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LIFE HISTORY OF LAKE HERRING OF GREEN BAY, LAKE MICHIGAN

By STANFORD H. SMITH

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ABSTRACT

Although the lake herring has been an important contributor to the commercial fish production of Green Bay, little has been known about it.

This study is based on field observations and data from about 6,500 lake herring collected over the period 1948 to 1952. Relatively nonselective commercial pound nets were a primary source of material for the study of age and growth. Commercial and experimental gill nets were used to obtain data on gear selectivity and vertical distribution.

Scales were employed to investigate age and growth. Age group IV normally dominated commercial catches during the first half of the calendar year and age group III the last half. At these ages the fish averaged about 10.5 inches in length. The season's growth started in May, was most rapid in July, and terminated near the end of October. The sexes grew at the same rate. Selectivity of fishing gear was found to influence the estimation of growth. Geographical and annual differences in growth are shown. Factors that might contribute to discrepancies in calculated growth are evaluated. Possible real and apparent causes of growth compensation are given.

The relation between length and weight is shown to vary with sex, season, year, and method of capture.

Females were relatively more plentiful in commercial catches in February than in May through December. The percentage of females decreased with increase in age in pound-net catches but increased with age in gill-net samples. Within a year class the percentage of females decreased with increase in age.

Most Green Bay lake herring mature during their second or third year of life. They are pelagic spawners with most intensive spawning over shallow areas. Spawning takes place between mid-November and mid-December, and eggs hatch in April and May. Lake herring ovaries contained from 3,500 to 11,200 eggs (averaged 6,375). Progress of spawning by age, sex, and length is given.

Lake herring were distributed at all depths in Green Bay in early May, were concentrated within 30 feet of the surface in late May, moved to deeper water in June, and were restricted to depths greater than 30 feet in July when temperatures in shallower water became unfavorably high (greater than 18° C.). In October, lake herring were again at all depths but were most abundant near the surface.

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By STANFORD H. SMITH, *Fishery Research Biologist*

The lake herring, or shallowwater cisco, *Leucichthys artedi* (LeSueur), occurs in all of the Great Lakes and in many inland lakes of the St. Lawrence, Hudson River, and upper Mississippi River drainages (Hubbs and Lagler, 1949), and has rather general distribution throughout Canada and Alaska in lakes and some rivers, and in Hudson and James Bays (Dymond 1933, 1943, and 1947). Close relatives of the lake herring have a circumpolar distribution in the glaciated areas of the Northern Hemisphere.

The lake herring is a member of the family Coregonidae, a complex and not well understood group of fish. Much confusion resulted from early attempts to describe this group in the Great Lakes (see Koelz 1929; pp. 311–314). The disagreement stemmed both from the fact that early workers studied only small numbers of specimens from one or a few localities and from the high degree of individual and geographic variability in size, shape, and taxonomic counts that characterizes this group. Koelz made a comprehensive taxonomic study of coregonids inhabiting the Great Lakes and Lake Nipigon based on about 15,000 specimens from many parts of each lake. He recognized the high degree of variability in the group and was able to organize the confused taxonomy. What had been described as several species by comparisons of a few specimens often were found to be representatives of a single species that varied greatly in form over its range. Koelz recognized the different species inhabiting the several lakes and thus established a system of nomenclature which has since been adequate for the species of the Great Lakes. He recognized all coregonids of the Great Lakes as belonging to the family Coregonidae and the genera *Coregonus* (Artedi) Linnaeus, *Leucichthys* Dybowski, and *Prosopium* Milner that had been described from studies of coregonids over their entire range.

A few authors have deviated recently from the system of classification used by Koelz and have placed *Leucichthys* and *Prosopium* in the genus *Coregonus*. I prefer to retain *Leucichthys* as a genus because it represents a well-defined group in North America. The *Leucichthys* group in Europe is ascribed to the subgenus *Argyrosomus*; however, European workers have written me that these fish are distinct from other coregonids of that continent.

The consolidation of all groups under the single genus *Coregonus* disregards the recognizable divergence of the phyletic lines represented by the three genera. It is true that the high degree of morphological plasticity characteristic of the coregonids sometimes causes morphometric and even gross appearances to approximate or, in isolated instances, to overlap each other. This superficial parallelism may occasionally hide the distinctness of the groups, but it cannot overrule the primary genetic divergence that is so clearly shown by the distributional pattern of each group.

For each genus there is a central range where its members are highly variable (*Coregonus* in Europe, *Prosopium* in northwestern North America, *Leucichthys* in northeastern North America), and where they are usually divided into several species. Range extensions of each group are characterized by lesser morphological variability and at the extremes only one or two relatively stable species remain. Ambient morphological divergences in isolated populations of one group may in some instances parallel developments common among members of another group and thereby tend to obscure the distinctness of the groups. Such occurrences cannot, however, be interpreted as incomplete separation of the groups. I believe the separate genera describe these phyletic lines in the clearest and most useful manner and should be retained in keeping with this basic purpose of modern taxonomy.

Because of its varied form in different localities, the lake herring is known by more than one common name. Names used in this work where other authors are quoted are sometimes cisco or tullibee rather than lake herring. These names are most often applied to the deep-bodied forms that occur in inland lakes and Lakes Erie and Ontario. Most lake herring from the upper Great Lakes, however, are of the characteristically shallow-bodied form that is most commonly termed "lake herring."

The lake herring is of major importance in the commercial fishery of Green Bay. Fluctuations in its abundance bring a degree of economic uncertainty to the people who depend upon this fish for part of their livelihood. Although the lake herring has been important in the commercial catch of Green Bay, little has been known about it. Knowledge of this species provides greater understanding of its reactions to changing environmental conditions, and also is required to develop management principles that would allow maximum utilization of the species without depleting the population.

A study of the life history of the Green Bay lake herring was initiated in 1948 when field collections of scales were made by Dr. Ralph Hile, of the United States Fish and Wildlife Service, as part of a cooperative project with the Wisconsin Conservation Department for the study of Green Bay fish populations. After 1950, field work was carried on by the author with the help of Leonard S. Joeris and Donald Mraz of the Sturgeon Bay field station of the Service's Great Lakes Fishery Investigations. During 1952, the research vessel FWS *Cisco*, operated by the Great Lakes Fishery Investigations, was available for approximately 1 week each in May, July, and October for the study of the distribution of lake herring in Green Bay. Some material on the lake herring of Green Bay was collected during parts of two other cruises of the *Cisco* in May and June.

The author is most grateful to Drs. Ralph Hile, John Van Oosten, and James W. Moffett, U. S. Fish and Wildlife Service, and to Dr. Karl F. Lagler, University of Michigan, for valuable guidance during the conduct of the study.

GENERAL FEATURES OF GREEN BAY

Green Bay is a nearly detached arm of Lake Michigan with its long axis roughly parallel to the northeast shore of the lake. Morphometric features of Green Bay and Lake Michigan are compared in table 1. The two bodies of water are similar in that they are long and narrow, but they differ greatly in depth and area. The greatest length of Green Bay is about 118 miles on a northeast-southwest axis between the upper end of Big Bay de Noc and the city of Green Bay, Wis. (fig. 1). The greatest width, about 23 miles, is on a northwest-southeast axis in the region of the northern island passages. The area of Green Bay included within a line drawn between the town of Fairport and the tip of the Door Peninsula near Gills Rock is approximately 1,590 square miles. The greatest depth, about 160 feet, is just northwest of Washington Island. The bay is relatively shallow—mean depth, 51 feet. One-third of its area is less than 30 feet deep and only 11 percent is more than 100 feet deep.

TABLE 1.—*Morphometric features of Lake Michigan and Green Bay*

[Data from the U. S. Lake Survey Chart Nos. 7 and 70, 1953 edition]

Measurement	Lake Michigan	Green Bay
Greatest length (miles)	307	118
Greatest width (miles)	118	23
Shoreline length (miles)	1,661	379
Area (square miles)	22,400	1,590
Volume (cubic miles)	1,165	15
Greatest depth (feet)	932	160
Mean depth (feet)	274	51

Four major channels in the northern island area with depths of 45 to 130 feet connect Green Bay with Lake Michigan. The manmade Sturgeon Bay Canal which is 160 feet wide and 20 feet deep joins the two bodies of water in the southern area at Sturgeon Bay. A study being carried on by the Great Lakes Fishery Investigations of the United States Fish and Wildlife Service has provided some data about the exchange of water between Green Bay and Lake Michigan. Although not as comprehensive as might be desired, the data do give a general idea of the water-exchange system between the lake and bay, and of water movements within the bay.

An outstanding feature of the water movements in Green Bay is the high degree of irregularity in direction and velocity. The direction and rate of water movements are believed to be governed mainly by wind and barometric pressure. Flow of water into the bay from rivers is believed to be of minor importance in the major water movements except during spring runoff. Movement

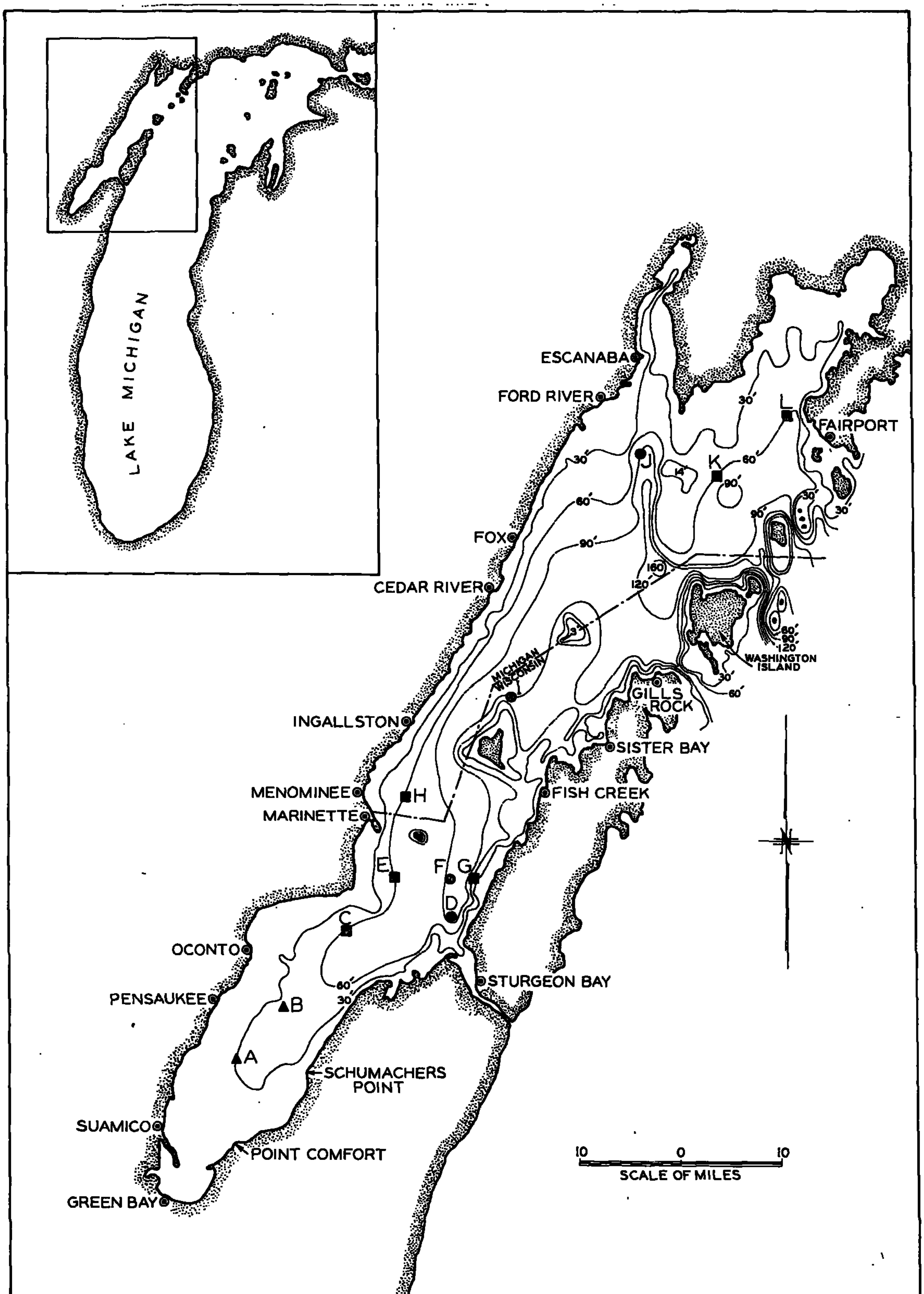

FIGURE 1.—Map of Green Bay showing locations of experimental gill-net stations. Triangles, shallow-water stations (A, 30 feet; B, 40 feet); squares, 60-foot stations; circles, 90-foot stations.

of Lake Michigan water into Green Bay is characterized more by surges than by a regular movement. Surges into the bay result primarily from seiche action set in motion by wind and pressure changes over Lake Michigan. The resultant currents in the bay cause a tremendous amount of mixing. In the northern passages the sequence of inflow, mixing, and outflow result in a great amount of water exchange between the bay and the lake. Evidence of a high degree of exchange in the northern area is found in the relatively clear, Lake Michigan-type water that lacks the deep green color produced by dense phytoplankton growth characteristic of the remainder of the bay. Definite lines of demarcation cannot be made on this basis, however, because of mixing of water masses. Clear lake water is sometimes observed in the Sturgeon Bay area, but here a sharp line of demarcation is usually present between the two types of water. This condition indicates that little mixing occurs before the lake water is returned with an outgoing surge through the canal.

In addition to water movements propagated by currents and water-level changes in Lake Michigan, the water in the bay itself is subject to indigenous seiches and currents caused by local conditions. The systems operating simultaneously in lake and bay, as they must most of the time, result in extremely complex and irregular water movements.

The water level in Green Bay is subject to almost continuous change. A change of a foot an hour is not uncommon and occasionally a drop of several feet in the southern end of the bay strands fishing boats in shallow harbors. Although a complex resonance pattern is characteristic of water-level charts of Green Bay, peaks occur at intervals of about 12 hours. The peaks show no relation to the movements of the moon. Typical spacing of the peaks within the 24-hour period can be completely disrupted by severe storms after which a new system is established with peaks occurring at different hours of the day but again at 12-hour intervals.

Some of the effects of water movements on the water temperatures in Green Bay will be shown later in a discussion of the distribution of lake herring.

ECONOMIC IMPORTANCE OF THE FISHERY

Green Bay supports one of the most productive commercial fisheries of the Great Lakes and the lake herring is a major contributor to the catch. Hile, Lunger, and Buettner (1953) showed that on the average 28.8 percent of the total pounds of all species taken in the State of Michigan waters of Green Bay consisted of herring. In 1952, the last year for which complete statistics and values are available, the lake herring catch of Green Bay (both Wisconsin and Michigan) amounted to 9,121,600 pounds and had a value to the fishermen of $456,080. This catch represented 94.1 percent of the production of this species in all of Lake Michigan and 38.7 percent of the lake herring production of all United States waters of the Great Lakes.

The commercial production of the lake herring in Green Bay is characterized by wide annual and seasonal fluctuations. The catch in Michigan waters of Green Bay ranged from 1,515,000 to 11,850,000 pounds (average 5,841,000 pounds) from 1891 to 1908 (Hile, Lunger, and Buettner, 1953) and averaged 82.4 percent of the total pounds of all species taken. In a later period (1929–49) there was a marked drop in the production to between 160,000 and 2,668,000 pounds (average 1,070,000 pounds) which contributed an average of 29.9 percent to the catch of all species. The production of lake herring in Michigan and Wisconsin waters during the years for which reliable records are available for both States (table 2) show wide variation seasonally and annually. Fluctuations of the catch are influenced primarily by weather, availability and abundance of other species with higher market value, and the abundance of lake herring itself. Thus, the causes of fluctuations are difficult to ascertain, but the great difference between the 1891–1908 and 1929–49 data on the Michigan waters of Green Bay (82-percent drop in average production) shown by Hile, Lunger, and Buettner indicates that the population must be subject to wide variations. The present study, however, has been conducted in years (1948–52) when total production has been high and relatively stable

(6,320,000 to 9,122,000 pounds) compared to the 10-year period after 1936.

TABLE 2.—*Commercial catch of lake herring in Wisconsin and Michigan waters of Green Bay, by quarters, 1936–53*

[In thousands of pounds]

Year	January-March	April-June	July-September	October-December	Total
1936	1,121	897	254	1,597	3,869
1937	1,475	1,127	246	1,254	4,102
1938	1,422	779	142	665	3,008
1939	381	513	158	449	1,501
1940	653	399	146	291	1,489
1941	382	347	129	442	1,300
1942	299	249	119	182	849
1943	330	428	303	223	1,284
1944	249	292	333	131	1,005
1945	581	791	1,003	1,289	3,664
1946	854	1,381	687	2,294	5,216
1947	1,686	1,223	544	1,832	5,285
1948	2,260	1,576	338	3,288	7,462
1949	1,354	1,622	303	3,041	6,320
1950	1,788	1,065	376	3,663	6,892
1951	1,322	593	747	5,049	7,711
1952	1,818	675	563	6,066	9,122
1953	587	842	384	4,081	5,894
Average, 1936–53	1,031	822	376	1,991	4,220
Percentage	24.4	19.5	8.9	47.2	

Note.—These data are from summaries of commercial catch records made by the U. S. Fish and Wildlife Service for Michigan waters and by the Wisconsin Conservation Department. Data for Wisconsin prior to 1942 included lake herring taken in that area of Lake Michigan adjacent to Green Bay, but catches in this area are characteristically small and are not believed to influence trends.

Because of highly seasonal production and rapid deterioration in handling and storage, the lake herring brings a low average price (5 cents per pound to the fishermen of Green Bay in 1952) and much of the catch is used for animal food. Given better markets and improved handling, the species may become a more important source of human food.

The lake herring has some small value as a sport fish. Its habit of feeding principally on small planktonic organisms and its disinclination to strike at lures has caused it to be overlooked by anglers using conventional methods. During recent years, however, fishermen have found that when lake herring are feeding on mayflies they will also strike at artificial flies. A sports fishery during the period of mayfly emergence is growing rapidly in popularity in the northern areas of Lakes Huron and Michigan. Some large lake herring are also taken with minnows as bait. A certain amount of angling for lake herring is carried on through the ice both on the Great Lakes and on inland lakes.

COLLECTION OF DATA

Scale samples and data on weight, length, sex, and state of development of sex organs were obtained on 4,390 specimens. Collections made between May 26, 1948, and January 22, 1952, were taken from commercial pound nets and gill nets as indicated in table 3. Scale samples of May, July, and October, 1952, were from fish captured in experimental gill nets. Table 4 lists all fish taken in experimental gill nets for which length and weight measurements and sex determinations were made; in some of the May collections, however, weight and sex data are missing.

TABLE 3.—*Collections of Green Bay lake herring from which scale samples were taken, 1948–52*

Date	Locality	Gear used [1]	Number of fish
1948			
May 26	Point Comfort	Pound net	262
Oct. 12	Schumachers Point	2⅜-inch gill net	152
1949			
Feb. 16	Schumachers Point	Pound net	345
May 13	Point Comfort	do	200
13	Pensaukee	do	241
Oct. 5	do	do	283
1950			
Feb. 22	Schumachers Point	do	341
27	Escanaba	do	166
June 21	Fish Creek	do	62
22	do	do	25
July 13	Ingallston	do	43
Sept. 14	Gills Rock	do	201
Nov. 29	Fox	do	107
30	Oconto	2⅜-inch gill net	108
Dec. 4	Sister Bay	Pound net	112
1951			
Feb. 20	Pensaukee	2⅜-inch gill net	168
20	do	Pound net	29
20	Ingallston	do	223
22	Schumachers Point	do	189
May 8	Point Comfort	do	143
June 15 [2]	Gills Rock	do	11
19	Pensaukee	do	80
21	Gills Rock	do	26
Aug. 20	Fox	do	59
29	Gills Rock	do	15
Nov. 11	Pensaukee	2½-inch gill net	80
Dec. 12	Gills Rock	1-inch gill net	79
1952			
Jan. 21	Escanaba	Pound net	90
22	Pensaukee	do	92
May 8	Station D	2-inch gill net	44
11	Station F	do	113
July 21	Station L	do	30
24	Station C	do	19
Oct. 22	Station B	do	46
23	Station D	do	19
24	Station I	do	187
Total			4,390

[1] See text, p. 95, for comments on mesh sizes of pound nets.
[2] This is a selected sample. All other samples are either random or represent the entire catch of one net.

TABLE 4.—*Lake herring taken in experimental gill nets in 1952*

Date [1]	Station [2]	Number of fish	Date	Station [2]	Number of fish
May 2	D	80	July 21	L	85
6	I	28	22	H	10
8	D	58	22	I	24
11	E	26	24	C	19
11	F	115	27	D	6
11	G	118	Oct. 22	A	15
22	E	85	22	B	46
22	F	31	22	C	143
22	G	31	23	D	19
25	A	13	24	H	140
25	B	32	24	I	187
25	C	5	25	J	179
June 11	J	81	25	K	130
12	K	19	25	L	139
12	L	46			
July 21	J	78	Total		2,039
21	K	51			

[1] Weight and sex data lacking for some May collections.
[2] See figure 1 for location.

Total length (tip of the snout to the end of the tail, lobes compressed) was recorded to the nearest 0.1 inch. Weights measured on a spring scale, with 18-ounce capacity, were recorded to the nearest 0.1 ounce. All lengths are given in inches and weights in ounces unless otherwise stated.

Samples from the commercial fishery were captured in standard fishing gear designed primarily for lake herring. Netting of pound nets used in the lake herring (and smelt, *Osmerus mordax*) fishery customarily has meshes (in the pot) of 1¼ to 2 inches, extension measure as manufactured. Nets of these mesh sizes are capable of capturing lake herring smaller than any taken from them during this study. Consequently, mesh size need not be considered as a selective factor in the treatment of samples from pound nets. Most small-mesh gill nets used in the Green Bay herring fishery have a mesh size of 2⅝ inches (allowable range 2¼ to 2¾ inches, depending on season, location, and conditions) extension measure. One collection in southern Green Bay was taken from a 2½-inch-mesh gill net on November 11, 1951. Experimental gill nets used to collect lake herring in the summer and fall of 1952 are described in Vertical Distribution in Green Bay (p. 128). All experimental gill nets were fished from the Service's research vessel *Cisco*.

Analyses and discussions in this report include all data that are believed pertinent to the solution of each particular problem. The exclusion of data of doubtful value in some instances causes discrepancies in the number of specimens listed in different tables. Whenever the excluded data are extensive or may influence results under alternate considerations, the reason for their omission is given. All collections of data used in this report are either taken from the entire catch of a net or are random samples unless otherwise stated.

EXAMINATION OF SCALES

Scales for age and growth analysis were taken when possible from the left side of the body in the area just above the lateral line and below the insertion of the dorsal fin. Van Oosten (1929, p. 274) stated that this area was selected "* * * after a careful examination had shown that its scales were less variable in shape and size, when compared one with another, than those of other parts of the body." Since the scales of lake herring are loosely attached and are frequently lost in nature, a liberal sample was taken to ensure the inclusion of non-regenerated scales. The scales from each fish were placed in an envelope on which were recorded the species, locality, date, length, weight, sex, condition of sex organs, gear, and name of collector. The "key" scales required to establish the body-scale relation were removed from approximately the center of the area from which routine samples were taken. The location was the same as that used by Van Oosten—the fourth row above the lateral line and immediately below the base of the first ray of the dorsal fin.

Some scales were mounted on glass slides in a glycerin-gelatin medium. Plastic impressions were made of the others. Each slide carried three or four scales of normal shape and without evidence of regeneration. The label on the slide bore the data shown on the envelope from which the scales were taken. Plastic impressions of scales were made by placing six or eight dry, uncleaned scales sculptured side down on a 1- by 3-inch strip of cellulose acetate bearing a serial number corresponding to that on the scale envelope. A second plastic strip was placed over the scales and the two strips were passed through a roller press set at the crushing pressure of cellulose acetate. (See Smith 1954.) The second strip of plastic holds the scales in position and ensures an even impression which produces a light, clear image. The numbered plastic strips bearing scale impressions were returned to the envelope and thus were not separated from the original data.

Before the plastic-impression method was adopted, careful microscopic comparisons were made of the scales and their impressions to be certain that replication was complete and without distortion. Butler and Smith (1953) who studied the reliability of scale impressions in age and growth studies found that growth calculations made from scale impressions did not differ significantly from those made from the scales themselves. About 500 of the scales used in this study were mounted in a glycerin-gelatin medium; plastic impressions were made of the remaining 3,900. All key scales used to establish the body-scale relation were mounted in glycerin-gelatin.

Scale measurements for growth computations were made from the magnified (×41) scale image projected on the screen of a microprojection device (described by Moffett 1952) and recorded to the nearest millimeter. The scale to be measured was oriented so that a line on the viewing screen bisected the image at its greatest anteroposterior diameter. Measurements of the total diameter and of diameters of growth fields circumscribed by annuli were made along this line. The total diameter was measured from the extreme anterior to the extreme posterior margins of the scale. Diameters of growth fields were measured from the inside edge of the first complete circulus outside the annulus.

Scale measurements of each fish were entered on IBM (International Business Machine) cards along with coded information concerning each fish. All subsequent computations and tabulations were made by means of the 602A IBM calculator and the 404 IBM tabulator at the Statistical Research Laboratory of the University of Michigan.

Ages were determined by counting the annuli or year-marks on the scales. Van Oosten (1929) clearly established the validity of this method for the age determination of the lake herring of Saginaw Bay. More recent authors reporting on this species (Carlander 1945; Cooper 1937; Fry 1937; Hile 1931, 1936; Pritchard 1931; Stone 1938; and others) have accepted the use of scale markings for age analysis of lake herring.

Nothing in the data on the Green Bay lake herring gives cause to question the validity of scales for age determination. Nevertheless, certain difficulties of interpretation were encountered. Accessory checks, or false annuli, occurred on scales of nearly all fish after the second year of life. The general appearance of these checks and their location with respect to the annuli on either side left little doubt as to their identity; however, the possibility of some errors of age determination cannot be discounted.

The regular appearance of accessory checks is not confined to the Green Bay stock. These false annuli on cisco scales have been reported by Hile (1936) in the cisco of Muskellunge Lake and by Fry (1937) in Lake Nipissing. Bauch (1949) described a fast-slow-fast growth pattern in a population of "kleinen Maräne," *Coregonus albula* L. (the European coregonid most similar to the lake herring), in Mochelsee. He attributed the midseason check in the scales to oxygen depletion and an accumulation of hydrogen sulfide in the hypolimnion which forced these fish, normally inhabitants of the deeper waters in summer, to live in upper strata where less favorable temperature conditions exist. Data on the Green Bay herring are inadequate to show the cause of accessory checks or even the time of their formation. Seemingly the formation of checks varies from fish to fish and possibly according to season and locality.

The characteristics of the annulus on the scales of Green Bay lake herring are similar to those described for scales in other populations. The circular ridges on the scale start forming on the anterior margin of the scale and grow posteriorly along the lateral fields. When growth stops completely and resumes again, growth of the unfinished circuli is not completed; instead a new circulus is started which encompasses the ends of those left incomplete at the cessation of growth.

Fish having scales without an annulus are designated as belonging to age group 0, those with one annulus to age group I, * * *. For convenience, each fish is held to pass into the next higher age group on January 1. Since annulus formation does not actually take place until spring or early summer, the convention requires that a "virtual" annulus be credited at the edge of the scale from January 1 until the new annulus is visible. Year classes are identified by year of hatching (spring) rather than year of egg deposition (fall). Thus, it is always possible to determine the year class of a fish by subtracting its age from the year of capture; for example, a fish

TABLE 5.—*Age composition of lake herring taken in commercial pound nets, by quarters, 1949–52*

[Dominant age groups indicated by asterisk]

Quarter and year	Number of fish	Percentage in age group—							Average age[1]
		I	II	III	IV	V	VI	VII	
January–March:									
1949	345			12.2	*74.2	13.6			4.01
1950	505			10.9	*74.8	13.5	0.8		4.05
1951	437		0.2	7.1	*80.1	12.6			4.05
1952	178			3.9	*87.1	8.4	0.6		4.06
All years, 1949–52	1,465		0.1	9.2	*77.8	12.6	0.3		4.04
April–June:									
1948	262		1.5	*53.6	42.2	2.7			3.46
1949	439			16.2	*73.3	9.1	1.4		3.96
1950	87			10.3	*72.4	14.9	2.4		4.09
1951	246		4.9	16.7	*67.5	10.1	0.4	0.4	3.86
All years, 1948–51	1,034		1.5	25.3	*64.0	8.2	0.9	0.1	3.82
July–September:									
1950	244	2.9	2.9	*50.8	40.5	2.9			3.38
1951	73	8.2	30.1	27.4	*32.9	1.4			2.89
All years, 1950–51	317	4.1	9.2	*45.4	38.8	2.5			3.06
October–December:									
1949	278	0.7	6.8	*76.3	15.1	0.7	0.4		3.09
1950	219	0.5	5.9	*68.9	24.7				3.18
All years, 1949–50	497	0.6	6.5	*73.0	19.3	0.4	0.2		3.13

[1] Average number of annuli.

belonging to age group III captured in 1949 belongs to the 1946 year class.

AGE COMPOSITION

The principal characteristics of the age composition of Green Bay lake herring taken in the commercial fishery (tables 5 and 6, and fig. 2) are the shift from older to younger fish during the calendar year and a strong tendency for the same age group to be dominant year after year during the same season.

In pound-net collections made during the first quarter (January–March), age group IV was

TABLE 6.—*Age composition of lake herring taken in commercial gill nets, in 1948, 1950, and 1951, and experimental gill nets in 1952, by quarters*

[Dominant age groups indicated by asterisk]

Quarter and year	Number of fish	Percentage in age group—						Average age[1]
		I	II	III	IV	V	VI	
January–March: 1951	166			3.0	*80.1	16.9		4.14
April–June: 1952	154			3.2	*85.1	11.1	0.6	4.09
July–September: 1952	48			35.4	*64.6			3.65
October–December:								
1948	152		3.9	*52.6	38.2	5.3		3.45
1950	108	1.9	4.6	*72.2	19.4	1.9		3.15
1951	80		2.5	*85.0	10.0	2.5		3.13
1952	250		0.4	*60.8	37.2	1.6		3.40
All years, 1948–52	590	0.3	2.4	*64.1	30.5	2.7		3.33

[1] Average number of annuli.

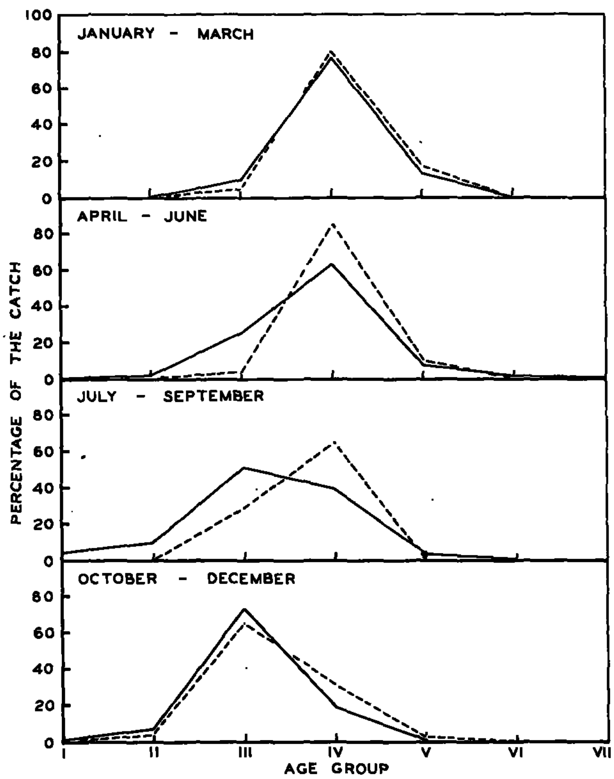

FIGURE 2.—Age composition of lake herring taken in commercial pound nets (solid line), and commercial and experimental gill nets (broken line) in various quarters, 1948–52.

without exception strongly represented (74.2 to 87.1 percent) and made up 77.8 percent of all fish taken over the period 1949–52. In April–June collections the IV-group was still strongest in 3 years (67.5 to 73.3 percent) and made up 42.2 percent of the sample in the remaining year. The percentage of IV-group fish dropped from 77.8 in the first quarter to 64.0 in the second, whereas the III-group increased from 9.2 to 25.3 percent. Age group III was dominant in the summer quarter (July–September) in one of the two samples (50.8 percent) as well as in combined data of 1950–51 (45.4 percent). The transition to dominance by age group III was complete in the fourth quarter (October–December), where it maintained this position in both years (68.9 and 76.3 percent) and in combined data for 1949–50 (73.0 percent). The dominance of the III-group (73.0 percent), which advances to age group IV on January 1, is only slightly less than that of the IV-group of the first quarter of the following year (77.8 percent). The mid-year shift of dominance from age group IV to age group III is also shown clearly by the average ages (table 5).

The much less extensive data on gill-net samples [1] (table 6 and fig. 2) suggest that the trend of age composition is much the same as for pound nets. Age group IV was dominant, but the average age was decreasing in the first three quarters and age group III was dominant in all samples of the fourth quarter.

Despite similar trends in the seasonal shift of age composition, gill nets in general took older fish than did pound nets. The small differences where large numbers of fish were concerned, however, indicated that during the years of this study both gears were cropping a similar segment of the population.

The age composition of the commercial catch demonstrated for Green Bay requires that a different year class be a major contributor to the fishery each year. The fishery, in turn, must then be very sensitive to fluctuations in success of year classes. Because of the resulting instability in the economy of small fishing communities it would be advantageous to devise some method of predicting good and poor year classes before they enter the fishery so that problems of high or low production could be anticipated. Unfortunately, this study has been conducted during a period of high and relatively stable production (see Economic Importance of the Fishery, p. 90) and no fluctuations or means of their detection were discernible. The catch and abundance (expressed as catch per unit-of-effort), however, are normally subject to wide fluctuations (Hile, Lunger, and Buettner, 1953).

The age composition of a representative sample of an entire population should normally show a preponderance of fish in the youngest age group, with progressively decreasing numbers as age increases. This pattern of diminishing numbers with age must exist in lake herring populations (even though it has never been demonstrated), for a population that regularly has fewer young fish than old must soon disappear. Since young lake herring have to be abundant, their scanty representation in samples of the population must be attributed either to the inability of collecting gear to capture them or to their absence from the area sampled.

It is believed that the scarcity of young herring in the 1948–52 samples was largely the result of their scarcity on the fishing grounds. A principal gear of capture, the pound net, was fully capable of taking lake herring as young as 1 or 2 years old had they been present in abundance. Pound nets from which lake herring were taken for this study were also designed to capture smelt. Because of their small size and slender form, smelt require smaller mesh sizes than do the lake herring and yellow perch (*Perca flavescens*), which constitute important portions of the commercial catch. Mesh sizes ranging from 1¼ to 2 inches, extension measure as manufactured, made even smaller by treatment with preservative, have been used in Green Bay since smelt became an important commercial species about 1940 (Hile, Lunger, and Buettner, 1953). Although this mesh was far smaller than was previously considered satisfactory to catch commercial-sized herring, its introduction did not result in any continuous appearance of smaller herring in the catch even though it regularly captured yearling smelt and perch. In southern Green Bay, large numbers of trout-perch (*Percopsis omiscomaycus*) 3 to 4 inches long are regularly taken.

The ability of pound nets to catch young herring was clearly demonstrated in the winter of 1944–45 when, according to Hile, Lunger, and Buettner,

[1] Collections from experimental and commercial gear are shown together in gill-net data. Figures presented in a later discussion on length at capture show that lake herring taken in the two types of gears at the same time of year have similar length distributions.

large numbers of "pin" herring were taken in pound nets. Scales from 78 specimens taken at Escanaba on May 27, 1945, revealed that all were fish of the 1943 year class and were nearing the end of their second year of life. Inasmuch as this has been the only phenomenal occurrence of small herring in smelt-type pound nets since they came into common use, it can be assumed that the appearance in numbers of young herring in 1945 could have resulted from a successful hatch in 1943 and that the abnormally plentiful young herring extended beyond their normal range into the shallow-water areas in which pound nets are located. Although lake herring average about 5 inches long at the end of their first year of life, which is within the size range of other small fish taken, none were ever present in our pound-net samples.

The lake herring is a relatively short-lived species. Hile (1936) reported the maximum age of XII in Trout Lake, Wisconsin. Although no other author has reported a fish this old, fish in age group XI have been reported by Fry (1937) in Lake Nipissing and by Hile in Clear Lake. Lake herring in age group X have been reported by Carlander (1945), Eddy and Carlander (1942), Stone (1938), and Van Oosten (1929). The lowest maximum age reached in any population was reported by Hile for Muskellunge Lake where the oldest fish belonged to age group IV. The oldest age groups in these populations are represented in the samples by only one or two individuals; in most lake herring stocks heavy mortality starts between the third and seventh years of life.

The oldest lake herring taken in Green Bay were two VII-group fish caught in pound nets in June 1951.[2] Only 17 representatives of age group VI were recorded during the course of this study.

The observed age compositions of several North American lake herring populations show that age groups II to V are best represented in the samples and that of these age groups III is usually the most common. Some of the differences among samples from various populations were undoubtedly the result of selectivity of collecting gear. It appears, nevertheless, that fish are much shorter lived in some populations than in others. Hile (1936) collected fish from several lakes with the same gill nets, and his data should be well adapted to a comparison of age composition in different bodies of water. Hile's data show that age groups II and III were best represented in the Muskellunge and Clear Lake populations, but that the oldest fish taken in Muskellunge Lake belonged to age group IV, whereas in Clear Lake ciscoes lived as long as 11 years and age group VII made up more than 11 percent of the samples. The difference between these two lakes in observed age composition is as great as that recorded elsewhere in the literature. It is possible that differences reported by other authors can be real and that the longevity does vary with local conditions.

Van Oosten (1929) showed that age group III (age group IV under his system of age designation) predominated in his samples from Saginaw Bay, all of which were taken from pound nets during the period October to December. This same age group dominated samples taken from Green Bay pound nets during the same time of the year (table 5).

SIZE AT CAPTURE

The lengths of lake herring captured in pound nets (table 7) and gill nets (table 8), varied both as to average and range among collections of the same year and of different years. Mean lengths for samples, however, show no distinct seasonal pattern, which is in marked disagreement with the well-established, seasonal changes in age composition (see p. 94). The data on age would suggest that the consistently older fish taken during the first half of the year should be longer than the predominantly younger fish taken in the second half. The discrepancy is explained by the length frequencies of age groups (table 9) which show a wide overlap of length distribution where length groups are frequently represented by fish of three ages. Differences between mean lengths of age groups III and V were only 0.4 to 0.7 inch in different years. Thus, lake herring of these age groups are similar in length regardless of age and no great changes in length should be expected to follow changes in age composition.

That there is a greater growth than is indicated by the average lengths of age groups is brought out in a later discussion of computed growth. The apparently poor growth suggested by the similar average lengths of different-aged fish in the commercial catch must be due either to a strong

[2] One of the VII-group fish was in a selected sample collected on June 15, 1951, and does not appear in discussions dealing with age. The other VII-group fish was in the June 19, 1951, collection.

TABLE 7.—*Length distribution of lake herring taken in pound nets, by month and year, 1948–52*

Total length (inches	May 1948	1949			1950						1951				January 1952
		Feb.	May	Oct.	Feb.	June	July	Sept.	Nov.	Dec.	Feb.	May	June	Aug.	
5.0 to 5.4							1								
6.0 to 6.4													1	2	
6.5 to 6.9							1						2	1	
7.0 to 7.4							1						1	3	
7.5 to 7.9				1			1							6	
8.0 to 8.4				4			3				1		2	21	
8.5 to 8.9	1			5	2	1	3	2			2		2	5	
9.0 to 9.4	5	1	4	7	8	1	6	3			4	1	3	6	1
9.5 to 9.9	41	35	12	12	36	9	10	8	3	3	10		9	2	4
10.0 to 10.4	98	160	103	29	172	14	11	16	21	12	60	8	20	3	8
10.5 to 10.9	67	95	186	82	190	35	4	59	45	64	181	47	27	7	56
11.0 to 11.4	28	44	111	100	81	16	2	82	32	29	146	49	21	10	73
11.5 to 11.9	18	8	19	27	11	9		24	3	3	26	28	12	5	34
12.0 to 12.4	2	2	5	10	3			6	1	1	7	6	3	2	4
12.5 to 12.9	1			2	2			1	2		1	1		1	2
13.0 to 13.4	1			2	1	1					2	1			
13.5 to 13.9				1								2	1		
14.0 to 14.4				1							1				
14.5 to 14.9					1	1							1		
15.5 to 15.9			1												
16.5 to 16.9													1		
Number of fish	262	345	441	283	507	87	43	201	107	112	441	143	106	74	182
Average length	10.5	10.5	10.7	10.8	10.6	10.8	9.5	10.9	10.8	10.8	10.8	11.2	10.7	9.3	11.1

TABLE 8.—*Length distribution of lake herring taken in gill nets, by month and year, 1948–52*

Total length (inches)	October 1948 [1]	November 1950 [1]	1951		1952 [3]		
			Feb.[1]	Nov.[2]	May	July	Oct.
7.5 to 7.9		1			1		
8.0 to 8.4		1					
8.5 to 8.9							1
9.0 to 9.4	1	1					
9.5 to 9.9			2		4	5	
10.0 to 10.4	4	4	12		26	16	9
10.5 to 10.9	18	21	44	5	63	17	64
11.0 to 11.4	33	33	87	20	46	5	104
11.5 to 11.9	55	26	15	28	13	6	58
12.0 to 12.4	23	14	6	16	3		5
12.5 to 12.9	14	5	2	9	1		
13.0 to 13.4	3	1		1			1
13.5 to 13.9		1		1			
14.0 to 14.4	1						
Number of fish	152	108	168	80	157	49	252
Average length	11.7	11.3	11.1	11.7	10.9	10.6	11.2

[1] Collections from 2⅜-inch-mesh commercial gill nets.
[2] Collections from 2½-inch-mesh commercial gill nets.
[3] Collections from 2-inch-mesh experimental gill nets.

TABLE 9.—*Length distribution of lake herring, by age group, taken from pound nets in January and February, 1949–52*

Total length (inches)	1949			1950				1951				1952			
	III	IV	V	III	IV	V	VI	II	III	IV	V	III	IV	V	VI
8.0 to 8.4								1							
8.5 to 8.9				2					1	1					
9.0 to 9.4		1		3	5				1	3			1		
9.5 to 9.9	9	24	2	9	27					10			4		
10.0 to 10.4	23	123	14	19	138	15			11	45	4	2	5	1	
10.5 to 10.9	8	71	16	17	143	29			13	152	14	2	48	4	
11.0 to 11.4	2	32	10	6	59	16			4	115	25	3	65	5	
11.5 to 11.9		3	5		5	5	1		1	18	7		28	4	
12.0 to 12.4		2			1	1	1			6	1		3	1	
12.5 to 12.9						2					1		1		1
13.0 to 13.4							1				2				
14.0 to 14.4											1				
14.5 to 14.9							1								
Number of fish	42	256	47	56	378	68	4	1	31	350	55	7	155	15	1
Average length	10.3	10.4	10.7	10.3	10.5	10.9	13.0	8.1	10.5	10.8	11.2	10.8	11.1	11.2	12.6

modification of the population by the fishery (that is, a selective destruction of the larger fish) or to a differential distribution of the fish according to size so that only a certain segment of the population is represented in the fishery. Since the second condition obviously would contribute to the first, it may be assumed that the commercial fishery exerts a strong modifying effect on the population. Natural mortality, of course, may also play an important but unmeasurable role in this process.

A progressive increase in length of lake herring of each age group in successive years from 1949 to 1952 (table 9) indicates that more rapid growth took place in the later years. This trend is also brought out in a later section on annual fluctuations in growth rate.

Small as variations were in the average lengths of lake herring collected at different times of the year (tables 7 and 8), November-May collections taken at about the same time but often at considerable distances apart, showed still smaller differences of no more than 0.2 inch. This similarity was not always present, however, for in collections of other months (June–October) large differences sometimes occurred. Examples of these small differences in average lengths of herring taken in different areas are given in the following table:

Date	Location	Average length (inches)
1949		
May 13	Suamico	10.8
13	Pensaukee	10.7
1950		
Feb. 22	Schumachers Point	10.6
27	Escanaba	10.5
Nov. 29	Fox	10.8
Dec. 4	Sister Bay	10.8
1951		
Feb. 20	Ingallston	10.7
20	Pensaukee	10.8
22	Schumachers Point	10.9
1952		
Jan. 21	Escanaba	11.1
22	Pensaukee	11.1

The weight of Green Bay lake herring at capture presents much the same picture as does length. Weights of fish of a given age are distributed over a wide range and each weight group is frequently represented by fish of three ages (table 10). Differences between age groups III and V varied only 0.6 ounce to 1.2 ounces in different years as would be expected when differences in length were small.

GROWTH

BODY-SCALE RELATION AND CALCULATION OF GROWTH

Van Oosten (1929) established the validity of computations of the growth of lake herring from the diameters of the entire scale and of growth fields within the several annuli. Since the publication of his work, most investigators reporting on growth of this species have accepted Van Oosten's conclusions.

The relation between body length and the anterior scale radius of lake herring was determined for the tullibee of Lake of the Woods by Carlander (1945). Carlander used the anterior radius because he found annuli difficult to locate in the posterior field. He demonstrated that the relation between scale radius and standard length was described satisfactorily by a third-degree equation. From a comparison of results of calculations from diameters and anterior radii Van Oosten (1929, p. 327) found that "* * * the diameter of a scale grows in length more nearly proportional with the body than does the anterior radius [and] * * * that the diameter dimension is less variable than the anterior radius * * *." Since no difficulty was experienced in locating annuli in the posterior field of scales of Green Bay lake herring, diameter measurements were used in this study to take advantage of the simple, direct-proportional relationship determined by Van Oosten. It was held desirable, nevertheless, to study the body-scale relation of the Green Bay lake herring to make certain that the procedure was valid in this stock.

If direct-proportion computations are to be valid, the body-scale ratio must be the same for all lengths of fish from the time of completion of the first annulus. Van Oosten (1929) found that after formation of this annulus the ratio of total scale diameter to body length was so nearly constant in the herring of Saginaw Bay that an assumption of constancy could be made. In the Green Bay lake herring the body-scale ratio exhibited no trend with increase in fish length (table 11). A *t*-test to determine whether such variations as did occur represented a significant trend confirmed the validity of the assumption that the ratio does not change with length ($0.8<p<0.9$). Since the fish from which these data were taken covered the full range from those that had just completed the first year of life to the largest and oldest fish collected,

TABLE 10.—*Weight distribution of lake herring, by age group, taken from pound nets in January and February, 1949–52*

Weight group (ounces)	1949			1950				1951				1952			
	III	IV	V	III	IV	V	VI	II	III	IV	V	III	IV	V	VI
2.0 to 2.4				3				1					1		
2.5 to 2.9		1		2	2				2	1			1		
3.0 to 3.4	1	3		4	13					3					
3.5 to 3.9	8	34	3	6	35	1				9			2		
4.0 to 4.4	20	102	11	17	96	11			9	33	3		5	1	
4.5 to 4.9	11	59	13	11	115	24			6	60	5	2	19	1	
5.0 to 5.4		28	5	8	81	15			12	144	12	5	42	3	
5.5 to 5.9	2	22	8	3	19	10	1		1	57	16		45	5	
6.0 to 6.4		5	3	2	10				1	28	12		23	2	
6.5 to 6.9		2	3		2	3	1			6	1		12	3	
7.0 to 7.4			1		4	1				5	2		4		
7.5 to 7.9					1	2				2			1		
8.0 to 8.4										2					1
8.5 to 8.9						1									
9.0 to 9.4											2				
10.5 to 10.9											1				
11.0 to 11.4							1				1				
14.0 to 14.4							1								
Number of fish	42	256	47	56	378	68	4	1	31	350	55	7	155	15	1
Average weight	4.3	4.5	5.0	4.3	4.6	5.1	9.5	2.4	4.7	5.2	5.9	5.1	5.5	5.7	8.4

TABLE 11.—*Relation between magnified (×41) scale diameter and total length of Green Bay lake herring*

Number of fish	Average total length [1] (inches)	Average scale diameter [1] (millimeters)	Average body-scale ratio [2]
2	5.8	101.0	17.4
8	6.2	113.0	18.2
14	6.7	126.3	18.8
13	7.2	129.8	18.0
9	7.7	139.1	18.2
8	8.2	153.8	18.7
13	8.7	163.8	18.8
9	9.2	168.7	18.3
24	9.8	175.2	18.0
43	10.2	186.6	18.2
81	10.7	194.5	18.2
72	11.2	202.6	18.1
23	11.6	212.9	18.3
15	12.2	224.3	18.4
6	12.6	230.2	18.3
2	13.2	241.0	18.3
1	14.0	249.0	17.8
1	14.9	260.0	17.5

[1] Means for fish within a ½-inch interval of total length.
[2] Means of the body-scale ratio computed for individual fish.

direct-proportion calculations are valid for all Green Bay herring. Thus, the method established for Saginaw Bay lake herring is applicable to the Green Bay stock as well.

The graphical representation of the relation between body length and scale diameter (fig. 3; see also table 11) is based on data for the sexes combined. Regression lines fitted to the data for the sexes separately exhibited no statistically significant differences. This body-scale relation is obviously linear. The fitting of a least-squares line to the means [3] of scale diameters and body lengths yielded the following equation:

$$L=0.01615+0.05486\ S,$$

where L is total length in inches and S is the magnified scale diameter in millimeters. The intercept of less than 0.02 inch on the axis of fish length is so small that calculations of growth from the least-squares equation are nearly identical with those that would be obtained if the intercept were assumed arbitrarily to be 0. In other words,

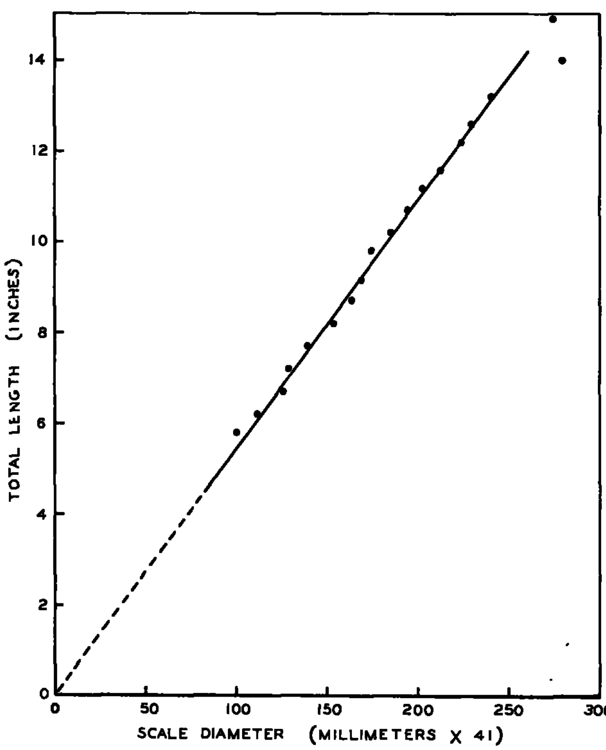

FIGURE 3.—Relation between total length of fish and magnified (×41) scale diameter in the Green Bay lake herring. The dots show empirical data; the slope of the line is the mean body-scale ratio.

[3] Weighted means are used to reduce error in slope of the least-squares regression due to scatter. Tests of statistical significance were based on individual measurements.

the body-scale ratio can be considered constant and the simple procedure of direct-proportion calculations can be followed. The lack of trend in the body-scale ratio with increase in length (table 11) and the close fit of the line in figure 3 (fitted on the assumption of no intercept and with a slope based on the mean body-scale ratio) to the empirical data justify this view.

To be sure, newly hatched lake herring do not have scales as would be indicated by the relationship just described. Fish (1932) and Pritchard (1930) in detailed descriptions of this species from hatching up to lengths of 17.5 to 20.0 millimeters (0.7 to 0.8 inch) did not mention the presence of scales. Van Oosten (1929) reported a lake herring 34 millimeters (1.3 inches) long which had not formed scales and stated that scale formation probably starts at a fish length of 35 to 40 millimeters (1.4 to 1.6 inches). Wohlschlag (1953) observed that the first scales were formed at a length of 40 to 60 millimeters (1.6 to 2.4 inches) in *Leucichthys sardinella* of an Alaskan lake. Thus, the body-scale regression does not exist until a body length of about 1.5 inches is reached. There must be a period before the end of the first year of life when scale growth is considerably faster than body growth, after which the linear relation with an apparent 0-intercept has become established.

TIME OF ANNULUS FORMATION

Because so few investigators of the growth of the lake herring have made collections throughout the year, information on the time of formation of the annulus or year-mark is scanty. A certain amount of data is available, however, on the annulus formation of species closely related to the lake herring.

Van Oosten (1923), studying scales taken at monthly intervals from whitefish (*Coregonus clupeaformis*) kept at the New York Aquarium, demonstrated that the annulus was completed by resumption of growth in March or April and that these fish ceased growing in August or September. He suggested that rising temperature was probably the primary cause of the resumption of growth and the development of sex products causes retardation or cessation of scale growth in late summer. In a later report Van Oosten (1929, p. 345) commented on annulus formation in the lake herring of Saginaw Bay that "* * * inasmuch as the formation of an annulus is causally related to the retardation of growth, it is safe to assume that in nature, too, the annulus of these species forms during the winter period." He left open the question as to just when in the winter the annulus does form. In his study of growth of the Lake Nipissing cisco Fry (1937, p. 18) stated that "Scales from fish captured in early spring place the date of the completion of the annulus, or rather of the initiation of the new season's growth, at some time in May." Dannevig and Dannevig (1937, p. 198), however, stated that in the brown trout (*Salmo trutta*) of southern Norway "The general opinion that the narrow ridges are formed during autumn and winter as a result of low temperatures does not hold good." They showed that in two lakes the scales of most trout had new growth outside a year-mark in the spring, whereas in two other lakes new growth occurred in the fall. They also reported that some annulus formation took place every month of the year. Although these findings are not directly applicable, it is believed that some of the characteristics of this not too-distantly related group are reflected in the scale growth of Green Bay lake herring.

From the data on annulus formation in the lake herring of Green Bay (table 12) it is seen that some fish had started new growth as early as May 8, the date of the earliest collection other than the midwinter samples in which no fish exhibited new growth. As the season progressed the percentage of fish with completed annuli increased, but a few individuals still gave no indication of new growth as late as June 19 to 21. In a July 13, 1950, sample and in all collections later than that date, annulus formation was complete.[4]

The data of table 12 indicate further that the younger fish form annuli earlier than do the older ones. With only the exceptions of the III-group and VI-group (a single fish) of the June 19–21 collections, the percentage of lake herring with new growth decreased with age. That this relation between age and time of annulus formation may be general among fish is indicated by observations in carp, *Cyprinus carpio*, by Frey (1942); white crappie, *Pomoxis annularis*, by Hanson

[4] Collections of June 21–22, 1950, have been excluded in this consideration. Fewer than half of the lake herring in these collections had completed annuli, but examination of the scales showed them to be much undersized; obviously the scales were removed from the back near the dorsal fin and thus came from a body region above that from which scales were regularly taken.

TABLE 12.—*Percentage of lake herring with completed annuli collected from pound nets during period of annulus formation*

[Number of fish in parentheses]

Date	Percentage with completed annuli in age group—					
	II	III	IV	V	VI	VII
May 8, 1951	100 (1)	46 (24)	14 (104)	0 (13)	------	------
May 13, 1949	------	55 (72)	4 (321)	0 (40)	0 (6)	------
May 26, 1948	100 (4)	45 (141)	20 (110)	29 (7)	------	------
June 19–21, 1951	73 (11)	79 (17)	63 (62)	50 (12)	100 (1)	0 (1)

(1937); rock bass, *Ambloplites rupestris*, by Hile (1941); and the Atlantic herring, *Clupea harengus*, by Hodgson (1924).

It appears also that within an age group the smaller fish tend to start the season's growth earlier than do the larger ones (table 13). With only three exceptions (age group IV of the May 8 sample and age groups III and V of the June 19–21 collections—the last two age groups represented by few fish), the lake herring that exhibited new growth had averaged smaller at the end of the preceding season than had fish whose current season's growth had not yet started. In some age groups the current-season increment was sufficiently great to eliminate the original difference of average length.

The relatively long period of annulus formation (at least 6 weeks and probably longer) and the correlation between age and the onset of new growth necessitate care in the determination of age for fish captured early in the growing season. For some individuals it may be difficult or even impossible to decide whether marginal growth represents a small full-season increment of the preceding year or unusually rapid growth made during the current season.

PROGRESS OF SEASON'S GROWTH

The data on the amount of growth and on the percentage of the season's growth completed on various dates of capture (table 14) exhibit some irregularities in trend, and on some dates rather large discrepancies occur among the figures for different age groups.[5] To some extent these irregularities and discrepancies can be attributed to the

[5] Collections of June 21–22, 1950, were omitted because of abnormal scale size which might have affected the computation of growth increments—see footnote 4 (p. 100).

TABLE 13.—*Relation between onset of new growth and total length of lake herring taken in pound nets during period of annulus formation, by age group, 1948–51*

[Length in inches]

Scale margin	Number of fish	Length before start of growth [1]	Total length at capture	Increment of new growth
May 26, 1948:				
Age group III:				
Not growing	77	10.31	10.31	----------
Growing	64	10.11	10.40	0.29
Age group IV:				
Not growing	88	10.64	10.64	----------
Growing	22	10.37	10.61	0.24
Age group V:				
Not growing	5	11.58	11.58	----------
Growing	2	11.40	11.55	0.15
May 13, 1949:				
Age group III:				
Not growing	32	10.63	10.63	----------
Growing	40	10.12	10.54	0.42
Age group IV:				
Not growing	308	10.81	10.81	----------
Growing	13	10.39	10.69	0.30
June 21–22, 1950:				
Age group III:				
Not growing	6	10.02	10.02	----------
Growing	3	10.17	10.53	0.36
Age group IV:				
Not growing	55	10.70	10.70	----------
Growing	8	10.44	10.69	0.15
May 8, 1951:				
Age group III:				
Not growing	13	10.68	10.68	----------
Growing	11	10.66	11.00	0.34
Age group IV:				
Not growing	89	11.11	11.11	----------
Growing	15	11.29	11.49	0.20
June 19–21, 1951:				
Age group II:				
Not growing	3	7.30	7.30	----------
Growing	8	8.24	8.50	0.26
Age group III:				
Not growing	2	10.85	10.85	----------
Growing	15	10.06	10.52	0.46
Age group IV:				
Not growing	23	10.75	10.75	----------
Growing	39	10.39	10.73	0.34
Age group V:				
Not growing	6	11.08	11.08	----------
Growing	6	11.48	11.73	0.25

[1] Length of growing fish calculated by scale measurement of recently formed annulus.

small numbers of fish in certain age groups. Another possible source of bias lies in the fact that collections were made in different calendar years in which the progress of growth may have been dissimilar. A real correlation appears to exist, however, between age and percentage of growth completed in samples captured during the period of annulus formation. In collections taken before July 13, for example, the percentage of growth completed decreased as age increased with only one exception—the III-group of the June 19–21 samples. In this collection, the II-group probably was not representative, because the actual amount of growth and the percentages were both smaller than in May.

Another factor bearing on the data of table 14 that should be mentioned, even though it cannot be evaluated, concerns the validity of the base employed for the computation of the percentages.

TABLE 14.—*Amount of season's growth in length completed by age groups, individually and combined, on various dates of capture*

[Expressed as calculated increments (inches) and as percentages of the full-season growth determined from samples of the same year class taken in January and February of the following calendar year]

Date and age group	Number of fish	Average new growth	Full-season growth	Percentage of growth completed
May 8, 1951:				
II	1	0.50	2.04	24.5
III	24	.15	1.33	11.3
IV	104	.03	1.05	2.9
Average percent	139			4.6
May 13, 1949:				
III	72	0.23	1.12	20.5
IV	321	.01	.89	1.1
Average percent	393			4.7
May 26, 1948:				
II	4	0.27	1.68	16.1
III	141	.13	1.03	12.6
IV	110	.05	.89	5.6
Average percent	255			9.6
June 19–21, 1951:				
II	11	0.19	2.04	9.3
III	17	.41	1.33	30.8
IV	62	.23	1.05	21.9
Average percent	90			22.0
July 13, 1950:				
II	1	0.70	2.04	34.3
III	17	.54	1.26	43.2
IV	21	.41	.95	43.2
Average percent	39			43.0
Aug. 20, 1951:				
II	15	1.27	2.04	62.3
III	17	1.18	1.33	88.7
IV	23	.87	1.05	82.9
Average percent	55			79.1
Sept. 14, 1950:				
II	6	1.48	2.04	72.5
III	107	.92	1.26	73.0
IV	78	.66	.95	69.5
Average percent	191			71.6
Oct. 5, 1949:				
II	19	1.72	1.76	97.7
III	212	1.09	1.12	97.3
IV	42	.93	.89	104.5
Average percent	273			98.4
Nov. 14, 1951:				
II	3	1.77	2.04	86.8
III	67	1.27	1.33	95.5
IV	8	1.20	1.05	114.3
Average percent	78			97.1
Nov. 29–Dec. 4, 1950:				
II	18	2.02	2.04	99.0
III	229	1.18	1.26	93.7
IV	75	.91	.95	95.8
Average percent	322			94.5

The full-season increments given in the table were determined from samples of the same year class taken in January and February of the next calendar year. A better estimate of the full-season growth could not be derived from the materials at hand. It will be brought out in a later section on seasonal changes in style of growth that the fishery removes lake herring selectively according to individual growth rate. By reason of this selective destruction, the early-winter samples may not be truly descriptive of the course of growth that would have taken place in an unexploited population. There is no reason to believe, however, that this source of bias has seriously affected the estimates of progress of the season's growth.

Despite the difficulties and possible sources of bias just discussed, the data of table 14 can be used to form a general idea of the normal course of the season's growth of lake herring. That this growth does follow a distinct and reasonably definite course is indicated by the unweighted means of the percentages of growth completed for the different dates of collection. These percentages are given graphically in figure 4; in the same figure a curve has been fitted by inspection to the empirical data. The progress of growth probably can be described best from the following percentages obtained from the curve.

Period of growth	Percentage of season's growth completed—	
	During period	At end of period
Before June	11	11
June	20	31
July	25	56
August	19	75
September	14	89
October	8	97
After October	3	100

From the preceding table it is seen that the greatest amount of growth in any single month took place in July (25 percent) and that the summer months, June to August, accounted for 64

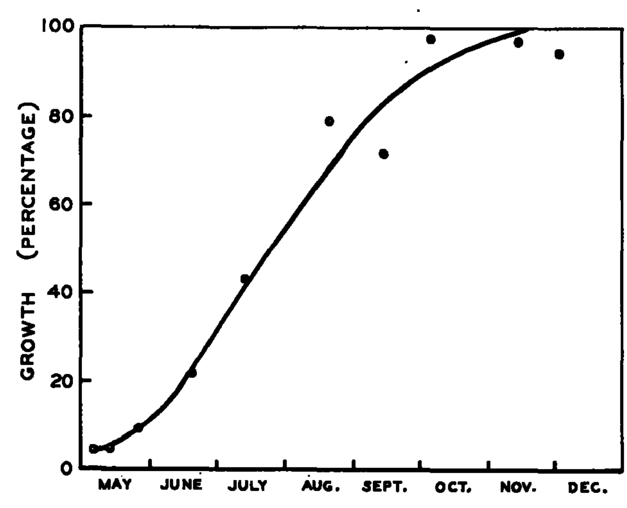

FIGURE 4.—Percentage of season's growth completed at time of capture. The dots show empirical data; the curve was drawn by inspection.

percent of the season's total. Growth started sometime in May (this belief is supported by earlier data on annulus formation) and for practical purposes it was complete at the end of October.

Hile (1936) made observations on midsummer progress of the season's growth in cisco populations of four Wisconsin lakes by a procedure similar to that just described. He found that growth had been completed by the end of July in Trout Lake and by the end of August in Muskellunge Lake, but in Silver Lake only two-thirds to three-fourths of the growth was completed in August. In Clear Lake, males had completed 64 percent of their season's growth in July and 81 percent in September and the females had completed 68 and 76 percent, respectively, in these months. Although no sex difference could be found in the progress of growth of the Green Bay lake herring, the trend did not differ greatly from that of the Clear Lake stock.

GROWTH CHARACTERISTICS OF LAKE HERRING IN GREEN BAY

Among the principal factors that must be considered in an analysis of the growth of lake herring in Green Bay are sex differences, either natural or resulting from selective destruction in the commercial fishery; correlation of growth rate with natural or fishery mortality; and geographical variation within the bay. The influence of each of these factors must be known in order to interpret properly the growth of the entire population.

Sex differences in growth

Only one of four stocks of ciscoes from northern Wisconsin lakes studied by Hile (1936) exhibited sex difference in growth rate. No significant differences in growth of males and females were found by Carlander (1945), Cooper (1937), Eddy and Carlander (1942), Stone (1938), or Van Oosten (1929) in populations of lake herring studied by them. Fry (1937, p. 65) did not discuss the influence of sex on growth rate but his data showed no consistent differences in calculated growth of the sexes up to age group VII beyond which males tended to be larger. Since Van Oosten and Stone used fish from pound nets, whereas the collections of the other authors were taken with gill nets, it appears that estimates of growth by males and females are not distorted by collecting methods. Differences in growth of the sexes in samples of the Green Bay lake herring population, though occasionally large, were distributed irregularly, showed no definite pattern, and favored neither sex. They disappeared almost completely in the best-represented age groups in the combined samples from pound nets (table 15) and gill nets (table 16). The sexes are accordingly combined in all subsequent treatment of growth data.

TABLE 15.—*Comparison of growth of male and female lake herring of age groups III and IV taken in pound nets, 1949–51*

[Calculated total length in inches]

Age group and sex	Number of fish	Length at end of year of life—			
		1	2	3	4
Age group III:					
1949:					
Males	123	5.5	8.1	9.9	------
Females	203	5.5	8.1	9.9	------
1950:					
Males	173	5.5	8.0	9.9	------
Females	164	5.3	8.0	9.8	------
Age group IV:					
1949:					
Males	242	5.4	7.9	9.5	10.6
Females	377	5.4	7.9	9.5	10.6
1950:					
Males	262	5.2	7.6	9.3	10.5
Females	332	5.2	7.7	9.3	10.5
1951:					
Males	255	5.2	7.7	9.5	10.8
Females	283	5.2	7.7	9.5	10.8

TABLE 16.—*Comparison of growth of male and female lake herring of age groups III and IV taken in gill nets, 1951–52*

[Calculated total length in inches]

Age group and sex	Number of fish	Length at end of year of life—			
		1	2	3	4
Age group III:					
1952: [1]					
Males	100	5.5	8.0	9.8	------
Females	74	5.3	8.0	9.8	------
Age group IV:					
1951: [2]					
Males	62	5.5	8.0	9.8	11.0
Females	79	5.4	8.1	9.9	11.1
1952: [1]					
Males	138	5.1	7.5	9.3	10.5
Females	117	5.0	7.5	9.3	10.6

[1] Collected from 2-inch-mesh experimental gill nets.
[2] Collected from 2⅜-inch and 2½-inch-mesh commercial gill nets.

Effect of gear selection on estimation of growth

From a review of the literature and from his own data Hile (1936, pp. 298, 306) held 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.

Hile concluded that—

* * * if these selected groups are eliminated the remaining growth data can be considered accurate and trustworthy within very narrow limits.

If Hile's assumptions are correct we should find close agreement between growth of best-represented age groups of herring taken in gill nets and herring of the same ages taken in the less-selective pound nets. This expectation is fulfilled by the data of table 17. Growth of the best represented age groups (III, IV, and V) was almost identical in pound-net and gill-net samples. In shorter age groups, I and II, the greater calculated lengths of herring from gill-net samples indicate that the larger, faster-growing individuals are selected by gill nets. This tendency for herring caught in gill nets to be larger than those taken in pound nets is still present though somewhat reduced in age group III. Because the effects of gill-net selection extends to ages as high as the III-group (which is frequently dominant), most detailed analyses of growth in later sections have been based on pound-net samples alone.

TABLE 17.—*Comparison of growth of lake herring taken in pound nets and in gill nets, by age groups*

[Calculated total length in inches]

Net [1]	Number of fish	Length at end of year of life—					
		1	2	3	4	5	6
Age group I:							
Pound	16	5.1					
Gill	2	6.2					
Age group II:							
Pound	78	5.2	8.1				
Gill	15	5.8	9.0				
Age group III:							
Pound	906	5.4	8.1	9.9			
Gill	404	5.5	8.2	10.0			
Age group IV:							
Pound	2,018	5.3	7.8	9.5	10.6		
Gill	475	5.2	7.8	9.5	10.7		
Age group V:							
Pound	208	5.0	7.4	8.9	10.1	11.0	
Gill	59	4.9	7.3	9.0	10.2	11.2	
Age group VI:							
Pound	11	5.0	7.8	9.7	11.0	12.1	13.1
Gill	1	5.3	7.1	8.6	10.2	11.3	12.0

[1] Collections from pound nets in 1948–52, and from 2 to 2½-inch-mesh experimental and commercial gill nets in 1948 and 1950–52.

Seasonal differences

The apparently slow growth indicated by small differences between lengths of lake herring of different age groups at capture, brought out in a previous discussion of the length frequencies of age groups, again suggests the possibility of selective destruction of fish of more rapid growth by the commercial fishery. If such a selective destruction is taking place and is strong, it should result in growth differences detectable in samples taken in the same year but several months apart. That selective destruction was sufficiently great to influence estimates of growth is indicated by the data of table 18. In every comparison, except the third year of life in the III-group taken in 1949, fish caught earlier in the year had higher calculated lengths than did those taken later. In 14 of 18 comparisons the advantage of the early-season over the late-season fish amounted to 0.4 inch or more. Because of the seasonal differences in growth patterns in fish of the same age group it is necessary to stratify samples according to seasons when making discriminating comparisons.

TABLE 18.—*Comparison of growth of lake herring, by age group, taken in pound nets at different seasons, 1949–51*

[Calculated total length in inches]

Location and date of capture	Number of fish	Length at capture	Length at end of year of life—			
			1	2	3	4
SOUTHERN GREEN BAY						
Age group III:						
Feb. 16, 1949	42	10.3	6.0	8.6	10.3	
Oct. 5, 1949	212	10.8	5.2	7.9	10.3	
Age group IV:						
Feb. 16, 1949	256	10.4	5.5	7.9	9.4	10.4
Oct. 5, 1949	42	11.2	4.8	7.4	9.0	10.3
NORTHERN GREEN BAY						
Age group III:						
Feb. 27, 1950	23	10.2	5.5	8.4	10.2	
Nov. 29, 1950	73	10.7	5.3	7.8	9.7	
Age group IV:						
Feb. 27, 1950	133	10.5	5.0	7.7	9.3	10.5
Nov. 29, 1950	31	11.0	4.9	7.3	8.9	10.1
Feb. 20, 1951	172	10.7	5.2	7.7	9.4	10.7
Aug. 20, 1951	23	11.1	4.8	7.3	9.0	10.3

Geographic differences

That environmental conditions must differ in the various parts of Green Bay is obvious (see General Features of Green Bay, p. 88). If environmental conditions influence growth and if the population is not regularly mixed by active migration or passive transport with currents, differences in the growth of lake herring captured in various sections of Green Bay should be detectable.

Differences between growth in northern and southern waters of the bay are indicated by comparisons of lake herring taken in pound nets at the same time of year at locations separated by considerable distances (table 19). In 10 comparisons of size at capture for fish of the same age, northern fish were shorter in six, and longer in two; lengths of the remaining two groups were

TABLE 19.—*Comparison of growth of lake herring, by age groups, taken in pound nets at the same time of year at different locations*

[Calculated total length in inches]

Date and locality	Area	Number of fish	Length at capture	Length at end of year of life—					Length increment				
				1	2	3	4	5	1	2	3	4	5
Feb. 22-27, 1950:													
Age group III:													
Escanaba	North	23	10.2	5.5	8.4	10.2			5.5	2.9	1.8		
Schumachers Point	South	33	10.3	5.9	8.6	10.3			5.9	2.7	1.7		
Age group IV:													
Escanaba	North	245	10.5	5.0	7.5	9.3	10.5		5.0	2.5	1.8	1.2	
Schumachers Point	South	133	10.5	5.4	7.9	9.5	10.5		5.4	2.5	1.6	1.0	
Age group V:													
Escanaba	North	9	11.5	4.8	7.4	9.1	10.5	11.5	4.8	2.6	1.7	1.4	1.0
Schumachers Point	South	59	10.8	5.0	7.2	8.7	9.9	10.8	5.0	2.2	1.5	1.2	0.9
Nov. 29-Dec. 4, 1950:													
Age group III:													
Fox	North	73	10.7	5.3	7.8	9.7			5.3	2.5	1.9		
Sister Bay	South	78	10.8	5.5	7.9	9.7			5.5	2.4	1.8		
Age group IV:													
Fox	North	31	11.0	4.9	7.3	8.9	10.1		4.9	2.4	1.6	1.2	
Sister Bay	South	23	10.9	5.2	7.5	9.0	10.1		5.2	2.3	1.5	1.1	
Feb. 20-22, 1951:													
Age group III:													
Ingallston	North	6	10.0	5.3	7.9	10.0			5.3	2.6	2.1		
Schumachers Point	South	22	10.7	5.8	8.7	10.7			5.8	2.9	2.0		
Age group IV:													
Ingallston	North	172	10.7	5.2	7.7	9.6	10.7		5.2	2.5	1.9	1.1	
Schumachers Point	South	154	10.9	5.4	7.9	9.7	10.9		5.4	2.5	1.8	1.2	
Age group V:													
Ingallston	North	41	11.1	4.8	7.2	8.8	10.1	11.1	4.8	2.4	1.6	1.3	1.0
Schumachers Point	South	12	11.5	5.0	7.5	9.0	10.4	11.5	5.0	2.5	1.5	1.4	1.1
Jan. 21-22, 1952:													
Age group III:													
Escanaba	North	79	11.1	5.0	7.7	9.7	11.1		5.0	2.7	2.0	1.4	
Pensaukee	South	76	11.1	5.5	8.0	9.8	11.1		5.5	2.5	1.8	1.3	
Age group IV:													
Escanaba	North	8	11.0	4.5	6.9	8.6	9.8	11.0	4.5	2.4	1.7	1.2	1.2
Pensaukee	South	7	11.5	5.1	7.7	9.3	10.6	11.5	5.1	2.6	1.6	1.3	0.9

equal in the two areas. Differences between growth of lake herring from northern and southern localities are much more apparent in the calculated lengths. Without exception northern fish grew less in their first year than did southern fish. Although growth increments of the northern fish were predominantly larger than those of southern fish in the second year and were without exception greater in the third year, the initial handicap of slower growth in the first year was overcome by the end of the third year of life in only 2 of 10 pairs of samples. By the end of the fourth year, however, the initial differences in size in the two areas had largely disappeared.

The significance of this comparison may be questionable in the light of information brought out in a later discussion (Growth Compensation, p. 109), that fish with poor first-year growth also tend to be slightly shorter at capture than fish having better growth in the first year. It is possible then that differences between calculated lengths of lake herring in northern and southern samples may be a reflection of differences in the length at capture. That such an explanation is not adequate is indicated, however, in the data of table 20 which gives comparisons of the growth histories of fish of the same age in the same ½-inch length interval. Northern Green Bay fish of the same length and age as the southern Green Bay fish at capture tended to be shorter than the southern at the ends of their first, second, and third years of life; but after the first growing season northern fish usually grew more than southern fish. This similarity of growth differences in selected length intervals and entire age groups is evidence that northern and southern fish do have different patterns of growth. The hypothesis of a north-south gradient is suggested by the fact that differences in first year's growth are greater in samples taken farther apart.

Annual fluctuations in growth rate

Since calculated growth histories of lake herring in Green Bay differ according to season and geographical location, studies of annual fluctuations in growth must be based on samples taken in the same location at the same time each year. The series of samples that best met these requirements were taken in the southern part of Green Bay in January or February in the years 1949 to 1952. The materials for the study of annual fluctuations in the growth based on these collec-

TABLE 20.—*Comparison of growth of lake herring, of same age and length at capture, taken in pound nets at the same time of year at different locations*

[Calculated total length in inches]

Length group and locality	Number of fish	Length at capture	Length at end of year of life—				Length increment			
			1	2	3	4	1	2	3	4
Feb. 22–27, 1950:										
Age group IV; 10.0–10.4 in.:										
Escanaba (north)	47	10.2	5.0	7.3	9.0	10.2	5.0	2.3	1.7	1.2
Schumachers Point (south)	91	10.3	5.2	7.6	9.2	10.3	5.2	2.4	1.6	1.1
Age group IV; 10.5–10.9 in.:										
Escanaba (north)	37	10.7	5.0	7.6	9.4	10.7	5.0	2.6	1.8	1.3
Schumachers Point (south)	106	10.7	5.5	8.0	9.6	10.7	5.5	2.5	1.6	1.1
Age group IV; 11.0–11.4 in.:										
Escanaba (north)	27	11.3	5.1	7.9	9.9	11.3	5.1	2.8	2.0	1.4
Schumachers Point (south)	32	11.2	5.6	8.3	10.0	11.2	5.6	2.7	1.7	1.2
Nov. 29–Dec. 4, 1950:										
Age group III; 10.0–10.4 in.:										
Fox (north)	16	10.3	5.1	7.5	9.3	-------	5.1	2.4	1.8	-------
Sister Bay (south)	8	10.3	4.9	7.3	9.3	-------	4.9	2.4	2.0	-------
Age group III; 10.5–10.9 in.:										
Fox (north)	35	10.7	5.4	7.9	9.7	-------	5.4	2.5	1.8	-------
Sister Bay (south)	44	10.7	5.5	7.9	9.6	-------	5.5	2.4	1.7	-------
Age group III; 11.0–11.4 in.:										
Fox (north)	18	11.1	5.2	7.9	9.9	-------	5.2	2.7	2.0	-------
Sister Bay (south)	21	11.1	5.6	8.1	9.9	-------	5.6	2.5	1.8	-------
Feb. 20–22, 1951;										
Age group IV; 10.0–10.4 in.:										
Ingallston (north)	33	10.3	5.1	7.4	9.0	10.3	5.1	2.3	1.6	1.3
Schumachers Point (south)	9	10.2	5.2	7.5	9.0	10.2	5.2	2.3	1.5	1.2
Age group IV; 10.5–10.9 in.:										
Ingallston (north)	74	10.7	5.1	7.7	9.4	10.7	5.1	2.6	1.7	1.3
Schumachers Point (south)	68	10.7	5.4	7.8	9.5	10.7	5.4	2.4	1.7	1.2
Age group IV; 11.0–11.4 in.:										
Ingallston (north)	43	11.1	5.4	8.0	9.8	11.1	5.4	2.6	1.8	1.3
Schumachers Point (south)	63	11.1	5.4	8.0	9.8	11.1	5.4	2.6	1.8	1.3
Jan. 21–22, 1952:										
Age group IV; 10.5–10.9 in.:										
Escanaba (north)	20	10.7	4.8	7.5	9.4	10.7	4.8	2.7	1.9	1.3
Pensaukee (south)	28	10.8	5.3	7.7	9.6	10.8	5.3	2.4	1.9	1.2
Age group IV; 11.0–11.4 in.:										
Escanaba (north)	32	11.2	5.1	7.8	9.8	11.2	5.1	2.7	2.0	1.4
Pensaukee (south)	33	11.1	5.6	8.2	9.9	11.1	5.6	2.6	1.7	1.2
Age group IV; 11.5–11.9 in.:										
Escanaba (north)	15	11.7	5.2	8.3	10.2	11.7	5.2	2.1	1.9	1.5
Pensaukee (south)	13	11.6	5.8	8.4	10.3	11.6	5.8	2.6	1.9	1.3

tions (table 21) are so arranged that in each section of the table the vertical columns show the calculated growth in different years of life but in the same calendar year, the horizontal rows give a comparison of the growth in different calendar years for the same year of life, and each diagonal row gives the growth history of a single year class. For the quantitative determination of annual fluctuations of growth the data were subjected to the analysis described by Hile (1941), a procedure involving the determination of the percentage change in growth from each year to the next. The chain of estimates thus obtained was then adjusted to a mean of 0.0 for the period of years covered by the data (table 22). The fluctuations show a trend toward an improvement of growth during the period covered and show a possible tendency to be cyclic. From a value slightly below average in 1944 (−2.1 percent), growth declined to a minimum of −6.5 in 1946 (fig. 5). The year 1947 was the first in a 4-year period of improvement that culminated in growth 9.1 percent above average in 1950.

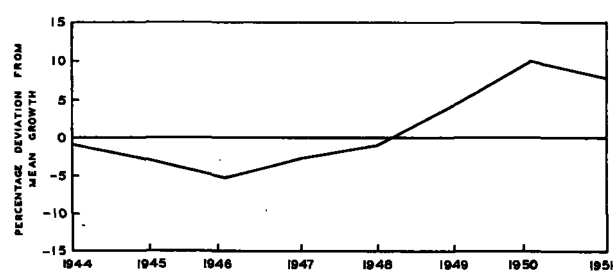

FIGURE 5.—Fluctuation of growth in length of lake herring from the 1944–51 mean.

Temperature is commonly considered an important factor in the determination of fluctuations in growth. Hile (1936, pp. 276–280) discussed the possible influence of air temperature on the growth of cisco populations in northeastern Wisconsin lakes and cited works of several authors who found a positive correlation between summer temperatures and the amount of growth of several European species of coregonids. Concerning the Wisconsin cisco populations Hile concluded—

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.

Van Oosten (1929) found no correlation between annual fluctuations in first-year growth and annual fluctuations in the air temperatures during the growing season for Saginaw Bay lake herring. More recently, Svärdson (1951) has shown that the growth of whitefish in Sweden was greater in hot summers than in cool.

The data for the Green Bay lake herring (table 22) give no evidence of a definite relation between fluctuations of growth and deviations of mean air temperatures or population density over the 8-year period 1944 to 1951.

TABLE 21.—*Annual calculated growth increments of lake herring from pound nets in southern Green Bay in January or February, 1949–52*

Age group and year of life	Annual growth increment (inches) in—							
	1944	1945	1946	1947	1948	1949	1950	1951
Age group III:								
3d year					1.7	1.7	2.0	2.0
2d year				2.6	2.7	2.9	2.9	
1st year			6.0	5.9	5.8	6.0		
Age group IV:								
4th year					1.0	1.0	1.2	1.3
3d year				1.5	1.6	1.8	1.8	
2d year			2.4	2.5	2.5	2.5		
1st year		5.5	5.4	5.4	5.5			
Age group V:								
5th year					0.8	0.9	1.1	0.9
4th year				1.1	1.2	1.4	1.3	
3d year			1.3	1.5	1.5	1.6		
2d year		2.4	2.2	2.5	2.6			
1st year	5.1	5.0	5.0	5.1				
Number of fish in age group:								
III			42	33	22	6		
IV		256	245	154	76			
V	47	59	12	7				

TABLE 22.—*Deviation of growth, air temperature during the growing season (May–October), and abundance of lake herring in southern Green Bay, from the average for the 8-year period, 1944–51*

Year	Percentage growth deviation	Mean temperature deviation ° F.[1]	Abundance[2]
1944	−2.1	2.0	−63
1945	−4.1	−1.8	−36
1946	−6.5	−0.1	24
1947	−3.8	1.4	24
1948	−2.1	0.8	28
1949	3.1	1.8	14
1950	9.1	−2.1	5
1951	6.7	−2.0	4

[1] Mean monthly deviations of air temperatures for the period May-October recorded by U. S. Weather Bureau at Green Bay, Wisconsin.
[2] Percentage deviation from average catch per unit-of-effort in pound and gill nets computed from Wisconsin commercial catch records for southern Green Bay (Wisconsin commercial fishing district M-1).

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Discrepancies in calculated growth

The systematic discrepancies among calculated growth histories of different age groups already noted for the Green Bay lake herring are a frequent, almost regular, characteristic of data on growth of fish. These differences occur among different age groups of the same year class as well as among age groups of different year classes. The pattern of the discrepancies varies from species to species and stock to stock. Most common is that which goes under the name of Lee's phenomenon of "apparent decrease of growth," in which the estimates of length at the end of various years of life decrease with increase in the age of the fish on which the estimate is based. In this "typical" situation, the calculated lengths in the earlier years of life show the greatest disagreements. More recent authors have tended to depart from this definition and to apply the term "Lee's phenomenon" to all systematic discrepancies among calculated lengths.

The literature on causes of Lee's phenomenon, in both the restricted and the broader sense, is extensive and to a considerable degree controversial. A review of the subject at this time could serve little purpose.[6] It may be useful, nevertheless, to list the principal factors that have been offered in explanation of systematic discrepancies in calculated lengths. These several factors, the significance of which will become clearer from later discussions, are as follows:

1. Use of wrong formula for growth calculations.

2. Selective action of fishing gear.

3. Biological segregation on basis of size or maturity.

4. Higher mortality rate (natural or in the fishery) of the fish with the more rapid growth.

In the consideration of discrepancies among calculated lengths of Green Bay lake herring, the first of these items is not significant since the validity of the method of calculation was established by a study of the body-scale relationship. The effects of gear selectivity (item 2) can be rendered insignificant by confining studies of growth discrepancies to samples taken by pound nets, which, as has been pointed out, were capable of capturing fish smaller than the smallest herring

[6] See Van Oosten (1929) and Hile (1936) for detailed discussions of the problem.

TABLE 23.—*Calculated total length of lake herring at the end of each year of life, by age group and year class, 1943–50*

[Pound-net samples only. Length in inches]

Year class and year of capture	Age group	Number of fish	Length at end of year of life—						
			1	2	3	4	5	6	7
1950 year class:									
1951	I	6	4.3						
1949 year class:									
1950	I	8	5.7						
1951	II	35	4.4	7.3					
1952	III	7	5.9	8.7	10.8				
1948 year class:									
1949	I	2	5.2						
1950	II	20	5.8	8.5					
1951	III	119	5.4	8.0	9.9				
1952	IV	155	5.3	7.9	9.7	11.1			
1947 year class:									
1949	II	19	5.8	8.9					
1950	III	340	5.4	8.0	9.8				
1951	IV	561	5.2	7.7	9.5	10.8			
1952	V	15	4.8	7.2	8.9	10.2	11.2		
1946 year class:									
1948	II	4	5.9	9.7					
1949	III	326	5.5	8.1	9.9				
1950	IV	594	5.2	7.7	9.3	10.5			
1951	V	83	4.9	7.4	9.0	10.3	11.3		
1952	VI	1	4.8	7.8	9.6	10.8	11.9	12.6	
1945 year class:									
1948	III	141	5.9	8.2	10.2				
1949	IV	619	5.4	7.9	9.5	10.6			
1950	V	88	4.9	7.3	8.8	10.0	10.9		
1951	VI	1	6.1	9.7	11.9	13.3	14.8	16.3	
1944 year class:									
1948	IV	110	5.1	7.7	9.6	10.6			
1949	V	89	5.1	7.4	8.8	9.9	10.9		
1950	VI	6	5.0	7.9	9.7	11.1	12.3	13.3	
1951	VII	1	5.0	8.3	10.0	11.3	12.6	13.6	14.6
1943 year class:									
1948	V	7	5.2	8.0	9.6	10.6	11.5		
1949	VI	3	4.8	7.5	8.9	10.1	11.0	12.0	

appearing in the samples. Such discrepancies as do appear, therefore, are to be attributed principally to factors 3 and 4.

The inconsistencies among the calculated growth histories of the different age groups of the several year classes [7] of the Green Bay lake herring (table 23) differ from Lee's phenomenon as originally described (Lee 1920). It is true that the estimates of length for a particular year of life did tend to decrease with increase in age of fish on which estimates were based. On the other hand, the size of the differences did not decrease with increase in the number of years of life as is characteristic of Lee's phenomenon. In all but one comparison between age groups represented by 15 or more fish the estimate of first-year length decreased with increase of age (the one exception is in age groups IV and V of the 1944 year class). The trends were similar for the second-, third-, and fourth-year calculated lengths, but exceptions were more numerous.

[7] The most discriminating comparisons are those among different age groups of the same year class, since these are not biased by annual fluctuations in growth.

It is believed that the discrepancies among the calculated lengths of the age groups of the Green Bay lake herring represent the combined effects of segregation according to size within the population and of selective destruction of the faster-growing individuals in the fishery made possible by that segregation. Because of the connection between these two factors it is difficult to judge their relative importance. In fact, an attempt to separate the two is not desirable, since they are essentially parts of a single process.

In the younger age groups, only the largest fish (a small percentage of the total) enter the pound-net fishery. (Note the small representation of age groups I and II in collections—table 17). Selection in the gill-net fishery is similar (table 17), but the effects of selective destruction probably occur later in gill nets than in pound nets. This biological selection (plus gear selection in gill nets) leads to the overestimation of the rate of growth in those age groups. At the same time, destruction of the larger, fast-growing fish modifies the growth characteristics exhibited by the remaining stock. As members of a year class grow older, bias to the immediate sample resulting from the selective capture of the larger fish declines, but the cumulative effects of destruction of the faster-growing individuals become increasingly important.

Ten populations of *Leucichthys artedi*, for which various authors have given figures of calculated growth of different age groups, have all exhibited Lee's phenomenon to some degree. Disagreements were large in only one of four cisco populations in northeast Wisconsin (Hile 1936). In the Irondequoit Bay cisco population the growth rate decreased with increased age among the younger age groups, but differences were random at the higher ages (Stone 1938). Fry (1937) found only small discrepancies among the estimates of the first-year growth of the Lake Nipissing cisco, but disagreements were large in later years.

The variation in the nature of the discrepancies in calculated growth of fish of different age in the several populations leads to the conclusion that the causes of Lee's phenomenon are not the same in all populations. Principal explanations of the phenomenon in lake herring advanced by various authors are—

1. Selective action of gill nets used in collecting samples.

2. Segregation as to maturity during the spawning run.

3. Segregation as to size, independent of maturity.

4. Higher mortality rate among fast-growing fish than among slow-growing.

Hile (1936) found that discrepancies in the calculated lengths of ciscoes in three of four Wisconsin lakes were the result of faulty sampling traceable to selective action of gill nets. Carlander (1945) attributed Lee's phenomenon in ciscoes of Lake of the Woods, Minnesota, to the selectivity of large-mesh gill nets, as well as to differential mortality of fast- and slow-growing fish as proposed by Hile (1936). Eddy and Carlander (1942) also found the phenomenon in ciscoes of Gull Lake, Minnesota.

Van Oosten (1929) and Cooper (1937), whose samples came from spawning-run lake herring in Saginaw Bay and Blind Lake, respectively, offered similar explanations of Lee's phenomenon. Their views are expressed adequately in the following quotation (p. 570) from Cooper's paper:

> * * * the lake herring first reaches maturity during its third, fourth, or fifth year of life, depending upon individual rate of growth; the more rapidly growing individuals of any one year class attain maturity first. It follows that the youngest year groups were represented in the catch (from the spawning grounds) only by their biggest individuals and, as older age groups were considered, more and more of those fish that had been smaller individuals in their earlier years appeared in the older groups. Therefore the younger age groups contained a larger proportion of fast-growing fish than did the older groups and, consequently, the computed lengths for the early years of life would be greater in the younger age groups than in the older. The persistence of the phenomenon in the older age groups (in groups in which all individuals are mature) may be explained on the basis of differential mortality, that is, on the assumption that the more rapidly growing fish die off earlier in life than the more slowly growing fish.

In Green Bay, as has been pointed out, segregation by size (and hence by rate of growth within a year class) appears to take place at all seasons.

Evidence was presented by Hile (1936) that a high natural mortality rate was correlated with rapid growth in the cisco population of Silver Lake. Cooper has suggested differential mortality as a possible factor in Lee's phenomenon. Hile also advanced the hypothesis that, if there was segragation of fast- and slow-growing fish with depth, the gill nets which were always fished on the bottom could not take equal samples of both. Fry (1937) demonstrated that faster-growing young fish were found in deeper waters of Lake Nipissing during the summer and were joined in successive years by more and more of the slower-growing members of the same year class. Behavior of this type explains why Lee's phenomenon might be found in samples taken in a certain location at a particular period of the year. Although a difference in seasonal distribution of fast- and slow-growing lake herring may exist in Green Bay and may be contributing to Lee's phenomenon there, it cannot be the main causative agent, because the phenomenon exists in samples collected at different depths and at different locations in the same and different seasons.

Growth compensation

Growth compensation—the tendency for the smaller fish at a particular age to have the more rapid subsequent growth—seems to be common among fish (Van Oosten 1929; Eddy and Carlander, 1942). The existence of growth compensation was mentioned in 4 of 14 publications on growth of lake herring (Carlander 1945, in Lake of the Woods tullibee; Eddy and Carlander, 1942, in the tullibee of 17 Minnesota lakes; Hile 1936, in the cisco of four Wisconsin lakes; and Van Oosten 1929, in the Saginaw Bay lake herring). Growth compensation seems to be a general occurrence in North American coregonids. It has been shown in the following stocks: Lake Michigan kiyi (*Leucichthys kiyi*) by Deason and Hile (1947); Reighard's chub (*L. reighardi*), longjaw cisco (*L. alpenae*) and bloater (*L. hoyi*) of Lake Michigan by Jobes (1943, 1949a, and 1949b); Lake Huron whitefish by Van Oosten (1939); and Lake Superior longjaw (*L. zenithicus*) by Van Oosten (1937). McHugh (1941) did not find growth compensation in several populations of Rocky Mountain whitefish (*Prosopium williamsoni*).

Of the authors who mentioned growth compensation in studies of lake herring only Hile (1936) and Van Oosten (1929) discussed its characteristics in any detail. Carlander (1945, p. 129) stated that—

> As was demonstrated for the ciscoes by Van Oosten (1929) and Hile (1936), growth compensation occurs in the Lake of the Woods tullibee but the compensation is not great enough to overcome any advantage in length which large individuals may hold at the end of the first year.

TABLE 24.—*Calculated growth of lake herring grouped by size in different years of life*

[Based on IV-group fish of Feb. 16, 1949, sample collected at Schumachers Point. Terminal groups contain 15 percent and middle groups 35 percent of total number of fish. Mean lengths for the year of life of grouping and corresponding growth increments are italicized. Maximum difference between lengths in parentheses]

Total length (inches)	Number of fish	Length at end of year of life—				Length increment			
		1	2	3	4[1]	1	2	3	4
1st year of life:									
3.7 to 4.9	38	*4.6*	7.4	9.1	10.3	*4.6*	2.8	1.7	1.2
4.9 to 5.5	90	*5.2*	7.7	9.3	10.3	*5.2*	2.5	1.6	1.0
5.5 to 6.0	90	*5.7*	8.1	9.5	10.5	*5.7*	2.4	1.4	1.0
6.0 to 6.7	38	*6.2*	8.5	9.8	10.8	*6.2*	2.3	1.3	1.0
		(1.6)	(1.1)	(0.7)	(0.5)				
2d year of life:									
6.0 to 7.4	38	5.0	*7.1*	8.9	10.1	5.0	*2.1*	1.8	1.2
7.4 to 7.9	90	5.3	*7.7*	9.3	10.4	5.3	*2.4*	1.6	1.1
7.9 to 8.4	90	5.6	*8.2*	9.6	10.5	5.6	*2.6*	1.4	0.9
8.4 to 9.4	38	6.0	*8.6*	9.9	10.9	6.0	*2.6*	1.3	1.0
		(1.0)	(1.5)	(1.0)	(0.8)				
3d year of life:									
8.1 to 9.0	38	5.0	7.2	*8.8*	10.0	5.0	2.2	*1.6*	1.2
9.0 to 9.4	90	5.3	7.7	*9.2*	10.2	5.3	2.4	*1.5*	1.0
9.4 to 9.9	90	5.6	8.1	*9.6*	10.5	5.6	2.5	*1.5*	0.9
9.9 to 10.9	38	5.8	8.4	*10.1*	11.1	5.8	2.6	*1.7*	1.0
		(0.8)	(1.2)	(1.3)	(1.1)				
4th year of life:									
9.3 to 10.0	38	5.2	7.4	8.9	*9.9*	5.2	2.2	1.5	*1.0*
10.0 to 10.4	90	5.4	7.8	9.2	*10.2*	5.4	2.4	1.4	*1.0*
10.4 to 10.9	90	5.6	8.0	9.5	*10.6*	5.6	2.4	1.5	*1.1*
10.9 to 12.1	38	5.7	8.3	10.0	*11.2*	5.7	2.6	1.7	*1.2*
		(0.5)	(0.9)	(1.1)	(1.3)				

[1] Length at capture.

The characteristics of growth compensation brought out by these authors for this species were similar, in that the shorter fish at the end of the first year of life tended to grow more in the following year than did the longer first-year fish. The studies demonstrated further that the initial advantage of the longer first-year fish was not completely overcome. This type of compensatory growth was also found in the Green Bay herring (table 24).

Previous investigators have examined the phenomenon of growth compensation by dividing fish into different length groups according to the first year's growth and comparing subsequent growth of these groups. It is not to be anticipated, however, that these first-year groupings will retain their identities in subsequent years; that is, individual growth will vary sufficiently so that a new grouping on a similar basis in later years will show some exchange of fish between the original groups. In lake herring both previous and subsequent growth of fish of the same length in a particular year of life varied widely (table 25). For example, the 47 lake herring that were 7.0 to 7.4 inches long in the second year of life had ranged from 3.5 to 5.9 inches in their first year and from 8.5 to 10.9 inches in their third year.

Because of the tendency for fish of a given length in a particular year of life to derive from fish of a considerable length range in earlier years and, in turn, to contribute to a wide range of length in subsequent years, it is to be anticipated that the growth of fish of different length groups will vary according to the year of life in which the grouping is made. This expectation is met by the data of table 24 in which length groupings of fish of a single age group are made on a similar basis (see caption of table) for each year of life. The maximum difference (difference between mean lengths of the terminal group) without exception was greatest for the year of grouping, and decreased consistently in previous and subsequent years of life. The decrease from the year of grouping toward earlier years reflects the diverse origin of the fish with respect to their positions in the length distributions in those earlier years. The decrease in the maximum difference in years of life following the year of grouping represents a tendency toward convergence of size.

Further information on these growth relationships is to be had from the annual growth increments of length shown at the right of table 24. Here it is seen that the increments in each year of life preceding the year of grouping tended to fall in the same order as in the grouping year itself, but that in subsequent years the increments tended to fall in the reverse order.

As a general biological phenomenon, growth compensation may reflect principles holding for

TABLE 25.—*Subsequent and/or previous frequency distribution of the calculated length of lake herring that had the same calculated length at the end of a particular year of life*

[Based on all age group III fish of the 1950 pound-net collections]

Year of grouping and calculated total length (inches)	Length frequency at end of year of life—											
	1	2	3	1	2	3	1	2	3	1	2	3
1st year of life:												
4.5 to 4.9	54											
5.0 to 5.4				90								
5.5 to 5.9							101					
6.0 to 6.4										65		
6.5 to 6.9		5			1			1				
7.0 to 7.4		22			17			3				
7.5 to 7.9		12	1		40			23			5	
8.0 to 8.4		9			30			51			28	
8.5 to 8.9		6	6		2	4		18	2		26	
9.0 to 9.4			15			17		2	10		4	2
9.5 to 9.9			19			44		2	35		2	21
10.0 to 10.4			10			20		1	41			23
10.5 to 10.9			3			5			10			17
11.0 to 11.4									2			2
12.0 to 12.4									1			
2d year of life:												
3.5 to 3.9	1											
4.0 to 4.4	4			1			1					
4.5 to 4.9	22			12			9			6		
5.0 to 5.4	17			40			30			2		
5.5 to 5.9	3			23			51			18		
6.0 to 6.4				5			28			26		
6.5 to 6.9							1			4		
7.0 to 7.4		47										
7.5 to 7.9					81							
8.0 to 8.4								120				
8.5 to 8.9			9			2					56	
9.0 to 9.4			16			21			6			
9.5 to 9.9			16			40			56			10
10.0 to 10.4			5			16			46			29
10.5 to 10.9			1			2			11			16
11.0 to 11.4									1			1
3d year of life:												
3.5 to 3.9	1											
4.0 to 4.4	1			2								
4.5 to 4.9	13			19			12			3		
5.0 to 5.4	16			44			21			5		
5.5 to 5.9	10			35			41			10		
6.0 to 6.4	2	1		21			23			17		
6.5 to 6.9		2		1			5			2		
7.0 to 7.4		13			16			8			1	
7.5 to 7.9		21			40			16			2	
8.0 to 8.4		6			56			46			11	
8.5 to 8.9					10			29			16	
9.0 to 9.4			43					3			5	
9.5 to 9.9						122					2	
10.0 to 10.4									102			
10.5 to 10.9												37

fish and also for other animals as well. Hile (1941, p. 305) stated that—

> A wealth of experimental evidence supports the view that among animals in general the inherent capacity for growth is lost chiefly through its exercise, and, conversely, the failure to grow does not entail necessarily the loss of the natural ability to grow.

In support of this statement he cited the work of several authors on such widely separated groups as mammals, fish, salamanders, and insects. Hodgson (1929), on the other hand, demonstrated that compensatory growth could be a perfectly natural result of comparisons of fish of different age (fish that have the same number of annuli that were of different ages because they hatched at different times during the season). Hodgson explained his view that growth compensation is "apparent" by comparing identical hypothetical growth curves that started at different points along the time axis.[8]

Later Hile (1941) applied Hodgson's principle to the sigmoid growth curve of the rock bass to explain the variety of relationships among the annual increments of different yearling size groups. A similar use of the growth curve of the Green Bay lake herring is presented in figure 6. Here the two growth curves are identical but fish *A* hatched and started to grow at time 0_A, whereas fish *B* hatched and started to grow at time 0_B. At time

[8] Hodgson (1929) felt that a bimodal length-frequency distribution of first-year sea herring resulted from a long irregular hatching period and estimated that hatching extended over about 3 months. Hile (1936) also attributed a bimodal first-year length-frequency distribution of ciscoes in certain year classes in two Wisconsin lakes to irregular weather conditions during the hatching period that resulted in irregular and prolonged hatching. It has been impossible to learn anything about the hatching of lake herring in Green Bay, but it is believed that hatching may extend over a period of several weeks since spawning occurs over a period of 4 to 6 weeks.

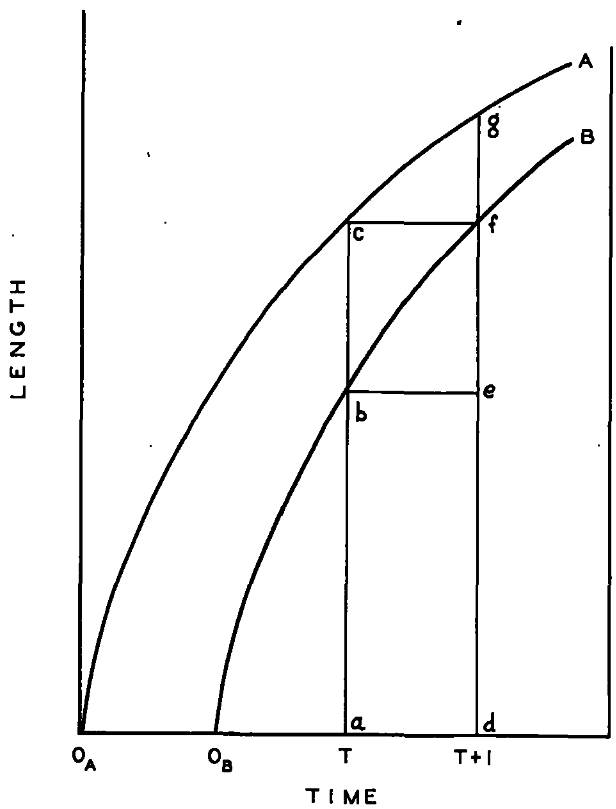

FIGURE 6.—The effects of differences in age (time of hatching) on the amount of growth during a later growing season.

T, which may mark the end of any growth period, fish A has attained length ac and fish B has attained the lesser length ab. During the interval from T to $T+1$ fish A, which had expended more of its ability to grow at time T, added the increment of length fg which is less than the increment ef added by younger fish B. This explanation of growth compensation as an apparent phenomenon is based on the premise that all fish have the same growth curve. Under this concept, the growth of fish during a particular time interval depends principally on the size it had attained at the beginning of the interval. The data presented in table 26 shows that this assumption is essentially correct, for fish of the same length at different ages tend to grow the same amount in the following year.

In a review of Hodgson's (1929) treatment of growth compensation, Ford (1933) offered the

TABLE 26.—*Growth exhibited by lake herring that were the same length at the end of different years of life*

[Total length in inches]

Length group and year of capture	Number of fish	Year of life at which computed lengths are grouped	Length at end of year of life—			Length increment	
			2	3	4	3	4
8.0 to 8.4 inches:							
1949	207	2	8.2	9.7	------	1.5	------
		3	------	8.2	9.8	------	1.6
1950	128	2	8.2	9.7	------	1.5	------
		3	------	8.2	9.6	------	1.4
1951	133	2	8.2	9.8	------	1.6	------
		3	------	8.2	9.7	------	1.5
8.5 to 8.9 inches:							
1949	81	2	8.6	10.0	------	1.4	------
	69	3	------	8.8	10.1	------	1.3
1950	46	2	8.7	10.0	------	1.3	------
	104	3	------	8.8	10.0	------	1.2
1951	57	2	8.7	10.1	------	1.4	------
	56	3	------	8.8	10.1	------	1.3
1952	26	2	8.6	10.2	------	1.6	------
	7	3	------	8.7	10.1	------	1.4
9.0 to 9.4 inches:							
1949	7	2	9.2	10.4	------	1.2	------
	201	3	------	9.2	10.3	------	1.1
1950	7	2	9.1	10.3	------	1.2	------
	221	3	------	9.2	10.4	------	1.2
1951	4	2	9.3	10.6	------	1.3	------
	146	3	------	9.2	10.6	------	1.4
1952	5	2	9.2	10.5	------	1.3	------
	25	3	------	9.3	10.7	------	1.4
Unweighted average	------	------	------	------	------	1.39	1.35

criticism that Hodgson employed curves of identical shape, although it is well known that growth may vary from individual to individual. Ford demonstrated that Hodgson's explanation could be supported from comparisons of growth along dissimilar curves starting at different points along the time axis.

From the hypothetical curves of figure 7 it can be shown that dissimilar curves starting at the same point on the time axis will also exhibit growth compensation. This compensation depends on the fact proved earlier that size, not age, at the start of a period of growth determines the amount of growth that will be made during the period. The form of three of the five curves of figure 7 is identical with that of the growth curves of figure 6, namely, 0_Acg, $0C$, and 0_Bbf. The curves $0cg$ and $0bf$ represent individual fish A and B whose growth up to time T departed from the typical. Fish A grew more (ac) and fish B grew less (ab) at time T than the typical fish which would follow curve $0C$. Since, however, length is more important than age as a determiner of growth within a period (table 26), fish A may be expected subsequently to grow along the curve cg or, in other words, to follow the same course as a normal fish hatched at time

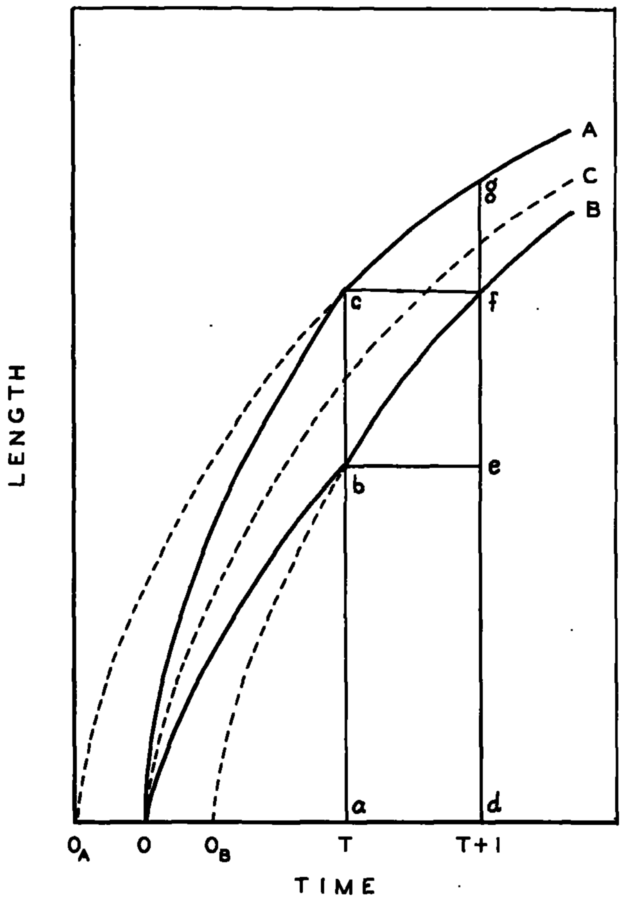

FIGURE 7.—The effect of size at the start of a growing season on the amount of growth during that season.

0_A. Similarly, the growth after time T of fish B should be that of a normal fish that hatched at 0_B. The compensatory effects of differences in the growth of these two typical fish (hatched at the same time) during the period $T-T+1$ is identical with the compensation between the two typical fish hatched at 0_A and 0_B in figure 6.

General growth in length

Distorting influences of the negative correlation between individual length of life and rate of growth make it impossible to establish a general curve that might represent the growth history of a typical, or "average," fish. Only growth of particular age groups can be shown. Curves in figure 8, based on data of all pound-net collections (table 17), are believed to be the most reliable means of representing the general growth of Green Bay lake herring taken in the commercial fishery. Age groups I, II, and VI are omitted from the data

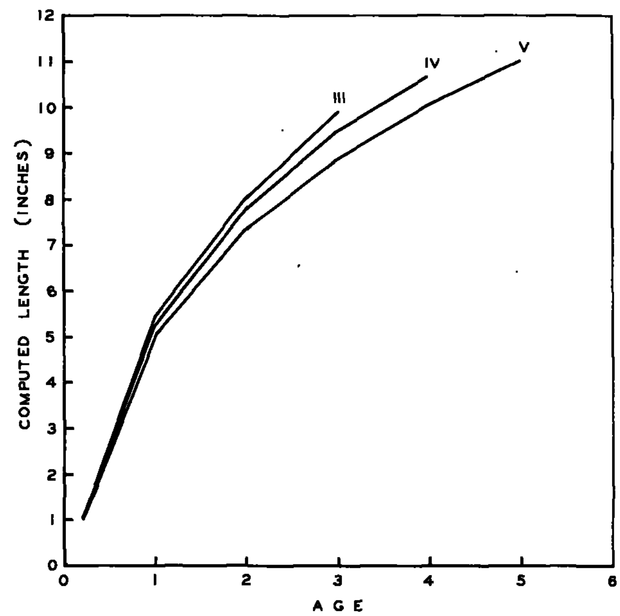

FIGURE 8.—Calculated growth in length of age groups III, IV, and V of Green Bay lake herring as determined for all fish of these age groups taken in pound nets, 1948–52.

because of the bias introduced by their almost complete absence from samples during some seasons, and because they are represented by small numbers of fish.

LENGTH-WEIGHT RELATION

GENERAL RELATIONSHIP

The variation of the volume of an object of constant shape with the cube of any linear dimension is a well known principle of mathematics. It can also be said that the weight of an object must vary with the cube of any linear dimension if the shape and specific gravity are both constant. If, however, the shape or specific gravity changes the relationship does not hold, but other relatively simple relationships ordinarily can be used to interpret the changes. The usefulness of the "cube law" in the study of the weight of animals was recognized by Herbert Spencer in 1871 according to a discussion of its application in this field by Thompson (1942). Hile (1936) reviewed the use of this principle in studies of the relation between the length and weight of fish.

The condition coefficient "C" determined by the formula $C=W/L^3$ (C=the coefficient, W=weight, and L=length) is widely employed by fishery workers as an index of changes in the form of fish that result from such phenomena as maturation and release of sex products or variations in the amount of fat or flesh. If the cube relationship is maintained throughout life then C is an unbiased expression of condition and it is possible to compare the coefficients of fish of different length. Thompson (1942) pointed out, however, that, "* * * inasmuch as the animal is continually apt to change its body proportions during life, k [his symbol for condition coefficient] also is continually subject to change." In this situation C becomes a function of length and the C values of fish of different length are not directly comparable as measures of departure from the "normal" for the stock. Hile (1936, p. 238) stated that—

> Although the cube law does appear to apply to the length-weight relationship in some species * * *, these instances appear to be the exceptions, for 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.

The situation is further complicated by the fact that not only does the length-weight relation deviate from the cube law, but it is not the same for different populations of the same species and it varies from year to year within the same populations (Hile 1936).

The relation between length and weight in most populations of fish is represented satisfactorily by the formula $W=cL^n$, where W=weight, L=length, and c and n are constants. However, since the relation between length and weight in a population varies with respect to sex, season, method of capture, and year of capture, as will be shown later, no single equation can describe the situation at all times and any general relationship that might be established is of necessity artificial. Nevertheless, a general length-weight equation based on all available data, regardless of sex, maturity, collecting gear, or season of capture, can be useful as an estimate of the average situation.

An estimate of the length-weight relation of Green Bay lake herring based on all data is

$$\log W = -2.4386 + 3.0729 \log L,$$

where W equals weight in ounces, and L equals total length in inches. Data upon which this estimate was based are shown in table 27. The weights computed from the mean length of fish in each length group are the basis of the curve in figure 9; the empirical data are shown by dots. Comparisons of calculated and actual weights

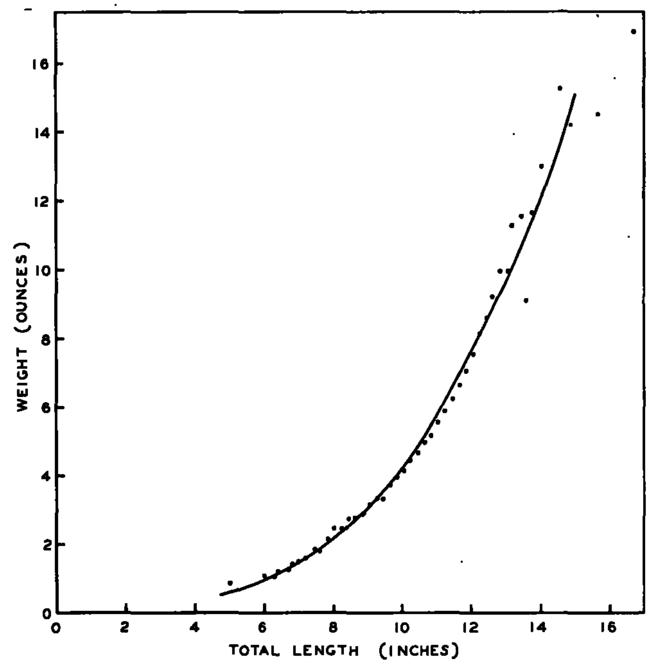

FIGURE 9.—Length-weight relation of the lake herring of Green Bay. The dots show the empirical data; the curve is the graph of the equation given in the text.

prove that this formula does not describe the empirical data precisely. Calculated weights are generally less than actual weights for fish under 9 inches, greater for fish between 9 and 12 inches, and less for fish longer than 12 inches. A close fit was hardly to be expected in view of the known heterogeneity of the material. Few fish under 9 inches and over 12 inches were taken, and these were not equally represented in all seasons (table 7). This variation in representation together with seasonal differences in weights of fish of the same length are responsible for the irregularities.

SEASONAL CHANGES IN WEIGHT

The study of seasonal changes in weight of Green Bay lake herring (table 28) is restricted to fish captured in the same calendar year (1949), in the same area (extreme southern Green Bay), and in the same gear (pound nets). In the 12 length intervals represented by 3 or more fish on all three collection dates the October fish were heaviest in 11 and the May fish were lightest in 11. February specimens were, of course, characteristically intermediate (10 of 12 comparisons). Over the length range at which all dates were represented, the October specimens averaged 4.8 percent

TABLE 27.—*Relation between the total length and weight of Green Bay lake herring*

[All collections combined]

Total length (inches)	Number of fish	Weight (ounces)	
		Empirical	Calculated
5.8 to 5.9	1	0.90	0.80
6.0 to 6.1	4	1.07	0.91
6.2 to 6.3	2	1.05	1.02
6.4 to 6.5	6	1.16	1.10
6.6 to 6.7	8	1.26	1.24
6.8 to 6.9	5	1.36	1.32
7.0 to 7.1	5	1.48	1.47
7.2 to 7.3	11	1.62	1.59
7.4 to 7.5	5	1.86	1.76
7.6 to 7.7	4	1.86	1.86
7.8 to 7.9	12	2.15	2.05
8.0 to 8.1	7	2.47	2.19
8.2 to 8.3	17	2.48	2.38
8.4 to 8.5	16	2.76	2.57
8.6 to 8.7	12	2.77	2.76
8.8 to 8.9	11	2.85	2.93
9.0 to 9.1	15	3.19	3.18
9.2 to 9.3	21	3.33	3.41
9.4 to 9.5	28	3.32	3.62
9.6 to 9.7	45	3.73	3.87
9.8 to 9.9	137	3.98	4.11
10.0 to 10.1	211	4.16	4.37
10.2 to 10.3	328	4.45	4.64
10.4 to 10.5	431	4.64	4.93
10.6 to 10.7	495	4.97	5.23
10.8 to 10.9	497	5.19	5.52
11.0 to 11.1	503	5.51	5.84
11.2 to 11.3	376	5.88	6.17
11.4 to 11.5	206	6.23	6.51
11.6 to 11.7	146	6.64	6.87
11.8 to 11.9	103	7.03	7.22
12.0 to 12.1	59	7.51	7.69
12.2 to 12.3	39	8.10	8.04
12.4 to 12.5	24	8.58	8.42
12.6 to 12.7	17	9.20	8.84
12.8 to 12.9	15	9.94	9.31
13.0 to 13.1	6	9.98	9.71
13.2 to 13.3	6	11.31	10.14
13.4 to 13.5	3	11.53	10.73
13.6 to 13.7	1	9.10	11.10
13.8 to 13.9	3	11.63	11.58
14.0 to 14.1	3	13.00	12.19
14.6 to 14.7	2	15.25	13.77
14.8 to 14.9	1	14.20	14.68
15.6 to 15.7	1	14.50	17.23
16.6 to 16.7	1	14.90	20.83

TABLE 28.—*Seasonal changes in weight of lake herring taken in pound nets in southern Green Bay during 1949*

[Weight in ounces]

Total length (inches)	February 16		May 13		October 5	
	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight
7.8 to 7.9					1	1.80
8.0 to 8.1					1'	2.10
8.2 to 8.3					3	1.97
8.4 to 8.5					2	2.35
8.8 to 8.9					1	2.90
9.0 to 9.1			1	2.80	1	2.20
9.2 to 9.3	1	2.90	1	3.60	4	3.22
9.4 to 9.5	2	3.45	3	3.03	7	3.45
9.6 to 9.7	7	3.57	3	3.30	3	3.70
9.8 to 9.9	26	3.86	8	3.48	4	3.52
10.0 to 10.1	50	4.01	26	3.85	8	4.11
10.2 to 10.3	73	4.30	46	4.15	12	4.33
10.4 to 10.5	66	4.45	69	4.27	27	4.82
10.6 to 10.7	34	4.71	73	4.53	34	5.18
10.8 to 10.9	32	5.00	75	4.82	30	5.27
11.0 to 11.1	22	5.42	62	5.05	41	5.70
11.2 to 11.3	15	5.68	36	5.45	51	5.98
11.4 to 11.5	9	5.85	23	5.67	14	6.30
11.6 to 11.7	3	6.23	5	6.34	12	6.62
11.8 to 11.9	3	6.76	4	6.20	9	7.12
12.0 to 12.1	2	6.65	5	7.02	7	7.61
12.2 to 12.3					3	8.06
12.4 to 12.5					2	8.55
13.0 to 13.1					1	9.10
13.2 to 13.3					1	9.30
13.4 to 13.5					1	12.20
14.0 to 14.1					1	13.40
15.6 to 15.7			1	14.50		

above and the May fish 4.6 percent below the unweighted mean for the three dates. The February specimens were slightly (0.2 percent) above the mean.

Seasonal changes in weights of fish are often associated with, and are used to follow, the development and release of sex products. Thompson (1942) showed a weight cycle for plaice following the spawning cycle, but he pointed out that immature fish also experience a seasonal weight fluctuation similar to that of mature fish. These seasonal changes, he believed, indicate a cycle of relative well-being originating in the variation of conditions that influence the addition or removal of body fat or tissue.

SEX DIFFERENCES IN WEIGHT

Because of the demonstrated seasonal changes in weight, studies of sex differences in weight are best made on samples taken within a short period of time. Actually the comparisons offered by the data in table 29 are based on collections of single days. On none of these dates were sex differences large. The weights of male and female lake herring of corresponding length were nearly the same in February (males 0.5 percent lighter than females). Females were the lighter in May (1.8 percent) but were heavier in October (3.4 percent). Sex differences probably are greater at the time of spawning in the latter part of November; unfortunately, adequate samples were not available for study of this point.

Carlander (1945) found no significant difference in condition coefficients of male and female tullibee from Lake of the Woods. Direct comparison of weights of male and female tullibee from Gull Lake (Eddy and Carlander, 1942) showed the females to be slightly heavier for their length than the males, but the difference was small. These authors did not consider possible seasonal variations in their presentation. Two of four populations of ciscoes in northeastern Wisconsin lakes (collections were made only during the summer) showed no differences in weight between sexes; in the other two stocks the males were the heavier in one and the females were the heavier in the other (Hile 1936). Van Oosten (1929) found little difference between average condition coefficients

TABLE 29.—*Weights of lake herring by sex and location taken in pound nets in southern Green Bay in 1949*

[Weight in ounces]

Total length (inches)	February 16, 1949 (Schumachers Point)				May 13, 1949 (Pensaukee and Suamico)				October 5, 1949 (Pensaukee)			
	Males		Females		Males		Females		Males		Females	
	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight
7.8 to 7.9											1	1.80
8.0 to 8.1											1	2.10
8.2 to 8.3											3	1.96
8.4 to 8.5											2	3.35
8.6 to 8.7											2	2.30
8.8 to 8.9											1	2.90
9.0 to 9.1							1	2.80	1	2.20		
9.2 to 9.3			1	2.90	1	3.60			2	3.55	2	2.90
9.4 to 9.5			2	3.45	1	3.20	2	2.95	3	3.40	4	3.50
9.6 to 9.7	3	3.70	4	3.47	1	3.50	2	3.20	1	4.30	2	3.40
9.8 to 9.9	5	3.86	21	3.86	2	3.50	6	3.48	3	3.47	1	3.70
10.0 to 10.1	11	4.00	39	4.01	11	3.82	15	3.86	2	4.10	6	4.11
10.2 to 10.3	25	4.32	48	4.30	21	4.11	25	4.17	6	4.05	6	4.61
10.4 to 10.5	29	4.46	37	4.44	33	4.34	36	4.21	9	4.72	18	4.88
10.6 to 10.7	12	4.82	22	4.65	29	4.55	44	4.52	11	5.10	23	5.23
10.8 to 10.9	11	5.07	21	4.97	38	4.88	37	4.76	19	5.15	11	5.46
11.0 to 11.1	10	5.48	12	5.38	23	5.16	39	4.99	19	5.70	22	5.71
11.2 to 11.3	3	4.43	12	5.75	18	5.41	18	5.48	17	5.83	34	6.05
11.4 to 11.5	2	5.55	7	5.94	5	5.90	18	5.61	4	6.07	10	6.40
11.6 to 11.7			3	6.23	1	7.10	4	6.15	5	6.40	7	6.78
11.8 to 11.9			3	6.76	2	6.80	2	5.60	3	6.53	6	7.41
12.0 to 12.1			2	6.65	3	7.20	2	5.70	2	7.70	5	7.58
12.2 to 12.3											3	8.07
12.4 to 12.5											2	8.55
13.0 to 13.1											1	9.10
13.2 to 13.3											1	9.30
13.4 to 13.5									1	12.20		
14.0 to 14.1											1	13.40
15.6 to 15.7					1	14.50						

of male and female lake herring of the spawning run (October–November) in Saginaw Bay (all lengths combined). Seasonal variations in differences of weight between the sexes in related species have been reported by Jobes for *Leucichthys reighardi* (1943), *L. alpenae* (1949a), and *L. hoyi* (1949b), and by Deason and Hile for *L. kiyi* (1947). Comparisons by Bauch (1949) of the mean condition coefficients of *Coregonus albula* of Mochelsee showed that females were slightly heavier than males during all seasons. In spawning-run samples of the same species from Keitelesee (Järvi 1920) ripe females were heaviest for their length and spent females were lightest (only slightly lighter than males).

ANNUAL DIFFERENCES IN WEIGHT

Annual fluctuations in the length-weight relation of Green Bay lake herring captured at the same time of year (January or February) in 1949 to 1952 generally were small (table 30). Weights of fish of the same length showed an upward trend from 1949 to 1952. The amount of change from year to year is indicated roughly by the following

TABLE 30.—*Weights of lake herring taken in pound nets during February 1949–51 and January 1952*

[Weight in ounces]

Total length (inches)	1949		1950		1951		1952	
	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight
8.0 to 8.1					1	2.40		
8.6 to 8.7					1	2.60		
8.8 to 8.9			2	2.30	1	2.60		
9.0 to 9.1			2	2.45	1	2.80		
9.2 to 9.3	1	2.90	3	3.13	2	3.50		
9.4 to 9.5	2	3.45	5	3.02	1	3.30	2	2.60
9.6 to 9.7	7	3.57	7	3.55	1	3.70		
9.8 to 9.9	26	3.86	27	3.71	9	3.88	3	4.03
10.0 to 10.1	50	4.01	48	4.01	13	4.21	3	4.03
10.2 to 10.3	73	4.30	74	4.35	29	4.50	2	4.70
10.4 to 10.5	66	4.45	101	4.57	40	4.71	7	4.80
10.6 to 10.7	34	4.71	77	4.79	81	5.02	22	5.04
10.8 to 10.9	32	5.00	62	5.00	61	5.16	30	5.17
11.0 to 11.1	22	5.42	43	5.30	78	5.41	38	5.55
11.2 to 11.3	15	5.68	22	5.55	53	5.71	29	5.74
11.4 to 11.5	9	5.85	19	5.87	14	6.17	19	6.12
11.6 to 11.7	3	6.23	3	6.80	10	6.37	11	6.20
11.8 to 11.9	3	6.76	5	6.46	5	6.62	10	6.60
12.0 to 12.1	2	6.65			4	7.42	1	6.80
12.2 to 12.3			3	7.50	2	7.80	2	6.45
12.4 to 12.5			1	7.90	2	8.55	1	7.80
12.6 to 12.7							2	7.80
12.8 to 12.9			1	8.70				
13.0 to 13.1					2	10.10		
13.2 to 13.3			1	11.00				
14.0 to 14.1					1	11.40		
14.8 to 14.9			1	14.20				
Mean deviation from average percent		−2.3		−1.8		1.3		1.7

mean percentages of deviations from the average weight for all years: 1949, −2.3 percent; 1950, −1.8 percent; 1951, 1.3 percent; and 1952, 1.7 percent. This period of increasing weight was also one of generally improving growth rate (table 22).

Hile (1936) found that the length-weight relation and condition coefficient varied from year to year in three of four populations of ciscoes in northeastern Wisconsin lakes. Annual differences in the length-weight relation were reported by Deason and Hile (1947) for *Leucichthys kiyi* and by Jobes for *L. reighardi* (1943), *L. alpenae* (1949a), and *L. hoyi* (1949b).

INFLUENCE OF METHOD OF CAPTURE ON WEIGHT

Discussions of seasonal and annual fluctuations, and sex differences in the length-weight relation have been based entirely on fish taken from pound nets. Gill-net samples were omitted from these comparisons because of the bias to length-weight data introduced by gill-net selectivity. Farran (1936) treated this problem in detail and established limits of selectivity (in terms of length and girth) of different sizes of mesh of gill nets in capturing marine herring. Deason and Hile (1947) demonstrated that within a sample of kiyi from Lake Michigan that was homogeneous as to age, sex, and locality and date of capture, the coefficient of condition decreased with increase in length of fish taken by gill nets of the same mesh size but increased in fish of the same length with increase of mesh size.

Although materials for the study of effects of gear selection on length-weight data in the Green Bay lake herring are scanty, those that are available (table 31) demonstrate conclusively that gill nets tend to take heavier fish than do pound nets operating in the same area and season, but because of the small numbers of fish on which the individual averages are based, a number of exceptions occurred. The records for females taken during the spawning season show almost no difference between samples from the two gears. The extent of the bias in the remaining comparisons is sufficiently great, however, to make exclusion of the gill-net samples desirable in detailed studies of the length-weight relation.

TABLE 31.—*Weights of lake herring taken in gill nets and in pound nets at different times of the year, 1950 and 1951*

[Weight in ounces]

Total length (inches)	November				February			
	Gill net [1]		Pound net [2]		Gill net [3]		Pound net [4]	
	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight	Number of fish	Average weight
Males:								
9.7 to 9.9	------	------	2	4.00	1	3.90	1	4.00
10.0 to 10.2	1	4.70	3	4.13	3	4.56	3	3.86
10.3 to 10.5	2	5.10	8	4.83	4	4.65	5	4.74
10.6 to 10.8	11	5.32	12	5.05	8	5.25	17	5.10
10.9 to 11.1	13	5.69	13	5.51	26	5.63	21	5.30
11.2 to 11.4	13	5.86	4	5.95	19	5.98	16	5.61
11.5 to 11.7	10	6.60	2	6.00	4	6.47	------	------
11.8 to 12.0	4	6.70	------	------	3	6.56	------	------
12.1 to 12.3	1	7.40	------	------	1	7.70	------	------
12.4 to 12.6	1	8.60	------	------	------	------	1	7.90
12.7 to 12.9	1	9.00	------	------	------	------	------	------
Total or average	57	5.99	44	5.16	69	5.66	64	5.24
Females:								
7.6 to 7.8	1	2.30	------	------	------	------	------	------
8.2 to 8.4	1	2.30	------	------	------	------	------	------
9.1 to 9.3	1	4.10	------	------	------	------	------	------
9.7 to 9.9	------	------	1	4.10	1	3.60	------	------
10.0 to 10.2	1	5.20	7	4.38	2	4.60	3	4.50
10.3 to 10.5	1	5.30	8	4.90	6	4.95	18	4.72
10.6 to 10.8	4	5.65	16	5.30	20	5.12	31	4.86
10.9 to 11.1	5	5.68	22	5.67	32	5.50	42	5.23
11.2 to 11.4	7	5.92	5	6.40	22	5.82	12	5.44
11.5 to 11.7	9	6.76	1	6.30	8	6.43	12	6.16
11.8 to 12.0	5	7.20	------	------	2	7.25	4	6.97
12.1 to 12.3	9	7.67	1	8.30	3	8.36	1	8.00
12.4 to 12.6	1	8.00	------	------	2	8.05	1	9.20
12.7 to 12.9	3	8.80	2	9.35	------	------	------	------
13.0 to 13.2	1	9.40	------	------	------	------	1	9.40
13.6 to 13.8	1	10.50	------	------	------	------	------	------
Total or average	50	6.65	63	5.54	98	5.67	125	5.30

[1] Collected from a 2⅜-inch-mesh gill net at Oconto on November 30, 1950.
[2] Collected from a pound net at Fox on November 29, 1950.
[3] Collected from a 2⅜-inch-mesh gill net at Pensaukee on February 20, 1951.
[4] Collected from a pound net at Schumachers Point on February 22, 1951.

GENERAL GROWTH IN WEIGHT

The differences in weight according to sex, season, and year of capture detract from the usefulness of the general growth curves of the Green Bay lake herring. The best means of depicting growth is to compute weights for the calculated lengths of the best-represented age groups for all pound-net data (table 17). Weights for age groups III, IV, and V calculated from the general length-weight relation (p. 114) are given in table 32. Growth curves for these age groups are given in figure 10.

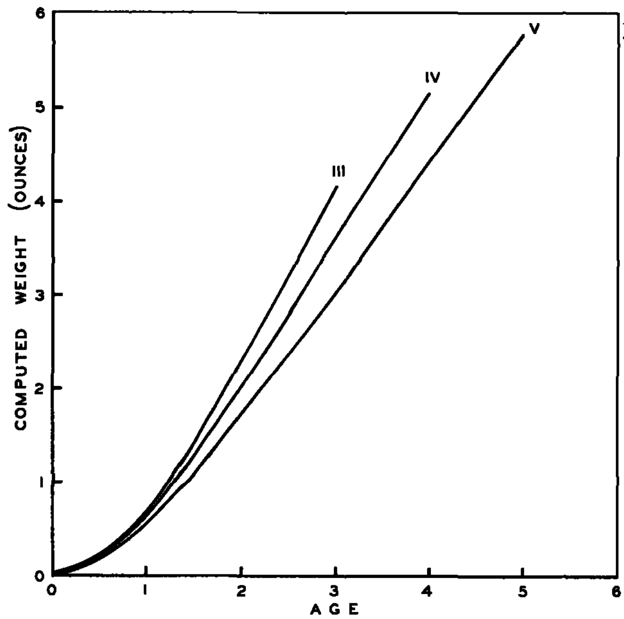

FIGURE 10.—Calculated growth in weight of age groups III, IV, and V of Green Bay lake herring as determined from calculated lengths for all fish taken from pound nets, 1948–52, and the length-weight relation for all fish of these age groups.

TABLE 32.—*Calculated growth in weight for the Green Bay lake herring of age groups III, IV, and V*

[Calculated from the general length-weight relation, p. 114, and lengths of fish taken in pound nets in 1948–52, table 17, p. 104]

Age group	Weight (ounces) at age—				
	1	2	3	4	5
III	0.65	2.25	4.18		
IV	.61	2.01	3.68	5.15	
V	.51	1.71	3.01	4.44	5.77

REPRODUCTION AND EARLY GROWTH

SEX COMPOSITION

As is common among fish, data on sex composition in lake herring populations are highly variable. Some factors that may contribute to variability of sex composition in samples from a population are:

1. Segregation of the sexes through various periods of the year including segregation resulting from sex differences in age and size at maturity.

2. Differences in mortality (natural or fishing) between the sexes.

3. Gear selectivity in relation to sex differences in activity and morphology.

To evaluate any of these factors would be difficult, particularly since they are interrelated and some or all of them may affect the sex composition of a sample.

Reports of various authors on different populations of lake herring (table 33) show sex composition, expressed as percentage of females, ranging from 29 percent in Blind Lake (Cooper 1937) to 73 percent in Trout Lake (Hile 1936). The Blind Lake collection was made during the spawning period but the paucity of females is not characteristic of spawning fish as may be seen by the sex composition of other samples collected during the spawning period—in Swains Lake (67 percent) and Saginaw Bay (51 percent).

Six out of 11 lake herring populations for which data have been published on the change of sex composition in relation to age (table 33) show a rise in the proportion of females with increase in age (Clear Lake, Gull Lake, Lake of the Woods, Muskellunge Lake, Swains Lake, and Trout Lake), 2 populations show a downward trend (Blind Lake and Saginaw Bay), and 3 exhibit no clear trend (Irondequoit Bay, Lake Nipissing, and Silver Lake). The 6 populations exhibiting an increase in the percentage of females with age were collected with gill nets and 1 (Swains Lake) was sampled exclusively during the spawning period. Of the 2 populations with a downward trend, 1 was sampled with pound nets (Saginaw Bay) and the other with gill nets (Blind Lake), and both sets of data were based on spawning-run collections. One of the 3 populations showing no trend was sampled with pound nets (Irondequoit Bay) and the other 2 were sampled with gill nets, and all represent samples from more than 1 month and year. It is obvious from these comparisons that the relation of sex composition to age as reported for different stocks is not clearly influenced by collecting gear or sexual activity at time of collection.

Some information on possible sources of bias in determining the sex composition of a population is brought out in the Green Bay data on fluctuations in the sex ratio according to age, gear of collection, and depth, season, and year of capture.

In pound-net samples, which made up the bulk of the Green Bay collections, the percentage of females was consistently higher in February than during other months of the year, and since no trend was shown in sex composition during the other months, the data for all but the February samples are combined in table 34. This seasonal

TABLE 33.—*Changes in sex composition with age for different lake herring populations*

[Number of fish in parentheses]

State and body of water	Percentage females in age group—											All ages	Gear used	Investigator
	0	I	II	III	IV	V	VI	VII	VIII	IX	X+			
Michigan:														
Blind Lake	100 (1)	67 (3)	35 (23)	29 (66)	24 (38)	30 (10)	20 (10)	0 (1)				29 (152)	gill	Cooper (1937).
Saginaw Bay			55 (11)	54 (818)	50 (1,434)	50 (539)	45 (124)	42 (19)	20 (5)			51 (2,950)	pound	Van Oosten (1929).
Swains Lake					20 (5)	64 (22)	71 (24)	68 (28)	100 (1)	100 (3)	100 (1)	67 (84)	gill	Brown and Moffett (1942).
Minnesota:														
Gull Lake			0 (2)	17 (24)	52 (112)	65 (342)	71 (168)	80 (10)				63 (658)	do	Eddy and Carlander (1942).
Lake of the Woods		48 (80)	49 (101)	54 (120)	59 (63)	63 (38)	67 (12)	100 (4)	0 (2)		0 (1)	54 (421)	do	Carlander (1945).
New York: Irondequoit Bay			39 (64)	66 (216)	38 (13)	37 (43)	57 (68)	59 (76)	64 (11)	100 (1)	50 (2)	57 (494)	pound	Stone (1938).
Ontario: Lake Nipissing			53 (156)	55 (334)	56 (350)	55 (293)	49 (255)	36 (97)	76 (21)	92 (13)	60 (5)	53 (1,524)	gill	Fry (1937).
Wisconsin:														
Clear Lake		42 (69)	47 (102)	48 (95)	47 (39)	45 (20)	50 (26)	66 (50)	68 (31)	75 (4)	100 (4)	51 (440)	do	Hile (1936).
Muskellunge Lake		50 (26)	57 (472)	60 (361)	0 (2)							58 (861)	do	Do.
Silver Lake		52 (66)	62 (26)	56 (86)	53 (160)	56 (133)	67 (24)	100 (1)				55 (496)	do	Do.
Trout Lake		50 (2)	62 (97)	67 (520)	78 (368)	93 (80)	92 (12)	100 (4)	80 (5)	100 (2)	33 (3)	73 (1,101)	do	Do.

TABLE 34.—*Sex composition of lake herring taken in pound nets, 1948–52*

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

Time of collection	Percentage females in age group—							All fish [1]
	I	II	III	IV	V	VI	VII	
1948: May		75 (1:3)	60 (57:84)	55 (50:60)	71 (2:5)			58 (110:152)
1949:								
February			74 (11:31)	67 (85:171)	68 (15:32)			68 (111:234)
May, October	100 (0:2)	63 (7:12)	61 (112:172)	57 (157:206)	60 (17:25)	33 (2:1)		59 (298:426)
1950:								
February			64 (20:36)	61 (148:230)	54 (31:37)	50 (2:2)		60 (201:306)
June, July, September, November, December	43 (4:3)	50 (10:10)	46 (153:128)	47 (114:102)	45 (11:9)	0 (2:0)		46 (294:252)
1951:								
February		100 (0:1)	71 (9:22)	57 (148:200)	56 (24:31)	100 (0:1)		59 (182:257)
May, June, August	100 (0:2)	44 (15:12)	47 (31:27)	43 (107:82)	19 (21:5)	100 (0:1)	100 (0:1)	42 (178:130)
1952: January			71 (2:5)	48 (81:74)	73 (4:11)	0 (1:0)		51 (90:92)
1949–52: January–February		100 (0:1)	69 (42:94)	59 (462:675)	60 (74:111)	50 (3:3)		60 (584:889)
1948–51: May–December	63 (4:7)	53 (33:37)	54 (352:411)	51 (428:450)	46 (51:44)	33 (4:2)	100 (0:1)	52 (880:960)

[1] Includes fish of unknown age.

difference in the percentage of females appears in the data for individual age groups as well as in the data for all ages combined.

The percentage of females in samples of lake herring taken from pound nets also showed a clear tendency to decrease during the period 1949 to 1952 (table 34). This trend is present in the best-presented age groups (III and IV) as well as in the data for all ages combined in both the January-February samples and the samples from the remaining months.

The change in sex composition with increase in age of lake herring taken in pound nets was irregular, but a downward trend in the percentage of females is evident in most series (table 34) and is conspicuous where data of all years for comparable periods have been combined (bottom of table). This trend would suggest that young females might be taken in the pound-net fishery at a higher rate than young males. A sex difference in mortality of this kind should result in a progressive reduction in the proportion of females within a year class. That this expectation is fulfilled consistently in the January-February collections is demonstrated by the following tabulation of percentages of females in samples of four different year classes at various ages (where represented by 25 fish or more).

Year class	Percentage females and age group in—			
	1949	1950	1951	1952
1945	67 (IV)	54 (V)	----------	----------
1946	74 (III)	61 (IV)	56 (V)	----------
1947	----------	64 (III)	57 (IV)	----------
1948	----------	----------	71 (III)	48 (IV)

The corresponding tabulation for collections made in months other than January and February demonstrates a similar trend but does contain one exception, the V-group of the 1944 year class.

Year class	Percentage females and age group in—			
	1948	1949	1950	1952
1944	55 (IV)	68 (V)	----------	----------
1945	60 (III)	57 (IV)	----------	----------
1946	----------	61 (III)	47 (IV)	19 (V)
1947	----------	----------	46 (III)	43 (IV)

In gill-net collections the percentage of females varied widely from sample to sample (table 35). Although the available data are insufficient for a study of annual and seasonal trends, they offer no evidence of disagreement with the trends established in pound-net data. The change in sex composition with age of gill-net caught fish, however, is the reverse of that of fish taken by pound nets. The gill-net samples show a clear tendency toward a higher percentage of females with increasing age. This progressive destruction by gill nets of females in the older age groups should tend to counteract the effect of pound nets in cropping younger females at a faster rate than males.

The combined effects of the selective destruction of the two fishing gears in determining differences in sex composition with season and age cannot be evaluated with data at hand. It is clear, however, that females are cropped more heavily than males during the winter (January-February) fishery by both pound nets and gill nets. The effects of this destruction of females are counteracted in part by the greater destruction of males in the remaining months of the year.

Records of the sex composition of samples of lake herring taken at various levels between the surface and bottom (see description of oblique

Table 35.—*Sex composition of lake herring taken in gill nets, 1948–52*

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

Time of collection[1]	Percentage females in age group—						All ages
	I	II	III	IV	V	VI	
1948: October	------	33 (4:2)	73 (22:58)	74 (15:43)	63 (3:5)	------	71 (44:108)
1950: November	100 (0:2)	40 (3:2)	43 (44:33)	62 (8:13)	0 (2:0)	------	47 (57:50)
1951:							
February	------	------	100 (0:5)	56 (58:75)	63 (10:17)	------	59 (69:98)
November	------	33 (2:1)	30 (47:20)	50 (4:4)	------	------	33 (54:26)
1952:							
May	------	------	20 (4:1)	44 (74:57)	53 (8:9)	100 (0:1)	45 (87:70)
July	------	------	53 (8:9)	68 (10:21)	------	------	61 (19:30)
October	------	100 (0:1)	42 (88:64)	42 (54:39)	75 (1:3)	------	43 (143:109)
All dates	100 (0:2)	40 (9:6)	47 (213:190)	53 (223:252)	59 (24:34)	100 (0:1)	51 (473:491)

[1] Collection from commercial gill nets—1948, 1950, 1951; collection from experimental gill nets—1952.

gill-net sets in Vertical Distribution in Green Bay, p. 128), yielded no evidence of segregation of the sexes according to depth in June or July, but they indicated a strong tendency in October toward a higher percentage of females in the deeper strata than in the shallower (table 36). This trend was much stronger in samples from nets fished in 60 feet of water than in 90 feet (fig. 11).

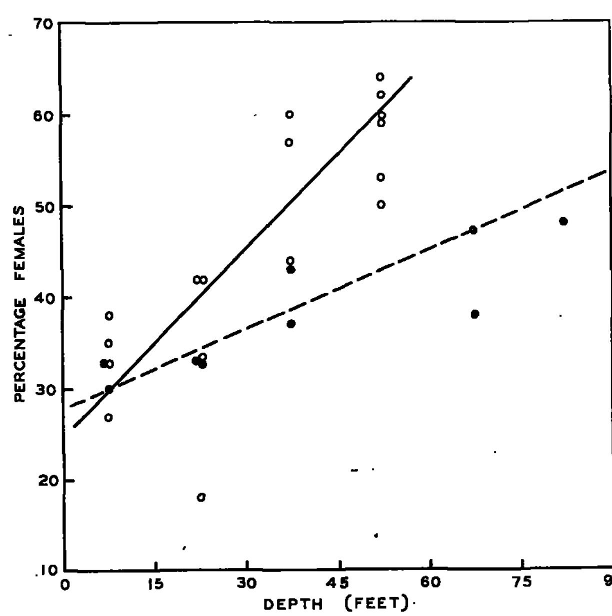

Figure 11.—Sex composition of lake herring taken at various depths in October 1952 in 2-inch-mesh experimental gill nets set obliquely from surface to the bottom. Open circles indicate the data for 60-foot stations and solid circles the data for 90-foot stations; the regression lines were fitted by least squares.

TABLE 36.—*Sex composition of lake herring taken at various depths in experimental 2-inch-mesh gill nets in 1952*

[Number of fish in parentheses]

Month, depth, and station [1]	Date taken	Percentage females at—						All depths
		0–15 feet	15–30 feet	30–45 feet	45–60 feet	60–75 feet	75–90 feet	
June:								
60 feet:								
K	12	50 (4)	0 (1)	67 (6)	63 (8)			58 (19)
L	12	(0)	50 (4)	71 (17)	60 (25)			63 (46)
90 feet: J	11	(0)	100 (1)	50 (10)	63 (32)	48 (23)	47 (15)	54 (81)
All depths		50 (4)	50 (6)	64 (33)	62 (65)	48 (23)	47 (15)	58 (146)
July:								
60 feet:								
C	24	(0)	0 (1)	38 (8)	80 (10)			58 (19)
H	22	(0)	(0)	50 (4)	33 (6)			40 (10)
K	21	0 (1)	33 (3)	35 (31)	38 (16)			35 (51)
L	21	(0)	44 (25)	73 (30)	63 (30)			61 (85)
90 feet:								
D	27	(0)	(0)	100 (1)	(0)	0 (1)	50 (4)	50 (6)
I	22	(0)	(0)	40 (5)	40 (15)	0 (2)	50 (2)	38 (24)
J	21	100 (1)	100 (2)	44 (9)	56 (18)	43 (21)	67 (27)	56 (78)
All depths		50 (2)	45 (31)	51 (88)	54 (95)	38 (24)	64 (33)	52 (273)
October:								
30 feet: A	22	47 (15)	(0)					47 (15)
40 feet: B [2]	22	43 (44)	100 (2)					46 (46)
60 feet:								
C	22	38 (37)	42 (36)	44 (41)	62 (29)			45 (143)
H	24	33 (40)	18 (40)	57 (35)	64 (25)			40 (140)
K	25	27 (30)	42 (26)	60 (30)	59 (44)			48 (130)
L	25	35 (49)	33 (30)	50 (30)	60 (30)			43 (139)
90 feet:								
D	23	45 (11)	50 (8)	(0)	(0)	(0)	(0)	47 (19)
I	24	33 (40)	33 (40)	43 (40)	53 (57)	38 (8)	100 (2)	42 (187)
J	25	23 (30)	33 (30)	37 (30)	50 (28)	47 (30)	48 (31)	40 (179)
All depths		35 (296)	34 (212)	48 (206)	57 (213)	45 (38)	52 (33)	43 (998)

[1] See figure 1 for location.
[2] Depths intervals 0-20 and 20-40.

Despite the clear-cut change in sex composition with increase of depth, the validity of an assumption that sexes are segregated according to depth in October is questionable. Since the gill nets used to obtain these collections were stationary the activity of the fish was a primary determinant of the number of fish taken by them. Accordingly, it is possible that changes in sex composition with depth do not reflect a corresponding difference in the actual relative abundance of males and females but that they are merely "apparent changes" traceable to sex differences in activity. In other words, the males may have been much more active than the females near the surface, whereas the activity of the sexes may have been equal or nearly equal at the greater depths. No evidence on the question of sex differences in activity is available from the present study or from published reports on the lake herring. Evidence has been published, however, that the males of the related kiyi of Lake Michigan become much more active during the spawning period (Hile and Deason, 1947). If a similar behavior is assumed for the lake herring, and if it is assumed further that the heightened activity of males starts in advance of the spawning period and that the fish near the surface are the ones closest to the spawning state (the lake herring is a pelagic spawner), then sex differences in activity rather than true segregation can explain the relation of sex composition of lake herring to depth in October samples which were taken about 3 weeks before spawning starts.

AGE AND SIZE AT MATURITY

A lake herring was considered immature if it was not in spawning condition when captured during the spawning season, or if the state of the gonads indicated that it would not spawn during the next spawning period following its capture. As most small lake herring captured in Green Bay were taken within a few months before the spawning period, at a time when all mature fish had well-developed gonads, little difficulty was experienced in distinguishing the immature individuals.

Published statements as to the age at which the lake herring matures frequently have been indefinite because of considerable individual variation among fish and because of questionable dependability of samples as a result of gear selection or segregation on the basis of maturity. Hile (1936) suspected that his estimates of percentage of maturity in the younger age groups were too high if the faster-growing fish of each age group matured first, since his gill nets did not take the smaller members of those age groups. Van Oosten (1929), who sampled only fish of the spawning run, felt that since immature fish did not participate in spawning activities they were not properly represented in the samples.

A summary of published data on the maturity of lake herring (table 37) shows that the age at which most fish mature in different populations varies from I to IV. Although lake herring maturing in the first year of life (age group 0) have never been reported, maturity in the second year (age group I) is common. The reason for later maturity in some populations is not clearly understood.

The Green Bay collections contained relatively few immature lake herring, all of which were in age groups 0, I, and II (table 38). The two 0-group fish taken (one male and one female) were immature. In age group I, 32 percent of the males and 11 percent of the females were mature. By the next year (age group II) most fish of both sexes had reached maturity (97 percent of the males; 88 percent of the females). This tendency for males to mature sooner than females was also found in the lake herring of Saginaw Bay (Van Oosten 1929) and Irondequoit Bay (Stone 1938). The three 2-year-old ciscoes taken in Lake Ontario by Pritchard (1930) were all mature females. The average lengths of mature and immature fish indicate that the larger members of an age group are more likely to be mature (table 38).

TABLE 37.—*Age at which lake herring of different populations reach sexual maturity*

[Arranged according to age at maturity]

Body of water	Age group in which—			Investigator
	Few fish mature	Some fish mature	Most or all fish mature	
Clear Lake, Wis.			I	Hile (1936).
Green Bay, Lake Michigan		I	II	Present work.
Lake of the Woods, Minn.		I	II	Carlander (1945).
Saginaw Bay, Lake Huron		I	II	Van Oosten (1929).
Trout, Silver, and Muskellunge Lakes, Wis.		I	II	Hile (1936).
Lake Erie			II	Clemens (1922).
Irondequoit Bay, Lake Ontario.		II	III	Stone (1938).
Blind Lake, Mich.		II	III	Clemens (1922).
Lake Oconomowoc, Wis.			III	Cahn (1927).
Lake Ontario	II	III	IV	Pritchard (1931).
Hudson Bay		III	IV	Dymond (1933).
Manitoba Lakes			IV	Bajkov (1930).

TABLE 38.—*Relations among age, length, and sexual maturity in the lake herring of Green Bay*

[Total length in inches]

Age group [1]	Mature		Immature		Percentage mature
	Number of fish	Total length	Number of fish	Total length	
Males:					
0			1	6.0	0
I	8	8.2	17	6.9	32
II	33	9.9	1	8.0	97
Females:					
0			1	5.8	0
I	2	8.6	16	7.8	11
II	30	9.3	4	8.2	88

[1] All fish older than age group II were mature.

HATCHING AND EARLY GROWTH

Almost nothing is known about the incubation, hatching, and early development of lake herring in nature. Cahn (1927) collected unhatched eggs in Lake Oconomowoc, Wisconsin, in March, but had no positive evidence as to the time of hatching. Pritchard (1930) observed that hatching takes place during April and early May in the Bay of Quinte, Lake Ontario, and he made daily collections of the growing fry from May 9 to June 1. These fry were found among reeds in shallow-water areas of protected bays, but apparently they moved toward the open water as they grew. On June 1 when the last individuals were collected, they were 20 millimeters long. After that date they could not be located again. Greeley and Greene (1931) collected young-of-the-year lake herring in the St. Lawrence River near Ogdensburg, N. Y., on June 6, 17, and 18, and at Waddington, N. Y., on June 28, in 1930. Since adult lake herring are unknown in the river, it is presumed that these fish came 78 miles downstream from Lake Ontario. The lengths of these young herring on different dates of collection were as follows:

Date	Number of fish	Length	
		Average	Range
June 6	15	21 mm	18 to 28 mm.
June 17, 18	142	28 mm	24 to 32 mm.
June 28	76	36 mm	29 to 45 mm.

The mean length of 21 millimeters of the June 6 collection corresponds closely with the length of 20 mm. recorded by Pritchard (1930) on June 1. Cahn (1927) took three young of the year with an average length of 62.5 mm. in a gill net fished on the bottom at 52 feet in Lake Oconomowoc on June 20, 1922. Fry (1937) caught 0-group ciscoes in the region of the thermocline in Lake Nipissing during late August 1933 to 1935. Hile (1937) found 17 young lake herring (average length, 65 mm.) washed upon the shore of Trout Lake during late summer. Reighard (1915) reported similar recoveries of young in Douglas Lake and Ward (1896) found small lake herring washed up on the shore of Lake Michigan following storms. Records of a few recoveries of small lake herring from shallow-water areas of the Great Lakes are on file in the Fish Division of the Museum of Zoology, University of Michigan.

Knowledge of the distribution and habits of young-of-the-year lake herring is scanty in Green Bay also. In spite of a constant lookout for them during all field work and attempts to locate them with midwater and bottom trawls during the summer of 1952 only two young-of-the-year lake herring have been taken from Green Bay. Both were captured in a 1-inch-mesh gill net from 17 fathoms of water off Gills Rock on December 12, 1951. One was a male 6.0 inches long and the other a female 5.8 inches long. Otter trawls of the same construction as those used in a search for small lake herring in Green Bay caught large numbers of yearling lake herring in Lake Superior in 1953 (often more than 1,000 in a 10-minute tow). The best catches were made at 5 to 15 fathoms in the Apostle Islands area near Bayfield, Wis., and along the southeastern shore of the Keweenaw Peninsula. These collections have not yet been studied, but examination of a few specimens showed that they were just starting their second year of life. Young-of-the-year lake herring 10 to 12 mm. long were taken in surface plankton tows on May 29 and 30 near Bayfield, Wis. These fry match the descriptions by Prichard (1930) and Fish (1932) of lake herring of the same length from Lakes Erie and Ontario. Further evidence that fry of the genus *Leucichthys* may be pelagic was obtained when fry of either *L. hoyi* or *L. reighardi* (my tentative identification) were collected by the author with a dip net in open water on Lake Michigan near North Manitou Island on July 30, 1952.

FECUNDITY

The number of eggs produced by female lake herring varies widely both within and between populations. Jordan and Evermann (1902) and Bean (1902) carried similar accounts of what must be the same fish—a 2½-pound female tullibee from the "western territories of Canada"—that held 23,700 eggs. Cahn (1927), using the volumetric method, estimated the number of eggs of a 465-gram (about 1 pound) female from Lake Oconomowoc at 15,238. Bajkov (1930) stated that the tullibee of the Canadian prairie provinces carry 15,000 to 20,000 eggs. Brown and Moffett (1942), using a partial-weight method, estimated the number of eggs in ovaries of 9 ciscoes from Swains Lake. The results of their study were as follows:

	Average	Range
Number of eggs	30,328	23,272 to 37,272.
Total length of fish	15.7 in	15.2 to 16.2 in.
Weight of fish	1.72 lb	1.48 to 1.86 lb.

No correlation was found between number of eggs and size or age of these fish. Scott (1951) also used the partial-weight method to estimate the egg count of 12 II-group and 6 III-group ciscoes from Lake Erie. His findings are summarized as follows:

	Average	Range
Age group II:		
Number of eggs	29,225	16,000 to 42,500.
Total length of fish [1]	13.4 in	11.7 to 14.4 in.
Weight of fish	1.18 lb	0.65 to 1.50 lb.
Age group III:		
Number of eggs	23,017	14,200 to 38,600.
Total length of fish [1]	15.3 in	13.8 to 16.6 in.
Weight of fish	1.65 lb	0.96 to 2.21 lb.

[1] This paper gave only standard lengths. Estimates of total length in this stock have been based on the assumption that the ratio of total length to standard length was 1.19—a value near the middle of the range of conversion factors listed by Carlander (1950).

Scott found that the number of eggs tended to increase with length and weight of the female. He pointed out, however, that the apparent decrease in the number of eggs with increasing age of the fish, as shown by his data, may be in error, since all age group III fish were ripe when collected and unknown numbers of eggs were lost in handling them. Stone (1938) estimated (by the volumetric method) the number of eggs of 104 Irondequoit Bay lake herring to average 24,095; the mean length of these fish was 13.4 inches. The average number of eggs per fish in the different age groups ranged from 13,723 in the 2-year-olds (average length, 11.9 in.) to 48,999 in the 8-year-olds (average length, 16.7 in.).

The number of eggs was estimated by the dry-weight method for 72 Green Bay lake herring. This method was developed by Paul H. Eschmeyer and George F. Lunger, of the Service's Great Lakes Fishery Investigations, in studies of the fecundity of lake trout; they have not published an account of the procedure. The general procedure with lake herring ovaries (which differs somewhat from that followed by Eschmeyer and Lunger for lake trout) is as follows:

The formalin-preserved ovaries are broken up thoroughly and the larger pieces of connective tissue are removed; the remaining materials are dried at 60° C. until there is no further weight loss; a sample of 100 eggs is removed and weighed (weighing is facilitated if the dried material is allowed first to reach moisture equilibrium with the atmosphere); the total number of eggs is computed from ovary weight and sample weight.

The dependability of the method was tested by making 38 estimates from 100-egg samples of 19 ovaries for which actual counts were made. The advantage of the dry-weight method in reducing error is clearly shown in the following comparisons:

Method	Percentage error		Investigator
	Mean	Range	
Dry weight	0.3	0.1 to 2.2	Present work.
Wet weight	6.7	0.4 to 21.0	Brown and Moffett (1942).
Volumetric	5.1	3.0 to 14.0	Stone (1938).

The number of eggs per fish in the Green Bay lake herring (table 39; fig. 12) varied widely but nevertheless exhibited a tendency to increase with length of the fish. In the entire sample of 72 fish with an average length of 11.2 inches, the average number of eggs was 6,375. Fish of different age but of the same length showed no difference in egg

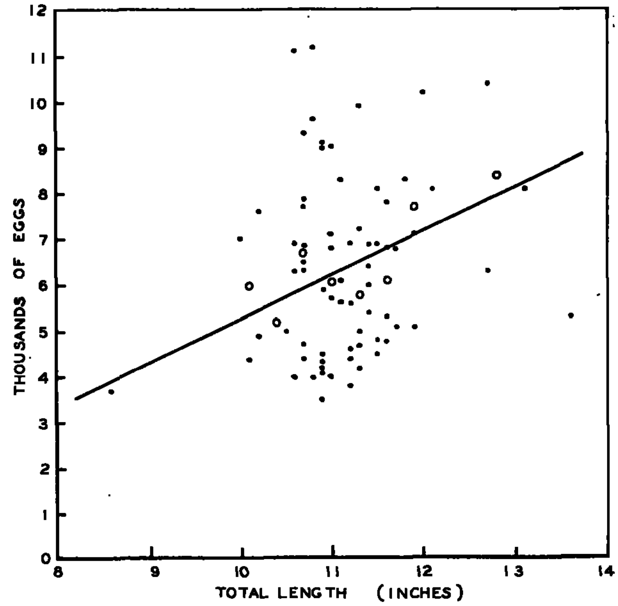

FIGURE 12.—Relation between length of Green Bay lake herring and number of eggs. The dots represent individual fish and circles are averages for 0.3-inch length groups; the line was fitted by least squares to the means of the 0.3-inch groups.

number (details of analysis are not presented here). The relative number of eggs (expressed as number of eggs per ounce of body weight), contrary to the actual number, showed a downward trend with increase in length (fig. 13). For the entire sample (61 fish—11 fish not weighed) the average number of eggs per ounce of fish was 1,012 (table 39). This value is below those for the ciscoes of Swains

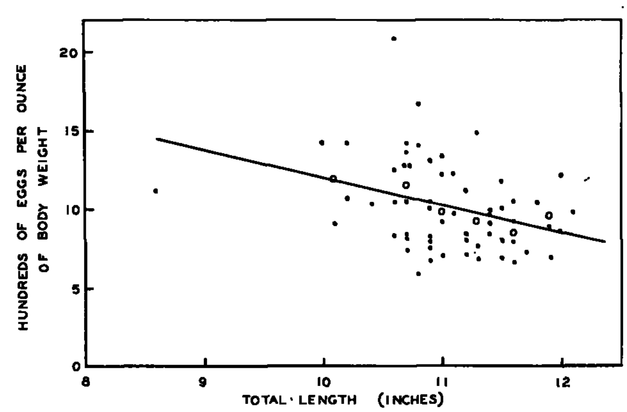

FIGURE 13.—Relation between length of Green Bay lake herring and the number of eggs per ounce of body weight. The dots represent individual fish and circles are averages for 0.3-inch length groups; the line was fitted by least squares to the means of the 0.3-inch groups.

Lake (1,103 eggs per ounce of fish), Lake Erie (1,546 eggs per ounce of age group II fish), and Irondequoit Bay (1,369 eggs per ounce of fish) as computed from data given by Brown and Moffett (1942), Scott (1951), and Stone (1938), respectively.

TABLE 39.—*Relation between the length of the individual lake herring and the number, weight, and size of the eggs it produces*

[Number of fish in parentheses]

Total length (inches)	Number of eggs per fish		Number of eggs per ounce of fish[1]	Average egg diameter (millimeters)	
	Average	Range		October	November
8.5 to 8.7	3,748 (1)	----------	1,102 (1)	1.61 (1)	-------
10.0 to 10.2	5,985 (4)	4,419 to 7,641	1,202 (4)	1.55 (2)	1.86 (2)
10.3 to 10.5	5,182 (2)	5,025 to 5,339	1,027 (1)	1.68 (1)	1.99 (1)
10.6 to 10.8	6,662 (15)	3,968 to 11,212	1,156 (16)	1.59 (12)	1.75 (3)
10.9 to 11.1	6,079 (16)	3,471 to 9,102	976 (15)	1.63 (12)	1.95 (4)
11.2 to 11.4	5,790 (14)	3,783 to 9,924	918 (11)	1.65 (11)	1.91 (3)
11.5 to 11.7	6,140 (11)	4,502 to 8,120	851 (9)	1.65 (10)	1.94 (1)
11.8 to 12.0	7,663 (4)	5,085 to 10,250	986 (3)	1.64 (3)	1.75 (1)
12.1 to 12.3	8,109 (1)	----------	977 (1)	-------	1.87 (1)
12.7 to 12.9	8,368 (2)	6,294 to 10,442	-------	-------	1.87 (2)
13.0 to 13.2	8,061 (1)	----------	-------	-------	1.98 (1)
13.6 to 13.8	5,304 (1)	----------	-------	-------	1.98 (1)
All lengths	6,375 (72)	3,471 to 11,212	1,012 (61)	1.62 (52)	1.88 (20)

[1] Records of weight were lacking for 11 fish.

The average egg diameters showed no tendency to change with increase of length but were larger in fish of the spawning run in November (1.88 mm.) than in the prespawning October specimens (1.62 mm.). Other analyses revealed no correlation between egg diameter and total number of eggs in individual fish.

SPAWNING

Time and factors of spawning

According to available records, lake herring in the latitude of the Great Lakes spawn sometime between mid-November and mid-December, and spawning activity at one location usually covers a period of 1 to 2 weeks. That the spawning date may differ with latitude is indicated by Dymond (1933), who found evidence that the lake herring of Hudson and James Bays spawn as early as September 10. Water temperature unquestionably is an important factor influencing the time of spawning. Cahn (1927) stated that ciscoes did not begin to spawn in Lakes Mendota and Oconomowoc, Wisconsin, until water temperature had dropped below 4° C., and that the temperature was either 3.1° or 3.0° C. at the time spawning ended (5 years of observations). To verify this apparent relation between temperature and spawning, Cahn (p. 100) held 25 ciscoes in tanks with the following results:

* * * The water was kept at a temperature of 4.5° C. during a period of four months [weeks?], covering the breeding season. In spite of the fact that fifteen of the confined fish were females, all heavy with eggs, not a single egg was laid during this time. In a second tank, exactly similar to the first, and with the same water supply, but cooled by means of ice to a temperature of 3.5° C., females from the first tank spawned within ten minutes after transfer.

A second experiment consisted in transferring two females into the second tank while the water was 4.5° C. After two hours in this tank, a large piece of ice was added and a careful record of the temperature kept. The first female spawned with the temperature at 3.6° C., the second at 3.4° C.

Monti (1929) found that whitefish did not spawn in Italian lakes where winter temperatures remained above 7° or 8° C. Evidence supporting the hypothesis of a critical breeding temperature was given by Pritchard (1930). During the spawning period of the lake herring, which starts in mid-November, the temperatures at a hatchery intake near Belleville in the Bay of Quinte, Lake Ontario, were—

Date	Temperature (° C.)	Date	Temperature (° C.)
Nov. 15	6.1	Nov. 23	4.4
16	7.8	24	3.3
17	6.1	25	3.3
18	4.4		

Stone (1938) recorded a temperature of 3.8° C. shortly before ciscoes started to spawn in Irondequoit Bay, Lake Ontario. He observed also that spawning started earlier in the southern end of the bay where water temperatures dropped sooner than in the northern end. Washburn[9] reported water temperatures near 3.3° C. during cisco spawning in Birch Lake, Michigan. Brown and Moffett (1942) found spawning at its peak in Swains Lake, Mich., on December 14, 1937, when

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

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the surface-water temperature was "* * * practically at the freezing point." They expressed the belief that spawning may have continued for several days after ice covered the lake.

Although the lake herring of Green Bay spawns from mid-November to mid-December, considera-able variation in the progress of spawning activities does take place. It is believed, however, that some spawning is going on every year some place in the bay during this entire period.

An example of the dynamic situation during the progress of spawning in Green Bay is offered by records of catches of a single pound net at Sister Bay in December 1950. On December 2 the catch consisted mostly of ripe fish ready to spawn; on December 3 about 50 percent of the fish were spent; on December 4 all of the 112 lake herring examined from the catch of this net were spent; furthermore, their gonads were in an advanced state of recovery—a condition typical of that found in February. This observation suggests that (1) Lake herring move in schools during the spawning period in Green Bay; (2) fish of one school do not necessarily complete spawning in the place at which they have started; and (3) schools in one area do not all spawn at the same time.

Differences in progress of spawning between various groups of fish most probably are the result of differences in the temperature regime in the several parts of this hydrographically complex bay (see General Features of Green Bay, p. 88). Available temperature records are inadequate for study of local differences during the spawning season. Records that have been made, however, show that the temperature drops through the 4° to 3° C. range during the last half of November and the first half of December when spawning takes place.

Spawning grounds

Most reports, particularly those concerning inland lakes, indicate that eggs of lake herring are laid in shoal areas 3 to 10 feet deep (Bean 1902; Cahn 1927; Pritchard 1930; Stone 1938). Although no evidence was given that spawning did not occur in deeper water, the regularly observed movement of fish into shoal areas and back to deep water clearly indicates that the shallower region must be the preferred spawning area. Wagner (1911, p. 76) reported that in Green Lake, Wisconsin, which is 237 feet deep, "Local fishermen generally believe that spawning takes place at a depth of about seventy feet, on marly bottom, but this is somewhat doubtful." Koelz (1929) related that lake herring spawn in water 60 feet deep at the western end of Lake Erie and in water 30 to 150 feet deep at the eastern end. In Lake Ontario, Koelz said a deep-water form spawns in 90 to 180 feet whereas shallow-water lake herring spawn in 60 feet of water. In Green Bay, spawning fish are most concentrated in water 10 to 60 feet deep but catches of both ripe and spent fish are observed from nets fished at depths down to at least 140 feet. Apparently, spawning takes place over practically all depths and in all sections of the bay.

Spawning lake herring in general show no preference for a particular bottom type. Spawning has been reported over boulders, gravel, sand, marl, clay, mud, and aquatic vegetation. In Green Bay, spawning takes place over areas of boulders, sand, and mud, with no clear indication of preference. The failure to select particular bottom types probably stems from the fact that lake herring are pelagic spawners. Evidence that eggs are extruded a considerable distance above the bottom is given by Pritchard (1930), who found eggs evenly scattered over the bottom with no evidence of local concentrations that would be expected if eggs were deposited near the bottom.

Spawning behavior

Few observations have been made of the spawning act of lake herring. Cahn (1927) described spawning activity of ciscoes in Lake Oconomowoc as being slow and deliberate with no chasing or darting about. In contrast with Cahn's observation, Bean (1902) described the night-time spawning activity of the tullibee in New York as being accompanied by "* * * constant loud splashing and fluttering." This type of activity has also been reported by Washburn (see footnote 9, p. 125) in Birch Lake, Michigan, where "The fish were seen darting about singly and in pairs, occasionally coming to the surface and splashing the water. The appearance of these fish on shoals would take place just before dark at or about sunset and continue until 10:00 p. m." Fishermen of Green Bay tell of similar jumping and splashing activity of lake herring during the spawning period. No observations have been reported on the part this activity plays in the spawning process. Brown and Moffett (1942, p. 149) observed ciscoes breaking water in Swains Lake in the early evening during the peak of the spawning period and remarked, "There was no concentration of these fish. Approximately as many were seen over deep water as were observed over the shallows." The greatest depth of Swains Lake is 64 feet.

Progress of spawning by age, sex, and size

Although the lake herring population of Green Bay, taken as a whole, may show irregular progress of spawning, there seems to be some pattern in the progress of spawning of individual segments of the population. The data of the only two samples that contained a good representation of both ripe and spent fish (table 40) show that, without exception, the longer fish tended to spawn before the shorter fish and that the percentage of spent males was greater than that of females. In both sexes the upward trend in the percentage of spent fish with increase of age suggests that older fish spawn earlier than do younger fish.

TABLE 40.—*Comparison of ripe and spent lake herring in spawning-run collections from Green Bay, by sex and age group, November 29–30, 1950*

[Length in inches]

Age group	Ripe		Spent		Percentage spent
	Number of fish	Total length (inches)	Number of fish	Total length (inches)	
Males:					
I	1	9.7	----	----	0
II	2	10.8	2	11.1	50
III	29	10.8	45	11.1	61
IV	8	11.1	12	11.2	60
V	----	----	2	11.8	100
Females:					
II	2	10.7	----	----	0
III	38	10.8	38	11.4	50
IV	14	11.0	18	11.9	56

Predation on eggs

Possibly the greatest mortality in the life cycle of lake herring takes place immediately after the eggs are laid. A common predator on these eggs is the lake herring itself. Stone (1938) found cisco eggs in 23 of 34 cisco stomachs collected during the spawning season. Pritchard (1931) found cisco eggs in 6 of 46 cisco stomachs. In Green Bay, 16 stomachs of 19 feeding lake herring taken on November 28, 1950, contained from 1 to 33 herring eggs. Although the lake herring commonly eats its own eggs, other species seem to to make greater inroads. Stone found from a few to 200 cisco eggs in stomachs of 20 of 36 brown bullhead (*Ameiurus nebulosus*) and believed this fish to be an important predator in Irondequoit Bay. Pritchard noted cisco eggs in the brown bullhead in Lake Ontario, but the yellow perch was a heavier consumer of cisco eggs (average of 275 eggs per stomach) during the peak of spawning. He also found cisco eggs in whitefish stomachs, but the numbers were small as whitefish were not present during the main spawning period. Rawson (1930) also reported that whitefish feed on cisco eggs. Jordan and Evermann (1902) found that the mud-puppy (*Necturus maculosus*) consumes cisco eggs in Lake Erie. These reports of predation on cisco eggs have been mostly incidental and have not been based on a special study of this problem. Since lake herring eggs, after being laid, lie unprotected on the bottom, variation in the amount of predation at this stage may influence the relative strength of a year class.

DISTRIBUTION AND MOVEMENTS

The distribution of lake herring during the summer months has been a subject of much comment in the literature (Cahn 1927; Fry 1937; Hile 1936; Hile and Juday, 1941; Koelz 1929; Nelson and Hasler, 1942; Pearse 1921; Reighard 1915; Scott 1931; Stone 1938; Van Oosten 1930; Wagner 1911). Although the observations of various authors are not exactly comparable because characteristics of the bodies of water studied were different, the distribution is similar in all lakes of the same type. Upon the warming of surface waters in the spring the lake herring, a stenothermic, cold-water animal, avoids this change by vacating shallow water. As warming continues and a thermocline develops, undesirable or intolerable temperatures of the epilimnion may cause the lake herring to be restricted to the thermocline and hypolimnion.

In the southern portion of their range lake herring are rarely found in lakes that do not develop thermoclines or where the hypolimnion becomes unusually warm. In Indian Village Lake, Indiana, near the extreme southern limit of the range, they have adapted themselves to conditions that might be considered intolerable elsewhere (Scott 1931). In lakes in which either the oxygen becomes depleted or undesirable gases are formed in the hypolimnion, lake herring are forced to inhabit the area of the thermocline. In years of such extreme stagnation lake herring must choose between the epilimnion with adequate oxygen and unsuitable temperatures, or the hypolimnion with inadequate oxygen and suitable temperatures. Cahn (1927) reported that in situations of this type heavy mortalities occur in southern Wisconsin lakes. During a period of extreme stagnation in Snow Lake, Indiana, Scott observed ciscoes coming to the surface, apparently in a state of asphyxiation. These fish recovered quickly, however, and returned to deeper water. According to Koelz (1929) the lake herring of Lakes Erie and Huron follow the normal pattern by descending into deep water during the midsummer months. Koelz reported that lake herring were taken in Lake Superior 1 mile off Grand Marais, Minn., in floating gill nets all year except late July and early August. Surface temperatures in this region are always relatively low.

Among the authors who have reported on the vertical distribution of the lake herring, only a few have given limnological records or experimental data from which judgment can be formed as to limiting values of the controlling factors. Most detailed consideration of the problem was given by Hile (1936) and Fry (1937). From Hile's data on the vertical distribution of ciscoes and on temperature and oxygen conditions during the general period of his fishing operations (he had no limnological records on the actual dates of lifting gill nets) in Muskellunge and Silver Lakes, it may be seen that ciscoes were taken only rarely at temperatures above 17° to 18° C., which marked the upper limit of their distribution, or at oxygen concentrations below 3 or 4 parts per million at the deeper limit of their distribution. Fry commented that he seldom took ciscoes in Lake Nipissing in water 20° C. or warmer. He mentioned oxygen depletion as a possible limiting factor for the lower limit of distribution, but considered carbon dioxide concentration to be of greater importance in making the hypolimnion uninhabitable. Hile did not mention carbon dioxide as a factor in the distribution of the cisco, but in a later publication on the bathymetric distribution of fish in several lakes of northeastern Wisconsin (Hile and Juday, 1941) skepticism was expressed as to the influence of both carbon dioxide and pH concentrations on the distribution of various species in those waters. Cahn's (1927) aquarium experiments indicated that ciscoes avoided temperatures above 17° C.

Of the several possible limiting factors mentioned by earlier investigators only temperature can be held important in Green Bay. Oxygen concentrations in the deeper waters of the bay during the summer of 1952 were always above 7 p. p. m. and the pH fell within the range 7.8 to 8.2. Although determinations were not made of carbon dioxide concentrations in deep water during the summer, the values for oxygen and pH constitute prima-facie evidence that carbon dioxide was not present in excessive amounts.

VERTICAL DISTRIBUTION IN GREEN BAY

The occurrence of lake herring in commercial nets in Green Bay gives some information about the vertical distribution of the herring. In months of cool weather (September or October to May or June) lake herring are commonly taken in pound nets fished in shallow areas and in gill nets fished at all depths. During other months, however, nets set in shallow water make only occasional catches, usually following a storm, and gill nets fished on the bottom in deeper water take few lake herring.

In 1952, a study was undertaken to determine the distribution of the lake herring before, during, and after the summer period when, according to the fishermen, the lake herring "disappear." Oblique gill-net sets,[10] similar to those used by Fry (1937), were employed to determine the depth at which lake herring were located. In these sets 140 linear feet of gill netting were fished in every 15-foot stratum. At station B, where the water was 40 feet deep, 140 feet of gill netting were fished in each 20-foot stratum. One end of the gang of nets was tied to an anchor and the other end to a 15-gallon-drum float. The depths at which segments of the nets fished were controlled by gallon-jug floats attached to the nets with lines whose lengths were multiples of 15 feet. To hold the nets tight, an anchor rope about equal in length to the gang was tied to the 15-gallon drum, pulled against the first anchor, and set with a long buoy line (see figure 14 for a diagram of an oblique set in 60 feet of water).

[10] These experimental nylon gill-nets were 280 feet long and 6 feet deep, and had mesh sizes of 1, ½, and 2 inches, extension measure. The 2-inch-mesh nets were used most extensively.

Table 41.—*Vertical distribution of lake herring taken in oblique sets of gill nets in different periods*

[Mesh sizes, extension measure, in inches]

Month, station, and depth	Date set and lifted	Mesh size	Number of fish	Percentage of catch at—					
				0–15 feet	15–30 feet	30–45 feet	45–60 feet	60–75 feet	75–90 feet
EARLY MAY:									
A (30 ft.)	3– 4	1½	0	0	0				
B (40 ft.)[1]	3– 4	1½	1	100	0				
C (60 ft.)	3– 4	1½	0	0	0	0	0		
D (90 ft.)	1– 2	1½	80	1	2	11	29	39	18
Do	8– 9	1	5	0	0	20	20	40	20
Do	8– 9	1½	7	42	0	0	29	29	0
Do	8– 9	2	45	9	4	45	33	7	2
E (60 ft.)	10–11	2	26	65	23	12	0		
F (90 ft.)	10–11	2	115	30	7	11	28	19	5
G (60 ft.)	10–11	2	118	70	12	10	8		
H (60 ft.)	5– 6	1½	0	0	0	0	0		
I (90 ft.)	5– 6	1½	28	7	7	14	11	21	40
J (90 ft.)	6– 7	1½	0	0	0	0	0	0	0
K (60 ft.)	7– 8	1½	0	0	0	0	0		
L (60 ft.)	7– 8	1½	0	0	0	0	0		
LATE MAY:									
A (30 ft.)	24–25	2	13	85	15				
B (40 ft.)[1]	24–25	2	32	94	6				
C (60 ft.)	24–25	2	5	60	40	0	0		
E (60 ft.)	21–22	2	85	60	34	4	2		
F (90 ft.)	21–22	2	31	87	10	0	0	0	3
G (60 ft.)	21–22	2	31	87	13	0	0		
JUNE:									
J (90 ft.)	10–11	2	82	0	1	14	39	28	18
K (60 ft.)	11–12	2	18	17	6	33	44		
L (60 ft.)	11–12	2	46	0	9	37	54		
JULY:									
A (30 ft.)	23–24	2	0	0	0				
C (60 ft.)	23–24	2	19	0	5	42	53		
D (90 ft.)	27–27	2	6	0	0	17	0	17	66
H (60 ft.)	21–22	2	10	0	0	40	60		
I (90 ft.)	21–22	2	24	0	0	21	63	8	8
J (90 ft.)	19–21	2	152	1	1	7	12	14	65
K (60 ft.)	19–21	2	90	1	3	78	18		
L (60 ft.)	19–21	2	197	0	13	53	34		
OCTOBER:									
A (30 ft.)	21–22	2	15	100	0				
B (40 ft.)[1]	21–22	2	46	96	4				
C (60 ft.)	21–22	2	379	45	37	11	7		
D (90 ft.)	22–23	2	19	58	42	0	0	0	0
H (60 ft.)	23–24	2	189	52	33	9	6		
I (90 ft.)	23–24	2	439	29	36	19	13	2	1
J (90 ft.)	24–25	2	1,220	14	21	28	26	9	2
K (60 ft.)	24–25	2	645	34	36	23	7		
L (60 ft.)	24–25	2	446	11	52	21	16		

[1] Depth intervals 0–20 and 20–40, one 280-foot net used from surface to bottom.

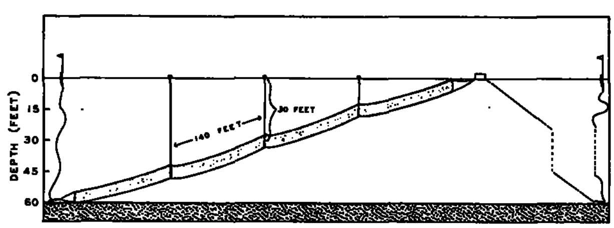

Figure 14.—Method of setting a gill net in an oblique position. Horizontal scale much reduced.

It was obviously impossible to avoid some sagging in the gang. The amount of sag was lessened by the action of currents which are almost always fairly strong in Green Bay.

Oblique sets of gill nets were fished at 12 stations in representative areas throughout Green Bay (fig. 1) from early May to late October 1952. One station (A) was established in 30 feet of water and another (B) in 40 feet in the shallow southern portion of the bay. Six stations (C, E, G, H, K, L) were located in 60 feet of water, and 4 stations (D, F, I, J) in 90 feet.

No lake herring were taken at the shallow-water station A (30 feet) in southern Green Bay and only one was caught at station B (40 feet) in early May (table 41); only a few were taken in late May (A, 13 fish; B, 32 fish) at which time they were found mostly in the upper 15 to 20 feet of water. No lake herring were obtained at the 30-foot station in July. A few were again taken at both stations in October (A, 15 fish; B, 46 fish) when lake herring were concentrated near the surface.

Since the distribution of fish varied randomly among individual 60- and 90-foot stations in southern, central, and northern Green Bay during any one season, data for stations of equal depth have been combined to show seasonal differences in distribution. The graphical representations of distribution of lake herring at 60-foot stations

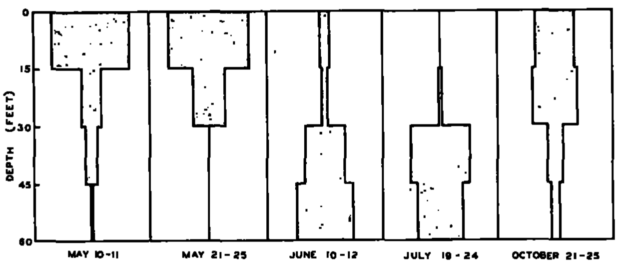

FIGURE 15.—Vertical distribution of lake herring taken in oblique sets of gill nets in 60 feet of water. The full width of the panel for each time period is 100 percent.

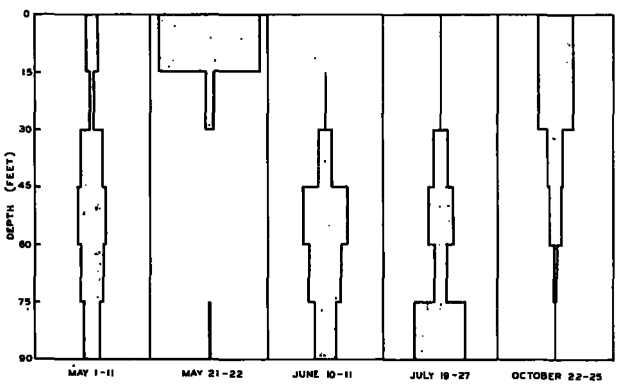

FIGURE 16.—Vertical distribution of lake herring taken in oblique sets of gill nets in 90 feet of water. The full width of the panel for each time period is 100 percent.

(fig. 15) and at 90-foot stations (fig. 16) are given as unweighted mean percentages for all stations where lake herring were caught.

Despite the concentration of lake herring in the upper 15-foot stratum at 60-foot stations (E and G) in early May (67.9 percent, fig. 15), evidence at 90-foot stations where nets were fished on the same and other dates in early May (table 41, fig. 16) suggests a possibly random distribution. In late May the lake herring were concentrated in the top 15-foot stratum at both 60- and 90-foot stations (69.0 and 87.1 percent); most of the remaining fish were at the 15- to 30-foot level (29.0 percent at 60-foot stations and 9.7 percent at 90-foot stations). Lake herring exhibited a strong tendency to move into water deeper than 30 feet in June (84.5 percent at 60-foot stations and 98.7 percent at the 90-foot station); the tendency toward concentration below 30 feet was still greater in July (94.4 and 99.3 percent at 60- and 90-foot stations). Lake herring were present in fair numbers except in deepest water (75 to 90 feet) in October but showed a decided tendency to be concentrated in the upper 30 feet (74.6 and 66.8 percent at 60- and 90-foot stations).

The general seasonal trend in vertical distributions from May to October may be summarized as follows. The first change was from a variable pattern in early May to a pelagic distribution in late May. In June and July the lake herring had descended to depths greater than 30 feet and by October they had resumed the pelagic habitat with the greatest concentration between the surface and 30 feet.

The distribution of lake herring during the spawning period in November and December has been brought out in the discussion of spawning activity. Distribution during winter and early spring is subject of much speculation. The few observations that have been made lead to the conclusion that schools of lake herring may be found at any depth.

The vertical distribution of lake herring showed no relation to temperature, except in the avoidance of water with temperature near or above 20° C. In early May when the water was relatively cool (3.2° to 7.6° C. at stations where lake herring were caught) and varied little with depth (table 42), the distribution of herring was largely random (table 41). Late May temperatures are available for only the shallow-water stations (A and B); the surface temperatures at these locations were 14.1° and 14.5° C. and bottom temperatures were 13.0° and 11.6° C.

Although the lake herring had moved toward greater depths in June, it cannot be assumed that increasing water temperature near the surface was the cause. The temperatures from the surface to 30 feet were between 12.3° and 15.1° C. (total range at all stations)—not greatly different from those at stations A and B in late May. The lake herring continued to be concentrated below 30 feet in July. During this month water temperatures at less than 30 feet (fig. 17 and table 42) usually were within the range of 18.3° to 21.5° C. (the range from 15.6° at 20 feet to 18.6° at the surface on July 24 represents a transitory situation following a severe storm). Since these July temperatures from the surface to 30 feet were mostly near or above the values considered critical for the lake herring (see p. 128), it is probable that temperature conditions held the lake herring in greater depths in July. This view is supported by the absence of lake herring at shallow-water station A

TABLE 42.—*Water temperature at or near experimental gill-net stations*

[Temperature records made with a bathythermograph. Depth of cast (feet) is indicated by deepest temperature recorded]

Period and station [1]	Day of month	Temperature (° C.) at depth of—										
		0 feet	10 feet	20 feet	30 feet	40 feet	50 feet	60 feet	70 feet	80 feet	90 feet	100 feet
EARLY MAY:												
A	3	12.1	9.1	8.6	-----	-----	-----	-----	-----	-----	-----	-----
B	3	13.1	8.4	7.4	6.9	-----	-----	-----	-----	-----	-----	-----
D	1	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	-----
D	8	9.2	8.0	6.9	6.6	6.2	5.8	5.4	5.3	5.2	5.1	5.0
E	10	6.6	6.6	6.5	6.5	6.5	6.5	6.3	5.9	-----	-----	-----
E	11	6.0	6.0	6.0	6.0	6.0	6.0	6.0	6.0	-----	-----	-----
F	11	6.9	5.9	5.6	5.5	5.2	4.8	4.3	4.3	4.3	4.3	-----
G	10	7.6	7.0	6.6	5.9	4.9	4.8	4.7	-----	-----	-----	-----
G	11	7.5	7.1	6.9	6.8	6.6	6.1	5.3	-----	-----	-----	-----
I	5	5.5	5.4	5.1	4.5	4.2	4.2	4.2	4.2	4.2	4.2	4.2
J	6	7.5	7.5	7.4	7.3	7.2	7.1	7.0	6.9	5.1	5.0	5.0
K	7	8.6	8.2	8.0	7.6	6.6	6.1	5.3	-----	-----	-----	-----
L	7	6.0	6.0	5.3	5.2	5.2	5.2	5.2	-----	-----	-----	-----
LATE MAY:												
A	24	14.1	13.8	13.1	13.0	-----	-----	-----	-----	-----	-----	-----
B	24	14.5	13.6	13.5	13.3	11.6	-----	-----	-----	-----	-----	-----
JUNE:												
J	10	12.9	12.9	12.8	12.8	12.6	12.2	11.1	8.4	7.5	7.3	-----
K	11	13.1	13.1	12.5	12.3	11.6	10.8	9.1	7.5	6.0	-----	-----
K	11	13.6	13.5	13.0	12.6	11.5	9.3	7.7	6.0	-----	-----	-----
L	11	15.1	15.0	14.4	13.7	11.2	7.3	6.2	-----	-----	-----	-----
JULY:												
A	23	20.5	20.5	20.5	20.3	-----	-----	-----	-----	-----	-----	-----
A	24	19.8	19.8	19.7	19.7	-----	-----	-----	-----	-----	-----	-----
B	24	19.6	19.3	18.3	11.4	10.2	-----	-----	-----	-----	-----	-----
C	23	19.9	19.9	19.6	18.5	12.0	9.6	9.0	9.0	9.0	-----	-----
C	24	18.6	16.9	15.6	14.7	14.2	13.0	9.6	9.1	8.7	-----	-----
D	22	20.2	20.1	19.9	11.5	9.8	8.8	7.9	7.8	7.6	7.5	-----
D	27	20.6	20.5	20.2	20.0	17.7	10.0	8.1	7.5	7.4	7.3	7.2
H	21	20.3	20.2	19.9	11.7	9.2	8.9	8.4	8.4	-----	-----	-----
I	21	21.3	21.1	21.0	20.4	18.0	12.6	8.5	7.9	7.2	6.9	6.8
I	22	21.5	21.5	21.2	19.5	14.6	10.1	8.4	7.2	6.8	6.8	6.7
J	19	20.5	19.9	19.2	18.5	13.9	10.6	9.9	8.9	8.3	8.0	8.0
J	21	21.4	21.2	19.7	18.5	14.5	12.9	11.5	10.1	10.0	9.0	8.7
K	19	20.3	19.7	19.1	19.0	17.0	11.0	10.2	10.1	-----	-----	-----
K	21	20.2	19.9	19.5	18.6	14.5	10.4	9.6	9.4	-----	-----	-----
L	19	20.7	19.4	18.7	15.6	14.0	11.5	-----	-----	-----	-----	-----
L	21	20.5	20.4	19.9	14.5	12.1	10.0	9.1	-----	-----	-----	-----
OCTOBER:												
A	21	8.4	8.4	8.4	8.4	-----	-----	-----	-----	-----	-----	-----
B	21	8.9	8.9	8.9	8.9	8.9	-----	-----	-----	-----	-----	-----
C	21	9.2	9.2	9.2	9.2	9.2	9.2	9.2	-----	-----	-----	-----
C	22	9.4	9.4	9.4	9.4	9.4	9.4	9.4	-----	-----	-----	-----
D	22	9.9	9.9	9.9	9.9	9.8	9.7	9.7	9.6	9.5	9.5	9.5
D	23	9.8	9.8	9.8	9.7	9.7	9.7	9.6	9.5	9.3	-----	-----
H	23	10.2	10.2	10.2	10.2	10.1	10.1	10.0	10.0	-----	-----	-----
I	23	10.1	10.1	10.1	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0
I	24	10.0	10.0	10.0	10.0	10.0	10.0	10.0	9.9	9.8	9.8	-----
J	24	9.5	9.5	9.4	9.3	9.3	9.3	9.3	9.3	9.3	9.3	9.3
K	24	9.7	9.6	9.4	9.4	9.4	9.4	9.4	9.4	-----	-----	-----
L	24	8.5	8.3	8.3	8.2	8.1	8.1	8.1	-----	-----	-----	-----

[1] See figure 1 for location.

where the temperatures on July 23 and 24 were 19.7° to 20.5° C. In October when the lake herring were again most plentiful from the surface to 30 feet, the water temperature was generally cool (8.1° to 10.2° C.) and the temperature gradients from top to bottom were insignificant (greatest difference 0.4°).

The one previous study of the vertical distribution of the lake herring in relation to size of fish was made by Fry (1937) in Lake Nipissing. Fry found that the movement from shallow water to the hypolimnion was not a mass descent but was "* * * an orderly succession of certain groups of individuals which migrate in order of size and sex." Consideration of the distribution in relation to sex was made earlier (p. 120) in the discussion of sex composition. In the summary o the length of lake herring taken at various depths (table 43) the sexes are combined, as no sex differences in length were found for fish taken in the same depth of water. Despite certain exceptions (usually at depths in which the catches were small) the average size of lake herring tended to decrease with increase in depth of water in all collecting periods. Davidoff [11] found a similar tendency for the larger ciscoes of Myers Lake, Indiana, to be near the surface.

The seasonal changes in the distribution of the lake herring must be a major cause of the highly

[11] Davidoff, Edwin B. 1953. Growth, response to netting, and bathymetric distribution of the cisco, *Leucichthys artedii* (Le Sueur) in Myers Lake, Indiana. M. S. thesis, Department of Fisheries, University of Michigan. [Typewritten.]

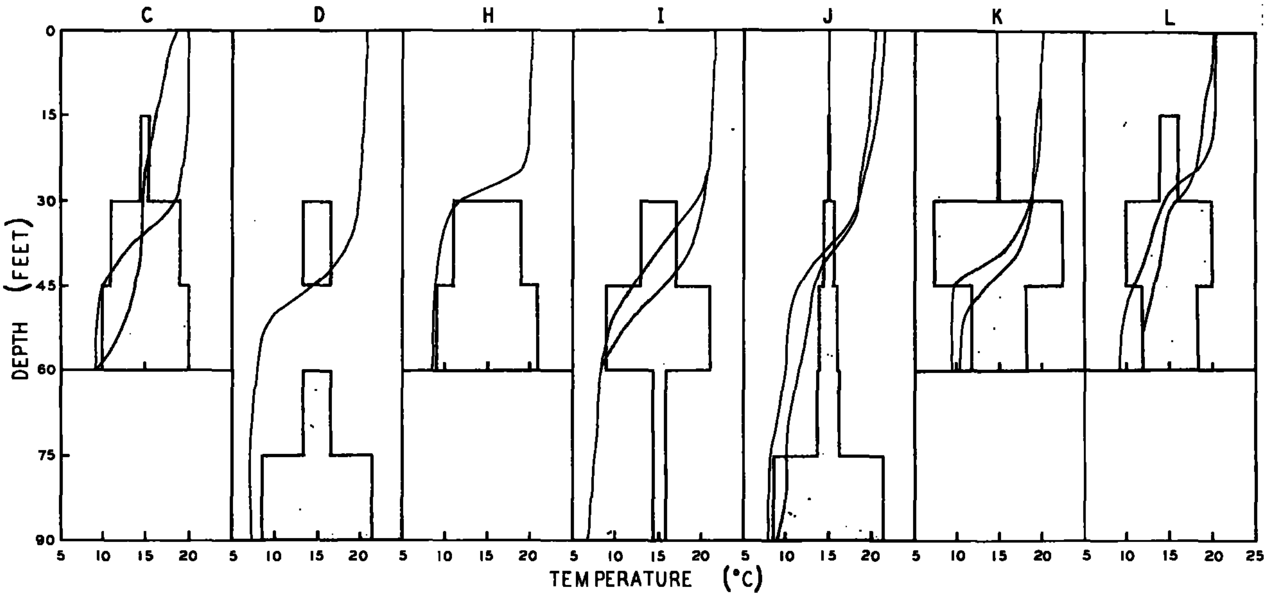

FIGURE 17.—Relation between temperature and vertical distribution of lake herring July 19–27, 1952. See figure 1 for locations of stations. The full width of the panel for each station represents 100 percent.

TABLE 43.—*Length of lake herring taken in oblique sets of gill nets, by depth and season, 1952*

[2-inch-mesh gill nets, all stations combined. Length in inches]

Depth (feet)	May 1–11		May 21–25		June 10–12		July 19–27		October 21–25	
	Number of fish	Total length	Number of fish	Total length	Number of fish	Total length	Number of fish	Total length	Number of fish	Total length
0 to 15	137	11.0	119	11.1	4	11.1	2	11.1	279	11.3
15 to 30	30	11.0	40	10.9	6	10.5	31	11.0	210	11.2
30 to 45	48	10.9	3	10.9	34	10.8	87	10.7	206	11.0
45 to 60	56	10.9	2	10.5	65	10.9	95	10.6	212	10.8
60 to 75	25	10.8	---	---	23	10.8	24	10.7	38	11.1
75 to 90	7	10.7	1	10.7	15	10.7	33	10.7	33	10.7

seasonal character of the fishery. Nearly half (47.2 percent) of the commercial catch is made during the fourth quarter of the year (fall) and a fourth (24.4 percent) during the first quarter (winter). (See table 2.) Production is much lower in the spring (19.5 percent) and summer quarters (8.9 percent).

Principal gear for taking lake herring are pound nets which fish from the surface to the bottom and are seldom set at depths greater than 35 to 40 feet, and gill nets which are set on the bottom at all depths but are effective only 6 to 11 feet above the bottom.[12] Thus, pound nets can take herring only when the fish are in the shallower inshore waters and gill nets can capture them only when the fish are near the bottom. From figures 15 and 16 it may be seen that in June and July most herring were in water too deep to be taken by pound nets. The same condition most probably held in August, September, and even early October. During the same period the lake herring should have been available to gill nets set in deeper water. Examination of the nets as they were lifted from oblique sets revealed, however, that most of the herring taken in the bottom 15-foot stratum were caught in the upper half of the net section. Because the fish are some 6 to 8 feet above the bottom, commercial fishing with gill nets during the summer period is not productive. The distribution pattern in which some, and at times most, lake herring are above the bottom and outside the 30- to 40-foot contour provides them a considerable degree of protection from commercial exploitation. In view of the relative inefficiency of present fishing gear, the probability of depletion by the present fishery is small.

[12] In State of Michigan waters gill nets may not be more than 11 feet deep (distance from float line to lead line); in Wisconsin the greatest depth allowed (stated in numbers of meshes) is about 6 feet.

MOVEMENTS AND ACTIVITY

Available evidence shows that the lake herring, as well as other coregonids in the Great Lakes, does not undergo extensive migrations. Principal source of information is the study of Smith and Van Oosten (1940), who reported the following percentage recaptures from Lake Michigan fish tagged from 1929 to 1931 near Port Washington, Wis.: 5.4 percent from 593 lake herring; 22.1 percent from 457 whitefish; 5.7 percent from 106 chubs (*Leucichthys* spp., other than lake herring); and 20.0 percent from 35 pilots, or round whitefish (*Prosopium cylindraceum quadrillaterale*). Lake herring were not recovered at distances greater than 50 miles from point of tagging, while lake trout and rainbow trout tagged in the same study were recaptured at distances as great as 125 to 225 miles away. The percentage distribution of recoveries was as follows:

Miles traveled from point of release	Lake herring	Whitefish	Chubs	Pilots
1 to 10	69	67	100	100
11 to 25	28	29		
26 to 50	3	1		
51 to 75		3		

Järvi's (1920) study of the "kleine Maräne," a species similar to the lake herring, in Keitelesee, Finland,[13] disclosed the presence of distinct stocks, with respect to growth and age composition, in different basins. In view of these differences he concluded that the movements of the "kleine Maräne" must be limited and that the few observed migrations probably resulted from unusual temporary conditions.

Local movements of the lake herring that have been observed probably are the result of thermal conditions or represent spawning and feeding activities. The vertical movement accompanying thermal stratification is not as great as the horizontal distances that must be traveled in Green Bay when the fish abandon the warming shallow-water areas to seek colder water. This distance amounts to about 10 miles in northern Green Bay and 25 miles in southern Green Bay. Similar distances are covered in the return to shallow-water areas prior to and accompanying spawning. In Lake Erie the summer and spawning movements, according to the distribution described by Van Oosten (1930) must involve distances of 100 miles or more.

[13] The greatest length of Keitelesee is 72 kilometers, or about 45 miles.

Cahn (1927) found that the ciscoes of Oconomowoc Lake were closer to the surface at night than during the day, and he interpreted this diurnal migration as a feeding movement. Järvi (1920) observed the same diurnal movement in the "kleine Maräne" of Keitelesee. He believed that the local horizontal movements of schools of "kleine Maräne," as well as the diurnal movements, were associated with feeding. Similar movements of lake herring schools in Green Bay are shown by the highly erratic catches of nets fished in the same locality day after day. A good example is found in the catches at Sister Bay on December 2, 3, and 4, 1950, where a pound net apparently took members of three different schools on three successive days (see p. 126).

There is some evidence that the strong currents, which are common in Green Bay, are responsible for movement of lake herring. These movements are reported by commercial fishermen who occasionally, following summer storms, take lake herring in shallow-water areas where they are not normally found during the summer period. These occurrences indicate that lake herring can be transported by currents.

SUMMARY

1. The lake herring occurs in many of the deeper, colder lakes of the northeastern section of the United States, over most of Canada and Alaska, and also in Hudson and James Bays. It is rarely found in rivers.

2. Green Bay is one of the most productive commercial fishing areas in the Great Lakes and the lake herring is a major contributor to the total catch in the bay. In 1952 Green Bay produced 38.7 percent of the total take of lake herring from all United States waters of the Great Lakes. The commercial catch fluctuates widely, but this study was conducted during years (1948–52) when production was high and relatively stable.

3. Green Bay is 118 miles long and 23 miles wide. Water exchange with Lake Michigan is relatively free in the northern end of the bay, but practically nil in the southern section. Water movements in the bay are complex and often are of considerable magnitude. They result in an unstable, almost continually changing environment within the bay.

4. Scales for studies of age, growth, and year-class strength were collected from 4,390 lake herring taken from pound and gill nets. Investigation of most phases of the life history was based on catches of pound nets, which are less selective with respect to size of fish than are gill nets. Length records were obtained for all and weight and sex data for most of the 2,039 lake herring taken from experimental gill nets.

5. Age determinations were made by examining the magnified image of scales projected on a screen. Fish with no annulus (year-mark) were assigned to age group 0, those with 1 annulus to age group I * * *. All fish were considered to pass into the next higher age group on January 1.

6. The maximum age of lake herring reported in any population is XII; the oldest fish from Green Bay belonged to age group VII. The best-represented age groups in the various populations for which there are published records are age groups II to V; age groups III and IV were the most plentiful in Green Bay. The commercial catch in Green Bay was dominated by age group IV in the period January to June and by age group III in July to December.

7. The age composition of lake herring from pound nets was not representative of the population, as young fish were seldom taken even though the mesh sizes (1½ to 2 inches, extension measure) were small enough to hold them. Yearling lake herring, as a rule, do not inhabit the relatively shallow, inshore areas where pound nets are fished.

8. The length of lake herring from the commercial pound nets and gill nets varied little from season to season. Even during the summer period of rapid growth the effects of individual increases in length were largely compensated by the selective destruction of the larger lake herring in the fishery and by the shift to a lower average age.

9. The relation between the total body length in inches (L) and the magnified ($\times 41$) scale diameter in millimeters (S) of Green Bay lake herring is described by the formula

$$L = 0.01615 + 0.05486\ S$$

Since the intercept is so small, its value was assumed to be 0, and lengths at the end of various years of life were calculated from scale measurements by direct proportion.

10. Annuli are formed on scales of the Green Bay lake herring in May and June. The progress of annulus formation is irregular, possibly because of different local environmental influences. The younger age groups and the smaller fish within an age group tend to form annuli earliest.

11. Growth within the season was described by a sigmoid curve. Growth started about the first of May and terminated near the end of October, with the fastest growth in July.

12. Males and females grew at the same rate.

13. Selective destruction of fast-growing individuals was so great that seasonal differences in style of growth were detectable, that is, lake herring taken early in the year had grown faster in earlier years than had fish of the same age group captured later in the same year.

14. Calculated length at the end of the first year of life increased from north to south. These first-year differences, almost surely of environmental origin, were rapidly reduced by compensatory growth in later years of life.

15. Annual fluctuations in growth in length indicated that conditions affecting growth of lake herring in Green Bay changed little from year to year. The growth rate was below average and decreasing from 1944 to 1946, improved from 1946 through 1950, and then declined somewhat in 1951. Growth was well above average during the period 1949–51.

16. The different age groups exhibited systematic discrepancies in calculated growth resembling those commonly termed Lee's phenomenon of "apparent decrease of growth rate." Selective destruction of the larger, faster-growing fish by the commercial fishery was held to be the most important of the various factors that may have contributed to the discrepancies.

17. Growth compensation takes place in Green Bay lake herring. It was shown that growth compensation will appear in the calculated growth of fish that follow identical growth curves but that are hatched at different times in the season. It was also demonstrated that length rather than age is the primary determinant of subsequent growth of the individual, and hence that growth compensation can occur among fish whose growth curves are different.

18. The general length-weight relation of the Green Bay lake herring is described by the equation

$$\log W = -2.4386 + 3.0729 \log L,$$

where W is weight in ounces and L is total length in inches.

19. Weight varied according to sex and to method, season, and year of capture.

20. Females were relatively more abundant in samples taken from pound nets in February than in May to December. They were also more plentiful in the younger age groups than in the older. The selective destruction of females in younger age groups may be a major factor in the progressive decline with increased age in the percentage of females in a year class.

21. The percentage of females in the Green Bay lake herring population declined continuously from 1949 to 1952.

22. The percentage of females in collections taken in oblique sets of gill nets increased with depth of water in October. This change in sex composition with depth may reflect an actual difference in the distribution of the sexes, but a difference in the activity of the sexes may have been a major factor.

23. Some Green Bay lake herring matured during their second year of life, and all had reached maturity by the end of the third year.

24. Lake herring spawn in Green Bay between mid-November and mid-December, but spawning of an individual school of fish may be completed in a fraction of this period. Fish of the same school do not necessarily complete spawning in one location. Within a school, the older fish and the larger fish of an age group tended to spawn first and the males spawned earlier than the females.

25. Lake herring are pelagic spawners; the eggs are broadcast and settle unprotected to the bottom. Inshore areas are preferred, but there is evidence that lake herring may spawn in Green Bay over water as deep as 140 feet.

26. The literature indicates that lake herring hatch in early spring (April–May) and that newly hatched fry are pelagic. Young-of-the-year lake herring have rarely been collected. They probably lead a bathypelagic existence where they are relatively immune from capture by the usual methods of collection.

27. Although the number of eggs produced by female lake herring (range, 3,471 to 11,212) varied widely for fish of the same total length as well as of different lengths, the number of eggs tended to increase with length of the fish. The relative number of eggs (i. e., number per ounce of body weight) tended to decrease with increase of length.

28. The lake herring of Green Bay were randomly distributed from top to bottom in early May, but they were concentrated in the upper 15 to 30 feet in late May. They descended to deeper water in June and were restricted to strata more than 30 feet below the surface in July when temperatures in shallower water were unfavorable (17° C. and above). In October, lake herring were again found at all levels but were most abundant in the upper 30 feet.

29. Lake herring are not migratory but they sometimes move considerable distances to avoid unfavorable temperatures. Local movements are probably associated with feeding or represent passive transport by currents.

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