LIFE HISTORY, TROPHIC RELATIONSHIPS, AND BATHYMETRIC DISTRIBUTION AND MOVEMENT OF AMERICAN SMELT, OSMERUS MORDAX (MITCHILL), IN GULL LAKE, KALAMAZOO AND BARRY COUNTIES, MICHIGAN

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ABSTRACT

LIFE HISTORY, TROPHIC RELATIONSHIPS, AND BATHYMETRIC DISTRIBUTION AND MOVEMENT OF AMERICAN SMELT, OSMERUS MORDAX (MITCHILL), IN GULL LAKE, KALAMAZOO AND BARRY COUNTIES, MICHIGAN

by Richard Greig Burbidge

American smelt represent a fishery of considerable importance but like many prolific species, they have flourished and are sometimes a problem. Ecological relationships of smelt are a source of controversy. Smelt are taken commercially only during short seasonal periods in fluctuating amounts. More must be known of life history, trophic relationships, and bathymetric distribution and movement before smelt can be effectively controlled and utilized.

The study of the natural history of smelt in Gull Lake was based on data from 286 smelt collected with gill nets, an Isaacs-Kidd midwater trawl, and hook and line, from December 1965 to November 1966. Physical measurements (length, weight, sex, age) were taken, and stomachs were analyzed. Echo recordings of fish distribution were obtained with a Furuno F-850-A (200 kc/sec) Fish Finder, from October to December 1966. The number and position of fish traces in each transect were recorded to demonstrate vertical and horizontal movement. Temperature and dissolved oxygen profiles were determined.

Gull Lake smelt were shown to be one genetic race; their growth was rapid, but mature individuals were smaller than smelt in other environments. Growth of young fish was comparable. A high natural mortality in the fourth year was indicated. There was a predominance of females at all ages, and females were larger than males.

Richard Greig Burbidge

Smelt in Gull Lake ate the most available food, but apparently had a preference for dipteran larvae. A change from night to daylight feeding, accompanied by a change to filter feeding, was indicated as larger dipteran larvae declined. Only a few fish were noted in stomachs of smelt. Evidence that smelt are prey of larger game fish was established.

Smelt were restricted to the colder hypolimnion in summer; in colder months they were distributed at all depths. Diel vertical and horizontal movements of the smelt population were demonstrated.

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By

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Introduction

The smelts (Osmeridae) comprise a group of anadromous fish of wide geographical distribution in northern latitudes. Their recorded distribution includes both North Atlantic, North Pacific, and Arctic coasts, forming an irregular, interrupted, distributional belt that encircles the Northern Hemisphere (Kendall, 1927).

The American smelt, Osmerus mordax (Mitchill), is found along the Atlantic coast of the United States from the Raritan River (40° 30') to the Gulf of St. Lawrence. They are abundant along northern shores of New Brunswick, and are found in many fresh-water lakes of Maine, New Brunswick, and Nova Scotia, where they have become landlocked (Goode, 1884).

The first shipment of smelt to the Great Lakes was in 1906, when eggs from New England were deposited in the St. Mary's River, Mich. (Van Oosten, 1937). This introduction was not successful for the species was never taken in that region. In 1912, 16 million eggs from Green Lake, Maine, were deposited in Crystal Lake, Mich.; success became apparent when large breeding runs were observed in 1919 (Creaser, 1926).

Smelt were first captured in Lake Michigan in 1923 (Van Oosten, 1937) and their ensuing dispersal and establishment in the Great Lakes recorded (Hankinson and Hubbs, 1922; Creaser, 1925; Savage, 1935; Van Oosten, 1937; Clarke, 1944; and Dymond, 1944). It is certain that the Crystal Lake population was the only source of smelt now present in Michigan and all the Great Lakes except Ontario, where the species has been present since historical time (Van Oosten, 1953).

Smelt have flourished in spite of a heavy mortality in 1942-43 which caused an estimated loss of 50 million lb. (Van Oosten, 1947).

Great Lakes commercial smelt production was 16 million lb. in 1960 (Baldwin and Saalfeld, 1962). Smelt are taken with pound, gill, and fyke nets, principally during the winter; most fishing is done in Green Bay (Van Oosten, 1953; Swanson, 1955). Canadian fishermen have successfully used trawls to harvest Lake Erie smelt (Ferguson and Regier, 1963).

Great Lakes smelt normally spawn at night in accessible streams during April and May at the beginning of their third growing season (Stevenson, 1944; Baldwin, 1950; Van Oosten, 1953). Sportsmen employ dip nets to harvest a quantity of smelt estimated to be greater than commercial catches (Schneberger, 1937).

Smelt have been a source of controversy since their establishment in fresh water. They are an item of considerable importance to commercial fishermen and sportsmen, but like many prolific species in a favorable new habitat they have flourished. In some areas smelt have become a menace to commercial fishermen (Schneberger, 1937). Knowledge of their life history may make effective control possible.

Smelt are considered important because of their varied ecological relationships with game species (Rupp, 1959). At this time these relationships are not certain. Extreme levels of abundance make it necessary to understand their role as predators, competitors, and prey (Gordon, 1961).

The species is abundant in certain ares of the Great Lakes, but cannot be taken in quantity except during short seasonal periods. Knowledge of their movements and distribution must be extended if the smelt fishery is to be profitable (Carr, 1964).

The present investigation of smelt in Gull Lake was undertaken to contribute to a description of the species and enhance the knowledge of its ecology. Information on the natural history of smelt may afford a better understanding of their economic potential, and their present and future biological and ecological role.

A total of 25,000 adult smelt from the Oden State Fish Hatchery were introduced in Gull Lake, Kalamazoo and Barry Counties, Mich., from 1950 to 1953 (Plainwell office of the Michigan Conservation Department, unpublished records). The first heavy spawning run was observed in 1956 in Prairieville Township Park Creek. Establishment has been successful except for a moderate mortality in 1962, and a heavy mortality due to a pathogenic bacteria in 1965.

Gull Lake smelt spawn at night in April in Prairieville Township Park Creek, Little Long Lake Creek, and along the shore between these streams at the beginning of their third growing season. Spawning smelt are protected so there is no dip netting. Sportsmen fish for smelt by hook and line in the winter.

Gull Lake is among the larger and deeper lakes of Michigan (Taube and Bacon, 1952). The basin is of glacial origin, formed probably during the last ice invasion. Surface area is 8.2 km^2; maximum depth is 33 m. The drainage is relatively small; inlets from Miller and Little Long Lakes, springs, and several other streams contribute to the water supply. A dam at Gull Lake Outlet controls the outflow of water to the Kalamazoo River. Sand, gravel, and rubble are the principal shoal bottom types. Marl, muck, and pulpy peat are found in deeper areas. A mixture of marl and pulpy peat is predominant.

Gull is an alkaline dimictic lake that thermally stratifies in summer (Hutchinson and Löffler, 1956). Water appears green due to fine particles of marl in suspension, and the penetration and back-scattering of predominantly green and blue light.

Gull Lake is well supplied with vegetation; at least 24 species of vascular plants have been recorded (specimens available in the Kellogg Biological station herbarium collection).

A wide variety of fish is present in Gull Lake (manuscript in preparation, C. W. Huver). The most common forage fish are the brook silversides (Labidesthes sicculus), logperch (Percina caprodes), and bluntnose minnow (Pimephales notatus). The white sucker (Catostomus commersoni), yellow bullhead (Ictalurus natalis), and longnose gar (Lepisosteus osseus) are common. Game fish include the smallmouth bass (Micropterus dolomieui), largemouth bass (Micropterus salmoides), green sunfish (Lepomis cyanellus), bluegill (Lepomis macrochirus), rock bass (Ambloplites rupestris), yellow perch (Perca flavescens), cisco (Coregonus artedii), rainbow trout (Salmo gairdneri), and lake trout (Salvelinus namaycush). Rainbow trout have been stocked annually since 1942, lake trout since 1943. Fishing pressure is moderate.

Emphasis is placed on rainbow trout, lake trout, and smelt. Ciscos, also cold-water fish, are native to the lake. Smallmouth and largemouth bass, bluegills, and yellow perch are the most important warm-water species.

A study would be incomplete without a consideration of life history, trophic relationships, and bathymetric distribution and movement. There is a distinct relation between these three aspects; a discussion of one phase would be impossible without incorporating the others.

Literature Review

Life History

Aspects of smelt life history are covered in the literature. Much has been based on samples collected during spawning runs, or within a restricted period, or that were too small. The nature and composition of a smelt population must be studied over a period of time if the fish is to be effectively controlled and utilised. Kendall (1927) summarized most early information on smelt life history and included studies on both marine and landlocked smelt.

The Fisheries Research Board of Canada initiated an investigation of smelt in the Miramichi River and Bay, New Brunswick. Various phases of this study were reported (McKenzie, 1943, 1944, 1946, 1947, 1948, 1956, 1958, 1964). Coastal smelt in Great Bay, New Hamp., were studied by Warfel, Frost, and Jones (1943).

New England smelt have been studied in lakes of New York (Greene, 1930; Zilliox and Youngs, 1958), New Hampshire (Hoover, 1936), and Maine (Rupp, 1959; Rupp and Redmond, 1966).

Smelt in Crystal Lake, Mich., were investigated by Creaser (1926) and Beckman (1942). Studies were conducted on Great Lakes smelt in Lake Michigan (Creaser, 1929a; Schneberger, 1937; Baten and Tack, 1952), Lake Huron (Baldwin, 1950), and Lake Superior (Bailey, 1964).

The present study is concerned with the length distribution, percent age composition, mean length and weight, length-weight relationship, sex ratio, and sexual dimorphism of smelt collected in Gull Lake over a 1 year period. The spawning phenomenon was not investigated in Gull Lake, but accounts are available (Creaser, 1926; Kendall, 1927; Greene, 1930; Schneberger, 1937; Hoover, 1936; Stevenson, 1944;

McKenzie, 1944, 1947, 1964; Baldwin, 1950; Van Oosten, 1953; Lievense, 1954; Rupp, 1959, 1965; Rothschild, 1961).

Trophic Relationships

Trophic relationships in lakes in which smelt were introduced has been a source of dispute, arising from variations in reports of the food and feeding habits of smelt. These can be attributed to small samples collected in one season, incorrect interpretation of results, and differences in habitat and size of fish. Smelt are often introduced as food for game fish, but many believe they reduce the number of game fish fry. Some fear smelt as competitors for the food of game fish.

Concern for the role of smelt began with Creaser (1926, 1929a, 1929b), who examined smelt from Lake Michigan and several Michigan lakes and found them feeding on crustaceans, insects, emerald shiners (Notropis atherinoides), and smelt and yellow perch fry. He concluded: "The smelt is...an enemy of all smaller fishes, including the young of the commercial species, as well as a competitor for the food of the adults of the larger species."

Creaser was supported by Doolittle (from Kendall, 1927) and Greene (1930), who observed small smelt in New England lakes feeding on zooplankton, but large individuals feeding primarily on other smelt and insect larvae.

In contrast, other studies in New Hampshire (Hoover, 1936), Green Bay (Schneberger, 1937), Lake Huron (Baldwin, 1950; Gordon, 1961), and Lake Erie (Ferguson, 1965) found smelt seldom eating fish, but feeding primarily on bottom fauna and zooplankton. Van Oosten (1953) summarized: "...nowhere have investigators found such species (game and commercial fish) present in the stomachs of smelt in any significant quantities."

Evidence that smelt are eaten by commercial and game fish was provided by Kendall (1927), Greene (1930), Dymond (1944), Tharratt (1959), and McCaig and Mullan (1960).

It was the purpose of the Gull Lake study to analyze the food and feeding habits of smelt collected over 1 year to determine their position in the nutritional scheme of the lake, and understand their role as competitors, predators, and prey.

Bathymetric Distribution and Movement

Diel bathymetric movements of marine fish have been noted by Hickling (1935), Welsh, Chace and Nunnemacher (1937), Brawn (1960), Johnson (1961), Manzer (1964), and Clarke and Backus (1964). Similar movements have been reported in fresh water for the cisco (Cahn, 1927), and white bass (Roccus chrysops) (McNaught and Hasler, 1961).

Recording echo sounders have been used to find fish and measure their movements. Hodgson (1950) reported on the use of echo sounders for pelagic fishing; Balls (1951), Richardson (1952), and Valdez and Cushing (1966) utilized these instruments to record vertical movements. Cushing (1952, 1954, 1957, 1963) has done much to perfect their use in fish distribution studies. Schaefers and Powell (1958) correlated midwater trawl catches with echo recordings. Clarke and Backus (1956) measured vertical movements of deep scattering layers. Northcote, Lorz and MacLeod (1964) recorded diel movements of fresh-water fish. Gordon and Larsen (1965) published on the application of echo recorders to fishery research.

Most research on smelt distribution has been concerned with locating areas where the fish could be effectively harvested. Sampling was done primarily with bottom nets and trawls so little is known of their bathymetric distribution and movements.

Vertical distribution of smelt has been studied in lakes of New York (Greene, 1930; Odell, 1932; Galligan, 1962) and the Great Lakes (Van Oosten, 1953; Gordon, 1963; Carr, 1962, 1964). That smelt have diel vertical movements was first reported by Kendall (1927), who suggested that they may ascend in the evening to feed. Sand and Gordon (1960) and Ferguson (1965) found a dispersal of Lake Erie smelt to midwater in late afternoon, and a return to bottom in the morning.

Materials and Methods

This study was based on data from 286 smelt collected in Gull Lake from 17 December 1965 to 12 November 1966, and echo recordings obtained from 7 October 1966 to 15 December 1966.

Smelt were collected with a 1/2-inch nylon gill net (100 x 6 ft), 1-inch nylon gill net (70 x 6 ft), 3-ft Isaacs-Kidd midwater trawl, and hook and line. A small otter trawl (3 m) and Gulf III sampler were utilized with no success.

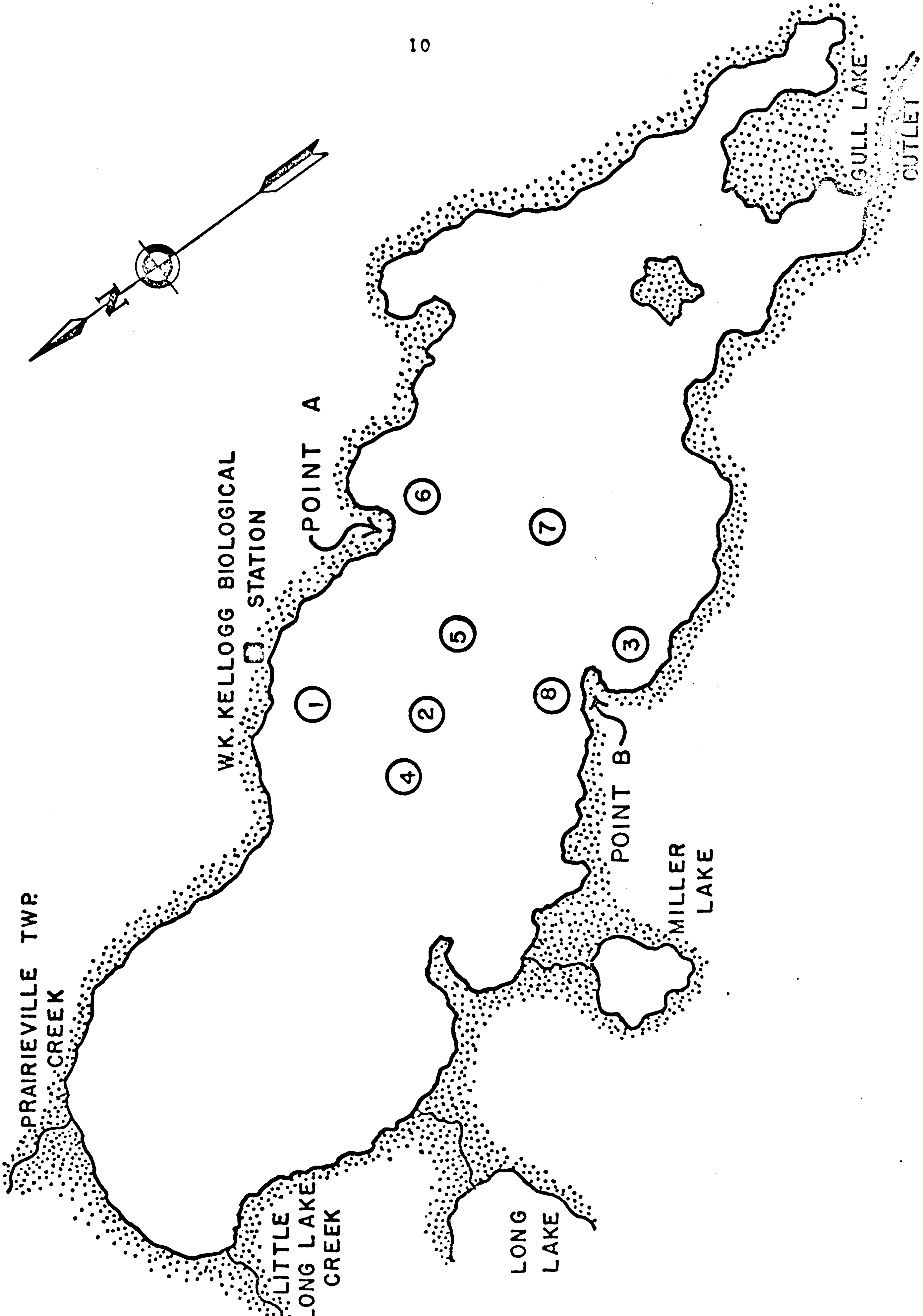
Gill netting operations were initiated in December 1965. The 1/2-inch gill net was fished on the bottom at Stations 1, 2, and 3 (Fig. 1) from December to June. During February it was set at Station 4 directly under the ice, and vertically from surface to bottom.

The 1/2-inch gill net was marked in meters and fished vertically at Station 5 from July to November to detect diel fish movements. The net was attached to two buoys at the surface, and rods were fastened to both ends to keep it open. It was set and recovered primarily at night at 2 and 3 hr intervals. Fish were removed and their depth recorded. The gear was anchored to a permanent buoy to minimize drift.

The 1-inch gill net was fished on bottom at Stations 6 and 7 in August. The Isaacs-Kidd trawl was towed at various depths from September to November. Runs from 10 min to 1 hr were made around Station 5, or from Station 5 to the north end of the lake. One February sample was obtained by fishing through the ice with hook and line at Station 8.

The selectivity of the gear was obvious. The midwater trawl captured age-group 0 or small age-group I smelt, while gill nets captured age-groups I to V. Smelt were not collected in January and

Fig. 1. Gull Lake, Kalamazoo and Barry Counties, Michigan. Station numbers and transect points are indicated.


N
PRAIRIEVILLE TWP.
CREEK
W.K. KELLOGG BIOLOGICAL
STATION
POINT A
1
2
3
4
5
6
7
8
POINT B
MILLER
LAKE
LITTLE
LONG LAKE
CREEK
LONG
LAKE
GULL LAKE
OUTLET

March when the lake was freezing and opening. A June sample was lost due to improper preservation.

Smelt were preserved in 5% formalin and returned to the laboratory for examination. Total length (tip of snout to tip of tail, lobes compressed) and standard length (tip of snout to end of vertebrae) were measured to the nearest millimeter. Weight was determined to the nearest 0.1 g. Sex was determined by gross inspection of the gonads. Sex of age-group 0 fish could not be determined with confidence.

Scales were removed from behind the dorsal fin, examined under a drop of water at 100 X, and aged according to a "shiny line" criterion (McKenzie, 1958; Bailey, 1964). A year of growth was considered to have begun after the April spawning run. Smelt captured in April had completed spawning.

Stomach contents were removed from the lower esophagus to the pyloric sphincter and examined in water under a stereomicroscope. Percent fullness was estimated on the basis that a full stomach was completely distended. Food items were sorted and the percent which each item composed of the entire mass was estimated (Lagler, 1952). Volume was measured with a sedimentation tube graduated to 0.1 ml; winter samples were too small to be measured accurately. Remains included all unidentified digested matter.

Temperature and dissolved oxygen were measured from July to November. Temperature was determined with a Whitney electric resistance thermometer. Water samples were obtained with a Van Dorn water bottle and analyzed for dissolved oxygen by an unmodified Winkler technique. All field work was done from a 27 ft inboard vessel or small boats.

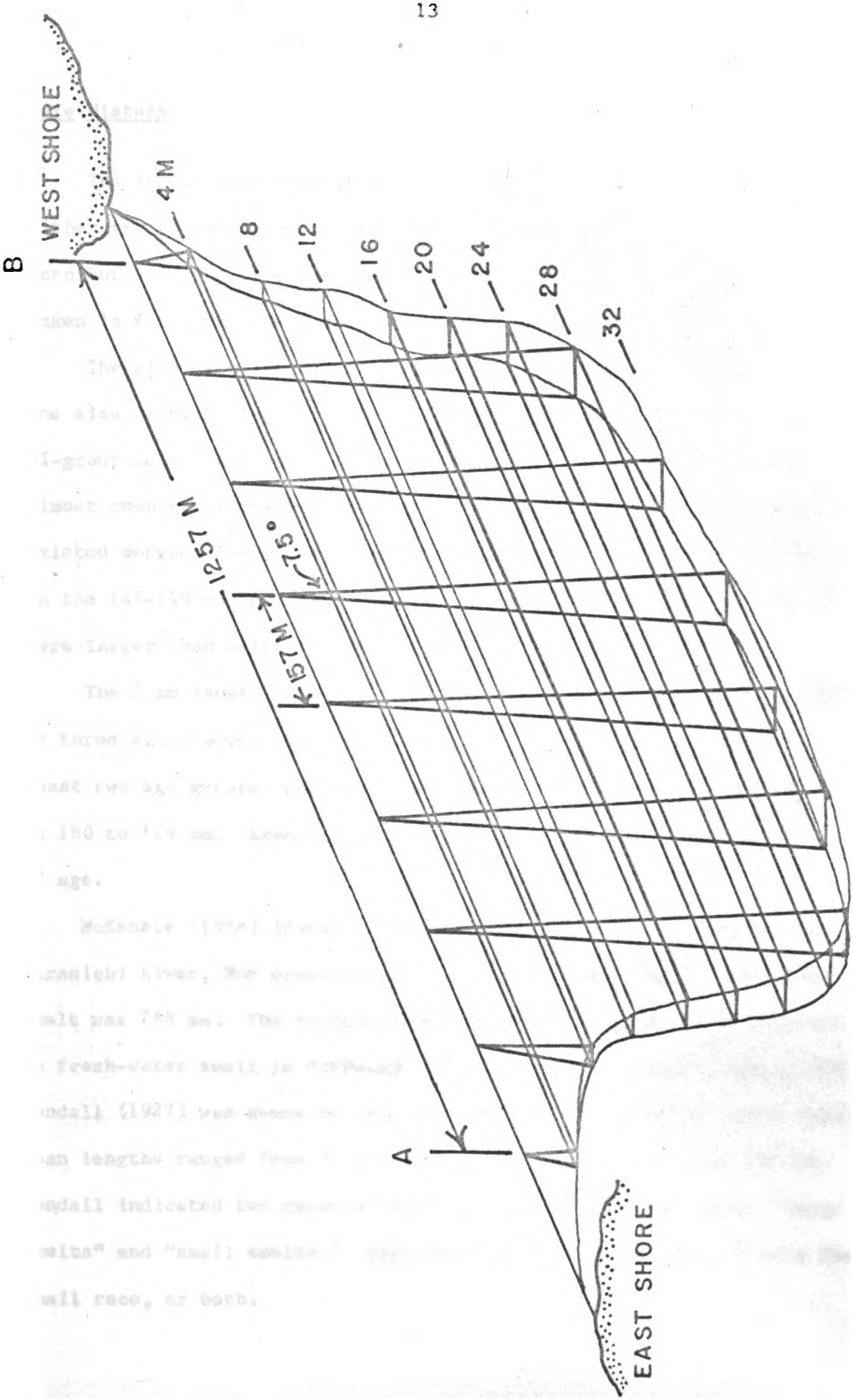
Echo sounding recordings were obtained with a 200 kc/sec Furuno "Triton" Model F-850-A White Line Fish Finder to determine the distribution and movement of fish. The sound wavelength in water (15 C) was 0.7185 cm. Sound pulse frequency was 170/min. Duration of the sound pulse was 0.0015 sec, so the sound pulse length was 2.156. The beam of sound was cone-shaped and symmetrical. The beam angle at half-power point was 5.5° (full-angle); at half-sound pressure it was 7.5° (full-angle) (personal communication, S. Kunitomo, Furuno Electric Company).

Transects were run with the echo sounder between Points A and B (Fig. 1) every hour at various times from October to December; engine speed varied from 500 to 1000 rpm. The instrument was set Gain 4, at a depth range of 0-40 fathoms. At this gain only echoes from fish were received (see Appendix). Individual fish echoes were recorded on dry electrosensitive paper as vertical traces approximately 0.5 mm wide and 3 mm long.

Each recorded transect was divided into eight vertical depth intervals of 4 m, and eight horizontal units of equal length (Fig. 2). The number of fish traces in each quadrat was recorded; the top of each trace was considered as the actual depth of the fish. The approximate volume of each quadrat included within the sound beam was calculated. The number of traces in each quadrat was divided by the volume to give a density of fish per cubic meter. The density in each quadrat was then converted to percent of the total number of fish in the transect.

The depth interval from 0 to 4 m was not included because the artificial surface line was 2 m deep. Further, the 28 to 32 m depth interval was not included because the bottom contour varied considerably. All transects were run in calm weather so the volume of water covered by the sound beam was consistent.

Fig. 2. Diagramatic representation of the Gull Lake sonar transect (Point A to Point B) showing quadrats included within the half-sound pressure beam of sound.


B
WEST SHORE
4 M
8
12
16
20
24
28
32
1257 M
7.5°
157 M
A
EAST SHORE

Results and Discussion

Life History

The length distribution of age-group 0 smelt did not overlap either sex of age-group I (Table 1). The gap between the two was attributed to the time they were collected; age-group 0 smelt were taken in fall, but age-group I fish were not captured until summer.

The size range of age-groups I to IV varied from 69 to 29 mm. The size range of I-group males overlapped the II-group by 39 mm; II-group males overlapped the III-group by 29 mm. Age-group I females almost completely overlapped II-group females. An obvious difference existed between age-group II and III females, except for one individual in the 145-149 mm interval. Females of age-groups I, II, III, and IV were larger than males in these groups.

The 5 mm length range intervals included individuals from as many as three age groups. Each interval from 140 to 199 mm included at least two age groups, and five age groups (I to V) were represented at 180 to 189 mm. Except for age-group 0, length was a poor index of age.

McKenzie (1958) investigated the marine smelt that spawn in the Miramichi River, New Brunswick, and found one size range. The largest smelt was 288 mm. The length distribution and maximum length attained by fresh-water smelt in different lakes is highly variable (Rupp, 1959). Kendall (1927) was aware of this and compared smelt from 21 Maine lakes. Mean lengths ranged from 58 to 305 mm. The largest smelt was 401 mm. Kendall indicated two races of smelt in some New England lakes, "large smelts" and "small smelts." Some have only the large race, or only the small race, or both.

Table 1. Total length distribution of Gull Lake smelt. Sex undetermined for age-group 0. M, male; F, female

Length (mm)	Age-group and sex										
	0	I		II		III		IV		V	
	M F	M	F	M	F	M	F	M	F	M	F
40-44	1										
45-49	1										
50-54	2										
55-59	1										
60-64	1										
65-69	4										
70-74											
75-79	1										
80-84											
85-89											
90-94											
95-99											
100-104											
105-109											
110-114											
115-119			1								
120-124											
125-129		1	1		1						
130-134		3	4	1							
135-139		3	7								
140-144		3	13	2							
145-149		13	12	2	6		1				
150-154		11	8	4	6						
155-159		9	17	8	5						
160-164		3	7	15	13	2					
165-169		1	8	6	11	1					
170-174			2	7	8						
175-179			1	5	6	1					
180-184			1		5			1		1	
185-189				1	2	1	1				
190-194						1	6		1		1
195-199							6	1	1		
200-204							1				
205-209							2		3		
Total	11	47	82	51	63	6	17	2	5	1	1

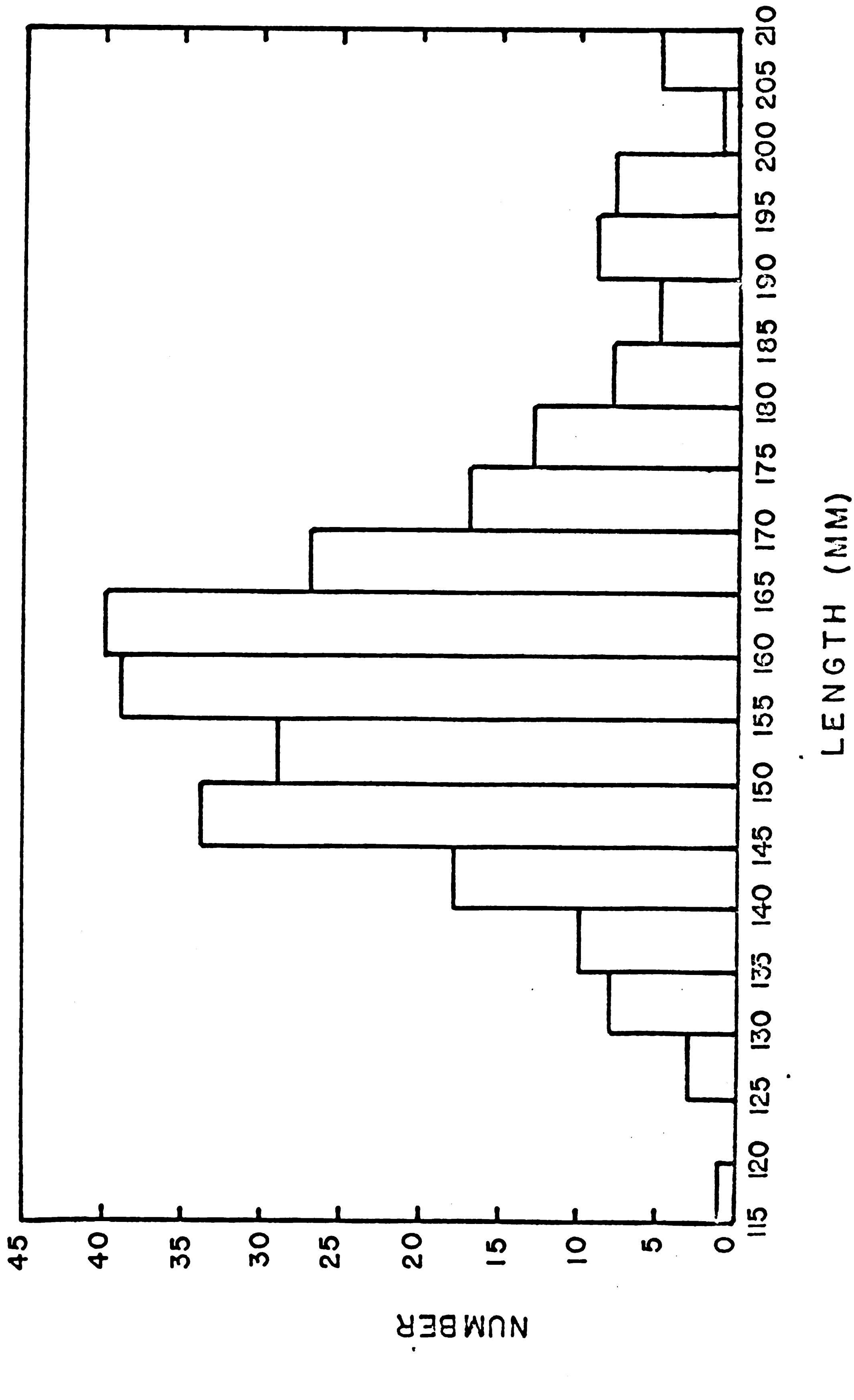
Greene (1930) presented evidence for large and small races in Lake Champlain. He said: "Differing growth rates, sizes at maturity, food selectivity and the fact that their apparent integrity has been preserved even though the two groups occur together throughout the lake, all point to a genetic rather than an environmental basis for the separation of the two groups." He did not find an anatomical basis for the two groups, and he found smelt with intermediate growth rates that could not be assigned to either race. Greene recorded a range for age-group II of 100 to 160 mm for the small race, and 150 to 240 mm for the large race.

Zilliox and Youngs (1958) studied Lake Champlain smelt and accepted the separate race theory without discussion. Rupp (1959) reported on large and small races in some Maine lakes, and found two distinct spawning runs; the large race spawned first and the smaller second. The largest smelt was 279 mm.

Creaser (1926) discovered that smelt in Crystal Lake matured at a large size and reached a length (305 mm) as great as some New England and salt water smelt. He concluded that large race smelt were introduced into the Great Lakes. Kendall (1927) supported Creaser by pointing out that Crystal Lake smelt came from a large race cultured at Green Lake Fish Hatchery, Maine. Evidence for the large race in the Great Lakes was given by Schneberger (1937) who found Green Bay smelt at 305 mm, and Dymond (1944) who found one 367 mm specimen in Lake Huron. Bailey (1964) recorded Lake Superior smelt at 280 mm.

The length distribution of Gull Lake smelt (Fig. 3) indicated that lengths were roughly divisible into four modes, with most fish in the first two. This could not be satisfactorily compared to the smelt of New England because of the absence of two size ranges. Gull

Fig. 3. Total length distribution of Gull Lake smelt. Age-group 0 is not included.


NUMBER
0
5
10
15
20
25
30
35
40
45
LENGTH (MM)
115
120
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210

Lake smelt were also far short of the maximum size attained by eastern smelt.

The length distribution of Gull Lake smelt was similar to Great Lakes, Miramichi River, and Crystal Lake smelt for there was only one size range, but maximum length in these areas was greater. This indicates that one genetic race was introduced in Gull Lake. This is probably a safe assumption because they came from the Oden State Fish Hatchery near Petosky, Mich. The small race seldom reaches a size over 150 mm (Creaser, 1926), so Gull Lake smelt are probably large race fish. If Gull Lake smelt are the large race, they did not have a comparable growth rate, which suggests that Gull Lake is less favorable for the growth of smelt. It may be a physically harsh environment, or there may be differences in diet to account for size differences. Gull Lake smelt have a growth rate between the two races of New England smelt.

The length distribution of age groups (Fig. 4) demonstrated that the first mode consisted primarily of age-group I smelt, and the second of age-groups I and II. The third mode resulted chiefly from age-group III, and the fourth from age-groups III and IV. Length curves for age-groups I and II overlapped and had the same slope and range. Individuals in the 160-164 mm interval were most numerous. The length range of age-groups I through IV was 110 to 214 mm, or a 104 mm difference. Age-groups 0 and V were not included because of a small sample. Only two individuals of age-group V were captured.

The length range of age-group I Gull Lake smelt was approximately the same as Lake Superior smelt (104 to 213 mm) (Bailey, 1964). Gull Lake age-groups II, III, and IV were smaller, indicating larger Gull Lake smelt fared less well than younger fish.

Fig. 5 illustrates the length distribution of Gull Lake male and

Fig. 4. Total length distribution of age groups of Gull Lake smelt.

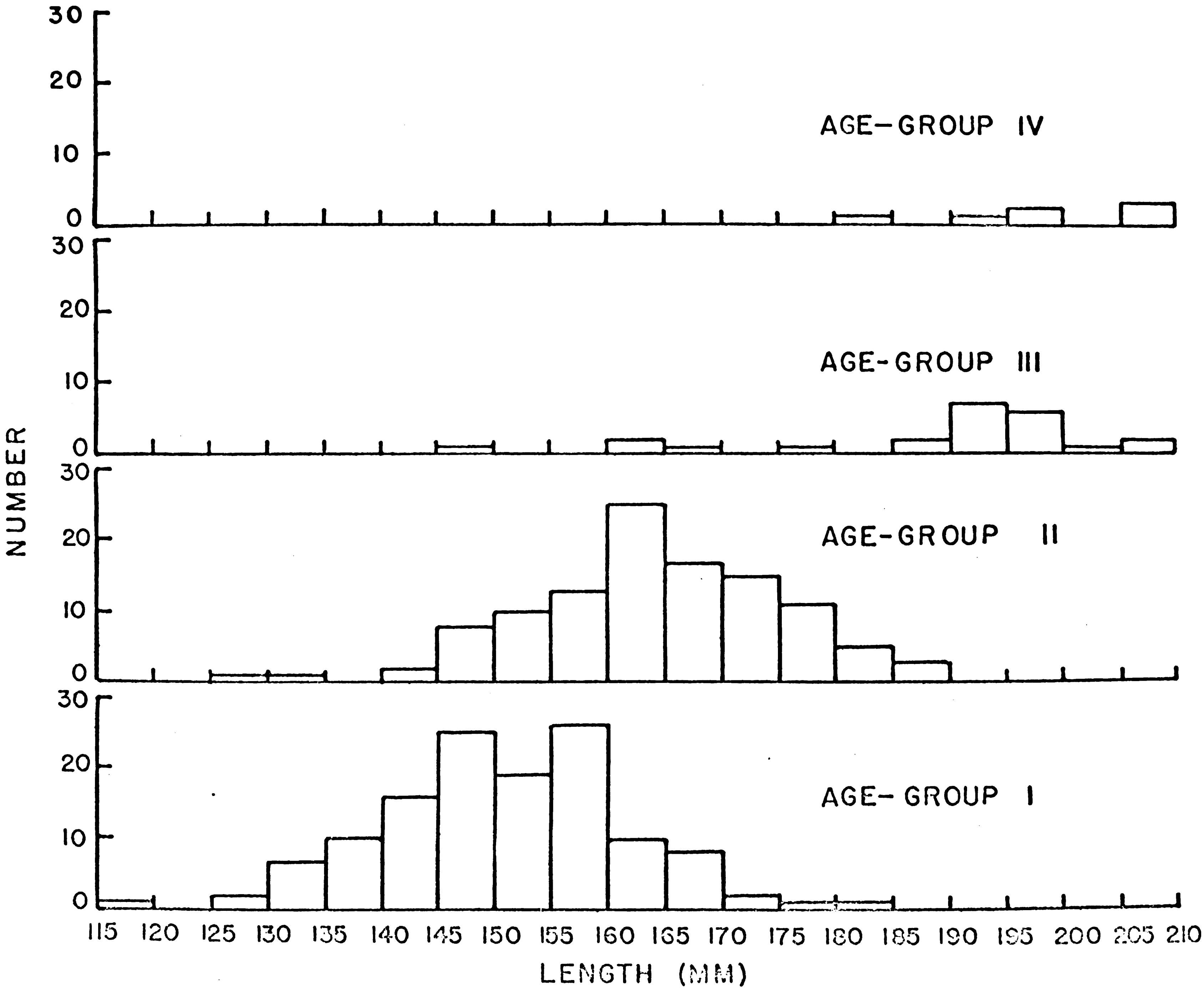
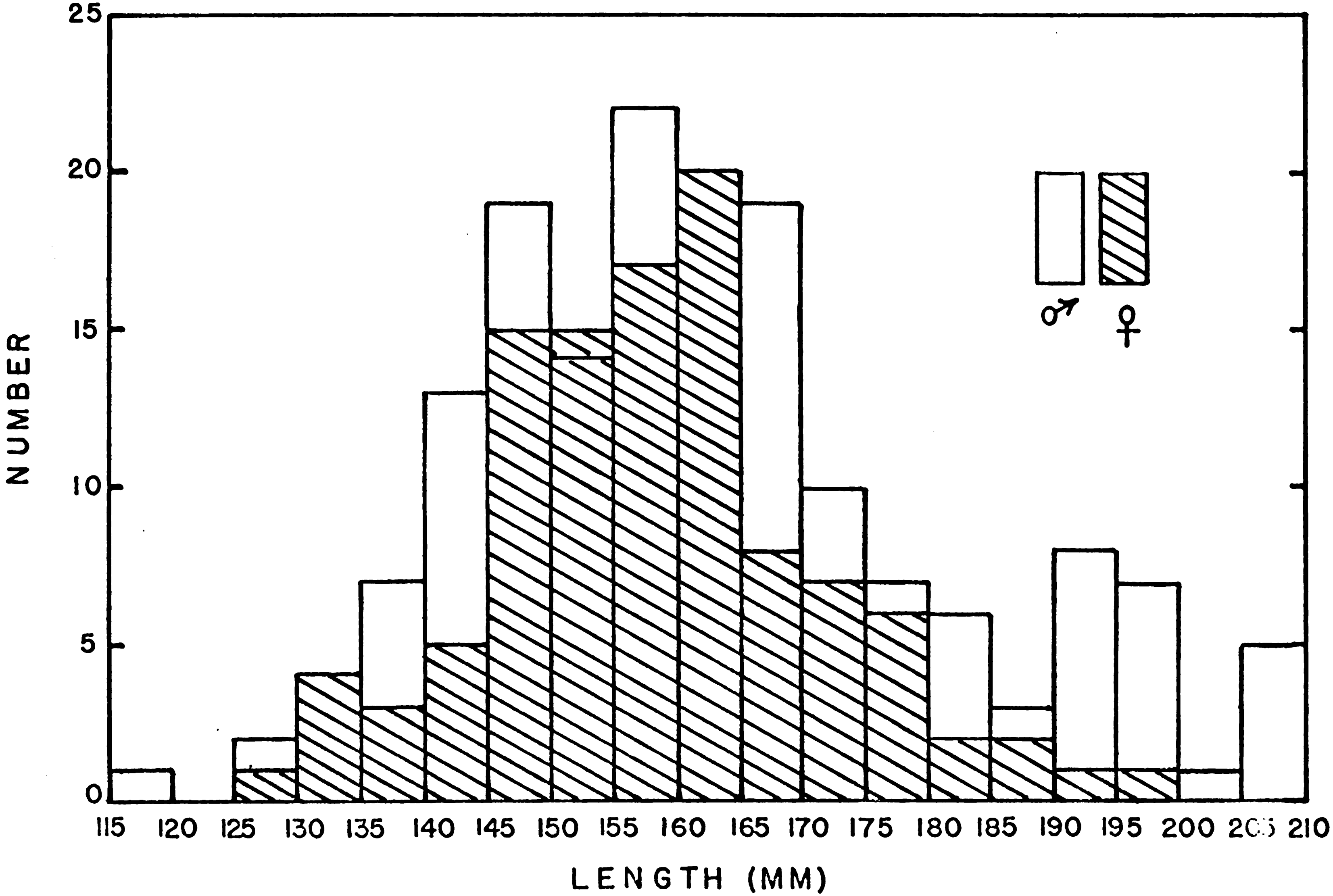

AGE-GROUP IV
AGE-GROUP III
AGE-GROUP II
AGE-GROUP I
NUMBER
0
10
20
30
115 120 125 130 135 140 145 150 155 160 165 170 175 180 185 190 195 200 205 210
LENGTH (MM)

Fig. 5. Total length distribution of male and female Gull Lake smelt. Age-group 0 is not included.


25
20
15
10
5
0
NUMBER
115 120 125 130 135 140 145 150 155 160 165 170 175 180 185 190 195 200 205 210
LENGTH (MM)
♂
♀

female smelt. There were fewer males than females in only one interval (150-154 mm). There was an equal number of each sex in the 130-135 and 160-165 mm intervals. The greatest difference existed in the 165-169 mm interval (19 females and 8 males); this difference was not highly significant ($P<0.10$) and could have resulted through sampling. Females had a total length range of 104 mm, and males 84 mm. The curves indicated that the sex ratio remained relatively constant for most length intervals.

The consistent predominance of females at all length ranges suggests that forces selecting females were important at all sizes. McKenzie (1958) and Bailey (1964) found a predominance of female smelt at all lengths. Smelt generally spawn at the beginning of the third growing season (Van Oosten, 1953). A pronounced mortality often occurs among fresh-water smelt during or shortly after spawning (Kendall, 1927). If males are in poorer condition than females during spawning, they may be more susceptible to disease, parasites, predation, starvation, or extreme weather. This could account for the fewer numbers of mature males. The fewer numbers of immature males could have resulted from behavioral differences that made them more susceptible to predation or less susceptible to capture.

That males are in poorer condition has not been proven, although it is known that males are more active than females during spawning, and may remain in the spawning stream for an entire night or throughout the day (Hoover, 1936). McKenzie (1964) said: "Mortality among the males (smelt) at spawning is at least partly responsible for this increase in the proportion of females with age." The increase in proportion of Gull Lake females may have been due to the accumulated effect of males dying while spawning, or decreased predation on larger females.

The percent age composition of Gull Lake smelt (Table 2) varied considerably with the month. April and May samples included only age-groups II and III. The July collection consisted of age-group II (84%) and older fish. Age-group I appeared in August, but most of the sample was age-group II (76%). The September sample was young due to the selectivity of the Isaacs-Kidd trawl. Age-group I smelt captured by gill net increased in the fall, and older individuals decreased. The December sample was comprised primarily of age-group I (89%). For the entire year, age-group I was dominant (45%), followed by age-group II (40%). The small number of age-group 0 smelt was not an indication of their numbers in Gull Lake, but of the inability of gill nets to capture them.

The percent age composition of Gull Lake smelt shows that few age-group I fish were taken until fall, and in fall the number of age-group II fish decreased. In spring and early summer age-group I fish were not much larger than the previous winter, and would pass through the nets. As they grew they were captured in increasing numbers, and were most numerous in the winter samples. Age-group II smelt were caught in decreasing numbers during the growing season because of a probable natural mortality. Bigelow and Welsh (1925) indicated that smelt, as schooling fish, probably associate in age groups. This would affect the catch during the year, particularly in winter and spring when nets were on the lake bottom where smelt were likely in schools.

The predominance of age-group I smelt in Gull Lake, excluding age-group 0, agreed with reports by Greene (1930) for Lake Champlain, Warfel *et al*. (1943) for Great Bay, New Hamp., and McKenzie (1964) for the Miramichi River. In these areas, as in Gull Lake, the number of

Table 2. Percent age composition of Gull Lake smelt. Number of individuals in brackets

Month	Age-group					
	O	I	II	III	IV	V
April			91.0(10)	9.0(1)		
May			50.0(1)		50.0(1)	
July			84.0(21)	8.0(2)	4.0(1)	4.0(1)
August		8.5(6)	76.0(54)	11.3(8)	4.2(3)	
September	27.3(3)	72.7(8)				
October	15.6(7)	55.5(25)	26.7(12)	2.2(1)		
November	3.2(1)	41.9(13)	45.2(14)	6.5(2)		3.2(1)
December		89.2(50)	3.6(2)	3.6(2)	3.6(2)	
January		100.0(3)				
February		77.4(24)		22.6(7)		
Total	3.8(11)	45.1(129)	39.9(114)	8.0(23)	2.5(7)	0.7(2)

smelt decreased with age, with few individuals in age-group V. This indicated that the Gull Lake sample was representative and not affected by sampling.

The mean total length (Table 3) and weight (Table 4) of Gull Lake smelt were computed. Age-group 0 smelt were collected during 3 months, so it was not possible to determine their total length or weight for one growing season. Increase in size of age-group I was best represented because active growth does not begin until early summer (McKenzie, 1958). Age-group II smelt were not collected in January and February, so their size at the growing season end was not known. The mean size of age-group III fish captured in July provided an estimate of the size of II-group fish at the end of the previous season; the number of age-group III smelt were too few to draw conclusions concerning their growth.

Fig. 6 represents the mean total length and weight of age groups of Gull Lake smelt. Differences between the mean lengths of age-groups I and II, and II and III were 23 and 24 mm. Differences between the mean weights of these groups was 5 and 12 g.

The length and weight of Gull Lake smelt age groups were not comparable to either race of Lake Champlain smelt. Mean total length for age-group III of the small race was 158 mm; for age-group I of the large race it was 208 mm. Starting with age-group I, Lake Superior smelt were 152, 185, 200, and 218 mm (total length), and 21.7, 43.5, 59.1, and 71.5 g (Bailey, 1964). Females were even larger. Starting with age-group I, Miramichi River smelt averaged 166, 195, 220, 244, and 260 mm (total length), and 29.4, 50.8, 73.0, and 90.5 g (McKenzie, 1958).

The length and weight of age-group I Gull Lake smelt were similar

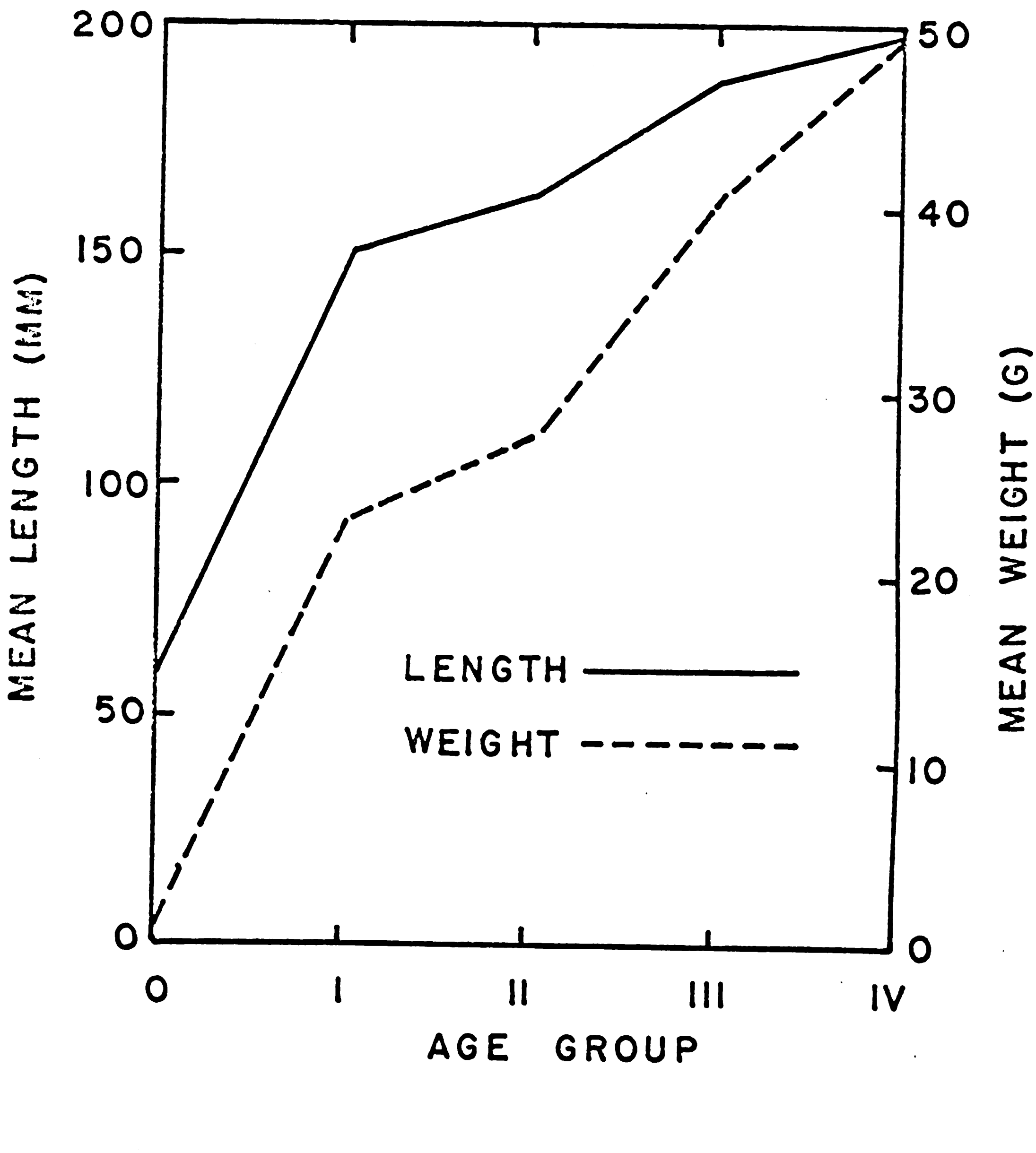
Table 3. Mean total length (mm) of Gull Lake smelt. Number of individuals in brackets

	Age-group					
Month	O	I	II	III	IV	V
April			150.9(10)	145.0(1)		
May			151.0(1)		180.0(1)	
July			164.9(21)	176.5(2)	197.0(1)	193.0(1)
August		135.5(6)	166.9(54)	191.1(8)	200.7(3)	
September	47.7(3)	136.6(8)				
October	64.7(7)	144.4(25)	161.4(12)	195.0(1)		
November	60.0(1)	144.8(13)	162.8(14)	189.0(2)		180.0(1)
December		155.5(50)	147.0(2)	190.0(2)	202.5(2)	
January		151.7(3)				
February		158.3(24)		191.3(7)		
Total	60.2(11)	150.1(129)	163.4(114)	187.8(23)	197.7(7)	186.5(2)

Table 4. Mean weight (g) of Gull Lake smelt. Number of individuals in brackets

	Age-group					
Month	O	I	II	III	IV	V
April			20.0(10)	18.9(1)		
May			23.0(1)		45.7(1)	
July			28.2(21)	36.2(2)	43.6(1)	41.4(1)
August		16.4(6)	29.6(54)	41.6(8)	53.9(3)	
September	0.8(3)	16.5(8)				
October	1.7(7)	19.5(25)	25.2(12)	43.9(1)		
November	1.3(1)	19.6(13)	27.4(14)	37.9(2)		34.2(1)
December		25.1(50)	22.0(2)	43.8(2)	48.0(2)	
January		24.3(3)				
February		27.8(24)		42.7(7)		
Total	1.4(11)	23.0(129)	27.6(114)	40.4(23)	49.6(7)	37.8(2)

Fig. 6. Mean total length and weight of age groups of Gull Lake smelt.


200
150
100
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0
50
40
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10
0
MEAN LENGTH (MM)
MEAN WEIGHT (G)
LENGTH
WEIGHT
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I
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IV
AGE GROUP

to Lake Superior smelt, and were probably similar to age-group I Miramichi smelt because these were captured in winter and measurements were high. Growth after the first year, however, advanced at a faster rate than Gull Lake smelt.

Food of young smelt consists primarily of smaller crustaceans in the ocean (Kendall, 1927), Great Lakes (Gordon, 1961), and fresh-water landlocked lakes (Greene, 1930). This would account for similar growth rates for the first 2 years. In the ocean smelt change to a fish, shrimp, *Mysis*, and other large crustacean diet; in the Great Lakes older smelt eat, in addition to smaller crustaceans, *Mysis*, amphipods, insects, and some fish. In New England lakes large smelt often feed exclusively on other smelt.

Gull Lake smelt fed primarily on small crustaceans and dipteran larvae, and did not change their diet with age. Within a smelt lifespan, efficiency of predation on larger food items would result in a conservation of energy, which could account for greater growth in other areas. That Gull Lake smelt did not have a diet similar to other areas was due to the fact that *Mysis* is not found in Gull Lake. In addition, smelt in Gull Lake were restricted to the colder hypolimnion in summer which prevented them from feeding on young and small fish in warm surface waters. In fall, when smelt were distributed at all depths, young fish were too large to be a subject of prey. There is also a possibility that annual production of zooplankton is less in Gull Lake, although there is no evidence of this.

The physical environment of Gull Lake may have adversely affected smelt growth in a manner not realized in other environments. Gull is large and relatively deep, with a cold (10 C) summer hypolimnion. In the fall there is a critical lack of oxygen in the hypolimnion that restricts the distribution of deep water fish. Rooted vegetation is found only on the shoals, so most of the lake is barren.

Genotype of smelt and abundance of competitive species probably do not influence smelt growth rates. Rupp and Redmond (1966) showed that these two factors had little or no effect in influencing length or longevity of smelt, whereas the physical environment and abundance of plankton fauna had a pronounced effect on growth rates.

Examination of length-weight data of Gull Lake smelt revealed little difference in the weight of each sex in each length interval (Table 5). A length-weight relationship was established using all fish, regardless of sex or maturity. Length intervals were 5 mm; lengths in each interval were averaged. The mean weight of smelt in each interval was the basis for the curve in Fig. 7.

The general length-weight equation, determined by fitting a straight line to logarithms of the mean lengths and weights was:

$$\log W = -4.67 + 2.76 \log L$$

where W = weight (g) and L = total length (mm).

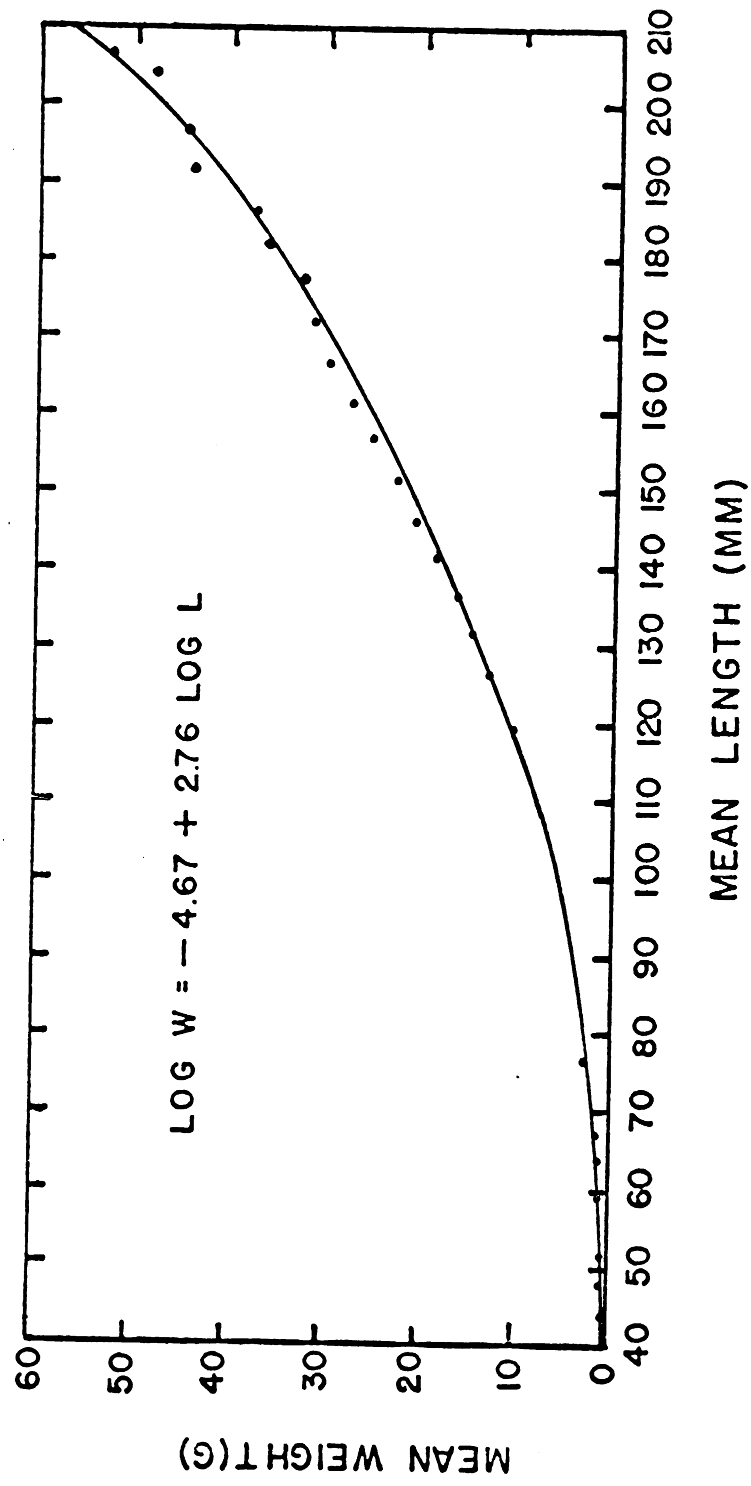
Beckman's (1942) data demonstrated that smelt in Crystal Lake weighed more than Gull Lake smelt at all lengths over 60 mm. There was evidence that Crystal Lake smelt fed on fish much of their lives, which could explain their greater weight. Gull Lake smelt were heavier than Miramichi smelt of equal length up to 184 mm. After 184 mm Miramichi smelt were heavier, which suggested a difference in the adult diets. The largest immature Miramichi smelt was 209 mm; the smallest was 140 mm.

The sex ratio of Gull Lake smelt (Table 6) varied with the age group; the greatest difference existed in age-group III ($P<0.05$). There was a significant difference ($P<0.05$) in age-group I. Females

Table 5. Total length-weight relationship of Gull Lake smelt. Number of individuals in brackets

Length (mm)	Mean length (mm)	Mean weight (g)			
		Immature	Males	Females	Total
40-44	44.0	0.5(1)			0.5(1)
45-49	48.0	0.8(1)			0.8(1)
50-54	51.5	1.0(2)			1.0(2)
55-59	59.0	1.2(1)			1.2(1)
60-64	64.0	1.5(1)			1.5(1)
65-69	66.8	1.7(4)			1.7(4)
70-74					
75-79	77.0	2.9(1)			2.9(1)
80-84					
85-89					
90-94					
95-99					
100-104					
105-109					
110-114					
115-119	119.0			10.8(1)	10.8(1)
120-124					
125-129	126.7		12.2(1)	14.7(2)	13.8(3)
130-134	132.4		14.4(4)	15.1(4)	14.8(8)
135-139	136.7		16.6(3)	16.5(7)	16.5(10)
140-144	141.8		18.3(5)	18.7(13)	18.6(18)
145-149	146.3		20.5(15)	21.0(19)	20.7(34)
150-154	151.7		22.4(15)	23.5(14)	22.9(29)
155-159	157.0		25.7(17)	25.7(22)	25.7(39)
160-164	161.8		27.4(20)	27.5(20)	27.5(40)
165-169	166.7		29.5(8)	30.3(19)	30.0(27)
170-174	171.6		31.2(7)	31.9(10)	31.6(17)
175-179	177.2		32.5(6)	32.9(7)	32.7(13)
180-184	181.4		40.0(2)	34.9(6)	36.2(8)
185-189	186.2		36.1(2)	39.0(3)	37.8(5)
190-194	191.7		42.8(1)	44.4(8)	44.2(9)
195-199	196.0		44.8(1)	44.7(7)	44.7(8)
200-204	204.0			48.5(1)	48.5(1)
205-209	206.6			53.3(5)	53.3(5)

Fig. 7. Total length-weight relationship of Gull Lake smelt.



LOG W = — 4.67 + 2.76 LOG L
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60
MEAN LENGTH (MM)
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80
90
100
110
120
130
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150
160
170
180
190
200
210

Table 6. Sex ratio of Gull Lake smelt

Age-group	Males	Females	Males (%)	Females (%)	Ratio M/F
I	47	82 *	36	64	0.573
II	51	63	45	55	0.810
III	6	17 *	26	74	0.353
IV	2	5	29	71	0.408
V	1	1	50	50	1.000
Total	107	168 *	39	61	0.637

* Significant difference ($P < 0.05$)

dominated in all groups except V. The proportion of females increased with age; the ratio of males to females was closest in age-group II. The total sex ratio was 168 females (61%) to 107 males (39%). This difference was highly significant (P<0.005). There was no evidence that the indicated sex ratio was influenced by smelt schooling according to sex.

Most published data on sex ratios were based on spawning season samples. Hoover (1936) and Langlois (1935) showed that smelt sex ratios fluctuate during the breeding season and even during the spawning night. Beckman (1942) sampled Crystal Lake smelt before and after the spawning season and found 61% females and 39% males, which agreed with the Gull Lake sample. Both Beckman and McKenzie (1964) found an increase in abundance of females with age.

The sex ratio of Gull Lake smelt strengthened the conclusion that females were selected during spawning because of a mortality of males. The decreasing proportion of males over the years would result from mortality during additional spawning seasons. There is one record (Michigan Conservation Department) of a large smelt kill in Gull Lake immediately after a spawning run (1960). The significant difference in age-group I could have resulted from a selective predation or a behavioral difference that made males less susceptible to capture. These factors could, of course, have been important at all ages.

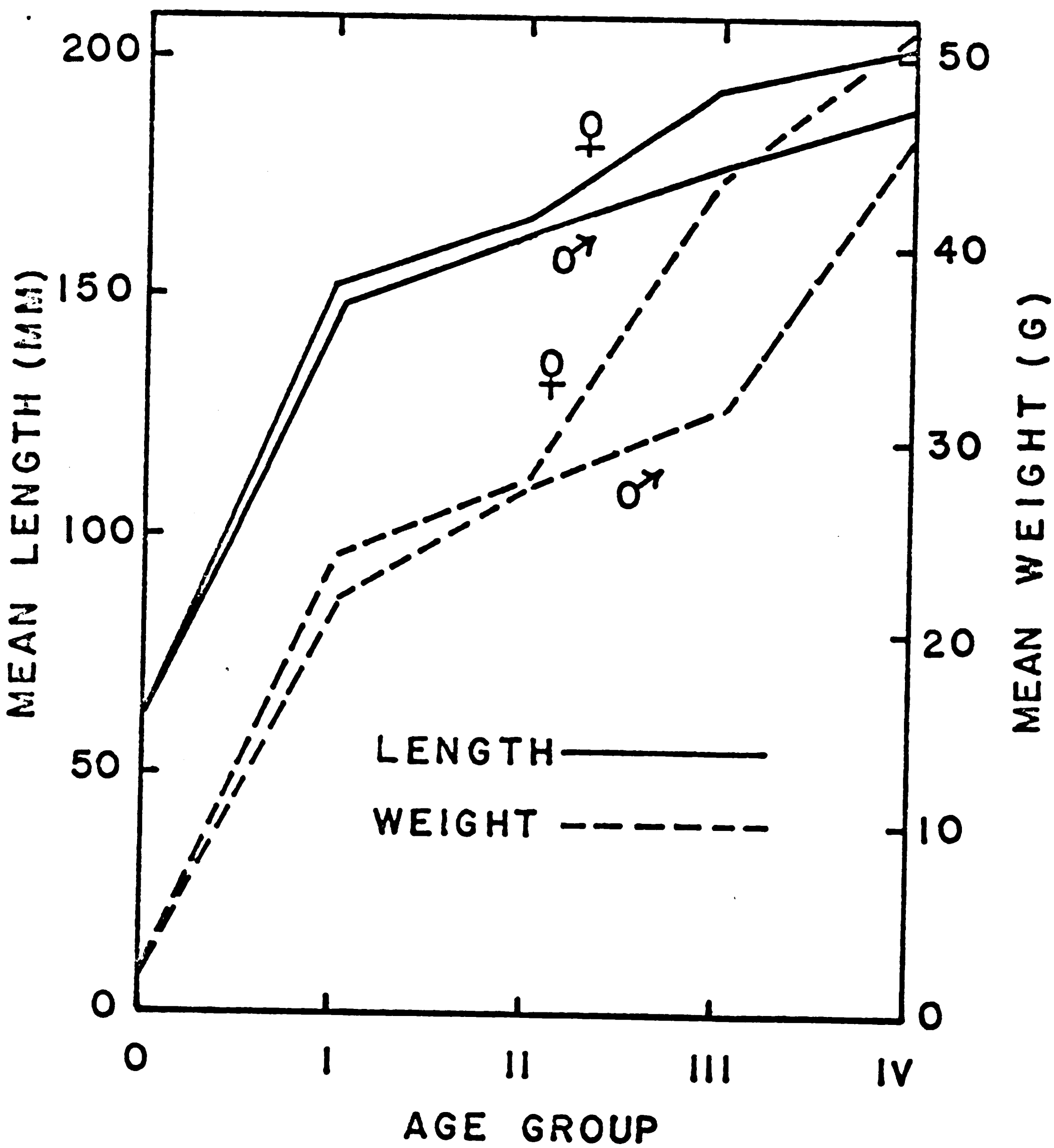
Size differences between the sexes of Gull Lake smelt were apparent (Table 7). Females were larger (mean length and weight) than males in each age group (Fig. 8). The smallest difference between sexes was in age-group II. Sexual dimorphism was most obvious and only significant (P<0.05) in age-group III, with a difference of 17.7 mm and 12.3 g. At this age smelt were sexually mature and had

Table 7. Sexual dimorphism of Gull Lake smelt. Number of individuals in brackets

Age-group	Males (mm)	Females (mm)	Males (g)	Females (g)
I	148.7(47)	151.0(82)	21.8	23.7
II	162.3(51)	164.4(63)	27.3	27.8
III	174.7(6)	192.4(17) *	31.3	43.6 *
IV	188.0(2)	201.6(5)	45.3	51.3
V	180.0(1)	193.0(1)	34.2	51.3

* Significant difference ($P < 0.05$)

Fig. 8. Sexual dimorphism of Gull Lake smelt.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10
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MEAN LENGTH (MM)
MEAN WEIGHT (G)
♀
♂
♀
♂
LENGTH
WEIGHT
0
I
II
III
IV
AGE GROUP

spawned once. Size differences in the sexes of age-groups IV and V should be partly attributed to a small sample. They indicated, however, that size differences between sexes increased with age.

Langlois (1935) cited three factors that enable him to distinguish between sexes of spawning smelt: color (males are darker); nuptial tubercles (pronounced in males); and size (females are larger). Color and nuptial tubercles are apparent only during spawning; size differences are apparent at all times.

Larger females and an increasing size difference between sexes of smelt with age were seen in Great Bay, New Hamp. (Warfel *et al*., 1943), Crystal Lake (Beckman, 1942), South Bay, Lake Huron (Baldwin, 1950), Lake Superior (Bailey, 1964), and the Miramichi River (McKenzie, 1958). Perhaps the slower growth rate of males could be attributed to their higher rate of metabolism, under endocrine influence in response to genetic and environmental forces (Lagler, Bardach, and Miller, 1962).

Trophic Relationships

Data on food and feeding habits of Gull Lake smelt were obtained from analysis of 286 stomachs. Food habits varied and were related to the season (Table 8). During May, July, and August smelt ate only *Chaoborus* and Tendipedidae larvae. There were no crustaceans eaten in these months. A few young smelt were eaten in August. In September the volume of *Chaoborus* decreased so cladocerans were equally important. In fall and winter the proportion of cladocerans and copepods increased until they were the primary food. Volume of copepods was greater than cladocerans in February and April. Ostracods were taken in small numbers from September to December. Tendipedids were eaten from April to October, but mainly in July and August.

Table 8. Food of Gull Lake smelt expressed in estimated percent of total volume

Month	Cladocera	Copepoda	Ostracoda	*Chaoborus*	Tendipedidae	Smelt	Remains
April	2.7	11.6		4.7	0.2		80.8
May					70.0		30.0
July				47.9	45.0		7.1
August				38.1	44.1	3.3	14.5
September	30.6	3.8	0.1	34.4			31.1
October	21.0	5.7	0.1	21.0	0.8		51.4
November	12.7	10.5	0.5	3.9			72.4
December	18.2	0.8	0.3	9.9			70.8
January	46.7			0.3			53.0
February	12.4	22.6		2.6			62.4
Total	10.5	4.5	0.1	23.2	18.1	1.0	42.6

Food for the year was dominated by Chaoborus and tendipedid larvae. Cladocerans and copepods were the only other items eaten in appreciable amounts. Only Chaoborus larvae were eaten regularly over the year.

A single food item could not be compared with that of another month because the amount of digested matter varied considerably. So that the importance of an item could be compared over a year, food was expressed in percent frequency of occurrence (Table 9). These data are illustrated in Fig. 9. Cladocerans were not eaten in July and August, but occurred in over 70% of the stomachs from September to February. They were found in all stomachs from September to January, and in fewest in October. Copepods also were not eaten in July and August, but were taken most frequently in October and November. They were eaten least frequently in December and January. Copepods occurred in most stomachs when cladocerans were least important.

Ostracods were most important in November. Chaoborus larvae appeared in most stomachs during summer, but decreased in fall as cladocerans and copepods were eaten more frequently. Tendipedid larvae were eaten primarily during July and August.

Cladocerans and copepods were not routinely identified, but stomachs were selected periodically and the contents identified to genus. Smelt were feeding almost entirely on the genera Daphnia, Cyclops, and Diaptomus. This was probably true for all smelt, for these were the only individuals recognized. Bosmina was the other cladoceran identified, but it was eaten only occasionally because of its small size.

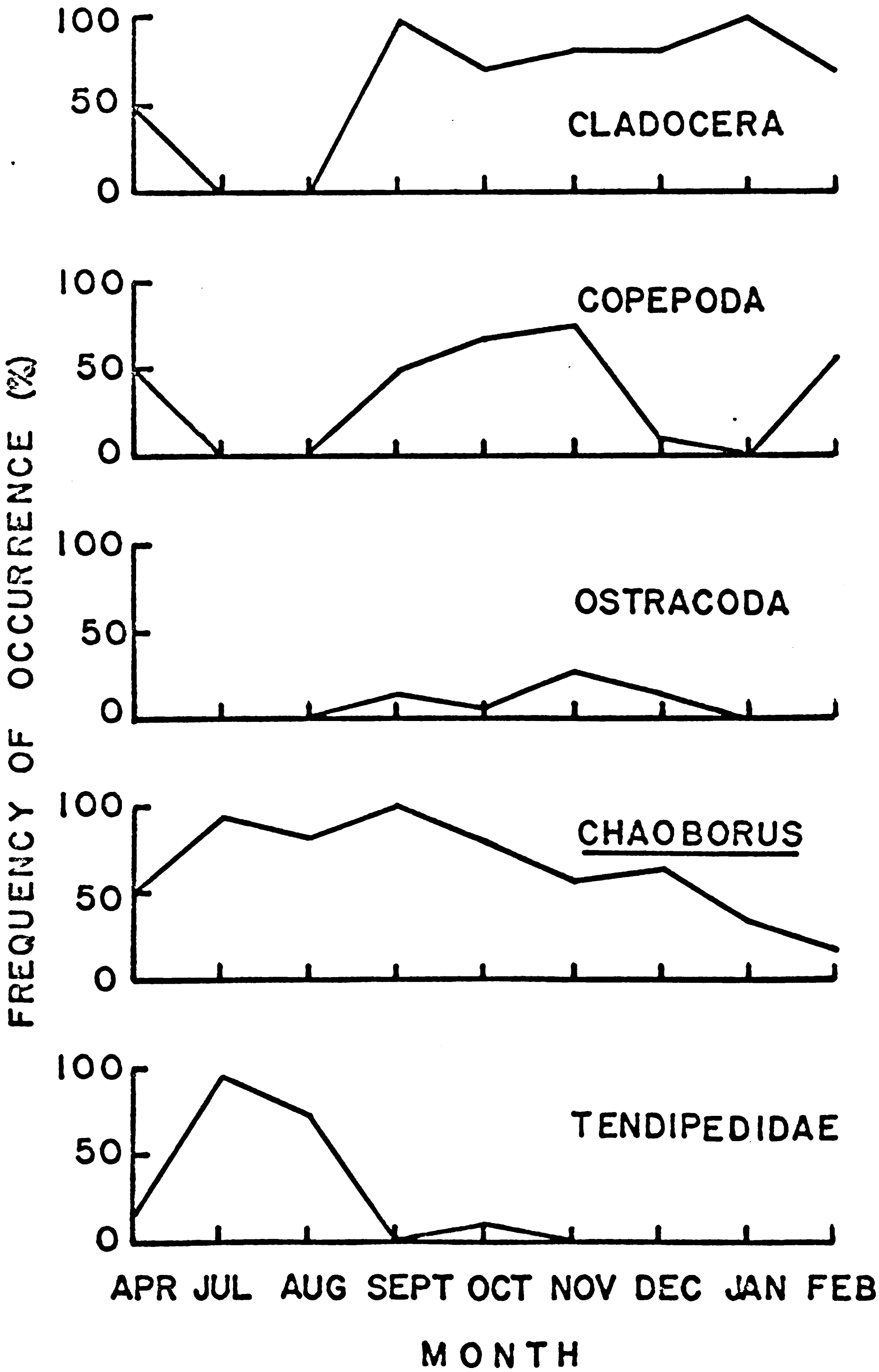
All ostracods were the free-swimming Cypria turneri Huff. Tendipes was the only tendipedid genus identified.

It has been stated that food of fresh-water smelt varies with its

Table 9. Food of Gull Lake smelt expressed in percent frequency of occurrence

Month	Cladocera	Copepoda	Ostracoda	*Chaoborus*	Tendipedidae	Smelt	Number
April	50	50		50	17		6
May					100		1
July				96	96		24
August				82	75	5	61
September	100	38	13	100			8
October	72	68	8	80	8		25
November	82	76	29	59			17
December	82	9	16	64			44
January	100			33			3
February	71	57		19			21
Total	46	25	7	70	35	1	210

Fig. 9. Food of Gull Lake smelt expressed in percent frequency of occurrence.


100
50
0
CLADOCERA
100
COPEPODA
50
0
100
OSTRACODA
50
0
100
CHAOBORUS
50
0
100
TENDIPEDIDAE
50
0
FREQUENCY OF OCCURRENCE (%)
APR JUL AUG SEPT OCT NOV DEC JAN FEB
MONTH

size and age. The character and arrangement of their teeth indicate carnivorous propensities, while their comparatively close-set gill rakers suggest minute planktonic food at certain stages of growth (Kendall, 1927). The food habits of Gull Lake smelt were in part similar to those of smelt in other areas, for the smaller and younger fish fed primarily on small crustaceans and insect larvae. However, similarities ended as adult smelt in other environments changed to a fish diet.

Crystal Lake smelt fed on the emerald shiner in fall and winter (Creaser, 1926; Beckman, 1942). Smelt in Mountain Lake, Mich., fed on young smelt and yellow perch in summer, in addition to an equal amount of copepods and insects (1929b).

Doolittle (from Kendall, 1927) found smelt over 150 mm in Sebago Lake, Maine, eating fish and insect larvae while smaller smelt fed primarily on zooplankton. Most fish eaten were smelt of all sizes. Reports in Kendall (1927) stated that the prevailing genera of zooplankton prey were *Cyclops*, *Diaptomus*, *Daphnia*, and *Bosmina*.

Greene (1930) found young and small race smelt in Lake Champlain feeding primarily on cladocerans and copepods. The prevailing genera were *Cyclops*, *Diaptomus*, *Daphnia*, *Bosmina*, and *Leptodora*. The larger race smelt fed primarily on other smelt and insect larvae. Greene suggested that the fish-eating habit of the larger race is not a characteristic acquired by their larger size, but "...size for size, they take many more fishes than the smaller race, and conversely, far less plankton." He concluded that there must be a racial basis for a physiological difference in food preferences. Mayfly (*Hexagenia*) larvae comprised most of the insect larvae eaten in Lake Champlain. In Saranac Lake *Chaoborus* and tendipedid larvae were prominent.

Great Lakes smelt are similar to those in Gull Lake because they do not feed extensively on fish. This was true in Lake Michigan (Creaser, 1929a), Green Bay (Schneberger, 1937), and Lake Huron (Baldwin, 1950). Fish were not eaten in significant numbers; only the sculpin (Cottus), burbot (Lota lota), and smelt were taken occasionally.

In Lake Huron young smelt fed primarily on Cyclops and Diaptomus (Gordon, 1961). Daphnia and Bosmina were taken in amounts varying with the season. Older smelt fed most frequently on crustaceans, and insects accounted for the greatest volume. Cladocerans and copepods comprised most of the crustaceans, except in November when smelt from deep water had eaten Mysis exclusively. Mayflies dominated the insect food. Dipterans were consumed only in July and August in pronounced numbers. Fish were eaten infrequently, usually shiners in summer and smelt in fall.

Observations on the food of Gull Lake smelt agreed most closely with food habits of Great Lakes smelt. Fish of both areas fed mainly on crustaceans and insects, and more often consumed their own species rather than other fish. With the exception of deep water Great Lakes fish that fed on Mysis, smelt from both areas depended on copepods, cladocerans, and dipteran larvae for the major portion of their diet.

As in the Great Lakes, food habits of Gull Lake smelt varied with the season, suggesting that they were eating fauna most abundant at the time. In summer large pupating dipteran larvae were eaten extensively. Pupation of the larvae in summer probably removed the largest individuals, so in the fall only smaller larvae were present. Total biomass may not have changed, but individual larvae would have been considerably smaller. Further, low temperatures may have affected the visual pigments of larvae, thus altering their migratory behavior. In the fall, therefore, vertical migrations of smaller larvae were significantly less extensive. In the fall cladocerans and copepods appeared in the stomachs of smelt. The peak of copepod consumption occurred when cladocerans were eaten least frequently, which would have occurred if there was a fall and late winter bloom of copepods. Cladocerans could have bloomed in summer and early winter.

These data indicate that Gull Lake smelt fed on food most available, but may have had a preference for dipteran larvae since crustaceans were abundant at all depths in summer. When larger dipteran larvae disappeared and vertical migrations of the remaining larvae decreased, smelt turned to a crustacean diet dominated by the most abundant organism. That there were no crustaceans eaten in summer indicates that smelt were seeking and eating individual dipteran larvae. This would not have been a great energy expenditure since large larvae were extremely abundant in the water column at night. In the fall smelt appeared to change to filter feeding for capturing crustaceans. This would explain the consumption of only larger genera; smaller animals and plants would have escaped through their gill rakers.

There was no evidence that Gull Lake smelt were feeding on the bottom; there were no bottom dwelling amphipods or clams eaten, though these are often found in bottom feeding Great Lakes smelt (Ferguson, 1965). Low oxygen conditions in summer may have limited the distribution of these food organisms on a large portion of the bottom of Gull Lake.

Gull Lake smelt did not prey on other fish even though they had the physiologic ability to do so. They were not generally as large as "fish eating" smelt in other areas, but larger individuals were comparable to smaller "fish eating" smelt. Smelt in Gull Lake were restricted to the colder hypolimnion in summer (Fig. 12), and could not associate with minnows and young fish in warm surface waters. In fall when adult smelt were near surface, young of smelt and other species would have been too large to be preyed upon. The only time smelt are in the habitat of small fish is during spawning when their consumption is limited. The formidable smelt dentition, which suggests fish capturing capabilities, evolved in the ocean where smelt feed on fish and relatively large fast-moving crustaceans (shrimp).

The dependence of smelt on crustaceans and insects suggests that they compete with the young of all associated species and adults of many (Gordon, 1961). In order to adversely affect other species by competition, however, smelt would have to have a rate of consumption so great that a food scarcity develops. There has been no evidence that this has happened. In Saginaw Bay where smelt have become plentiful in recent years, yellow perch collected from 1943 to 1955 were heavier, length for length, than perch collected from 1929 to 1930 (El-Zarka, 1959).

Feeding habits of Gull Lake smelt varied with the season (Table 10). Data from Tables 8 and 10 are plotted in Fig. 10. There were no smelt captured by gill net in daylight during the entire study period; evidently smelt could see and avoid the white net. It is probably safe to assume that most smelt were captured at night, and that feeding activity data for the year were comparable.

Sampling methods must be considered in a comparison of feeding activity. From July to November smelt were captured at night and fixed every 2 or 3 hr, so values, particularly percent remains, were not comparable. The low water temperature during those months would have slowed the rate of digestion so values for percent remains may not have been too high. The February value was correct because these

Table 10. Seasonal feeding habits of Gull Lake smelt

Month	Number	Number with food	Percent with food	Stomach fullness (%)
April	11	6	54.5	6.8
May	2	1	50.0	25.0
July	25	24	96.0	48.2
August	71	61	85.9	34.6
September	11	8	72.7	29.1
October	45	25	54.8	14.0
November	31	17	54.8	18.7
December	56	44	78.6	13.4
January	3	3	100.0	18.3
February	31	21	67.7	6.8
Total	286	210	73.4	22.0

Fig. 10. Seasonal feeding habits of Gull Lake smelt.

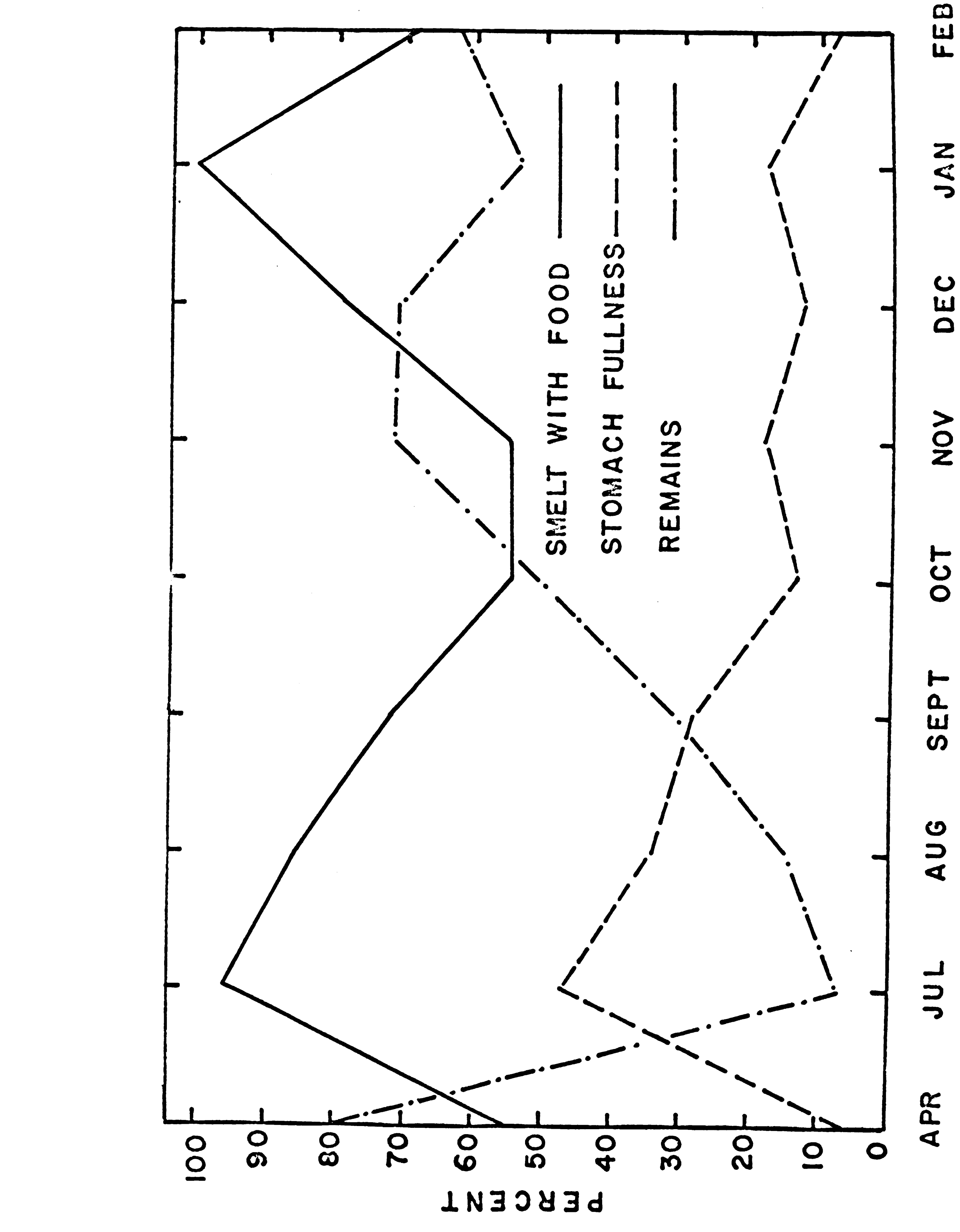
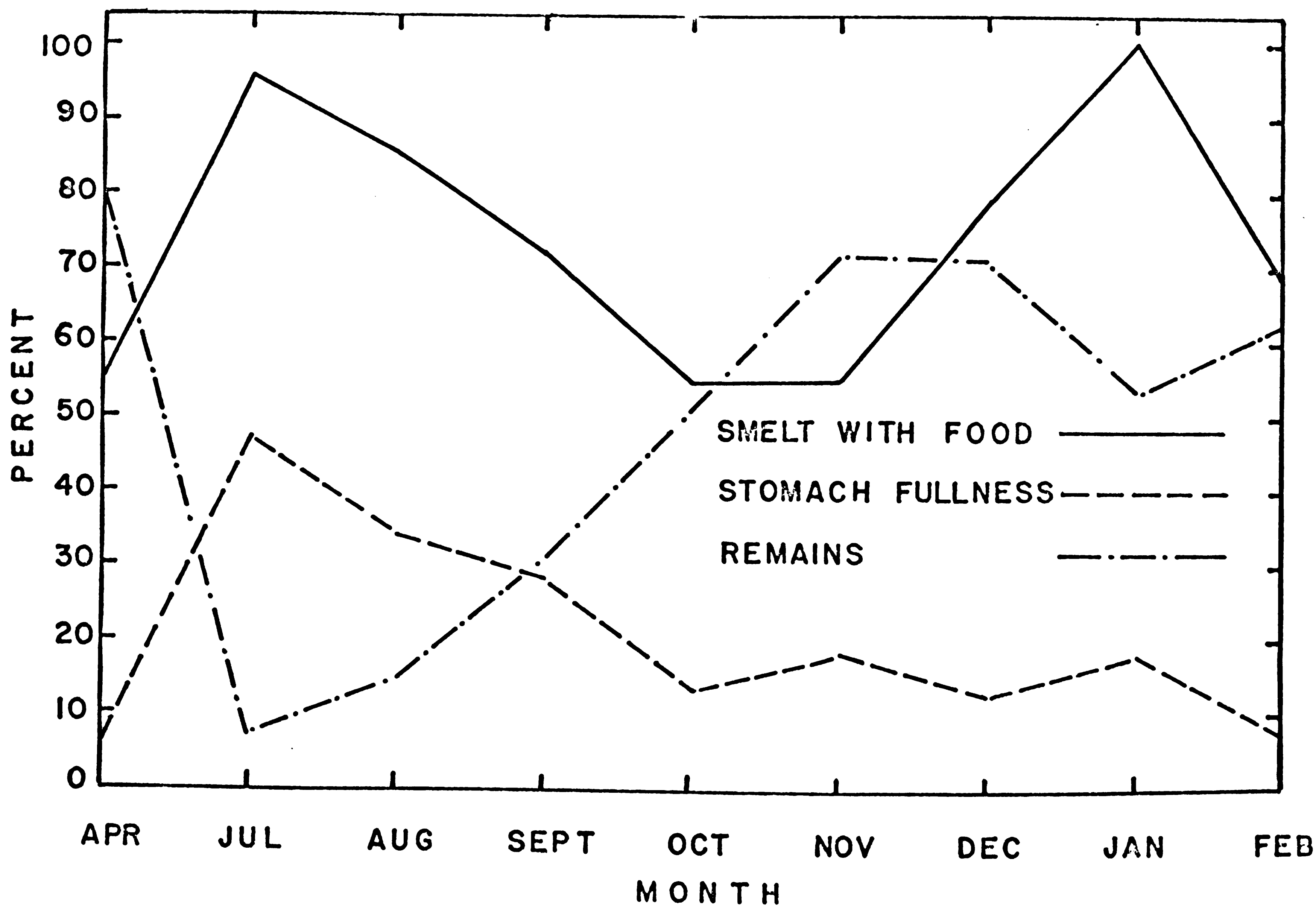

SMELT WITH FOOD
STOMACH FULLNESS
REMAINS
PERCENT
0
10
20
30
40
50
60
70
80
90
100
APR
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MONTH

Fig. 10. Seasonal feeding habits of Gull Lake smelt.


PERCENT
100
90
80
70
60
50
40
30
20
10
0
APR
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MONTH
SMELT WITH FOOD
STOMACH FULLNESS
REMAINS

smelt were captured at night and frozen immediately.

The highest proportion of stomachs with food occurred in July and January. The proportion decreased steadily from July to October. Feeding activity increased slightly in winter. Percent fullness was highest in July, and decreased through April. There was not an appreciable increase in amount of food eaten in winter; more fish may have been feeding but individuals were not eating more. Percent remains was least in summer when most stomachs were full. The proportion of digested material increased in fall, peaked in November and December, decreased slightly in January and February, and was greatest in April.

These data indicate that smelt changed from feeding at night in summer to late afternoon or early evening in the fall. If smelt were all captured at night, the amount of digested matter would not have increased if they had continued to feed at night. The decrease in the number with food and stomach fullness was probably in part due to a decreased metabolism associated with lower temperatures, but mainly due to a change in the time of feeding.

Further evidence that the peak feeding activity of smelt changed from night to late afternoon or early evening was obtained by evaluating diel feeding habits (Table 11). Results from July did not indicate a change in diel feeding activity. The percent of empty stomachs, fullness, and remains did not change significantly, although in early morning of 29 July smelt appeared to feed less. In August there was a definite change in feeding activity from early evening to morning, which indicated that smelt were feeding most intensely in late evening or early morning. In October and November there was a strong indication that smelt were feeding in late afternoon or early evening. It was not possible to predict from these data when smelt were specifically feeding, but a

Table 11. Diel feeding habits of Gull Lake smelt

Date and time	Number	Stomachs empty (%)	Stomach fullness (%)	Remains (%)
15 July				
2115-0005	9	0.0	65.6	5.6
0005-0310	2	0.0	50.0	7.5
0310-0555	4	0.0	63.8	3.0
29 July				
2310-0345	5	0.0	32.0	5.2
0345-0545	5	20.0	20.0	14.8
3 August				
2005-2240	17	11.8	17.6	15.7
2240-0730	13	0.0	65.4	7.5
9 August				
2000-2200	8	37.5	13.8	54.0
2200-0005	10	10.0	26.5	9.4
0355-0730	9	22.2	28.9	18.6
11 October				
1945-2240	4	0.0	30.0	70.0
2240-0035	8	50.0	12.5	55.0
0035-0230	11	27.2	19.5	48.8
0230-0430	8	62.5	3.1	85.0
11 November				
2030-2230	6	16.7	36.7	60.0
2300-2400	10	20.0	30.0	71.3
0030-0900	7	71.4	4.3	85.0

change from night to an earlier feeding peak was indicated.

That smelt were feeding only at night in summer was further confirmed by the fact that only dipteran larvae were eaten. Smelt could not have eaten dipterans during the day because the larvae inhabit the mud on the lake bottom at this time (Woodmansee and Grantham, 1961). In Gull Lake it appeared that once larger dipteran larvae decreased, night feeding offered no advantage, so smelt fed on crustaceans during the day. If they changed to filter feeding, they would have benefited from the light of day in locating aggregations of zooplankton. Small numbers of dipteran larvae were eaten in fall so there was still some feeding in early evening. This agreed with Ferguson (1965) who found Lake Erie zooplankton-eating smelt feeding most actively at dusk and dawn, with minimal feeding in early morning darkness.

Little was done in Gull Lake to determine the role of smelt as food for game fish. A northern pike (Esox lucius) weighing approximately 4 lb. had eaten two adult smelt. In a 5 year study of Gull Lake fish, Huver (personal communication) found that lake trout, yellow perch, smallmouth bass, largemouth bass, and rainbow trout had preyed on smelt.

There is some evidence that smelt in other areas are eaten by the lake trout, yellow perch, northern pike, rock bass, largemouth bass, burbot, brook trout (Salvelinus fontinalis), lake whitefish (Coregonus clupeaformis), walleye (Stizostedion vitreum vitreum), white perch (Roccus americanus), Atlantic salmon (Salmo salar), sauger (Stizostedion canadense), and chain pickerel (Esox niger) (Kendall, 1927; Greene, 1930; Dymond, 1944).

Tharratt (1959) suggested that smelt may be the primary food of Lake Huron yellow perch. McCaig and Mullan (1960) studied fish in Quabbin Reservoir, Mass., after smelt were introduced, and found a significant increase in the growth of lake and brown trout (*Salmo trutta*). This suggests that smelt may be important to the growth and success of some game fish as their individual size and abundance make them ideal prey.

Bathymetric Distribution and Movement

Temperature and dissolved oxygen were measured in Gull Lake during the period of gill netting operations (Fig. 11). The lake was thermally stratified in July and August, with little change in upper and lower temperature limits. The thermocline was between 6 and 15 m (11 and 24 C). In September the upper waters cooled; in October the thermocline was less definite and decreased in depth until 4 November when the lake was homothermous.

In July dissolved oxygen was constant from surface to bottom (8.5 mg/l). In August high oxygen concentrations in the thermocline were due probably to increased phytoplankton production; oxygen decreased to a near critical level in deep water. In September and October there was little change in high oxygen levels at the surface, but there was little or no oxygen below 20 m until the lake "turned over" in late October. By 5 November oxygen levels were high (over 10 mg/l) and constant from surface to bottom.

The bathymetric distribution of Gull Lake smelt was determined during 4 months of vertical gill netting (Table 12). These data were expressed as percent of total catch for each month (Fig. 12). Smelt were captured primarily during darkness. In July and August almost all smelt were captured between 8 and 20 m. In August no smelt were taken below 20 m. Smelt captured in October were evenly distributed from surface to bottom. In November smelt captures were weighted

Fig. 11. Gull Lake temperature (C) and dissolved oxygen (Mg/l) profiles.

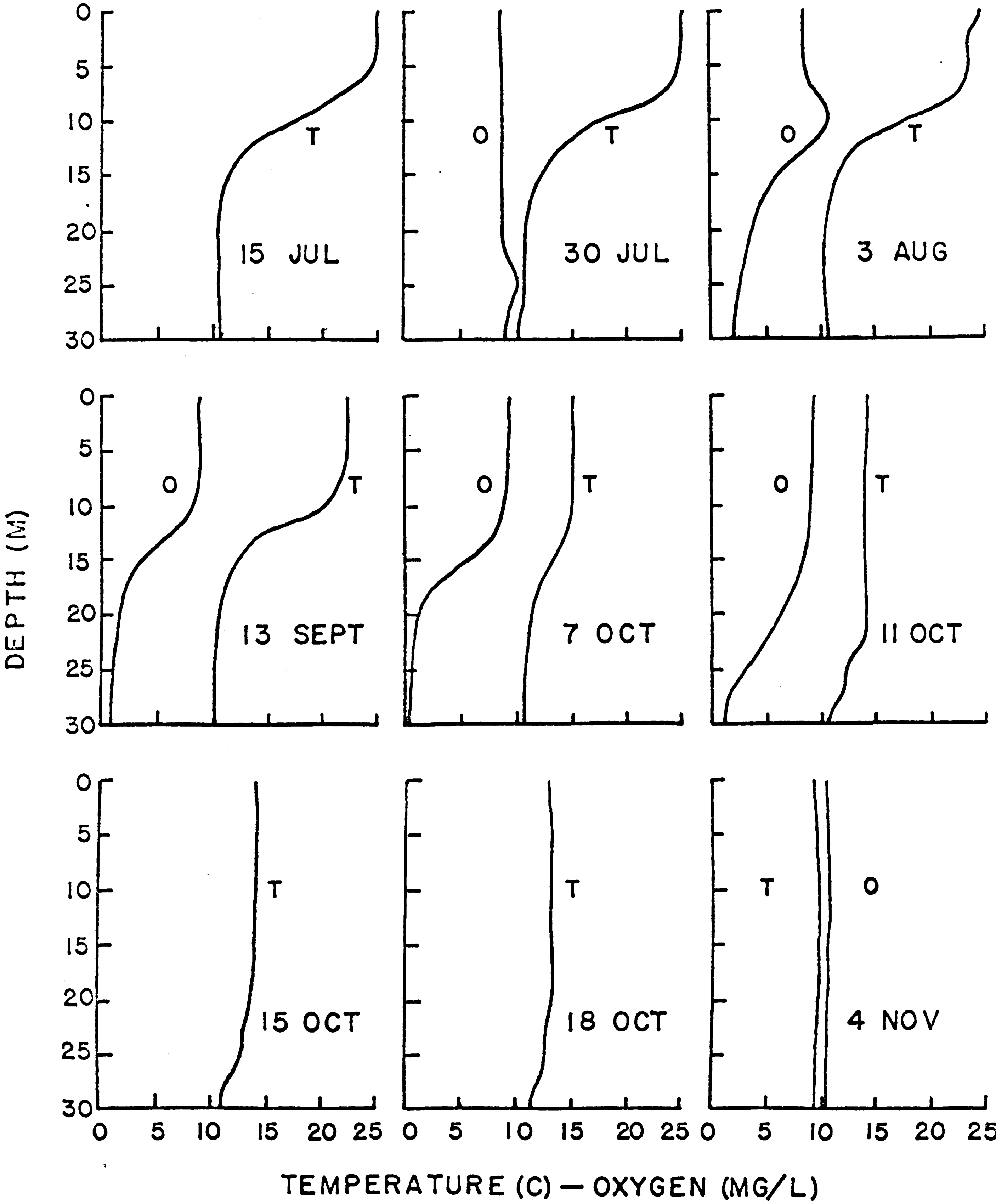

DEPTH (M)
0
5
10
15
20
25
30
T
15 JUL
O
T
30 JUL
O
T
3 AUG
O
T
13 SEPT
O
T
7 OCT
O
T
11 OCT
T
15 OCT
T
18 OCT
T
O
4 NOV
0 5 10 15 20 25
TEMPERATURE (C) — OXYGEN (MG/L)

Table 12. Seasonal bathymetric distribution of Gull Lake smelt

Depth (m)	July	August	October	November
1-4			8	2
5-8			4	5
9-12	5	24	6	3
13-16	8	23	8	3
17-20	9	13	6	3
21-24			2	1
25-28	3		2	
29-32				
Total	25	60	36	17

Fig. 12. Seasonal bathymetric distribution of Gull Lake smelt expressed in percent of catch for each month.

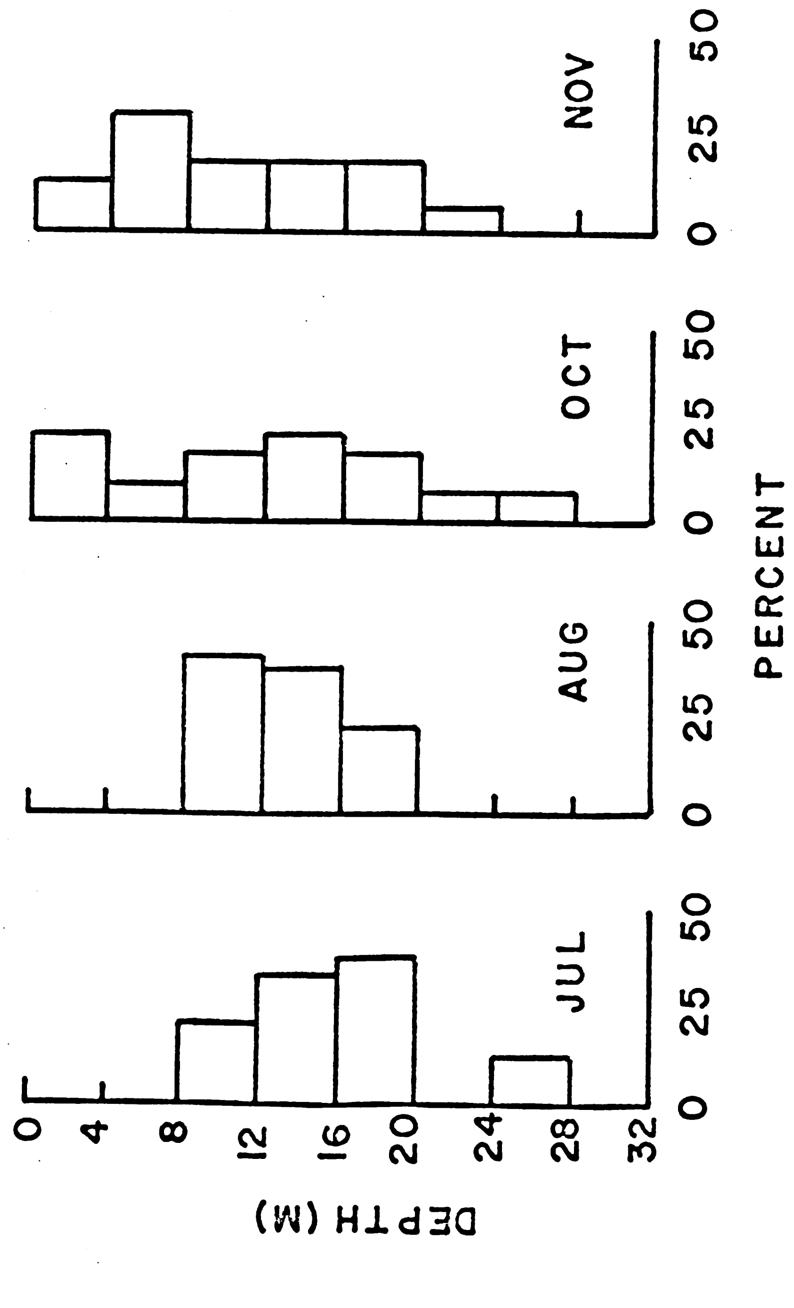
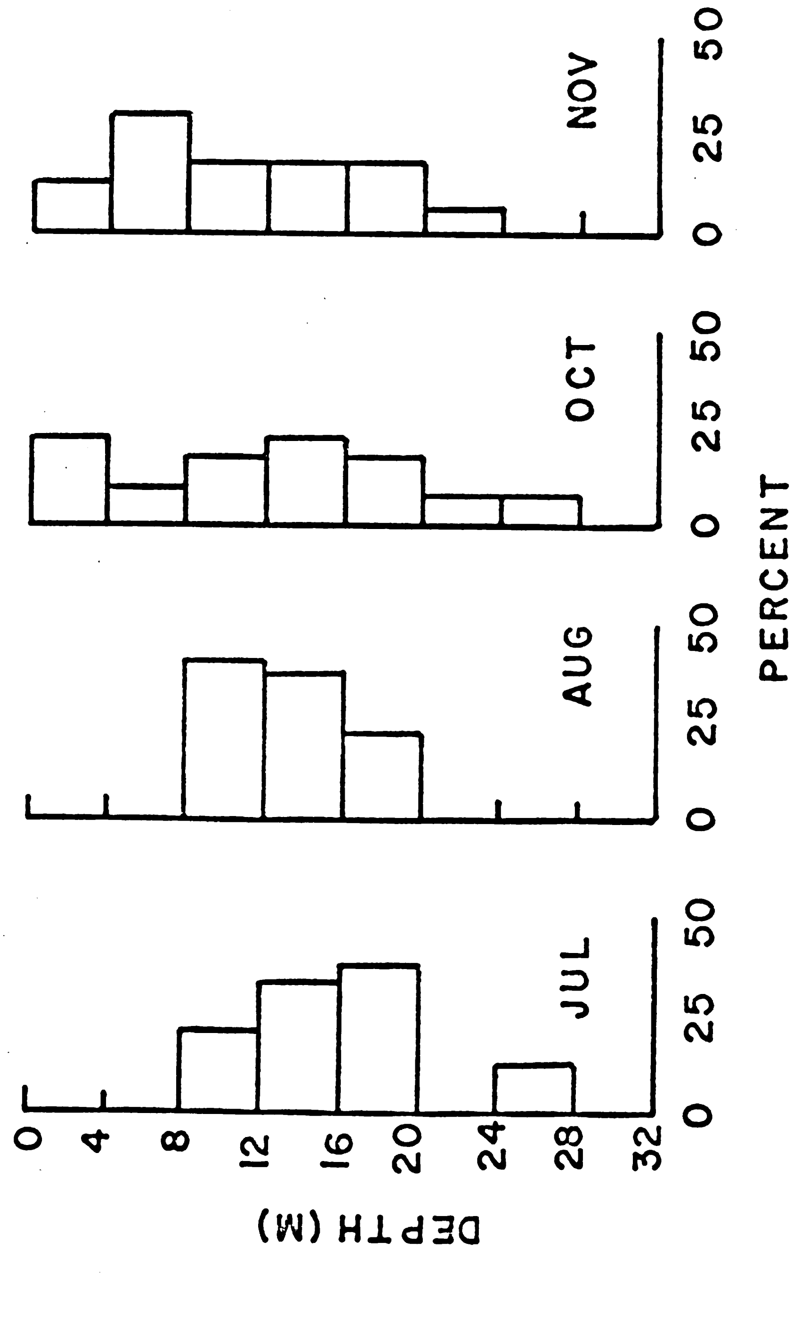

DEPTH (M)
0
4
8
12
16
20
24
28
32
0
25
50
JUL
AUG
OCT
NOV
PERCENT

Fig. 12. Seasonal bathymetric distribution of Gull Lake smelt expressed in percent of catch for each month.


JUL
AUG
OCT
NOV
0
25
50
PERCENT
0
4
8
12
16
20
24
28
32
DEPTH (M)

toward the surface, although numbers were too few to draw conclusions. The observed distribution showed a predominance of smelt in midwater at night. No fish were collected below 28 m because the net was short of the bottom.

Echo recordings obtained at night in July and August supported the gill netting results and showed little smelt activity of any kind below 20 m.

Although smelt are sometimes found in warm water (Kendall, 1927), they are a cold water species confined to deeper water during summer thermal stratification. In summer smelt have been recorded in lakes of New York below 12 m (Odell, 1932), and in the Great Lakes from 18 to 34 m (Van Oosten, 1953) and 27 to 45 m (Gordon, 1963). They were found at a thermal preference of 12.8 C in Lake Champlain (Greene, 1930), 6.6 to 8.3 C in Cayuga Lake (Galligan, 1962).

The bathymetric distribution of Gull Lake smelt appeared to be controlled by levels of dissolved oxygen, temperature, and their own feeding habits. Except for 11 October, smelt captured in the 4 months illustrated in Fig. 12 were collected under conditions of sufficient oxygen at all depths. On 11 October there was 0.0 mg/l below 27 m, but fish were counted on echo recordings at 26 m where oxygen was 0.8 mg/l. In September and early October there were no fish observed below 1.0 mg/l. As the 1.0 mg/l isopleth was depressed with fall turnover, fish moved downward with it. Pearse and Achtenberg (1921) and Bardach (1955) demonstrated that an oxygen deficiency limited the depth of yellow perch, and that fish are dependent on a minimum level of oxygen tension. It was assumed that Gull Lake smelt did not venture much below a certain minimum level of oxygen (1.0 mg/l).

Since there was sufficient oxygen during the 4 months of vertical gill netting, temperature and feeding were the two primary factors that influenced smelt bathymetric distribution. In July and August smelt were feeding extensively on Chaoborus and Tendipedidae larvae; larvae were observed by echo recorder concentrated between the surface and 20 m at night. This would explain why smelt captured at night were almost all above 20 m, but the fact that they were not above 8 m had to be attributed to a temperature (22 C) beyond which they would not pass. This suggested that temperature was a more critical factor than their feeding habits. Ferguson (1958) in laboratory experiments showed that temperature acting alone could control the distribution of fish, and suggested that a thermocline may act as a thermal or density barrier. He also presented evidence that although light, feeding activity, and social behavior may interfere with precise temperature selection, temperature is the main controlling factor of fish distribution when oxygen is not a consideration. Fry (1947) defined the preferred temperature of fish as the "region in an infinite range of temperature, at which a given population will congregate with more or less precision." He defined the temperature corresponding to the maximum point of an activity curve as a "true optimum, a temperature at which the internal economy of an organism can function best to give a particular response to a given stimulus." Fish, therefore, tend to congregate at a temperature at which, in terms of energy gain and loss, a given activity can be most efficiently carried on.

Smelt generally do not penetrate the thermocline and move into warmer water. The advantage smelt in Gull Lake would have gained by moving into warmer water to increase their feeding space, assuming they could have adapted to the temperature, would have been offset by an increased metabolism and energy loss. In October and November, when the lake was not stratified and surface temperature was 14 C, smelt were collected at all depths. Smaller dipteran larvae were not concentrating in upper waters at that time. Smelt were not in upper waters for feeding purposes, but were feeding primarily on crustaceans at all depths.

The vertical gill net was lifted every 2 or 3 hr from July to November to determine if there was vertical movement in the smelt population (Table 13). Since most smelt were captured in midwater in July and August, movement was not observed. From October to November the number of captured smelt was small, but a movement and dispersal downward at night was indicated. In early evening most smelt were captured in upper waters, but in early morning they were captured in deep water as well.

Pennak's (1943) quartile curve method was applied to data obtained from the echo recordings between Points A and B (Fig. 2) to depict vertical movement of smelt. One modification of the method was made: to permit the determination of the first, second, and third quartile depths on the basis of percent ages in 4 m intervals, linear interpolation was employed so quartile curves could be tabulated to the nearest meter. The quartile depths were determined from a cumulative frequency column and plotted in Figs. 13 and 14. Pennak's method was devised for zooplankton migrations, but since a finite number of fish in a known volume of water was considered, it was considered a valid method for recording fish movement.

A total of three dates were combined for the 24 hr transect series in Fig. 13. Although the dates were widely spaced, other echo recordings from this study showed that the trends illustrated were representative for those times at all dates. There was a marked diel variation in

Table 13. Diel bathymetric distribution of Gull Lake smelt

	Depth (m)							
Date and time	1-4	5-8	9-12	13-16	17-20	21-24	25-28	29-32
15 July								
2115-0005				5	4			
0005-0310			2					
0310-0555			1	1	2			
30 July								
2310-0345			1		3		1	
0345-0545			1	2			2	
3 August								
2005-2240			10	5	2			
2240-0740			8	8	10			
9 August								
2000-2200			1	6	1			
2200-0005			5	4				
11 October								
1945-2240	1	1	1	1				
2240-0035	2	1	1	1	2		1	
0035-0230	2	1	1	5	1	1		
0230-0430	2	1	1	1	2		1	
18 October								
1930-2130			1					
2130-2330	1		1					
0130-0730					1	1		
4 November								
2230-0015			1					
0015-0215	2					1		
7 November								
1730-0845		1	1	1	1			
11 November								
2030-2230		2						
0030-0900		2	1	2	2			

Fig. 13. Diel vertical distribution and movement of Gull Lake fish illustrated by the quartile curve method. Shaded areas indicate an absence of fish. Vertical dashed lines denote sunset and sunrise. Three dates are represented: 15 December (1300-1800 hr); 4-5 November (1900-0900 hr); 15 October (1000-1200 hr).

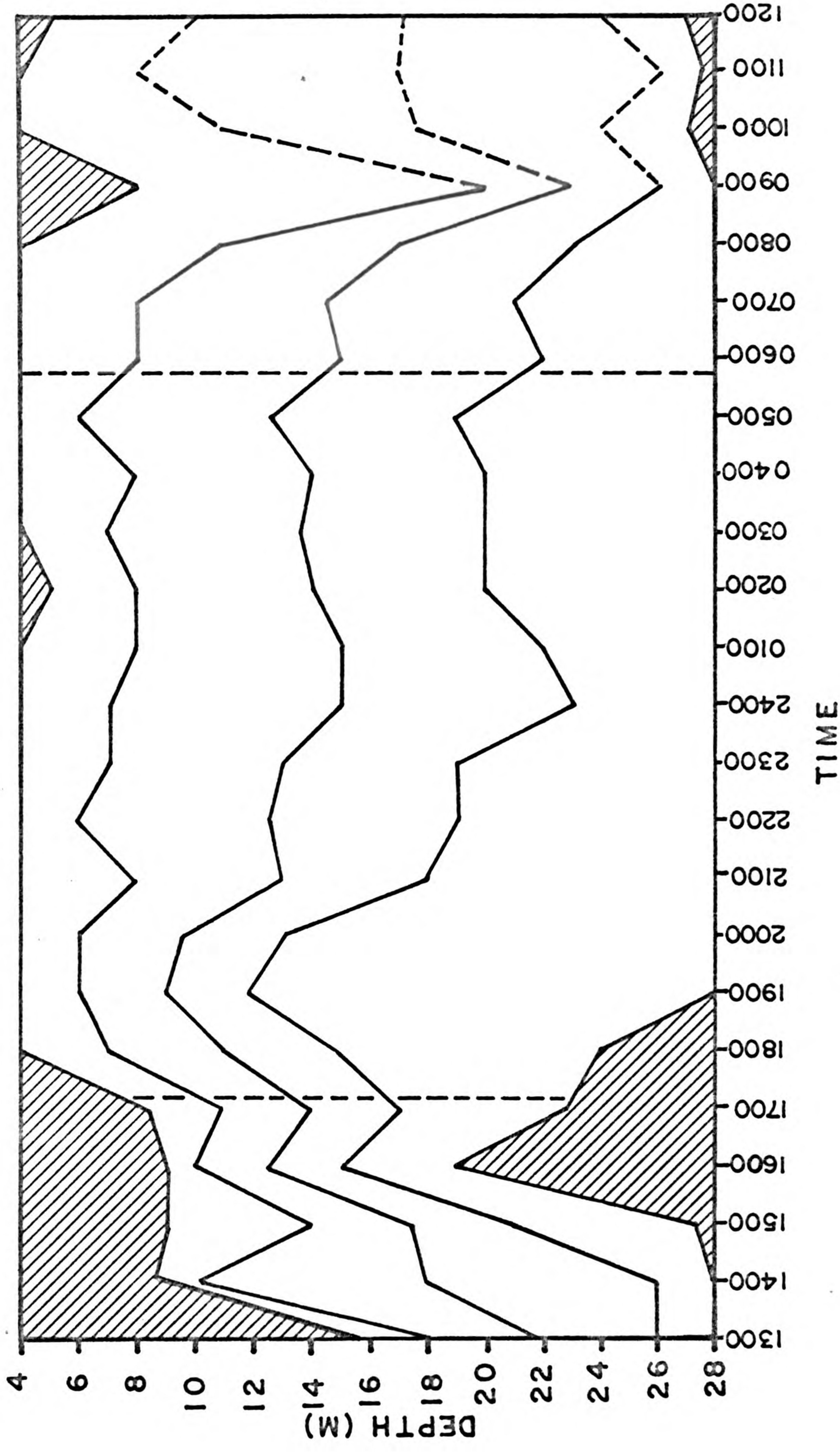
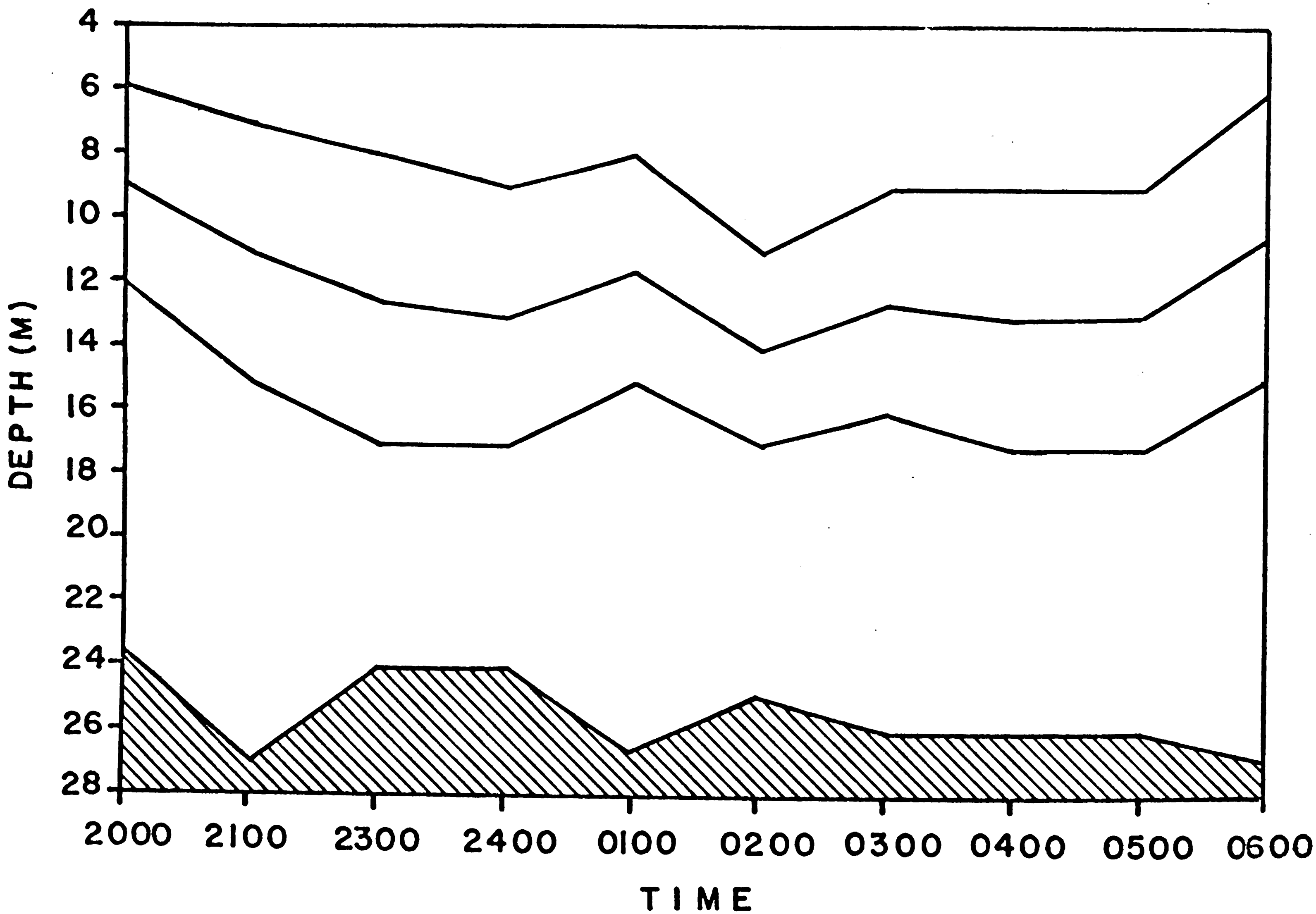

DEPTH (M)
4 6 8 10 12 14 16 18 20 22 24 26 28
TIME
1300 1400 1500 1600 1700 1800 1900 2000 2100 2200 2300 2400 0100 0200 0300 0400 0500 0600 0700 0800 0900 1000 1100 1200

Fig. 14. Diel vertical distribution and movement of Gull Lake fish illustrated by the quartile curve method (11-12 October). Shaded areas indicate an absence of fish. Oxygen deficiency below 26 m.


4
6
8
10
12
14
16
18
20
22
24
26
28
DEPTH (M)
2000
2100
2300
2400
0100
0200
0300
0400
0500
0600
TIME

numbers of fish found within the transect (Table 14). Fig. 13 and Table 14 show that at 1300 hr the few fish (7) recorded were below 16 m. Numbers did not increase appreciably until 1800 hr. There was a vertical rise of fish until 1900 hr when 75% was above 12 m. The absence of fish in upper and lower waters during that period indicated they were moving simultaneously toward the surface.

After 1900 hr fish increased and had an apparent downward movement and dispersal. By 2400 hr they were evenly distributed from surface to bottom, except for a greater density from 4 to 8 m that did not change until 0700 hr. At 0100 hr there was another rise that peaked at 0500 hr. The maximum number of fish was at 0600 hr. After 0600 hr numbers decreased and fish moved toward bottom; by 0900 hr 75% were below 20 m. Another sharp rise at 1000 hr resulted from a school in shallow water. They may have been smelt, but should not be considered because the rest of the fish were concentrated in deep water. It was probably a littoral school moving to deeper water.

Because the three quartiles coincided in the evening and morning, all fish appeared to move simultaneously in one direction. At night a constant proportion remained above 6 to 8 m, while the remainder dispersed and moved downward.

The results in Fig. 14 strengthened the previous data. Numbers of fish during this series (11-12 October) were larger, but a similar movement was observed. From 2000 to 2300 hr there was a general movement downward ending at 0200 hr. The 50% quartile dropped from 9 to 14 m. The upper half appeared to move downward more than the lower half. The largest number was at 0200 hr; beyond 0200 hr the apparent numbers decreased while fish again moved toward the surface. The absence of fish on bottom was attributed to an oxygen deficiency.

Table 14. Number of fish in each sonar transect expressed as percent of maximum number for one transect

Date and time	Number	Percent of maximum
15 December		
1300	7	3.2
1400	5	2.3
1500	9	4.1
1600	5	2.3
1700	8	3.7
1800	59	27.2
4-5 November		
1900	46	21.2
2000	67	30.9
2100	61	28.1
2200	59	27.2
2300	87	40.1
2400	86	39.6
0100	98	45.2
0200	93	42.9
0300	140	64.5
0400	144	66.4
0500	133	61.3
0600	217	100.0
0700	136	62.7
0800	83	38.2
0900	36	16.6
15 October		
1000	56	25.8
1100	55	25.3
1200	42	19.4
11-12 October		
2000	195	49.8
2100	260	66.3
2300	232	59.2
2400	200	51.0
0100	338	86.2
0200	392	100.0
0300	372	94.9
0400	313	79.8
0500	347	88.5
0600	110	28.1

Work with echo recorders should be considered with reservation because of the difficulty of relating echo traces to species. In Gull Lake differences between individual traces and schools could not be distinguished. Conclusions concerning species recorded had to be drawn after considering the behavior and habitats of all species present, and by utilizing other sampling methods when traces were recorded.

Of the major species present in Gull Lake, the logperch, bluntnose minnow, yellow bullhead, longnose gar, smallmouth bass, largemouth bass, rock bass, green sunfish, and bluegill were restricted to the littoral zone; the white sucker was restricted to the benthic zone; brook silversides and young bluegills were found in the upper limnetic region; and the cisco, rainbow trout, lake trout, and smelt were considered lower limnetic forms. The yellow perch was most abundant in shallow water but ranged into all parts of the lake (Greene, 1930; Odell, 1932; Lagler et al., 1962).

Fish associated with the upper limnetic (surface) region and those restricted to the littoral zone were not included in the analysis of fish movement because the 0 to 4 m interval, including the major zone of rooted vegetation, was omitted. If the littoral zone fish had been counted, they would not have contributed to an observed vertical movement because they were restricted to bottom. SCUBA operations at night revealed most littoral fish resting on bottom, so there was little movement in any direction.

Benthic fish are restricted to bottom in deeper water, except during oxygen depletion. Their contribution to numbers of fish counted was lessened by excluding all fish traces below 28 m. Very few traces were recorded close to bottom at any depth, so benthic fish were probably scarce.

Ciscos exhibit diel vertical movements (Cahn, 1927). In Gull Lake, however, the few captured by fishermen and gill nets indicate the population is small. Rainbow and lake trout are not abundant in Gull Lake (Kalamazoo Gazette, 5 March 1967). These species do not reproduce successfully in lakes of Michigan (Taube and Bacon, 1952), so they are stocked annually.

Hasler and Villemonte (1953) showed that physoclistous yellow perch cannot have an extensive vertical migration, and that at night they remained close to shore in contact with bottom in a state of "sleep". In Gull Lake yellow perch would not have been in midwater at night; they may have been recorded in daylight but would not have been moving vertically.

The 1/2 inch gill net, which captured yellow perch when on bottom, was fished vertically at night at Station 5 (Fig. 1). In 4 months 138 (88.4%) smelt, 16 (10.2%) yellow perch, and 2 (1.4%) ciscos were captured. In 8.7 hr the Isaacs-Kidd trawl captured 34 smelt, 1 brook silversides, and 1 yellow perch between 4 and 16 m, and 95 young bluegills between 5 and 10 m. Most bluegills were less than 20 mm, and were captured primarily during September before echo recordings were evaluated. These data and knowledge of the habits and behavior of other fish in Gull Lake provide strong evidence that most fish recorded were smelt, and that recorded vertical movements applied to the smelt population.

Smelt are known to be schooling animals (Kendall, 1927). They were probably in deep water during the day and accustomed to seeing one another. As darkness approached they may have lost their tendency to school and moved independently in the water column, toward surface in the evening and back toward bottom at dawn. In approaching daylight they probably schooled again in deep water, leaving the transect free of individual fish.

The fish recorded in Gull Lake, assumed to be mostly smelt, exhibited vertical movements similar to most other aquatic animals, which according to Clarke and Denton (1962) "...are thought to be deepest in the daytime, to ascend at dusk, to sink or become more scattered during the night, and to rise again at dawn before descending for the new day." They suggested that animals in the sea which find upper waters unsafe in the bright light of day, hide in the depths and move into food-rich upper waters at night, thus extending their feeding space and food source while reducing the effectiveness of predators.

Clarke and Denton (1962) emphasized that vertical migrations of animals are more closely correlated with the strength and rate of change of penetrating daylight than any other stimulus (e.g. temperature and pressure). Clarke and Backus (1964) felt it was unlikely that temperature has an effect on vertical migrations. Clarke and Backus (1956) suggested that aquatic animals do not remain at or move with an optimum illumination, but are stimulated to move vertically by a reduction in light. Once the stimulus is received, animals move steadily toward surface even though it means moving into higher intensities. This possibility was referred to by McNaught and Hasler (1964).

Brawn (1960) indicated that changes in light intensity may have initiated diel changes in depth of Atlantic herring (*Clupea harengus harengus*). Richardson (from McNaught, 1961) concluded that diel vertical movements of Atlantic herring and sprat (*Clupea spattus*) were in direct response to light.

Many studies on fish behavior show a close correlation between diel vertical movements of fish and their food. Welsh *et al.* (1937) found pelagic fish in the Sargasso Sea moving vertically with their primary food (copepods). McNaught and Hasler (1961) suggested that white bass followed vertically moving aggregations of Daphnia by means of an acute sense of smell. Northcote et al. (1964) found the peamouth (Mylocheilus caurinus) moving with and feeding on rising insect larvae and cladocerans at night.

The question arises as to whether fish anticipate the rise of zooplankton and move toward surface in response only to light, if they follow dense aggregations of zooplankton upward that are known to respond to light, or if they respond to other unknown or combination of factors.

Ferguson (1965) found that the smelt in Lake Erie ascended from bottom in late afternoon, remained dispersed in midwater during the night, and descended abruptly to bottom at dawn. The evening ascent was accompanied by active feeding on zooplankton. The morning descent may or may not have been accompanied by zooplankton feeding. Since smelt were not feeding at night, Ferguson could not justify their movement to midwater on the basis of food procurement, but suggested light as the factor to which they were responding. He felt that smelt were feeding while ascending and descending simply because they were most active at those times, for as Swift (1964) has demonstrated for the brown trout, it "feeds becuase it is active, and is not active because it is feeding."

In the fall the diel vertical movements and feeding activity of Gull Lake smelt were similar to those of Lake Erie smelt. It was shown that Gull Lake smelt were not feeding at night, probably because of an absence of larger dipteran larvae concentrating in upper waters in the fall. Since they were not feeding at night, they would not have been moving into upper waters for food procurement. It appeared that the only factor to which smelt were responding was light.

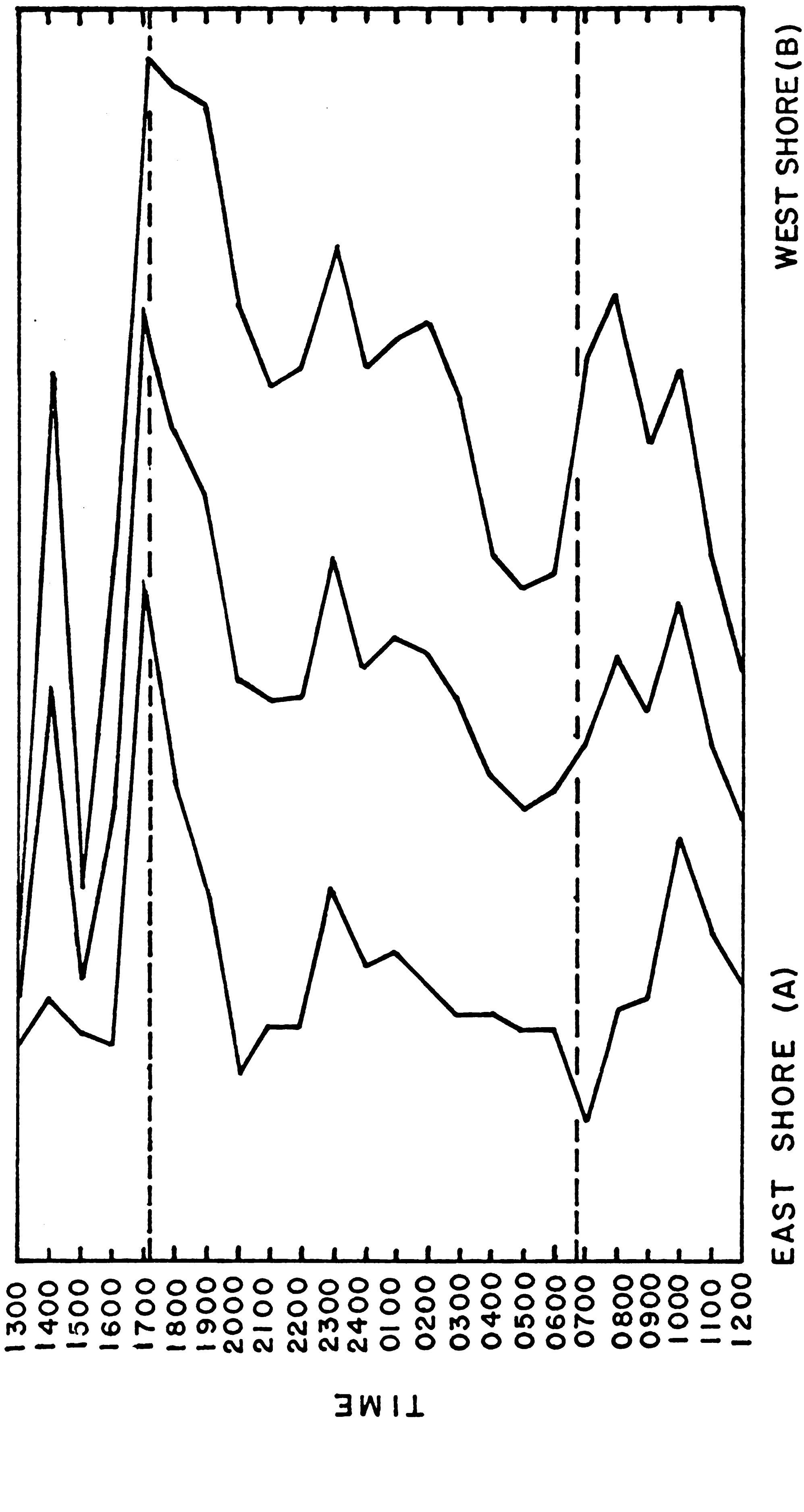
This observed behavior may have evolved for feeding in the summer months when great concentrations of pupating dipteran larvae migrate to upper waters at night. During these months smelt may have actively followed dense aggregations of larvae upward, but they were probably responding mainly to light since they continued their vertical movements in the fall. This migration behavior insured that smelt had access to an abundant supply of food where and when they were relatively safe from predators.

The quartile curve method was used to measure horizontal movements toward or away from shore. Quartiles were determined from a horizontal cumulative frequency column. The position of each quartile was determined to the nearest 0.1 of an interval by linear interpolation.

Fig. 15 illustrates the horizontal movement of fish for the 24 hr series considered in Fig. 13. In the early afternoon fish were concentrated near the east shore. In late afternoon there was a dispersal and movement to the west until 1700 hr when 75% were concentrated in the west half of the transect. From 1800 hr until morning fish were evenly distributed, and fluctuated from east to west. There was a movement toward the east shore in the morning.

Except for the period from 0700 to 0800 hr, the closeness of fit of the three quartiles suggests there was little movement toward or away from opposing shores by significant numbers of fish at any one time. In other words, fish did not appear to move from both shores outward in the evening at the same time, but seemed to shift either east or west together. Only between 0700 to 0800 hr was there a universal movement toward both shores. From 1000 to 1200 hr a majority returned back to the east shore, where they were first

Fig. 15. Diel horizontal distribution and movement of Gull Lake fish illustrated by the quartile curve method. Horizontal dashed lines denote sunset and sunrise. Three dates are represented: 15 December (1300-1800 hr); 4-5 November (1900-0900 hr); 15 October (1000-1200 hr).

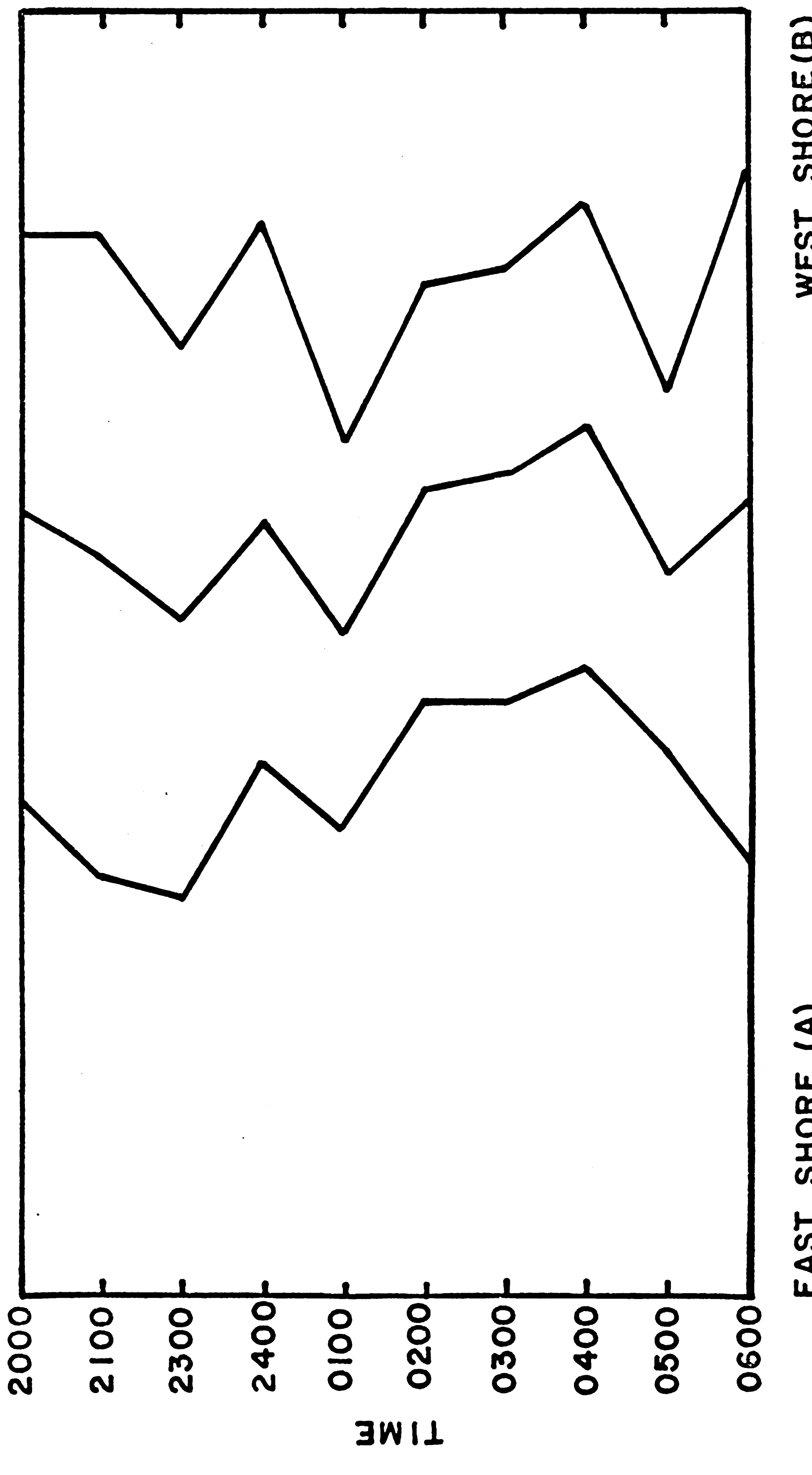

EAST SHORE (A)
WEST SHORE (B)
1300
1400
1500
1600
1700
1800
1900
2000
2100
2200
2300
2400
0100
0200
0300
0400
0500
0600
0700
0800
0900
1000
1100
1200
TIME

observed at 1300 hr the previous day.

The same horizontal movement was demonstrated on 11-12 October (Fig. 16). Fish were concentrated toward the west shore the entire evening, and exhibited periodic east or west fluctuations. The fish again appeared to move as a whole; equal movement away from opposing shores was not observed. Between 0500 and 0600 hr there was universal movement toward both shores.

These data suggest that although there was not a simultaneous movement away from both shores in the evening, there may have been a slight movement toward the shores at dawn. There was a possibility that fish moved out from the west shore in the evening, were concentrated more toward the middle at night, and returned to the east shore in the morning. Although movement toward or away from shore may not have been universal, schools may have dispersed in the evening and formed in the morning near either of the shores. Unfortunately, there were too few data to determine whether schools were forming and dispersing along just one shore, or if they were on both shores away from the echo recorder.

Fig. 16. Diel horizontal distribution and movement of Gull Lake fish illustrated by the quartile curve method (11-12 October).


TIME
2000
2100
2300
2400
0100
0200
0300
0400
0500
0600
EAST SHORE (A)
WEST SHORE (B)

Summary and Conclusions

The study of American smelt in Gull Lake revealed distinct relationships between aspects of their life history, trophic patterns, and bathymetric distribution and movement. The maximum size and mean length and weight of age groups of Gull Lake smelt were less than smelt in other environments. Younger fish were of comparable size, but differences increased with age. The physical environment may have adversely affected growth, but the primary influencing factor was apparently a difference in diets of mature fish.

Smelt of similar size and genetic background in other areas changed their food habits with age and fed on large crustaceans (*Mysis*) and fish. Smelt in Gull Lake fed on small crustaceans and insect larvae, and did not feed on large crustaceans and fish at any time. *Mysis* is not found in Gull Lake, but the absence of fish in their diet was probably the major factor responsible for their smaller size.

A study of the bathymetric distribution of Gull Lake smelt demonstrated that they were restricted from feeding on fish. In summer they were confined to the colder hypolimnion, and did not penetrate the thermocline to feed on young fish in warm surface waters. By fall when adult smelt were in upper waters, potential prey had grown so they were too large to be fed upon. Therefore, the mid-summer distribution of smelt and the kinds and distribution of other fish in the lake indirectly affected smelt growth rate.

Percent age composition of Gull Lake smelt was related to natural mortality and selectivity of sampling gear. Few age-group III and older fish indicated a high mortality in the 4th year. Fewer mature males than females could have been caused by a mortality of males in poor condition during spawning. Fewer immature males could have resulted from behavioral differences that made them more susceptible to predation or less susceptible to capture. A smaller male could have resulted from a higher metabolism.

Gull Lake smelt fed on the most available food, but probably had a preference for large dipteran larvae. Pupating dipterans were eaten exclusively in summer when crustaceans were also abundant. Data indicated a change from night to daylight feeding, accompanied by a change to filter feeding, when the composition of dipteran larvae populations changed so that only smaller larvae with limited vertical movements were present.

Smelt in Gull Lake exhibited diel vertical movements that could have evolved from feeding on dipteran larvae in upper waters at night. However, it was most closely related to changes in light intensity because the migrations continued after smelt no longer fed on insect larvae.

Life history data give insight into the population dynamics of smelt. Their rapid growth and relatively short lifespan emphasize the need for harvesting smelt after they first spawn (beginning of third growing season) and before natural mortality is too great (4th year). Gear could be developed to exclude younger smelt.

Food habits studies suggest that smelt could be introduced as food for game and commercial species in cold deep lakes that strongly stratify in summer, without fear of competition for food or predation on valuable fry.

Data on bathymetric distribution and movement indicates that smelt may be effectively captured using midwater trawls at night. This would extend the fishing season and reduce fluctuations in existing catches.

It is clear that additional work is needed before the role smelt play in the aquatic environment is completely understood, and before they can be effectively controlled and utilized.

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Appendix

The beam of sound from the Furuno echo sounder gave an uninterrupted picture of fish distribution within the Gull Lake transect (Fig. 2) because of the slow boat speed and the high number of soundings per min. The methods utilized were determined to be valid after experimentation with empty glass vials. The sound pulse is reflected by any plane that represents a boundary between two media, and the strength of reflection is determined by the difference in density and speed of sound in the original and new medium (Midttun, U. S. Bureau of Commercial Fisheries, unpublished report). Studies on acoustic characteristics of fish demonstrate that, although the swim bladder occupies only 5 to 8% by volume in fresh-water species, it accounts for 40 to 80% of the signal reflected back. This is explained by the fact that acoustic reflectivity of fish flesh is about 4.6%, bone about 26%, and air 100% (Jones and Pearce, 1958; Cushing and Richardson, 1955). The appearance of the trace is dependent primarily on the size of the swim bladder. Air filled glass vials comparable in size to swim bladders gave approximately the same echo response as fish.

A glass vial (60 by 7 mm) was fastened to a weighted line so the vial rested horizontally like the swim bladder of a fish. The vial was suspended at various depths and scanned with the echo sounder. At 30 m and gain 4, the vial returned an echo comparable to traces that were counted as fish, at that depth and gain. It was assumed, therefore, that all smelt were recorded at all depths at that gain, since the surface area of air bladders of age-group I smelt were comparable in size to the plane surface area of the vial. Age-group 0 smelt are usually associated with the surface; at those depths an echo would have been reflected without difficulty.

At a high gain an individual Chaoborus, because of its hydrostatic organs, is recorded as strongly as a fish echo. After experimentation it was decided that at gain 4 Chaoborus larvae were not recorded; only random strong echoes assumed to be fish remained.

Sound energy was sufficient to return an echo from all fish at all depths within the half-sound pressure angle because of the narrow sound beam. Due to the directivity of sound from the transducer face, however, weaker sound waves were emitted over an area larger than the half-sound pressure angle, particularly in upper waters. That the sounder was on gain 4 tended to reduce this effect, but values for fish numbers in upper waters may have been too high. This was lessened by not including the 0 to 4 m interval. The scattering of sound from the transducer face was of some value because it probably recorded fish between the main sound pulses. At 500 rpm the boat traveled 1.1 ft between pulses, at 1000 rpm it traveled 2.0 ft, which meant that a triangle of water 8 ft and 15.3 ft deep respectively was not included within the half-sound pressure pulses. However, fish in this water were probably reached by sound waves outside the half-sound pressure beam.