LIFE HISTORY OF LAKE HERRING IN LAKE SUPERIOR

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ABSTRACT

The average annual commercial catch of lake herring (*Coregonus artedi*) in U.S. waters of Lake Superior was nearly 12 million pounds in 1929–61. This production contributed 62.4 percent of the total U.S. take of lake herring for the Great Lakes. About 90 percent of the annual catch is taken from small-mesh gill nets during the November-December spawning season.

The life-history studies were based on 12,187 fish collected in 1950–62; past growth was computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich.

Age group IV dominated the catch in each year's collection at each port, followed by age groups III and V. The average age of the lake herring in the commercial samples was 3.9 years at Bayfield, Portage Entry, and Marquette, and 4.1 years at Duluth. With few exceptions, the mean age of the females exceeded that of the males.

The strength of the year classes varied considerably at each port but generally declined over the 1946–55 period. Fluctuations were similar at Bayfield and Marquette, but at neither port resembled closely the fluctuations at Portage Entry. Year classes 1954 and 1955 were, however, well below average at all three ports.

Females were larger than males (largest difference was 0.6 inch) at all ports except Marquette where the males held a slight advantage. With only one exception, the average lengths of the age groups were larger in 1956–59 than in 1950–55. The largest increase from the earlier to the later period was 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

The weight of the lake herring in the combined samples increased as the 3.170 power of the length. Lake herring of corresponding lengths were heavier in 1956–61 than in 1950–55 (greatest increase was 8.8 percent at Bayfield). Port-to-port differences in average weight among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight.

The calculated lengths and weights of fish from Duluth were smallest, followed by those from Bayfield, Portage Entry, and Marquette. With only one exception, the calculated lengths and weights of lake herring taken in 1956–59 were greater than those taken in 1950–55.

The trends in annual fluctuations of growth in length and weight were closely correlated among the three ports. Growth was generally below average in 1945–53 and above average in 1954–59.

The percentage of females equalled or exceeded that of the males in all age groups above I. The percentage of females, all age groups combined, was 68.5. The first mature males appeared in the 8.5- to 8.9-inch group; the first mature females were in the 9.5- to 9.9-inch group. All males were mature at lengths greater than 11.4 inches, and all females at lengths greater than 11.9 inches. The youngest mature lake herring belonged to age group II, and all fish older than age group III were mature. Spawning of Lake Superior lake herring normally is at its peak during the last week in November and the first week in December. The average number of eggs produced by female Lake Superior lake herring was 6,351.

Crustacea were the most common food and were found in 83 percent of the 146 stomachs examined.

The distribution of lake herring may be influenced by temperature, abundance of plankton, and spawning. The fish are most common near the surface in early summer, migrate to deeper water as the surface water warms, and are randomly distributed between the surface and about 20 fathoms in the late fall.

The lake herring, *Coregonus artedi* LeSueur, occurs in all of the Great Lakes and in the deeper inland waters of the St. Lawrence River, Hudson River, and Mississippi River drainages (Hubbs and Lagler, 1947). The name "lake herring"

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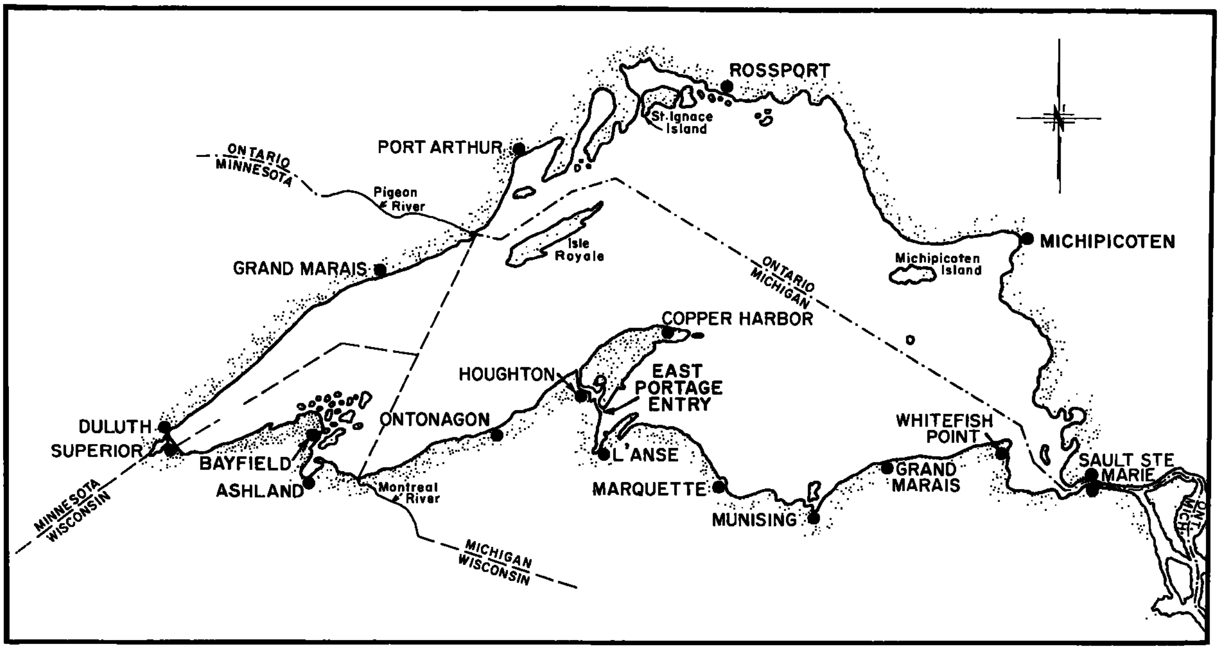

FIGURE 1.—Map of Lake Superior.

undoubtedly originates from the resemblance and analogous ecological position to the Atlantic marine herring, *Clupea harengus*. Both are pelagic and feed largely on plankton. They are the basis of considerable commercial fishing and also serve as forage for the more valuable food fishes—the marine forms for cod and other predators, and the fresh-water forms for the once-abundant lake trout.

The lake herring did not gain high importance in the Great Lakes fisheries until the early 1900's when it assumed first position in the total Great Lakes production; it has held this rank to the present time. The average production in U.S. waters in 1929–61, the most recent years for which dependable statistics are available for all Great Lakes, was nearly 19 million pounds. The catch of 24,371,000 pounds in 1948 was the highest recorded in that period, but Lake Erie alone produced greater catches before the collapse of the fishery there in 1925. Production in the Great Lakes in most recent years has not equalled that of the earlier years, but continues to be substantial (nearly 21 million pounds, for example, in 1954).

The lake herring (usually known as cisco in Lake Erie and in small lakes) is a member of an extremely complex genus. The coregonines have confused taxonomists for many decades, and even though researchers have added greatly to the amount of data available, the group is still not well understood. The confusion stems from the difficulty in describing a group which varies widely in size, shape, and systematic characters, and in which the morphology is affected by the environment. The deepwater members of the genus, known collectively as chubs, are often difficult and sometimes impossible to identify by species at the smaller sizes. The separation of lake herring from chubs, however, rarely causes difficulty.

Numerous papers have been published on the age, growth, and ecology of *C. artedi* of the smaller lakes but the only major publications on the species in the Great Lakes have been those of Van Oosten (1929), Scott (1951), and Smith (1956). This paper is the first contribution to the life history of the lake herring in Lake Superior.

MATERIALS AND METHODS

The studies of the Lake Superior lake herring were based on 12,187 specimens collected from commercial and experimental gill nets fished at various locations and dates during 1950–62. The main study of age and growth was based on 3,779

TABLE 1.—*Ports and dates of collection of Lake Superior lake herring used in study of age and growth*

Date	Port	Gill net mesh size	Number of fish
		inches	
1950			
Dec. 4	Bayfield	[1]	103
Dec. 5	Portage Entry	[1]	96
Dec. 15	Marquette	2½	68
1951			
Nov. 20	Marquette	2⅜	106
Nov. 27	Bayfield	2⅜	147
Nov. 27	Portage Entry	2⅜	123
1952			
Nov. 11	Bayfield	2⅜	125
Nov. 24	Portage Entry	2⅜	106
Dec. 11	Marquette	2⅜	101
1953			
Nov. 20	Marquette	2⅜	84
Dec. 1	Portage Entry	2⅜	91
1954			
Dec. 1	Portage Entry	2½	96
Dec. 6	Bayfield	2¼	161
Dec. 10	Marquette	2½	102
1955			
Dec. 2	Portage Entry	2⅜	85
Dec. 5	Marquette	4½	95
1956			
Nov. 6	Marquette	2⅜	72
Nov. 11	Portage Entry	2⅜	143
1956			
Nov. 19	Bayfield	2⅜	93
Dec. 5	Marquette	2⅜	83
Dec. 10	Portage Entry	2⅜	100
1957			
Nov. 25	Portage Entry	2⅜	106
Nov. 26	Marquette	2⅜	81
Nov. 27	Bayfield	2¼	105
Dec. 3	Duluth	[1]	47
Dec. 4	Bayfield	2¼	92
Dec. 6	Duluth	[1]	43
Dec. 9	Portage Entry	2⁷⁄₁₆	103
Dec. 9	Marquette	2⁷⁄₁₆	78
1958			
Nov. 25	Portage Entry	2⁷⁄₁₆	118
Dec. 1	Marquette	2⅝	117
Dec. 3	Duluth	2¼–2½	122
Dec. 10	Bayfield	2½	116
1959			
Nov. 24	Duluth	2⅜	113
Dec. 1	Portage Entry	2⅜–2½	125
Dec. 1	Marquette	2½	123
Dec. 8	Bayfield	[1]	110
Total			3,779

[1] Mesh size unkown.

fish from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., (fig. 1) during the fall spawning seasons of 1950–59 (table 1). The mesh sizes of the commercial gill nets ranged from 2¼ to 2⅝ inches, extension measure (the sample collected at Marquette in 1955 came from 4½-inch-mesh trout nets). The 2⅜-inch-mesh gill nets were by far the most common in the fishery. Scale samples and data on length, weight, sex, and state of gonads were obtained from each fish.

The remainder of the samples came from experimental gill nets fished from the Bureau's research vessel *Siscowet* (fig. 2) in western Lake Superior (table 2), from special collections during the 1961 spawning run at Bayfield, and from the summer lake herring fishery at Marquette. The numbers of fish employed in the individual phases of the life-history study varied according to the appropriate materials available or the number of specimens required. The numbers and sources of the fish used for each particular study are listed in the text.

All collections used in this report represent the entire catch or net-run samples.

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

Whenever possible, the scales for the study of age and growth were removed from the left side of the body at a point midway between the lateral

TABLE 2.—*Lake herring taken in experimental gill nets by the M/V* Siscowet *in western Lake Superior, 1958–61*

Date	Number of fish
1958	
June	323
July	62
August	45
September	774
October	53
November	208
December	80
1959	
April	6
May	23
June	9
July	289
August	4
September	32
October	177
November	886
December	272
1960	
April	66
May	57
June	20
July	53
September	176
October	217
November	269
December	621
1961	
May	2
June	5
July	6
September	120
October	10
November	245
December	74
Total	5,184

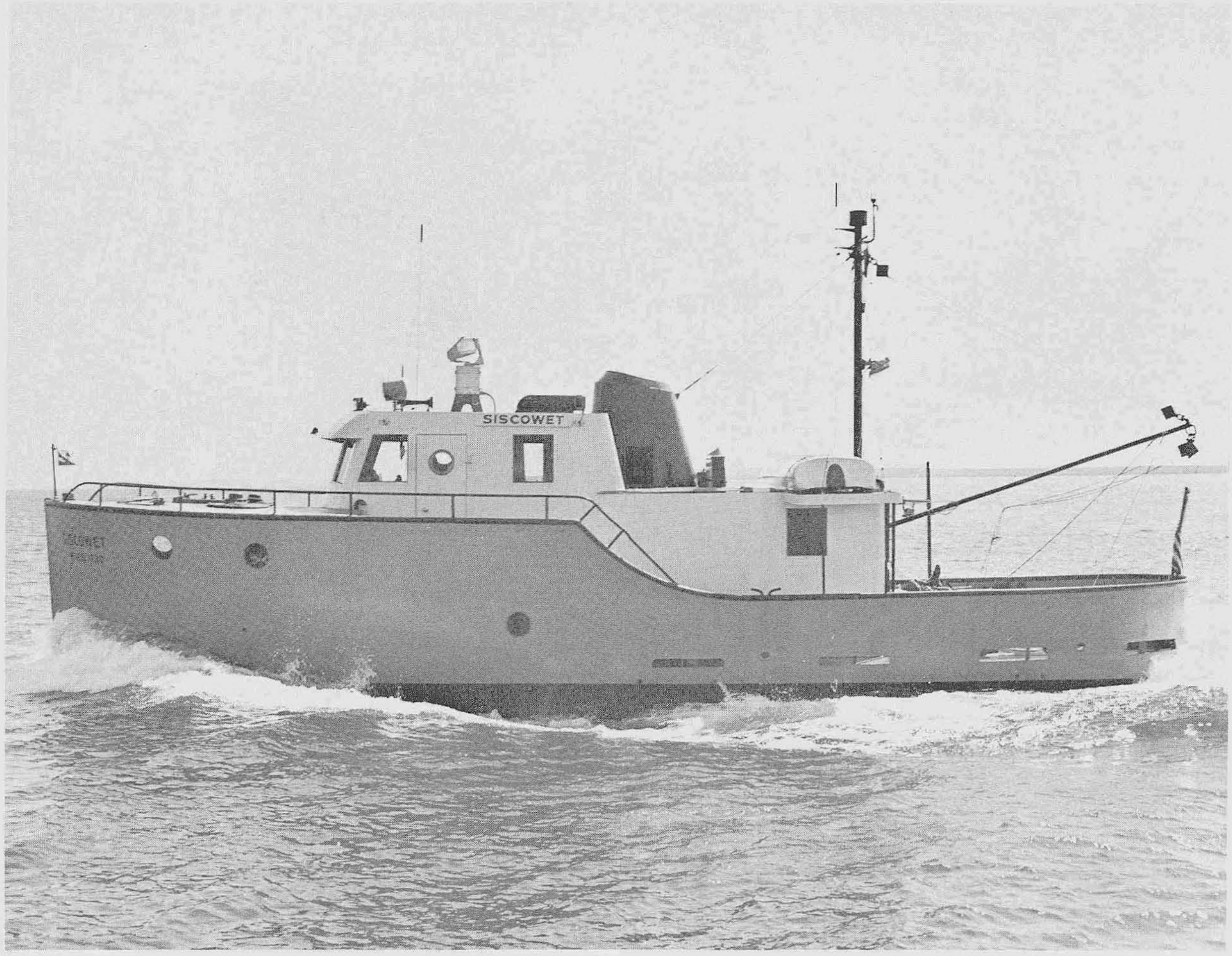

FIGURE 2.—M/V *Siscowet.*

line and the middle of the base of the dorsal fin. Scales were not always available from this area, however, particularly on fish which had been choked through the gill nets, thus leaving them devoid of scales in the midriff. Under these circumstances, the scales were removed from wherever they could be found, usually from a point posterior to the dorsal fin.

Plastic impressions of scales were made in cellulose acetate (Smith, 1954) and were magnified 43 diameters by means of a microprojector (Moffett, 1952). Diameters of scales and growth fields were measured through the focus along a line that roughly bisected the anterior field, and were recorded to the nearest millimeter.

Some difficulty was encountered in distinguishing accessory marks or false annuli from the true annuli. If doubt as to true age was great, the specimen was excluded from the analysis. It is felt that these few exclusions (about 3 percent) made the age determinations reasonably dependable.

Age groups are designated by Roman numerals corresponding to the number of annuli. All the fish were considered to have passed into the next age group on January 1. For fish of all spawning-run collections, the numbers of completed growing seasons ran one greater than the indicated ages. The annulus formation offered no difficulties in age determinations since the samples for the age and growth studies were all collected during the fall spawning run, whereas the annulus is laid down in the early summer.

Calculations from scale measurements of lengths at time of completion of earlier annuli were made by direct proportion. The validity of this method was demonstrated for Saginaw Bay (Lake Huron) lake herring by Van Oosten (1929) and for Green Bay (Lake Michigan) lake herring by Smith (1956). Materials available in the present study were unsuitable for the determination of the body-scale relation for lake herring of Lake Superior.

An instructive discussion of the various phases of this paper requires a preliminary statement on the probable extent to which various sources of bias affect the data. The major bias to the data from the spawning-run samples can be traced to four sources: gear selection; segregation on the basis of maturity; selective fishing mortality; and time of capture within the spawning season. These sources may act independently or collectively to prejudice estimates of age composition, relative strength of the year classes, size at capture, growth, sex composition, and annual fluctuations in size and growth. The first two factors have so much in common that certain of their effects cannot be separated, and together they make possible the selective fishing that leads to the progressive change in the actual growth of the survivors.

Bias from gear selection affects estimates of age composition through failure of the gear to take representative samples of the younger age groups which actually may be present on the spawning grounds. The selection of only the larger members of the younger age groups causes overestimates of average size and calculated lengths. The possibility of selecting the small members of the older age groups also exists, but the scarcity of old fish and the reduction of growth with age probably make this selection insignificant. Changes from cotton to nylon twine, in mesh sizes, and subtle changes in the hang of the net may bias comparisons among samples, especially those dealing with changes in the average size, growth, and weight. During 1950–55 the 2⅜-inch-mesh net was the most common, although samples were collected from 2½-inch-mesh nets in Marquette in 1950 and 1954 and at Portage Entry in 1954. One sample was collected from 2¼-inch-mesh nets at Bayfield in 1954. In the years following 1955, the fishery adjusted the mesh size to conform with the increased size of the fish at all ports except Bayfield (comparable data are not available for Duluth). At Portage Entry, the 2⁷⁄₁₆- and 2½-inch-mesh nets were in common use, and at Marquette the mesh sizes ranged from 2⅜-inch in 1956 to 2⅝-inch mesh in 1958, 1960, and 1961. At Bayfield, despite the increased size of the fish, the mesh sizes actually decreased during 1956–61 from 2⅜- in 1956 to 2⁵⁄₁₆-inch mesh in 1961.

Successively larger meshes would be expected to capture fish of larger size, and the shorter fish captured should have a greater relative girth (and hence, be heavier than fish of the same length captured in nets with smaller meshes). Deason and Hile (1947) found that *C. kiyi* of the same length captured in nets of successively larger meshes had successively greater values of the coefficient of condition, *K*.

Other questions arise relating to comparisons among samples taken from different makes of twine. The mesh sizes recorded in the data were those ordered by the fishermen and not necessarily the actual size as fished. Different twine companies supply different mesh sizes on identical orders; some produce mesh sizes which are scant whereas others give accurate meshes. Also, lots of twine of the same general material (e.g., cotton, linen, or nylon) have different shrinkage under use. When the fisherman receives the twine he may hang the net on the one-half basis (i.e., 4 feet of twine, flat mesh, hung on 2 feet of maitre) or tighter, such as two-third basis (6 feet of twine on 4 feet of maitre). The selective action of the gill nets may vary according to their hang—a tightly hung net has a lesser tangling action and hence may be more selective than one hung loosely.

Undoubtedly the most severe source of bias in the spawning-run collections was segregation on the basis of maturity. Since only mature individuals were found on the spawning grounds, I-group fish were entirely lacking and age groups II and III were poorly represented. Age group IV was the first age at which all of the lake herring were mature; consequently, fish of this age group were persistently dominant in the samples. Only the faster growing of the younger age groups were mature. Bias from segregation according to maturity is made more complicated by sex differences in attainment of maturity. Since females mature at a greater size and age than do males, overestimates of growth and underestimates of numbers among younger fish are more severe for them. Data on sex ratio by age are impaired correspondingly.

The production of about 90 percent of the annual catch under the conditions just described leads to selective fishing mortality according to growth rate and sex. This selective destruction modifies the growth and sex ratio of a year class as it passes through the fishery. At the younger ages males are subjected to greater mortality than females, and the faster growing fish of both sexes are eliminated. The survivors of a year class have slower growth, and fewer males than would be characteristic of a year class which had not been subjected to a selective fishery or to no fishery at all. In some situations the longer exposure of males to selective fishing could make them appear to grow more slowly than females whether or not the sexes actually grew at different rates. The selective destruction probably does not end until all of the fish are mature and fully vulnerable to the gear.

Records of age composition and hence also judgments of year-class strength may be affected by the time of capture within the spawning season. Collections made in the early days of the season often had an unduly high percentage of fish in the younger age groups (the early-maturing males of the population reach the spawning grounds first). Conversely, samples collected during the last few days of the season frequently included disproportionately large numbers of fish in the older age groups (see section on reproduction). This source of bias is most damaging at the extremes of the season—the time of capture is of little consequence during the main season.

COMMERCIAL FISHERY FOR LAKE HERRING

The lake herring has been the principal species in the commercial production in U.S. waters of Lake Superior since 1908 (Koelz, 1926). Between 1891 and 1907 the lake trout occupied first place in poundage produced, and in the years prior to 1891 the whitefish was the principal species taken.

The statistical records of lake herring production in Lake Superior for 1929–61 (table 3) are from Lake Fish issued annually by the Bureau of Commercial Fisheries and those for Ontario are issued by the Province.

The first published record of lake herring production in Lake Superior is for 1867 in Ontario. The first record of production in the U.S. waters of Lake Superior is for 1879, but in 1879–1928 the statistics often included the catch of small chubs and in some years the catch of round whitefish (*Prosopium cylindraceum*). Only since about 1929 can the records for lake herring production in the U.S. waters of Lake Superior be termed reasonably dependable.

TABLE 3.—*Production (thousands of pounds) of lake herring in Lake Superior, 1929–61*

Year	United States				Canada	Grand total
	Minnesota	Wisconsin	Michigan	Total	Ontario	
1929	8, 571	2, 625	1, 516	12, 712	2, 529	15, 241
1930	8, 368	705	2, 341	11, 414	2, 745	14, 159
1931	5, 363	662	886	6, 912	1, 396	8, 308
1932	5, 123	362	540	6, 026	962	6, 988
1933	5, 203	650	941	6, 794	1, 744	8, 538
1934	8, 017	2, 946	2, 068	13, 031	2, 157	15, 188
1935	7, 911	2, 422	2, 782	13, 115	1, 506	14, 621
1936	5, 243	2, 856	3, 657	11, 757	2, 789	14, 546
1937	5, 623	2, 991	3, 170	11, 784	2, 378	14, 162
1938	5, 715	2, 485	2, 394	10, 594	1, 917	12, 511
1939	6, 590	3, 119	3, 357	13, 066	1, 435	14, 501
1940	7, 381	4, 909	4, 213	16, 502	1, 201	17, 703
1941	5, 724	6, 160	5, 954	17, 838	1, 433	19, 271
1942	4, 697	5, 035	5, 113	14, 844	1, 393	16, 237
1943	5, 079	4, 435	4, 360	13, 874	1, 209	15, 084
1944	5, 069	4, 712	4, 446	14, 227	1, 481	15, 708
1945	4, 398	6, 538	3, 109	14, 045	1, 708	15, 753
1946	3, 443	6, 342	3, 357	13, 142	1, 511	14, 653
1947	2, 904	4, 641	3, 263	10, 808	1, 017	11, 825
1948	3, 890	6, 291	4, 524	14, 705	1, 285	15, 991
1949	4, 054	5, 028	4, 122	13, 204	1, 255	14, 459
1950	2, 489	3, 953	1, 715	8, 158	505	8, 663
1951	2, 249	5, 347	2, 829	10, 424	763	11, 187
1952	2, 683	5, 890	3, 448	12, 021	993	13, 014
1953	2, 667	5, 356	2, 415	10, 439	745	11, 184
1954	2, 854	5, 575	3, 393	11, 823	920	12, 743
1955	2, 332	4, 359	3, 443	10, 134	708	10, 842
1956	2, 600	4, 158	3, 719	10, 478	821	11, 299
1957	3, 177	3, 162	5, 017	11, 355	1, 696	13, 051
1958	2, 870	2, 496	4, 850	10, 216	1, 744	11, 960
1959	2, 408	2, 862	6, 242	11, 512	2, 833	14, 345
1960 [1]	1, 863	2, 255	6, 693	10, 806	2, 117	12, 923
1961 [1]	1, 580	2, 559	7, 306	11, 445	1, 505	12, 950

[1] Materials supplied for this report in advance of general release for all species.

Lake Superior contributed an average of 62.4 percent to the total U.S. production of lake herring for the Great Lakes in 1929–59. (This percentage unquestionably was much lower before the collapse of the highly productive Lake Erie cisco fishery in 1925.) The annual percentage contribution ranged from 39.7 percent in 1931 to 92.0 percent in 1959. The high figure for 1959 did not reflect a particularly great yield in Lake Superior but rather a very low catch of lake herring in the other Great Lakes.

In the U.S. waters of Lake Superior the catch of lake herring was 12.7 million pounds in 1929, dropped to 6 million pounds in 1932, and reached nearly 18 million pounds in 1941, the highest production recorded. Since 1934 the take has exceeded 10 million pounds in all years but one (1950).

Although the catch of lake herring has contributed nearly three-fourths (74.2 percent) to the 1929–59 total U.S. production of Lake Superior, the value of the lake herring represented less than one-third (30.4 percent) of the total. The annual percentage contribution to the total value of the fishery ranged from 17.7 percent ($67,000) in 1932 to 56.9 percent ($854,000) in 1941. In recent years the lake herring has contributed a relatively high percentage to the total value of the fishery due to the drastic decline of the high-priced lake trout.

Reasons for the relatively low value of the lake herring stem from strongly seasonal production, capture and handling procedures, and technological problems. On the average, about 90 percent of the annual production occurs during the November-December spawning run when the market is soon glutted. Individual catches, often running as large as 10 tons, are piled in the gill net tugs and brought to shore where they are picked from the nets in warm sheds. Little care is taken in picking the fish from the nets. The rough treatment of this highly palatable but delicate fish often produces an inferior product hardly fit for human consumption. Even those fish which are removed carefully from the nets and well iced soon become soft and unappetizing. Frozen lake herring readily dehydrate and suffer objectionable oxidation of the fat.

In the early years, nearly all of the lake herring were salted; large quantities were shipped to economically depressed areas in the east and southeast. With the advent of mink farming in the early 1940's, a large percentage of the lake herring was sold for mink food. The 1961 lake herring production at Bayfield, Wis., was divided about equally between salt herring and mink food.

The distribution of the catch of lake herring among the different states has shifted markedly during the period for which sound statistics are available. Minnesota dominated the catch in 1929–40, Wisconsin held the lead in 1941–56 (exception was 1942 when Michigan occupied first place), and Michigan had the largest catch in 1957–61.

The 1929–61 average annual production of lake herring from Canadian waters of Lake Superior was 1,527,000 pounds, only 11 percent of the lake's total. The catch exceeded 2 million pounds in only 7 years and was below 1 million in 8 years.

TABLE 4.—*Average catch (pounds) of Lake Superior lake herring per 1,000 feet of gill nets lifted in November–December 1929–59*

[Number of feet of nets lifted (in thousands of feet) is in parentheses]

Year	Minnesota	Wisconsin	Michigan[1]	Year	Minnesota	Wisconsin	Michigan[1]
1929	---------	---------	303 (3,235)	1948	---------	---------	279 (13,815)
1930	---------	---------	248 (5,656)	1949	268 (8,906)	688 (7,086)	330 (11,128)
1931	---------	---------	170 (8,830)	1950	286 (5,240)	490 ---------	224 (6,714)
1932	---------	---------	175 (2,421)	1951	352 (4,100	745 (7,100)	395 (6,783)
1933	---------	---------	186 (3,549)	1952	348 (5,343	765 (7,566)	445 (6,293)
1934	---------	---------	194 (7,326)	1953	444 (3,217)	670 (7,901)	396 (4,995)
1935	---------	---------	205 (8,709)	1954	320 (4,697)	542 (10,217)	449 (6,699)
1936	---------	---------	226 (12,182)	1955	303 (4,439)	641 (6,749)	469 (5,812)
1937	---------	---------	155 (15,831)	1956	330 (3,996)	665 (6,101)	409 (6,267)
1938	---------	---------	165 (11,901)	1957	317 (4,944)	483 (6,370)	419 (9,811)
1939	---------	---------	164 (18,110)	1958	301 (4,038)	472 (5,172)	356 (9,738)
1940	---------	---------	264 (13,092)	1959	218 (4,940)	424 (6,590)	295 (14,517)
1941	---------	---------	266 (17,909)	1960	190 (3,076)	548 (3,825)	299 (13,033)
1942	---------	---------	230 (16,676)	1961	192 (3,760)	715 (3,331)	345 (11,739)
1943	---------	---------	206 (15,735)				
1944	---------	---------	232 (13,210)	Average			
1945	---------	---------	216 (13,006)	1949–61	298 (4,669)	604 (6,501)	372 (8,733)
1946	---------	---------	282 (9,854)				
1947	---------	---------	173 (15,900)	1929–61	---------	---------	278 (10,317)

[1]Based on the November–December catch per unit effort for statistical districts 1–4 and 6. To obtain the grand averages in the column, the catch per unit effort in each district was weighted by the percentage contribution of the district to the total State of Michigan catch in 1929–43.

Although recent production of lake herring in U.S. waters is not significantly below that of the 1929–61 mean of 11,794,000 pounds, some evidence exists that the abundance has declined in certain areas of the lake, particularly in Minnesota. The catch per unit effort during the 2-month spawning season in Minnesota (table 4) reached a peak of 444 pounds per 1,000 linear feet of net lifted in 1953, but the trend was downward after that year and the 1960–61 catch per unit effort (mean of 191 pounds) was the lowest for the 13-year period. Much of the decline in Minnesota can be traced to the near collapse of the fishery in the Duluth area, which in the years prior to 1955, contributed the major portion of Minnesota's production. The average annual catch per unit effort at Duluth in 1951–53 was over 300 pounds. An erratic decline in abundance after 1953 reduced the catch per unit effort to only 68.5 pounds in 1960 (the catch per unit effort increased slightly to 91.7 pounds in 1961).

TABLE 5.—*Average catch of Lake Superior lake herring per 1,000 linear feet of gill nets lifted in November-December, 1950–59, according to weight and number of fish*

Year	Minnesota [1]		Wisconsin [1]		Portage Entry		Marquette	
	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish
1950			490	1,307	200	471	265	643
1951			745	2,055	426	1,082	325	722
1952			765	1,826	462	1,001	472	967
1953					421	999	320	656
1954			542	1,262	504	1,320	213	425
1955					519	1,154	273	588
1956			665	1,565	451	949	242	471
1957	317	757	483	991	453	928	330	468
1958	301	669	472	995	381	664	269	439
1959	218	425	424	807	305	554	267	442
1960	190	380	548	913	313	538	271	434
1961			715	1,395	334	534	431	651
Average: 1950–55			636	1,613	422	1,005	311	667
1956–61			551	1,111	372	695	302	484
Percentage decrease			13.4	31.1	11.8	30.8	2.9	27.4

[1] Data were lacking to calculate the numerical catch per unit effort for Minnesota in 1950–56 and for Wisconsin in 1953 and 1955.

Some evidence of declining abundance exists also in Wisconsin waters where the catch per unit effort during the 2-month spawning season declined from a mean of 649 pounds per 1,000 feet of gill nets lifted in 1949–55 to 551 pounds in 1956–61. The catch per unit effort in 1961 (715 pounds), however, was the highest since 1952 (765 pounds). On the other hand, little evidence of a decline exists in those Michigan waters in which substantial catches were made each year since 1929. The average catch per 1,000 feet of gill nets in 1956–61 (354 pounds) was slightly below that of 1949–55 (387 pounds), but far above the 1929–61 mean of 278 pounds.

A measure of abundance according to numbers of fish caught per unit effort, rather than pounds of fish, may better describe changes in population density. Since the average size of the lake herring captured was greater in 1956–61 than in 1950–55, fewer individuals were required to reach the same weight in the later period. The data are inadequate to make comparisons between the early and late periods at Duluth since samples were taken only in 1957–60. The catch per unit effort in pounds at Bayfield declined 13.4 percent from 1950–55 to 1956–61 (table 5). The catch per unit effort in numbers,[1] on the other hand, declined 31.1 percent (from 1,613 in 1950–55 to 1,111 in 1956–61). The decrease in catch per unit effort according to weight from the early to the later period was 11.8 percent at Portage Entry and 2.9 percent at Marquette. The number of fish caught per 1,000 feet of gill nets lifted decreased 30.8 percent at Portage Entry and 27.4 percent at Marquette.

Fishing effort, based on the number of linear feet of gill nets (in units of 1,000 feet) lifted during the 2-month spawning season, varied from state to state and year to year (table 4). Fishing effort in Minnesota ranged from 3,076 units in 1960 to 8,906 units in 1949 (the 1949–61 mean was 4,669). The fishing effort in Wisconsin exceeded that of Minnesota in all years except two (1949 and 1961). The number of units exceeded 10,000 in 1954, and the 1949–61 mean was 6,501. Fishing effort in Michigan[2] exceeded 10,000 units lifted in 1936–49 (exception in 1946 when the value was 9,854 units) and in 1959–61. Over 18,000 units of gill nets were lifted during the 2 spawning months in 1939. The 1949–61 mean was 8,733 units, well below the 1929–61 average of 10,317.

The interpretation of data on catch per unit effort for lake herring in terms of actual availability is difficult because of the recent changeover from cotton to nylon gill nets. This change took place much later and at a slower pace in Lake Superior than did the changeover to nylon trout nets. Not until 1958 or 1959 were the majority of Wisconsin lake herring fishermen using nylon nets, and a few fishermen were still fishing cotton nets in 1961. Since the cotton lake herring nets were commonly used only once a year, during the fall spawning season, they lasted many years. The fishermen were reluctant to replace perfectly good cotton nets with new, expensive nylon.

Extensive observations on the relative efficiency of cotton and nylon lake herring nets have not been made. The Bureau's research vessel *Cisco* provided comparisons between the catch of chubs in nylon and linen gill nets in Lake Michigan. Nylon gill nets took 2.2 times as many chubs as linen nets of corresponding mesh fished in the same gang. The Bureau vessel *Siscowet* obtained only one comparison between catches of lake herring in nylon and cotton nets. In this experiment the nylon nets took 4.3 times as many lake herring as did cotton nets fished in the same gang.

[1] The numerical catch per unit effort was based on the catch per unit effort in pounds divided by the average weight of the fish in the sample.

[2] Total November–December effort for statistical districts 1–4 and 6.

Since the conversion to nylon nets has taken place slowly over the past 5 to 8 years and dependable conversion factors on the relative efficiency of the two types of nets for taking lake herring are unavailable, it appears impossible to undertake any adjustment in the statistics. Fishing intensity, therefore, may have been underestimated and the availability or abundance, based on the catch per unit effort, may have been to the same degree overestimated more and more as nylon nets replaced cotton nets.

ANNULUS FORMATION AND PROGRESS OF THE SEASON'S GROWTH

Smith (1956) determined that some lake herring started new growth in Green Bay as early as May 8 in 1950, and that annulus formation was completed by July 13. Van Oosten (1929) suggested that annulus formation occurred during the winter for the lake herring of Saginaw Bay.

Information on the time of annulus formation is scarce from Lake Superior since lake herring were difficult to catch during the spring and early summer. The only reliable data came from Marquette where an early-summer lake herring fishery developed in 1961 and continued in 1962.

The earliest collection was made on May 3, 1962 (table 6), and included several fish which had already begun new growth. As late as July 27 (a full 2 weeks after annulus formation was completed in Green Bay), a few individuals still gave no indication of new growth. New growth had started on all of the lake herring collected on August 21, 1961, and on all fish collected later that season.

Among the best represented age groups (IV–VI), the younger fish started new growth earlier than did the older ones. On June 28, for example, 94 percent of the IV-group and 86 percent of the V-group fish had a completed annulus as contrasted with a percentage of 65 for age group VI. On July 27, the percentages were 100 and 96 for age groups-IV and V but only 88 percent for VI-group fish.

TABLE 6.—*Percentage of lake herring with completed annuli collected at Marquette during period of annulus formation*

[Number of fish in parentheses]

Date	Percentage with completed annuli in age group						Ages combined
	III	IV	V	VI	VII	VIII	
1962							
May 3	17 (46)	11 (101)	8 (109)	0 (70)	5 (22)	0 (4)	8 (352)
1961							
June 28	50 (4)	94 (16)	86 (20)	65 (17)	64 (11)	20 (5)	73 (73)
July 27	88 (8)	100 (21)	96 (25)	88 (25)	60 (5)	75 (4)	91 (88)
Aug. 28	100 (14)	100 (26)	100 (27)	100 (12)	100 (6)	----	100 (85)

The period of annulus formation for lake herring in Lake Superior exceeds 8 weeks. Extreme care is needed in age determination for fish captured during the spring and early summer.

The data on the amount and percentage of the season's growth were taken from samples collected at Marquette during the summer of 1961 and in the spring of 1962 (table 7). Collections were not available in 1961 until late June when the summer fishery started. Since the summer fishery ended in late September, the estimate of full season's growth was based on samples of the same year class collected in May 1962. Special arrangements were made to obtain these samples before the regular summer fishery began in late June.

The records of table 7 exhibit some irregularities in trend which probably can be attributed to the small numbers of fish on which certain estimates were based. Ten of 29 estimates were based on fewer than 10 fish. The most reliable data are those for age groups IV, V, and VI, where all 15 percentages are based on more than 10 fish and 12 on 20 or more.

Despite the irregularities in the data, a general idea of the progress of the season's growth can be formed from the weighted means of the percentages of growth completed for the different dates (fig. 3).

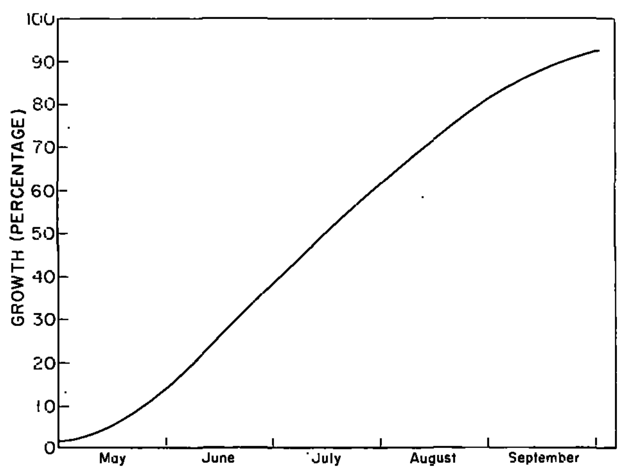

FIGURE 3.—Percentage of season's growth completed at time of capture, age groups combined. The curve was drawn freehand on the basis of data of table 7.

TABLE 7.—*Amount of season's growth in length (inches) completed by age groups on various dates of capture*

[The full season's growth of fish caught in 1961 determined from samples of the same year class collected on May 3, 1962]

Age group and item	Date of collection					Full-season growth in 1961
	May 3, 1962 [1]	June 28, 1961	July 27, 1961	August 21, 1961	September 25, 1961	
Age group III:						
Current-season growth	0.08	0.19	0.76	1.16	1.09	1.58
Percentage completed	5.1	12.0	48.1	73.4	69.0	100.0
Number of fish	46	4	8	14	5	77
Age group IV:						
Current-season growth	0.04	0.47	0.84	1.07	1.15	1.28
Percentage completed	3.1	36.7	65.6	83.6	89.8	100.0
Number of fish	101	16	21	26	20	184
Age group V:						
Current-season growth	0.02	0.35	0.68	0.83	0.99	0.96
Percentage completed	2.1	36.5	70.8	86.5	103.1	100.0
Number of fish	109	20	25	27	26	207
Age group VI:						
Current-season growth	0.00	0.42	0.51	0.63	0.82	0.89
Percentage completed	0.0	47.2	57.3	70.8	92.1	100.0
Number of fish	70	17	25	12	14	138
Age group VII:						
Current-season growth	0.01	0.42	0.33	0.56	0.49	0.79
Percentage completed	1.3	53.2	41.8	70.9	62.0	100.0
Number of fish	22	11	5	6	5	49
Age group VIII:						
Current-season growth	0.00	0.04	0.39	----------	0.85	0.85
Percentage completed	0.0	4.7	45.9	----------	100.0	100.0
Number of fish	4	5	4	----------	2	15
Average percentage: [2]						
All age groups	2.3	38.0	60.9	80.1	92.0	100.0
Age groups III–V	3.0	34.1	65.4	82.6	94.5	100.0
Age groups VI–VIII	0.3	42.8	53.7	70.8	85.8	100.0

[1] Current-season growth made in 1962; percentage computed from full-season growth of fish of same age in 1961.
[2] Weighted means.

The following percentages were obtained from the curve in the same figure:

Period of growth	Percentage of season's growth completed	
	During period	At end of period
Before May	2.3	2.3
May	11.5	13.8
June	25.0	38.8
July	22.5	61.3
August	20.0	81.3
September	11.2	92.5
After September	7.5	100.0

The greatest amount of growth in any single month took place in June (25.0 percent) and by the end of August, 81.3 percent of the season's growth was completed. Over two-thirds of the season's growth was in June–August and 90 percent in May–September.

Growth of Green Bay lake herring started sometime in May and ended in October (Smith, 1956). The greatest amount of growth took place in July. Hile (1936) found that growth of lake herring (ciscoes) in northeastern Wisconsin was complete by the end of July in Trout Lake, near the end of August in Muskellunge Lake, in early September in Sliver Lake, and in early October in Clear Lake. Differences in the length of the growing season contributed importantly to differences of growth rate in the four populations.

Growth of the related *C. kiyi* of northern Lake Michigan (Deason and Hile, 1947) was 39 percent completed by June 14, 80 percent by July 9, and 100 percent completed by September 7.

AGE COMPOSITION AND YEAR-CLASS STRENGTH

AGE COMPOSITION

The age composition of the spawning-run samples varied relatively little from year to year and port to port. Age group IV dominated the catch in each year's collection at each port. Indeed, the contribution of the IV group (table 8) exceeded 50 percent in all but 8 collections (Duluth, 1957 and 1959; Bayfield, 1958; Portage Entry, 1955 and 1958; and Marquette, 1955, 1956, and 1959). The highest percentage of IV-group fish was 68.1 (Bayfield, 1957) and the lowest was 37.0 percent (Bayfield, 1958). The average percentage for the IV group for the combined collections was 53.2.

Fish of age group III were second in abundance in 16 of the 31 collections. The percentage contribution ranged from 11.0 (Bayfield, 1959) to 40.6 (Portage Entry, 1954) and averaged 24.8. The V

TABLE 8.—*Age composition of Lake Superior lake herring according to port and year of capture*

[Averages are unweighted]

Port and year of capture	Number of fish	Percentage age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								*Years*
1957	90	5.6	15.6	42.2	34.4	2.2	-----	4.1
1958	122	2.5	31.1	50.8	15.6	-----	-----	3.8
1959	113	0.9	21.2	37.1	24.8	14.2	1.8	4.4
Average	-----	3.0	22.6	43.4	24.9	5.5	0.6	4.1
Bayfield:								
1950	103	-----	37.9	61.1	1.0	-----	-----	3.6
1951	147	-----	26.5	60.6	12.9	-----	-----	3.8
1952	125	-----	19.2	55.2	22.4	3.2	-----	4.1
1954	161	-----	16.8	66.5	16.1	0.6	-----	4.0
1956	93	2.2	16.1	58.0	23.7	-----	-----	4.0
1957	197	3.0	20.8	68.1	8.1	-----	-----	3.8
1958	116	5.2	24.1	37.0	27.6	5.2	0.9	4.0
1959	110	2.7	11.0	59.1	24.5	1.8	0.9	4.2
Average	-----	1.6	21.6	58.3	17.0	1.3	0.2	3.9
Portage Entry:								
1950	96	-----	31.2	61.5	7.3	-----	-----	3.7
1951	123	0.8	18.7	56.1	22.8	1.6	-----	4.1
1952	106	0.9	20.8	54.8	22.6	0.9	-----	4.0
1953	91	3.3	39.6	53.8	3.3	-----	-----	3.6
1954	96	4.2	40.6	52.1	3.1	-----	-----	3.5
1955	85	-----	20.0	43.5	34.1	2.4	-----	4.2
1956	243	2.1	35.8	56.3	5.8	-----	-----	3.6
1957	209	3.8	22.5	58.9	14.8	-----	-----	3.8
1958	118	0.8	22.0	39.9	36.5	0.8	-----	4.1
1959	125	1.6	14.4	54.4	28.0	1.6	-----	4.1
Average	-----	1.8	26.6	53.1	17.8	0.7	-----	3.9
Marquette:								
1950	68	1.5	22.1	63.2	13.2	-----	-----	3.9
1951	106	0.9	19.8	59.5	19.8	-----	-----	4.0
1952	101	-----	20.8	53.4	23.8	2.0	-----	4.1
1953	84	-----	38.1	52.4	8.3	1.2	-----	3.7
1954	102	1.0	19.6	57.8	20.6	1.0	-----	4.0
1955	95	2.1	21.1	41.0	34.7	1.1	-----	4.1
1956	155	3.9	27.1	44.5	21.9	2.6	-----	3.9
1957	159	4.4	28.9	55.4	9.4	1.9	-----	3.8
1958	117	6.0	31.6	52.1	10.3	-----	-----	3.7
1959	123	1.6	34.1	43.2	19.5	1.6	-----	3.9
Average	-----	2.1	26.3	52.3	18.2	1.1	-----	3.9
Grand total or average	3,779	2.0	24.8	53.2	18.4	1.5	0.1	3.9

group ranked second in 14 collections; it ranged from 1.0 percent (Bayfield, 1950) to 36.5 percent (Portage Entry, 1958), and averaged 18.4 percent for the combined collections. Age groups III and V were equally represented in the 1951 Marquette collection. Other age groups were sparsely represented or entirely lacking. The youngest fish were members of the II group (mean percentage contribution, 2.0). The VI group appeared in 18 collections (mean percentage, 1.5) but VII-group fish (the oldest in the samples) were taken only at Duluth in 1959 and at Bayfield in 1958 and 1959. The mean age ranged from 3.5 years in 1954 at Portage Entry to 4.4 years at Duluth in 1959. The mean ages of the combined years' collections from the several ports differed little—4.1 years at Duluth and 3.9 years at Bayfield, Portage Entry, and Marquette. The average age of fish taken in the 1950–55 period of relatively slow growth differed little from that of the faster growing fish captured in 1956–59.

The records of age composition according to sex (table 9) show a higher percentage contribution for females than for males in all age groups above III (exceptions were the VII group at Duluth and the IV group at Marquette). The differences in percentage contribution of the sexes were greatest at Duluth; the percentage of males in the III group was twice that of the females, and the percentage of females was slightly larger than that of the males in age group IV. The percentage of females was twice that of males in age group V and nearly four times in the VI group.

TABLE 9.—*Age composition of Lake Superior lake herring according to sex and port, 1950–59*

Port and sex	Number of fish	Percentage in age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								*Years*
Males	135	6.7	33.3	42.3	14.8	2.2	0.7	3.8
Females	190	-----	16.3	44.8	30.5	7.9	0.5	4.3
Bayfield:								
Males	452	2.9	26.5	55.5	14.2	0.9	-----	3.8
Females	600	0.7	17.5	62.2	17.8	1.5	0.3	4.0
Portage Entry:								
Males	584	3.1	30.7	50.3	15.4	0.5	-----	3.8
Females	708	1.0	23.4	57.0	17.9	0.7	-----	3.9
Marquette:								
Males	701	2.1	27.5	52.2	17.3	0.9	-----	3.9
Females	409	2.9	25.2	50.6	19.3	2.0	-----	3.9

With few exceptions the average age of the females exceeded that of the males in each of the collections (table 10). The difference between the mean ages of the sexes among the combined collections from each port ranged from nil at Marquette to 0.5 year at Duluth.

TABLE 10.—*Average age of Lake Superior lake herring according to port, year of capture, and sex*

Year of capture	Duluth		Bayfield		Portage Entry		Marquette	
	Males	Females	Males	Females	Males	Females	Males	Females
1950	-----	-----	3.6	3.6	3.8	3.7	3.8	4.1
1951	-----	-----	3.8	3.9	4.0	4.3	4.0	4.1
1952	-----	-----	4.3	4.0	3.8	4.1	4.1	4.0
1953	-----	-----	-----	-----	3.5	3.7	3.8	3.7
1954	-----	-----	3.9	4.1	3.4	3.9	4.0	4.0
1955	-----	-----	-----	-----	4.1	4.3	4.1	4.3
1956	-----	-----	4.0	4.7	3.5	3.7	3.8	4.0
1957	4.0	4.2	3.5	3.9	3.8	3.9	3.6	3.9
1958	3.5	4.0	3.8	4.6	4.2	4.1	3.7	3.7
1959	3.9	4.7	3.7	4.3	3.9	4.2	3.7	4.1
All years	3.8	4.3	3.8	4.0	3.8	3.9	3.9	3.9

YEAR-CLASS STRENGTH

Fluctuations in the strength of year classes of fish have been the subject of extensive research since Hjort (1914) demonstrated the significance of year-class abundance in the fluctuations of productivity of major marine fisheries. The literature in this field is so widely known and has been summarized so frequently that a review of it would not be appropriate in this paper. Even a listing of studies of year classes in the Great Lakes is not required in view of El-Zarka's (1959) broad coverage of the subject.

The evaluation of the relative strength of year classes usually has been based on data on the percentage age composition of samples in a series of years. On occasion, the records have permitted only the identification of certain year classes of unusual strength or weakness (Van Oosten and Hile, 1949—Lake Erie whitefish; Jobes, 1952—Lake Erie yellow perch). In other circumstances it has been possible to arrange year classes ordinarily (Hile, 1941—Nebish Lake rock bass) or from a series of comparisons to set up a system of "ranks" (Hile, 1954—Saginaw Bay walleye). El-Zarka (1959—Saginaw Bay yellow perch) attempted to improve the precision of estimates of year-class strength by subjecting his data on percentage age composition to an analysis of year-to-year change similar to the one used by Hile (1941) for the study of annual fluctuations of growth rate.

Instructive as these uses of data on age composition may be, much more effective judgments can be made of the strength of year classes if catch-effort data are available on the fishery from which samples were obtained. Records of catch per unit of fishing effort make it possible to estimate the availability of each age group in terms of numbers of fish. The study of fluctuations in the strength of year classes of lake herring in Lake Superior accordingly has been based on the application of age-composition data for spawning-run samples to statistics on the catch (in pounds) per 1,000 linear feet of small-mesh gill nets during the spawning months of November and December. The procedures followed are similar to those employed by Pycha (1961) in his study of the year classes of walleye in northern Green Bay, Lake Michigan. El-Zarka (1959) had recognized the value of this approach but was unable to use it because of the small numbers of legal-sized fish in certain of his samples.

The application of data on age composition to statistics on catch per unit effort is illustrated best by a hypothetical example. Let it be assumed that a sample containing 223 lake herring weighed 69.1 pounds and that the catch of lake herring of the same port in the same year was 341 pounds per 1,000 feet of gill net lifted in November and December. It is then computed that 1,000 feet of commercial nets took $341/69.1=4.935$ times as many lake herring as were in the sample. Numbers per unit effort for individual age groups are then calculated by multiplying the number in the age group by the ratio 4.935; for example, an age group that contributed 43 fish to the sample was produced in the commercial fishery at the rate of $43\times4.935=189$ individuals per 1,000 feet of net. It was by this procedure that the records of table 11 were obtained. Data are given only for age groups III, IV, and V since other age groups were poorly represented or lacking in the samples.

Numbers of fish caught per unit effort were estimated for certain age groups as indicated by footnote in table 11. All figures for the III groups of the 1946 year class and the V groups of the 1955 year class were estimated; at Bayfield, additional estimates were needed to fill gaps created by the lack of collections in 1953 and 1955. These estimations required first the determination of the ratios of the average numbers of fish in different age groups from all available samples at a port; the appropriate ratios were then applied to available data on year classes to obtain estimates for missing data. The actual computation for age group III of the 1946 year class at Bayfield illustrates the procedure. From all available Bayfield samples it was determined that the average number of lake herring in age group III amounted to 0.378 times the average number in age group IV and 1.317 times the average number in age group V. The following two estimates then were made of the number per unit effort for the missing III group of the 1946 year class; $0.378\times799=302$; $1.317\times265=349$. The mean of the two estimates, 326, was entered in table 11. All other estimates were obtained similarly.

The relations among the succesive samples of the same year class off a port varied widely in samples from all three ports (table 11). The

TABLE 11.—*Numbers of lake herring caught per lift of 1,000 linear feet of small-mesh gill nets by year class and age group, off three Lake Superior ports*

[Based on samples from commercial landings during the spawning season and on catch-effort statistics for November and December]

Port and age group	Year class										Average
	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	
Bayfield:											
III	[1] 326	495	545	351	[1] 317	212	[1] 224	252	206	240	317
IV	799	1,245	1,008	[1] 816	839	[1] 926	908	675	368	478	806
V	265	409	[1] 352	203	[1] 241	371	80	274	198	[1] 160	255
Total	1,390	2,149	1,905	1,370	1,397	1,509	1,212	1,201	772	878	1,378
Portage Entry:											
III	[1] 280	147	202	208	392	594	231	340	209	146	275
IV	290	607	549	533	637	502	534	547	265	301	477
V	247	226	33	38	393	55	137	243	155	[1] 94	162
Total	817	980	784	779	1,422	1,151	902	1,130	629	541	914
Marquette:											
III	[1] 199	142	143	201	250	83	124	128	135	139	154
IV	406	430	517	344	246	242	210	259	229	191	308
V	143	230	54	88	204	103	44	45	86	[1] 84	108
Total	748	802	714	633	700	428	378	432	450	414	570

[1] Estimated by procedure explained in text.

records for the year classes in the Portage Entry samples illustrate this variability. The strongest year class (1950) and the third strongest (1953) held their ranks by reason of catches well above the 10-year average (given in right-hand column of table 11) at all three ages; similarly, the weakest year class (1955) yielded catches well below average as the III group and the IV group (V group estimated), and the next to the weakest (1954) was taken in below-average numbers at all three ages (though near average as age group V). The next to strongest year class (1951), on the contrary, held that position because of tremendous numbers caught as age group III (over twice the mean of 275); its representation was only moderately above average as age group IV and was extremely low as age group V. The 1947 year class held a rank above average only because of a strong upward trend of the catches; the numbers were far below average as age group III, above average as age group IV, and highest (relatively) as age group V. The catches of the remaining year classes from Portage Entry can be described best as variable but without clear trend. Two examples should illustrate the situation. The 1947 year class was weakly represented as age group III, but catches as age groups IV and V were sufficient to bring the total above average. In the 1952 year class, the poor catches as age groups III and V were counterbalanced by the good catch as age group IV to bring the total near the mean.

Numerous causes can be advanced for the discrepancies among successive samples of certain year classes, but no clear demonstration or evaluation can be offered for any of them. Random error unquestionably played a role because none of the annual samples was truly large and some were undesirably small (table 1). Major sources of bias were weather, nature of previous fishing on the year class, and changes of gear specifications.

The shortness of the spawning season in late November and early December makes the success of fishing highly sensitive to weather. Near the height of spawning, a storm that is severe enough to damage gear and disperse the schools depresses the catch per unit effort and causes underestimates of the strength of year classes represented in the year's sample. Conversely, exceptionally calm, favorable weather can make the catch per unit effort higher than normal. Should the weather, by mischance, cause the catch per unit effort to be abnormally high or low in 2 or all of the 3 years in which a year class is present in numbers, a severe misjudgment must result. It was not possible to relate weather conditions to the behavior of estimates of year-class strength at successive ages. Storms cannot be classified satisfactorily as to the expected effect on catch per unit effort, and furthermore the effects of a single storm are not uniform for all gear in an area. It is only to be hoped that biases from weather conditions were not cumulative for many year classes and that for most they were compensatory.

Intensity of fishing or fishing conditions that influence the vulnerability of a year class in its first year or years of exploitation can influence later estimates of its strength. If, for example, a year class is highly vulnerable to the nets and fished heavily as age group III, the original numbers may be so reduced that catches as age groups IV and V are relatively low. If both age groups III and IV are removed in large numbers, the return per unit effort as the V group may be extremely small. Low vulnerability and low removal at the earlier ages should have the reverse influence. Effects of earlier fishing against year classes may well have contributed to the discrepancies among age groups and to the upward or downward trends described for the Portage Entry samples and present in those from the other two ports.

As was pointed out in the section on materials and methods, many fishermen increased the mesh size of lake herring gill nets during the years of sampling. A second change of gear was the gradual conversion from cotton to nylon twine. The change of mesh size was an adjustment to the increase in the mean size of the lake herring and tended to maintain the capacity of the gear to take fish in constant relation to the true abundance of lake herring on the grounds. Fishermen who did not increase mesh size as fish size increased probably lowered the relative efficiency of their nets. The conversion from cotton to nylon almost certainly increased the catching power of the nets. It is not possible, however, to offer quantitative estimates of the effects of either the increases of mesh size or the change in netting material.

Other possible sources of bias to the samples could be stated but the chance that any of them were significant is too small to justify even a listing.

Even though the discrepancies that appear in the data for certain year classes at each port can be explained logically, the explanations do not weaken the necessary conclusion that certain of the estimates of year-class strength are less precise than might be wished. The method which appears least biased for judging the strength of each year class is one based on the number of fish caught per unit of effort for the three age groups combined.

The apparent strength of the year classes (see year-class totals of table 11) varied considerably but not excessively at each port. The richest year class at Bayfield (1947—2,149 fish at three ages) was 2.78 times as strong as the weakest (1954—772 fish). The strongest year class at Portage Entry (1950) yielded catches that were 2.63 times those of the weakest (1955), and at Marquette the catches of the 1947 year class were 2.12 times those of the 1952 year class. These 2.12- to 2.78-fold fluctuations may appear substantial but they are trivial in comparison with the 88.5-fold fluctuation of year-class strength determined by Pycha (1961) for the Green Bay walleye.

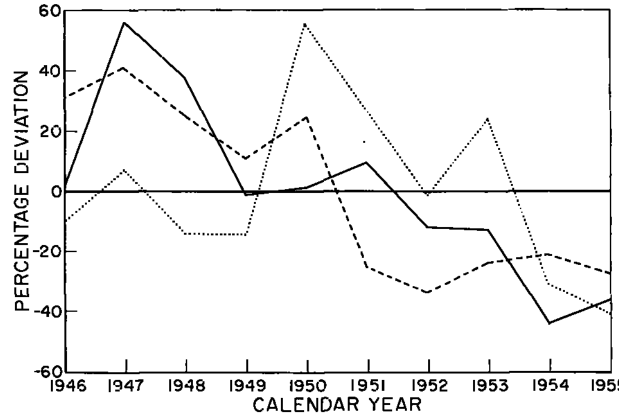

Figure 4.—Fluctuations in the relative strength of the year-classes 1946–55 of lake herring from Bayfield (solid line); Portage Entry (dotted line); and Marquette (dashes).

The year-to-year fluctuations of year-class strength at each port are grasped best from the data of table 12 (see also fig. 4) in which each year-class total of table 11 is expressed as a percentage deviation from the mean for the 10 year classes. It is obvious at once that fluctuations at Bayfield and Marquette had many

Table 12.—*Fluctuations of year-class strength of lake herring off three Lake Superior ports*

[Percentage deviations computed from year-class totals of table 11]

Year class	Percentage deviation from average for port		
	Bayfield	Portage Entry	Marquette
1946	0.8	−10.6	31.3
1947	55.9	7.3	40.7
1948	38.2	−14.2	25.3
1949	−.6	−14.7	11.1
1950	1.4	55.7	22.8
1951	9.5	26.0	−24.9
1952	−12.1	−1.3	−33.7
1953	−12.8	23.7	−24.2
1954	−44.0	−31.1	−21.0
1955	−36.3	−40.8	−27.4

similarities but exhibited only limited agreement with those off Portage Entry.

The deviations from average at Bayfield and Marquette were on the same side of the average for 8 of 10 year classes. Year classes off the two ports agreed particularly well in 1947 (the best year class at each port) and 1948 when year classes were strong and in 1952–55 when all four year classes were decidedly below average. Agreement was poor in 1946, 1949, and 1950 which produced year classes near average at Bayfield and above average at Marquette; the 1951 year class produced the worst disagreement—9.5 percent above average at Bayfield and 24.9 percent below at Marquette.

The closeness of the agreement between year-class fluctuations at Bayfield and Marquette is brought out by the coefficient of correlation ($r=0.726$) between the deviations from average. This value of the coefficient is significant at the 2-percent probability level ($r=0.716$ at $p=0.02$; $df=8$).

The data for Portage Entry agreed clearly with those for Bayfield and Marquette in 1954 and 1955 when the year classes were decidedly weak off all three ports but showed most limited agreement in other years.

Data for Bayfield and Portage Entry agreed in some measure in 1947 and 1951 when year classes were above average at both ports. Year classes of 1946, 1949, 1950, and 1952 were near average at one of the two ports but departed from average by at least 10.6 percent and as much as 55.7 percent at the other. Major disagreements between Bayfield and Portage Entry were provided by the year classes of 1948 and 1953.

The only consequential agreement between records for Portage Entry and Marquette, aside from the previously mentioned 1954 and 1955 year classes, was provided by the year classes of 1947 and 1950. The agreement for 1952 was unimportant, and disagreements were major for the year classes of 1946, 1948, 1949, 1951, and 1953.

No attempt has been made yet to inquire into the factors of year-class fluctuation in Lake Superior stocks of lake herring or into the reasons for the broad similarities of these fluctuations at Bayfield and Marquette and the apparently independent fluctuations at Portage Entry. A longer series of data is needed.

SIZE AT CAPTURE

LENGTH AND WEIGHT OF THE AGE GROUPS

Data on length and weight of the age groups (table 13) provide comparisons by sex, port, and two periods of capture (1950–55 and 1956–59). The females were longer than the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held an advantage (7 of 10 comparisons) at Marquette. Among the best represented age groups (III–V), sex differences in average length were small. The largest advantage for the females was 0.6 inch (V groups in the Duluth collections); the largest for the males was 0.2 inch at Marquette (III group in the 1950–55 and the IV group in the 1956–59 samples)

TABLE 13.—*Average total lengths and weights of the age groups of male and female lake herring according to port and period of capture*

Age group and sex	Duluth		Bayfield				Portage Entry				Marquette			
	1957-59		1950-54		1956-59		1950-55		1956-59		1950-55		1956-59	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
	Inches	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*	*Inches*	*Ounces*
II:														
Males	11.3	6.3	--------	--------	11.7	7.0	11.3	6.3	11.9	7.4	11.7	7.0	12.6	8.8
Females	--------	--------	--------	--------	11.8	7.2	11.5	6.7	12.0	7.6	11.3	6.3	12.3	8.2
III:														
Males	11.3	6.3	11.0	5.8	11.8	7.2	11.4	6.5	12.0	7.6	11.7	7.0	12.7	9.0
Females	11.9	7.4	11.3	6.3	11.9	7.4	11.5	6.7	12.0	7.6	11.9	7.4	12.7	9.0
IV:														
Males	11.9	7.4	11.1	6.0	11.8	7.2	11.4	6.5	12.1	7.8	11.9	7.4	12.9	9.6
Females	12.1	7.8	11.5	6.7	12.2	8.0	11.8	7.2	12.3	8.2	12.0	7.6	12.7	9.0
V:														
Males	11.6	6.8	11.5	6.7	11.9	7.4	11.5	6.7	12.6	8.8	12.2	8.0	12.9	9.6
Females	12.2	8.0	11.8	7.2	12.4	8.4	11.8	7.2	12.7	9.0	12.1	7.8	12.8	9.3
VI:														
Males	12.3	8.2	12.8	9.3	12.8	9.3	11.1	6.0	11.6	6.8	12.8	9.3	14.0	12.3
Females	12.8	9.3	12.5	8.6	12.7	9.0	11.6	6.8	12.8	9.3	11.7	7.0	13.2	10.3
VII:														
Males	15.6	17.2	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
Females	12.4	8.4	--------	--------	12.8	9.3	--------	--------	--------	--------	--------	--------	--------	--------

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It is difficult, if not impossible, to distinguish possible true sex differences in the growth of Lake Superior lake herring from the effect of bias from segregation by size and maturity and the resulting selective action of the fishery on the population. Since male lake herring mature at a slightly younger age than do females, a substantially larger percentage of males than females were represented in age groups II and III at all ports except Marquette (table 9). The intensive lake herring fishery at the ports west of Marquette selectively destroyed these early-maturing, fast-growing males in the younger age groups, leaving the slower growing, late-maturing members of the sex to represent the older age groups. This phenomenon may well lead to low estimates of size for males in the older age groups. Since the lake herring from Marquette grew faster than those from the other ports, proportionately larger numbers of mature females were represented in the younger age groups. The sex ratio, therefore, was more nearly equal in age groups II and III and the fishery which has never been intensive at Marquette, was not particularly selective toward the males.

A detailed discussion of table 13 is not desirable as more discriminating information is given in the section on calculated growth. Most of the lake herring, regardless of age, fell within the 11- to 13-inch range and weighed 6 to 10 ounces. The small difference in size among the age groups is surely a result of the highly selective gill nets, segregation by maturity, and of selective fishing mortality.

With only one exception (that of the VI-group males in the 1956–59 Bayfield collections), the average size of the age groups was larger in 1956–59 than in 1950–55. Among the best represented age groups (III–V), the increase in length from the early to the late period ranged from 0.4 inch to 1.1 inches (11.5 to 11.9 inches for the V-group males at Bayfield and 11.5 to 12.6 inches for the V-group males at Portage Entry). In general, the average size of the lake herring increased from the western to the eastern part of the lake. Lake herring of age groups III–V from the 1956–59 Marquette collections were 0.6 so 1.4 inches longer and 1.3 to 2.7 ounces heavier than fish of the same age from Duluth.

LENGTH DISTRIBUTION OF THE SAMPLES

The length-frequency records for the samples (table 14), by port and period of capture, indicate generally compact distributions. The range in length from the shortest to the longest fish was greatest (6.9 inches) in the Duluth samples and smallest (3.9 inches) in the 1950–55 Portage Entry collections. The Duluth samples were represented by both the shortest (9.0 inches) and the longest (15.9 inches) fish taken in all of the collections.

TABLE 14.—*Length distribution of Lake Superior lake herring according to port for the periods 1950–55 and 1956–59*

[Asterisks indicate modes]

Total length	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54 [1]	1956–59	1950–55	1956–59	1950–55	1956–59
Inches							
9.0–9.4	1	--------	--------	--------	--------	--------	--------
9.5–9.9	4	3	--------	--------	--------	--------	--------
10.0–10.4	12	21	1	5	1	1	--------
10.5–10.9	13	106	18	61	13	2	5
11.0–11.4	43	*198	58	180	60	15	11
11.5–11.9	61	130	155	*235	183	91	46
12.0–12.4	*114	53	*167	102	*201	143	116
12.5–12.9	55	17	89	11	139	*195	*148
13.0–13.4	19	6	21	2	66	91	141
13.5–13.9	1	1	6	1	24	13	71
14.0–14.4	1	--------	1	--------	7	3	12
14.5–14.9	--------	--------	--------	--------	--------	2	2
15.0–15.4	--------	--------	--------	--------	--------	--------	--------
15.5–15.9	1	--------	--------	--------	1	--------	2
Number of fish	325	535	516	597	695	556	554
Average length	11.9	11.3	12.0	11.6	12.2	11.9	12.8
Percentage over 11.9 inches	58.8	14.4	55.0	19.4	63.0	80.4	88.8

[1] Samples were not collected in 1953 and 1955.

The length composition clearly changed from 1950–55 to 1956–59 at two of the three ports. From the earlier to the later period, the modal length increased 1.0 inch at Bayfield (from 11.0–11.4 to 12.0–12.4 inches) and 0.5 inch at Portage Entry (11.5–11.9 to 12.0–12.4 inches). The mean length increased 0.7 inch (from 11.3 to 12.0 inches) at Bayfield and 0.6 inch (11.6 to 12.2 inches) at Portage Entry. The mode at Marquette (12.5–12.9 inches) was the same for the two periods but the mean length increased 0.7 inch (11.9 to 12.8 inches). Port-to-port differences of modal length were greatest in the 1950–55 samples; the mode was 11.0–11.4 inches at Bayfield, 11.5–11.9 inches at Portage Entry, and 12.5–12.9 inches at Marquette. The average lengths increased from 11.3 inches at Bayfield to 11.6 at Portage Entry and 11.9 at Marquette.

The percentage of fish longer than 11.9 inches varied with differences in modal and mean lengths. The percentage of lake herring 12.0 inches long or longer in the 1950–55 collections was 14.4 at Bayfield, 19.4 at Portage Entry, and 80.4 at

Marquette. The percentages were higher in 1956–59 at all ports—58.5 percent at Duluth (no earlier data), 55.0 percent at Bayfield, 63.0 percent at Portage Entry, and 88.8 percent at Marquette.

LENGTH DISTRIBUTION OF THE AGE GROUPS

The records on the length-frequency distributions of the age groups have been limited to one example, that of the 1957 Marquette collection (table 15). It is not believed that the additional information to be gained would warrant the large expansion of tabular material to show the length distributions of the age groups for each year or period at each port. The 1957 Marquette sample was selected because it illustrates the general characteristics of all the samples.

TABLE 15.—*Length distribution of the age groups of Lake Superior lake herring captured at Marquette, 1957*

Total length	Age group				
	II	III	IV	V	VI
Inches					
11.0–11.4			1	1	
11.5–11.9	1	3	7		
12.0–12.4	1	14	16	5	1
12.5–12.9	3	16	24	3	
13.0–13.4	2	9	31	4	1
13.5–13.9		4	8	2	
14.0–14.4			1		
14.5–14.9					
15.0–15.4					
15.5–15.9					1
Total	7	46	88	15	3
Average length	12.6	12.7	12.8	12.7	13.6

Typical of the length distributions of the age groups of Lake Superior lake herring are the small ranges of length and the extensive overlap of the age groups. The range in length of the age groups of the 1957 Marquette sample was only 1.9 inches for age group II to 3.9 inches for the VI-group fish. Despite the small range, overlap was extensive. The length interval of 12.0–13.4 inches was represented by all five age groups.

LENGTH-WEIGHT RELATION

GENERAL RELATION

The data on general length-weight relation of the Lake Superior lake herring (table 16) were based on fish from all of the collections regardless of port, year, or season of capture, type of gear, sex, or state of maturity. The length-weight relation does vary according to port and year of capture, and between ripe and fully spent females, but it was held that the best estimate of the general

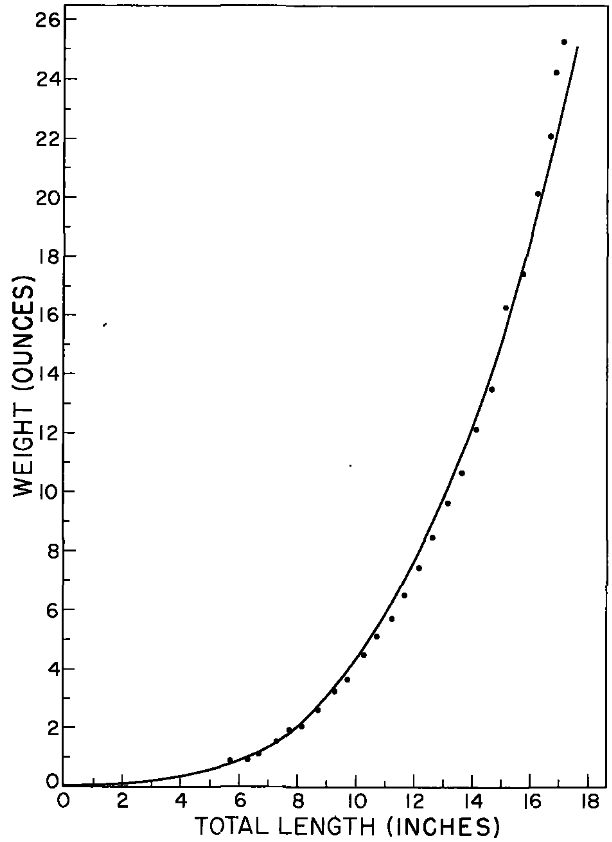

FIGURE 5.—Length-weight relation of Lake Superior lake herring. The curve represents the calculated weights and the dots the empirical weights.

relation is one based on all available fish. The empirical weights at different lengths are given graphically by dots in figure 5. The curve is a graph of the following equation derived by fitting a straight line (by least squares) to the logarithms of the average lengths and weights:

$$\text{Log } W = -2.54688 + 3.17008 \log L,$$

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

Although the calculated weights were higher than the empirical weights for fish between 9.2 and 15.2 inches long, the agreement between the empirical and calculated values was acceptable. The largest disagreement was at 17.55 inches where the empirical weight (28.50 ounces) was 3.52 ounces above the calculated weight (24.98 ounces); only 2 fish were weighed, however, at

Table 16.—*Length-weight relation of Lake Superior lake herring of the combined collections, 1950–59*

Number of fish	Total length	Weight	
		Empirical	Calculated
	Inches	*Ounces*	*Ounces*
12	5.73	0.83	0.72
20	6.27	.97	.96
11	6.63	1.14	1.14
13	7.24	1.53	1.51
24	7.72	1.86	1.85
20	8.18	2.13	2.22
25	8.70	2.69	2.70
25	9.22	3.26	3.25
29	9.70	3.66	3.81
72	10.28	4.54	4.58
444	10.76	5.11	5.30
1,216	11.23	5.76	6.07
1,896	11.68	6.51	6.87
2,068	12.19	7.42	7.87
1,314	12.68	8.41	8.92
682	13.17	9.66	10.05
284	13.65	10.68	11.26
118	14.17	12.18	12.68
101	14.67	13.56	14.15
72	15.20	16.22	15.84
47	15.66	17.51	17.41
35	16.22	20.74	19.46
23	16.66	22.15	21.18
11	17.18	25.26	23.35
2	17.55	28.50	24.98

this interval. Most disagreements were less than 0.5 ounce.

INCREASE OF WEIGHT FROM 1950–55 TO 1956–61

The annual data on the length-weight relation of Lake Superior lake herring have been combined for 1950–55 and 1956–61. This arbitrary division seems to be best for showing the long-term changes in weight for the 12-year period. Year-to-year differences in 1950–55 were without trend at each of the ports, but weights of fish of the same length showed a definite upward trend from 1956 through 1961. The data of table 17 are based entirely on records of weights of spawning-run male lake herring. Although the weights of the females exhibited trends similar to those of the males, these trends were often obscured by sample differences in the proportions of ripe, partially spent, or spent fish. Weight differences between fully ripe and spent females are considered too severe for the data to be included in this study. Deason and Hile (1947), for example, demonstrated that the loss of weight of the female *C. kiyi* at spawning amounted to 11.8 percent, whereas the loss of weight of males was altogether unimportant (mean percentage loss, 1.6).

The differences of weight in the two collecting periods were strongly consistent. Among comparisons of length intervals represented by 10 or more fish in each period, lake herring captured in 1956–61 were without exception heavier than those of the same length taken in 1950–55 (table 17).

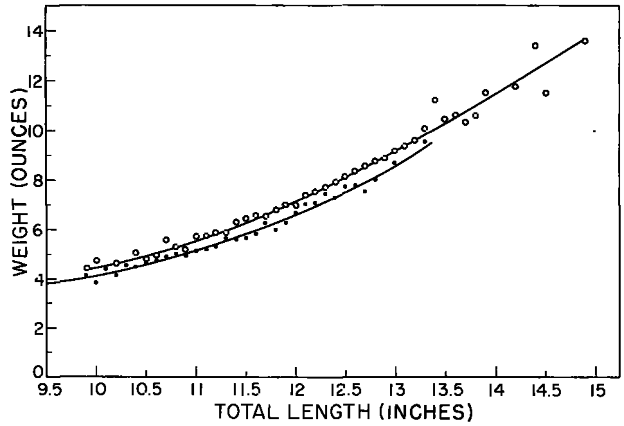

Figure 6.—Weights of Bayfield lake herring captured in 1950–54 (solid dots) and in 1956–61 (open dots). The curves were fitted by inspection.

The percentage increase in weight, length for length, ranged from 4.1 to 13.4 at Bayfield (fig. 6). The percentage increases in weight at the other ports ranged from 2.3 to 6.9 at Portage Entry and from 2.7 to 9.7 at Marquette. The average percentage increase in weight was greatest at Bayfield (8.8 percent), followed by Marquette (5.2 percent), and Portage Entry (4.4 percent). When the numbers of fish were small, lake herring caught in 1950–55 occasionally were heavier than those of the same length taken in 1956–61, but even here the 1956–61 fish were heavier in the great majority of the comparisons.

Despite the fact that mesh sizes of the commercial gill nets were frequently larger in 1956–61 than in 1950–55, lake herring of the same length were heavier during the later period regardless of the mesh size of the net from which they were taken.

Port-to-port differences in average weights among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight. Comparisons of weights for length intervals represented by 5 or more fish from each port revealed the Marquette lake herring to be the heaviest in 9 of 14 comparisons, fish from Portage Entry ranked second in 9 of 14 comparisons, and the Bayfield lake herring were lightest in 13 of 14 comparisons. In 1956–61, the Marquette lake herring were heaviest in 7 of 11 comparisons, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small and without trend.

TABLE 17.—*Weights of spawning-run male lake herring taken in Lake Superior during 1950–55 and 1956–61*

Total length	Duluth		Bayfield				Portage Entry				Marquette			
	1956–60 [1]		1950–54 [2]		1956–61		1950–55		1956–61		1950–54 [3]		1956–61	
	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	Number of fish	Average weight
Inches		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*		*Ounces*
9.5	1	3.80	1	3.90										
9.6	1	3.90												
9.7	2	4.25												
9.8							1	4.0			1	3.89		
9.9	1	4.50	4	4.15	1	4.40								
10.0			1	3.84	1	4.70					1	4.08		
10.1	3	4.27	3	4.41										
10.2	2	4.35	7	4.19	1	4.60	2	4.53	1	4.70				
10.3	2	4.70	4	4.52			1	4.30			1	4.36		
10.4	7	4.66	11	4.49	2	5.00	4	4.77						
10.5			16	4.70	2	4.75	4	4.79			13	4.78		
10.6	3	5.23	21	4.78	3	4.93	7	4.89			1	4.87		
10.7	2	5.25	34	4.85	4	5.58	16	5.05	3	4.87	8	5.31	1	5.30
10.8	7	5.14	49	4.95	6	5.28	18	5.19	3	5.37	9	5.13	1	5.90
10.9	4	5.38	45	4.97	5	5.16	23	5.26	3	5.27	4	5.62	1	5.50
11.0	7	5.36	48	5.17	8	5.64	32	5.32	8	5.54	11	5.23	1	5.20
11.1	8	5.85	38	5.21	5	5.72	35	5.48	7	5.60	18	5.69	1	6.30
11.2	10	5.70	48	5.36	19	5.81	41	5.66	11	6.05	31	5.76		
11.3	6	6.20	38	5.61	24	5.84	57	5.78	9	5.73	44	5.81	3	6.63
11.4	9	6.14	21	5.64	19	6.22	50	5.91	9	6.11	61	6.02	3	6.63
11.5	13	6.29	23	5.66	23	6.40	55	6.14	5	6.24	77	6.14		
11.6	12	6.41	15	5.89	34	6.51	53	6.18	21	6.47	65	6.13	4	6.42
11.7	8	6.75	10	6.26	22	6.56	54	6.36	28	6.68	80	6.37	5	7.06
11.8	10	6.87	10	5.99	39	6.79	33	6.46	24	6.71	100	6.48	7	8.02
11.9	15	7.09	4	6.28	29	6.93	38	6.70	19	6.88	90	6.77	4	6.66
12.0	13	7.07	5	6.65	34	6.99	54	6.83	21	6.98	123	6.89	13	7.56
12.1	16	7.17	12	7.00	32	7.38	32	7.04	12	7.23	102	7.07	18	7.70
12.2	12	7.68	2	7.02	29	7.43	33	7.09	14	7.42	92	7.26	18	7.63
12.3	9	7.49	5	7.47	21	7.66	18	7.27	12	7.77	72	7.47	19	7.96
12.4	5	7.82	1	7.23	36	7.93	12	7.47	14	7.76	86	7.59	19	7.94
12.5	10	7.98	1	7.72	24	8.10	8	7.46	11	8.06	69	7.71	22	8.08
12.6	9	8.46	2	7.78	27	8.31	4	7.74	11	8.36	69	8.01	24	8.24
12.7	7	8.67	2	7.53	19	8.53	4	7.99	13	8.12	56	8.24	26	8.46
12.8	4	8.15	1	8.01	18	8.77	3	8.25	8	8.85	33	8.32	28	8.59
12.9	5	8.92			11	8.88			5	8.72	27	8.69	24	9.11
13.0	4	8.80	1	8.61	9	9.14	1	8.25	7	9.14	9	8.95	32	9.06
13.1	3	9.30			14	9.34			6	9.43	14	9.09	28	9.48
13.2	2	8.85			7	9.59			5	9.84	7	9.16	28	9.56
13.3	3	9.27	1	9.52	4	10.08			3	10.13	3	9.71	26	9.69
13.4	1	7.20			1	11.20			5	9.62	4	9.52	24	10.05
13.5					6	10.37			1	10.20	2	10.14	24	10.14
13.6	4	9.65			4	10.58	1	11.57	10	10.25			26	10.06
13.7					2	10.30			3	10.27	1	12.35	11	10.54
13.8					1	10.60			2	10.45	1	10.51	12	10.90
13.9					1	11.50			1	11.50	1	11.61	11	10.87
14.0									2	10.75			9	10.67
14.1									3	11.10	1	9.88	3	11.23
14.2					1	11.80							4	12.12
14.3											1	12.70	3	11.60
14.4					1	13.40			1	12.80			3	12.53
14.5					1	11.50			1	11.30			3	11.67
14.6													1	13.10
14.7													3	12.67
14.8													1	14.50
14.9					2	13.60					1	16.58		
15.5													1	17.99
15.8											1	17.81	1	15.40

[1] Samples were not collected in 1961. [2] Samples were not collected in 1953 and 1955. [3] Appropriate samples were not available for 1955.

CALCULATED GROWTH

GROWTH IN LENGTH

The growth rate of the Lake Superior lake herring varied considerably but in general tended to be faster in the later collections. A division in the data accordingly was made to separate a period of relatively slow growth (1950–55) from a period of more rapid growth (1956–59). A detailed discussion of annual fluctuations in growth is presented in a later section.

The calculated lengths of the sexes (data not given here) revealed slightly higher values for the females at Duluth, Bayfield, and Portage Entry, and greater lengths for the males at Marquette. The differences were small, never exceeding 0.6 inch. True sex differences in growth rate have been observed in only one stock of lake herring, that of Clear Lake in northeastern Wisconsin, where Hile (1936) demonstrated that the calculated lengths of the females were up to 0.3 inch longer than those of the males.

TABLE 18.—*Calculated total length of lake herring taken at Duluth in 1957–59*

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	9	4.8	8.5	[1] 11.3					
III	76	4.8	7.4	9.9	[1] 11.5				
IV	142	4.2	6.8	8.9	10.7	[1] 12.0			
V	78	3.9	6.3	8.1	9.8	11.1	[1] 12.0		
VI	18	4.1	6.5	8.2	9.7	10.9	11.9	[1] 12.7	
VII	2	3.9	6.6	8.3	9.6	10.8	12.3	13.3	[1] 14.0
Grand average [2]		4.3	6.8	9.0	10.6	11.6	12.5	13.3	14.0
Number of fish		325	325	325	316	240	98	20	2

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

Since it appears impossible to distinguish true sex differences in growth of Lake Superior lake herring from the effect of bias through the selective action of the fishery on a population segregated by maturity, the sexes have been combined for the study of calculated growth.

The major difficulties in the estimation of growth of Lake Superior lake herring arise from the systematic decline in calculated growth rate with an increase in age. These discrepancies were similar in the data for all of the collections at each port (tables 18 through 24). The situation is described best by a few examples. First-year calculated lengths of lake herring from Duluth decreased from 4.8 inches for the II group to 3.9 inches for age group V (table 18); at Bayfield, the decrease was from 5.6 inches for the II group to 4.3 inches for the VI group in the 1956–59 collections (table 20). Second-year calculated lengths decreased from 9.6 inches (II group) to 5.7 inches (VI group) in the 1956–59 Portage Entry samples (table 22) and from 9.8 inches for age group II to 6.5 inches for age-group VI in the 1956–59 Marquette collections (table 24). A detailed review of the comments of other investigators on this kind of disagreement is not considered necessary here since systematic discrepancies of this type have been observed repeatedly among the lake herring and other species and have been discussed at length in the literature. Most investigators agree that the high calculated lengths of the younger age groups and the low values for the older fish can be traced to two major sources of bias: gear selection of the larger fish in the younger age groups and the progressive destruction of the faster growing fish by the fishery. These sources of bias, combined with segregation by maturity of the spawning-run samples, undoubtedly account for the discrepancies among the calculated growth histories of Lake Superior lake herring.

TABLE 19.—*Calculated total length of lake herring taken at Bayfield in 1950–54* [1]

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
III	129	4.8	7.6	9.4	[2] 11.2			
IV	328	4.5	7.0	8.7	10.4	[2] 11.3		
V	74	4.4	6.7	8.4	9.8	11.0	[2] 11.7	
VI	5	4.5	6.7	8.4	9.7	10.8	11.8	[2] 12.6
Grand average [3]		4.6	7.1	8.8	10.5	11.2	11.9	12.7
Number of fish		536	536	536	536	407	79	5

[1] Samples were not collected in 1953.
[2] Average length at capture following completion of current-season growth.
[3] Based on the successive addition of mean increments beyond the fifth year of life.

The two major sources of bias to estimates of growth are to some degree compensating. The best estimates of general growth are held, therefore, to be those based on records from all the fish from each of the spawning-run collections. Fish collected by the *Siscowet* and from the summer commercial fishery have been omitted from the study to permit comparisons among the spawning-run collections at the various ports.

The extent of the variation of growth of Lake Superior lake herring according to port and period of capture is seen best from the summary in table 25. The fish from Bayfield were the slowest growing in the 1950–55 samples, and those from Marquette had the fastest growth (fig. 7). Portage Entry lake herring grew faster than the Bayfield fish but more slowly than those from Marquette. First-year calculated lengths ranged from

Table 20.—*Calculated total length of lake herring taken at Bayfield in 1956–59*

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	17	5.6	9.3	[1]11.7					
III	96	4.9	7.8	10.2	[1]11.8				
IV	296	4.7	7.4	9.2	10.9	[1]12.0			
V	97	4.6	6.9	8.6	10.1	11.3	[1]12.2		
VI	6	4.3	6.6	8.4	9.8	11.0	11.8	[1]12.7	
VII	2	4.8	6.4	7.8	9.0	10.2	11.3	12.3	[1]12.8
Grand average [2]		4.7	7.4	9.4	10.9	11.8	12.7	13.6	14.1
Number of fish		514	514	514	497	401	105	8	(2)

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

Table 21.—*Calculated total length of lake herring taken at Portage Entry, 1950–55*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	9	5.6	8.7	[1]11.4				
III	167	5.0	7.6	9.8	[1]11.4			
IV	322	4.8	7.2	9.0	10.6	[1]11.6		
V	94	4.6	6.7	8.3	9.9	10.9	[1]11.7	
VI	5	4.3	5.7	6.9	8.3	9.8	10.7	[1]11.4
Grand average [2]		4.8	7.2	9.1	10.7	11.4	12.2	12.9
Number of fish		597	597	597	588	421	99	5

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

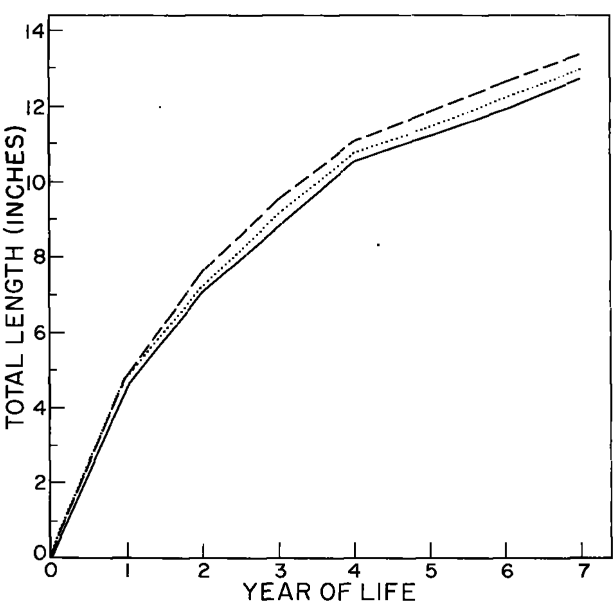

Figure 7.—General growth of Lake Superior lake herring of the 1950–55 collections from Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Table 22.—*Calculated total length of lake herring taken at Portage Entry, 1956–59*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	16	5.6	9.6	[1]11.9				
III	178	4.9	7.9	10.2	[1]12.0			
IV	375	4.6	7.2	9.1	11.0	[1]12.2		
V	123	4.6	6.8	8.6	10.4	11.7	[1]12.7	
VI	3	3.5	5.7	7.2	8.9	10.6	11.8	[1]12.2
Grand average [2]		4.7	7.4	9.4	11.1	12.1	13.1	13.5
Number of fish		695	695	695	679	501	126	3

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

Table 23.—*Calculated total length of lake herring taken at Marquette 1950–55*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	5	5.5	9.6	[1]11.6				
III	129	5.1	8.0	10.2	[1]11.8			
IV	302	4.7	7.5	9.4	10.9	[1]11.9		
V	115	4.5	7.2	8.8	10.3	11.4	[1]12.2	
VI	5	4.4	6.8	8.5	9.9	10.9	11.9	[1]12.6
Grand average [2]		4.8	7.6	9.5	11.0	11.8	12.6	13.3
Number of fish		556	556	556	551	422	120	5

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

4.6 inches at Bayfield to 4.8 inches at Portage Entry and Marquette. At the end of 4 years of life the calculated lengths were 10.5 inches at Bayfield, 10.7 inches at Portage Entry, and 11.0 inches at Marquette. Sixth-year calculated lengths were 11.9 inches at Bayfield, 12.2 inches at Portage Entry, and 12.6 inches at Marquette.

TABLE 24.—*Calculated total length of lake herring taken at Marquette, 1956–59*

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
		Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
II	22	5.3	9.8	[1] 12.5				
III	167	5.5	8.6	10.9	[1] 12.7			
IV	271	4.8	7.6	9.7	11.5	[1] 12.8		
V	85	4.6	7.2	8.9	10.6	11.8	[1] 12.8	
VI	9	4.5	6.5	8.1	9.9	11.2	12.3	[1] 13.4
Grand average [2]		5.0	7.9	10.0	11.7	12.5	13.5	14.6
Number of fish		554	554	554	532	365	94	9

[1] Average length at capture following completion of current-season growth.
[2] Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 25.—*Calculated total length* [1] *of Lake Superior lake herring according to port for the years 1950–55 and 1956–59*

Year of life	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54 [2]	1956–59	1950–55	1956–59	1950–55	1956–59
	Inches	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
1	4.3	4.6	4.7	4.8	4.7	4.8	5.0
2	6.8	7.1	7.4	7.2	7.4	7.6	7.9
3	9.0	8.8	9.4	9.1	9.4	9.5	10.0
4	10.6	10.5	10.9	10.7	11.1	11.0	11.7
5	11.6	11.2	11.8	11.4	12.1	11.8	12.5
6	12.5	11.9	12.7	12.2	13.1	12.6	13.5
7	13.3	12.7	13.6	12.9	13.5	13.3	14.6
8	14.0		14.1				

[1] Calculated lengths beyond the fifth year of life are based on the successive addition of mean increments.
[2] Samples were not collected in 1953 and 1955.

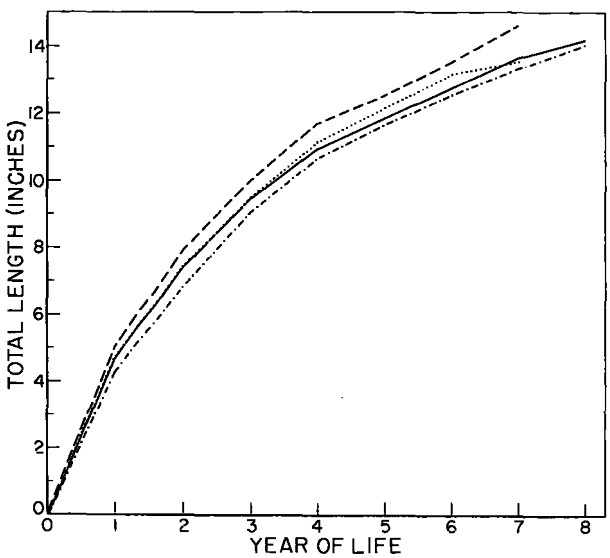

FIGURE 8.—General growth in length of Lake Superior lake herring of the 1956–59 collections from Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Growth in 1956–59 also increased from the western to eastern ports (fig. 8). The lake herring from Duluth grew 4.3 inches in the first year, those from Bayfield and Portage Entry grew 4.7 inches, and the Marquette fish grew 5.0 inches. In the fourth year of life the calculated lengths of lake herring were 10.6 inches at Duluth, 10.9 inches at Bayfield, 11.1 inches at Portage Entry, and 11.7 inches at Marquette. At the end of 6 years of life the calculated lengths were 12.5 inches at Duluth, 12.7 inches at Bayfield, 13.1 inches at Portage Entry, and 13.5 inches at Marquette.

Dryer (1963) found a similar west-to-east change in the growth of whitefish of Lake Superior. The slowest growing stocks were those from Bayfield; the growth rate increased to the east where the fastest growing fish were from Whitefish Bay. Smith (1956) observed that lake herring from northern Green Bay grew less in their first year than did those from southern Green Bay but grew faster than the southern fish in subsequent years. By the end of the fourth year the differences in size had largely disappeared.

With only one exception (that of the first-year calculated length of the Portage Entry fish) the calculated lengths of lake herring taken at all ports in 1956–59 were greater than those of the 1950–55 collections (fig. 9). The fish taken in the later period at Bayfield were 0.1 inch longer in the first year, 0.6 inch longer in the third, and 0.8 inch longer in the sixth year of life. At Portage Entry the first-year calculated length (4.7 inches) of the 1956–59 fish was 0.1 inch less than that of the 1950–55 samples, but beginning in the second year of life the calculated lengths of the fish taken in the later period were without exception the longer (the largest difference was 0.9 inch in the sixth year of life). Lake herring taken in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life.

GROWTH IN WEIGHT

The weights in table 26 were computed from the general length-weight equation given on page 509 and correspond exactly with the lengths of table 25. Questions relating to the reliability of the calculated lengths apply, therefore, to the calculated weights.

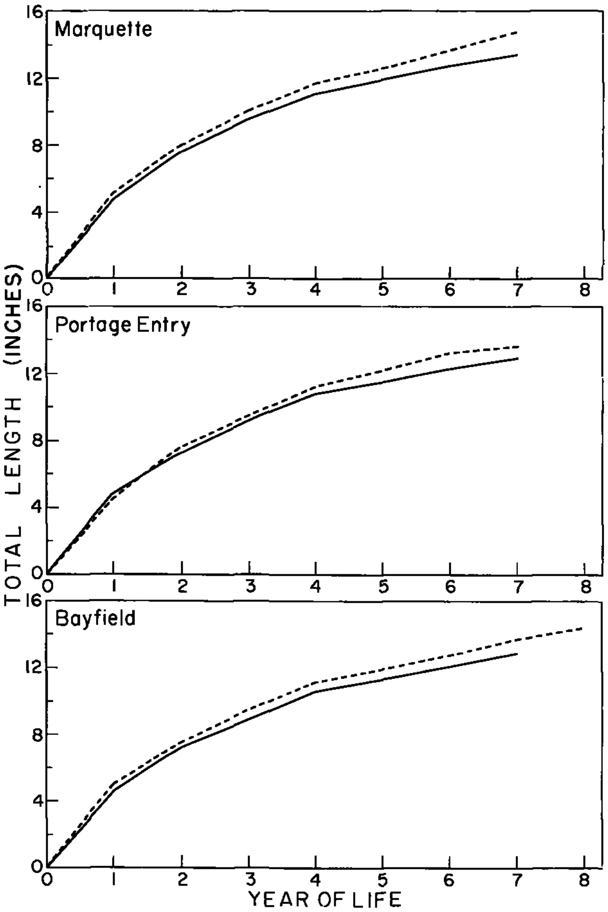

FIGURE 9.—General growth in length of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette. Growth in 1950–55, solid line; in 1956–59, broken line.

TABLE 26.—*Calculated weight of Lake Superior lake herring according to port for the years 1950–55 and 1956–59*

[Weights were computed from the calculated lengths of table 25 by means of the general length-weight equation. Increments in parentheses.]

Year of life	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54[1]	1956–59	1950–55	1956–59	1950–55	1956–59
	Ounces	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
1	0.40	0.43	0.52	0.58	0.52	0.58	0.60
	(0.40)	(0.43)	(0.52)	(0.58)	(0.52)	(0.58)	(0.60)
2	1.22	1.40	1.60	1.43	1.60	1.78	2.00
	(0.82)	(0.97)	(1.08)	(0.85)	(1.08)	(1.20)	(1.40)
3	3.04	2.82	3.58	3.18	3.58	3.64	4.33
	(1.82)	(1.42)	(1.98)	(1.75)	(1.98)	(1.86)	(2.33)
4	5.20	5.05	5.68	5.30	6.00	5.80	7.02
	(2.16)	(2.23)	(2.10)	(2.12)	(2.42)	(2.16)	(2.69)
5	6.84	6.16	7.20	6.49	7.80	7.20	8.61
	(1.64)	(1.11)	(1.52)	(1.19)	(1.80)	(1.40)	(1.59)
6	8.61	7.40	9.10	8.00	10.10	8.84	11.10
	(1.77)	(1.24)	(1.90)	(1.51)	(2.30)	(1.64)	(2.49)
7	10.60	9.10	11.37	9.60	11.10	10.60	13.98
	(1.99)	(1.70)	(2.27)	(1.60)	(1.00)	(1.76)	(2.88)
8	12.38	--------	12.69	--------	--------	--------	--------
	(1.78)	--------	(1.32)	--------	--------	--------	--------

[1] Samples were not collected in 1953 and 1955.

The calculated weights of lake herring from the various ports differed little at the end of the first year (from 0.4 ounce at Duluth to 0.6 ounce in the 1956–59 Marquette samples), but in subsequent years of life differences among ports and between periods of capture were sometimes considerable.

In 1950–55 the lake herring from Bayfield had the slowest growth in weight (fig. 10). The fish reached 1.4 ounces during the second year of life, and by the seventh year they were 9.1 ounces. Portage Entry fish grew slightly faster than those from Bayfield, reaching 9.6 ounces at the end of 7 years of life. Growth at Marquette was similar to that of fish from the other ports during the first year but was faster in subsequent years; at the end of 7 years the lake herring from Marquette were 1 ounce heavier than those from Portage Entry and 1.5 ounces heavier than the Bayfield fish.

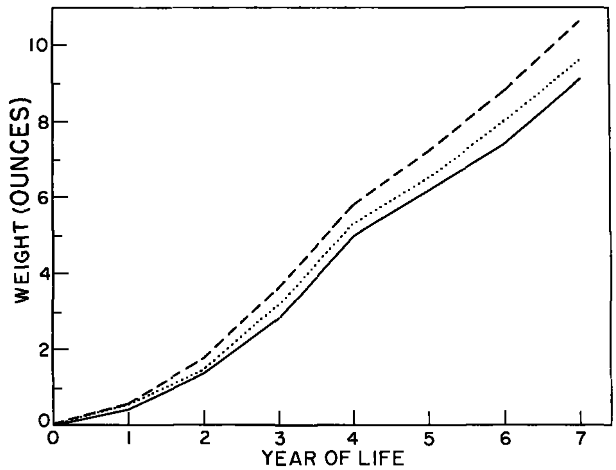

FIGURE 10.—General growth in weight of Lake Superior lake herring in 1950–55 at Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Growth in weight was faster during 1956–59 than in 1950–55 at all ports. At the end of 6 years of life, for example, the fish from Bayfield were 1.7 ounces heavier in 1956–59 (9.1 ounces) than in 1950–55 (7.4 ounces). At Portage Entry the VI-group fish were 2.1 ounces heavier (increase from 8.0 to 10.1 ounces) and at Marquete they were 2.3 ounces heavier (increase from 8.8 to 11.1 ounces).

Port-to-port differences of growth in weight had a general west-to-east trend toward faster growth during 1956–59 also (fig. 11). Duluth lake herring

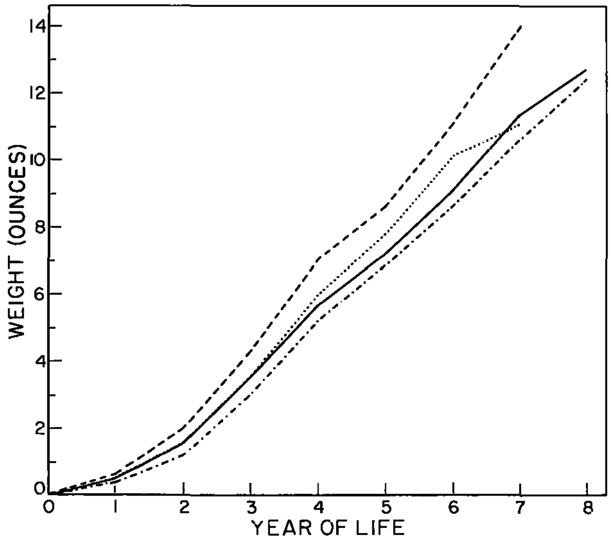

FIGURE 11.—General growth in weight of Lake Superior lake herring in 1956–59 at Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

weighed 0.4 ounce in the first year, those from Bayfield and Portage Entry grew 0.5 ounce, and at Marquette they grew 0.6 ounce. At the end of 7 years the fish weighed 10.6 ounces at Duluth, 11.4 ounces at Bayfield, 11.1 ounces at Portage Entry, and 14.0 ounces at Marquette.

The second-year increments of weight were more than twice that of the first year's growth at all of the ports except Portage Entry in 1950–55, and third-year growth was double the second-year increments at Duluth and at Portage Entry in 1950–55. The increments in weight reached a peak in the fourth year of life at all ports except Bayfield in 1956–59 and Marquette where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956–59.

ANNUAL FLUCTUATIONS IN GROWTH

FLUCTUATIONS OF GROWTH IN LENGTH

Voluminous data and discussions have been published on the extent of annual fluctuations of growth and on the various factors affecting the growth of fish. Temperature and population densities probably have been most commonly considered but the results have been varied and often inconclusive. A discussion of this vast literature need not be undertaken here. Excellent reviews and references to publications on factors of growth have been given by Hile (1936), Van Oosten (1944), and Watt (1956).

The number of studies on factors affecting the growth of lake herring has not been large. Hile (1936), who considered the possible influence of air temperature and population density on the growth of cisco populations in northeastern Wisconsin, concluded that the failure of variations of both factors to operate in the same direction in the same years may obscure the effect of each of them. Van Oosten (1929), Carlander (1945), and Smith (1956) found no correlation between annual fluctuations in growth of lake herring and air temperatures.

The data on annual fluctuations of growth in length of Lake Superior lake herring are separated according to port (tables 27, 28, and 29). Data are given only for age groups III, IV, and V; other groups were not adequately represented. The Duluth samples have been omitted since the collections, available only for 1957–59, cover too few years for a satisfactory study of annual fluctuations.

The growth increments are arranged in the following manner: the columns show the growth for different years of life in a particular calendar year; the horizontal rows show growth in a particular year of life in the different calendar years; and the diagonal rows show the growth history of an age group belonging to a year class that can be identified by the calendar year in which the first-year growth was made. The data for different age groups had to be kept separate because of the systematic discrepancies described in the section on calculated growth in length.

Although examination of the growth increments of lake herring from the various ports reveals strong though irregular trends toward improved growth in the later years, a procedure based on the actual percentage change from one calendar year to the next offers a more precise estimate of growth fluctuations. This method was described in detail by Hile (1941).

The largest annual fluctuations in growth occurred at Bayfield (table 30). Growth was poorest in 1945 and 1946 when the percentage deviations from the 15-year (1945–59) mean were −14.7 and −23.5 percent. Growth improved irregularly to 12.0 percent above average in 1951

TABLE 27.—*Annual increments of growth in length of Lake Superior lake herring captured at Bayfield, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6						0.7	0.7	0.7		0.7		0.7	1.0	1.0	1.2
5					1.6	1.0	1.1		1.4		1.1	1.4	1.2	1.6	
4				2.0	1.3	1.6		1.4		1.5	1.8	1.4	1.3		
3			1.0	1.3	1.5		1.5		1.6	1.7	1.8	1.5			
2		1.3	2.1	2.8		1.3		2.4	2.1	2.3	2.0				
1	4.7	4.3	4.6		4.7		4.5	3.9	4.6	4.5					
Number of fish	(1)	(19)	(28)		(26)		(22)	(16)	(32)	(27)					
Age Group IV:															
5						0.9	1.0	1.0		1.0		1.0	1.1	1.2	1.1
4					1.6	1.5	1.9		1.9		1.9	1.9	1.6	1.9	
3				1.7	1.8	1.6		1.9		1.9	1.9	2.2	1.3		
2			2.4	2.4	2.6		2.3		2.4	2.5	2.5	3.4			
1		4.7	4.4	4.6		4.7		4.7	4.6	4.6	4.7				
Number of fish		(63)	(89)	(69)		(107)		(54)	(134)	(43)	(65)				
Age group III:															
4						1.7	2.1	1.5		1.4		1.6	1.6	1.3	1.4
3					2.0	1.9	2.5		2.3		2.4	2.4	2.4	2.8	
2				2.5	2.6	2.4		2.8		2.7	3.2	2.8	2.9		
1			4.9	4.6	5.0		4.9		4.8	4.7	5.4	5.3			
Number of fish			(39)	(39)	(24)		(27)		(15)	(41)	(28)	(12)			

TABLE 28.—*Annual increments of growth in length of Lake Superior lake herring captured at Portage Entry, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6						0.7	0.7	0.7	1.0	0.9	0.8	0.9	1.0	1.0	1.1
5					1.3	1.0	1.0	1.0	1.0	1.3	1.5	1.3	1.4	1.3	
4				1.3	1.5	1.4	1.7	1.8	1.7	1.8	1.7	1.8	1.8		
3			1.8	1.6	1.9	1.6	1.9	1.5	1.8	1.8	1.8	1.7			
2		2.2	2.2	2.2	1.9	2.0	2.1	2.1	2.2	2.3	2.3				
1	4.4	4.5	4.7	4.7	4.3	4.6	4.5	4.3	4.7	4.8					
Number of fish	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)					
Age group IV:															
5						1.1	.9	.9	1.1	1.0	.6	1.2	1.3	1.2	1.2
4					1.4	1.6	1.6	1.7	1.6	1.7	1.8	1.9	2.0	1.9	
3				1.9	1.9	1.9	1.8	1.9	1.9	1.9	2.0	2.1	2.2		
2			2.8	2.5	2.6	2.2	2.1	2.3	2.6	2.6	2.9	2.6			
1		4.6	4.6	4.7	4.9	5.2	5.5	4.6	4.5	4.7	4.5				
Number of fish		(59)	(69)	(58)	(49)	(50)	(37)	(137)	(123)	(47)	(68)				
Age group III:															
4						1.6	1.9	1.7	1.7	1.6	1.8	1.9	1.9	1.5	1.8
3					2.2	2.0	2.2	2.2	2.1	2.1	2.3	2.3	2.3	2.5	
2				2.9	2.7	2.5	2.6	2.5	3.0	2.9	3.0	3.9	2.5		
1			4.9	4.8	5.0	5.1	5.3	4.9	4.8	5.0	5.0	5.2			
Number of fish			(30)	(23)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)			

TABLE 29.—*Annual increments of growth in length of Lake Superior lake herring captured at Marquette, 1950–59*

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*
6						1.0	0.7	0.9	0.9	0.9	0.7	0.9	1.1	1.2	1.1
5					0.9	1.1	1.0	1.3	1.3	1.1	1.1	1.3	1.6	1.2	
4				1.1	1.5	1.6	1.5	1.6	1.7	1.6	1.8	1.7	1.7		
3			2.0	1.4	1.6	1.6	1.7	1.7	1.8	1.6	2.0	1.8			
2		2.5	2.9	2.8	2.7	2.7	2.4	2.7	2.6	2.2	2.6				
1	4.5	4.5	4.4	4.4	4.4	4.6	4.8	4.4	4.4	4.9					
Number of fish	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)					
Age group IV:															
5						1.0	1.1	1.2	1.0	1.0	1.0	1.1	1.3	1.5	1.3
4					1.6	1.4	1.6	1.7	1.8	1.8	1.8	1.8	2.0	1.9	
3				1.8	2.0	2.0	2.0	1.9	2.0	2.1	2.1	2.2	2.1		
2			2.7	2.8	2.8	2.7	2.7	2.3	2.7	2.8	2.9	2.9			
1		4.6	4.7	4.6	4.8	4.8	4.9	4.9	4.9	4.6	4.8				
Number of fish		(43)	(63)	(54)	(44)	(59)	(39)	(69)	(88)	(61)	(53)				
Age group III:															
4						1.6	1.5	1.5	1.8	1.7	1.6	1.8	1.8	1.9	1.9
3					2.4	2.0	2.4	2.2	2.1	1.9	2.2	2.5	2.6	2.2	
2				2.9	3.4	2.8	2.8	3.1	4.0	4.2	4.1	4.5	3.6		
1			4.7	5.0	5.3	5.3	5.5	4.8	5.0	5.0	4.9	5.4			
Number of fish			(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)			

but then fell to −3.6 percent in 1952. Beginning in 1953, growth improved progressively (exception in 1957) to 1959 when a maximum value of 16.3 percent above average was reached.

Growth at Portage Entry remained below average in 1945–53 (percentage range, from −0.4 to −5.2) and was above average in 1954–59 (exception in 1958). Growth improved steadily from 1952 to 1956 when the value of 8.9 percent above average was reached. The percentage declined in 1957 and 1958 but recovered to 8.7 percent in 1959.

TABLE 30.—*Percentage deviation of growth in length of Lake Superior lake herring from the 1945–59 mean*

Year	Percentage deviation at			Year	Percentage deviation at		
	Bayfield	Portage Entry	Marquette		Bayfield	Portage Entry	Marquette
1945	−14.7	−4.4	−9.3	1953	−0.9	−0.7	3.1
1946	−23.5	−2.3	−9.3	1954	.1	1.2	-1.5
1947	−6.1	−.5	−6.0	1955	6.3	2.5	4.8
1948	−.2	−2.8	−7.9	1956	7.7	8.9	11.2
1949	1.8	−2.5	−1.8	1957	1.0	3.4	11.2
1950	−6.8	−4.1	−.7	1958	10.6	−1.8	6.2
1951	12.0	−.4	−.7	1959	16.3	8.7	−.5
1952	−3.6	−5.2	−1.8				

The percentages of departure from average growth at Marquette fell below the mean in 1945–52 (range, −0.7 to −9.3) and were above average in 1953–58. The maximum value of 11.2 percent occurred in 1956 and 1957, after which the growth rate declined to −0.5 percent in 1959.

With few exceptions, the percentage deviations of growth in length of Lake Superior lake herring at all ports were below average in 1945–53 and above average in 1954–59 (fig. 12). Improvement in growth was especially marked in 1953–56.

To obtain a better measure of the similarity of the long-term changes of growth at the three localities, coefficients of correlation were calculated for the actual annual deviations from average. The coefficients are as follows:

Ports	r
Bayfield–Portage Entry	0.595
Bayfield–Marquette	.618
Portage Entry–Marquette	.601

The coefficients between annual fluctuations in growth were significant at a probability level between 2 and 1 percent (absolute values of r at the 2- and 1-percent levels of significance are 0.592 and 0.641). Conditions as a whole are apparently undergoing a progressive change favorable to improved growth at the three ports. Temperature alone was not responsible for the growth fluctuations of Lake Superior lake herring. Meterological conditions should operate similarly over the entire lake and hence should have similar effects on trends in the growth at all three ports. The temperature records give no evidence, however, for a major upward trend since 1954.

The inverse relation which appears to exist between the upward trend in improved growth and the downward trend in abundance of lake herring at the various ports suggests that the decrease in population density may have contributed to the

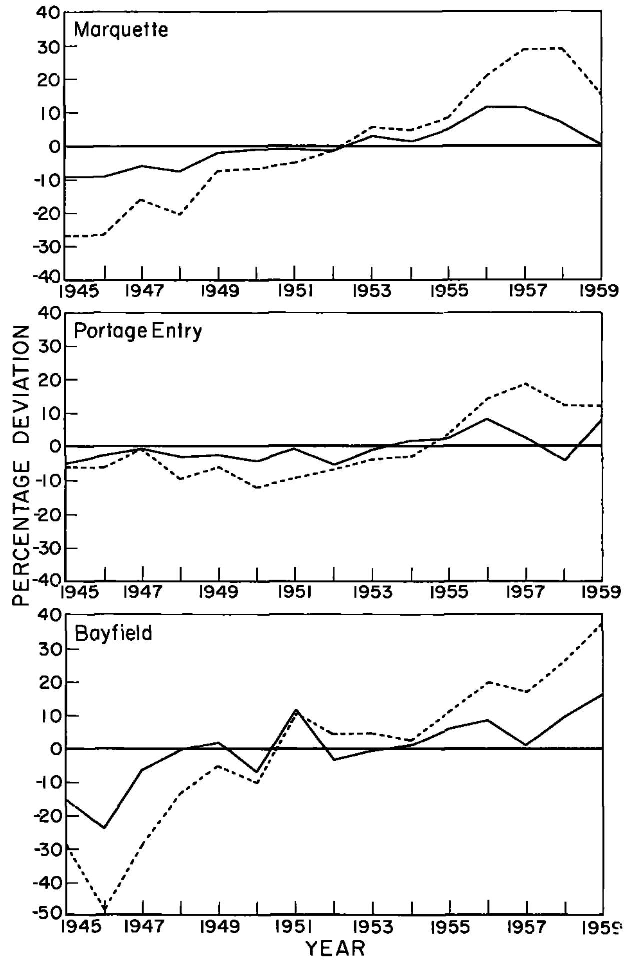

FIGURE 12.—Annual fluctuations of growth in length (solid line) and weight (broken line), of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette.

change. A statistically significant correlation between growth (in both length and weight) and abundance could not be established, however. The number of years covered by the data may have been inadequate for a sound statistical analysis. Data on fluctuations of both growth and of abundance in terms of numbers of fish were available only for the 10 years 1950–59. Data on both growth and abundance in terms of pounds of fish were available for 15 years (1945–59) in Michigan waters only.

FLUCTUATIONS OF GROWTH IN WEIGHT

The annual increments of growth in weight (tables 31, 32, and 33) are arranged in the same manner as those of length in tables 27, 28, and 29. Since the calculated weights were based on the calculated lengths, the trends in annual fluctuations of growth in weight for Lake Superior lake herring were similar to those of growth in length (fig. 11). Growth in weight was below average at Bayfield in 1945–50, at Portage Entry in 1945–54, and at Marquette in 1945–52. Growth was above average at all of the ports after 1954.

The correlation between annual fluctuations of growth in weight of Lake Superior lake herring at the three ports was even closer than that for length. The values of r follow:

Ports	
Bayfield–Portage Entry	0.651
Bayfield–Marquette	.889
Portage Entry–Marquette	.823

The coefficients were well beyond the 1-percent level of probability, and 2 were beyond the 0.1-percent level.

TABLE 31.—*Annual increments of growth in weight of Lake Superior lake herring captured at Bayfield, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6						1.1	1.0	1.4		1.0		1.2	1.7	1.9	2.2
5					2.2	1.3	1.8		1.9		1.7	2.1	1.8	2.2	
4				1.6	1.2	2.0		1.2		1.8	1.8	1.8	1.3		
3			0.5	.7	1.4		.8		1.2	.9	1.4	1.0			
2		0.4	.7	1.1		.4		.8	.6	.8	.6				
1	0.5	.4	.5		.5		.5	.3	.5	.5					
Number of fish	(1)	(19)	(28)		(26)		(22)	(16)	(32)	(27)					
Age group IV:															
5						1.4	1.5	1.7		1.7		1.7	2.0	2.1	2.1
4					2.1	1.9	2.5		2.6		2.7	2.6	2.3	2.8	
3				1.4	1.4	1.3		1.6		1.6	1.6	2.0	1.4		
2			.9	.8	1.0		.8		.9	.9	.9	1.6			
1		.5	.4	.5		.5		.5	.5	.5	.5				
Number of fish		(63)	(89)	(69)		(107)		(54)	(134)	(43)	(65)				
Age group III:															
4						2.5	3.0	2.2		2.1		2.5	2.6	2.2	2.6
3					1.9	1.8	2.6		2.5		2.5	2.8	3.0	3.6	
2				1.0	.9	1.0		1.2		1.2	1.5	1.5	1.5		
1			.6	.5	.6		.6		.5	.5	.7	.7			
Number of fish			(39)	(39)	(24)		(27)		(15)	(41)	(28)	(12)			

TABLE 32.—*Annual increments of growth in weight of Lake Superior lake herring captured at Portage Entry, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6						1.2	1.2	1.3	1.7	1.6	1.5	1.8	1.8	2.2	2.4
5					1.8	1.5	1.5	1.5	1.5	1.9	2.4	2.1	2.4	2.2	
4				1.6	1.7	1.8	2.0	2.1	2.0	2.2	2.0	2.4	2.4		
3			1.2	1.1	1.5	1.0	1.2	1.0	1.2	1.2	1.5	1.4			
2		0.8	.8	.8	.7	.6	.7	.8	.7	.8	.9				
1	0.4	.4	.5	.5	.4	.5	.4	.4	.5	.5					
Number of fish	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)					
Age group IV:															
5						1.9	1.4	1.5	1.8	1.7	1.2	2.2	2.4	2.6	2.2
4					1.9	2.2	2.2	2.3	2.2	2.5	2.4	2.6	3.1	2.8	
3				1.8	1.6	1.8	1.5	1.8	2.0	1.7	1.8	2.1	2.0		
2			1.1	.9	1.0	.8	.9	1.2	1.0	.9	1.3	.9			
1		.5	.5	.5	.6	.6	.7	.5	.5	.5	.5				
Number of fish		(59)	(69)	(58)	(49)	(50)	(37)	(137)	(123)	(47)	(68)				
Age group III:															
4						2.5	2.8	2.6	2.6	2.4	2.9	3.1	3.2	2.8	3.0
3					2.4	2.0	2.2	2.4	2.3	2.3	2.5	2.7	3.2	2.8	
2				1.3	1.2	1.1	1.2	1.2	1.4	1.3	1.5	2.3	1.2		
1			.6	.5	.6	.6	.7	.6	.5	.6	.6	.6			
Number of fish			(30)	(23)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)			

TABLE 33.—*Annual increments of growth in weight of Lake Superior lake herring captured at Marquette, 1950–59*

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1943	1954	1955	1956	1957	1958	1959
Age group V:	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
6						1.8	1.3	1.7	1.7	1.8	1.4	2.0	2.3	2.6	2.6
5					1.3	1.7	1.6	2.1	2.1	1.7	1.9	2.1	2.6	2.2	
4				1.5	2.0	2.1	1.9	2.0	2.2	2.3	2.3	2.2	2.4		
3			1.7	1.2	1.3	1.3	1.5	1.4	1.7	1.3	1.4	1.7			
2		0.8	1.1	1.1	1.0	1.0	.8	1.2	.9	.8	1.1				
1	0.5	.5	.4	.4	.4	.5	.5	.4	.4	.6					
Number of fish	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)					
Age group IV:															
5						1.7	1.9	2.2	1.8	1.8	1.8	2.1	2.8	3.3	2.8
4					2.1	2.0	2.3	2.5	2.6	2.5	2.8	2.8	3.1	3.0	
3				1.7	2.0	1.9	2.0	1.9	1.9	2.1	2.2	2.2	2.2		
2			1.0	1.2	1.1	1.2	1.2	.8	1.2	1.2	1.2	1.3			
1		.5	.5	.5	.5	.5	.6	.6	.6	.5	.5				
Number of fish		(43)	(63)	(54)	(44)	(59)	(39)	(69)	(88)	(61)	(53)				
Age group III:															
4						2.5	2.5	2.6	3.1	3.1	2.9	3.8	4.0	4.5	3.8
3					2.5	2.5	2.9	2.6	2.7	2.5	3.2	3.6	4.0	3.2	
2				1.3	1.8	1.4	1.4	1.9	2.3	2.7	2.6	3.0	2.3		
1			.5	.6	.7	.7	.7	.5	.6	.6	.6	.7			
Number of fish			(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)			

The range of the percentage fluctuations of growth in weight (table 34) was much greater at each port than was that of growth in length (table 30). This difference is largely due to the nature of the length-weight relation, namely, the increase of weight approximately as the cube of the length. Consequently, the increment of weight corresponding to a particular increment of length depends not only on the amount of growth in length but also on the length of the fish at the time the growth is made. For example, a lake herring that weighs 2 ounces at a length of 8 inches will weigh 4.3 ounces upon reaching a length of 10 inches, a gain of 2.3 ounces. A 10-inch fish that experiences the same 2-inch growth (from 10 to 12 inches) increases its weight from 4.3 to 7.6 ounces, a gain of 3.3 ounces. Both the large size of the fish and the large increments of length contributed to the excellent growth in weight in the more recent years.

The curves of fluctuations of growth in length and weight are further affected by differences with respect to the years of life that exerted greatest influence on the year-to-year percentage changes. Under the procedure of Hile (1941) for estimates of growth fluctuations, the earlier years of life dominated the estimates of fluctuations of growth in length by reason of their larger increments. The data on weight, on the other hand, were least affected at lower ages since the increments of weight were smallest during the earlier years of life. In the later years of life, the weight increments were large when those of length were small.

Similar discrepancies between estimates of fluctuations of growth in length and weight were found by Hile (1954) for walleye and by El-Zarka (1959) for yellow perch in Saginaw Bay.

TABLE 34.—*Percentage deviation of growth in weight of Lake Superior lake herring from the 1945–59 mean*

Year	Percentage deviation at			Year	Percentage deviation at		
	Bayfield	Portage Entry	Marquette		Bayfield	Portage Entry	Marquette
1945	−28.3	−6.0	−26.8	1953	4.6	−3.4	5.4
1946	−48.4	−6.0	−26.8	1954	2.2	−2.5	4.2
1947	−28.3	−.4	−16.4	1955	11.5	3.8	8.1
1948	−13.6	−9.3	−20.3	1956	19.9	15.2	20.5
1949	−5.7	−6.0	−7.6	1957	16.5	17.1	28.3
1950	−9.9	−12.0	−7.0	1958	26.4	12.7	28.3
1951	11.5	−9.5	−5.7	1959	37.0	12.7	16.0
1952	4.6	−6.6	−.2				

REPRODUCTION

SEX COMPOSITION

Segregation by maturity in the spawning run, in combination with sex differences in age at first maturity and sex differences in the time of arrival of fish on the grounds, limited the use of spawning-run samples for the study of sex composition. The collections from Bayfield in 1959 and 1961 offer examples of the effects of time of capture within the spawning period. A net-run sample collected on November 19, 1959, contained only 3 percent females, and a later sample from the same area on December 8 included 82 percent females. In 1961, net-run samples of lake herring were collected each day the nets were lifted during 15 days of the spawning season (table 35). The number of females exceeded that of the males in all but the first and third days of collection. Had the production of spawning-run fish begun earlier in the season,[3] the percentage of males undoubtedly would have been higher during the first few days. The percentage of females increased steadily after November 23 (exceptions on November 27 and 28) to December 3, when they contributed 93 percent to the total. The advantage of the females decreased slightly in the last 2 days of the season.

Smith (1956) was able to demonstrate differences in the sex ratio according to age, year of collection, depth, season, and gear of capture. His samples from pound nets contained a higher percentage of females in February than during other months; the percentage of females in the samples decreased during 1949–52; the percentage of females decreased with an increase in age in pound net collections and increased with increase in age in gill net collections; in October, females were relatively more plentiful in the deeper than in shallow water.

TABLE 35.—*Changes in the sex ratio of Lake Superior lake herring during the 1961 spawning season at Bayfield*

[The age groups have been combined]

Date	Number of males	Number of females	Percentage of females
Nov. 20	85	67	44.1
22	87	123	58.6
23	80	75	48.4
24	57	97	63.0
25	57	156	73.2
26	50	150	75.0
27	41	97	70.3
28	53	147	73.5
29	38	155	80.3
30	28	122	81.3
Dec. 1	26	132	83.5
2	21	129	86.0
3	10	132	93.0
4	19	144	88.3
6	23	123	84.2
Combined samples	675	1,849	73.3

Comparable data from Lake Superior did not disclose differences in the sex ratio according to season (with the exception of the spawning season), geographical location, or depth. Since all of the samples came from gill nets, sex data for fish from different gears could not be compared.

The data on sex composition of Lake Superior lake herring were collected during the summer (no fish collected later than September 27 were used in the study of the sex ratio) at: Two Harbors, Minn; Bayfield, Wis.; and Marquette, Mich. The samples for the various dates at these ports were so similar that the collections have been combined (table 36).

[3] The fishermen did not start intensive fishing until they could be assured of good catches.

The number of females equalled or exceeded that of the males in each age group except the I group (only 1 fish). In the later years, the advantage of the females increased from 52.3 percent for age group III to 81.8 percent for group VII (the percentage dropped to 71.4 percent for age group VIII). For all age groups combined, the percentage of females was 68.5.

TABLE 36.—*Sex composition of age groups of Lake Superior lake herring*

[Based on summer collections]

Age group	Number of males	Number of females	Percentage of females
I	1		0.0
II	20	20	50.0
III	63	69	52.3
IV	56	146	72.3
V	51	154	75.1
VI	37	87	70.2
VII	8	36	81.8
VIII	4	10	71.4
Combined samples	240	522	68.5

AGE AND SIZE AT MATURITY

Variation is considerable in the age and size at maturity among different populations of lake herring. Most of the lake herring are mature at age group II in the lakes of northeastern Wisconsin (Hile, 1936), Saginaw Bay (Van Oosten, 1929), Green Bay (Smith, 1956), and Lake Erie (Clemens, 1922); at age group III in Lake Ontario (Stone, 1938), Blind Lake, Mich. (Cooper, 1937), Lake Oconomowoc, Wis. (Cahn, 1927), and Lake Superior; and at age group IV in Hudson Bay (Dymond, 1933) and Manitoba Lakes (Bajkov, 1930). Differences in the age and size at maturity often can be correlated with the growth rates of the stocks; fish which have particularly slow growth may mature at a higher age but at a length below that of faster growing specimens (Alm, 1959). This phenomenon was demonstrated among various stocks of whitefish in Lake Superior (Dryer, 1963), but a similar correlation does not appear to exist among all populations of lake herring. Indeed, lake herring from Trout, Silver, and Muskellunge Lakes in northeastern Wisconsin (Hile, 1936) are among the slowest growing for which growth data have been published, but these fish matured at a younger age than those from the faster growing stocks of Lakes Superior and Ontario.

The limited data on the age and size at maturity for Lake Superior lake herring (tables 37 and 38) came from records of nonspawning-run samples. Nearly all of the fish taken in the spawning-run samples were mature. The youngest mature lake herring in Lake Superior belonged to age group II (table 37), and all fish older than the III group were mature. The percentage maturity was higher for males than for females in age groups II and III. All lake herring shorter than 8.5 inches were immature, and all fish longer than 11.9 inches were mature (table 38). The first mature male appeared in the 8.5- to 8.9-inch group and all the males were mature at lengths greater than 11.4 inches. The first mature females appeared in the 9.5- to 9.9-inch group and all were mature at lengths greater than 11.9 inches.

SPAWNING

Spawning of the lake herring in the Great Lakes region takes place some time between mid-November and mid-December. Most investigators agree that water temperature is the main factor influencing the onset of spawning. Various observations and experiments (Cahn, 1927; Pritchard, 1930; Stone, 1938; Brown and Moffett, 1942; Smith, 1956) have shown that spawning does not occur until water temperatures drop below 39.0° F. (3.9° C.).

The earliest spent lake herring from Lake Superior was caught on November 12 in Keweenaw Bay in 1951, and ripe fish were observed as late as December 20 in the Apostle Islands area in 1960. The bulk of the spawning normally takes place during the last week of November and the first week of December. Water temperatures during this time ranged from 40° F. to 37° F. (4.4° C. to 2.8° C.).

Prespawning fish appear on shallow (3 to 6 fathoms) reefs in the Apostle Islands in mid-October. Lake herring are fished commercially on these reefs from mid-October to late November, but the catches rarely include spent fish. The fishermen follow the lake herring off the reefs into about 20 fathoms where large-scale spawning first occurs. As the spawning season progresses, the fishermen move into deeper water and the last large catches are taken from water 60 to 70 fathoms deep. Koelz (1929) stated that spawning lake herring at Marquette were first found in 8 or 9 fathoms but later moved out to 14 or even 20.

Table 37.—*Relation between age and sexual maturity of Lake Superior lake herring*

[All fish younger than age group II were immature; all fish older than age group III were mature]

Age group and sex	Number immature	Number mature	Percentage mature
Males:			
II	9	7	44
III	5	22	81
Females:			
II	14	5	26
III	6	20	77

Table 38.—*Relation between length and sexual maturity of Lake Superior lake herring*

[All fish shorter than 8.5 inches were immature; all fish longer than 11.9 inches were mature]

Total length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
Inches						
8.5–8.9	1	1	50	—	—	—
9.0–9.4	4	4	50	4	—	0
9.5–9.9	4	4	50	3	1	25
10.0–10.4	3	6	67	6	3	33
10.5–10.9	—	6	100	2	8	80
11.0–11.4	1	4	80	2	10	83
11.5–11.9	—	6	100	1	6	86

Scanning with the fish magnifier of the depth recorder aboard the *Siscowet* during the 1961 spawning season in the Apostle Islands region, confirmed earlier suggestions (Smith, 1956) that the lake herring are pelagic spawners. Night scanning during the peak of the season revealed a heavy concentration of fish (presumably lake herring) at 5 to 15 fathoms below the surface in water 35 fathoms deep. A midwater trawl towed 10 fathoms below the surface took small numbers of lake herring and a 5-foot nylon-cloth, ⅛-inch-mesh net (usually used for the collection of larval fish) towed at 20 fathoms caught small numbers of lake herring eggs. The eggs undoubtedly were drifting toward the bottom after release from the fish. Additional evidence of pelagic spawning comes from the north shore of Lake Superior where commercial gill nets floated 7 fathoms below the surface in 80 fathoms of water take large numbers of spawning lake herring.

These findings do not prove that lake herring are exclusively pelagic spawners. Most of the commercial production from the south shore of the lake comes from nets set on the bottom. The fish move to the bottom sometime during the night; spawning may continue there.

Evidence from Lake Superior supports earlier findings that spawning lake herring show no preference for a particular bottom type.

FECUNDITY

Fecundity studies of lake herring by earlier authors demonstrated that the number of eggs varied widely according to stock and individuals within a stock. Smith's (1956) detailed account of these findings revealed, in general, that the number of eggs tended to increase with length and weight of the female, but the number of eggs per ounce of body weight decreased with increase in length. The average diameters of eggs from Green Bay lake herring showed no change with increase in length of the female, and the egg diameter and the total number of eggs per individual fish were not correlated.

The fecundity of Lake Superior lake herring was investigated from 30 fully ripe females collected in 1950–54 at Marquette and Portage Entry. The formalin-preserved ovaries were broken up thoroughly and the connective tissue removed. The eggs were then set aside to dry at room temperature for 24 hours or until all signs of moisture had disappeared. A sample of 500 eggs was removed and weighed to the nearest 0.0001 g., and the total number of eggs was computed from their total weight (determined to the nearest 0.0001 g.) and the sample weight.

The dependability of this method was tested by making 14 estimates from 500-egg samples ot one pair of ovaries for which an actual count was made. The actual number of eggs counted was 7,523, and the estimates ranged from 7,407 to 7,609. The extreme percentage errors were −1.54 and 1.14. The mean of the absolute values of the percentage errors was 0.63.

The fecundity data for Lake Superior lake herring exhibited identical trends to those described by earlier investigators. The number of eggs tended to increase with fish length, and the number of eggs per ounce of body weight to decrease with increase in length (table 39). The average number of eggs ranged from 4,314 for fish in the 10.6- to 10.8-inch size group to 10,250 for a 14.0-inch fish. The average for the entire sample was 6,351 eggs. The average number of eggs per ounce of body weight ranged from 1,006 for fish in the 10.9- to 11.1-inch size group to 746 for those in the 12.4- to 12.6-inch group. The average number of eggs per ounce of fish for the entire sample was 842.

Comparable data from Lake Superior and Green Bay (Smith, 1956) reveal that the Lake Superior lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight (table 40). The production of eggs from individual Green Bay lake herring was larger for each length interval for which comparable data were available (exception at 11.5 to 11.7 inches). The number of eggs per ounce of fish was also higher for Green Bay lake herring in 4 of 6 comparisons. The unweighted means for each sample showed that Green Bay lake herring produced over 1,000 more eggs per individual fish and nearly 100 more eggs per ounce of fish.

The egg diameters of Lake Superior lake herring were measured for only one 11.4-inch female.

TABLE 39.—*Relation between the length of Lake Superior lake herring and the total number of eggs and the number per ounce of weight*

[Number of fish in parentheses]

Total length	Number of eggs per fish		Average number of eggs per ounce of fish
	Average	Range	
(Inches)			
10.6–10.8	4,314 (2)	3,834–4,794	828
10.9–11.1	5,802 (4)	3,728–9,417	1,006
11.2–11.4	5,354 (4)	4,515–6,922	896
11.5–11.7	6,719 (7)	4,712–8,579	978
11.8–12.0	5,425 (4)	4,735–5,912	787
12.1–12.3	6,075 (3)	5,310–7,514	792
12.4–12.6	5,495 (2)	5,305–5,684	746
12.7–12.9	7,726 (3)	6,970–8,685	793
13.9–14.1	10,250 (1)	------------	754
All lengths	6,351 (30)	3,728–10,250 ------------	842 (30)

TABLE 40.—*Number of eggs per fish and per ounce of weight produced by lake herring of Green Bay (Lake Michigan), and Lake Superior*

[The data for Green Bay are from Smith (1956). Number of fish in parentheses]

Total length	Average number of eggs per fish		Average number of eggs per ounce of fish	
	Green Bay	Lake Superior	Green Bay	Lake Superior
(Inches)				
10.6–10.8	6,662 (15)	4,314 (2)	1,156 (16)	828 (2)
10.9–11.1	6,079 (16)	5,802 (4)	976 (15)	1,006 (4)
11.2–11.4	5,790 (14)	5,354 (4)	918 (11)	896 (4)
11.5–11.7	6,140 (11)	6,719 (7)	851 (9)	978) (4)
11.8–12.0	7,663 (4)	5,425 (4)	986 (3)	787 (4)
12.1–12.3	8,109 (1)	6,075 (3)	977 (1)	972 (3)
All lengths [1]	6,741	5,615	977	881

[1] Unweighted means.

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The mean diameter of 48 eggs was 1.88 mm., exactly that found by Smith (1956) from 20 specimens taken in November in Green Bay.

FOOD HABITS

Stomach contents were examined from 146 lake herring collected on various dates in 1950–60 at Bayfield, Wis., and Marquette, Mich. (table 41).

Crustacea, found in 83 percent of the stomachs examined were by far the most common food of lake herring. Copepods (*Diaptomus*, *Epischura*, and *Limnocalanus*) were found in all of the stomachs of small lake herring (5.6–6.4 inches) in the May sample, in 93 percent of the stomachs of the June–July and September–October collections, and in 66 percent of the stomachs of the December sample. The total frequency of occurrence for copepods was 71 percent. Cladocera (*Daphnia*) ranked second (36 percent), and Mysidacea (*Mysis relicta*), important only in the December sample, were in 19 percent of the total stomachs examined.

Insects were not found in the May or December collections but were in 61 percent of the June–July samples and in 23 percent of the September–October collections. Of the insects that were positively identified, Formicidae and Diptera were most common.

Fish eggs (lake herring) were found in 62 percent of the stomachs in the December sample. Although the lake herring is known to prey on its own eggs, a question arises as to whether lake herring eggs are a preferred food or if they are eaten incidentally with plankton. Since the major foods of the lake herring are pelagic, the eggs may simply be eaten as they drift toward the bottom after being released by pelagic spawners. Some eggs could, of course, have been taken from the bottom. The consumption of fingernail clams and water mites, though rare, gives evidence of occasional bottom feeding.

The common food found in the lake herring stomachs during various seasons of the year gives strong support to the belief that the lake herring is primarily pelagic.

TABLE 41.—*Food in stomachs of Lake Superior lake herring collected at Bayfield and Marquette, 1950–60*

Item	Percentage occurrence in seasonal samples				All dates
	May 3, 1960	June 6–July 30, 1959	Sept. 17, 1958 Sept. 30–Oct. 2, 1959	Dec. 5, 1950	
Number of stomachs	5	43	43	55	146
Length of fish [1]	5.6–6.4	4.3–13.0	5.3–16.5	11.0–12.9	5.6–16.5
Food item:					
Crustacea (total)	100	93	93	66	83
Copepoda	100	84	58	10	71
Cladocera		44	74	2	36
Mysidacea		9	5	40	19
Amphipoda				2	2
Unidentified remains		12	19	33	21
Insecta (total)		61	23		25
Formicidae		7			2
Diptera		7	5		4
Lepidoptera		2			1
Homoptera		2			1
Hymenoptera [2]		2			1
Hemiptera		2			1
Thysanoptera		2			
Unidentified remains		33	19		15
Pelecypoda			2		1
Rotatoria		2	2	6	3
Hydracarina			2	2	1
Fish remains				2	1
Fish eggs				62	23
Chlorophyta	40	72		4	24
Diatoms		35	7		12
Unidentified debris		7	12	35	19

[1] Total length, inches.
[2] Exclusive of the ants.

DISTRIBUTION

The seasonal distribution of the lake herring has been a subject of considerable speculation among fishermen as well as researchers. That the fish disappear in Lake Superior during the summer cannot be disputed. Prior to 1960 the only summer fishery for lake herring on the lake existed along the north shore and at Isle Royale where floated nets yielded small catches. A small summer lake herring fishery developed in 1960–62 at Marquette where bottom nets set at about 20 fathoms produced some good catches.

Koelz (1929) caught only a few stragglers in his experimental nets at depths of 10 to 100 fathoms during the summer in Lake Superior and reported that fishermen believed they had seen schools of lake herring near the surface in the open lake at that season.

In the course of the 1958–61 studies of fish populations in western Lake Superior by the research vessel *Siscowet*, special cruises collected information on the seasonal changes in the areal and depth distribution of the lake herring. Experimental fishing was carried out in several locations among the Apostle Islands with standard gill nets (300 feet each of 2- to 2¾-inch mesh), bull nets (gill nets 300 feet long, 100 meshes deep, with mesh sizes of 2⅜ and 2½ inches), and bottom and midwater trawls. The bottom trawls were a semiballoon type with a 31-foot headrope, 2½-

TABLE 42.—*Number of lake herring caught per 1,000 linear feet of 2- to 2¾-inch-mesh gill nets set on the bottom at various depths in western Lake Superior, 1958–61*

[Number of lifts in parentheses]

Time period and item	Depth of water (fathoms)								
	<10	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89
April 27–June 30									
Number of fish	5 (3)	8 (11)	12 (21)	11 (6)	0 (2)	4 (15)	2 (4)	0 (4)	3 (4)
July 1–Sept. 13									
Number of fish	0 (2)	8 (22)	10 (21)	1 (5)	3 (14)	3 (6)	7 (1)	-----	2 (2)
Sept. 14–Oct. 14									
Number of fish	13 (3)	35 (16)	4 (18)	2 (3)	0 (4)	0 (1)	0 (2)	7 (2)	-----
Oct. 15–Nov. 15									
Number of fish	85 (22)	0 (2)	4 (3)	23 (1)	-----	19 (4)	-----	-----	-----
Nov. 16–Dec. 20									
Number of fish	287 (7)	330 (2)	42 (3)	98 (3)	201 (2)	284 (7)	280 (3)	-----	66 (4)

inch-mesh body, and ½-inch-mesh cod end. The midwater trawl was converted from a bottom trawl to full-balloon type and was equipped with trawl plane floats. The standard gill nets were fished on the bottom at depths of 2 to 89 fathoms, and the bull nets were floated at different depths below the surface or set obliquely from the surface to the bottom. The floating and "oblique" nets were suspended at the desired distance below the surface from a series of floats. A limited amount of drift-netting (nets attached to unanchored boat, allowed to drift freely) was carried out in various parts of the open lake but few lake herring were captured. The bottom trawls were fished at 5 to 60 fathoms, and the midwater trawl was employed when pelagic schools of fish were observed on the sensitive echo-sounder aboard the vessel. The data gained from this experimental fishing failed by far to bring out clearly the movements and distribution of the lake herring, but they did add materially to the hitherto negligible information on the subject.

Some explanations are required to permit an instructive account of the depth distribution of lake herring in Lake Superior from the records of tables 42 and 43. The time covered may be subdivided according to seasonal thermal conditions and the spawning season. Prior to July 1, the water of western Lake Superior was generally homothermous although surface temperatures occasionally reached 50° F. in late June. The surface water began to warm fairly rapidly in early July, and a pronounced thermocline soon developed. This condition persisted until about mid-September when the early fall storms mixed the water and the depth of the epilimnion increased to 80–100 feet. By mid-November (the beginning of the spawning season) the water was again almost homothermous at temperatures of about 43° F.

The depths listed in table 42 are the depths of water in fathoms where the nets were set; the nets fished 1 fathom of water immediately above the bottom. In table 43, the listed depths show the range and mean (in fathoms) that the bull nets were fished below the surface. The change of catch with the depth the nets were fished below the surface did not vary with the maximum depth of the water.

The catch of lake herring from gill nets set on the bottom was small at all depths and periods except during the spawning season (table 42). During April 27–June 30, the largest catch was only 12 fish per 1,000 linear feet (taken at 20–29 fathoms). At no depths below 39 fathoms did the catch exceed four fish. Between July 1 and

TABLE 43.—*Number of lake herring caught per 1,000 linear feet of 2⅜- and 2½-inch-mesh bull nets fished at various depths below the surface in western Lake Superior, 1958–60*

[Number of lifts in parentheses. Temperatures ° F.]

Time period and item	Depth of water fished (fathoms)—range and mean (in parentheses)								
	<6.5 (3.3)	3.3–9.8 (6.6)	6.7–13.2 (10.0)	10.0–16.5 (13.3)	13.3–19.8 (16.6)	16.7–23.2 (20.0)	20.0–26.5 (23.3)	23.3–29.8 (26.6)	26.7–33.2 (30.0)
May 17–June 30:									
Number of fish	51	29	20	-----	-----	-----	-----	-----	-----
Average temperature	46°	42°	39°	-----	-----	-----	-----	-----	-----
	(4)	(4)	(1)	-----	-----	-----	-----	-----	-----
July 1–Sept. 13:									
Number of fish	19	27	25	23	7	2	4	4	0
Average temperature	67°	56°	45°	42°	41°	39°	39°	39°	39°
	(13)	(9)	(7)	(7)	(5)	(4)	(6)	(4)	(3)
Sept. 14–Oct. 5:									
Number of fish	140	127	133	110	104	50	12	17	2
Average temperature	55°	55°	55°	52°	47°	45°	44°	42°	44°
	(6)	(13)	(8)	(9)	(9)	(6)	(6)	(4)	(3)

September 13, few lake herring were captured, all at depths below 10 fathoms. The data suggest a widely scattered distribution between 10 and 69 fathoms during this period. In the early fall (September 14–October 14), most of the lake herring were taken in the 10- to 19-fathom stratum; they disappeared almost entirely at depths below 39 fathoms (exception was the catch of 7 fish per 1,000 linear feet of net at 70–79 fathoms). The prespawning fish began to concentrate on shallow reefs in October 15–November 15. Small-mesh gill nets set on the lake trout spawning reefs (3 to 6 fathoms) during mid-October often caught large numbers of lake herring which were nearly ripe. The period November 16–December 20 (which includes the lake herring spawning season) yielded relatively large numbers of lake herring at all depths. (The small numbers of fish taken at 20–39 fathoms is misleading because these sets were made for another species on grounds not frequented by lake herring.)

Water temperatures on the bottom were relatively low during all seasons. The highest temperature (53.5° F.) was recorded at 15 fathoms on September 30, and the lowest (34.9° F.) was at 24 fathoms on December 13.

Because the small catches of lake herring in the bottom nets suggest a pelagic life for the species, a better description of their depth distribution should be obtained from the records of catches from floating and "oblique" sets of bull nets (table 43). During May 17–June 30, the lake herring were most abundant (51 per 1,000 linear feet) at depths less than 7 fathoms. The catch of 29 fish at 3–10 fathoms and 20 fish at 7–13 fathoms suggested a decrease in abundance with an increase in depth. The average water temperature during this period ranged from 46° F. at 3 fathoms to 39° F. at 10 fathoms. No sets were made below 13 fathoms during the period. From July 1 to September 13 the largest numbers of lake herring were caught at 3–17 fathoms. The decrease in the number of fish between the surface and 7 fathoms may be the result of relatively high water temperatures in the surface layers (67° F.). Good catches of lake herring were rare in water warmer than 60° F. Lake herring were scarce below 17 fathoms. Since the lake herring are principally plankton feeders during the summer and the heaviest concentration of plankton occurs in the upper water levels, their depth distribution may be determined by the abundance of food at various depths. On July 9, 1959, the *Siscowet* collected several plankton samples with a series of Clarke-Bumpus plankton samplers towed at 2, 7, and 20 fathoms below the surface. The concentration of plankton at 2 fathoms was extremely heavy; it was much lighter at 7 fathoms, and at 20 fathoms practically no plankters were captured.

The best catches in the bull nets were made during September 14–October 5. At this time the fish were abundant at depths to 20 fathoms (140 fish per 1,000 linear feet at 0–7 fathoms to 104 fish at 13–20 fathoms). The increase in the catch in the shallowest water followed a decrease in average water temperature to 55° F. The fish at this time apparently were moving toward the inshore areas prior to the late-fall spawning.

The catch of lake herring in bottom trawls was practically nil regardless of season, depth, or temperature of water. The midwater trawl towed 10 fathoms below the surface at night during the spawning season took only small numbers of lake herring.

The data from the catches of bottom nets and bull nets suggest that the vertical distribution of the lake herring may be influenced by temperature, abundance of plankton, and spawning. Very little is known of the horizontal movements of the species, although the available evidence indicates a random areal distribution in the inshore areas during April–June, a wide scattering during the summer (possibly small scattered schools in the open lake), an inshore movement in early fall when the fish begin to form larger schools in advance of spawning, and finally, the spawning season when they can be caught at widely varied depths and locations. Our recorded catches were affected, to be sure, by changes in activity as well as numbers. Heightened activity was probably an important factor in the fall catches, especially in the spawning season.

SUMMARY

1. The lake herring has been the principal species in the commercial production of Lake Superior since 1908. The 1929–61 average annual catch in U.S. waters was nearly 12 million pounds, 62.4 percent of the total U.S. production of lake herring for the Great Lakes. Minnesota dominated the catch in 1929–40, Wisconsin held the

lead in 1941–56 (exception in 1942), and Michigan had the largest catch in 1942 and 1957–61.

2. Small-mesh gill nets (2¼- to 2⅞-inch mesh) are the principal gear for catching lake herring in Lake Superior. On the average, about 90 percent of the annual production is landed during the spawning season in November and December.

3. Although recent production of lake herring in U.S. waters is not significantly below the 1929–61 mean, evidence exists that abundance has declined in certain areas of the lake. The decline from 1950–55 to 1956–61 in numbers of fish caught per unit effort of fishing was 31 percent at Bayfield and Portage Entry, and 27 percent at Marquette.

4. The life-history studies were based on 12,187 lake herring collected from commercial and experimental gill nets fished at various locations in Lake Superior in 1950–62. Individual growth histories were computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., during the fall spawning seasons of 1950–59. Growth was computed from scale measurements by direct proportion. Fish used in other phases of the study came from experimental gill nets and from the summer commercial lake herring fishery.

5. Some fish had begun new growth by May 3, although annulus formation was not complete until mid-August. Over 90 percent of the season's growth was complete by the end of September.

6. The age composition and mean age of the commercial samples varied moderately by year of capture and port. Age group IV dominated the catch each year at each port and contributed 53.2 percent of the total, followed by age group III (24.8 percent) and age group V (18.4 percent). The remaining age groups (II, VI, and VII) combined, contributed only 3.6 percent. The mean age of all the years' collections was 3.9 at Bayfield, Portage Entry, and Marquette, and 4.1 at Duluth. With few exceptions the average age of the females exceeded that of the males. The differences between the mean ages of the sexes did not exceed 0.5 year.

7. Although estimates of year-class strength were affected by several sources of bias, a ranking was nevertheless made on the basis of the number of fish of various ages taken per unit effort of fishing. The strength of the year classes declined irregularly at all of the ports during the period (1946–55) for which data were available. The values (given as percentage deviations from the mean) ranged from 55.9 in 1947 to −44.0 in 1954 at Bayfield, from 55.7 in 1950 to −40.8 in 1955 at Portage Entry, and from 40.7 in 1947 to −33.7 in 1952 at Marquette. Fluctuations of year-class strength were similar at Marquette and Bayfield. Only the 1947 and 1950 year classes showed better than average strength at each port. Year classes 1954 and 1955 were weak at all ports.

8. The average total length of the females of an age group at capture was longer than that of the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held a slight advantage (7 of 10 comparisons) at Marquette.

9. With only one exception (that of the VI-group males in the 1956–59 Bayfield samples), the average length of the age groups was larger in 1956–59 than in 1950–55. The increase in average length from the early to the late period ranged from 0.4 inch for the V-group males at Bayfield to 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

10. The length distributions of the age groups typically had small ranges and extensive overlap. The length range of the age groups in the 1957 Marquette sample, for example, were as small as 1.9 inches (age group II) and did not exceed 3.9 inches (VI-group fish). The length interval of 12.0–13.4 inches was represented by all five age groups.

11. The relation between the total length in inches (L) and the weight in ounces (W) of Lake Superior lake herring from all of the collections, was described by the equation, $\log W = -2.54688 + 3.17008 \log L$.

12. The weights of lake herring of corresponding lengths were heavier in 1956–61 than in 1950–55. The average percentage increase in weight, length for length, was 8.8 percent at Bayfield, 5.2 percent at Marquette, and 4.4 percent at Portage Entry. Port-to-port differences in average weight among fish of the same length in 1950–55 showed a west-to-east trend toward increased weight. In 1956–61 the Marquette lake herring were generally heaviest, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small.

13. The growth rate of Lake Superior lake herring varied according to port and period of capture. The fish from Duluth in 1956–59 were the slowest growing, followed in rank by those from Bayfield, Portage Entry, and Marquette. With only one exception (that of first-year calculated lengths of the Portage Entry fish), the calculated lengths of lake herring taken in 1956–59 were greater than those of fish taken in 1950–55. Lake herring caught in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life. Growth in length was greatest during the first year of life in both collecting periods (from 4.3 inches at Duluth to 5.0 inches at Marquette in 1956–59). With few exceptions, the annual increments of growth in length decreased progressively until the fifth year of life, after which the increments were 1.0 inch or less.

14. Growth in weight also increased from the western to eastern ports and from the early to late collecting period. The first-year calculated increments were small (less than 0.7 ounce) in both collecting periods. The increments increased progressively to a maximum in the fourth year of life at all ports except Bayfield and Marquette in 1956–59, where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956–59.

15. The trends of annual fluctuations in growth in length were similar at the three ports. In general, growth was below average in 1945–53 and above average in 1954–59. The quality of growth for all years of life expressed as percentage deviation from the 1945–59 mean, ranged from a low of −23.5 at Bayfield in 1946 to a maximum of 16.3 at Bayfield in 1959.

16. The annual fluctuations of growth in weight were similar to those of growth in length. Growth in weight was below average at Bayfield in 1945–50, at Portage Entry in 1945–54, and at Marquette in 1945–52. Growth was above average at all of the ports after 1954.

17. No correlation could be established between fluctuations of growth and changes in temperature or the abundance of lake herring.

18. The number of females equalled or exceeded that of the males in each age group except I (only 1 fish) from the nonspawning-run samples. The advantage of the females progressively increased from 52.3 percent for age group III to 81.8 percent for group VII. The percentage of females was 68.5 for all age groups combined.

19. The youngest mature lake herring in Lake Superior belonged to age group II, and all fish older than III were mature. The shortest mature male appeared in the 8.5- to 8.9-inch group, and all males were mature at lengths greater than 11.4 inches. The first mature females appeared at 9.5–9.9 inches, and all were mature at lengths greater than 11.9 inches.

20. Major spawning of Lake Superior lake herring normally takes place during the last week of November and the first week of December. Water temperature at this time usually is between 37° F. and 40° F. The fish are pelagic spawners; the eggs are broadcast and settle to the bottom at depths ranging from 20 to 80 fathoms. The spawning fish show no preference for a particular bottom type.

21. The number of eggs produced by female lake herring (range 4,314 to 10,250) tended to increase with fish length, and the number of eggs per ounce of body weight decreased with increase in length. Lake Superior lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight than do lake herring from Green Bay, Lake Michigan.

22. Crustacea were by far the most common food and were found in 83 percent of 146 stomachs examined from Lake Superior lake herring. Other food included insects and fish eggs (presumably those of lake herring).

23. The vertical distribution of the lake herring may be influenced by temperature, abundance of plankton, and spawning. During the early summer, the fish are most common near the surface where plankton is most abundant. As the surface water warms in midsummer, the lake herring move to deeper levels, despite the high concentration of plankton near the surface. After September 13, they were randomly distributed from the surface to about 20 fathoms, and during the spawning season, they were captured in good numbers at all depths down to 90 fathoms.

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