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BUREAU OF FISHERIES

AGE AND GROWTH OF THE CISCO
LEUCICHTHYS ARTEDI (LE SUEUR), IN THE
LAKES OF THE NORTHEASTERN
HIGHLANDS, WISCONSIN

By RALPH HILE

Bulletin No. 19

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By RALPH HILE, Ph. D., Assistant Aquatic Biologist, U. S. Bureau of Fisheries

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INTRODUCTION

In 1927 the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries instituted a cooperative study of the life histories of the fishes that inhabit the lakes of the highland district of northeastern Wisconsin. By the arrangements agreed upon, the survey furnished facilities for the conduct of field operations and staff members of the two organizations cooperated in the collecting and investigation of the research materials. The limnological laboratories of the survey at Trout Lake, Wis., served as headquarters for all field operations.

During the summer and early autumn of 1927 Dr. Stillman Wright of the Bureau, with the aid of an assistant made collections of fishes from several lakes of the region. In 1928, when it was impossible for Dr. Wright to be in direct supervision of the field work, the collections were made by Dr. Joseph Goldsmith and an assistant. A part of the collections for the years 1927 and 1928 served as a basis for a preliminary report on the growth of the rock bass in Trout and Muskellunge Lakes (Wright, 1929). In 1929 Dr. Wright found it necessary to devote his entire time to limnological investigations on Lake Erie and collecting operations were suspended during that year.

The collection of data for the investigation of the life histories of the fishes of the region was resumed in 1930. During this season the field work was carried on by Dr. Edward Schneberger of the survey and Dr. Ralph Hile of the Bureau. (In 1931 the collecting of materials was continued under the supervision of these 2 investigators with the aid of 2 assistants.) In 1932, when it was impossible for Dr. Hile to participate in the field operations, the collections were made by Dr. Schneberger, aided by one assistant.

Although the materials collected have afforded data on a number of species, the investigations have centered upon the life histories of three forms: The yellow perch, *Perca flavescens* Mitchill; the rock bass, *Ambloplites rupestris* Rafinesque; the cisco or lake herring, *Leucichthys artedi* (Le Sueur). Dr. Schneberger has given his attention to the study of the perch and Dr. Hile to the study of the rock bass and the cisco. The small collections of game fishes collected in the various years formed a part of the material used by Juday and Schneberger (1930, 1933) in their studies on the growth of game fishes in Wisconsin.

The ultimate aim of these studies of the fishes of northeastern Wisconsin is a more precise evaluation of the various environmental factors in their relation to the growth and abundance of the different fish forms. Since 1925 the survey has been conducting extensive limnological investigations on the lakes of the region.² The fish collections that were made for the growth studies have served also as material for study by survey staff members of food habits and parasitic infestation in the various species. The general consideration of the relationship between growth and environment awaits the termination of these several lines of investigation. In the present publication references will be made to relationship between growth and certain environmental factors, but no exhaustive discussion of the question will be undertaken.

In the investigation of the ciscoes an attempt was made to select the populations for study from "type" lakes. The selection of the four lakes with which this study is primarily concerned was based principally on the amount of fixed CO₂ present in

² For a history of the survey's operations consult Juday and Birge (1930). Annual summaries of the survey's activities appear in the Bureau's reports on Progress in Biological Inquiries (Rich, 1926; Higgins, 1928a, 1928b, 1930, 1931a, 1931b, 1932, and 1933).

the water. This factor was considered to be a fair index of the general productive capacity of the various waters. Size and form of basin were also taken into account in the selection of the lakes. Trout Lake is the second largest and the deepest lake of the region. In comparison with the surrounding bodies its water is relatively hard. Muskellunge is a lake intermediate as to size and as to the amount of fixed CO₂. Silver Lake is a small lake with intermediate conditions with respect to fixed CO₂. Clear Lake has an area approximately equal to that of Muskellunge Lake. Its water contains an unusually small amount of fixed CO₂.

Table 1 gives for each lake the details of location, area, depth, and also data relative to the physical and chemical nature of the waters. The two lakes, Allequash and Tomahawk, from which small samples of scales were obtained for growth study, are included in the table.

TABLE 1.—Description of the 6 lakes of which cisco populations were studied

[The characteristics, color, pH, conductivity, fixed CO₂, and organic content of plankton refer to average surface conditions. These data were furnished by the Wisconsin Geological and Natural History Survey]

Lake	Location	Length in kilometers	Width in kilometers	Surface area (hectares)	Maximum depth (meters)	Volume in 1,000 cubic meters	Secchi disk transparency (meters)	Color platinum cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO ₂ in milligrams per litre	Organic matter of plankton in milligrams per litre
Clear	Town 39N, range VIII	2.10	1.83	373	26.5	—	6.3	0	6.6	17	2.2	0.84
Muskellunge	Town 41E, range VII	3.30	1.18	375	19.3	26,172	4.0	4	7.3	40	10.0	1.16
Silver	Town 41N, range VII	1.69	.64	87.3	19.5	9,884	5.5	4	7.5	62	15.0	.85
Trout:												
North basin	Town 41 and 42N, range VI and VII	3.60	2.10	532	29.0	69,017	5.0	6	7.8	73	18.5	.66
South basin		4.51	3.86	1,051	35.5	149,020	4.5	3	7.6	77	18.7	.92
Allequash	Town 41N, range VIII	2.41	1.41	142	7.5	—	1.5	30	7.9	67	16.9	1.48
Tomahawk	Town 38 and 39N, range VI and VII	7.24	3.00	1,476	22.5	—	4.2	8	7.6	69	16.7	.78

¹All ciscoes collected from Trout Lake were taken in the south basin.

Juday and Birge (1930) published a general description of the northeastern highland lake district. Thwaites (1929) described the glacial geology of a part of Vilas County in which all but two (Clear Lake and Tomahawk Lake) of these lakes are located. Chemical, physical, and biological data concerning the various lakes have appeared from time to time in the publications of the limnological laboratory of the survey.

From time to time in the following discussion different species of fish will be mentioned by their common names. Because of the considerable local variation in the common names of fishes it is thought well to list the scientific names of the various species mentioned, along with their common names:

Bluegill, <i>Helioperca incisor</i> (Cuvier and Valenciennes).	Perch, yellow perch, <i>Perca flavescens</i> Mitchill.
Burbot, <i>Lota maculosa</i> Le Sueur.	Pike-perch, <i>Stizostedion vitreum</i> (Mitchill).
Ciscoes or chubs, <i>Leucichthys</i> spp.	Rock bass, <i>Ambloplites rupestris</i> Rafinesque.
Cisco, lake herring, <i>Leucichthys artedi</i> (Le Sueur).	Sauger, <i>Stizostedion canadense</i> (Smith).
Lake trout, <i>Cristivomer namaycush</i> (Walbaum).	Smallmouth black bass, <i>Micropterus dolomieu</i> Lacépède.
Largemouth black bass, <i>Aplites salmoides</i> (Lacépède).	Sucker, <i>Catostomus commersonnii</i> (Lacépède).
	Whitefish, <i>Coregonus clupeaformis</i> (Mitchill).

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I wish to acknowledge the assistance and cooperation of the members of the staff of the Wisconsin Geological and Natural History Survey. Dr. Chancey Juday offered much valuable advice, particularly in the selection of lakes for study, and supplied needed limnological information. Dr. Edward Schneberger was completely in charge of the 1932 collecting operations.

Dr. John Van Oosten, in charge of the Great Lakes fishery investigations of the Bureau of Fisheries, gave much valuable advice (both as to field procedure and methods of analysis of data) during the execution of this work, and gave his assistance freely in the interpretation of difficult scales. Dr. Van Oosten also made a critical examination of the manuscript.

Dr. Carl L. Hubbs, curator of fishes in the Museum of Zoology of the University of Michigan, read the original manuscript and offered valuable suggestions for its improvement.

Harry C. Carver, professor of mathematics and insurance in the University of Michigan, read the section of the manuscript on the relationship between length and weight.

Dr. Peter Okkelberg, secretary of the Graduate School of the University of Michigan, checked the accuracy of my translation of portions of Huitfeldt-Kaas' (1917) publication. The reference to Olofsson's (1932) paper is based on an abstract prepared by R. W. Eschmeyer of the Michigan Institute for Fisheries Research.

The determination of age and the calculation of growth of the 1928 collection of the Trout Lake cisco are entirely the work of Dr. Stillman Wright, formerly of the Bureau of Fisheries.

MATERIALS

The investigation of age and growth has been based upon the determination of ages for 3,882 specimens and the calculation of growth for 3,694 specimens. Specimens other than those whose ages were determined have been used incidentally for other purposes such as the study of vertical distribution of the cisco and the density of population. Koelz (1931) described material from each of the six lakes whose populations are considered in this study. According to Koelz 3 subspecies of *Leucichthys artedi* are represented in these 6 populations. Clear Lake is the type locality for *L. artedi clarensis* Koelz. The same form is accredited to Muskellunge, Silver, and Allequash Lakes. Koelz described the Trout Lake cisco as *L. artedi clemensi* Koelz, and the form occurring in Tomahawk Lake as *L. artedi wagneri* Koelz. However, Hile (MS.) in a paper now in press has demonstrated that the ciscoes of these lakes at present are not susceptible of division into subspecies, but should be considered merely as populations of the species, *L. artedi*.

Table 2 lists the locality and year of capture of the ciscoes used in the life-history studies. The 1931 material includes 658 preserved specimens collected for a morphometric study to appear in a later publication, while all the 1932 Muskellunge Lake specimens and 95 of the 1932 Clear Lake specimens were preserved.

TABLE 2.—Year of collection and number of specimens in the collections used in the study of age and growth of the cisco

Lake	Year of collection				Total number
	1928	1930	1931	1932	
Trout.....	182	508	610	—	1,300
Muskellunge.....	281	245	616	188	1,330
Silver.....	135	118	378	—	631
Clear.....	—	—	249	191	440
Allequash.....	47	66	—	—	113
Tomahawk.....	68	—	—	—	68
Total.....	713	937	1,853	379	3,882

The relatively limited data from the small collections from Allequash and Tomahawk Lakes are not considered in the general discussions of this paper, but are treated in a special section (appendix A).

METHODS

GEAR USED IN COLLECTING

With the exception of a small number of 0-group individuals picked up on the beaches of Trout Lake all samples used in this investigation were collected by means of gill nets. The 1928 collections were made in nets of the following sizes of mesh: ³ 1½, 1½, 1¾, 2, 2½, and 3 inches, and in Trout Lake a 1¼ by 8-inch trammel. The trammel used in the capture of Trout Lake ciscoes would operate as a 1¼-inch gill net. In this year no net records were kept for individual specimens. It is unlikely, however, that in any of the three populations (Trout Lake, Muskellunge Lake, Silver Lake) ciscoes were taken either in the 2½-inch- or 3-inch-mesh nets.

The nets used in 1930 had also been used in 1928. However, the discarding of worn-out nets at the close of the 1928 season was so extensive that the only sizes of mesh available in 1930 for the capture of ciscoes in the three lakes named in the preceding paragraph were 1½ and 2 inches. These same nets were used in the early part of the 1931 collecting season. The depth of these nets varied from 3 to 4½ feet.

The gill nets used in 1930 and in the early part of the 1931 season were in a sorry state of repair. Not only were many of the meshes broken, but holes of considerable size were of frequent occurrence. The making of repairs was not feasible as the thread had deteriorated to the extent that even ordinary handling and use of the nets frequently produced new tears in the webbing.

The gear was completely replaced on July 22, 1931, after which date the following sizes of mesh were used: 1¼, 1½, 1¾, 2, 2¼, 2½, and 3 inches. Each net was 50 yards long and approximately 6 feet deep; 5-inch leads were used as a precaution against tangling of leads in the webbing. All Clear Lake samples (1931 and 1932) were taken in the new gear, but only a few lifts of the new gear were made in the other lakes.

The question of gill net selectivity, particularly with reference to the use of gill net samples for the study of age and growth, is considered in a special section (pp. 294–306).

METHODS OF FISHING

The new nets purchased in 1931 were fished in gangs containing 1 net of each of the 7 mesh sizes. In sets of the old nets the larger mesh sizes, known to be ineffective on the cisco populations that were being sampled, were occasionally

³ Throughout this paper, sizes of mesh, unless otherwise indicated, are presented as stretched measure.

omitted. No attempt was made to arrange the nets in any definite order as to size of mesh. In general it was customary to intersperse the larger mesh sizes with the smaller. All sets were made on the bottom.

The nets were lifted and reset once each day. At least once each week they were removed from the water, stretched on a reel, and allowed to dry thoroughly. At intervals of about a month all the nets were treated with copper soap after a method suggested by Harry Hansen, formerly of the Bureau of Fisheries.

The 1928 data contain only scattered information as to the depth from which the various samples were taken. During 1930 observations were made regularly as to the general depth and the nature of the bottom in the region in which the nets were set. Later it was found desirable to possess more precise information on the matter of depth. Accordingly in 1931 and 1932 soundings were made to determine the depth at which each particular net was set. Routine records were kept as to the condition of the weather (cloudiness, precipitation, and strength and direction of the wind). Catches from the different sizes of mesh were placed separately in labeled pails. After the return to the field laboratory counts of the number of fish taken in each net were added to the field notes.

FIELD DATA RECORDED FOR INDIVIDUAL SPECIMENS

Scale samples were taken in the field from all specimens except those preserved for morphometric studies. (The treatment of preserved specimens will be discussed later.) The scale samples were removed whenever possible from the left side of the body dorsal to the lateral line and ventral to the dorsal fin. Scales were stored in standard Bureau of Fisheries scale envelopes. On each serially numbered envelop were recorded date, locality, species, length, weight, sex, state of maturity,⁴ and gear.⁵ The field numbers included in the day's catch were cataloged.

The standard length (from the tip of the snout to the end of the vertebral column) was measured for each individual fish. Enough measurements of the total length (from the tip of the snout to the line connecting the tips of the extended caudal fin) were made to obtain a reliable figure for the ratio between standard and total length.⁶ All lengths were measured with a steel tape in a straight line between the points indicated, not along the curvature of the body, and were recorded to the nearest millimeter. Throughout this paper the unit of length can be assumed to be the millimeter.

The smaller individuals were weighed on a Chatillon spring platform balance of 500-gram capacity with calibrations at 2-gram intervals. Weights of these fish were estimated to the nearest gram. Weight records above 500 grams were obtained by means of a Chatillon spring platform balance of 5-kilo capacity and with calibrations at 20-gram intervals. Weights of these larger fish were estimated to the nearest 5 grams. Toward the close of the 1931 collecting season the smaller balance developed a fluctuating error that was at no point greater than 2 grams. This balance was replaced by a new instrument at the beginning of the 1932 season.

⁴ A fish whose sexual condition showed that it would spawn in the coming autumn was listed as mature, whether or not it may have spawned previously.

⁵ Sex, maturity, and gear were not recorded for the 1928 samples.

⁶ The ratio, total length in standard length, has the following values: Clear Lake, 0.84; Trout Lake, 0.84; Silver Lake, 0.85; Muskellunge Lake, 0.85; Allequash Lake, 0.84. The ratio was not determined for the Tomahawk Lake cisco.

TREATMENT OF PRESERVED SPECIMENS AND RESULTING SHRINKAGE

Part of the fish preserved for morphometric study were weighed and measured while fresh. These specimens were provided with individual, serially numbered tin tags. Other specimens to be preserved were divided into small groups which were wrapped in cheesecloth. Within each package was included a label bearing a record of date, locality, and usually of gear. The specimens were held in a 10-percent formalin solution until the close of the season. Upon removal from the formalin solution the fish were soaked in water about 4 days and then transferred permanently to a 70-percent solution of alcohol.

Since the preserved specimens—most of which were not weighed and measured in the field—constituted a part of the material used for a study of growth, it was of some importance to know the extent of the shrinkage brought about by the preserving fluids. Data on this question were obtained from 99 ciscoes from Clear Lake and from 105 ciscoes from Muskellunge Lake, all taken in 1932. These fish were weighed and their lengths measured at the time of capture. The dates of capture for the Clear Lake specimens were July 12 to July 19; for those from Muskellunge Lake, July 28 and July 29. The individuals of both collections were reweighed and remeasured October 10 and October 11, 1932. At this time they had been in alcohol about 5 weeks. The measurements and weighing of both the fresh and preserved material were made by the same method and by the same individual (Dr. Schneberger).

The ratio between preserved length and fresh length was 1.000:1.019 for the Muskellunge Lake cisco. This value of the shrinkage factor agrees closely with the figure, 1.016, determined by Van Oosten (1929) for the Lake Huron herring. Since the populations from Silver Lake and Trout Lake do not have greatly dissimilar length ranges (approximately 125–200 millimeters) the shrinkage factor based on the Muskellunge ciscoes has been used in correcting for shrinkage the lengths of the preserved specimens from these two lakes.

In the Clear Lake cisco, where the length range is much greater, the relative amount of shrinkage was found to vary at different lengths. The lengths of preserved specimens from this lake were corrected according to the following shrinkage factors:

Length interval:	Shrinkage factor	Number of specimens
350.....	1.005	16
250-349.....	1.010	65
150-249.....	1.028	18

The shrinkage factors for weight were 1.181 for the Muskellunge Lake ciscoes and 1.144 for the Clear Lake ciscoes. However, the individual shrinkage in weight varied so widely that it was not considered valid to employ a weight shrinkage factor for the purpose of making individual corrections. Only those preserved specimens that were weighed when fresh were used for the study of growth in weight.

PREPARATION AND EXAMINATION OF SCALE MATERIAL

Scales were soaked in water and cleaned by means of a dissecting needle and a small camel's-hair brush. Three scales from each fish were mounted on a microscope slide in a gelatin-glycerin medium prepared according to a formula presented by Van Oosten (1929). No regenerated scales or scales with abnormal or irregular shape

were mounted. On the label of each slide were recorded the field number, laboratory number, date and locality of collection, species, sex, maturity, length, weight, and gear. The scales were studied by means of the projection apparatus described by Van Oosten (1923). The magnifications used were X19 for scales of the Clear Lake ciscoes and X40.5 for scales of all other fish.

MISCELLANEOUS CONSIDERATIONS

It is the policy throughout this paper to apply toward the solution of each particular question all suitable data available. As a result of this procedure there appear certain discrepancies in the number of specimens listed in the tables pertaining to different phases of the general problem of the life history of the cisco. Since discrepancies of this sort, if unexplained, may prove a considerable annoyance to a reader, attention will be called to the causes for at least the most important of them.

Table 2 lists the fish upon which determinations of age were made. These specimens, with the exception of the 1932 Muskellunge Lake collections, separated into age groups and year classes, appear in the growth tables 3 to 7. The tables of general growth in length (10 to 14) are based on fewer specimens than tables 3 to 7 since certain indicated age groups were eliminated because of selection by gear. (The 17 0-group Trout Lake ciscoes were also omitted in the computation of the general growth curve.) The tables for growth in weight (15 to 18) are based on fewer specimens than those for growth in length since part of the preserved fish used in the growth study were not weighed before preservation. Of course, the study of the length-weight relationship and of condition was based only on specimens weighed in the field.

In the listing of catch per unit effort of gill nets (section on the relationship between density of population and rate of growth) it was, of course, valid to include fish that had not been aged. Similarly in the determination of the average length of all fish taken in a particular size of gill net (section on selective action of gill nets) it was also valid to include unaged fish. Further, the grand average length used for comparing the average length of an age group as determined from the combined catch of several different sizes of mesh with the average lengths of the same age group as based on the catch of individual sizes of mesh may include certain fish for which net records were not available. (Net records were lacking for a large part of the preserved fish.) The data of tables 40 and 73 are based in part on catches of Muskellunge Lake ciscoes taken in 1932 for morphometric investigations and included only incidentally in this study. None of the 1928 data is included in the analysis of net catches.

The 1928 data also lacked records of sex and maturity and hence could not be included in the sections on sex ratio and age at maturity.

Although some of these discrepancies are mentioned in the general discussions, a general statement of their origins was considered advisable.

THE SCALE METHOD

ASSESSMENT OF AGE AND CALCULATION OF GROWTH

The treatment here of the growth data of the cisco is based upon the use of the scale method. Van Oosten (1929) established the validity of the method for this species in his study of the life history of the Lake Huron herring. It is assumed that

the method is equally valid for the populations considered in this investigation. As will appear later, the results of the analysis of the growth material presented here seem to justify the assumption. Throughout this paper the individual ages are designated as the number of years of life that have been completed. Although the cisco spawns in late autumn or early winter, the life of the individual is assumed to begin the following spring when hatching takes place. During the first year of its life the individual is a member of the 0 group, during the second year it is a member of the I group, etc. Fish hatched in the same year belong to the same year class, regardless of their age at the time of capture.

Two examinations for age determination were made of the scales of each individual specimen. At the second examination either a definite assignment of age was made for the troublesome scales or the slides were marked as unreadable. At the time of the final examination one of the three scales on the slide was measured. This scale was selected on the basis of clearness of markings and symmetry of form. The diameters of the different growth areas were measured along the anteroposterior axis of the scale. For this measurement the ruler was placed in such a position that its edge passed through the focus of the scale and approximately bisected the posterior field (that portion of the scale which is exposed in its natural position on the fish). Scale measurements were made with a tested millimeter ruler and recorded to the nearest millimeter (occasionally the nearest half millimeter).

The assessment of age was based on the determination of the number of annuli or lines of discontinuity between growth areas of succeeding years. Two difficulties were encountered in the determination of individual ages. The later annuli of the older individuals (particularly those of the slower-growing populations) were sometimes so crowded together as to make their recognition difficult or even impossible. In the latter case the scales were discarded. Accessory annuli (summer checks) were not infrequent, but their characteristically indefinite appearance and their position with respect to the true annuli were such that they were ordinarily easily recognizable. Somewhat less than 5 percent of the total number of scales examined were discarded as unsatisfactory for the determination of age.

Accessory checks were found to occur regularly in all the samples of the scales of the Muskellunge Lake cisco. They could be separated from the true annuli quite easily in the growth fields of the earlier years, and consequently they presented no great difficulty in the age and growth analysis of the earlier (1928-31) collections which were composed almost entirely of I-, II-, and III-group fish. In 1932, however, IV-group fish were present in abundance for the first time. In this year's collection the presence of accessory annuli, along with the IV-group's excessively slow growth during the fourth year of life, made the separation of the III group and the IV group of that year's collection both difficult and uncertain. Because of these difficulties and because of the abundance of data from the preceding years, the 1932 collections were not used in the computation of a general growth curve for the Muskellunge Lake population. However, certain of the data from the 1932 Muskellunge Lake samples will be used from time to time for other purposes.

Van Oosten (1929) demonstrated that after the formation of the first annulus the ratio of the total scale length to body length is so nearly constant in the lake herring that the assumption of the absolute constancy of the ratio affords the most

satisfactory means for the calculation of growth during the various years of the individual's existence. The formula used in the calculation of growth was:

$$L_n = D_n \frac{L_T}{D_T}$$

where

L_T = length of fish at time of capture;

D_T = total diameter of scale;

L_n = length of fish at end of n^{th} year of life;

D_n =diameter of scale within the n^{th} annulus.

Tables 3 to 7 present the data for the calculated growth in length for the ciscoes of Trout, Muskellunge, Silver, and Clear Lakes. Since no difference in the growth of the two sexes was apparent in the fish of the first three lakes the data for these lakes as presented represent a combination of males and females. In the data for the Clear Lake cisco the sexes are treated separately.

TABLE 3.—*Calculated growth of Trout Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life											
					1	2	3	4	5	6	7	8	9	10	11	12
1919	1931	XII	1	226	80	104	117	130	148	169	180	190	199	211	218	224
1920	1931	XI	2	205	75	103	119	130	142	152	162	172	180	198	204	224
1922	1931	IX	2	200	83	112	127	140	154	168	180	190	198	211	218	224
1923	1931	VIII	2	192	87	115	134	145	156	169	179	190	198	211	218	224
1924	1928	IV	5	192	87	115	134	145	156	169	179	190	198	211	218	224
	1931	VII	17	147	85	120	133	143	156	169	179	190	198	211	218	224
	1928	III	4	175	80	113	128	141	153	162	174	190	198	211	218	224
	1930	V	61	143	84	123	137	148	156	164	174	190	198	211	218	224
1925	1931	VI	12	167	82	116	135	148	160	174	190	198	211	218	224	224
	1928	II	102	165	79	116	132	145	156	164	174	190	198	211	218	224
	1930	IV	90	134	82	117	137	147	156	164	174	190	198	211	218	224
	1931	V	79	156	82	118	135	145	154	164	174	190	198	211	218	224
1926	1928	*I	2	128	81	118	135	145	154	164	174	190	198	211	218	224
	1930	III	347	149	79	117	139	146	154	164	174	190	198	211	218	224
	1931	IV	269	148	78	115	135	146	154	164	174	190	198	211	218	224
	1930	*II	36	140	91	127	137	146	154	164	174	190	198	211	218	224
1928	1931	III	173	142	84	120	137	146	154	164	174	190	198	211	218	224
1929	1931	*II	61	136	87	127	137	146	154	164	174	190	198	211	218	224
1930	1930	0	17	66	106	117	127	137	146	154	164	174	190	198	211	224
	1931	*I	2	128	106	117	127	137	146	154	164	174	190	198	211	224

TABLE 4.—Calculated growth of Muskellunge Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life			
					1	2	3	4
1925.....	1928	III	10	172	105	142	162	---
1926-----	1928	II	252	160	99	147	---	---
1927-----	1928	*I	19	137	97	---	---	---
-----	1930	III	14	166	85	132	157	---
1928-----	1931	IV	2	176	90	143	161	17
-----	1930	II	214	162	95	143	---	---
1929-----	1931	III	347	166	96	145	163	---
-----	1930	*I	17	148	103	---	---	---
1930-----	1931	II	258	149	98	138	---	---
-----	1931	*I	9	136	96	---	---	---

TABLE 5.—Calculated growth of Silver Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life						
					1	2	3	4	5	6	7
1923	1923	V	10	182	76	115	142	161	175	-----	-----
	1928	IV	69	177	79	125	150	166	-----	-----	-----
1924	1930	VI	3	197	72	112	134	161	177	192	-----
	1931	VII	1	201	77	111	135	158	172	186	196
	1928	III	46	165	73	127	157	-----	-----	-----	-----
1925	1930	V	25	193	74	120	145	165	185	-----	-----
	1931	VI	21	194	78	119	142	158	177	189	-----
	1928	II	9	157	90	140	-----	-----	-----	-----	-----
1926	1930	IV	58	183	78	126	152	173	-----	-----	-----
	1931	V	108	188	80	126	150	168	182	-----	-----
	1928	*I	1	133	95	-----	-----	-----	-----	-----	-----
1927	1930	III	25	181	77	134	167	-----	-----	-----	-----
	1931	IV	102	183	80	132	159	176	-----	-----	-----
	1930	II	7	173	99	151	-----	-----	-----	-----	-----
1928	1931	III	61	177	83	137	166	-----	-----	-----	-----
1929	1931	II	19	171	104	151	-----	-----	-----	-----	-----
1930	1931	*I	66	141	105	-----	-----	-----	-----	-----	-----

TABLE 6.—Calculated growth of Clear Lake ciscoes (males) to the end of each year of life for the different year classes at each age

[illegible]

TABLE 7.—Calculated growth of Clear Lake ciscoes (females) to the end of each year of life for the different year classes at each age

[illegible]

From an examination of the tables for Trout, Muskellunge, and Clear Lakes it will be noticed that "Lee's phenomenon" of "apparent decrease in the calculated growth" as it is determined from successively older groups of individuals, while possibly present, is not a source of any great discrepancies, especially where large numbers of individuals are involved. On the whole the calculated growths based on different age groups in the same year's collection or upon samples of the same year class taken at different ages, agree satisfactorily for corresponding years of life, with the exception of the large calculated growths obtained for the younger age groups (marked with asterisks in the tables) in the Trout Lake and Muskellunge Lake collections. These large growths can be explained as the result of the selective action of the gill nets used for their capture. (See section on gill net selectivity.) The small but fairly consistent discrepancies that appear in the corresponding calculated growths of older year groups of the Trout Lake fish may be partly the result of slight changes in the body scale ratio. It is probable that selective action of gear plays a role here also. At any rate the discrepancies are of such small magnitude that they affect but little any conclusions that might be drawn concerning the growth of the population as a whole.

LEE'S PHENOMENON IN THE SILVER LAKE CISCO

In the Silver Lake data (table 5) there appear much more pronounced disagreements among the corresponding calculated growths of different age groups than are present in the other three populations. Not only are these discrepancies relatively large, but the comparison of any two age groups shows that in general they tend to be cumulative with increased age. These discrepancies appear in the comparisons of calculated growths based on the same year class but taken in different seasons as well as in calculated growths based on the different age groups of a single year's collection. To illustrate these two points there may be examined (table 5) first the calculated growths of the III, V, and VI groups of the 1925 year class and second the calculated growths of the III, IV, V, and VI groups of the 1931 collection. With certain exceptions in the first year of life it will be noticed that each successively older age group tends to give smaller values for the calculated lengths for corresponding years of life. Thus it may be seen that the observed discrepancies in the calculated growths depend on the differences in the age of the groups studied.

It will be noticed further that the apparent change of growth rate as it appears in the fish older than the II group differs from Lee's phenomenon as it ordinarily occurs, in that it is the calculated growths of the later rather than the earlier years of life that are affected most.

The calculated lengths of the Silver Lake ciscoes at the end of the first year of life require some special consideration. If size of sample is taken into account, the calculated growths for the first year of life show fairly good agreement for all age groups older than II. The calculated growths for the first year of life as based on the II group are somewhat less than those based on the I group, but those of both groups are considerably greater than the growths based on the older-age groups. The high calculated growths for the first year of life as based on the I group can be explained in part by the selective action of the gill nets used in collecting the samples, for there is reason to believe that even the smallest mesh of these nets may have taken only the larger individuals of this group. Such an explanation, however, does not seem to hold for the fish of the II group, since on the basis of comparisons with samples from other lakes the range of size of the Silver Lake II group seems to be such that very little

selection by gear could have taken place. Some other explanation must be sought, therefore, for the high growth values of this age group.

Since disagreements in the calculated growth data of fish are generally attributed in part to changes with age in the growth relation between body and scale, it was deemed advisable to study this relationship in the Silver Lake cisco. The 1931 collection was selected as best suited for this purpose. As was mentioned previously (p. 216) the scale samples used in this entire investigation were all taken from the same region of the body. Selections of scales for mounting and for measuring were made on the basis of distinctness of the annuli and symmetry of form rather than on size. As a consequence of this procedure the relationship between the length of body and the diameters of the scales measured should be comparable in the different age groups of a single sample.

As may be seen in table 8 the average ratio between the body length and the magnified diameters of the scales does not vary greatly from one age group to another. The generally made assumption of a linear relationship between scale size and body size tends to the determination for the Silver Lake cisco of the equation:⁷

$$L = 10.7 \text{ mm} + 1.078 D,$$

where L = length of body in millimeters,

and D = the (magnified) diameter of the scale in millimeters.

TABLE 8.—The body-scale ratio for the different age groups of the Silver Lake cisco collected in 1931, and the average diameters of scales as measured at the magnification $\times 40.5$

[D_T is total diameter. The diameters within the different growth areas of the scales are indicated by the subscript figure]

Age	Number of specimens	Body-scale ratio	D_T	D_1	D_2	D_3	D_4	D_5	D_6	D_7
VII.....	1	1.16	174.0	67.0	96.0	117.0	137.0	149.0	161.0	170.0
VI.....	21	1.16	168.3	67.5	104.0	123.7	139.5	153.6	164.5	-----
V.....	108	1.13	167.9	70.9	112.6	133.8	150.5	162.6	-----	-----
IV.....	102	1.13	161.9	71.0	117.5	140.8	155.7	-----	-----	-----
III.....	61	1.15	155.7	72.6	119.5	145.7	-----	-----	-----	-----
II.....	19	1.18	145.8	88.0	128.7	-----	-----	-----	-----	-----
I.....	66	1.17	121.3	90.2	-----	-----	-----	-----	-----	-----

Table 9 gives a comparison of the calculated growths of the 1931 Silver Lake collection first as they were determined on the assumption of a constant body scale ratio at all ages and second as they appear after correction for the changing body-scale relationship indicated by the above equation. It will be noticed that while the "correction" produced changes in the actual values of the individual average calculated lengths, it did little toward the elimination of the discrepancies between the calculated growths of the different age groups. For example, it may be seen that the maximum discrepancy in the calculated growth for the first year of life (between the calculations for the I group and the VI group) was reduced from 28 millimeters in the uncorrected to 24 millimeters in the corrected data—an improvement in agreement of only 4 millimeters. Similarly, the improvements in the agreement in the calculated lengths for the later years of life are unimportant when they

⁷ It is realized that a more precise evaluation of the body-scale relationship might have been obtained through the use of "key" scales selected from exactly the same location in each fish. However, the complete failure of the "correction" equation to eliminate the discrepancies in the calculated growths of the Silver Lake cisco together with the fact that no corrections are needed in the other three populations made any detailed study of the body-scale relationship in these cisco populations unnecessary.

are considered in relation to the total discrepancy. Thus it may be seen that the observed discrepancies in the calculated growth of the Silver Lake cisco did not originate in a change of the body-scale relationships with increasing age.

TABLE 9.—*Calculated growth of the Silver Lake cisco, collection of 1931*

Age	Length	Uncorrected calculated lengths							Corrected calculated lengths						
		L ₁	L ₂	L ₃	L ₄	L ₅	L ₆	L ₇	L ₁	L ₂	L ₃	L ₄	L ₅	L ₆	L ₇
VII	201	77	111	135	158	172	186	196	84	116	138	160	173	187	196
VI	194	78	119	142	158	177	189		84	123	145	160	178	189	
V	188	80	126	150	168	182			86	129	152	169	182		
IV	183	80	132	159	176				86	135	160	176			
III	177	83	137	166					89	139	167				
II	171	104	151						108	152					
I	141	105							108						

Further light is thrown on the question by the examination of the actual average measurements of the growth areas of the scales upon which the Silver Lake growth calculations were based (table 8). The comparison of the diameter measurements of table 8 with the corresponding calculated lengths of table 9 shows clearly that the disagreements in the calculated growths of the different age groups appear also in the actual scale measurements upon which the growth calculations were made. Van Oosten (1929) also observed that Lee's phenomenon was to be found in actual scale measurements as well as in calculated growths.

The "apparent change in growth rate" in the Silver Lake cisco must, then, be considered a real change rather than an apparent change due to changing body-scale relationships. Since, as was pointed out previously, the phenomenon appears consistently both in comparisons between different age groups of the same year class and in comparisons between different age groups of different year classes taken in the same calendar year, it cannot be explained either on the basis of inherent differences in the capacity for growth in different year classes, or on the basis of varying environmental conditions affecting growth in different years. It must rather be considered the result of some selection factor correlated with the length of time intervening between the years for which the computations and scale measurements were made and the year when the fish was captured. Attention will be called briefly to possible sources of selection.

POSSIBLE CAUSES OF LEE'S PHENOMENON IN THE SILVER LAKE CISCO

SELECTION BY GEAR

A more detailed consideration of the question of the selective action of the gear used will be presented later in this paper. (See section on selective action of gill nets.) It may be stated here, however, that this factor most probably does not operate on the Silver Lake ciscoes except in the I group and that therefore it cannot explain Lee's phenomenon in these fish.

SELECTION DUE TO DISSIMILAR DISTRIBUTION WITHIN THE LAKE OF THE VARIOUS ELEMENTS OF THE POPULATION

Since the gill nets used in collecting the cisco samples for these studies were set directly on the bottom they fished only the lower few feet of water. If it is assumed that the larger individuals of the population tend to lead a more pelagic existence

than the smaller ones, then the more rapidly growing fish within an age group would be less subject to capture by nets set on the bottom than the slower growing individuals within the same group. Further, the effect of such segregation would be greater as age increases. The above-mentioned assumption would serve well to explain decreasing growth as it has been observed in the Silver Lake cisco, but data for its verification are not available. The chief objection to such an explanation lies in the fact that it is the smaller fish not the larger that would normally be expected to lead the more pelagic existence.

SELECTION DUE TO DIFFERENTIAL MORTALITY, CORRELATED WITH GROWTH RATE

It has been observed repeatedly that poikilothermous organisms tend to grow more slowly and reach a greater age in northern latitudes. The phenomenon appears to depend on the relation of temperature to the rate of metabolism. It is not wholly unreasonable to assume that the individual rate of metabolism might affect the individual growth rate and the individual length of life. Were mortality greater among individuals of more rapid growth, those individuals that survived longest would be those that had actually grown most slowly. The early growth as calculated from these slow growing survivors of the older age groups would naturally be small. Further, the effect on calculated lengths of this selection through differential mortality would tend to be increased with greater age, and thus discrepancies of the type observed in the Silver Lake data would be explained.

The relation between individual growth rate and individual length of life has been studied experimentally by several investigators. Osborne et al. (1917) found that a temporary preliminary stunting delayed maturity and extended the life span of rats. Titcomb et al. (1928) and McCay et al. (1931) found that trout that did not grow lived longer than those which showed growth on a similar diet. Zabinski (1929) by effecting a retardation of growth was able to prolong life in the black beetle and the roach. McCay (1933) presented a brief discussion of the general problem of the relationship of rate of growth to longevity.

OTHER POSSIBLE CAUSES

It is recognized that the three possible causes of Lee's phenomenon in the Silver Lake cisco discussed in the preceding paragraphs are by no means the only possible explanations of the observed discrepancies in calculated growth as based on fish of different age. These three suggested explanations were emphasized because they appear to be the most plausible in the face of the available data. Other explanations should be mentioned briefly along with the reason for their rejection.

1. Growth may be better in some calendar years than in others. This explanation cannot be accepted as the growth discrepancies were found to occur between members of the same year class, captured at different ages.
2. Portions of the scale may be resorbed after being laid down. The examination of the scales offered no evidence for any kind of resorption.
3. The scale fields may contract after being laid down. The nature of the structure of scales makes this explanation totally unacceptable. (See Van Oosten, 1929.)
4. More than one annulus per year may be formed. The clarity of scale markings on the Silver Lake cisco was superior to that of the Trout Lake and Muskellunge Lake ciscoes; yet the measurements of the scales of the last two populations gave

quite consistent results in the calculation of growth. Accessory annuli were rare in the Silver Lake cisco scales. With the elimination of the more questionable scales it appears unreasonable to assume that the number of errors in the determination of ages was sufficient to account for the observed large discrepancies in the calculated growths. Certainly accessory annuli cannot account for the decrease with age in the diameter of the first growth field.

5. The individuals of the population may have segregated themselves on the basis of maturity with the result that the smaller, immature members of each age group may have been absent from the samples. This explanation lacks plausibility in the face of the strong evidence presented later (p. 268) that some if not most fish mature as members of the I group, while all II-group fish certainly can be considered mature. It should be mentioned further that segregation on basis of maturity would be expected to be most pronounced at the spawning time, not in midsummer when the cisco is confined in Silver Lake to a narrow stratum of water in the lower part of the thermocline and the upper part of the hypolimnion.

Regardless of the explanation or explanations accepted as to the cause of Lee's phenomenon in the Silver Lake cisco, it appears that the observed discrepancies do not affect the validity of the method used in this paper for the calculation of growth from scale measurements. Nevertheless, there remains the question as to why the phenomenon should be peculiar to the Silver Lake population.

GENERAL GROWTH CURVES FOR THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

GROWTH IN LENGTH

For each population considered here all collections were combined⁸ to give a general growth curve (fig. 1). The indicated lengths at the end of the various years of life are in general the grand average of all calculated lengths for these years. In the Trout Lake and Clear Lake ciscoes, however, the irregularities in the later years, that result largely from the small samples, were smoothed in accordance with the observed data on the annual calculated growth increments.

The Silver Lake growth data raise a question as to the value and significance of any "general" growth curve in this population. The presentation of a general growth curve involves the tacit assumption that this curve can be taken to represent the course of growth of an individual that is typical of the population as a whole. However, the Silver Lake growth curve was derived from the combination of several age groups whose growth histories were fundamentally different. It appears characteristic of the Silver Lake cisco that individual growth history and individual life span are definitely correlated. Consequently the combining of all age groups to obtain a general growth curve involves the lumping together of a mass of heterogeneous growth material. The typical individual that such a curve is purported to represent is probably nonexistent. Nor can the growth curve obtained from a single age group be considered homogeneous. A sample of III-group fish, for example, can be expected to contain fish that would normally have died within the year of collection, and along with them others that would have survived to their fifth, sixth, or seventh year, or even longer. All these different groups within a single age group would have different types of growth.

⁸ Certain age groups, however, were eliminated as unreliable because of selection by gear. These were: Trout Lake, all I groups and the II groups of 1930 and 1931; Muskellunge Lake, all I groups; Silver Lake, all I groups. For Clear Lake no groups needed to be eliminated.

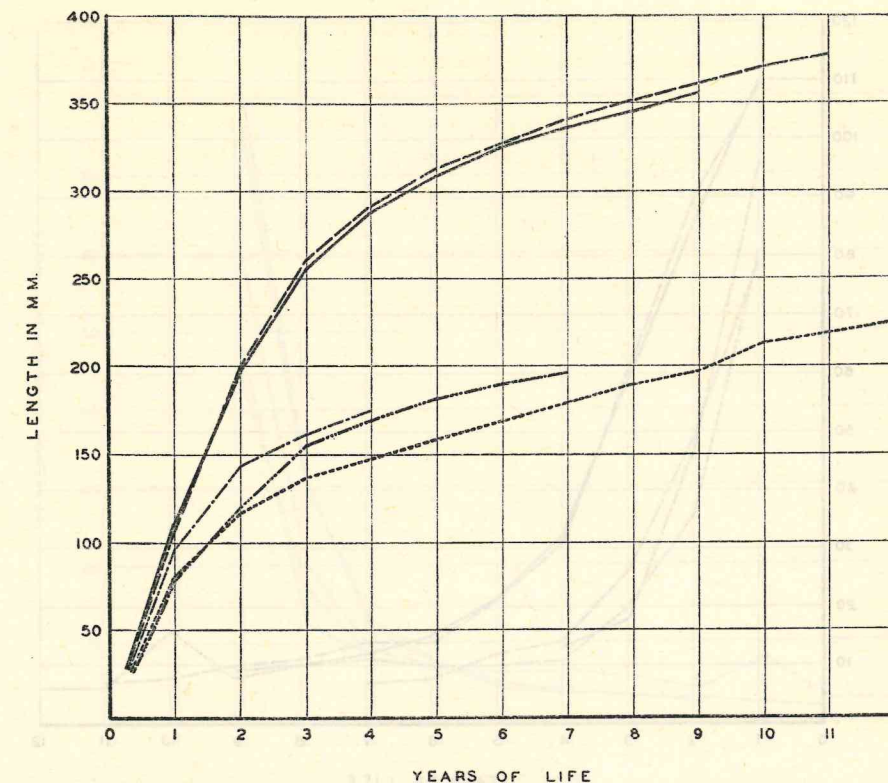


FIGURE 1.—General growth curves showing the average calculated standard length of the cisco (in millimeters) at the end of each year of life. Trout Lake, ---; Muskellunge Lake, - - -; Silver Lake, - . . -; Clear Lake (males), —; Clear Lake (females), — — —.

Tables 10 to 14 give for each population the calculated length at the end of each year of life, and the increase, both absolute and percentile, during each year of life. These data are presented graphically in figures 1 to 3.

TABLE 10.—Trout Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined. Sexes combined]									
Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1.....	12	225	6	2.7	26.....	6	168	10	6.3
3.....	11	219	6	2.8	114.....	5	158	10	6.8
3.....	10	213	16	8.1	499.....	4	148	11	8.0
5.....	9	197	8	4.2	1,080.....	3	137	20	17.1
10.....	8	189	10	5.6	1,182.....	2	117	36	44.4
14.....	7	179	11	6.5	1,182.....	1	81	81

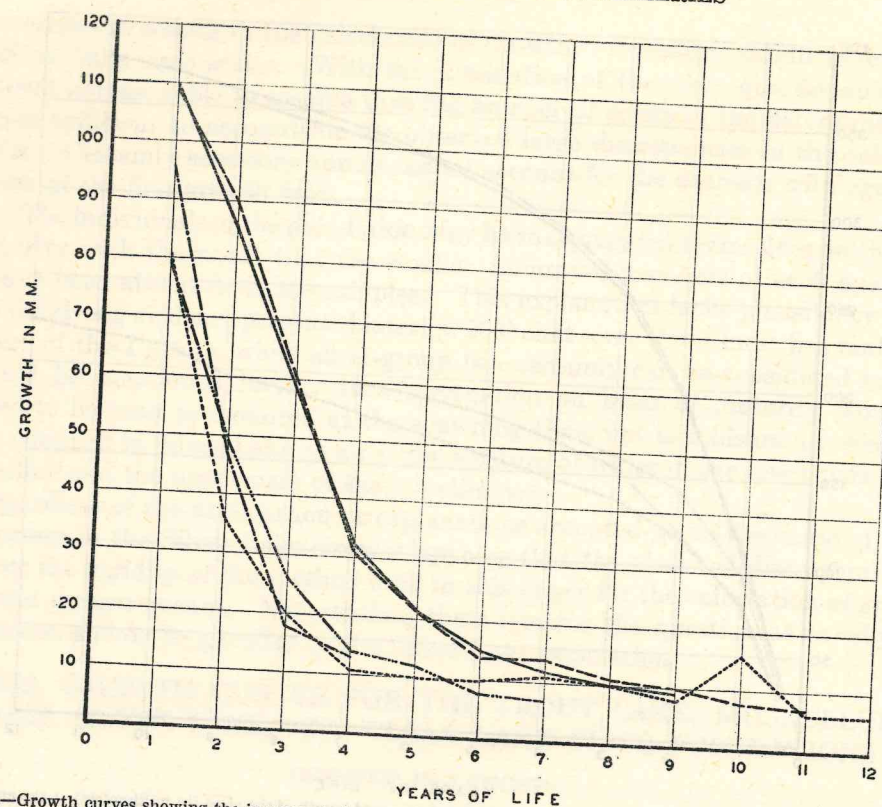


FIGURE 2.—Growth curves showing the increment of growth (in millimeters) in length of the cisco for each year of life. Trout Lake, ---; Muskellunge Lake, - . -; Silver Lake, . . . -; Clear Lake (males), —; Clear Lake (females), — — —.

TABLE 11.—Muskellunge Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life
[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
2	4	174	13	8.1	1,097	2	143	47	49.0
373	3	161	18	12.6	1,097	1	96	96	

TABLE 12.—Silver Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life
[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	7	196	7	3.7	529	3	155	26	20.2
25	6	189	8	4.4	564	2	129	49	61.2
168	5	181	12	7.1	564	1	80	80	
397	4	169	14	9.0					

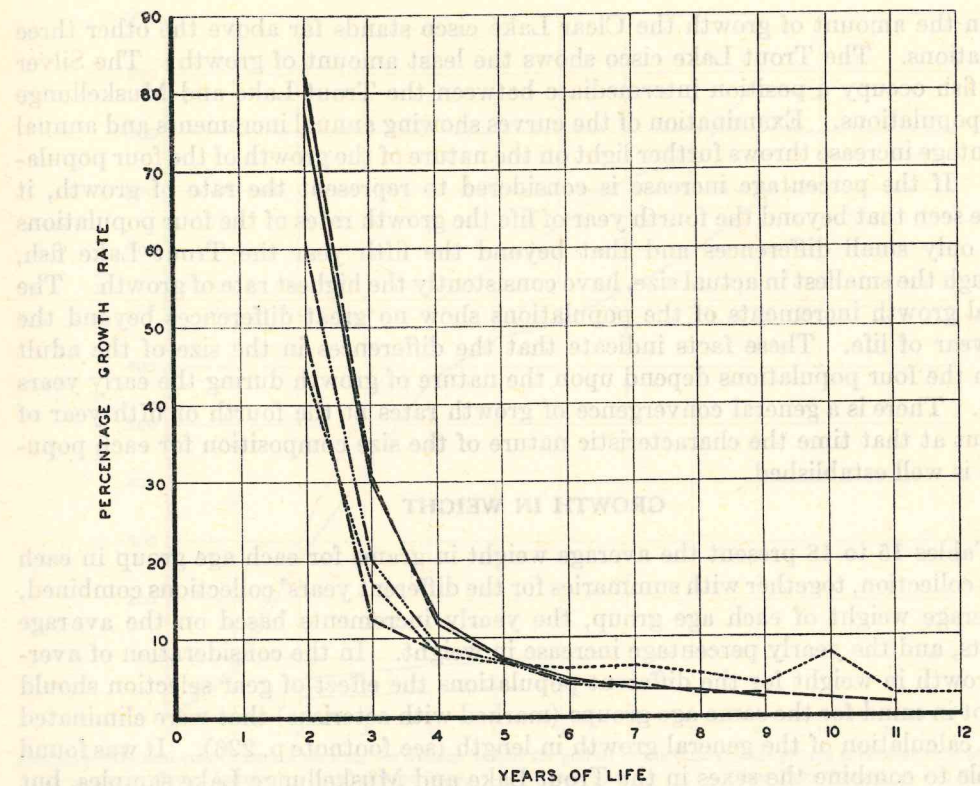


FIGURE 3.—General growth curves showing the percentage increase in length of the cisco in each year of life. Trout Lake, ---; Muskellunge Lake, - . -; Silver Lake, . . . -; Clear Lake (males), —; Clear Lake (females), — — —.

TABLE 13.—Clear Lake cisco—males—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life
[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	9	354	9	2.6	73	4	287	32	12.5
11	8	345	10	3.4	122	3	255	59	30.1
28	7	335	12	3.7	176	2	196	86	78.2
41	6	323	15	4.9	216	1	110	110	
62	5	308	21	7.3					

TABLE 14.—Clear Lake cisco—females—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life
[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	11	376	7	1.9	83	5	312	21	7.2
4	10	369	8	2.2	101	4	291	31	11.9
7	9	361	10	2.8	147	3	260	61	30.7
28	8	351	11	3.2	195	2	199	90	82.6
61	7	340	14	4.3	224	1	109	109	
74	6	326	14	4.5					

In the amount of growth the Clear Lake cisco stands far above the other three populations. The Trout Lake cisco shows the least amount of growth. The Silver Lake fish occupy a position intermediate between the Trout Lake and Muskellunge Lake populations. Examination of the curves showing annual increments and annual percentage increase throws further light on the nature of the growth of the four populations. If the percentage increase is considered to represent the rate of growth, it will be seen that beyond the fourth year of life the growth rates of the four populations show only small differences and that beyond the fifth year the Trout Lake fish, although the smallest in actual size, have consistently the highest rate of growth. The annual growth increments of the populations show no great differences beyond the fifth year of life. These facts indicate that the differences in the size of the adult fish in the four populations depend upon the nature of growth during the early years of life. There is a general convergence of growth rates at the fourth or fifth year of life, but at that time the characteristic nature of the size composition for each population is well established.

GROWTH IN WEIGHT

Tables 15 to 18 present the average weight in grams for each age group in each year's collection, together with summaries for the different years' collections combined, of average weight of each age group, the yearly increments based on the average weights, and the yearly percentage increase in weight. In the consideration of average growth in weight for the different populations the effect of gear selection should be kept in mind for the same age groups (marked with asterisks) that were eliminated in the calculation of the general growth in length (see footnote p. 226). It was found possible to combine the sexes in the Trout Lake and Muskellunge Lake samples, but not in the Clear Lake and Silver Lake collections. The females of the Clear Lake population grow in weight much more rapidly than do the males, while the males from Silver Lake tend toward a slightly better growth than do the females.

TABLE 15.—Trout Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection; selection probably affected the II-group weight values only slightly. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	100 ΔW/W
	1928	1930	1931			
XII			172 (1)	172 (1)		
XI			119 (2)	119 (2)		
VII			111 (2)	111 (2)		
VI			50 (2)	50 (2)		
V			45 (23)	47 (32)	3	6.4
IV	42 (17)	54 (9)	39 (139)	41 (255)	6	14.6
III	37 (61)	37 (347)	36 (129)	37 (537)	4	10.8
II	31 (102)	*32 (36)	*33 (50)	31 (102)	6	19.4
I	*26 (2)		*27 (2)	*26 (4)		

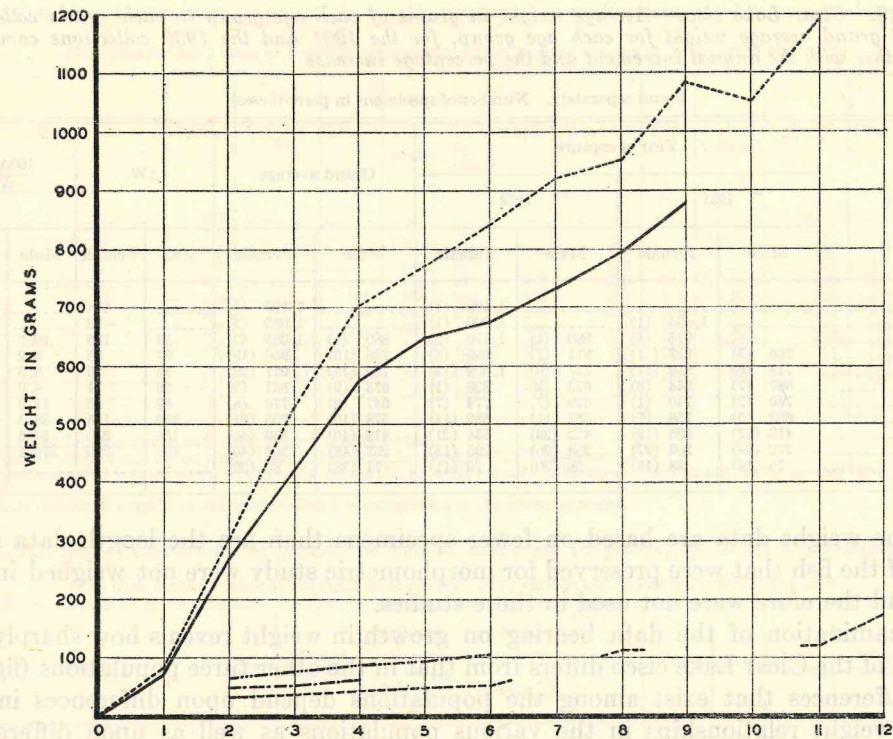


FIGURE 4.—General growth curves showing the average weight (in grams) of the different age groups of cisco at time of capture in summer. Trout Lake, ---; Muskellunge Lake, — · —; Clear Lake, · · · ·; Clear Lake (males), —; Clear Lake (females), — — —.

TABLE 16.—Muskellunge Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	100 ΔW/W
	1928	1930	1931			
IV	55 (10)	49 (14)	60 (2)	60 (2)	9	17.6
III	50 (252)	45 (214)	51 (266)	51 (290)	5	10.9
II	*33 (19)	*39 (17)	*31 (9)	*35 (45)		

TABLE 17.—Silver Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1930 and the 1931 collections combined, together with the annual increment and the percentage increase

[Sexes separately. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture					Grand average		ΔW		$\frac{100\Delta W}{W}$	
	1928	1930		1931							
	Male and female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
VI	-----	-----	106 (3)	-----	104 (8)	-----	104 (11)	-----	11	-----	11.6
V	81 (10)	98 (10)	99 (15)	95 (12)	92 (22)	96 (22)	95 (37)	10	11	11.6	13.1
IV	68 (69)	86 (23)	87 (35)	86 (13)	80 (22)	86 (36)	84 (57)	4	11	4.9	15.1
III	59 (46)	86 (13)	74 (12)	76 (10)	73 (13)	82 (23)	73 (25)	16	12	24.2	19.7
II	50 (9)	68 (3)	64 (4)	64 (4)	60 (8)	66 (7)	61 (12)	-----	-----	-----	-----
I	*28 (1)	-----	-----	*32 (24)	*35 (25)	*32 (24)	*35 (25)	-----	-----	-----	-----

TABLE 18.—Clear Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1931 and the 1932 collections combined, together with the annual increment and the percentage increase

[Sexes separately. Number of specimens in parentheses]

Age	Year of capture				Grand average		ΔW		100ΔW W	
	1931		1932							
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
XI										
X										
IX		1,035 (1)		1,190 (1)		1,190 (1)		128		12.1
VIII		915 (1)		1,090 (1)		1,062 (2)		23		-2.1
VII	760 (3)	937 (11)	880 (1)	1,170 (2)	880 (1)	1,085 (3)	84	135	10.6	14.2
VI	718 (6)	859 (17)	811 (7)	969 (8)	796 (10)	950 (19)	67	33	9.2	3.6
V	687 (7)	844 (8)	625 (2)	1,000 (12)	729 (15)	917 (29)	56	76	8.3	9.0
IV	710 (2)	740 (1)	629 (7)	820 (1)	673 (9)	841 (9)	26	71	4.0	9.2
III	603 (5)	756 (7)	567 (11)	680 (14)	647 (9)	770 (8)	69	65	11.9	9.2
II	413 (17)	525 (19)	422 (23)	534 (21)	418 (40)	530 (40)	151	175	38.3	33.0
I	272 (28)	303 (27)	259 (20)	295 (13)	267 (48)	306 (40)	151	230	56.6	77.7
	75 (18)	88 (15)	68 (20)	70 (11)	71 (38)	80 (26)	196	220	276.1	275.0

The weight data are based on fewer specimens than are the length data since most of the fish that were preserved for morphometric study were not weighed in the field and therefore were not used in these studies.

Examination of the data bearing on growth in weight reveals how sharply the growth of the Clear Lake cisco differs from that in the other three populations (fig. 4). The differences that exist among the populations depend upon differences in the length-weight relationships in the various populations as well as upon differences in the amount of growth in length. The questions of form and changes in form, and of the relationship between length and weight are considered in a separate section (pp. 237-247.)

COMPARISON OF THE GROWTH OF THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS WITH THAT OF CISCO POPULATIONS IN OTHER REGIONS

Data on the growth of the cisco or lake herring have been published for Lake Erie by Clemens (1922), for Oconomowoc and Pine Lakes in southern Wisconsin by Cahn (1927), for Lake Huron by Van Oosten (1929), for Lake Ontario by Pritchard (1931), for the Indian Village Lakes in northern Indiana by Hile (1931), and for Hudson Bay by Dymond (1933). Tables 19 and 20 present a comparison of the growth of these populations with that of the populations of the present investigation. The lengths (table 19) are expressed in millimeters, the weights (table 20) in grams, and the ages in both tables as the number of years of life completed. The methods of presentation of the various authors were altered to conform to this uniform method of expressing length, weight, and age. Dymond did not include data on growth in weight of the Hudson Bay cisco. The largest fish in his collection was a female, 383 millimeters long and weighed 793 grams.

TABLE 19.—Comparison of growth in length, expressed in millimeters, of 11 cisco populations

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout ¹	Muskellunge ¹	Silver ¹	Clear ¹		Huron ²	Ontario ³	Erie ³	Indian Village ³	Oconomowoc ⁴	Pine ⁴	Hudson Bay ³
				Male	Female							
XII	225											
XI	219											
X	213											
IX	197			354	361			345		386	345	
VIII	189			345	351	292	303	285		362	330	336
VII	179		196	335	340	274	297	275	374	336	314	324
VI	168		189	323	326	258	270	255	336	315	283	308
V	158		181	308	312	244	253	235	342	282	246	290
IV	148	174	169	287	291	235	233	215	316	223	195	284
III	137	161	155	255	260	218	226	190	301	174	162	214
II	117	143	129	196	199	185	196	160	260	135	125	184
I	81	96	80	110	109	127	129	125				

¹ Calculated lengths at the end of the year of life indicated.

² A combination of calculated lengths and actual lengths measured in November.

³ Actual measured lengths at time of capture during the growing season. The ages of the fish are really greater than indicated here.

⁴ Actual measured lengths in midwinter after the completion of the growing season.

TABLE 20.—Comparison of growth in weight, expressed in grams, of 10 cisco populations

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout	Muskellunge	Silver		Clear		Huron	Ontario	Erie	Indian Village	Oconomowoc	Pine
			Male	Female	Male	Female						
XII	172											
XI	119											
X							1,190				696	436
IX							1,062				623	406
VIII							880	1,085			611	343
VII	111						796	950			527	262
VI							729	917			445	190
V	50						488	269		810	366	120
IV	47						454	213		782	257	85
III	41	60	96	84	578	705	159	181	128	523	166	60
II	37	51	82	73	418	530	143	159	85	462	105	45
I	31	46	66	61	267	306	100	105		278		
					71	80		31				

It should be mentioned that the length data of table 19 are not in all cases strictly comparable from one population to another. The data for Trout, Muskellunge, Silver and Clear Lakes are all calculated lengths; the data for Lake Huron are a combination of calculated lengths and actual lengths measured in November; the data for Lake Ontario, Lake Erie, the Indian Village Lakes, and Hudson Bay represent actual measurements of fish caught during the growing season; and the data of Oconomowoc Lake and Pine Lake are actual average measurements of fish taken in the winter after the close of the growing season. These small differences in the manner of presentation should not affect the value of the data for purposes of comparison.

Though growth in length of the cisco varies widely in different localities, certain consistent likenesses as to the manner of growth are apparent. The greatest growth in length occurs in the first year of life. The growth of the second year is large but less than that of the first. Growth decreases markedly in the third year of life. Throughout the later years the annual increment of growth in length tends to remain fairly constant. Growth in weight is too greatly complicated by the questions of differences in form and of change of form to permit a general description of the style of growth with respect to this character.

Willer (1929) called attention to the fact that certain fishes can be said to possess a typical species growth curve that retains a characteristic form regardless of the extent to which external factors influence the actual amount of growth. With respect to growth in length the cisco seems to possess such a species growth curve.

It will be noticed in table 19 that the populations showing the greatest (Clear Lake, Indian Village Lakes) and the least (Trout Lake) amount of growth are found in small, inland lakes. Such a situation might be expected in view of the greater diversity of habitat furnished by the smaller bodies of water. The growth in the different populations cannot be classified according to latitude or region, but rather, the differences in growth seem to depend upon purely local conditions within the individual lake or possibly upon the genetic make-up of the local stock.

A population showing a greater amount of growth in length than another does not necessarily show a greater amount of growth in weight. Two examples will illustrate this situation. (See tables 19 and 20.) At all ages beyond the seventh year the Oconomowoc Lake cisco is longer than either the males or females of the Clear Lake cisco, and yet at all ages the weights of the Oconomowoc fish are less than those of the Clear Lake fish of corresponding age. Secondly, at the age of 7 years the weights of the Clear Lake and the Indian Village Lakes ciscoes are approximately equivalent. At the same time the length of the Indian Village Lakes fish at the age of 7 years is greater than that attained by the Clear Lake⁹ males in the ninth year and equal to the length reached by the Clear Lake females in the tenth or eleventh year. These discrepancies between growth in length and growth in weight find their origin in the different length-weight relationships in the various populations. Populations may differ both as to general body form itself and as to the manner of change of form with increase in length.

RANGE OF LENGTH IN INDIVIDUAL AGE GROUPS; MAXIMUM LENGTH AND WEIGHT

Tables 21 to 25 show for the four lakes under consideration here the length distribution of the different age groups in each year's collection. On the whole, length is a poor index of age. The amount of overlap between consecutive age groups is so great that in most instances a fish of a given length might have any of several different ages. This is particularly evident in the Trout Lake data of table 21. In the rapidly growing Clear Lake population, however, the positions of both sexes of the first three age groups (I, II, and III) stand out clearly in the length frequencies. In the 1931 Silver Lake collection the I group is well separated from the remainder of the sample. The Muskellunge Lake collection of 1931 shows a fairly distinct separation of the II and III groups, but a greater abundance of other age groups in the collections of this year might have obscured this division.

⁹ The average lengths of the Clear Lake fish measured at the time of capture were: IX group, male, 355 millimeters; X group, female, 377 millimeters; XI group, female, 378 millimeters.

TABLE 21.—Length frequencies (5-millimeter intervals) of each age group of the Trout Lake cisco in each year's collection

Length	I		II			III			IV			V		VI	VII	VIII	IX	XI	XII
	1928	1930	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931	1931	1931	1931	1931	1931	1931
225 to 229																			1
220 to 224																			
215 to 219																		1	
210 to 214																			
205 to 209																			
200 to 204																			
195 to 199																1	1		
190 to 194																2	1		
185 to 189												1				1		1	
180 to 184																1			
175 to 179												1			3				
170 to 174													1		2	1			
165 to 169															1				
160 to 164															2				
155 to 159															3	2			
150 to 154															1				
145 to 149			2	13															
140 to 144			9	6		3	120	9	4	29	74				21	1			
135 to 139			30	6		15	94	41	5	15	98				8				
130 to 134			43	4		15	1	2	12										
125 to 129			16	4		8													
120 to 124			1	2															
Average	128	128	134	140	136	143	149	142	147	156	148	167	156	165	175	192	200	205	226

TABLE 22.—Length frequencies (5-millimeter intervals) of each age group of the Muskellunge Lake cisco in each year's collection

(The 1932 III and IV groups are not included because of the high degree of uncertainty in their separation)

Length	I				II				III			IV
	1928	1930	1931	1932	1928	1930	1931	1932	1928	1930	1931	1931
180 to 184					1				2			3
175 to 179					3							13
170 to 174					14	14						73
165 to 169					28	46	3		2	4	5	126
160 to 164					88	92	20	8	3			111
155 to 159					78	35	24	6				20
150 to 154					27	18	60	7				1
145 to 149					12	5	93	1				
140 to 144					6		50					
135 to 139					1		5					
130 to 134					5		3					
125 to 129					8							
Average	137	148	136	140	160	162	149	156	172	166	166	176

TABLE 23.—Length frequencies (5-millimeter intervals) of each age group of the Silver Lake cisco in each year's collection

Length	I		II			III			IV			V		VI		VII
	1928	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931
205 to 209												2				
200 to 204									1			1		6	1	5
195 to 199						1			13	13		5		13	2	
190 to 194						2	1		19	13		1	8	26		8
185 to 189						6	6	3	12	22	2	7	28			4
180 to 184						7	6		19	37	4	2	21			
175 to 179						1	5	20	19	6	17	1	14			
170 to 174						2	9	2	19	24	6	10	2			
165 to 169			2	3		12	1	8	12		2					
160 to 164			2			3	15		1	4						
155 to 159			1													
150 to 154			3													
145 to 149			2													
140 to 144			14													
135 to 139			21													
130 to 134			17													
125 to 129			1													
120 to 124			1													
Average	133	141	157	173	171	165	181	177	174	183	183	182	193	188	197	201

TABLE 24.—Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (males) in each year's collection

Length	I		II		III		IV		V		VI		VII		VIII		IX
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	
360 to 369																	
350 to 359																	
340 to 349										1							1
330 to 339											3		1	5	1		
320 to 329							2	1		2	1		5	1	2		
310 to 319					1	2		3	1	3	2		2	2			
300 to 309					1	2		4	1	5				1			
290 to 299					10	10		2									
280 to 289					8	4											
270 to 279					3	4			1								
260 to 269			5	1													
250 to 259			5	8	3												
240 to 249			14	4		1											
230 to 239			5	5													
220 to 229			3	1													
210 to 219			1														
200 to 209	1		1	1													
190 to 199	1																
180 to 189	4	5															
170 to 179	8	10															
160 to 169	5	5															
Average	178	176	253	254	285	290	317	314	325	320	326	320	331	336	338	345	355

TABLE 25.—Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (females) in each year's collection

Length	I		II		III		IV		V		VI		VII		VIII		IX		X		XI
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	
380 to 389																					
370 to 379																					
360 to 369																					
350 to 359																					
340 to 349																					
330 to 339																					
320 to 329																					
310 to 319																					
300 to 309																					
290 to 299																					
280 to 289																					
270 to 279																					
260 to 269																					
250 to 259																					
240 to 249																					
230 to 239																					
220 to 229																					
210 to 219																					
200 to 209																					
190 to 199																					
180 to 189																					
170 to 179																					
160 to 169																					
150 to 159																					
Average	186	176	264	262	302	308	334	329	338	342	339	320	344	362	354	356	351	368	376	379	378

There are some disagreements between the length distributions of fish of the same age, but taken in different seasons. Some of these differences, particularly in the younger age groups, are due to the variation in the time of the collection of the sample within the growing season. The I groups of Clear Lake will serve as an example. (See tables 24 and 25.) In 1932 these ciscoes were collected from July 12 to July 19, while in 1931 they were taken during two periods, July 22 to July 28 and September 3 to September 5. Since the September samples averaged more in length (the average length of the September fish was about 200 millimeters) than the July samples, their presence accounts for the greater upward extension of the length distribution of the 1931 I-group Clear Lake ciscoes. However, at least some

of the other differences between the length distributions of fish of the same age may be accounted for by the actual differences in the growth histories of the year classes they represent. This appears to be true, for example, in the II groups from Muskellunge Lake (table 22). The 1931 II-group fish from this lake were much smaller in average size than those of the preceding 2 years. The examination of the tabulation of calculated lengths for these various groups (table 4) likewise shows that the 1931 II group (1929 year class) actually grew less during the first and second years of life than did the 1929 and 1930 II groups (year classes of 1927 and 1928).

In table 26 are given the data relative to the longest and the heaviest fish taken from each population. (Data concerning the lengths and weights of the oldest fish taken may be obtained from tables 3 to 7.) There is sufficient variation in individual growth that the largest individual need not necessarily be the oldest. In the Silver Lake collections and for both sexes of the Clear Lake samples the largest fish are from 1 to 4 years below the observed maximum age. It is true further that the largest fish with respect to length is not always the heaviest (for example, see the data on the longest and the heaviest fish from Silver Lake). The differences among the maximum sizes attained in the different populations are more striking if size is considered in terms of weight. The Clear Lake fish reach a weight approximately 17 times as great as those from Muskellunge Lake, 10 times as great as those from Silver Lake, and 7 times as great as those from Trout Lake.

TABLE 26.—Data concerning the longest and the heaviest cisco in each of the 4 lakes

Lake	Year of capture	Age	Length in millimeters	Weight in grams	Sex
Trout	1931	XII	226	172	Female.
	1932	IV	180	70	Do.
Muskellunge	1932	V	188	110	Male.
	1930	VI	206	120	Female.
Silver	1930	VII	204	910	Do.
	1932	VIII	368	910	Male.
Clear	1931	X	1,383	1,210	Female.
	1932	VII	383	1,210	Do.

¹ This fish was not weighed before it was preserved. The length recorded includes a correction for shrinkage.

The maximum size attained depends both upon rate of growth and upon the maximum age of survival. The Trout Lake cisco is the slowest growing of the four populations, yet a few individuals survive to such an age as to reach a size greater than is attained by the fish in either Silver or Muskellunge Lakes. It is probable that further collections might change the order of arrangements of the lake with respect to the maximum size reached by the cisco, as well as the absolute maximum values for length and weight.

CONDITION AND THE RELATIONSHIP BETWEEN LENGTH AND WEIGHT

Weight in fishes may be considered a function of the length. If form and specific gravity¹⁰ were constant throughout life the relationship could be expressed by the equation,

$$W = cL^3, \quad (1)$$

where

W = weight,

L = length,

and

c = constant.

The above equation is a statement of the well-known cube law. Actually, in nature, the value of c is not constant for a species or population but is subject to a

¹⁰ Reibisch (1908) could find no appreciable seasonal variation in the specific gravity of the plaice. Keys (1928) pointed out that the hydrostatic equilibrium that exists between the fish and its environment renders great fluctuations in specific gravity unlikely.

wide range of variation. The values of c under various definitions (coefficient of condition, condition factor, length-weight factor) have been used widely by fisheries investigators as measures of individual or average seasonal and regional differences in the condition or "degree of well-being" of fishes. Some investigators have used the coefficient as a measure of the state of sexual development. Others have considered condition to apply only to the state of nourishment and have removed the gonads before taking the weight for the calculation of the coefficient. Yet others have used the coefficient merely as a measure of relative heaviness and have recognized the effect of both the state of sexual development and of the state of nourishment on the determination of its value.

In addition to its use as a means of estimating condition, the equation (1) has been employed also to describe the general length-weight relationship in populations of fishes, and thus serve as the basis for the calculation of unknown weights of fish of known length or of unknown lengths of fish of known weight. The use of the equation in this latter capacity has met with indifferent success, due to the failure of the cube law to describe accurately the relationship of length to weight in many forms of fishes. Fulton (1904) who applied the law to the relationship of length to weight in several marine species stated:

The law in regard to the increase in weight according to the cube of the length, although broadly true, does not accurately apply in the case of the fishes examined. With scarcely an exception, the weight at a given length is greater than the weight calculated from the law, so that if the specific gravity of the fishes remains constant they must increase somewhat more in other dimensions than in length.

Although the cube law does appear to apply to the length-weight relationship in some species (Crozier and Hecht, 1914; Hecht, 1916), these instances appear to be the exceptions, for the observations of Fulton in regard to the inadequacy of the cube law in describing the length-weight relationship in fishes have been repeated by numerous investigators and on many forms of fishes. In recent years a much more satisfactory method of describing the length-weight relationship in fishes has been developed through the use of the more general equation:

$$W = CL^n, \quad (2)$$

where

W = weight,

L = length,

and

c = constant.

In this equation the values of both C and n are determined empirically.

Such a relationship has been determined by Järvi (1920), Tjurin (1927), Clark (1928), Keys (1928), Fraser (1931), Hart (1931, 1932), Tester (1932), Walford (1932), and Schultz (1933).

Some of the above authors have, however, confused the two entirely distinct issues of describing condition and expressing the length-weight relationship, and have abandoned the use of coefficients of condition based on the cube relationship in favor of those based on an empirically determined exponent (C in $W = CL^n$). That coefficients calculated from the cube relationship and from empirically determined exponents are in no sense of parallel significance as measures of condition appears from the following simple illustration.

A fish with a length of 1 foot and a weight of 1 pound will show on the basis of the cube relationship a coefficient of condition of 1.00. In conformity with a rather general usage this quantity may be designated as K . If this fish doubles its length without change of form or of specific gravity its weight at the length of 2 feet will be 8 pounds, and the value of K will continue to be 1.00. If, however, the weight at 2 feet is 10 pounds instead of 8 the value of K at this greater length will be 1.25, and it will be known that a change of form¹¹ has occurred along with growth in length. It may be considered that 2 pounds of the weight of this 10-pound fish represent its change of form; this change is measured directly in the increased value of K . The 10-pound fish is 25 percent heavier than the 8-pound fish and is 25 percent *relatively* heavier than the 1-pound fish (that is, the 10-pound fish corresponds in form to a fish that would have a weight of 1.25 pounds at the length of 1 foot). Thus it may be seen that values of K , by reason of their calculation from the cube relationship are direct and quantitative measures of form or relative heaviness, and in this sense are directly comparable between fishes of any length.

Now if the weights of 1 pound at the length of 1 foot and of 10 pounds at 2 feet were to represent actual average conditions within a population, the corresponding length-weight equation would be:

$$W = 1.00L^{3.32193}$$

The coefficients of condition calculated from this higher empirical exponent are 1.00 both for the fish at the length of 1 foot and weight of 1 pound and for the fish at the length of 2 feet and weight of 10 pounds. Thus it may be seen that the coefficient C fails entirely to measure in any way the change of form that occurred with increase in length. Further, the value of C for a fish that weighs 8 pounds at the length of 2 feet is 0.80, and from this value it would appear that a fish that doubles its length without change of form actually suffers a loss of condition. Since the assumption is hardly tenable that a fish can suffer such a great loss of condition without undergoing any change of form or relative heaviness it must be concluded that values of C calculated from empirically determined exponents fail to serve as satisfactory measures of condition. Questions concerning the use of C as a coefficient of condition will receive further consideration in connection with the presentation of the data of this investigation on condition and the length-weight relationship in the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake. At the present time, however, a brief review will be presented of the observations and opinions of authors who have used or suggested the use of C in equation (2) as a coefficient of condition.

The observations of Järvi (1920) should be included in this review, although in justice to that author it should be emphasized that he was concerned primarily with the calculation of unknown lengths and weights from a general length-weight relationship rather than with the measure of condition. Järvi's data are of particular interest here since he included a comparison of coefficients based on the cube relationship and as determined from equations of the type, $W = CL^n$, with empirically determined exponents. His coefficients for the males, the ripe females, and the spent females of the kleine Maräne (*Coregonus albula*) were, on the basis of the cube relationship,

¹¹ The term "form" as employed throughout this section carries with it no implications as to details of shape, but refers only to relative heaviness of stature.

0.00848, 0.00989, and 0.00830, respectively.¹² The coefficients as calculated from formulas with empirically determined exponents were, for the males, ripe females, and spent females, 0.0050, 0.0020, and 0.0056, respectively. The exponents in these last three formulas were 3.2 for the males, 3.64 for the ripe females, and 3.16 for the spent females. The comparison of the coefficients derived by the two methods shows clearly that those based on empirical exponents fail completely to reflect the relative heaviness of the fish groups to which they pertain. While the values of K based on the cube relationship show that the ripe females are on the average the relatively heaviest group, followed in order by the males and the spent females, the values of the coefficients calculated from equations with empirical exponents follow exactly the reverse order. Thus on the basis of the values of C of equation (2) the relatively heaviest group of fish would appear to be in the poorest condition. If the values of the two types of coefficients are compared in relation to the values of the exponents, n , it appears that while the values based on the cube relationship depend on the relative heaviness of the fish upon which they are based, the values of the coefficients calculated from equations with empirical exponents depend primarily not on the heaviness of the fish but rather on the value of the exponents. A large value of n is associated with a small value of the coefficient—and the reverse.

Clark (1928) appears definitely to have confused the two problems of describing condition and expressing the length-weight relationship. From her study of condition and the length-weight relationship in the California sardine (*Sardina caerulea*) Clark concluded: "The weight of sardines increases at a rate slightly greater than the cube of the length. For the data studied the correct formula for the weight-length factor was found to be $F = \frac{1000 W}{L^{3.15}}$. But for the purpose of the present study the formula $F = \frac{1000 W}{L^3}$ was sufficiently accurate."

Clark evidently believed that the coefficient of condition (weight-length factor), to be accurate, should tend to hold a constant value at all lengths of the fish, for she stated: "The more a species departs from this general weight-length relationship [cube relationship], the greater the error involved in the factor." Concerning the changes in the value of the factor with increasing length she observed further: "Due to the error introduced from calculating F on the basis of the cube of the length, the curve resulting from the equation $F = \frac{1000 W}{L^3}$ rises consistently throughout the range of sizes represented in the commercial catch at San Pedro."

Clark's conclusion that the failure of the cube law to describe the length-weight relationship makes inaccurate the use of coefficients of condition (weight-length factors) based on the cube relationship is scarcely justifiable, particularly in view of the fact that coefficients based on empirical exponents fail to reflect differences in form or relative heaviness while those based on the cube relationship offer a direct measure of relative heaviness independent of general length-weight relationships and comparable as measures of relative heaviness between fish of any length. Clark actually studied variations in the weight-length factor on the basis of values calculated from the cube relationship, but did so only because she considered that the use of these values introduced "only a minor error into the work."

¹² In the data from which these coefficients were determined weights were recorded in grams and lengths in centimeters.

Clark's data on the correlation between weight-length factors (calculated from the cube relationship) and the fat content of the sardine offers convincing evidence that measures of condition should be calculated from the cube relationship. Her data show conclusively that variations with length in the value of the weight-length factor are reflected closely in corresponding variations with length in the fat content of the sardine. Inasmuch as relative heaviness is thus showed to be dependent on fatness (condition), changes with length in relative heaviness must be considered also to represent changes of condition. In view of this fact it does not appear valid to measure condition in terms of a quantity that tends to be constant for fish of all lengths regardless of actual changes that may occur in relative heaviness of form with change in length. Since the quantity C in the equation $W = CL^n$ tends toward this constancy and fails to measure relative heaviness it must fail also to measure the differences of fatness (condition) upon which differences in relative heaviness depend.

Tester (1932) likewise appears to have confused the two problems of measuring condition and describing the general length-weight relationship. Concerning his method of determining the general length-weight relationship in the smallmouth black bass (*Micropterus dolomieu*) he stated:

Following the method used by Hart (1931) and others the relationship between length and weight for bass from Perch Lake [Ontario] was obtained by plotting average lengths against average weights on double logarithmic paper and deriving the natural slope of the resultant straight line drawn through the points. It was found that the weight increased by the power 3.1(7) of the length. * * *

Tester assumed, however, that the failure of the cube law to describe the length-weight relationship made the use of coefficients of condition based on the cube relationship invalid. Concerning the equation, $K = \frac{100 W}{L^3}$, employed by Hile (1931) to describe condition in several species of Indiana lake fish, Tester stated:

This equation is only approximate and might be better expressed—

$$K = \frac{100 W}{L^x}$$

In the case of the Perch Lake bass the power x would have a value 3.1(7). If the power $x=3$ is used, the value of K tends to increase with the length of the fish whereas it should remain constant.

Tester used the value $x=3.1(7)$ as determined from the Perch Lake bass to compute coefficients of condition for his smaller samples from Phantom Lake, Lake Nipissing, and Georgian Bay, but observed that, "To be strictly accurate, the value x should be determined separately for each of the latter three bodies of water. * * *"

Had Tester actually determined the value of the exponent for each of the bass populations he studied he would probably have become aware of the difficulties involved in the use of coefficients of condition based on empirical exponents.

Schultz (1933) expressed the relationship of length to weight in the bay smelt (*Atherinops affinis oregonia*) by the equation $W = FL^{2.59}$. He also employed the quantity F as a measure of seasonal changes in weight, dependent on the state of development of the gonads. That Schultz considered the length-weight factor, F , identical in significance with factors calculated from the cube relationship is apparent from the following statement: "The length-weight factor, F , was used to estimate the state of development of the gonads, as has been done by D'Arcy Thompson (1917),

Van Oosten (1929), Clark (1928b), Weymouth (1918 and 1923), Reibisch (1911), Crozier and Hecht (1915), and others.¹³

Of the above authors some employed the cube relationship in the study of the length-weight relationship (Thompson, Van Oosten, Weymouth (1918), Crozier and Hecht), while others used empirical exponents (Clark, Weymouth (1923)).

Because of the serious objections to the use of coefficients of condition based on empirical exponents, condition in this investigation has been measured by coefficients calculated from the cube relationship. The comparison of the equations $W=KL^3$ and $W=CL^n$ reveals an interesting connection between condition and length in populations that deviate from the cube relationship. The equation, $W=CL^n$, may be written in the form:

$$W=f(L)\cdot\phi(L), \quad (3)$$

where

$$\begin{aligned} f(L) &= CL^m, \\ \phi(L) &= L^3, \end{aligned}$$

and

$$m=n-3.$$

Thus it may be seen that where weight can be expressed as a parabolic function of the type $W=CL^n$ condition can be expressed by a similar function of length. While this definition of condition as a function of length is valid only insofar as the equation (3) actually describes the length-weight relationship, the failure of equation (3) has no effect on the value of coefficients calculated from the cube relationship as measures of relative heaviness. Where the coefficient of condition does behave as a parabolic function of length (hyperbolic if $m < 0$), the value of $m=n-3$ measures the rate of change of form or condition.¹⁴

In order to have the most complete data for the study of condition the value of $f(L) = \frac{W}{L^3}$ was calculated for each individual specimen. Since lengths were recorded

¹³ This statement of Dr. Schultz as it pertains to the studies of other investigators is in some points inaccurate. Van Oosten made no use of the coefficient of condition to study the state of sexual development but was interested primarily in deriving a general length-weight equation; he did, however, quote Thompson (1917) as to the effect of sexual state on the value of the coefficient. Clark used the weight-length factor chiefly as a measure of the state of nourishment or fatness as the following statement shows: "The monthly and yearly fluctuations in the weight-length factors of sardines were due, therefore, to some changes in the composition of the body tissue of the fish, presumably an increase or decrease in the fat content, and not to the amount of food in the alimentary tract, or to the growth of the sex organs." Weymouth (1918 and 1923) was concerned with the general length-weight relationship and not with any individual or seasonal fluctuations in the length-weight factor. Reibisch's coefficient was calculated neither from $W=KL^3$ nor $W=CL^n$, but was a "Dickenkoeffizient" with the formula $\delta = \sqrt{\frac{40000}{\pi} \frac{G}{L^3}}$, (G =weight in grams, L =length in centimeters). Reibisch discussed the effect of sexual state on the state of nourishment, but, in order to make δ describe only the state of nourishment, removed the gonads before weighing. Crozier and Hecht were concerned with the determination of a general length-weight equation. They stated: "All the fish examined (over 400) were either spent or unripe; so we are sure that none of the weights recorded are influenced by the ripening of the gonads." (The date of issue of Crozier and Hecht's paper was 1914, not 1915.)

¹⁴ The differential equations corresponding to the equations $W=CL^n$, and $f(L)=K=CL^m$ are:

$$\begin{aligned} \frac{dW}{W} &= n \frac{dL}{L}, \\ \text{and} \\ \frac{dK}{K} &= m \frac{dL}{L}. \end{aligned}$$

Now $\frac{dW}{W} \cdot \frac{1}{\frac{dL}{L}}$, $\frac{dL}{L} \cdot \frac{1}{\frac{dL}{L}}$, and $\frac{dK}{K} \cdot \frac{1}{\frac{dL}{L}}$, where t =time, are the relative rates of change in weight, length, and condition, respectively. The exponent n describes the ratio of the relative rates of change of weight and length, while m describes the ratio of the relative rates of change of condition (form) and length. If $n=3$, $m=0$, and growth proceeds without change of form. If $n \neq 3$, then $m \neq 0$, and the values of the exponents measure the rate of change of form.

in millimeters and weights in grams, the actual values of $f(L)$ were quite small. To avoid the use of such small decimals the coefficient of condition K as actually used was defined:

$$K=f(L) \times 10^5 \quad (4)$$

In the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake populations the variation of condition with length, and of weight with length conforms closely over certain length intervals with the conditions defined by equation (3). Consequently it was possible to determine equations describing condition and weight as functions of length by fitting parabolic equations to the observed average values of K at different lengths.

The assumed relationship between K and L indicates a linear relationship between the logarithms of their values:

$$\log K = a + m \log L, \quad (5)$$

where

$$a = \log C + 5.$$

It is possible to determine the values of C and m by fitting a straight line to the logarithms of corresponding values of K and L . The determined values of C and m can be used in writing not only the equation for K as a function of length but also for writing the equation for weight as a function of length.¹⁵

Table 27 contains the equations obtained for $K=C \times 10^5 L^m$ and $W=CL^n$. The data from which the equations were determined are found in tables 28 to 31. The tables mentioned last contain also a comparison of actual weights with theoretical weights calculated from the length-weight equations of table 27.

TABLE 27.—Equations for $K=C \times 10^5 L^m$ and $W=CL^n$ as determined for the various cisco collections

Lake	Year of collection	Sex	Number of specimens	Range of L	$K=C \times 10^5 L^m$	$W=CL^n$
Trout	1928	♂, ♀	138	125-154	$K=6.5232 L^{-0.32741}$	$W=6.5232 \times 10^{-5} L^{2.67259}$
	1930	♂, ♀	483	125-169	$K=4.8834 L^{-0.38967}$	$W=4.8834 \times 10^{-5} L^{2.61033}$
	1931	♂, ♀	338	125-164	$K=38.7640 L^{-0.69245}$	$W=38.7640 \times 10^{-5} L^{2.30755}$
	1928	♂, ♀	263	145-179	$K=4.568.9 L^{-1.02900}$	$W=4.568.9 \times 10^{-5} L^{1.97100}$
Muskellunge	1930	♂, ♀	244	140-179	$K=567.36 L^{-1.32462}$	$W=567.36 \times 10^{-5} L^{1.67538}$
	1931	♂, ♀	505	130-179	$K=141.92 L^{-0.94932}$	$W=141.924 \times 10^{-5} L^{2.05068}$
	1932	♂, ♀	93	145-179	$K=182.87 L^{-0.86815}$	$W=182.87 \times 10^{-5} L^{2.00085}$
	1930-31	♂	110	130-199	$K=0.25532 L^{0.25370}$	$W=0.25532 \times 10^{-5} L^{2.74627}$
Silver	1930-31	♂	160	135-204	$K=0.12322 L^{0.46379}$	$W=0.12322 \times 10^{-5} L^{2.43672}$
	1931	♂	85	160-359	$K=0.10104 L^{0.80330}$	$W=0.10104 \times 10^{-5} L^{2.80530}$
Clear	1931	♀	105	170-379	$K=0.04555 L^{0.84491}$	$W=0.04555 \times 10^{-5} L^{2.64491}$
	1932	♂	100	160-379	$K=0.04954 L^{0.82476}$	$W=0.04954 \times 10^{-5} L^{2.62476}$
	1932	♀	85	150-389	$K=0.03652 L^{0.88489}$	$W=0.03652 \times 10^{-5} L^{2.88489}$

¹⁵ For the purpose of fitting the equations the specimens were divided into length groups (10 millimeters in the Clear Lake cisco, 5 millimeters in the other populations) and the average values of K and L determined for each interval. A straight line was fitted to the logarithms of these values by the equating of moments. Combinations of the sexes and of different years' collections were made wherever the data justified the procedure. In Trout Lake and Muskellunge Lake the sexes were combined in each year's collection. In Silver Lake the sexes were treated separately, but the 1930 and 1931 collections were combined. In Clear Lake each sex and each year's collection received separate treatment. The data upon which the equations were based include only the size ranges for which adequate numbers of specimens were available.

TABLE 28.—Trout Lake ciscoes.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

[Sexes combined]

1928				1930				1931			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
128.....	29	28	1.33	127.....	25	26	1.22	128.....	28	29	1.38
132.....	31	30	1.31	132.....	27	27	1.18	133.....	31	31	1.32
137.....	33	34	1.31	137.....	31	31	1.17	137.....	33	32	1.25
142.....	37	36	1.28	143.....	34	33	1.14	142.....	36	35	1.24
147.....	40	40	1.27	147.....	36	36	1.15	147.....	39	39	1.21
150.....	43	44	1.28	152.....	40	40	1.13	152.....	42	42	1.21
				157.....	43	43	1.12	156.....	45	45	1.18
				162.....	48	48	1.14	162.....	49	49	1.15
				166.....	51	51	1.11				

TABLE 29.—Muskellunge Lake ciscoes.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

[Sexes combined]

1928				1930				1931				1932			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
147.....	44	45	1.40	142.....	36	36	1.24	134.....	33	32	1.34	145.....	38	39	1.24
152.....	46	45	1.28	147.....	38	37	1.18	137.....	34	33	1.28	153.....	46	44	1.27
157.....	48	48	1.25	153.....	41	42	1.16	142.....	37	37	1.30	157.....	47	46	1.22
162.....	50	51	1.21	157.....	43	43	1.11	147.....	40	41	1.28	162.....	50	49	1.18
166.....	52	53	1.16	162.....	45	46	1.08	152.....	42	44	1.26	167.....	52	52	1.12
172.....	55	58	1.13	166.....	47	48	1.04	157.....	45	46	1.19	172.....	55	55	1.08
176.....	57	54	.98	172.....	50	49	.97	162.....	48	49	1.15	176.....	57	58	1.05
				177.....	53	52	.94	166.....	51	49	1.08				
								172.....	55	55	1.09				
								176.....	57	54	.99				

TABLE 30.—Silver Lake ciscoes.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

1930-31, male				1930-31, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
132.....	29	30	1.28	138.....	30	30	1.15
137.....	32	32	1.24	142.....	34	35	1.19
143.....	37	36	1.23	147.....	38	37	1.16
172.....	69	70	1.36	167.....	58	55	1.19
177.....	76	77	1.37	172.....	65	67	1.32
182.....	83	84	1.39	177.....	72	74	1.32
187.....	91	91	1.39	182.....	79	81	1.33
191.....	98	99	1.42	187.....	87	89	1.34
197.....	108	106	1.38	192.....	95	95	1.35
				196.....	102	102	1.34
				201.....	111	108	1.33

TABLE 31.—Clear Lake ciscoes.—Values of length, theoretical weight, actual weight, and K at 10-millimeter length intervals

1931, male				1931, female				1932, male				1932, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
167.....	62	68	1.47	177.....	73	76	1.38	168.....	57	59	1.26	155.....	42	43	1.13
174.....	72	70	1.37	182.....	83	85	1.36	176.....	69	68	1.24	175.....	68	68	1.26
182.....	84	80	1.34	197.....	108	106	1.39	183.....	79	79	1.29	180.....	76	75	1.29
203.....	124	124	1.48	201.....	116	122	1.51	215.....	141	138	1.39	195.....	106	100	1.43
204.....	195	195	1.53	231.....	193	184	1.49	234.....	192	182	1.42	255.....	268	268	1.62
234.....	241	240	1.62	244.....	237	226	1.54	245.....	227	226	1.53	265.....	314	309	1.69
246.....	268	272	1.67	256.....	280	284	1.69	255.....	262	244	1.47	274.....	338	351	1.64
253.....	316	316	1.70	266.....	321	312	1.68	264.....	297	292	1.53	290.....	394	433	1.62
265.....	351	330	1.62	275.....	365	352	1.69	273.....	335	370	1.82	306.....	520	529	1.81
282.....	392	385	1.71	283.....	406	385	1.69	288.....	407	434	1.75	315.....	594	588	1.90
293.....	448	445	1.77	296.....	480	462	1.77	294.....	437	443	1.85	324.....	695	650	2.05
301.....	493	465	1.71	303.....	522	546	1.96	302.....	484	508	1.80	334.....	704	724	1.90
316.....	582	595	1.89	314.....	589	570	1.84	315.....	565	563	1.90	345.....	812	821	1.98
322.....	624	663	1.99	327.....	686	712	2.05	326.....	634	657	1.90	356.....	984	923	2.18
333.....	700	708	1.92	335.....	752	766	2.04	334.....	695	708	1.91	365.....	1,002	1,012	2.06
343.....	777	803	2.00	345.....	833	866	2.07	343.....	767	773	1.92	373.....	1,107	1,091	2.12
350.....	834	850	1.98	353.....	905	933	2.12	352.....	847	840	1.82	384.....	1,198	1,212	2.12
				362.....	997	1,036	2.18	365.....	960	885	1.79				
				371.....	1,088	1,048	2.05								

The comparisons of theoretical and actual weights show that the equations of table 27 fit the observed data in a quite satisfactory manner, for in general the agreement between actual and calculated weights is good. The discrepancies between actual and calculated weights are greater in the Clear Lake samples (table 31) than in those of the other three lakes. This might be expected not only because of the smaller numbers of fish in the Clear Lake collections but also because of the much greater size range shown by the ciscoes of this lake.

The equations themselves (table 27) contribute interesting information relative to the problem discussed previously (pp. 238-242) concerning the use of *C* as a coefficient of condition. The examination of the values taken by $C \times 10^5$ shows how widely this quantity can vary not only within different populations of the same species but also in different sexes and in different years' collections of the same population. Certainly the value 0.03652 (Clear Lake females, 1932) cannot be compared directly as a measure of condition with the value 4,568.9 (Muskellunge Lake, 1928), particularly in view of the fact that the higher value of *C* pertains to the slenderer form. Nor can the higher values of *C* shown by the males in the Clear Lake equations be interpreted as showing the males of this population to be in better condition than the females. The actual values of *K* and of weight for length show that the reverse is true. The table shows yet other examples that demonstrate clearly that values of *C* cannot be compared either between the sexes or between different years' collections of the same population, much less between different populations.

If the variations in the value of *C* are examined in relation to variations in the values of the exponents, *m* and *n*, it may be seen again that the values taken by *C* depend on the values taken by *n*. If *n* is high, *C* is small—and the reverse. Thus it may be seen that here as in Järvi's data the values of *C* do not depend on relative heaviness but on the rate of change in relative heaviness as measured by the exponents, *m* and *n*.

The examination of the values taken by *n* show further that this quantity is not fixed either for a species or a population. The values of the exponent not only vary tremendously from lake to lake but also vary considerably from year to year in the

samples of a single population. It will now be shown that not only does n vary from population to population and from year to year in the same population but further that in two populations, at least, the values of n determined for a single year's sample apply only to the length intervals for which the equations were fitted and do not hold for fish whose lengths lie outside these length ranges.

If the equation, $K=C \times 10^5 L^m$, for each year's collection of the Muskellunge Lake cisco is solved for $L=100$ millimeters the following values of K are obtained: 1928, $K=2.59$; 1930, $K=1.93$; 1931, $K=1.80$; 1932, $K=1.86$. These values of the coefficient of condition indicate a fairly robust body form. Ciscoes of such heavy build are indeed found among the larger fish of the Clear Lake population (table 31), but it is very unlikely that such heavily built individuals may be found at the length of 100 millimeters in the Muskellunge Lake cisco population, or in any population of the same species. This view is supported by the comparison of the K values upon which the 1928 length-weight relationship was determined (table 29) with those of the 15 fish that were less than 145 millimeters long. Eight of these 15 fell in the 125-129 millimeter length interval and had an average value of 1.23 for the coefficient of condition, K ; the 5 individuals in the 130-134 millimeter interval had an average K value of 1.25; while 2 single individuals whose lengths were 138 and 144 millimeters had K values of 1.29 and 1.34, respectively. These data show that in 1928 the values of K in Muskellunge Lake ciscoes less than 145 millimeters long were much lower than the theoretical length-weight equation (based on specimens more than 145 millimeters long) indicated they should be.

The 1931 data for Trout Lake furnish another example of the failure of a length-weight equation to describe the length-weight relationship for fish outside the length range for which the equation was determined. The length-weight equation for 1931 (see table 27) was based on specimens whose lengths ranged from 125 to 164 millimeters. The same collections contained five large fish (189 to 225 millimeters long). Since the 1931 length-weight equation for Trout Lake indicates a continuous decrease of K with increase in length, these large fish would be expected to show small values for the coefficient of condition. Table 32 which contains a comparison of actual and theoretical values of weight and K for these five fish shows that they fail completely to fulfill this expectation, for the actual values of weight and K are far above the theoretical values calculated from the length-weight equation.

TABLE 32.—Values of length, weight, and K for the 5 longest individuals of the 1931 Trout Lake cisco collection

Age	Length	Calculated weight	Actual weight	Calculated value of K	Actual value of K
VIII	189	69	100	1.03	1.48
XI	192	72	90	1.02	1.27
VIII	203	82	122	.98	1.46
XI	218	97	148	.93	1.43
XII	226	105	172	.91	1.49

Observations on the failure of a single value of n to hold for all lengths of fish within a population have been made previously by Clark (1928), Walford (1932), and Schultz (1933).

Materials for the comparison of condition in the different populations and in different years are to be found in tables 28 to 31 and 33. The last-named table

shows the variation in K according to age, while the earlier tables show the variation of K with length. On the whole the changes of K with age depend on differences in the average length of the various age groups. In Clear Lake in particular large differences in average lengths of age groups are associated with large differences in the average value of K , while smaller differences in average length are associated with smaller differences in the average value of K .

TABLE 33.—Value of K according to age groups

[Number of specimens in parentheses]

Age	Trout Lake			Muskellunge Lake			Silver Lake		
	1928	1930	1931	1928	1930	1931	1928	1930	
								Male	Female
XII			1.49 (1)						
XI			1.35 (2)						
X									
IX			1.47 (2)						
VIII									
VII			1.14 (2)						1.39 (3)
VI		1.17 (9)	1.13 (23)				1.34 (10)	1.38 (10)	1.37 (15)
V	1.32 (17)	1.15 (99)	1.21 (139)			1.10 (2)	1.29 (69)	1.42 (23)	1.37 (35)
IV	1.23 (61)	1.13 (347)	1.24 (129)	1.11 (10)	1.06 (14)	1.13 (266)	1.30 (46)	1.38 (13)	1.34 (12)
III	1.30 (102)	1.16 (36)	1.30 (50)	1.23 (252)	1.07 (214)	1.26 (229)	1.29 (9)	1.28 (3)	1.26 (4)
II	1.24 (2)		1.28 (2)	1.24 (19)	1.18 (17)	1.28 (9)	1.19 (1)		
I									

Age	Silver Lake, 1931		Clear Lake			
	Male	Female	1931		1932	
			Male	Female	Male	Female
XII						2.20 (1)
XI						2.00 (1)
X					2.15 (1)	2.36 (2)
IX					2.12 (1)	2.16 (8)
VIII					1.97 (3)	2.09 (12)
VII					2.00 (6)	2.50 (1)
VI		1.36 (8)	1.96 (7)	2.06 (8)	1.82 (2)	1.93 (7)
V	1.40 (12)	1.34 (22)	1.88 (2)	2.10 (1)	1.83 (11)	1.90 (14)
IV	1.41 (13)	1.28 (22)	1.86 (5)	2.03 (7)	1.70 (23)	1.82 (21)
III	1.31 (10)	1.29 (13)	1.73 (17)	1.86 (19)	1.66 (27)	1.64 (13)
II	1.30 (4)	1.25 (8)	1.66 (28)	1.66 (27)	1.56 (20)	1.27 (11)
I	1.22 (24)	1.18 (25)	1.38 (18)	1.39 (15)	1.25 (20)	

The analysis of the data was made to include the examination of variation of K with size in fish of the same age and the variation of K with age in fish of the same size. Without presentation of the extensive tabular material that would be necessary to show the detailed results of these analyses it may be stated that the variation of K with length within an age group proceeds in the same direction as the variation of K with length in the population as a whole, and that, on the whole, the value of K appears to be independent of age in fish of the same length.

The tables 28, 29, 30, 31, and 33 show further that condition varies from year to year in the same population. In both Trout Lake and Muskellunge Lake the ciscoes were slenderer in 1930 than in 1928 or 1931. In Silver Lake the lack of sex records for 1928 makes a comparison of that year with later years difficult. There is some indication, however, that in 1928 the Silver Lake cisco may have been in poorer condition than in 1930. In Clear Lake there do not appear to be any notable differences in the condition of the cisco in 1931 and 1932.

With respect to average condition, from poorest to best, the populations fall in the following order: Muskellunge Lake (sexes combined), Trout Lake (sexes combined), Silver Lake females, Silver Lake males, Clear Lake males, and Clear Lake females.

The order of the four populations of this investigation with respect to average condition is the same as their order with respect to average duration of life (p. 267). The indicated association between condition and longevity finds support in the observation (table 32, p. 246) that in Trout Lake survival to an advanced age appears to be accompanied by, if not contingent upon, a departure from the general tendency for condition to become poorer with increased length.

The study of condition and of the length-weight relationship in these four cisco populations may well be concluded with an illustration of how progressive change of condition is reflected in a progressive change in body proportions. In order to determine the intensity of the excess vertical and lateral growth that produced the heavy body form in the older and larger Clear Lake ciscoes the relationship of length to depth and width was studied in 95 preserved specimens collected in 1932. Since the relationship of length to weight in the Clear Lake cisco can be expressed satisfactorily by a parabolic equation it was assumed that a similar relationship may hold between length and width and length and depth. On the basis of this assumption the following equations were derived:

Male—46 specimens:

$$\text{Depth} = 5.052 \times 10^{-2} L^{1.2939}$$

$$\text{Width} = 0.656 \times 10^{-2} L^{1.5502}$$

Female—49 specimens:

$$\text{Depth} = 5.230 \times 10^{-2} L^{1.2899}$$

$$\text{Width} = 0.173 \times 10^{-2} L^{1.7879}$$

L =length in millimeters.

TABLE 34.—Clear Lake ciscoes, 1932—Comparison of theoretical and actual values of body depth and body width

Males					Females				
Length	Calculated depth	Actual depth	Calculated width	Actual width	Length	Calculated depth	Actual depth	Calculated width	Actual width
165.....	37	36	18	19	150.....	34	34	13	13
175.....	40	38	20	19	165.....	38	37	16	20
181.....	42	44	21	21	172.....	40	40	17	19
206.....	50	49	25	26	190.....	46	48	20	24
235.....	59	62	31	31	265.....	69	68	37	36
255.....	66	68	35	35	274.....	73	72	39	35
266.....	69	69	37	36	295.....	80	80	45	41
284.....	76	79	42	41	305.....	84	85	48	47
292.....	78	81	44	43	314.....	87	87	50	49
316.....	82	81	46	47	324.....	90	86	53	45
302.....	86	87	49	43	334.....	94	92	56	54
316.....	90	89	51	51	345.....	98	99	59	64
326.....	93	91	54	56	355.....	102	105	63	67
334.....	96	92	56	63	362.....	105	111	65	69
345.....	97				376.....	110	111	69	65
					383.....	113	109	72	59

Table 34 shows the lengths, depths, and widths from which the above equations were calculated. The data of the same table also make possible the comparison of actual measured depths and widths with theoretical values calculated from the equations. If due consideration is given the small number of specimens the agreement between the actual and theoretical values of depth and width is, in general, good.

The equations show that both the males and females of the Clear Lake cisco grow more rapidly in depth and width than in length. The differential growth of the dimension, width, proceeds more rapidly than the differential growth of the dimension, depth, that is, the change to a heavier stature proceeds more rapidly along the lateral than along the vertical axis. The comparison of the equations for the two sexes shows further that the differential growth in depth proceeds at approximately the same rate in the males and the females, while the differential growth in width proceeds more rapidly in the females than in the males. It is this higher differential growth in width that accounts for the higher K values in the Clear Lake females.

Values of K for cisco populations have been presented by Van Oosten (1929) and by Hile (1931). The former author found K to have an average value of 1.13 for the Lake Huron herring (0.01126 in his method of presentation). The sexes showed no consistent differences, and there was only a slight tendency for the value of K to increase with increase in length. Hile's data on the cisco of the Indian Village Lakes (Indiana) were too scanty to afford any information on the change in the value of K with change in length. The largest value of K which he found for any age group was 1.79, the smallest, 1.56. Since both Van Oosten and Hile employed the cube relationship for the calculation of K values, their results can be compared directly with those of this study.

A comparison of the values of K in the Lake Huron herring and the Indian Village Lakes cisco with those of the populations of this study shows that the Lake Huron herring is a very slender fish of approximately the same relative heaviness as the Muskellunge Lake cisco, while the Indian Village Lakes cisco is more heavily built than the Trout Lake, Muskellunge Lake, and Silver Lake ciscoes, but slighter in form than the Clear Lake cisco.

LENGTH OF GROWING SEASON

It was not possible in this investigation to follow the course of the season's growth in the different populations by means of a systematic collection of specimens at different times throughout the spring, summer, and autumn. Since all collections were made in July, August, and early September, and the single year's collections within a single lake were frequently made within a period of only a few days, any estimate of the course of growth during the growing season or of the length of the growing season in the different lakes must depend largely upon an indirect approach. However, the fact that the growth materials from each lake represent collections in 2 or more years makes possible at least a rough estimate of the length of the growing season in each lake. The following example will illustrate the method by which these estimates may be made:

The 1928 collection of the Trout Lake cisco contained 102 specimens of the II group (1926 year class). These fish had an average length of 134 millimeters at the time of capture (July 21, 28, and 29). The calculation of their earlier growth from scale measurements indicated that their average length at the beginning of the 1928 growing season (end of second year of life) was 117 millimeters. Thus it may be seen that these II-group fish of 1928 had grown 17 millimeters between the beginning of the growing season and the time of their capture in late July. The question now arises as to what part of the total 1928 growth of the II group this 17-millimeter increment may represent. The presence of this same (1926) year class in the 1930 collections as the IV group and in the 1931 collections as the V group makes a quite reliable answer to this question available, for it is possible to calculate the total

1928 growth from the scale measurements of each of these later collections of the year class. The 1930 IV-group samples indicated that the 1926 year class had a total growth of 19 millimeters in 1928, while the 1931 V group gave an average calculated growth of 17 millimeters for the same year. The combination of the 1930 and 1931 data gives a calculated total growth of 18 millimeters for the 1926 year class in the calendar year 1928. Since the 1928 specimens themselves had grown 17 millimeters at the time of their capture in late July it is apparent that the 1928 II group had practically completed its season's growth at the time of capture of the samples.

It is obvious that comparisons of the sort given above, to be most dependable, should be based on different years' collections of the same year class. By such a procedure errors that might arise from unequal growth of the same age fish in different calendar years are completely avoided. The confining of comparisons to different years' collections of the same year class of course limits this type of analysis to those year classes that are well represented in more than 1 year's collection. However, for the question at hand dependability is more important than a diversity of material.

Since data of the above type throw light only on the probable time at which growth ends, the presentation of the available data on the amount of the season's growth already made by the different populations at the time of capture of the samples should be preceded by a brief consideration of probable time at which the season's growth begins. Juday and Birge (1930) stated that in the lakes of this region "The ice disappears about the 1st of May; the shallower lakes usually lose their covering of ice a few days before the larger and deeper lakes." From these facts it may be considered valid to assume that in general growth does not occur in any of the four populations of this study before early May, and that the time at which growth begins does not differ by more than 1 or 2 weeks from one lake to another.

Table 35 shows a comparison of the amount of calculated growth made by three age groups of the Trout Lake cisco between the beginning of the growing season and the time of capture of the samples, with the total calculated growth for the season as determined from later years, collections of the same year class. The data for the 1928 II group which were used to illustrate the method of comparison have already been discussed. It may be seen at once that the 1930 III and IV groups agree with the 1928 II group in indicating that the season's growth of the Trout Lake cisco is practically if not entirely complete by the end of July. The growing season for the Trout Lake cisco is not longer than 3 months and, since growth may not start at once upon the disappearance of the ice, may actually be somewhat less than 3 months.

TABLE 35.—*Calculated growth of 3 age groups of the Trout Lake cisco up to the time of capture in the summer, compared with the growth for the entire summer calculated from collections of the same year class in later years*

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on later collections of	
				1930	1931
1926	July 21, 28, 29, 1928.....	II	17 (102)	19 (99)	17 (79)
1928	July 29, 30, 31, 1930.....	IV	9 (99)	-----	9 (79)
1927	Do.....	III	10 (347)	-----	11 (269)

Only one year class (1928) occurred in sufficient numbers in more than 1 year's collection of the Muskellunge Lake cisco to make possible a comparison of growth up to time of capture with the total season's growth. The 1930 II group (see table 4) had an average calculated growth of 19 millimeters for the 1930 season up to the time of capture, August 28 and 29. The 337 specimens of this same year class taken as the III group of 1931 showed an average calculated growth of 18 millimeters for the entire 1930 season. Although these data can scarcely be taken to demonstrate a shrinkage of 1 millimeter in the average size of the 1930 II group between the time of capture of the samples and the time of the formation of the third annulus, they do indicate that the season's growth of the Muskellunge Lake cisco is complete at the end of August.

It is, of course, possible that growth in the Muskellunge Lake cisco may be complete several weeks before the end of August. The 1928 and 1931 collections were taken earlier in the summer but, unfortunately, no comparisons are possible between the data of any age groups of the samples of these 2 years and data based on collections of the same year class in other years. In the 1928 collections (made July 1 to July 4) only the II group was well represented and none of the 1926 year class individuals was taken in any of the later collections. The 1931 collections (made July 14 to 28—over 80 percent of the former date alone) cannot be compared with the 1932 collections since for reasons discussed previously (p. 219) the 1932 catches were not included in the Muskellunge Lake growth data. It is possible, however, to compare the season's growth before capture of the 1928 and 1931 II groups with the grand average of 18 millimeters calculated growth in the third year of life, based on the combination of all age groups above the II group and all years' collection. These comparisons show that the 1928 II group which had grown 13 millimeters at the time of capture in early July was still 5 millimeters short of the average growth of fish in the third year of life, while the 1931 II-group fish which had grown 11 millimeters up to the middle of July still lacked 7 millimeters of having attained the average for third-year growth. These two comparisons, particularly the latter, indicate that the Muskellunge cisco is growing actively throughout July and that in all probability this growth extends at least into early August. Consequently the Muskellunge Lake cisco may be accredited with a slightly longer growing season than the Trout Lake cisco.

Since it was felt that the prominence of Lee's phenomenon in the growth data of the Silver Lake cisco made the comparison of age groups separated by more than 1 year of life inadvisable, none of the 1928 material was used in the study of length of the growing season in that lake. Table 36 shows the comparison of the 1930 calculated growth of three age groups of the Silver Lake cisco up to the time of capture in the middle of August with the total 1930 growth of these age groups calculated from 1931 collections of the same year classes. It may be seen that at the time of capture of the 1930 samples, August 9 to 15, the season's growth of the Silver Lake cisco was approximately two-thirds to three-quarters complete. From this fact it may be concluded that the Silver Lake cisco is still growing throughout the month of August and that the growing season probably extends on into early September. It may be concluded, therefore, that the growing season of the Silver Lake cisco is longer than that of either the Trout Lake or the Muskellunge Lake cisco.

TABLE 36.—Calculated growth of 3 age groups of the 1930 Silver Lake cisco collections up to the time of capture in the summer, compared with the growth for the entire summer of 1930 calculated from collections of the same year classes in 1931

[Number of specimens in parentheses]

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on 1931 collections
1925	Aug. 9, 10, 15, 1930.....	V	8 (25)	12 (21)
1926	Do.....	IV	10 (58)	14 (108)
1927	Do.....	III	14 (25)	17 (102)

The 1931 Clear Lake cisco samples were collected in two groups, the first from July 22 to 28, and the second from September 2 to 5. Tables 37 and 38 show the calculated growth during 1931 up to these 2 periods of capture for 7 age groups (sexes considered separately) and also the entire 1931 growth for these age groups as calculated from 1932 collections of the same year classes. Although there are several irregularities in the tables it can be seen at once that much of the season's growth occurred after the latter part of July and that growth was by no means entirely completed in early September. If all age groups are considered together, the males taken in late July had completed 64 percent of their 1931 growth while those taken in early September had completed 81 percent of the season's growth; the same data for the females are 68 percent for the July samples and 76 percent for the September samples. From these facts it may be concluded that the growth of the Clear Lake cisco probably continues through September and possibly into October, and further that the growing season of the Clear Lake cisco is longer than in any of the other three lakes.

TABLE 37.—Calculated growth of 7 age groups of the Clear Lake cisco (males) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections
1924.....	VII	8 (7)	5 (1)	11 (7)	1928.....	III	27 (16)	33 (10)	42 (11)
1925.....	VI	9 (6)	10 (5)	13 (9)	1929.....	II	51 (27)	61 (7)	70 (23)
1926.....	V	13 (2)	14 (2)	16 (2)	1930.....	I	55 (16)	77 (4)	105 (20)
1927.....	IV	18 (6)	22 (4)	24 (7)					

TABLE 38.—Calculated growth of 7 age groups of the Clear Lake cisco (females) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections
1924.....	VII	9 (16)	7 (5)	12 (8)	1928.....	III	31 (18)	36 (7)	44 (14)
1925.....	VI	12 (6)	12 (6)	18 (12)	1929.....	II	55 (27)	60 (8)	77 (21)
1926.....	V	12 (1)	13 (1)	16 (1)	1930.....	I	63 (14)	78 (4)	105 (13)
1927.....	IV	26 (2)	26 (2)	32 (7)					

While the Clear Lake cisco undoubtedly has an advantage over the other three populations in the length of the growing season, this advantage may not be as great as might at first be suspected. The autumn of 1931, in which year the length of the growing season of the Clear Lake cisco was estimated, was abnormally warm. The records¹⁶ of the United States Weather Bureau station at Minocqua, about 6 kilometers west of Clear Lake, show that the air temperature in September 1931, was 4.5° F. above the normal, while in October and November it was 3.0° F. and 6.5° F. above normal, respectively. This warm autumn may have extended the growing season of the Clear Lake cisco beyond its normal limit. If this is true the growth beyond early September in normal years may not be as much as 20 percent or more of the season's growth as tables 37 and 38 would indicate.

If the length of the growing season in the different lakes is considered in relation to the growth rates of the various populations, it may be seen that poorest growth occurs in the lake with the shortest growing season (Trout Lake) while the best growth occurs in the lake with the longest growing season (Clear Lake). The two lakes (Muskellunge and Silver Lakes) in which the growth rate was intermediate also have growing seasons of intermediate length. Thus it appears that differences in the length of the growing season are important contributing factors toward differences in growth rates. However, these differences in the length of the growing season can by no means explain entirely the observed differences in the amount of growth in the four populations. The growth of the Clear Lake cisco up to July, for example (tables 37 and 38), is well in excess of that found in Trout Lake cisco (table 35) or the Silver Lake cisco (table 36) of corresponding ages at any time in the growing season or for the entire growing season.

RELATIONSHIP BETWEEN DENSITY OF POPULATION AND RATE OF GROWTH

It was stated in the introduction that these studies on the growth of the cisco have been made on populations from "type" lakes that were selected on the basis of their biologically productive capacities as estimated chiefly from the amounts of fixed carbon dioxide in their waters. It was hoped that the comparison of the growth of the various populations might yield information as to the extent and nature of the effect of the natural richness of the waters upon the growth rates of the fish populations that live in them. The investigators who collaborated in planning and initiating the studies of which the present one is a part harbored no delusions to the effect that the relationship between the growth of fishes and the environment is in any sense simple. It was nevertheless surprising to find early in the investigation of the growth of the cisco that the growth rates of the populations did not fall at all in the order of the estimated productive capacities of the lakes in which they occurred, but rather that the reverse was true. Trout Lake with 18.7 parts per million of fixed CO₂ contains the slowest growing cisco of the four populations, while the cisco of Clear Lake, in which body there occur only 2.2 parts per million of fixed CO₂, stands out by far as the fastest growing of the four stocks. In Silver Lake and Muskellunge Lake where the amounts of fixed CO₂ are intermediate in value (Silver, 15.5 parts per million; Muskellunge, 10.0 parts per million) the growths of the cisco populations are also intermediate.

It can hardly be concluded that an inverse causal relationship exists between the growth rate of the cisco and the fixed CO₂ content of the lake it inhabits. Rather

¹⁶ Climatological Data of the United States by Sections, vol. 18, 1931.

it would appear that the growth rate of the cisco in these lakes depends primarily on some factor other than that of the productive capacity of the lake as that capacity is estimated from the concentration of bound CO_2 in its waters. If it is assumed that the various stocks do not differ greatly in their hereditary capacities for growth and that environmental conditions are in general comparable, then it may be expected that the amount of growth in the various populations will depend in large measure upon the availability of food. The determining factor is then the amount of food available to each individual fish. If the poorest growth occurs in the lake that produces the greatest amount of food, it may be assumed that here in all probability the number of feeding individuals is so great and the competition for food so strong that these individuals cannot secure a sufficient amount of food to maintain their normal rate of growth. On the other hand, if a relatively rapid growth occurs in a lake with a scanty basic supply of food it may be assumed that the feeding population in that lake is so small that in spite of the scarcity of food the individuals are still able to secure sufficient nourishment to maintain rapid growth.

This conception of a dependence of growth upon density of population is based primarily upon the assumption that there exists a competition for food. If food is present in a quantity greater than the maximum which the population can utilize for purposes of maintenance and growth, then an increase in the density of the population should not affect its growth rate until that point is passed where the food available becomes less than the maximum quantity which the population can use. From this point on a continued increase in the density of population involves a decrease in the ration of the individual fish and reduces the amount of individual growth. If the density of the population becomes sufficiently great, there is finally reached the point at which the food supply suffices only for purposes of maintenance and there is no excess for growth.

The evidence that investigators have presented to show a relationship between density of population and rate of growth in fishes has been of two sorts: (1) Change in rate of growth accompanying transfer from a thickly populated to a sparsely populated region, and (2) change in rate of growth accompanying changes in the density of the population within the same region.

European investigators have conducted numerous experiments that show the effect on growth rate of transplanting young plaice from the overcrowded coastal nursery grounds to less densely populated areas with more abundant food. The classic of all such experiments is the Danish work of transplanting young plaice from the overcrowded nursery grounds at the entrance of the Limfjord to the thinly populated areas of the inner broads. Although three-fourths of the fish are retaken within the year following the time of their liberation, their increase in size is so great that a continuation of these transplantation operations, which were begun in 1892, has proved profitable up to the present time.¹⁷

Borley (1912) gave the results of experimental transplantation of plaice from the English coastal waters to the Dogger Bank. He believed that there was "at least a doubling of the growth" (in length). In the same paper Borley reviewed the results of similar experiments by Dutch and Danish investigators. Lee and Atkinson (1912) also reviewed the results of earlier transplantation experiments. A good general review of European plaice transplantation experiments may be found in Blegvad's paper published in 1933.

¹⁷ There was no transplantation in 1917. Johansen (1928) summarized the results of the transplantation operations in the Limfjord up to that time.

The study of the relationship between the density of population in marine fishes and their rate of growth received considerable stimulation from the observation of the conditions that resulted from the almost complete suspension of fishing operations in the North Sea during the World War. During the war there occurred an accumulation of the stock of plaice. Large fish became more plentiful but the average rate of growth decreased. With the resumption of fishing on a large scale the accumulated population was largely fished out. Large fish became relatively scarce and the average rate of growth increased. Further investigations disclosed the fact that in general in regions with a dense population of plaice the rate of growth tended to be low and vice versa.¹⁸

Bückmann (1932) expressed the relationship between growth in weight and the density of population as being inversely proportional and referred to it as a "Verein-fachtes Wachstumgesetz" which he defined: "Die Gewichtszunahme verhält sich umgekehrt proportional zur Bestandsdichte." Bückmann expressed this law by the equation,

$$w^1 = w \frac{n}{n^1},$$

where w is the weight increase per individual in a population of n individuals and w^1 is the increase in weight that would occur if the number of individuals were changed from n to n^1 . Bückmann recognized the law to be inexact and mentioned certain disturbing influences. He pointed out that it is incorrect to assume that all the food consumed is applied toward increase in size. A certain definite amount is utilized to maintain individual metabolism. The percentage of the food that is so used varies according to the total amount of food available to each individual. Further, the efficiency with which a fish makes use of its food varies according to the abundance of food at hand.¹⁹ Yet another complicating factor is the competitive action of other species. Bückmann developed a growth formula that contained correcting factors for these sources of error.

Russell (1932) made a somewhat similar analysis of the relationship between growth and population density in fishes.

In some species fluctuations in the density of the population appear to have no effect on the rate of growth. Concerning the haddock Bowman (1932) stated:

It cannot be inferred from the results of the extensive and continuous investigations that, in comparable areas, the average growth rates of successive broods in their first year of life vary with differences in brood densities.

Hjort (1932) pointed out that growth in the Norwegian cod and herring stocks is remarkably uniform from year to year and quite independent of the density of the stock. He contended that growth was determined by specific conditions in the sea rather than by the numbers of fish in the population.

Marine populations, particularly round fishes, can wander freely over extensive areas. It is possible for them to seek out those regions with the most suitable food conditions, and in some instances it is probable that the role of food as a limiting factor for growth is insignificant as compared to other environmental influences. Within the restricted limits of a small inland lake a closer dependence of the growth

¹⁸ The following papers listed in the bibliography touch upon the question of the relationship between density of population in marine fishes (largely the plaice) and their rates of growth: Strodtmann and Langhammer (1925), Heincke and Bückmann (1926), Garstang (1926), Jensen (1928) and (1932), Bückmann (1932), Bowman (1932), Hjort (1932), and Russell (1932). These papers are only representative of the rather voluminous literature of the subject.

¹⁹ Bückmann referred to Dawes' (1930, 1931) feeding experiments with plaice.

rate upon the density of the population might be expected. Here ordinarily it is impossible for underfed fish to move to an area with more abundant food; they must subsist as best they can upon the food supply available within the lake. If the lake contains a "natural" population, a population not disturbed by any extensive removal of individuals through a fishery, then it may be assumed that in all probability a competition for food exists, and that this competition may in some lakes be quite severe. Several examples of the dependence of fish growth upon the density of the population have been observed in fresh-water lakes.

The Norwegian farmers have long recognized the disadvantages of an overcrowded stock in trout lakes. The appearance of emaciated and undersized individuals is taken as an indication that a more intensive fishery is desirable. Through the regulation of the intensity of the fishery they "keep the trout under discipline" (Huitfeldt-Kaas reviewed by Rugde (1923) in the Salmon and Trout Magazine). In another paper Huitfeldt-Kaas (1927) stated, "Very great rapidity of growth is shown by fish [trout] in lakes with quite small stock * * * This type of growth I think can suitably be termed 'slender stock type'."

Surbeck (1921) stated that the decrease in numbers in the stock of the "Balchen" (*Coregonus schintzii helveticus* Fatio) in Vierwaldstättersee following 1900 was accompanied by a significant increase in individual size.

Järvi (1920 and 1924) was able to show that in the "kleine Maräne" (*Coregonus albula*) of the Finnish lakes the poorest growth occurred when the fish were most plentiful and the best growth occurred when the fish were scarce. The fishermen consider the presence of large young fish in the early catches of the fishing season as an indication that the year will be bad.

Pirognikoff (1927) stated that the decline of the intensity of the fishery for the rudd (*Rutilus rutilus lacustris* Pallas) in Lake Chani and the consequent increase in the abundance of that form was accompanied by a distinct decline in the rate of growth.

Hart (1931) found that whitefish taken in different parts of Lake Ontario showed different rates of growth, which he was able to explain in part by the selective action of the gear used in collecting the samples, but stated with reference to the slow growth of the fish taken at Pleasant Point, "An explanation on the grounds of detrimentally keen competition for food in the first years in the neighborhood of a much frequented spawning ground is a tempting one."

In his studies of the trout (*Salmo kamloops* Jordan) of the Kamloops district, British Columbia, Mottley (1932) observed that the opening of a lake to intensive fishing was followed not only by a decrease in the abundance of trout but also by an increase in their "size for age." He advocated that an annual determination of growth rates be included in the data upon which stocking policies for the lakes of the region are based.

Juday and Schneberger (1933) reported the discovery of abundant populations of undersized smallmouth black bass in two small lakes in Vilas County, Wis. They considered the inferior growth of these bass as the results of a too great density of the populations in relation to the amount of available food.

On the basis of experimental studies on young trout Willer (1929) asserted that crowding operates as an inhibitor to growth in a manner over and above the effect it may have in producing competition for food. He considered this "Raumfaktor" to account for the irregularities found by him (Willer, 1924), and by Järvi (1920) in

the growth of the kleine Maräne and stated that he had found the same situation in the smelt (Willer, 1926).

In view of the numerous demonstrations by other investigators of a relationship between density of population and growth rate in fishes it was considered advisable in this study to investigate the relative densities of the four cisco populations with particular reference to a possible relationship between these densities and the observed differences in the growth rates of the various stocks.²⁰

An important source of difficulty in the study of the relationship between population density and growth rate lies in the fact that the estimation of the density of a fish population, either absolute or relative, is at its best difficult and in a large measure uncertain. Ordinarily the chief sources of information are the results of experimental fishing and the statistics of the commercial yield. In the present investigation dependence must be placed entirely upon the size of the catch per unit of effort as based on the action of experimental gear (gill nets). In this connection some of the chief difficulties and sources of error in the gathering and the interpretation of data on the gill-net catches should be mentioned.

Gill nets fish from a fixed position, and their effectiveness is dependent upon the movements of the fish. If the amount of movement varies according to time, locality, or population, such variations will be reflected in the catch of the net. The effect of the movements of the cisco is complicated by a tendency for the fish to shoal or move in groups. Group movements cause a great variation in the catch from day to day from nets set in exactly the same location.

Further difficulty lies in the fact that the catches of the same net or the same group of nets in different lakes are not always directly comparable.²¹ For example, the seven mesh sizes of the "new" gear employed in collecting the samples for the later part of this investigation failed to take equally adequate samples of all the age groups in the different populations. The Clear Lake catches probably represent reliable samples of the I group and all older groups as well. In Silver Lake and Muskellunge Lake, however, the I groups cannot be considered adequately represented, while in Trout Lake the representation of the II group as well as the I group are to be considered too small. The comparison of the Clear Lake catches with those in which the I and II groups are absent or poorly represented would of course lead to a too high estimate of the relative density of the Clear Lake population.

It must be recognized also that the fishing effort represented by a series of nets varies from one lake to another, for obviously no effort can be accredited to a net that is wholly ineffective for the capture of the members of a particular population. On the other hand, in a population with a wide length range two or three sizes of mesh may be necessary to capture a sample directly comparable to the catch of a single mesh size in a population with a more compact size range. Because of these difficulties it is not possible on the basis of gill-net catches to derive "index numbers" that can be taken directly as reliable measures of relative densities in populations of greatly dissimilar size ranges. In general, however, the examination of the catch of each size of mesh in each lake will, in spite of these aforementioned difficulties, give a fairly good idea of relative population densities in different lakes.

²⁰ It is realized that competition for food is not at all confined to competition among individuals of the same species. With the possible exception of the Muskellunge Lake cisco population, however, the competition of other species is probably of insignificant importance in this study. At present there are available few data on the degree of competition between the Muskellunge Lake cisco and the perch that occur abundantly in the same regions of the lake. (See the section, Fishes Associated with the Cisco.)

²¹ For a more detailed discussion of the action of gill nets see the section, "The selective action of gill nets."

In the comparison of net catches from different lakes it is important further to know whether observed differences in net catches result from real differences in population densities or whether they depend merely upon the actual positions in which the nets were set within the lakes. For this purpose it is necessary to have some knowledge of the vertical distribution of the cisco in each of the lakes whose populations are to be compared. The importance of such information will appear from the following discussion of the vertical distribution of the cisco in Trout, Muskellunge, Silver, and Clear Lakes. Particular attention will be given the question of the relationship between the vertical distribution of the cisco and the temperature and oxygen concentration in the different lakes. The data on the vertical distribution of temperature and O_2 in Silver Lake were taken from Juday and Birge (1932, table VI) and those for Trout Lake, Muskellunge Lake, and Clear Lake were supplied by Dr. Chancey Juday from the records of the Wisconsin Geological and Natural History Survey.

The cisco collections from Trout Lake were taken during July, both in 1930 and 1931, and in nets set on the bottom²² at depths of from 15 to 33.5 meters. Nets set anywhere within this region always took good catches of ciscoes while nets set in shallow water (less than 7.5 meters) for the capture of other species caught ciscoes only rarely. The few that were taken in the shallow water nets can be considered stragglers. From the examination of the data of table 39 it can be seen that in Trout Lake in middle and late summer there lies below the depth of 10 or 12 meters a large body of cold water with a good supply of oxygen. It is in this region that the cisco lives during this season of the year, and it is in this region that the samples used for study of density were collected.

TABLE 39.—Trout Lake, July 1, 1931, and Aug. 27, 1931. Relationship of temperature and dissolved oxygen to depth

[O_2 in milligrams per liter]					
July 1, 1931			Aug. 27, 1931		
Depth in meters	Temperature in $^{\circ}C.$	O_2	Depth in meters	Temperature in $^{\circ}C.$	O_2
0.....	25.4	7.77	0.....	19.9	8.60
5.....	19.4	8.75	5.....	19.9	8.80
10.....	13.5	9.71	10.....	16.8	8.45
15.....	9.5	8.89	15.....	9.8	7.00
20.....	8.3	8.31	20.....	8.4	5.40
25.....	7.6	7.20	25.....	7.8	3.80
28.....	7.5	7.07	28.....	7.6	2.00
31.....	7.3	5.71	31.....	7.3	.56

It is in Muskellunge Lake that the late-summer habitat shows the most marked restriction to a limited stratum. The record of the first three lifts in the 1930 collecting season shows how closely the number of specimens taken depends upon the depth at which the nets are set. On August 27, 1930, nets were lifted in Muskellunge Lake from a depth of 17.5 meters. The total catch was a single sucker. The nets were then reset at a depth of from 7 to 11.75 meters. The catch on August 28 was: 38 perch, 17 suckers, 3 smallmouth black bass, 1 rock bass, and 226 ciscoes. Most of the ciscoes were taken in the nets set at a depth greater than 9 meters. The position

²² It should be remembered throughout these discussions for all lakes that the nets were always set on the bottom at the recorded depths. They actually fished the stratum of water, 3.5 to 6 feet thick, immediately above the bottom.

of the nets was again shifted, this time to depths of 7 meters and shallower. The catch on August 29 was: 60 perch, 13 suckers, 8 smallmouth black bass, 3 rock bass, and only 13 ciscoes. Thus it may be seen that at the end of August 1930, ciscoes occurred on the bottom in abundance only within a rather limited region. They were not plentiful in depths less than 9 meters and were absent in the deeper portion of the hypolimnion.

Most of the ciscoes collected from Muskellunge Lake in 1931 were taken in a single set made July 14 at a depth of 9.5 to 10 meters. Although there are no 1931 data that may be used to set the upper and lower limits of the vertical range of the Muskellunge Lake cisco in that year, nets set at depths less than 8 meters for the capture of other species failed to take ciscoes.

The results of the rather extensive fishing of the 1932 collecting season (table 40) give the most complete information concerning the vertical distribution of the cisco in Muskellunge Lake. From these samples which were taken at different times in July and early August it appears that approximately two-thirds of the fish were captured in nets set at depths between 11 and 13 meters (the fish were taken in the stratum of water 6 feet thick immediately above the bottom). Data on the O_2 and temperature conditions in Muskellunge Lake in the late summer of 1932 based on the results of a vertical series of temperature and O_2 concentration determinations made August 25 (table 41) offer an explanation of the concentration of the cisco into such a narrow stratum and suggest that such a concentration most probably occurs every year. The data of table 41 indicate that in Muskellunge Lake in late summer, oxygen is almost completely lacking in the hypolimnion and may be abundant in the upper part only of the thermocline. As a result of this deficiency of oxygen in the deeper strata the ciscoes are forced out of the cooler strata and by reason of their preference for cool water and their need of oxygen become concentrated in that stratum of water that has the lowest temperature available and yet contains sufficient oxygen to support life.

TABLE 40.—Muskellunge Lake cisco, 1932—Vertical distribution of the cisco

[The data show the catch per day's fishing of 100 square yards of gill net, set at different depths. In parentheses are given the number of lifts upon which each average lift was based]

Depth in meters	Size of mesh (in inches)			Depth in meters	Size of mesh (in inches)		
	1¼	1½	1¾		1¼	1½	1¾
Less than 5.....	0.0 (1)	0.1 (10)	0.1 (9)	11 to 13.....	42.0 (1)	93.4 (5)	0.5 (2)
5 to 7.....	.0 (1)	.1 (9)	.0 (10)	13 to 15.....	1.5 (2)	17.0 (1)
7 to 9.....	.8 (5)	11.2 (4)	.5 (4)	No depth record.....	21.5 (2)	26.3 (3)	.0 (2)
9 to 11.....	10.3 (6)	29.0 (6)	1.5 (10)				

TABLE 41.—Muskellunge Lake, Aug. 25, 1932—Relationship of temperature and dissolved oxygen to depth

[O_2 in milligrams per litre]								
Depth in meters	Temperature in $^{\circ}C.$	O_2	Depth in meters	Temperature in $^{\circ}C.$	O_2	Depth in meters	Temperature in $^{\circ}C.$	O_2
0.....	21.3	8.02	10.....	14.5	5.33	15.....	10.5	0.56
5.....	21.3	8.70	11.....	13.8	2.67	19.....	10.1	.24
8.....	20.7	8.25	12.....	12.0	.43			

Because of the heavy concentration of the Muskellunge Lake ciscoes within a narrow stratum in late summer, it is apparent that the catch of ciscoes in a particular net will vary greatly according to the depth at which the net was set. To obviate this difficulty the estimate of the relative density of the population of the Muskellunge Lake cisco was based only on catches of nets set in the depths at which the cisco is most abundant. These depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

The conditions of life that the Muskellunge Lake cisco finds in middle and late summer in the upper strata of the thermocline are probably far from the optimum for the species. Not only is the water temperature higher than they would normally be expected to select but the crowding itself and the probable competition with the perch that inhabit the same region in large numbers (p. 293) may be expected to make for quite unsatisfactory feeding conditions. In view of these unsatisfactory conditions of life the poor condition (p. 248) of the individuals of this population in contrast to those of other lakes in which chemical conditions are better, and their short life span are not surprising.

That the existence of conditions that force the cisco into unsuitable strata of water may have damaging effects on the population was pointed out by Cahn (1927), who stated that when "the cisco is forced into water far warmer than it ordinarily selects * * * the result is often disastrous", and a high mortality occurs. Scott (1931) showed that where there is formed a "thermocline notch" in the oxygen curve the disappearance of the oxygen from the hypolimnion may force a sudden movement of the ciscoes from the hypolimnion to the upper strata of water. His observations on the cisco of Snow Lake, northeastern Indiana, showed that no great mortality results from this sudden move, but rather that the fish are only temporarily incapacitated. After floating for a short time at the surface they make a recovery and remain in the epilimnion for the remainder of the season. Such a forced removal into an undesirable habitat, either sudden or gradual, doubtless entails considerable shock to the individual fish. It is readily conceivable that a temporary stoppage of growth might occur, and that the occurrence of accessory annuli such as appear in the Muskellunge Lake cisco scales can be thus explained.

The Silver Lake cisco agrees with the Muskellunge Lake cisco in showing a rather sharply delimited vertical distribution. In the summers of both 1930 and 1931 ciscoes were taken only in nets set in depths between 10.5 and 15.5 meters. The dates of collection in 1930 were August 9, 10, and 15; in 1931, July 17 and August 22. The reason for this concentration within a 5-meter stratum appears from the examination of the data of table 42, which shows the relationship between depth and the temperature and O₂ concentration in Silver Lake on August 28, 1931. If the data of table 42 are considered in relation to the known vertical distribution of the cisco in Silver Lake, it would appear that a preference for cool water keeps the ciscoes from entering the warmer strata less than 10 meters deep, while a deficiency of oxygen prevents them from occupying the lower portions of the hypolimnion. Thus in late summer the Silver Lake cisco is confined to a narrow stratum in the upper part of the hypolimnion and the lower part of the thermocline. The catch of nets set between the depths of 10.5 and 15.5 meters can be taken to represent the relative abundance of the Silver Lake cisco at that time.

TABLE 42.—Silver Lake, Aug. 28, 1931—Relationship of temperature and dissolved oxygen to depth
[O₂ in milligrams per litre. From Juday and Birge (1932)]

Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
7	20.2	9.20	11	9.4	9.80	14	7.7	1.60
8	18.8	9.90	12	8.6	7.60	15	7.2	.60
9	14.7	13.20	13	8.2	4.40	18	6.8	.00
10	11.4	11.70						

The field records of lifts of ciscoes in Clear Lake indicate that in this lake the cisco occurs in all parts of the hypolimnion from midsummer to early autumn. (The dates of collection were July 22 to 28, 1931, Sept. 3 to 5, 1931, and July 12 to 19, 1932.) This distribution of the cisco in Clear Lake suggests that it may at all times find a plentiful supply of oxygen throughout the hypolimnion. Such an assumption is supported by the data on the temperature and dissolved oxygen conditions in this lake based on a vertical series taken August 19, 1932 (table 43). These data show that at this time of the year there is in Clear Lake a plentiful supply of oxygen at all depths. Thus it is valid to assume that the net samples captured at different depths in the hypolimnion may be taken to represent the relative abundance of the cisco in Clear Lake.

TABLE 43.—Clear Lake, Aug. 19, 1932.—Relationship of temperature and dissolved oxygen to depth
[O₂ in milligrams per litre]

Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
0	20.9	8.07	12	12.4	9.46	23	8.4	4.51
5	20.9	7.91	15	9.9	7.93	26	8.0	3.25
10	18.5	8.07	20	8.6	6.03			

The data for the comparison of the relative density of the four cisco populations (table 44) represent the catch of 100 square yards of gill net fished over a period of 24 hours. The lifts upon which the data are based were all made from depths at which the cisco occurred in abundance at the time of capture. These depths include the entire hypolimnions of Trout Lake and Clear Lake and the 10.5–15.5 meter stratum of Silver Lake, while in Muskellunge Lake the depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

TABLE 44.—Catch in number of ciscoes per 100 square yards of gill net per 24 hours' fishing
[Data arranged according to lake, year of capture, and mesh of net]

Lake	Year of capture	Size of mesh						
		1¼	1½	1¾	2	2¼	2½	3
Trout	1930		104.8					
	1931	161.0	73.0	11.0	2.8			
	1932		106.1					
Muskellunge	1930		143.9					
	1931	142.0	93.4	1.5				
	1932		31.6		50.0			
Silver	1930		30.0	176.0	45.0			
	1931	162.0	1.4	2.3	3.5	3.7	5.5	7.5
	1932	.1	.9	1.9	.7	2.4	4.3	3.8

¹ This size of mesh was not represented in the gear of the preceding years.
² The data for the 1932 Muskellunge Lake collections are presented in detail in table 40.

From the examination of the data of table 44 it may be seen that the various populations show considerable differences in their relative densities at the time of capture in the depths from which the samples were taken. The Muskellunge Lake fish appear to be the most abundant although Trout Lake is not far behind. The Silver Lake data show a relative abundance slightly less than that in Trout Lake or Muskellunge, while the Clear Lake cisco population may be considered relatively sparse.

The estimate of the relative densities of the four cisco populations at the time of capture is not, however, of primary importance in this investigation. Since this section is concerned chiefly with the relationship between density of population and rate of growth the most significant comparison of population densities must include a comparison of densities throughout the entire growing season rather than at some particular time within the growing season. It was pointed out in the section on the length of the growing season that growth of the Trout Lake cisco is practically complete at the end of July; the Muskellunge cisco completes its growth by the end of August, possibly sooner; the season's growth of the Silver Lake fish is two-thirds to three-quarters complete in mid August; and the Clear Lake cisco has completed well over half its season's growth by late July. From these facts it is apparent that the relative density of the four populations in late spring and the first half of the summer is more significant than their relative densities at the time the samples were collected. There is strong evidence that in Muskellunge Lake and Silver Lake at least the densities of the cisco populations earlier in the growing season were less than at the time of capture in late summer. The concentration of these populations in late summer within a narrow stratum may be considered the result of the temperature and oxygen condition at that time. It is most probable that in late spring and early summer no such concentration existed, since in the early season oxygen would be expected to occur at all depths in the hypolimnion. Consequently the relative densities for the Muskellunge Lake and Silver Lake fish in table 44 must be considered too high as compared to those from Trout Lake and Clear Lake.

If attention is given to the relative densities during the entire growing season the most probable arrangement of the lakes from the most dense to the least dense population is: Trout, Muskellunge, Silver, Clear. This is the same order these lakes show with respect to growth rate in weight (with slowest growth in Trout Lake and fastest growth in Clear Lake). The growth rates of the four populations are approximately in the reverse order of the productive capacities of the lakes as estimated from the amount of bound CO_2 in their waters (Clear Lake was estimated as the least productive, followed in order by Muskellunge, Silver, and Trout). Thus it appears that the growth rates of these populations are determined primarily by their relative densities rather than by the basic productive capacities of the waters they inhabit. Although it is recognized that crowding itself may possibly impede growth to a certain extent independently of its effect in creating competition for food, and that various physical-chemical factors may affect growth rate directly, it is believed that the differences in growth rate in these four populations depend in large measure on the varying degrees of competition for food in the different lakes. It is further probable that variation in the intensity of competition for food from lake to lake may be related to the observed differences in the length of the growing season of the different stocks. (See preceding section.)

AGE COMPOSITION OF THE SAMPLES AND THE RELATIVE ABUNDANCE OF YEAR CLASSES

Because of its importance in the study of commercial fisheries the question of age composition of the stock and of the existence of dominant year classes has in recent years received a great amount of attention. It is now well known that the success of different years' hatches as measured in terms of the number of young produced is subject to a wide range of variation from one year to another. The hatches of some years may be so successful that that particular year class may dominate in the fishery over a period of 1 or several years. Yet other hatches may be so unsuccessful as to make only minor contributions to the stock. The common occurrence of relatively successful and unsuccessful year classes has been demonstrated in many species of fish of commercial importance. The study of the age composition of the commercial catch over a period of years has served as a most valuable tool in the investigation of fluctuations in abundance. In both Europe and America the known age composition of the commercial stock, together with the observed rate of falling off of a year group from year to year, has been used by fisheries investigators as a basis of prediction of the probable yield of the fishery for the approaching season.

In spite of the extensive researches that have been made on the subject of fluctuations little is known as to the causes that make a year class good or bad. Hjort (1914) stated that while the basic causes of fluctuations in abundance are unknown, it appears that fluctuations "have their origin in certain conditions prevailing at a very early period in the life of the fish." He repeated this opinion in 1926. Storrow (1932) pointed out that not only are the factors that determine the success or failure of a year class complex, but also that the difficulty of observing the fish in its natural environment is great. He called attention further to the failure of attempts to simulate natural conditions in the laboratory, a convincing proof of inadequate knowledge of optimum conditions.

The most thorough-going studies on the question of fluctuations in abundance in coregonids and their causes are those of Järvi (1920, 1924, 1930). He was able to show not only a great variation in the abundance of different year classes of the "kleine Maräne" (*Coregonus albula*) but also a distinct connection between such variations in abundance and weather conditions in the spring just after the time of hatching. If there are strong winds at this critical period many of the delicate newly hatched young are destroyed by the wave action. Järvi found, however, that strong winds at the time of spawning are less harmful.

Huitfeldt-Kaas (1917) found that in some years in Lake Mjøsen almost all the spawning run individuals of *Coregonus albula* are taken in the commercial fishery before they have had an opportunity to spawn, and that poor year classes may result.

Because of the manner (collecting with gill nets) in which the samples were obtained in the present investigation the study of the relative abundance of the various age groups in the four cisco populations and along with it the consideration of the relative abundance of the different year classes must be approached with great caution. (The limitations of gill net samples in the study of relative abundance of age groups and year classes are discussed in the section on the selective action of gill nets.) The age composition of a gill-net sample must in general be considered as descriptive of the sample rather than of the population as a whole. Exceptionally, however, the representatives of some particular year class may appear so prominently or be so scarce at all of the ages at which that year class appears in different

collecting years that it may be possible to designate the year class as good or poor. The examination of the age composition of the different years' collections in each of the four lakes (tables 45 to 48) does indicate the presence of certain year classes that can be termed relatively good or relatively poor.

In the Trout Lake collections (table 45) the year classes of 1926 and 1927 appear to represent good years for the production of young. The former year class as the II group of 1928 made up more than half of that year's collection, and 3 years later as the V group of 1931 it was still relatively abundant, comprising 13 percent of the total collection in this latter year. By reason of gear selection the 1927 year class (I group of 1928) was almost entirely lacking in the 1928 collections. This year class was, however, dominant in the collections of the later years, first as the III group of 1930 and then as the IV group of 1931. These conclusions as to the "goodness" of the 1926 and 1927 year classes are supported by the comparison of the relative abundance of corresponding age groups in the different years' collections. The 1926 year class furnished the greatest relative abundance of any II group in any year ²³ (56.0 percent of 1928 collection) and also of any V group (13.0 percent of the 1931 collection). Similarly the 1927 year class furnished the greatest relative abundance of any III group (1930) and of any IV group (1931). It should be mentioned further that the presence of these two relatively successful groups contributed toward the progressive increase from year to year in the average age and average size of the fish in the collections obtained from Trout Lake.

TABLE 45.—Age composition of the samples of the Trout Lake cisco
[The percentages are given in parentheses]

Year of capture	Age											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1928.....	2 (1.1)	102 (56.0)	61 (33.5)	17 (9.3)								
1929.....												
1930.....		36 (9.2)	247 (63.2)	99 (25.3)	9 (2.3)							
1931.....	2 (0.3)	61 (10.0)	173 (28.4)	269 (44.1)	79 (13.0)	12 (2.0)	4 (0.7)	5 (0.8)	2 (0.3)		2 (0.3)	1 (0.2)

In the Muskellunge Lake collections (table 46) the year class of 1928 (II group of 1930, III group of 1931) may be considered relatively successful. This year class, as the III group composed 55.6 percent of the 1931 collections, whereas in preceding years the III group composed a negligible portion of the total collection. The similarity of the age composition of the 1928 and the 1930 collections suggests the possibility that the 1926 year class may have been exceptionally abundant and that a collection in 1929 would have shown a high percentage of III-group individuals. However, the almost total absence of all age groups above the II group in the 1928 and 1930 collections suggests also the possibility that heavy mortality may regularly reduce the numbers of Muskellunge ciscoes early in life, and that the great relative abundance of the III group in 1931 may depend not only on the great relative abundance of the 1928 year class but also in part on the failure of this year class to suffer this customary great mortality. The scarcity of I-group individuals in all Muskellunge Lake collections may be considered the result of selectivity by gear.

²³ The great abundance of II-group fish in 1928 may depend in part on the smaller mesh gill nets used in that year.

TABLE 46.—Age composition of the samples of the Muskellunge Lake cisco

[The percentages are given in parentheses]

Year of capture	Age			
	I	II	III	IV
1928.....	19 (6.8)	252 (89.7)	10 (3.6)	
1929.....				
1930.....	17 (6.9)	214 (87.3)	14 (5.7)	
1931.....	9 (1.5)	258 (41.9)	347 (55.3)	2 (0.3)

The study of the age composition of the Silver Lake collections (table 47) reveals the presence of one year class (1926) which may be considered good and of one year class (1929) which may be considered poor. The 1926 year class was dominant in the collections of 2 of the 3 years, as the IV group of 1930 and as the V group of 1931. The scarcity of 1926 year class individuals as the II group in the 1928 collection can be explained on the basis of gear selectivity. The 1929 year class must be considered relatively poor because of its relative scarcity as the II group of the 1931 collections. This scarcity can hardly be the result of selection by gear as the individuals of the age groups on either side are more than three times as numerous. The great abundance of I-group fish in 1931 as compared with 1930 is the result of the introduction of smaller meshed nets in the first-named year. The lack of individual net records makes it impossible to determine the reason for the scarcity of I-group fish in 1928. However, the 1930 year class can safely be considered more abundant than the 1929 year class. The 1924 year class which was dominant as the 1928 IV group may possibly represent a good production year.

TABLE 47.—Age composition of the samples of the Silver Lake cisco

[The percentages are given in parentheses]

Year of capture	Age						
	I	II	III	IV	V	VI	VII
1928.....	1 (0.7)	9 (6.7)	46 (34.1)	69 (51.1)	10 (7.4)		
1929.....							
1930.....		7 (5.9)	25 (21.2)	58 (49.2)	25 (21.2)	3 (2.5)	
1931.....	66 (17.5)	19 (5.0)	61 (16.1)	102 (27.0)	108 (28.6)	21 (5.6)	1 (0.3)

The Clear Lake samples (table 48) present much more definite and consistent indications of the presence of successful and unsuccessful year classes than were found in the other three lakes. Figure 5 shows graphically the year class composition for the 1931 and 1932 collections. The agreement between the 2 years in the relative abundance of the different year classes is close. Since the individuals of each year class were a year older in 1932 than in 1931, and consequently of a different size range, this close agreement between the year class composition of the 2 years' collections may be taken as strong evidence for a high degree of reliability of the Clear Lake samples both as to year class and as to age composition.

TABLE 48.—Age composition of the samples of the Clear Lake cisco

[The percentages are given in parentheses]

Year of capture	Age										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1931.....	38 (15.3)	69 (24.5)	51 (20.5)	14 (5.6)	6 (2.4)	23 (9.2)	29 (11.6)	16 (6.4)	1 (0.4)	2 (0.8)	1 (0.5)
1932.....	31 (16.2)	33 (17.3)	44 (23.0)	25 (13.1)	14 (7.3)	3 (1.6)	21 (11.0)	15 (7.9)	3 (1.6)	1 (0.5)	1 (0.5)

It can be seen at once from the examination of table 48 and figure 5 that in Clear Lake the 1926 year class (V group of 1931, VI group of 1932) was very unsuccessful,

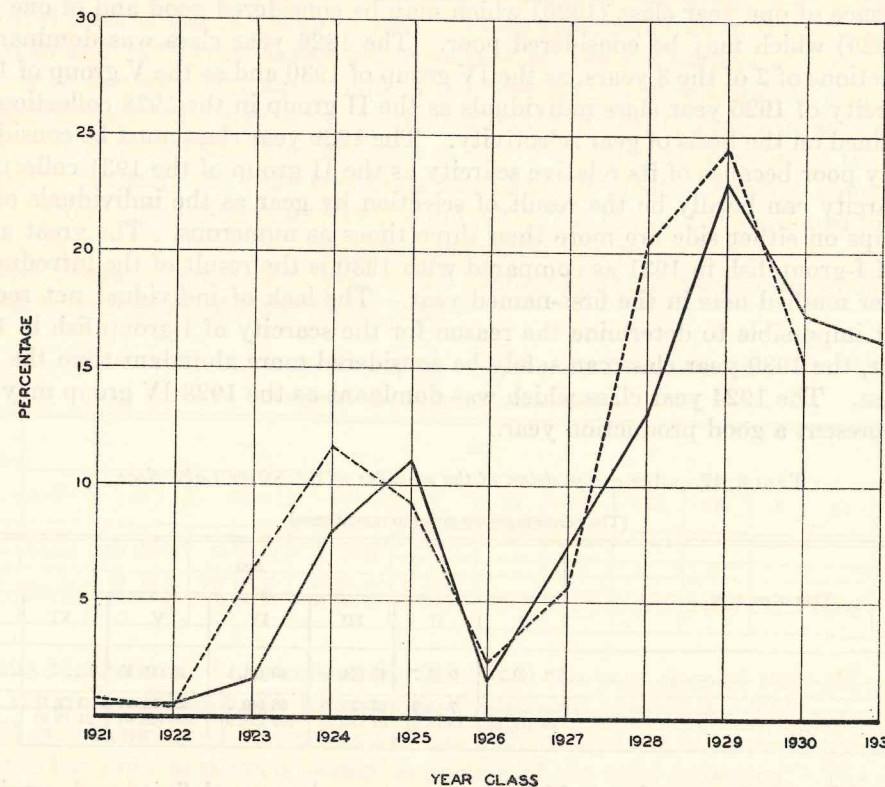


FIGURE 5.—Percentage representation of the different year classes in the Clear Lake cisco collections. 1931, broken line; 1932, solid line.

while the 1929 year class (II group of 1931, III group of 1932) which was dominant in the collections of both years may be termed good. It can be considered valid to state further that the 1924 and 1925 year classes (VII and VI groups of 1931) and probably the 1928 year class (III group of 1931) were more successful than those of 1926 and 1927 (V and IV groups of 1931), and that the 1929 year class (II group of 1931) was more successful than either that of 1930 (I group of 1931) or 1931 (I group of 1932).²⁴

In the comparison of the relative abundance of different year classes in Clear Lake some consideration should be given the matter of the age of the samples upon

²⁴ In contrast to the other 3 populations the I-group samples of Clear Lake can be considered representative. (See the section on "The selective action of gill nets.")

which the estimations are based. For example, the 1927 year class which as the IV group composed 5.6 percent of the 1931 collection and as the V group composed 7.3 percent of the 1932 collection must be considered to represent a much less successful year than the 1924 year class which as the VII group of 1931 composed 11.6 percent of that year's collection and a year later as the VIII group made up 7.9 percent of the 1932 collection. Although the 1924 year class individuals in both years' collections combined were only about one and one-half times as numerous as those of the 1927 year class, the former year class, by reason of its 3 years greater age, had suffered the reducing effect of natural mortality over a longer period of time. Consequently the 1924 year class as compared with the 1927 year class may be considered much more successful than the comparison of the representation of the two groups in the collections would indicate. A similar line of reasoning leads to the conclusion that the 1925 year class (VI group of 1931) also represents a very successful year. The same conclusion may possibly apply to the 1923 year class which was well represented as the VIII group of 1931.

In the preceding discussion it was shown that in each population there existed a considerable variation in the numerical abundance or successfulness of the various year classes. The years that appear to have had a production of relatively successful year classes were: Trout Lake—1926, 1927; Muskellunge Lake—1928; Silver Lake—1926; Clear Lake—1924, 1925, 1929. In Silver Lake the 1929 year class was poor, and in Clear Lake the 1926 and 1927 year classes must be considered relatively unsuccessful.

Since the four populations show no agreement in the matter of goodness or poorness of the various year classes, it may be concluded that in each population the success of the individual year classes depends on the purely local conditions within the lake. This conclusion is of particular interest in view of the rather general opinion that fluctuations in the relative abundance of year classes have their origin in differences in weather conditions from one year to another. Inasmuch as these four lakes are grouped closely together (the maximum distance between any two of them is about 18 kilometers) they must all be subjected to approximately the same weather conditions.

It must be remembered that relative abundance is not a wholly reliable index of absolute abundance. A poor year class may appear quite numerous in comparison to a yet poorer one. Järvi (1920) gave an excellent illustration of this fact when he pointed out that the great relative abundance of third year fish in some years' catches of the "kleine Maräne" depended not upon the actual abundance of that particular age group but was rather the result of the scarcity of fish in their second year of life.

The data of tables 45 to 48 make possible a comparison of longevity in the four populations. The Muskellunge Lake cisco has definitely the shortest average life span. The Trout Lake cisco falls second and the Silver Lake cisco third, while the average life span of the Clear Lake cisco is quite long. A possible explanation of these differences among the four populations as to the average length of life was mentioned in the section on condition in the different populations.

AGE AT MATURITY AND SEX RATIO

Although the collections of the cisco were made in July, August, and early September, several months before the time of spawning in November, the development of the gonads was such as to leave little doubt as to the sexual maturity of the

individual. Fish that would have spawned the following autumn could be distinguished easily from those which would not have spawned at that time. The former were considered here as matured fish even though they may not have spawned previously.

Sexual maturity occurs at an early age in each of the four populations. All the Clear Lake fish with the exception of a few I-group individuals were mature or maturing. Since there is good reason to believe that the I-group samples from Clear Lake are representative, it may be concluded that in this population the first spawning occurs in the autumn of the second year of life. Practically all the I-group individuals in the samples from Trout, Muskellunge, and Silver Lakes would have spawned the following autumn. There is reason to believe, however, that in these populations the nets used for collecting the samples took only the larger I-group individuals. The smaller members of the age group may have been immature. In all three populations, however, all II-group individuals indicated that they would spawn in the autumn.

The ciscoes of the four populations considered in this investigation attain sexual maturity at an earlier age than has been found by some investigators of this species. Clemens (1922), referring to *L. artedi* in Lake Erie, stated that first spawning is "probably at the end of the third summer." The ciscoes of the inland lakes of southern Wisconsin spawn at the age of 3 years (Cahn 1927). Van Oosten (1929) found that in the Saginaw Bay herring only a few fish matured in the second year, and that the majority matured in the third and fourth years of life. Van Oosten's data were based on the examination of individuals from the spawning run. In the Lake Ontario cisco Pritchard (1931) found a few females but no males mature at 2+ years. He stated further that several individuals of both sexes were mature at 3+ years, while spawning was general at 4+ years. Dymond (1933) found that in Hudson Bay the cisco does not mature "until the fourth and probably the fifth year."

The sex ratio expressed as the number of females per 100 males was determined by age groups for each of the four populations. These data are presented in table 49.

TABLE 49.—Sex ratio according to age in each of the four populations

[The ratio is expressed as the number of females per 100 males. The numbers of specimens are shown in parentheses. The age groups which were composed entirely of one sex are indicated by the sex symbols. The Clear Lake data were obtained by combining the 1931 and 1932 collections. The data for the remaining three lakes are based on the combination of the 1930 and 1931 collections]

Lake	Age					
	I	II	III	IV	V	VI
Trout.....	100 (2)	162 (97)	204 (520)	354 (368)	1,367 (88)	1,100 (12)
Muskellunge.....	100 (26)	130 (472)	151 (361)	151 (361)	1,367 (88)	1,100 (12)
Silver.....	110 (66)	160 (26)	126 (86)	111 (160)	129 (133)	200 (24)
Clear.....	72 (69)	89 (102)	94 (95)	86 (39)	82 (20)	100 (26)

Lake	Age						Average
	VII	VIII	IX	X	XI	XII	
Trout.....	♀ (4)	400 (5)	♀ (2)	-----	♂ (2)	♀ (1)	267 (1,101)
Muskellunge.....	♀ (1)	137 (861)	-----	-----	-----	-----	137 (861)
Silver.....	194 (50)	210 (31)	300 (4)	♀ (3)	♀ (1)	-----	124 (496)
Clear.....	-----	-----	-----	-----	-----	-----	104 (440)

With the exception of the irregular data of Silver Lake, the females tend to become relatively more abundant as age increases. The tendency toward a progressively greater preponderance of females finds an extreme condition in Trout Lake where male individuals are rare beyond the IV group. The Clear Lake fish differ from those of the other three lakes in that the males outnumber the females in the first five age groups. In the VI group the numbers are equal while in the age groups above 6 years the females are much more numerous than the males. Differences among the populations in the rate of change of the sex ratio with increased age are reflected in the average sex ratio for each population as based on the combination of all age groups.

It is believed that the data of table 49 are a reliable index of the sex composition of the four populations. Cahn (1927) and Van Oosten (1929) pointed out that males arrive at the spawning ground earlier than the females. European investigators of coregonids have observed frequently that not only do males arrive at the spawning grounds earlier than females but that they remain there longer. As a consequence, if samples are taken from the spawning run the conclusions concerning the sex ratio would not only be affected by the time within the spawning period of the taking of the sample but also would tend to contain a too high percentage of males. The collections used in this investigation are not open to such a criticism. All samples were taken during the summer, several months before the spawning time, and there is no evidence pointing toward a segregation of the sexes at this period of the year.

The data relative to the sex ratio in the four populations differ from those given by Cahn (1927) for the lakes, Mendota and Oconomowoc, in southern Wisconsin and by Van Oosten (1929) for the Lake Huron herring. Cahn found 101 males and 62 females in his collections from Lake Mendota and 429 males as against 315 females in his samples from Oconomowoc Lake. He combined the collections from the two lakes to obtain a ratio of 100 males to 71.2 females. Cahn attributed the greater abundance of males to the relatively higher mortality of the females during the warm weather of late summer. His data on sex ratio were not correlated with age.

Van Oosten (1929) found males and females approximately equally abundant (49.5 percent males) in his samples of the Lake Huron herring taken at Bay City, Mich. He did, however, find differences in the sex ratio in the different age groups. Females were the more numerous in the younger age groups (I and II in the method of age designation used in this paper) while the males were the more abundant in the older age groups. Van Oosten attributed the shifting sex ratio to an earlier attainment of sexual maturity on the part of the females and a consequent tendency for them to appear in the commercial catch at an earlier age.

The change with age in the sex ratio of the four cisco populations of this study must be explained on the basis of a differential mortality of the two sexes. Since there is no fishery for the cisco in these lakes, there can be no disturbance of the natural relationship through the catching of more individuals of the one sex than of the other. The reason for the observed differences in differential mortality in the four lakes presents a problem difficult of explanation. Attention should be called to the fact that with respect to the relative abundance of males in the entire samples the lakes fall in the same order that they show with respect to the amount of growth in weight, that is the population with the slowest growth (Trout Lake) has relatively fewest males. The possible significance of this parallelism will be considered later.

Willer (1929) suggested that selective destruction by carnivorous forms might affect the sex ratio in the kleine Maräne (*Coregonus albula*). In the younger groups the heavier, less agile female would fall prey to predators more readily than the males. In the older groups the heavier females would be protected by virtue of their size as the predatory fish would select the slenderer males as prey of more suitable proportions. Such an assumption does not serve to explain the change with increase in age in the sex ratio of the four populations of the present investigation. Though the Trout Lake stock shows the most rapid shift toward a preponderance of females, the growth of the two sexes in this lake is the same both with respect to length and weight. Furthermore, the greatest changes in sex ratio occur between age groups that show only slight differences in average length and weight. The situation in Muskellunge Lake is similar to that in Trout Lake. In Silver Lake the males tend to be slightly heavier than females of the same age while in Clear Lake the females are distinctly heavier than the males. Yet in both populations, particularly in the Clear Lake cisco, females are relatively more abundant than males in the older age groups.

In view of the fact that the greatest progressive change in the sex ratio with increase in age occurs in the population in which there is least reason to expect selection on the basis of sex by the carnivorous forms which prey on that population, it must be concluded that the differential mortality upon which the changing sex ratios depend is not the result of selection by predators. The differential mortality of the two sexes is probably the result of basic differences in their innate physiological mechanisms, differences that vary in their manifestations from one population to another, and whose effects appear to be associated to some extent with the growth rate of each particular population.

The above suggestion of an explanation of the differential mortality of the sexes of the cisco is in agreement with the conclusions of Geiser (1923, 1924, a, b,) ²⁵ who held that females are inherently better fitted than males to survive adverse environmental conditions. The explanation of the sex ratio on these grounds assumes particular interest when it is considered in relationship to the correspondence between sex ratio and growth rates in the four cisco populations of this study. It was pointed out (p. 269) that in these populations slow growth is associated with a relative paucity of males. It appears logical to assume that the environmental factors that doubtless contributed to the observed differences in growth rate may at the same time have produced corresponding differences in the sex ratios of these same populations. Thus the very slow growth of the Trout Lake cisco may be associated with very adverse environmental conditions that also produce an exceptionally high mortality among the less viable males. This excessive mortality of males as compared to females would produce the observed rapid change with increased age in the sex ratio and the relatively high abundance of females in the population as a whole. Similarly, the better growth in Muskellunge Lake and Silver Lake may be taken to represent conditions less adverse than those in Trout Lake. In these less adverse environments of Muskellunge and Silver Lakes the mortality of males as compared to females is less than in Trout Lake, and females are relatively less abundant in the populations as a whole. Finally, the favorable conditions that permit such excellent growth in the Clear Lake cisco are reflected in the slowly changing sex ratio and the almost equal representation of the two sexes in that population.

²⁵ In these papers Geiser included comprehensive reviews of the literature on the subjects of sex ratios and differential mortality of sexes, not only in the fishes but in other animal groups as well.

ANNUAL INCREMENTS OF GROWTH

VARIATION IN THE AMOUNT OF GROWTH IN DIFFERENT CALENDAR YEARS

Tables 50 to 54 show the calculated annual growth increments for each of the best represented age groups in the collections of each cisco population. (In Clear Lake all age groups below the IX group were included.) The arrangement of the tables is such that each horizontal row shows the growths in different calendar years of fish of the same age and in the same year of life. The vertical columns show growth increments for the same calendar year but for fish that are either of different age or in different years of life, sometimes both. Each diagonal row shows the growth increments in the different calendar years of a single age group in a single year's collection. The calendar year corresponding to the first year of life of any particular age group is the year of birth, while the year of capture of each age group is one year later than the calendar year of the last growth increment shown in the table for that age group.

TABLE 50.—Annual calculated growth increments in millimeters of the Trout Lake cisco, ages III to V, according to calendar year and year of life

Age	Year of life	1924	1925	1926	1927	1928	1929	1930	Average
V	5						12	9	10.5
	4					13	10		11.5
	3				19	17			18.0
	2			34	37				35.5
	1		82	81					81.5
IV	4				10		10	11	10.3
	3			13		19	20		17.3
	2		35		36	37			36.0
	1	85		82	78				81.7
	3				14		22	17	17.7
III	2					38	36		37.7
	1		84		79	84			82.3

TABLE 51.—Annual calculated growth increments in millimeters of the Muskellunge Lake cisco, ages II and III, according to calendar year and year of life

Age	Year of life	1925	1926	1927	1928	1929	1930	Average
III	3			20		25	18	21.0
	2		37		47	49		44.3
II	1	105		85	96			95.3
	2			48		48	40	45.3
	1		99		95	98		97.3

TABLE 52.—Annual calculated growth increments in millimeters of the Silver Lake cisco, ages II to VI, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	Average
VI	6							15	12	13.5
	5						16	19		17.5
	4					27	16			21.5
	3				22	23				22.5
	2			40	41					40.5
V	1		72	78						75.0
	5					14		20	14	16.0
	4				19		20	18		19.0
	3			27		25	24			25.3
	2		39		46	46				43.7
IV	1	76		74	80					78.7
	4					16		21	17	18.0
	3				25		26	27		26.0
	2			46		48	52			48.7
	1		79		78					79.0
III	3					30		33	29	30.7
	2				54		57	54		55.0
	1			73		77	83			77.7
II	2					50		52	47	49.7
	1				90		99	104		97.7

TABLE 53.—Annual calculated growth increments in millimeters of the Clear Lake cisco (males), age groups I to VIII, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII	8										9.4
	7										12.1
	6										16.1
	5										20.1
	4										30.0
VII	3										50.0
	2										86.0
	1	118	85	45	31	18	17	12	7	11	113.0
	7		108	87	55	29	23	16	13		12.1
	6										16.1
VI	5										20.1
	4										30.0
	3										50.0
	2										86.0
	1										113.0
V	7										12.1
	6										16.1
	5										20.1
	4										30.0
	3										50.0
IV	2										86.0
	1										113.0
	7										12.1
	6										16.1
	5										20.1
III	4										30.0
	3										50.0
	2										86.0
	1										113.0
	7										12.1
II	6										16.1
	5										20.1
	4										30.0
	3										50.0
	2										86.0

TABLE 54.—Annual calculated growth increments in millimeters of the Clear Lake cisco (females), age groups I to VIII, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII	8										11.5
	7										14.0
	6										17.5
	5										24.0
	4										32.5
VII	3										53.0
	2										88.0
	1	112	87	54	33	22	15	13	11	12	108.5
	7		105	89	52	32	26	20	15		15.5
	6										17.0
VI	5										25.5
	4										37.0
	3										58.0
	2										85.0
	1										108.0
V	7										16.0
	6										22.0
	5										37.0
	4										63.0
	3										81.5
IV	2										101.5
	1										28.0
	7										45.0
	6										72.0
	5										79.5
III	4										103.0
	3										38.5
	2										77.5
	1										90.0
	7										103.0
II	6										73.5
	5										94.0
	4										103.0
	3										102.0
	2										111.0

The examination of tables 50 to 54 shows that the amount of growth made by fish of the same age and in the same year of life varies considerably from one calendar year to another. This variation is doubtless to a certain extent random and of no particular significance. In each population, however, there may be detected certain calendar years that by reason of the consistently good or poor growth made in them may be considered good or poor growth years. For example, the growth of the Silver Lake cisco and the Muskellunge Lake cisco (possibly that of the Trout Lake cisco also) appears to have been better than average in the year 1929 while the Clear Lake cisco shows excellent growth for 1931. On the other hand, growth in the first three of the above populations appears to have been relatively poor in 1930, while the Clear Lake cisco shows poor growth for 1926 and 1927 at least.

The relative positions of the different calendar years with respect to goodness or poorness of growth may be brought out more clearly by simple methods of analysis. In the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations the relative position of each calendar year was determined on the basis of the percentage deviation from average growth in that particular year. As an illustration of the method of determining the deviation from average growth consider the growth of the Silver Lake cisco in the calendar year 1924 (table 52). The calculated first year growth of 72 millimeters of the VI group (year class of 1924) represents a —4.0 percent deviation from the average of 75-millimeter growth for VI-group fish in the first year of life; the 39-millimeter growth of the V group (1923 year class) in its second year of life represents a —10.8 percent deviation from the average growth of 43.7 millimeters for V-group fish in the second year; and finally the 79-millimeter first year's growth of the III group (year class of 1924) represents a 0.0 percent deviation from the average of 79-millimeter growth for III-group fish in the first year of life. The mean of these three deviations is —4.9, and it may be considered that the growth of the Silver Lake cisco in 1924 was 4.9 percent below average. The deviations from average growth for each calendar year calculated by the above method are shown in table 55 for Trout, Muskellunge, and Silver Lakes.

TABLE 55.—Percentage deviation from average growth in the different calendar years

Lake	Calendar year								
	1923	1924	1925	1926	1927	1928	1929	1930	1931
Trout		4.0	0.0	—5.2	—3.2	3.8	5.6	—4.2	
Muskellunge			10.2	—7.4	—3.2	1.4	9.1	—13.0	
Silver	—0.9	—4.9	—0.9	—0.7	—0.5	—1.7	7.7	—8.0	
Clear	3.3	—4.1	—5.1	—8.5	—8.5	—0.4	3.2	3.1	17.1

In criticism of the above method of determining the relative position of the different calendar years as to the amount of growth, it should be mentioned that the evaluation of the different years depends on comparisons that are based on different combinations of year classes and age groups, and that the evaluation of a single calendar year is based not upon a single comparison with all other calendar years involved but rather is the average of a group of comparisons no one of which involves more than 3 calendar years. If one of these single comparisons should happen to involve, for example, 3 poor-growth years the resultant percentage deviations would give too high an estimate of the relative goodness of these growth years as compared to calendar years not involved in the comparison. Similarly, a comparison that involves 3 good-growth

years will give too low an estimate of the goodness of growth in these years as compared with years not involved in this particular comparison. The possible distorting effect of examples such as those just given is obviated in large measure, however, by the fact that the evaluation of the goodness of growth of a single year involves comparisons with so many other calendar years that the effect of a single distorted comparison will tend to be greatly reduced.

In Silver Lake (table 52), for example, the evaluation of the year 1927 is based on comparisons that involve all other years from 1924 to 1930, inclusive. At the best, however, the evaluation of growth in different calendar years shows only their relative positions, and a general shifting of values might be expected to follow the

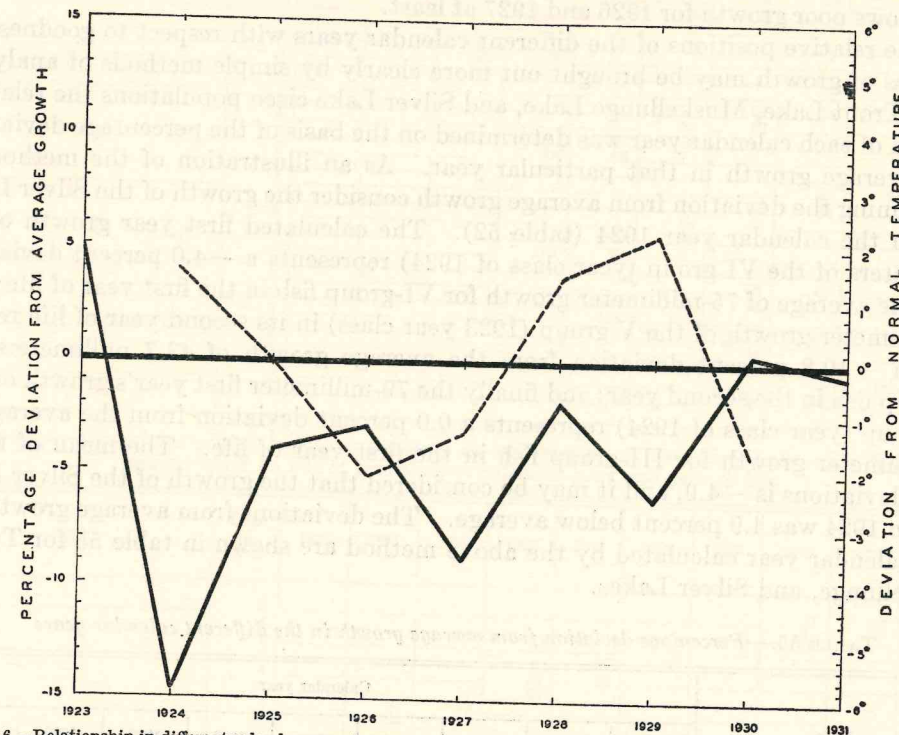


FIGURE 6.—Relationship in different calendar years between the deviation of the growth of the Trout Lake cisco from the average and the deviation of the air temperature from the normal during the cisco's growing season. Deviation from the average growth, broken line; deviation from normal temperature, solid line.

elimination or addition of another calendar year in the comparisons. The method of comparing goodness of growth in Trout, Muskellunge, and Silver Lakes in different calendar years has the advantage that all the single comparisons are based on fish of the same age, and that any possibility of a distortion through Lee's phenomenon is thereby eliminated.

The fact that collections of the Clear Lake cisco were made in only 2 consecutive calendar years makes necessary a slightly different procedure in the comparison of growth in that lake in different calendar years. In Clear Lake the evaluation of the goodness of growth by the method employed in the other three populations would mean that the estimate of the relative position of a single calendar year would be based not on comparisons with several other calendar years but on comparisons with only the single years immediately preceding and immediately following the year in

question. Since, as will be brought out presently, the calendar years 1924 to 1927, inclusive, were all below average as to goodness of growth, while the years 1929, 1930, and 1931 were all above average, the limitation of the estimate for a poor year, as for example 1926, to comparisons with two other poor years, 1925 and 1927, or of a good year as 1930 to comparisons with other good years, 1929 and 1931, would lead inevitably to erroneous conclusions concerning the goodness of growth in these years. To avoid this difficulty the evaluation of the different years was based on the comparison of total growth in each calendar year with that of the preceding year.

An illustration will be given of the method used in the evaluation of goodness of growth of the Clear Lake cisco in different calendar years. (See table 53.) In 1924

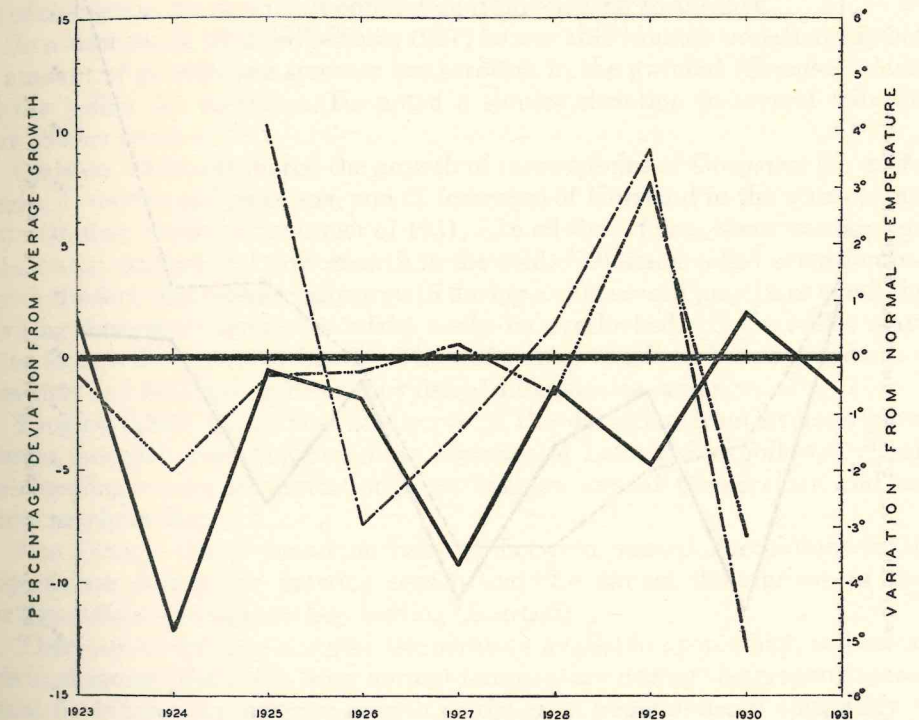


FIGURE 7.—Relationship in different calendar years between deviation of growth of Muskellunge Lake cisco and of Silver Lake cisco from average, and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, Muskellunge Lake cisco — — —; Silver Lake cisco — . . . —; deviation from normal temperature, ———.

the first year's growth of the VIII-group fish was 108 millimeters. This growth was 10 millimeters or 8.5 percent less than the first year's growth of the preceding year (118 millimeters in 1923). Thus the calendar year 1924 shows a —8.5-percent deviation from 1923 as to goodness of growth. Similarly the 1925 growths of 87 (VIII group, second year of life) and 102 (VII group, first year of life) show a total of 189 or a deviation of —3.1 percent from the total corresponding growth of 195 millimeters in 1924. The position of 1925 with respect to 1923 is the sum of the deviations, —8.5 and —3.1 or —11.6 percent. A continuation of this procedure shows the position of each calendar year with respect to the year, 1923. In order to make the relative positions of the different years describe their deviations from average growth rather than from 1923 growth, the mean value of all the deviations as computed from 1923 as the starting point was subtracted from the individual devia-

tion of each year. The final figures after a combination of the sexes (table 55) indicate that growth in 1923 was 3.3 percent above average. Although the Clear Lake data of table 55 were obtained by a different method from the data pertaining to the other three lakes, the fact that all these "deviations from average growth" are used only to show relative positions of the different calendar years makes a comparison of the data of all four lakes valid.

The data of table 55 are presented graphically in figures 6 to 8. The examination of the curves reveals a certain degree of correspondence as to goodness or poor-

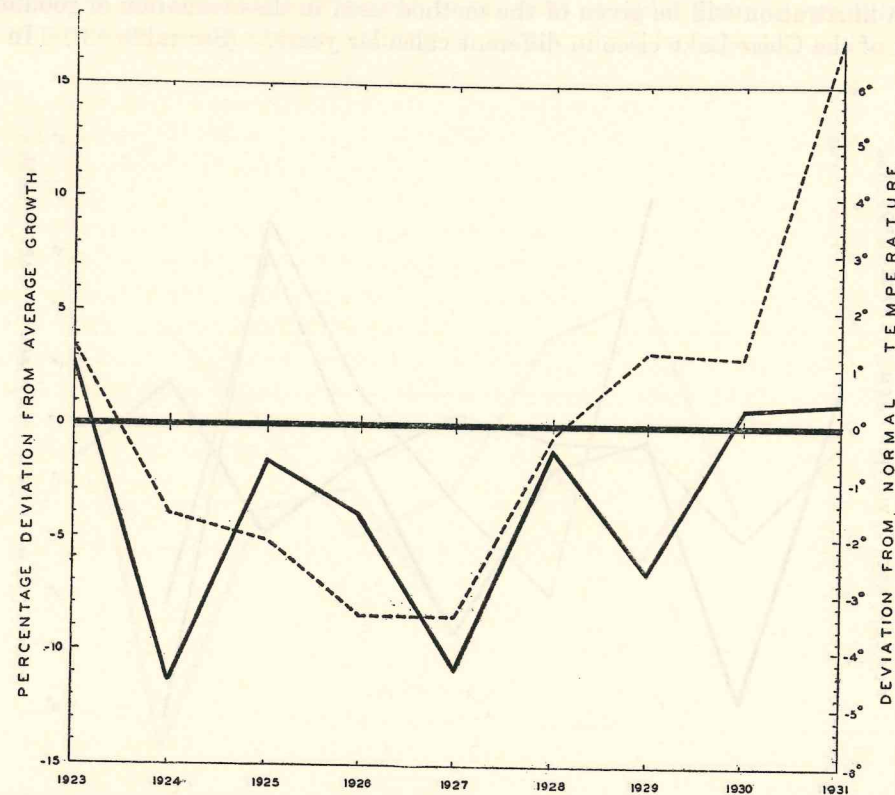


FIGURE 8.—Relationship in different calendar years between the deviation of growth of Clear Lake cisco from average and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, broken line; deviation from temperature, solid line.

ness of growth for certain populations and over certain periods of years. For example, Trout, Silver, and Muskellunge Lakes agree in showing improvement in growth from 1928 to the relatively good year 1929, followed by a distinct drop to the relatively poor year of 1930. Similarly Trout, Muskellunge, and Clear Lakes agree in showing poor growth in 1926 and 1927.

Agreements of the sort just pointed out suggest that the amount of growth in different calendar years may possibly be determined in part by factors that affect all four lakes. The failure of any general agreement of the growth deviation curves indicates, however, that local conditions that exist within a single lake also exert a powerful influence on the amount of growth in different calendar years.

The most apparent influence that might affect growth similarly in all lakes is the average temperature during the growing season, while growth within a single

lake might be expected to vary somewhat with annual fluctuations in the abundance of the population within that particular lake. References to the literature on the question of the change in growth rate that accompanies change in the density of population have been made previously (pp. 254-257). Some mention should be made of the much less numerous observations on the relationship between annual fluctuations in average temperature and annual fluctuations in growth, particularly as these observations have been made with reference to coregonids.²⁶

Huitfeldt-Kaas (1917) demonstrated a close correlation between first-year growth and average annual temperature in the lagesild or pollan (*Coregonus albula*) of Mjøsen and Storsjø. At the same time he recognized the possible effect on growth rate of changes in the density of population from one year to another.

In a later paper (Huitfeldt-Kaas, 1927) he was able to show a relationship between the amount of growth and summer temperature in the gwiniad (*Coregonus lavaretus*) and the pollan (*C. albula*). (He noted a similar situation in several tribes of the trout (*Salmo eriox*).)

Olofsson (1932) compared the growth of three species of *Coregonus* (*C. wartmanni borealis*, *C. wartmanni generosus*, and *C. lavaretus*) of Norrland in the warm summer of 1930 with that in the cold summer of 1931. In all three forms there was large growth in the warm summer and slow growth in the cold. Olofsson called attention particularly to the fact that occasionally growth during a cold season may be so small that the year ring formed on the scales might easily be overlooked. Some scales may even fail to form a distinct year band. The differences observed between growth of the years 1930 and 1931 were exhibited by fish of different sizes and ages.

Krogus (1933) found that the curve of the deviation from average growth in different calendar years for *Coregonus lavaretus* of Lake Baikal followed closely the corresponding curves for deviation from average annual temperature and average annual precipitation.

Van Oosten (1929) found no relation between annual fluctuations in the air temperatures during the growing season and the annual fluctuations in the first year's growth in the Saginaw Bay herring (*L. artedi*).

There are no records of water temperature available upon which to base a comparison of annual deviation from normal temperature during the growing season and annual deviation from average growth in the cisco populations of this study. It is possible, however, to make a comparison between annual deviation from average growth and annual deviation from normal air temperature²⁷ in the region. For this purpose the records of the meteorological stations at Big St. Germaine Dam and Rest Lake Dam were taken as representative for Trout, Muskellunge, and Silver Lakes, while the records of the Minocqua station were taken as representative for Clear Lake.²⁸

Since the lengths of the growing seasons (pp. 249-253) are not the same in the different lakes the annual deviations from normal summer temperature were calculated

²⁶ Although his work does not deal with the coregonids, mention should be made of Segerstrale's (1932, 1933) observations on the relationship between summer temperature and the growth of fishes in southern Finland. This work dealt with the perch (*Perca fluviatilis*) and several species of cyprinids. Segerstrale found that the amount of growth during the summer is a quantity highly sensitive to the average summer temperature.

²⁷ Climatological Data for the United States, U. S. Department of Agriculture, Weather Bureau, vols. X-XVIII, 1923-31.

²⁸ Muskellunge Lake lies about 3 kilometers east of Trout Lake, and Silver Lake lies about 1 kilometer off the southwest corner of Trout Lake. The St. Germaine weather station is about 13 kilometers southeast of Trout Lake while the Rest Lake station lies at an approximately equal distance to the northwest of Trout Lake. The town of Minocqua is about 6 kilometers due west of Clear Lake.

from different combinations of months. The St. Germaine and Rest Lake data were used to determine the annual deviation from normal temperature for the periods May to July and May to August, both inclusive. The former period of time may be taken to correspond approximately to the growing season of the Trout Lake cisco, and the latter to the growing seasons of the Silver Lake and Muskellunge Lake ciscoes. The annual deviation from normal temperature for the longer Clear Lake growing season (May to September, inclusive) were determined from the Minocqua station data. In these calculations of deviations from normal temperature, records for a single month were found to be occasionally lacking in the data for a station. For these few gaps in the data the corresponding records of the nearest neighboring station were substituted. This substitution is justifiable for the corresponding deviations from normal temperature at the different stations were almost always close to each other in value.

Table 56 shows the annual deviations from normal air temperatures as based on the different combinations of months and for the weather stations mentioned in the preceding paragraph. These data are presented graphically in figures 6 to 8 along with the corresponding curves of deviation from average growth. The examination of these curves shows that there is little evidence of a connection between annual deviation from average growth and annual deviation of the air temperature from the normal during the growing season. In the Trout Lake data (fig. 6) the years (1924, 1928, and 1929) with better than average growth were years with subnormal temperature for the period, May to July. On the other hand, 1930 with a temperature slightly above normal was a poor growth year. The year 1929 was a good growth year in both Muskellunge Lake and Silver Lake (fig. 7), while 1930 was a year of poor growth. Yet the air temperature for the period, May to August, was below normal in 1929 and above normal in 1930. Certain other years, however, show both subnormal temperature and growth below average (for example, Silver Lake, 1924). There is some indication that in Clear Lake (fig. 8) there may be some slight connection between annual variations in growth and annual variations in average air temperature over the period May to September. It may be seen that in Clear Lake all the calendar years with poorer than average growth (1924 to 1928, inclusive) showed subnormal temperatures during the growing season while 3 of the 4 years with better than average growth (1923, 1929, 1930, 1931) had temperatures above normal during the growing season. The year 1929 showed growth slightly above average, but temperature below normal. In general, however, the Clear Lake curves for annual deviation of the cisco's growth from the average and the annual deviation of the air temperature during the growing season from normal show a rather conspicuous lack of parallelism.

TABLE 56.—Average deviation of air temperatures from normal during the growing season of the cisco
[Deviations are in degrees Fahrenheit; 1.8° F.=1.0° C.]

Stations	Months	1923	1924	1925	1926	1927	1928	1929	1930	1931
St. Germain Rest Lake..	May, June, July.....	2.0	-5.8	-1.6	-1.2	-3.5	-0.7	-2.4	0.2	-0.2
Do.....	May, June, July, August.....	.8	-4.8	-0.2	-0.7	-3.6	-0.5	-1.9	.8	-0.6
Minocqua.....	May, June, July, August, September.....	1.1	-4.5	-0.6	-1.6	-4.3	-0.4	-2.6	.3	.4

The failure of the data discussed in the preceding paragraph to show any clear dependence of growth in different calendar years on the temperature of the air during

the growing season should not be taken to show that in these four cisco populations the amount of growth in a particular summer does not depend in part on the temperature of the lakes' waters during the growing seasons of the several stocks. It must be recognized first that fluctuations in air temperature may not offer a perfect index of fluctuations in water temperature. A more probable explanation of the failure of annual fluctuations in temperature and in growth to show correspondence is that annual differences in growth are so closely dependent on some other factor or factors that the effect of annual differences in temperature are almost completely obscured. There is reason to believe that in the populations of this investigation the annual fluctuations in the goodness of growth may show some dependence on annual fluctuations in the densities of the different populations.

It has been shown previously (p. 262) that the growth rates (in weight) of these four populations follow the inverse order of the relative densities of their populations. In view of this demonstrated relationship between growth rate and density of population it might well be expected that within a single population changes in the density of the cisco may be accompanied by changes in its growth rate.

In the study of the age composition of the cisco samples from Trout Lake (table 45, p. 264) it was pointed out that the years 1926 and 1927 saw the production of abundant year classes, and that as the result of the abundance of these two groups the 1930 Trout Lake cisco samples were on the average composed of older fish than the 1928 samples while the 1931 samples were composed of older fish than either the 1928 or 1930 collections. This accumulation of old fish together with the contributions of young in the years later than 1927 probably caused the density of the population to be rather high in 1930. This increase in the density of the population may account in part for the drop in growth from 1929 to 1930.

The data for the Muskellunge Lake cisco also afford evidence for a dependence of growth variations on variations in population density. While the 1928 and 1930 collections contained only a few individuals more than 2 years old, a large number of the 1928 year class individuals were present as the III group in 1931. (See p. 264.) The great abundance of the III group in 1931 suggests that an accumulation of the stock may have been occurring in Muskellunge Lake in 1929 and 1930. This accumulation may possibly account for the drop in the amount of growth from 1929 to 1930.

The age and year class composition data for the Silver Lake cisco (table 47, p. 265) show that here as in Trout Lake there was probably an accumulation of the stock in 1930. In the examination of the data of table 47 it should be remembered that the large number of 1931 I-group fish causes the representation of the older age groups of the 1931 samples to appear relatively too low; the gear used in 1928 and 1930 captured few I-group individuals. If due consideration is given to the absence of the I-group fish in the 1928 and 1930 collections the relative abundance of the older age groups in the 1931 Silver Lake collections must be recognized to be higher than in 1930, while the 1930 collection in turn shows a greater abundance of old fish than the 1928 collection. In Silver Lake as in Trout Lake and Muskellunge Lake the accumulation of older fish was accompanied by a decrease in growth from 1929 to 1930.

It should be mentioned that the data upon which a suggested explanation of the drop in growth from 1929 to 1930 in Trout, Silver, and Muskellunge Lakes was based fail to offer any logical explanation for the improvement of growth from 1928

to 1929. Unfortunately there are no 1929 collections upon which to base a comparison of the age composition of that year with the years 1928, 1930, and 1931.

In the Clear Lake cisco the evidence for a dependence of annual fluctuations in the amount of growth on annual fluctuations in the density of the population is somewhat stronger than in the Trout, Muskellunge, and Silver Lake populations. The years 1923, 1924, and 1925 (p. 265, table 48, fig. 5) were undoubtedly excellent years for the production of young. The presence of three successive good hatches must have led to a considerable accumulation of the cisco stock. Corresponding with this accumulation the amount of growth per year decreased from 1923 to 1927 (fig. 8). The production of young was poor in 1926 and 1927. The occurrence of 2 poor production years combined with natural mortality could be expected to lessen the crowding of the population. The growth improved from 1927 to 1929, fell back a little in 1930, and improved again in 1931.²⁹

The relationship indicated in the Trout Lake, Muskellunge Lake, Silver Lake ciscoes, and especially in the Clear Lake cisco, between annual fluctuations in population density and annual fluctuations in growth is in agreement with Järvi's observations (1920, 1924) on the kleine Maräne (*Coregonus albula*).

The failure of variations in the amount of growth in different calendar years to show any close general dependence on either annual variations in temperature or annual variations in population density suggests that possibly these variations in growth depend closely on both factors, and that the failure of these factors to operate in the same direction in the same year tends to obscure the effect of each of them.

BIMODALITY IN THE CALCULATED GROWTH FOR THE FIRST YEAR OF LIFE

The examination of the frequency distributions of the calculated growth for the first year of life in the best represented age groups (tables 57 to 60) shows that some of these distributions have a distinct bimodality, which appears to be characteristic for a year class and present regardless of the age of the fish upon which the calculated growths were based.

TABLE 57.—Trout Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class								
	1926			1927		1928		1929	
	II	IV	V	III	IV	II	III	II	
	1928	1930	1931	1930	1931	1930	1931	1931	
110.....									
105.....	1				1	1			1
100.....	1				1	1			2
95.....	4	1	1	7	4	5	6		6
90.....	6	2		14	4	8	15		13
85.....	7	8		17	16	6	34		20
80.....	9	21	15	32	24	7	26		12
75.....	15	30	23	74	48	5	31		16
70.....	30	20	27	85	78	3	31		6
65.....	26	11	6	83	72		26		1
60.....	3	6	2	30	18				
55.....				5	3				

²⁹ The good growth in 1931 may have been in part due to the climatic conditions of that year as well as to the reduced number of ciscoes in the stock. The temperature over the period, May to September, inclusive, was only slightly above normal (table 56) but the autumn temperatures were exceptionally high (p. 253). It is probable that the warm autumn of 1931 gave the Clear Lake cisco a longer growing season in that year than it usually enjoys.

TABLE 58.—Muskellunge Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class				Length	Year class			
	1926	1928		1929		1926	1928		1929
		II	II				III	II	
	1928	1930	1931	1931		1928	1930	1931	1931
125.....	2		2		90.....	20	39	28	
120.....	6	2	7		85.....	35	41	64	
115.....	28	8	16	3	80.....	29	26	60	
110.....	24	20	46	7	75.....	17	12	17	
105.....	35	21	39	33	70.....	1	2	5	
100.....	27	17	37	60	65.....	2			
95.....	16	21	26	72					

TABLE 59.—Silver Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class							
	1924		1925		1926		1927	
	IV	III	V	VI	IV	V	IV	III
	1928	1928	1930	1931	1930	1931	1931	1931
120.....								
115.....								
110.....								
105.....								
100.....								
95.....								
90.....	5		1		1	2	8	2
85.....	8		3	3	9	11	8	4
80.....	17	6	2	4	10	36	20	9
75.....	22	11	9	7	16	29	21	16
70.....	12	17	2	4	11	16	26	9
65.....	3	7	6	1	7	6	5	3
60.....	2	5	2	1	2	1	4	2
55.....					1			

TABLE 60.—Clear Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class									
	1924		1925		1928		1929		1930	
	VII	VIII	VI	VII	III	IV	II	III	I	I
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932
140.....										
135.....							1		2	3
130.....							1		3	1
125.....		1			1		1		5	6
120.....	2						1		7	5
115.....	3	1		2	1	1	4		3	4
110.....	1	2	1	1	5	3	11		13	1
105.....	8	1	5	2	10	5	11		8	9
100.....	5	3	8	6	11	3	24		6	7
95.....	9	1	7	7	12	4	12		4	2
90.....	3	4	1	2	7	7	7		1	1
85.....		1	1	1	5	2	1		4	

This bimodality of the length frequencies of the calculated growth for the first year of life may be found in the 1928 year class from Trout Lake and in the 1926 and 1928 year classes from Muskellunge Lake. All the other year classes from these two lakes, and all year classes from Silver Lake and Clear Lake, where the samples are large enough to give reliable results show unimodal distributions for the calculated growth of the first year of life. The fact that bimodality in the first year's growth occurs only in two populations and in only one or two year classes of these populations suggests that the occurrence of the phenomenon depends on the nature of the local conditions within each lake and that these conditions vary from year to year.

The most reasonable explanation for bimodality in the first year's growth lies in the assumption that in certain years there are two hatchings rather than a single one. In early spring a period of warm weather with brilliant sunshine and no strong winds can warm the waters of the shallow littoral region to a temperature several degrees above that of the main body of the lake. At such a time the development of the eggs of the cisco would be accelerated and some might hatch. If, however, there occurred before the completion of hatching season a period of cold, windy weather the temperature of the water of the littoral region would undergo a sudden drop of several degrees.³⁰ The development of the unhatched eggs would be retarded, and their hatching might be delayed for several days or even weeks. Such a situation would explain the observed cases of bimodality in the amount of growth during the first year of life. Eggs that develop in more exposed regions of a lake or in a lake more swept by winds would be less affected by fluctuations in weather conditions.

GROWTH COMPENSATION

The phenomenon of "growth compensation"—the tendency for individuals that grow relatively slowly in the early years of life to grow relatively rapidly during the later years—has been observed by numerous investigators and in several species of fish. The only study of growth compensation in the cisco was made by Van Oosten (1929) on the Saginaw Bay herring of Lake Huron. He concluded that "the large fish of an age group were the large fish in each preceding year of life * * * but that the differences between the small and large yearlings diminished each year of age—that is, the small yearlings were rapid growers and the large yearlings slow growers." Thus he found that compensation did occur, but that it was not sufficient to overcome completely any advantage in length which a large individual might hold at the end of the first year of life.

A comparison of growth compensation in age groups with unimodal and bimodal length distributions at the end of the first year of life should yield information as to the effect of the dispersion of the length frequency in early life upon the manner of growth in later life. In the 1931 collection from Muskellunge Lake (table 58) the distribution of the calculated lengths at the end of the first year is unimodal in the II group and bimodal in the III group. Both age groups are represented by large samples (258 for the II group and 347 for the III group). For these reasons they were selected as the basis for a study of growth compensation.

Table 58 shows the frequency distributions of the calculated lengths for both age groups at the end of the first year of life. The calculated length distributions of the

³⁰ Forel (1892) pointed out that the development of high temperatures in the littoral region depends on days of great calm and brilliant sunshine, and that this warming process proceeds slowly. The negative changes in temperature proceed much more rapidly. Forel observed that with a strong south wind the temperature of the littoral waters at the port of Geneva at times dropped as much as 6° C. to 8° C. or more from one day to another.

same groups at the end of the second year of life appear in table 61. Table 62 shows the frequency distribution of the increments of growth during the second year of life. All of these data are presented graphically as percentage frequencies in figure 9.

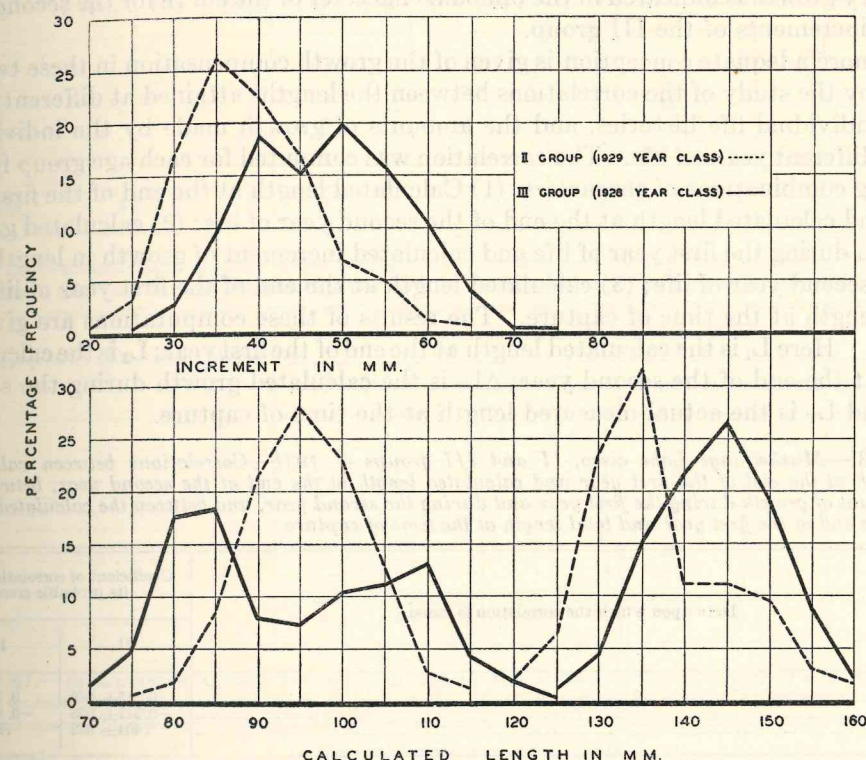


FIGURE 9.—Percentage frequency distribution of the 1931 samples of 1928 and 1929 year classes of Muskellunge Lake cisco with respect to calculated lengths at end of first year of life (below at left), the calculated lengths at end of second year of life (below at right), and calculated increments of growth during second year of life (above).

TABLE 61.—Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated length at the end of the second year of life as based on the II group and the III group

Age group	Length interval									Total number
	120-124	125-129	130-134	135-139	140-144	145-149	150-154	155-159	160-164	
II.....	5	16	61	82	28	29	25	8	4	258
III.....		4	16	53	76	92	67	31	8	347

TABLE 62.—Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated growth during the second year of life as based on the II group and the III group

Age group	Length interval												Total number
	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	
II.....	1	8	44	68	58	44	18	13	3	1			258
III.....		1	16	35	65	53	69	55	37	14	1	1	347

Examination of the data shows that during the second year of life of the III-group fish there occurred sufficient growth compensation to change the length distribution of the group from the bimodal to the unimodal condition. The existence of intense compensatory growth is indicated in the bimodal character of the curve for the second-year growth increments of the III group.

A more adequate conception is given of the growth compensation in these two age groups by the study of the correlations between the lengths attained at different times in the individual life histories, and the amounts of growth made by the individuals during different years of life. The correlation was computed for each age group for the following combinations of characters: (1) Calculated length at the end of the first year of life and calculated length at the end of the second year of life; (2) calculated growth in length during the first year of life and calculated increment of growth in length during the second year of life; (3) calculated length at the end of the first year of life and actual length at the time of capture. The results of these computations are given in table 63. Here L_1 is the calculated length at the end of the first year; L_2 is the calculated length at the end of the second year; ΔL_1 is the calculated growth during the second year; and L_T is the actual measured length at the time of capture.

TABLE 63.—*Muskellunge Lake cisco, II and III groups of 1931—Correlations between calculated length at the end of the first year and calculated length at the end of the second year, between the amount of growth during the first year and during the second year, and between the calculated length at the end of the first year and total length at the time of capture*

Data upon which the correlation is based	Coefficient of correlation and its probable error	
	II	III
L_1 and L_2	0.513±.046	0.708±.027
L_1 and ΔL_1	-0.311±.056	-0.826±.017
L_1 and L_T404±.052	.399±.045

Tables 64 to 67 show the data from which the correlations between L_1 and L_2 and between L_1 and ΔL_1 were calculated. The examination of tables 64 and 65 shows clearly that in both the II group and the III group the smaller fish at the end of the first year of life tend to be the smaller fish at the end of the second year of life, and that this tendency is the greater in the III group. Tables 66 and 67 show that in both age groups the individuals that grew least in the first year of life tend to grow most in the second, and that here again the tendency is more pronounced in the III group than in the II group.

TABLE 64.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, II group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life									Total
	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	
160 to 164.....										4
155 to 159.....										8
150 to 154.....					1	2	2	2		25
145 to 149.....					5	7	10			29
140 to 144.....					7	4	8			28
135 to 139.....					13	6	3			22
130 to 134.....					15	28	7			51
125 to 129.....					22	16	3			41
120 to 124.....					6	5				11
Total.....	1	4	22	56	72	60	33	7	3	258

TABLE 65.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, III group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life											Total	
	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124		125-129
160 to 164.....								1	1	2	3	1	8
155 to 159.....				1			4	5	10	8	2	1	31
150 to 154.....			2	4	5	5	9	16	20	4	2		67
145 to 149.....	1	3	11	18	14	7	12	11	13	2			92
140 to 144.....		1	20	22	6	10	10	5	2				76
135 to 139.....		8	19	15	3	4	2	1					53
130 to 134.....	1	4	6	4									16
125 to 129.....	1	1	2										4
Total.....	5	17	60	64	28	26	37	39	46	16	7	2	347

TABLE 66.—*Relationship between amount of growth in millimeters during the first year of life and the amount of growth during the second year of life in the Muskellunge Lake cisco, II group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life									Total
	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	
65 to 69.....					1					1
60 to 64.....					2					3
55 to 59.....					4					13
50 to 54.....					5					18
45 to 49.....					7					44
40 to 44.....					6					58
35 to 39.....					17					68
30 to 34.....					15					44
25 to 29.....					3					8
20 to 24.....					1					1
Total.....	1	4	22	56	72	60	33	7	3	258

TABLE 67.—*Relationship between amount of growth in millimeters during first year of life and amount of growth during the second year of life in the Muskellunge Lake cisco, III group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life												Total
	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	
75 to 79.....	1												1
70 to 74.....		1											1
65 to 69.....		3											14
60 to 64.....		5											37
55 to 59.....		4											55
50 to 54.....		3											69
45 to 49.....		1											53
40 to 44.....													65
35 to 39.....													35
30 to 34.....													16
25 to 29.....													1
Total.....	5	17	60	64	28	26	37	39	46	16	7	2	347

On the basis of the data that have been presented it is possible to draw the following conclusions concerning growth compensation as it is indicated in the two age groups considered here:

(1) Growth compensation occurs in both the group with a unimodal distribution of calculated lengths at the end of the first year of life and the group with a bimodal distribution of these lengths (negative correlation of L_1 and ΔL_1).

(2) Growth compensation is more intense in the group with the greater dispersion of the calculated lengths at the end of the first year of life (higher negative correlation between L_1 and ΔL_1 in the III group). The tendency toward compensation can lead to a bimodal distribution of the growth increments for the second

year, and can within a single season change the length distribution of the group from a bimodal to a unimodal condition.

(3) When the length distribution at the end of the first year of life is unimodal and the dispersion small, individual length at the end of the first year of life exerts more effect on individual length at the end of the second year of life, than the amount of growth during the first year of life exerts on the amount of growth during the second year of life. (In the II group the positive correlation of L_1 and L_2 is greater than the negative correlation between L_1 and ΔL_1 .) In the group with the greater dispersion and the bimodal distribution of lengths at the end of the first year of life the situation is reversed, that is, there is a closer connection between the amount of growth during the first year of life and the amount of growth during the second year of life than there exists between the length at the end of the first year and the length at the end of the second year. (In the III group the negative correlation between L_1 and ΔL_1 is greater than the positive correlation between L_1 and L_2 .)

(4) In spite of the growth compensation that occurs there is a tendency for the individual to hold throughout life a part of any advantage in length which it may hold at the end of the first year of existence. Compensation reduces individual advantage in length, but does not obliterate it (positive correlation in both groups between L_1 and L_T).

GROWTH RELATIONSHIPS IN THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

Throughout the preceding sections attention has been called repeatedly to the order in which the cisco populations of the four lakes arrange themselves with respect to certain characteristics such as growth rate, sex ratio, condition, and the like. In view of the apparent high degree of correspondence among certain of these orders of arrangement it is considered advisable to present the data concerning them in a summarized form, together with a brief discussion and review of the possible significance of the observed correlations. Table 68 shows that arrangement of the lakes with respect to the amount of bound carbon dioxide in their waters and to the amount of organic matter in the plankton, and also with respect to certain phases of the life history of the cisco. Although these data demonstrate a close dependence of certain phases in the life history of the cisco on the conditions of its animate and inanimate environment, as will appear in the following discussion, any attempt to describe these relationships in precise terms of cause and effect meets with serious difficulty.

TABLE 68.—Order of the 4 lakes with respect to the concentration of bound CO_2 and the abundance of organic matter in the surface plankton, and also with respect to certain phases of the life history of the cisco

Item	Lakes			
	Clear	Muskellunge	Silver	Trout
Growth in length.....	1	2	3	4
Growth in weight.....	1	3	2	4
Bound CO_2 in water.....	4	3	2	1
Density of population.....	4	2	3	1
Length of growing season.....	1	3	2	4
Sex ratio (females per 100 males).....	1	3	2	4
Organic matter in plankton.....	4	2	3	1
Condition (K).....	4	1	3	2
Average length of life.....	1	4	2	3

Before entering into the discussion of the relationship between growth rate and the environmental factors that may affect it, attention should be called to the fact that the order of the four lakes with respect to growth in length is not the same as their order with respect to growth in weight. Although the Muskellunge Lake cisco shows better growth in length than the Silver Lake cisco, its growth in weight is inferior to that of the Silver Lake population. The reason for this reversal of order lies in the very poor condition of the Muskellunge Lake fish. Weight unquestionably furnishes a better measure of increase in living matter than does length, but for the purposes of the present discussion it will probably be sufficient to consider both populations merely as intermediate between the extreme conditions represented by the Trout Lake cisco and the Clear Lake cisco.

PHYSICAL-CHEMICAL FACTORS

Certain factors may be ruled out immediately as inadequate for the observed differences in the growth rates of the four populations.

Temperature fails to account for the observed differences in growth rate. Since all four lakes are located within a short distance of each other the climatic conditions that affect each of them are essentially the same. Differences in the size and form of the various basins may lead to differences in average water temperature during the summer, but here it should be pointed out that while the cisco finds its coldest summer habitat in Trout Lake and Clear Lake, the populations of these two lakes represent the extremes in growth rate.

Oxygen conditions also fail to explain the differences in the growth rates of the four populations. Here, as was the case with temperature, Trout Lake and Clear Lake resemble each other most closely. Each possesses large masses of well oxygenated water in the hypolimnion, the favorite habitat of the cisco.

The abundance of bound CO_2 and the closely related hydrogen-ion concentration and conductivity are the only physical-chemical characteristics known to show any correlation with growth rate. Growth rate in length and the abundance of bound carbon dioxide stand in an inverse relationship to each other. It is hardly reasonable to assume that an abundance of bound CO_2 impedes growth directly or that a scarcity of bound CO_2 accelerates it. The effect of the abundance of CO_2 on growth rate is probably indirect and operative through its modification of the biological nature of the cisco's environment.

In general, the amount of bound CO_2 in a lake's waters is roughly indicative of the biological productive capacity of that lake. In view of this fact it would hardly be expected that the poorest growth of the cisco would occur in the lake with the greatest concentration of bound CO_2 . This apparently paradoxical situation is explained, however, if it is assumed that an abundance of bound CO_2 makes not only for a greater production of food organisms, but also makes for a much greater abundance of the ciscoes themselves, and that the abundance of the ciscoes in turn determines their growth rates. Such an assumption has the support of the observed fact that the cisco population is most dense in Trout Lake with the greatest amount of bound CO_2 and sparsest in Clear Lake with the least amount of bound CO_2 , while Muskellunge Lake and Silver Lake with intermediate concentration of bound CO_2 have populations of intermediate densities.

DENSITY OF POPULATION

The section on the relationship between density of population and growth rate inclined toward the opinion that differences in the severity of competition for food related to differences in the densities of the various populations are largely responsible for differences in the growth rates of the four cisco stocks. This opinion was presented as the most logical, even in the face of the facts, first that the actual existence of any competition for food in any one of the four populations remains to be demonstrated, and second that there exists a strong possibility that crowding may impede growth independently of competition for food (Willer's "Raumfaktor").

As to the causes of the observed differences in the densities of the four populations it may be seen, as was mentioned previously, that the greatest density of the cisco population occurs in the lake with the heaviest concentration of bound CO_2 (Trout Lake) while the least density occurs in the lake with the lightest concentration of bound CO_2 (Clear Lake). The positions of Silver Lake and Muskellunge Lake are reversed with respect to the concentration of bound CO_2 and the density of population, but both are intermediate to the conditions found in Trout Lake and Clear Lake.

Since it is generally held that the success or failure of a hatching of fish depends primarily on conditions that determine the survival of the young at a very early stage, it does not appear unreasonable to hold that differences, traceable to the concentration of bound CO_2 , in the amount and kind of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four populations. A study of the plankton cycle in each lake should throw light on the subject.

There does not appear to be any complete correlation between the amount of organic matter in surface samples of plankton taken during the summer and the density of the cisco populations. Although Clear Lake with the least amount of organic matter in the surface plankton has the sparsest cisco population, Trout Lake, with the densest cisco population does not have the greatest amount of organic matter in the surface plankton.

It is possible further that these differences in the densities of the cisco populations may depend on yet other factors such as the availability of suitable spawning areas or the destruction of eggs and young by predators.

Regardless of whether it is held that differences in growth rate depend directly on differences in population density or that both are dependent on yet other factors, it must be admitted that growth rate and density of population show a very close correlation.

LENGTH OF THE GROWING SEASON

In the general section under this title it was pointed out that differences in the growth rates of the four cisco populations can be explained in part by actual differences in the length of the cisco's growing season in the various lakes. The Trout Lake cisco has definitely the shortest growing season, followed by the Muskellunge Lake cisco, the Silver Lake cisco, and the Clear Lake cisco in the order named. Thus it may be seen that in the four populations the length of the growing season follows the same order as their growth rates (in weight) and the inverse order of their densities of population.

These differences in the length of the growing season cannot be accounted for on the basis of temperature and oxygen conditions for the same reasons that temperature and oxygen conditions fail to account for the differences in growth rate. (See p. 287.)

It is possible that an explanation of the differences in the lengths of the growing season may be found in the study of the plankton cycles in the four lakes. Particular attention should be given to the abundance at all times of the season, and in the strata actually inhabited by the cisco, of the plankton forms most commonly taken by that species.

A second possible explanation of the differences in the length of the cisco's growing season in the various lakes is suggested by the fact that in fishes in general the termination of the season's growth in adult fish is coincident with the onset of the development of the gonads preliminary to spawning. (The determination of the length of the growing season in the four cisco populations was based almost entirely on mature and maturing individuals.) Since the average size (weight) of the spawning individuals of the four populations follows the same order as their growth rates and the lengths of their growing season, it is suggested that the development of the gonads in small spawners may begin earlier in the season than in large spawners, and that the slowness of growth of a slow-growing population may be thereby accentuated.

PARASITIZATION

The only published data on the incidence and severity of parasitization in the cisco populations of Trout, Muskellunge, Silver, and Clear Lakes are those presented by Dr. Chancey Juday in the Bureau of Fisheries' report on Progress in Biological Inquiries 1931 (Higgins, 1932). Juday summarized the data then available as follows:

Thirty ciscoes from Silver Lake were examined for parasites, and cestodes were found in the intestines of all of them; 80 percent of them also had Acanthocephala. In Muskellunge Lake 80 percent of the ciscoes contained cestodes and 20 percent were free of visceral parasites. In Trout Lake 16 percent were negative, 82 percent had cestodes in their intestines, and 10 percent also had Acanthocephala. The ciscoes from Clear Lake, on the other hand, were 96 percent negative; only 2 specimens out of 60 examined yielded any parasites. These fish were found to be feeding almost exclusively on Daphnia, and this may be partly responsible for the very small parasite infestation. Clear Lake also has very soft water, and the snail population, as a result, is relatively small, so that the danger of parasite infestation from this source is correspondingly small.

Although the above data show that the Clear Lake cisco with the fastest growth rate has the lightest parasite infestation, the relationship between parasite infestation and growth rate in the remaining three populations is not clear. The solution of the problem concerning the relationship between growth rate and parasite infestation in the cisco awaits the examination, within each population, of the effect of individual parasitization on individual growth rate.

CONDITION

In the section that dealt with condition and the relationship between length and weight it was pointed out that the order of the four lakes with respect to the average condition of their cisco populations, from poorest to best, is: Muskellunge, Trout, Silver, Clear. While this arrangement does describe the order of the lakes with respect to condition as based on the samples taken, it is open to the criticism that because of the variation of K with length, additional samples taken in yet other years and showing different length distributions of the fish might possibly bring about a change in the arrangement. The determination of an average value of K within a population depends, first, on the manner of change of K with length and, second, on the length distribution of the fish used.

It is quite possible that the most significant phase of the study of condition in these four cisco populations does not lie in the determination of average values of K for the different stocks but lies rather in the study of the change of condition with increasing length. This is particularly true since the separation of the lakes with respect to the manner of change of K with increased length is much sharper than it is with respect to the average value of K in the entire population. The significance of the changes of K with length will become more apparent with the examination of

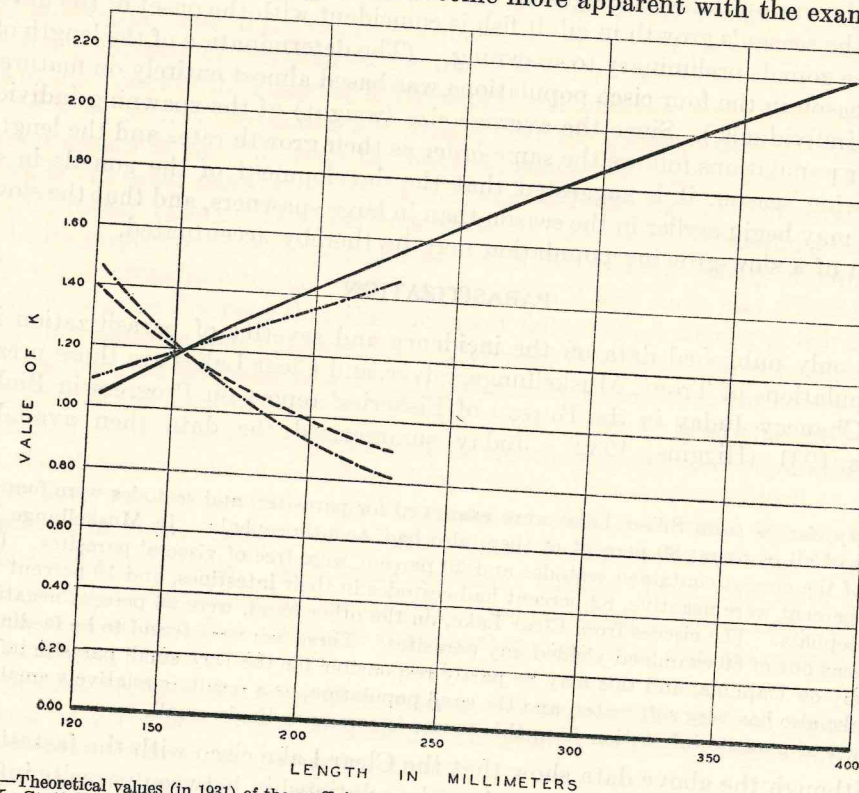


FIGURE 10.—Theoretical values (in 1931) of the coefficient of condition (K) at different lengths, calculated from equations of the type $K = C \times 10^5 L^m$. Trout Lake, ---; Muskellunge Lake, - - -; Silver Lake (females), . . .; Clear Lake (females), — · — ·.

the equations that describe K as functions of length. These equations for 1931 (the only year in which samples were taken from all four lakes) are:³¹

Muskellunge Lake:

$$K = 141.924 L^{-0.94932}$$

Trout Lake:

$$K = 38.7640 L^{-0.69245}$$

Silver Lake (females):

$$K = 0.12322 L^{0.45372}$$

Clear Lake (females):

$$K = 0.04555 L^{0.64991}$$

The theoretical values of K at different lengths, calculated from the above equations appear in table 69 and are presented graphically in figure 10.

³¹ For the purposes of this discussion one equation from each lake is sufficient. The equations for the males of Silver and Clear Lakes may be found in table 27.

TABLE 69.—Theoretical values of the coefficient of condition (K) at different body lengths, calculated from equations based on 1931 collections

Lake	Length in millimeters															
	130	140	150	160	170	180	190	200	210	220	230	250	270	290	310	330
Trout.....	1.332	1.266	1.207	1.154	1.107	1.064	1.025	0.989	0.956	0.926	0.898	-----	-----	-----	-----	-----
Muskellunge.....	1.397	1.302	1.220	1.147	1.083	1.026	0.975	0.928	0.886	0.848	0.813	-----	-----	-----	-----	-----
Silver (females).....	1.122	1.160	1.197	1.232	1.267	1.300	1.332	1.357	1.394	1.424	1.453	-----	-----	-----	-----	-----
Clear (females).....	1.077	1.131	1.182	1.233	1.283	1.331	1.379	1.426	1.471	1.517	1.561	1.648	1.733	1.815	1.895	1.974
															2.051	2.126
																2.200

The remarks, made previously (p. 246), concerning the validity of using length-weight equations for the calculation of unknown lengths or weights outside the range of the empirical data apply likewise to the calculation of unknown values of K for lengths outside the range of empirical data. However, it may be pointed out further, on purely mathematical grounds, that the K equations cannot possibly be used for the calculation of K values in very small fish, since as length approaches zero the values of K increase without limit in the equations with negative exponents and approach zero in the equations with positive exponents.

In the 1931 K equations it may be seen that the order of the four populations with respect to the value of the exponent, m , which describes the rate of change of K with change of length, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake. The differences in these rates of change are reflected in the forms of the curves of figure 10. Here it may be seen that the Muskellunge Lake cisco loses condition rapidly with increase in length. The Trout Lake cisco also loses condition with increase in length, but at a slower rate than does the Muskellunge Lake cisco. In Silver Lake the condition of the cisco improves with increase in length, although this improvement is not as rapid as it is in the Clear Lake cisco. The courses of the curves indicate further that at a length of between 150 and 160 millimeters the conditions of all four populations are closely similar.

If the above facts are examined in relation to the growth rates of the four populations it may be seen that, while the Clear Lake cisco with the most rapid growth shows the most rapid progressive improvement in condition, the Trout Lake cisco with the least rapid growth does not show the most rapid loss of condition. Although the Muskellunge Lake cisco shows better growth than the Trout Lake cisco with respect to both length and weight, the loss of condition with increase in length proceeds considerably more rapidly in the former population. This fact demonstrates at least a partial independence between the factors that determine growth rate and the factors that determine condition. Further, the fact that the factors which bring about a rapid loss of condition in one population may fail to reduce the growth rate of this population below that of a second stock with a less rapid loss of condition may be construed as a strong argument for the operation of the "space factor" in the determination of growth rate.

The data of table 68 show that the arrangement of the four lakes with respect to average condition and the rate of change of condition follows the reverse order of their arrangement with respect to the average abundance of the organic matter in the surface samples of plankton. (The greater number of these plankton samples were taken during the summer months.) Although the abundance of organic matter in surface samples of plankton may not serve as a wholly reliable index of the abundance of plankton forms most commonly taken by the ciscoes and in the strata of

water inhabited by that species, the data do show that the cisco suffers the most rapid loss of condition with increase in length and shows the poorest average condition in the lake (Muskellunge) with the most eutrophic environment, while the most rapid gain in condition and the best average condition are found in Clear Lake with the most oligotrophic environment. While it is hardly to be inferred that a mere abundance of food causes loss of condition in the cisco or that a scarcity of food makes for better condition, it is quite probable that the cisco does not thrive in the physical and chemical conditions most conducive to a large production of food organisms. The eutrophic environment of Muskellunge Lake may, for example, force the cisco to live under such undesirable conditions of temperature and dissolved oxygen that it fails to thrive even in the presence of abundant food, while in Clear Lake favorable physical and chemical conditions may make it possible for the cisco to reach the best of condition on a substantially smaller basic abundance of food.

Average longevity and condition appear to be more closely correlated than average longevity and growth, for the four populations follow exactly the same order with respect to the two first-named characteristics. Such a relationship is logical. With particular reference to the populations whose K equations show negative exponents, it appears probable that the progressive loss of condition with increase in length may bring the cisco to a point of emaciation beyond which survival is impossible. Since length is a function of age the imposition of a limit on the length that can be attained places also a limit on age. It has been pointed out previously (p. 246) that in the Trout Lake cisco the few very old individuals taken had not followed the same length-weight relationship that held for the main body of the population.

The relationship between individual condition and individual parasite infestation is not known. The Clear Lake cisco with the lightest parasite infestation of any of the four populations is the population with the best condition.

SEX RATIO

The cisco population of the four lakes follow the same order with respect to growth in weight and the average relative abundance of males. In the section on sex ratio it was pointed out that the less viable males probably suffer greater mortality under adverse conditions that produce slow growth, and hence that 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.

GENERAL REMARKS

The failure of certain of the growth relationships of the cisco to conform to generally accepted principles and theories suggests that, on the basis of our present knowledge, generalizations concerning these relationships are scarcely safe. A satisfactory understanding of the growth relationships of the cisco can be attained only after exhaustive studies into the biology of this form. Further, the great plasticity and adaptability of the cisco makes advisable the study of its biology in the greatest possible diversity of habitats.

An illustration of the dangers of making generalizations concerning the growth and biology of the cisco is offered by the examination of the relationship between

condition (K) and environmental factors. The data of this study indicate that the cisco is in the best condition in the most oligotrophic environment and in the poorest condition in the most eutrophic environment. However, the situation found in the Indian Village Lake (Indiana) shows that such a relationship cannot be considered general for this plastic species. Although the lakes of northeastern Indiana are of the extreme eutrophic type and the Indian Village Lake cisco lives under what are apparently the most undesirable conditions with respect to temperature and oxygen conditions (Scott, 1931), the Indian Village Lake cisco shows excellent growth and is in better condition than any but the Clear Lake population of this study (p. 249).

FISHES ASSOCIATED WITH THE CISCO

There is little resemblance among the fish associations of which the four cisco populations are parts. In table 70 are recorded the numbers of individuals of all species taken in the nets used for the cisco. Fish are considered to have been taken along with the cisco if they were taken in a net of any mesh set at the same time and approximately the same depth as the nets that caught ciscoes.

TABLE 70.—Numbers of individuals of other species of fish taken in the net catches along with the cisco samples

Species	Lakes			
	Trout	Muskellunge	Silver	Clear
Cisco.....	1, 197	1, 863	524	465
Perch.....		1, 543	1	5
Pike-perch.....				37
Rock bass.....		8		1
Sucker.....		130		
Lake trout.....	32			
Whitefish.....	32			
Burbot.....	1			
Smallmouth black bass.....		14		

In Trout Lake the fish taken with the cisco were all typical deep-water forms. There is no evidence that the deeper regions of the lake are invaded by individuals of the shallow-water forms. The trout were mostly large individuals that were caught and held by the teeth in small mesh nets.

The situation in Muskellunge Lake is unusual. The close association of the cisco with shallow-water forms is the result of the deficiency in oxygen that drives the ciscoes up from the lower, cooler strata of the lake.

In Silver Lake the cisco is practically isolated, at least during the late summer. The single perch taken at a depth of 14.5 meters may be considered a straggler.

In Clear Lake the pike-perch that were taken regularly along with ciscoes appear to be distributed generally throughout the region occupied by the cisco in this lake. The five perch were taken at depths between 19.5 and 24.5 meters. The rock bass was captured at a depth of 15.5 meters. Since both rock bass and perch are known to be plentiful in the shallow water of this lake their presence in the hypolimnion may be considered more or less as accidental.

In all the lakes the nature of the associations of which the ciscoes are part probably undergoes considerable change according to the time of year.

SELECTIVE ACTION OF GILL NETS

REVIEW OF PREVIOUS INVESTIGATIONS

Since the collections upon which the present investigation is based were made by means of gill nets, it is of importance to have some measure of the selective action of the nets used upon the various populations sampled. Several investigators have presented observations on the selective action of gill nets, and some of these observations have been made with specific reference to the problem of securing samples for the study of age, growth, and length distributions within a population.

Much of the published material on the selective action of gill nets has been included incidentally in growth and life history studies. Other data have been presented in routine fishery reports. Because of the generally scattered nature of these data on gill-net selectivity and because of the importance to fisheries biologists of having a more adequate idea of the reliability of the samples that they take with gill nets, the presentation of the data of this investigation on the question of gill-net selectivity will be preceded by a brief review of the literature³² on the subject.

The problem presented by the selective action of gill nets in the collection of materials for scientific investigations has been known for several decades. The Report on the Sea and Inland Fisheries of Ireland for 1902 and 1903³³; Part II—Scientific Investigations, contained in the report of the scientific adviser the statement that the investigation of herring shoals met a great difficulty in the selective action of the nets used in the commercial fishery. It was stated further, however, that the results of fishing nets of different meshes together (these experiments were made in another connection) indicated "that the selection is much less in practice than it would seem to be in theory. * * *

Delsman (1914) in his study of the age and growth of the North Sea and Zuider Zee herrings presented data to show that the selective action of the gear used in obtaining samples can exert an important effect on the nature of the results obtained from the study of those samples. He compared samples of drift nets and of seines of different sizes of mesh. From his observations he concluded:

Fänge an derselben Stelle mit Netzen verschiedener Maschenweite gemacht, werden verschieden sein und die Zusammensetzung des Fanges nach Grösse und Alter wird von der Maschenweite abhängen. Fischt man dagegen mit demselben Netz an verschiedenen Stellen * * * so werden auch die Fänge verschieden sein, und die Verschiedenheiten in ihrer Zusammensetzung werden durch die Zusammensetzung der Heringsschwärme im Meer bedingt werden.

Bjerkan (1917) disagreed with Delsman as to the great importance of selectivity of gear in determining the nature of herring samples from drift nets. From the comparison of trawl and drift-net catches he concluded that selection through the failure of drift nets to take smaller fish "cannot be very material." He pointed out further that "drift caught samples may point to the presence of rich year classes of very different ages." As to the effect of mesh size on the composition of drift net catches he stated further that "the size of mesh in the nets used affects the composition of the catches, but not to such an extent as might have been expected."

Further data on the action of drift nets were presented by Borley and Russell (1922). In connection with the study of the herring trawl fishery they measured the

³² No claims are made as to the completeness of this review; it should, however, bring together a sufficient mass of the miscellaneous data on the subject to furnish a good general conception of the nature of the problem of gill-net selectivity.

³³ Published in 1905.

catches of herring in drift nets of three sizes of mesh.³⁴ They summarized their results as follows:

According to these samples the finer-meshed nets caught the larger fish. The conclusion to be drawn is that the size distribution of the drift-net catch is probably not determined to any great extent by the selective action of the net.

Buchanan-Wollaston (1927) included with his discussion of the selective action of a trawl net certain observations as to the method of selection in drift nets. He called attention to the fact that drift nets do not capture all fish in the same manner. He pointed out that certain large individuals are retained by the maxillary barbs; some small individuals are held only because of the gill covers; while the majority are held between the gill covers and the dorsal fin. The different types of net action may lead to discontinuity in the length distribution of the catch.

Hodgson (1927) presented the analysis of data from the catch of herrings in three drift nets of different-size mesh.³⁵ Although the number of specimens was not great his results showed clearly that selective net action can lead to erroneous conclusions concerning the size and age composition of a population and also lead to inaccurate determinations of average lengths for the various age groups. Later the same author (Hodgson, 1933) presented the results of further experiments on the selective action of drift nets. These experiments were conducted with particular reference to the effect on the herring stock of the size of mesh in the drift nets employed in the commercial fishery. On the basis of two separate experiments Hodgson concluded:

that there is a very definite and subtle gradation in the length of the herrings caught by nets of even slightly different meshes, and it is also plain that the whole character of a fishery can be changed by the use of different nets.

These investigations were all concerned with a single marine fishery—the drift-net fishery for herring. The opinions of the different investigators, however, show considerable disagreement.

Of greater interest with respect to the present study are the data concerning the selective action of gill nets as they are fished in fresh water. In the following paragraphs certain of the available data with respect to the selective action of gill nets are mentioned briefly. The various investigations are treated in general in the chronological order of their appearance without any attempt at grouping according to variety or kind of fish concerned.

Järvi (1920) compared the catches of the kleine Maräne (*Coregonus albula*) taken by seine with those taken by a series of seven nets having meshes ranging from 10 to 15 millimeters (bar measurement). The length compositions of the samples from the two sources agreed well.

Järnefelt (1921) noticed that his growth curves for several species of fish showed irregularities that could be traced to the selective action of the nets that he used in obtaining his samples. Concerning these irregularities Järnefelt stated: " * * * dass es ebenso viel Senkungen der Kurve gibt wie Netze verschiedener Maschenweite benutzt werden." However, Segerstråle (1933) held that the irregularities observed by Järnefelt and others in growth curves resulted to a large extent from inaccurate methods of calculating growth from scale measurements, and that

³⁴ The sizes were 30, 31, and 33 meshes to the yard (bar measurement).

³⁵ The nets used had 35, 38, and 48 meshes to the yard (bar measurement).

irregularities in growth curves resulting from the selective action of nets are on the whole small.

Creaser (1926) in connection with his study of the growth of the sunfish (*Eupomotis gibbosus*) observed that gill nets are "particularly selective in their collecting" and advocated the use of a wide range of mesh size in gathering material for biological investigation, but included no data on the selective action of gill nets.

Koelz (1926) pointed out that in the Lake Ontario chub (*Leucichthys* spp.) fishery an increase of a quarter inch in the stretched measure of the mesh (from 2½ to 2¾ inches) reduced the number of fish taken by more than half.

Pritchard (1928) presented data on the selective action of six different sizes of mesh as that action affected the individual weight of Lake Ontario chubs (*Leucichthys* spp.). (The mesh size of his gill nets ranged from 1½ to 3 inches, stretched measure.) On the basis of his observations he stated, "The difference of one-quarter of an inch in the size of mesh may mean to the fishermen either a profitable or a 'starvation' industry." In a later paper (Pritchard, 1931) he presented the numbers of chubs of all species taken in nets of 12 different sizes of mesh (1¼ to 5 inches). Some data were included on the average lengths of the fish taken in different mesh nets. The data of Pritchard's 1931 paper agree with his earlier findings in indicating that a very small increase in the size of mesh may produce a great decrease in the number of fish taken.

Hart (1928) published detailed data on the length distribution of pike-perch and saugers of Lake Nipigon and Lake Abitibi taken in 6 different sizes of mesh ranging from 1½ to 4½ inches, stretched measure. Although Hart confined his discussion to the question of the proper legal mesh size in the commercial fishery, his data on the length distribution of the catches in different mesh size show clearly that a single size of mesh can take these spiny-rayed fish over a considerable length range. In a later paper (Hart, 1931) the same author pointed out that observed differences in the growth rate of the whitefish (*Coregonus clupeaformis*) in different parts of Lake Ontario could be explained in part by the tendency for the gill nets used in collecting samples from some localities to take only the larger fish of the younger age groups while pound-net samples were largely free from such selection. A more detailed consideration of the selective action of gill nets on whitefish appeared in Hart's (1932) study of the population statistics of Shakespeare Island Lake. (His experimental gear included 11 sizes of mesh, 1½ to 5 inches.) Hart found a correlation of 0.84 ± 0.01 between size of mesh and size of fish in Shakespeare Island Lake, while in Nipigon the correlation between the same variables was 0.51 ± 0.02 . He pointed out further that "large fish may be taken in small meshed nets although small fish are practically never taken in nets of coarse mesh."

Lechler (1929), referring to the selectivity of gill nets used in the fishery for the Reinanke (*Coregonus fera*) held that the selective action of the net is quite sharp. He stated: "Die Zusammensetzung der Fänge nach den Jahresklassen und damit die Grösse der Fische ist eine Funktion des Umfangs und direkt von der Netzmaschenweite abhängig." Further experiences caused him to modify this view slightly, for in a later publication (Lechler, 1930) he observed, "Die Fängigkeit der Netze ändert sich je nach der Beschaffenheit eines Bestandes."

Wright (1929) eliminated the younger age groups from his growth data on the rock bass (*Ambloplites rupestris*) as the selective action of the nets caused these early groups to have too high average values for length.

Haakh (1929) in his study of the age and growth of several species of fish in the Bodensee found that net selection led to inaccurate determinations of the average length of some age groups.

Wagler (1927, 1930a, 1930b, 1932, 1934) in his investigations of the coregonids of Bodensee and other north alpine lakes mentioned repeatedly the distorting effect of the selective action of the gill nets used in taking his samples for the study of age and growth. The effects of the selection were noticeable particularly in the high average lengths determined for the younger, smaller age groups and in the great variation in the relative abundance of the different year classes as determined from the various gill nets used. Wagler held that a close relationship exists between net selection and maximum girth of the individual fish (cf. Lechler, 1929). Elster (1934) in his study of the Blaufelchen (*Coregonus wartmanni*) expressed opinions similar to those of Wagler.

Van Oosten (1929b) in his discussion of the problems of the commercial fisheries of the Great Lakes pointed out the complex nature of the question of selectivity in the gill nets of the commercial fishery and included a small amount of data on the number and size of small trout (*Cristovomer namaycush*) and several species of chubs (*Leucichthys* spp.) taken in 2½- and 2¾-inch mesh nets.

In a later paper Van Oosten (1933) published a preliminary report of experimental chub net investigations conducted by the United States Bureau of Fisheries in Lake Michigan waters, 1930-32. The data presented included average catch per net, expressed in pounds and number of fish, for the lake trout and the chub in five different sizes of mesh. The meshes used were all of commercial fishery size, and varied from 2¾ to 3 inches, stretched measure. The variation in the catch of chubs in nets of different size mesh was striking. In lower Lake Michigan nets of 2¾-inch mesh caught more than twice as many chubs as did nets of 2½-inch mesh, and eight times as many as nets of 3-inch mesh.

In view of the marked disagreement that the preceding review shows to exist among some authors as to the nature and scope of the selective action of gill nets, it appears probable that each species and each locality offers its own special problem of gear selection.

The selective action of gear as size of mesh affects the amount of total catch (with respect both to numbers and weight) is particularly noteworthy. The existence of an intensive commercial fishery employing a more or less standard size mesh can, however, exaggerate the differences of catch between two different sizes of mesh. Ordinarily all the commercial gear of the same type used in a region for the capture of a species or group of species of similar size will meet approximately the same specifications particularly with reference to the size of mesh. Consequently there tends to be a great reduction in numbers in that portion of the population most liable to capture by the standard commercial gear. The withdrawal of large quantities of commercial size fish produces an abnormal condition in size distribution of the population as a whole. The introduction of nets of other, noncommercial sizes of mesh may then lead to comparisons that do not describe accurately the fishing action of the nets in question. Data based on catches from a population unaffected by commercial fishing might be expected to show somewhat less sharp selectivity than those from a population subjected to heavy fishing. It will be seen that the data of the present investigation tend to support this view.

SELECTIVE ACTION OF GILL NETS USED IN COLLECTING SAMPLES OF CISCOES FROM TROUT, MUSKELLUNGE, SILVER, AND CLEAR LAKES

In this investigation, although other phases of selectivity will be considered briefly, the study of the selective action of gill nets will be concerned primarily with the effect of selection upon the determination of growth in the various populations. The analysis will involve particularly the comparison of average lengths as determined for a single age group from samples taken in nets of different sizes of mesh. The analyses will show the basis for the elimination of certain selected groups in the computation of general growth curves (see footnote, p. 226) and will furnish a better idea of the validity of the use of gill-net samples in the study of growth. Such analysis is of especial importance here since different ranges of mesh sizes were employed in taking the different years' collections.

Attention should be called to certain criteria that are of general value in determining the reliability of gill-net samples for growth study. It may be pointed out that in general a sparse representation in a sample of a young age group whose average length is near the lower limit of effectiveness of the nets used, is a source of suspicion as to the reliability of the sample of that particular group. If this same sparsely represented group gives calculated growths that are in serious disagreement with those of the older age groups it should be eliminated from the data used for the study of growth in the population as a whole. A further check on the reliability of the material that represents a particular age group lies in the comparison of the average lengths for the group as determined from samples in different sizes of mesh and as determined from the different combinations of such samples. The examination of the length distributions of the catch of nets of different size mesh may also give an idea as to the adequacy of the sampling with respect to particular age groups.

As was mentioned in the introduction the 1928 data do not include records of gear for individual fish. For this reason the 1928 data cannot be used in the study of gill-net selectivity.

For purposes of convenience the gear used in 1928, 1930, and the early part of the 1931 season will be designated throughout this section as "old",³⁶ and the gear used during the latter part of the 1931 season and through the 1932 season will be known as "new." Descriptions of the two groups of nets were included in the section on methods.

Tables 71, 72, 74, 75, 76, and 77 show the effect of size of mesh on the determination of average size of the different age groups in the populations of Trout, Muskellunge, Silver, and Clear Lakes. Because of the generally small number of specimens upon which the average of lengths of the various age groups depend, attention must be given to the general trend of the differences that result from differences in gear rather than to the actual amount of the difference in any specific case. Since each population represents a distinct and separate problem in the study of selectivity, the data for each lake will be discussed separately.

TROUT LAKE

With the exception of a single specimen all the ciscoes collected in Trout Lake in 1930 were obtained from 1½-inch mesh nets, while the 1928 samples were probably taken in nets of 1¼-inch (trammel), 1¾-inch, 1½-inch, and perhaps a few in 1¼- and

³⁶ Although the "old" gear as fished in 1930 and in the early part of 1931 included 5 different sizes of mesh, only the 1¼-inch and 2-inch nets caught ciscoes. All collections from Clear Lake were made with the new gear. The date of change in gear was July 22, 1931.

2-inch mesh nets. In 1928 the average length of 182 ciscoes was 138 millimeters, and in 1930 the average length of 490 individuals was 150 millimeters. The smaller average size of the fish of the 1928 collection may be accounted for by the use of mesh sizes smaller than 1½ inches and by the relatively greater abundance of young fish in that year's samples. The relative abundance of the different age groups as well as the average lengths of these age groups in the samples of the 2 years may be found in table 3.

TABLE 71.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Trout Lake cisco, 1931 collection

[The first 2 rows show the average lengths of 5 age groups as based on samples taken July 22 in 1¼- and 1½-inch mesh gill nets. The third row shows the average of the 2. The fourth row shows the average lengths of the various age groups based on all fish taken in 1½-inch mesh gill nets in 1931. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
1¼ inches.....	124 (1)	134 (22)	139 (14)	147 (18)	155 (2)	140 (61)
1½ inches.....	137 (16)	137 (16)	143 (20)	149 (15)	158 (4)	145 (58)
Averages combined.....	124 (1)	135 (38)	141 (34)	148 (33)	157 (6)	-----
Average of all 1931 1½-inch samples.....	132 (1)	137 (39)	142 (159)	148 (246)	156 (77)	147 (522)

A single set of the "new" gear lifted July 22, 1931, provides the only data for Trout Lake for the comparison of growth as based on samples taken in nets with different size mesh. These data appear in table 71. In the first row appear the average lengths for the various age groups as based on fish taken in the 1¼-inch mesh net. The second row gives the same information for the sample from the 1½-inch mesh net. It will be seen that while the average length of all ciscoes taken in the 1½-inch mesh net was 5 millimeters greater than that of the ciscoes from the 1¼-inch mesh net, the differences between samples of the same age group varied from 2 to 4 millimeters and averaged only about 3 millimeters. The third row shows the average lengths of the different age groups as based on the combination of the July 22 samples taken in the 1¼- and 1½-inch mesh nets while the bottom row shows for comparison the average lengths of the various age groups as based on all the ciscoes taken in Trout Lake in the 1931 season in 1½-inch mesh nets. It may be seen that with the exception of the I group the averages based on the 1½-inch mesh net samples for the entire season differ but little from those based on the combined catches from 1¼- and 1½-inch mesh nets. While the necessity for the elimination of the I group from the Trout Lake growth data is at once apparent, the problem presented by the II group requires further consideration. In spite of the rather close agreement between the average length of the II-group fish as determined from samples from nets of 1¼- and 1½-inch mesh, the sparse representation of this age group in both the 1930 and 1931 collections (table 3) throws suspicion on the reliability of the samples. This suspicion is supported by the high calculated lengths at the end of the first and second years of life as based on both the 1930 and 1931 II groups. Consequently both of the groups were eliminated from the Trout Lake growth data. The II group of 1928, for which year no individual net records are available, was, however, retained, first because of its abundant representation in that year's collection, second because of the good agreement between its calculated growth and the corresponding calculated growth both of older age groups of the same year's collection and of samples of the same (1926) year class taken in the later years, 1930 and 1931, and finally because of the

knowledge that smaller mesh sizes were used in 1928 than in 1930 and the early part of 1931.

The relationship of net size to fish size (new nets, 1931) in the Trout Lake cisco is shown in figure 11.

MUSKELLUNGE LAKE

The old gear was used in the collection of ciscoes from Muskellunge Lake in 1928, 1930, and 1931. In the last 2 years all the fish were taken in the $1\frac{1}{2}$ -inch mesh net. In 1928 the gear used included the following sizes of mesh: $1\frac{1}{8}$ -, $1\frac{1}{2}$ -, $1\frac{3}{4}$ -, and 2-inch. The 2-inch mesh was probably not effective. Data on the average lengths of the various age groups in these years' collections will be found in table 4. In 1932

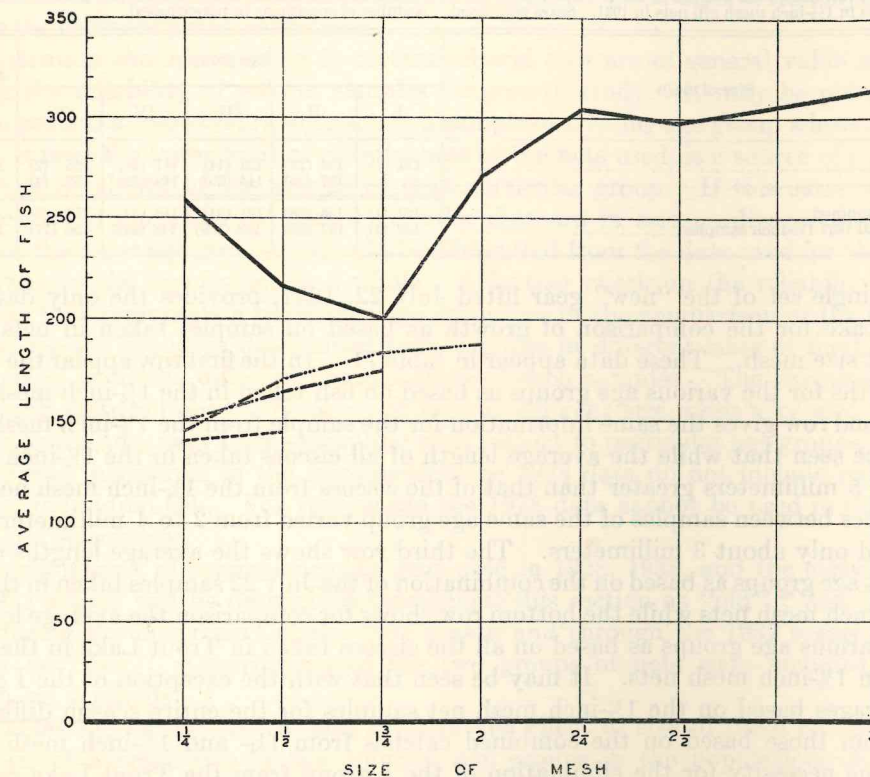


FIGURE 11.—Relationship between size of mesh of gill nets (stretched measure, in inches) and the average standard length in millimeters of the ciscoes taken. Trout Lake, ---; Muskellunge Lake, —; Silver Lake,; Clear Lake, —.

all the specimens were taken in three ($1\frac{1}{4}$ -, $1\frac{1}{2}$ -, and $1\frac{3}{4}$ -inch) of the seven sizes of mesh used in the new gear.

The 1932 material provides the only data for the study of the effect of mesh size on the average size of fish taken and for the comparison of the average lengths of the various age groups as based on samples from nets of different sizes of mesh. Scale examinations were made for 201 specimens of the 1932 collection, but ages could be estimated for only 189 of this number. The results of these determinations appear in table 72.³⁷ The table shows considerable differences between the nets of

³⁷ These data represent all the fish taken in the $1\frac{3}{4}$ -inch mesh net in 1932 and lifts of the $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets on July 28, 29, and 30, and Aug. 3, 1932. The numerical representations of the $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets are comparable, while that for the $1\frac{3}{4}$ -inch net is by comparison too high. This high representation of the $1\frac{3}{4}$ -inch net samples has probably caused the grand average length for the IV group to be too high, but it had little effect on the grand average length for the III group.

different mesh size both in the average size of the fish and in the relative abundance of the different age groups.³⁸ Selectivity according to length appears to be greater in the Muskellunge Lake cisco, where the $1\frac{1}{2}$ -inch mesh net caught fish 14 millimeters longer than the $1\frac{1}{4}$ -inch mesh sample, than in the Trout Lake cisco (table 71) where the fish from the $1\frac{1}{2}$ -inch mesh net were only 5 millimeters longer than those from the $1\frac{1}{4}$ -inch mesh net. It will be noticed further that nets of the same size mesh caught larger fish in Muskellunge Lake than in Trout Lake (fig. 11).

TABLE 72.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Muskellunge Lake cisco, 1932 collection
[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
$1\frac{1}{4}$ inches.....	137 (12)	152 (7)	159 (11)	168 (3)	-----	150 (33)
$1\frac{1}{2}$ inches.....	150 (3)	158 (12)	162 (59)	168 (59)	172 (1)	164 (150)
$1\frac{3}{4}$ inches.....	-----	166 (5)	177 (12)	-----	-----	174 (18)
Average.....	139 (15)	156 (24)	162 (75)	170 (74)	172 (1)	-----

The question of the reliability of the 1930 and 1931 collections is largely a question of the reliability of samples from $1\frac{1}{2}$ -inch mesh nets, for the collections of these 2 years were taken in nets of this size mesh. The 1928 samples may be considered as reliable as the 1932 samples. The data of table 72 show that in spite of the selection that does occur the $1\frac{1}{2}$ -inch mesh net samples, with the exception of the I group, give averages for the lengths of the different age groups that differ insignificantly from the corresponding averages based on the catch of nets of three different sizes of mesh. It is, therefore, a safe conclusion that with the elimination of the I groups the length data obtained from $1\frac{1}{2}$ -inch nets in the preceding seasons are accurate within the range of a very few millimeters.

TABLE 73.—Length frequencies of Muskellunge Lake ciscoes taken in 1932 in nets of different mesh size
[Sexes combined. The frequencies represent 18 lifts for the $1\frac{1}{4}$ -inch mesh net, 38 for the $1\frac{1}{2}$ -inch mesh net, and 37 for the $1\frac{3}{4}$ -inch mesh net]

Length	$1\frac{1}{4}$ -inch net	$1\frac{1}{2}$ -inch net	$1\frac{3}{4}$ -inch net	Total	Length	$1\frac{1}{4}$ -inch net	$1\frac{1}{2}$ -inch net	$1\frac{3}{4}$ -inch net	Total
185 to 189.....	-----	2	1	3	145 to 149.....	18	48	-----	66
180 to 184.....	-----	6	-----	6	140 to 144.....	24	20	-----	44
175 to 179.....	-----	27	3	30	135 to 139.....	40	4	-----	44
170 to 174.....	-----	102	4	106	130 to 134.....	7	-----	-----	7
165 to 169.....	2	157	2	161	Total.....	154	813	18	985
160 to 164.....	13	186	1	200	Average length..	146	160	174	-----
155 to 159.....	24	170	1	195					
150 to 154.....	21	91	-----	112					

The above conclusion is supported by the examination of the length frequencies of the total catch of Muskellunge Lake ciscoes in each mesh size in the entire 1932 season (table 73). In the length frequencies of the $1\frac{1}{4}$ -inch net samples there occurs at the 145 to 149 millimeter interval a depression that marks the separation of the I

³⁸ It was pointed out previously (p. 219), that because of slow growth in the later years and the common occurrence of accessory annuli the separation of the later age groups above the II group in the 1932 Muskellunge Lake samples was difficult. As a consequence, the average lengths listed for the III-group and the IV-group samples may be slightly in error. Any error that exists should not, however, impair greatly the general usefulness of the data for the purpose of studying the effect of net selection on the determination of the average lengths of age groups.

group from fish of greater age. Since the bulk of the II-group fish must lie above this depression it can be seen that their length distribution lies well within the range of efficiency of the 1½-inch mesh net. The fish taken in the 1¼-inch net are so few in number that they would have little effect in the determination of growth.

SILVER LAKE

The "old" gear was used in the collection of all the 1928 and 1930 samples of ciscoes from Silver Lake and for the first sample taken in 1931 (July 17). A gang of the "new" nets was used in taking the only other sample of this year in this lake (Aug. 22, 1931). In the sets of the old gear in 1930 and 1931 ciscoes were taken in 1½- and 2-inch mesh nets only; in 1928 they were probably taken in the 1½- and 1¼-inch meshes also. In the new gear they occurred in the 1¼-, 1½-, 1¾-, and 2-inch mesh nets.

Table 74 shows the average length of fish taken in different mesh sizes and the effect of net selectivity on the determination of the average length of the various age groups of the 1930 collection (5 lifts of 1½-inch nets, 3 of 2-inch nets) while table 75 gives similar information for the 2 lifts made in 1931.

TABLE 74.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1930 collection

[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	II	III	IV	V	VI	
1½ inches	173 (7)	178 (16)	182 (34)	190 (4)	198 (1)	186 (66)
2 inches	186 (9)	188 (24)	193 (20)	196 (2)		190 (64)
Average	173 (7)	181 (25)	183 (58)	193 (25)	197 (3)	

TABLE 75.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1931 collection

[The data in the upper part of the table are based on a lift of the "old" nets, July 17. The data in the lower part are based on a lift of the "new" gear, Aug. 22. The grand average for the year includes a number of preserved fish for which no net records were available. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group							Average length
	I	II	III	IV	V	VI	VII	
1½ inches	143 (6)	168 (5)	174 (3)	173 (3)				163 (18)
2 inches			189 (3)	187 (5)	192 (14)	198 (5)		191 (26)
Average	143 (6)	168 (5)	182 (6)	182 (8)	192 (14)	198 (5)		
1¼ inches	141 (51)	172 (3)	175 (3)	172 (1)	195 (2)			146 (60)
1½ inches	146 (6)	170 (6)	176 (4)	173 (6)	187 (7)			171 (30)
1¾ inches		174 (2)	178 (22)	182 (25)	186 (23)	193 (4)		183 (83)
2 inches			174 (1)	184 (12)	190 (18)	192 (2)	201 (1)	188 (37)
Average	142 (57)	171 (11)	177 (30)	181 (44)	188 (50)	193 (6)	201 (1)	
Grand average for 1931	142 (66)	171 (19)	177 (61)	183 (102)	188 (108)	194 (21)	201 (1)	

The data in tables 74 and 75 show rather large differences in the average size of fish taken in nets of different sizes of mesh. Although the fish taken in the 2-inch-mesh net of the old gear in 1930 were only 4 millimeters longer than those taken in the 1½-inch net, the 1931 samples taken in the same gear showed a difference of 28 millimeters, while the 2-inch-mesh net fish of the 1931 collection in the new gear had an average length 17 millimeters above the average for those from the 1½-inch net. A comparison with the Trout Lake and Muskellunge Lake data (tables 71 and 72, fig. 11) shows that the selection of the nets is sharper in the Silver Lake cisco than

in either of the former populations. The difference in average length between fish taken in 1¼- and 1½-inch-mesh nets was for example 5 millimeters in Trout Lake, 14 millimeters in Muskellunge Lake, and 25 millimeters in Silver Lake. Further, the difference in average length between fish taken in 1½- and 1¼-inch-mesh nets in Muskellunge Lake was 10 millimeters while in the Silver Lake cisco this difference was 12 millimeters.

Tables 74 and 75 show also that the average length for a particular age group varies considerably in samples taken by nets of different size mesh. Although certain irregularities occur (as might be expected from the small size of the samples) there is a general tendency for the samples from larger mesh nets to show distinctly higher average lengths for a given age group than do the samples from nets of smaller mesh. Further examination shows, however, that this tendency does not in general affect the validity of the averages of age groups based on the combination of the samples of several nets.

In the analysis of the data of tables 74 and 75 to establish the validity of the growth data for the Silver Lake cisco, it should be pointed out first that all ages above the II group in the 1931 sample taken in the new nets must be considered to have adequate representation throughout their entire length range. This is apparent from the fact that these older age groups are relatively scarce in the 1¼-inch-net catch, while at the other extreme a 2¼-inch-mesh net that was fished in the string failed to take any ciscoes at all. Since these average lengths of the older age groups from the new net sample can be considered reliable they can be used as a basis for the estimation of the reliability of the corresponding average lengths as determined from the old net samples. The fact that the average lengths for corresponding age groups of the 1930 and 1931 old net collections resemble each other on the whole more than either of them resembles the average lengths based on the 1931 new net collection suggests that the addition of the 1¼- and 1½-inch nets may have increased the reliability of the Silver Lake samples. The differences between the corresponding average lengths of the older age groups of the old and new net samples are not, however, of sufficient magnitude to invalidate the use of the earlier materials collected by the old gear.

The II-group samples present a more difficult problem. The general scarcity of II-group individuals in the collections of the old gear would indicate that its length range may lie just below the range of efficiency of the 1½-inch net, even though this size mesh was very efficient in Trout and Muskellunge Lakes in the taking of fish whose lengths were well below the observed average length (about 170 millimeters) for the Silver Lake II group. The 1931 sample with the new gear shows, however, that it is very unlikely that the Silver Lake II group has suffered serious selection by gear, as that selection affects average length, in any of the samples. The scarcity of the II-group fish in this sample taken in the new gear must be considered to show that this group in 1931 actually was less abundant than the neighboring age groups, for there is no reason to hold that the same nets that took 57 I-group and 30 III-group fish should fail to take II-group individuals in equal numbers provided they were equally abundant in the population. These facts together with the good agreement between the average lengths of the II-group samples as based on old and new gear samples make the retention of the II-group fish in the growth data advisable.

Since there is no means of demonstrating the reliability of any of the I-group samples they must be considered, at the best, questionable. They were accordingly eliminated from the growth data.

CLEAR LAKE

All Clear Lake specimens were collected with the "new" nets. Tables 76 and 77 show the average lengths of the different age groups according to the gear by which they were captured. Because of differences in growth rate the sexes are treated separately. Table 78 and figure 11 present the length frequencies and the average length of the catch according to mesh size for the total 1931 and 1932 catch of ciscoes from Clear Lake. The Clear Lake data differ from those of the three populations just considered in two important respects. First, the relationship that increase in size of mesh is correlated with an increase in the average size of the fish taken does not hold for Clear Lake as it did in the other three lakes; while the differences in the average size of the fish taken in different meshes are great, the larger mesh does not always take the larger fish (table 78, fig. 11). Second, in Clear Lake, fish were taken in all seven of the sizes of mesh used, and were most abundant in nets that were totally ineffective in all the other three populations, that is, nets whose mesh size was greater than 2 inches. The circumstance that the largest mesh (3 inches) took the greatest number of fish indicates that in making these collections it would have been desirable to use additional nets of mesh size greater than 3 inches. There is, however, reason to believe that the selection resulting from failure to fish with larger mesh nets affects chiefly the relative abundance of the larger fish in the sample. The increase in size of mesh from 2¼ to 3 inches had little effect on the average length of the individuals captured. If this trend were to continue, nets of a mesh size greater than 3 inches would be expected to add to the number of large fish without producing any important upward extension of the size range of the sample.

TABLE 76.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931–32 collections

[(Males) Number of specimens in parentheses]

Size of mesh	Age group									Average length
	I	II	III	IV	V	VI	VII	VIII	IX	
1½ inches.....	173 (12)	236 (3)	254 (1)	311 (1)	-----	-----	336 (3)	-----	-----	212 (16)
1¾ inches.....	176 (24)	245 (3)	291 (4)	-----	307 (3)	310 (1)	-----	341 (1)	-----	185 (28)
2 inches.....	190 (2)	250 (12)	286 (5)	314 (4)	328 (4)	326 (2)	333 (5)	347 (3)	-----	275 (14)
2¼ inches.....	-----	256 (25)	289 (12)	319 (6)	-----	328 (2)	329 (1)	334 (2)	355 (1)	296 (35)
2½ inches.....	-----	267 (5)	291 (18)	324 (4)	338 (2)	324 (3)	334 (6)	344 (4)	-----	281 (49)
3 inches.....	-----	-----	-----	-----	-----	-----	-----	-----	-----	307 (42)
Average.....	176 (38)	254 (48)	289 (40)	318 (15)	323 (9)	324 (8)	334 (15)	343 (10)	355 (1)	-----

TABLE 77.—Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931–32 collections

[(Females) Number of specimens in parentheses]

Size of mesh	Age group											Average length
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
1¼ inches.....	155 (1)	-----	-----	-----	-----	-----	336 (1)	-----	-----	-----	-----	246 (2)
1½ inches.....	179 (5)	-----	-----	-----	-----	-----	350 (1)	351 (1)	364 (1)	-----	-----	245 (8)
1¾ inches.....	180 (12)	279 (1)	-----	-----	-----	-----	356 (3)	357 (1)	-----	-----	-----	227 (17)
2 inches.....	186 (7)	263 (7)	301 (1)	325 (1)	338 (1)	-----	336 (1)	360 (3)	376 (1)	-----	-----	268 (22)
2¼ inches.....	201 (1)	259 (4)	300 (9)	323 (3)	-----	371 (1)	351 (9)	360 (2)	-----	-----	-----	316 (29)
2½ inches.....	-----	265 (14)	308 (14)	332 (6)	335 (3)	342 (4)	357 (6)	351 (7)	-----	-----	378 (1)	315 (54)
3 inches.....	-----	260 (14)	310 (15)	332 (8)	347 (4)	334 (4)	350 (11)	358 (7)	352 (1)	379 (1)	-----	319 (65)
Average.....	181 (26)	263 (40)	307 (39)	330 (17)	341 (8)	342 (9)	352 (30)	355 (22)	360 (3)	372 (2)	378 (1)	-----

AGE AND GROWTH OF THE CISCO

TABLE 78.—Length frequencies of Clear Lake ciscoes taken in nets of different mesh size
[The 1931 and 1932 collections and the sexes are combined]

Length	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	Total
150 to 159.....	1	-----	-----	-----	-----	-----	-----	1
160 to 169.....	-----	4	6	-----	-----	-----	-----	10
170 to 179.....	-----	10	17	3	-----	-----	-----	30
180 to 189.....	-----	3	12	-----	-----	-----	-----	15
190 to 199.....	-----	-----	-----	2	-----	-----	-----	2
200 to 209.....	-----	-----	1	1	1	-----	-----	3
210 to 219.....	-----	-----	-----	-----	-----	-----	-----	1
220 to 229.....	-----	-----	-----	-----	-----	-----	-----	1
230 to 239.....	-----	-----	-----	2	3	-----	-----	5
240 to 249.....	-----	-----	2	-----	1	-----	-----	3
250 to 259.....	-----	-----	-----	1	7	8	-----	16
260 to 269.....	-----	-----	-----	-----	5	12	8	32
270 to 279.....	-----	-----	-----	2	11	-----	-----	26
280 to 289.....	-----	-----	-----	3	9	4	-----	17
290 to 299.....	1	-----	-----	2	4	7	-----	16
300 to 309.....	-----	-----	-----	-----	8	10	-----	22
310 to 319.....	-----	1	-----	2	6	6	-----	22
320 to 329.....	-----	-----	-----	3	7	13	-----	33
330 to 339.....	-----	-----	-----	2	6	11	-----	26
340 to 349.....	1	2	-----	2	10	12	-----	30
350 to 359.....	-----	1	1	1	3	6	-----	29
360 to 369.....	-----	2	-----	2	5	1	-----	25
370 to 379.....	-----	1	1	-----	2	2	-----	13
380 to 389.....	-----	-----	-----	1	-----	1	-----	2
Total.....	3	24	44	35	64	103	108	382
Average length.....	259	217	201	271	306	299	315	-----

The Clear Lake samples with the exception of the I groups do not show as close dependence between the determination of the average length of individual age groups and the size of mesh by which the sample was taken (tables 76 and 77) as was observed in the other three populations. The proof of the reliability of the Clear Lake growth data must be based, therefore, on a demonstration that the population was adequately sampled throughout its length range rather than on a comparison of the average lengths of age groups as determined from samples from nets of different mesh size. It was pointed out in the preceding paragraph that the sampling of the larger fish was probably adequate. The scarcity of fish in the 1¼-inch net can be taken to show that the younger age groups were also adequately sampled. Accordingly, no age groups were eliminated from the Clear Lake samples.

RELATIVE ABUNDANCE OF AGE GROUPS IN GILL NET SAMPLES

The examination of tables 71, 72, 74, 75, 76, and 77 shows that on the whole the selectivity of nets is much more sharp in its effect on the number of fish in a given age group than in its effect on the determination of the average length of that age group. The following examples will illustrate this point. In Muskellunge Lake (table 72) the average lengths of the III-group fish in the 1¼- and 1½-inch-mesh nets were 159 millimeters and 162 millimeters, respectively; however, the 1¼-inch net took only 11 fish of this age group while the 1½-inch net took 59. In Silver Lake (table 75, data on lift of new nets) the III-group sample of the 1½-inch mesh had an average length only 2 millimeters less than the III-group sample from the 1¼-inch net, but was nevertheless represented by only 4 fish as compared with the 22 fish from the 1¼-inch-mesh net. In the same day's collection the V-group samples from the same two sizes of mesh had practically identical average lengths, but were more than three times as numerous in the 1¼-inch-mesh net as in the 1½-inch net. In Clear Lake (tables 76 and 77) the fish of the older age groups were more abundant in the samples of the 2½- and 3-inch-mesh nets, but the average lengths of these older age groups as determined from 2½- and

3-inch-net samples failed to be consistently higher than the average lengths determined for the same age groups from samples that were taken in smaller meshes.

From the above examples it may be concluded that selection by numbers is much sharper than selection by length. Apparently nets of different mesh size, which in their operation upon a population take samples that disagree only slightly as to average length, may take their samples with unequal degrees of facility, with the result that while their catches agree closely in average length they may differ markedly as to the actual number of fish taken. Table 78 (catch of $2\frac{1}{4}$ -, $2\frac{1}{2}$ -, and 3-inch nets) shows such a situation. If small differences in the sizes of mesh are accompanied by large differences in the number of fish captured from a certain size range, then small differences in the average sizes of different groups of fish may be expected to produce large differences in their numerical abundance in the catch of a particular size mesh.

From the above conclusions it can be seen that a series of nets that may take quite reliable samples of particular age groups, as average length is concerned, may at the same time fail to capture the members of these age groups in numbers corresponding to their actual relative abundance in the population of which they are part. Consequently gill-net samples must be employed with extreme caution in the study of the relative abundance of age groups and year classes.

GENERAL CONCLUSIONS

If the collections from the four lakes are considered as a whole it may be stated that the action of a gill net of specified mesh is predictable only with reference to the specific nature of the population to be sampled. The action of a net of specified mesh depends first upon the range of length and abundance of the fish within the population and second upon those morphological characteristics that determine in what manner the fish is held captive. A demonstration of the reliability of a sample obtained by use of gill nets from one population does not indicate that the same gear will obtain an equally reliable sample from a second, different population.

On the question of the use of gill-net samples for growth studies it was demonstrated that the analysis of growth data with respect to size of mesh of the gear in which samples are taken aids in the detection of age groups whose appearance in the sample is by reason of selection not representative. These age groups should be eliminated completely from the data. Such selected age groups were detected in three of the four populations considered here. It was demonstrated further that if these selected groups are eliminated the remaining growth data can be considered accurate and trustworthy within very narrow limits. No such high degree of reliability can be claimed for gill-net samples in the study of the relative abundance of the different age groups.

SUMMARY

1. This study of the growth of the cisco was based on the determination of age of 3,882 specimens and the calculation of growth from scale measurements of 3,694 specimens. The data for Trout, Muskellunge, Silver, and Clear Lakes are presented in the general paper while the smaller samples from Allequash and Tomahawk Lakes are treated separately in an appendix.

2. It was assumed that Van Oosten's (1929) demonstration of the validity of the scale method in *Leucichthys artedii* can be considered to apply to the four cisco popu-

lations of the present investigation. The consistent results obtained appear to justify the assumption.

3. The calculation of growth from scale measurements was based on the assumption that body length and scale diameter show a constant ratio at all lengths beyond that at which the first annulus is laid down. In the Silver Lake cisco alone were there any discrepancies between growth as calculated from fish of different age and as determined empirically that might throw doubt on the validity of the assumption.

4. It was demonstrated that Lee's phenomenon in the Silver Lake cisco does not depend on changing body-scale relationships with increase in length and age, but rather that the growth discrepancies are reflected in the actual scale measurements upon which the calculated growths were based.

5. Among the suggestions for the explanation of Lee's phenomenon in the Silver Lake cisco were: (1) Selection by gear, (2) selection due to dissimilar distribution within the lake of the various elements of the population, and (3) selection due to differential mortality correlated with individual growth rate (greater mortality among individuals with more rapid growth).

6. The four populations (Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake ciscoes) show wide differences in the amount and rate of growth both in length and weight. Their order with respect to growth rate in length, from minimum to maximum, is: Trout Lake, Silver Lake, Muskellunge Lake, Clear Lake; the order with respect to growth in weight is: Trout Lake, Muskellunge Lake, Silver Lake, Clear Lake.

7. On the basis of data on the growth of the cisco in this and other publications a "cisco-type" of growth was described.

8. On the whole the high degree of overlap of the length distributions of consecutive age groups of the cisco makes length alone a poor index of age.

9. Because of individual variation in growth rate the largest fish within a population is frequently not the oldest.

10. Condition was described in terms of the quantity K in the equation, $W=K \times 10^{-5} L^3$ (W =weight in grams; L =length in millimeters). It was pointed out that coefficients of condition calculated from the cube relationship describe relative heaviness independently of the general length-weight relationship, and are more satisfactory measures of condition than the quantity C in the equation $W=CL^n$ where the value of n is determined empirically.

11. The four cisco populations show wide differences with respect both to average condition and the manner of change of condition with change in length. The Muskellunge Lake cisco and the Trout Lake cisco show a loss of condition with increase in length (the rate of loss of condition is the more rapid in the former population). The Silver Lake cisco and the Clear Lake cisco, on the other hand, show improvement of condition with increase in length (the rate of improvement in condition is the greater in the Clear Lake cisco). The order of the four lakes with respect to the average condition of the fish in the samples, from minimum to maximum, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake.

12. In all four populations the relationship between length and weight may be described over certain length intervals by equations of the type, $W=CL^n$, where W =weight, L =length, and C =a constant. In some of the populations, at least, these equations cannot be extended to lengths outside the range of the empirical data.

13. The approximate date at which the season's growth of the cisco is completed in each of the lakes is: Trout Lake, end of July; Muskellunge Lake, late August; Silver Lake, early September; Clear Lake, late September or early October. Growth probably begins in all four populations shortly after the disappearance of the ice at about the 1st of May. The data show that the length of the cisco's growing season depends on the local conditions within each lake and not on the climatic conditions that are approximately the same for all four lakes.

14. The bathymetric distribution of the cisco in middle and late summer is highly sensitive to conditions of temperature and dissolved oxygen concentration. A knowledge of the vertical distribution of the cisco is important in the comparison of the densities of the populations of different lakes.

15. The order of the four lakes with respect to the density of their cisco populations, from the minimum to the maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake.

16. The large differences observed in the relative abundance of the various year classes show that the degree of success of the hatch of the cisco in different calendar years is subject to a wide range of variation. Since the years that saw relatively successful or unsuccessful hatches of the cisco are not the same in different lakes, it must be concluded that the relative abundance of a particular year class depends (as does the length of the growing season) on the local conditions within each individual lake, and not on general climatic conditions that would affect all lakes in the same manner.

17. In the Clear Lake cisco sexual maturity appears to be general at the end of the second year of life. In the other populations the cisco is known to be mature at the end of the third year of life, while some, at least, mature in the second year.

18. The order of the four lakes with respect to the sexratio of the cisco populations (expressed as the number of females per 100 males), from minimum to maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake. The differences among the populations with respect to the sex ratio depend on differences in the differential rates of mortality of the two sexes.

19. The available data indicate a close connection between certain phases of the life history of the cisco and the nature of its animate and inanimate environment.

20. The order of the four lakes with respect to the rate of growth of their cisco populations (in weight) is the same as their order with respect to the length of the cisco's growing season, and the reverse of their order with respect to the density of their cisco populations.

21. The observed differences in the length of the cisco's growing season in different lakes cannot account entirely for the observed differences in growth rate, but probably serve only to accentuate differences that already exist.

22. Suggested explanations of differences in the length of the cisco's growing season in different lakes were: (1) That they may depend on differences from lake to lake in the nature of the plankton cycle, and (2) that the smaller spawners of slow-growing populations may begin the development of the gonads, preliminary to autumn spawning, earlier in the season than do the larger spawners of the rapidly growing populations. (The four lakes follow the same order with respect to growth rate, length of the growing season, and the average size of mature fish.)

23. The correlation between density of population and growth rate may depend on differences in the severity of the competition for food, or upon the operation of a

"space-factor", whereby crowding alone impedes growth independently of the abundance of food.

24. Since, with the exception of a reversal of the positions of the closely similar Muskellunge Lake and Silver Lake populations, the four lakes arrange themselves in the same order with respect to the density of their cisco populations and with respect to the concentration of bound CO_2 in their waters, it was suggested that differences (traceable to the concentration of bound CO_2) in the kind and abundance of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four cisco populations.

25. Although the relationship between parasite infestation and growth rate has not been thoroughly investigated in the cisco it is known that the Clear Lake cisco, which has by far the best growth of any of the four populations, is practically free of parasites (96 percent negative), while the slower-growing populations from Silver, Muskellunge, and Trout Lakes have a heavy infestation of intestinal parasites (80 percent, or more, positive).

26. The best growth of the cisco occurs in Clear Lake with the smallest amount of organic matter in the surface plankton, but Muskellunge Lake, with the greatest amount of organic matter in the surface plankton does not have the slowest-growing cisco population.

27. The order of the four lakes with respect to the value of the sex ratio (females per 100 males) is the reverse of their order with respect to the rate of growth (in weight). It was suggested that the same factors that determine the rates of growth may cause the differential mortality rate of the less viable males to be greater in the slower-growing populations.

28. The Clear Lake cisco with the most rapid growth is in the best average condition (highest average value of K) and shows the most rapid improvement of condition with increase in length, but the Muskellunge Lake cisco with the poorest average condition and the most rapid loss of condition with increase in length is not the population with the slowest growth.

29. The at least partial independence of the factors that determine growth rate and the factors that determine condition may be construed as a strong argument for the operation of the "space-factor" in the determination of growth rate.

30. The order of the four lakes with respect to the average condition of their cisco populations and the rate of change of condition with increase in length is the reverse of their order with respect to the abundance of organic matter in the surface plankton. Thus it appears that the poorest condition is found in the most eutrophic environment and the best condition in the most oligotrophic environment.

31. Longevity and condition appear to be correlated. The average life span of the cisco is shortest in Muskellunge Lake where the average condition (K) is poorest and increase in length is accompanied by a rapid loss of condition, and the longest in Clear Lake where the average condition is best and condition improves as length increases.

32. In a general review and summary of the growth relationships of the cisco, it was brought out that some of these relationships fail to conform to generally accepted theories. The need was mentioned for a broader knowledge of the biology of the cisco based on observations in a great diversity of habitats. Attention was called to the danger of premature generalizations concerning the growth relationships and the biology of this very plastic species.

33. In each cisco population the amount of growth made by fish in the same year of life but in different calendar years was found to vary considerably. There is no apparent correlation between these variations in the amount of growth in different calendar years and annual variations in the average air temperature during the growing season. There is some indication that annual fluctuations in the density of each individual population may affect the amount of growth made in different calendar years, but with the possible exception of Clear Lake the data in support of such a relationship are not convincing.

34. The 1928 year class of Trout Lake and the 1926 and 1928 year classes of Muskellunge Lake show a bimodal distribution of the calculated lengths at the end of the first year of life. It was suggested that the reason for these bimodal distributions lies in exceptional weather conditions that bring about two hatchings in the spring. However, the effectiveness of weather conditions in bringing about two hatchings appears to depend on local conditions within each lake.

35. The 1928 year class in Muskellunge Lake which has a bimodal distribution of the calculated lengths at the end of the first year of life, and the 1929 Muskellunge Lake year class, which has an unimodal distribution of the calculated lengths at the end of the first year of life, were used as the basis of a study of the effect of the distribution of lengths at an early stage in the life history on the phenomenon of growth compensation in later years. It was found that growth compensation is much more intense in the group with the greater dispersion of the length distribution at the end of the first growing season. In both groups the larger fish at the end of the first year of life tend to be the larger fish at the end of the second year of life and at the time of capture in the third or fourth summer. Growth compensation in later years reduces the advantage of the large first year fish but fails to eliminate it completely.

36. The fish associations of which the ciscoes are part vary from lake to lake. In midsummer the cisco is taken in Trout Lake only with the typical deep water forms, the whitefish, the lake trout, and the burbot; in Muskellunge Lake large numbers of perch and other shallow-water fish are taken with the cisco; in Silver Lake the cisco spends the summer in practical isolation; and in Clear Lake the pike-perch is relatively abundant in the strata inhabited by the cisco.

37. Because of the scattered nature of the available published data, a review was made of earlier investigations concerning the selective action of gill nets.

38. The examination of the size and age composition of the gill-net samples showed that the action of a net or group of nets in taking samples of a cisco population cannot be predicted on the basis of experiences with other populations of the same species, but that each population presents its own problem of gill-net selectivity. Although gill nets are very selective in their operation, the judicious elimination of selected age groups can make gill-net samples highly reliable for the determination of growth curves. Extreme caution must be employed, however, in the use of gill-net samples for the study of age and year class composition.

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APPENDIX A. GROWTH OF THE CISCO IN ALLEQUASH AND TOMAHAWK LAKES

Small collections of ciscoes were obtained from Allequash Lake in 1928 and in 1930 and from Tomahawk Lake in 1928. Since it is unlikely that any further collections of ciscoes will be made in either of these lakes in the near future, the available growth data for each of the populations are being presented at this time.

Tables 1 and 2 show the average length, average weight, average value of *K*, and the calculated length at the end of each year of life in each age group for each of the three collections. The most noteworthy features of the growth in these two populations are the slow growth during the first year of life in the Allequash fish, the generally excellent growth of the Tomahawk Lake cisco, and the indication that in the Allequash Lake cisco the year 1929 was one above the average in the amount of growth. (It should be pointed out that 1929 was a good growth year in the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations.) The I group of the 1930 Allequash collection shows a particularly high growth for the 1929 season. It is, of course, true that the selective action of gear would be expected to cause a too high calculated growth for this group in any year but selection can hardly explain such a great growth as that which is present here in 1929, for it may be seen that in 1929 the calculated growth for the first year of life is 29 millimeters greater than that calculated for 1927 from the 1928 I group.

TABLE 1.—*Allequash Lake cisco*

[Length, weight, value of *K*, and calculated length at the end of each year of life. Division of data is according to year class and year of capture. Sexes combined]

Year class	Year of capture	Age	Number of specimens	Weight in grams	<i>K</i>	Length in millimeters	Year of life			
							1	2	3	4
1925	1928	III	3	54	1.50	155	54	101	127	
1926	1928	II	17	45	1.51	144	59	107		
	1930	IV	1	140	1.67	203	49	98	138	175
1927	1928	I	27	25	1.36	123	64			
	1930	III	12	108	1.56	190	58	115	165	
1928	1930	II	11	71	1.54	167	54	133		
1929	1930	I	42	42	1.43	143	93			

TABLE 2.—*Tomahawk Lake cisco, 1928*

[Length, weight, value of *K*, and calculated length at the end of each year of life for each age group. Sexes combined]

Year class	Age	Number of specimens	Weight in grams	<i>K</i>	Length in millimeters	Year of life				
						1	2	3	4	5
1923	V	1	156	1.53	217	81	138	172	193	210
1924	IV	16	146	1.59	209	78	141	174	198	
1925	III	39	125	1.58	199	76	140	182		
1926	II	11	99	1.61	183	81	155			
1927	I	1	35	1.42	135	83				

Because of the poor growth in the first year of life the general growth of the Allequash Lake cisco differs from that of all four populations considered in the main body of this study. The closest resemblance is probably with the Silver Lake cisco. The growth of the Tomahawk Lake cisco although poorer than that of the Clear Lake cisco is distinctly better than that found in Trout, Muskellunge, and Silver Lakes.

In both Allequash and Tomahawk Lakes the high values of *K* indicate good condition.

The exceptional conditions under which the Allequash cisco lives should be mentioned. (See table 1 of general paper.) Formerly there existed a rather general belief that the coregonids as a stenothermic form adapted to a cold-water habitat were limited in their distribution to the larger, deeper, lakes. Willer (1924) showed that such a generalization did not apply to the distribution of the kleine Maräne, *Coregonus albula*, in the lakes of East Prussia. Scott (1931) called attention to the exceptional conditions under which the cisco lives in Indian Village Lake (Indiana). This lake is small and shallow (6.4 meters) and in midsummer there is "only a trace" of oxygen below 4 meters. Allequash Lake is another example of a shallow-water habitat for the cisco. The cisco here must not only adjust itself to a wide annual range of temperature variation but also to unusual associates in the form of other species of fish. Along with the 70 ciscoes captured in 1930 were taken 1 blue gill, 15 suckers, 22 pike-perch, 32 rock bass, and 182 perch.