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A STUDY OF THE FEEDING HABITS OF FOUR SPECIES OF FISH, Alosa pseudoharengus, Coregonus hoyi, Perca flavescens, AND Osmerus mordax, AT THREE SITES ON LAKE MICHIGAN, AS COMPARED TO THE ZOOPLANKTON, PHYTOPLANKTON AND WATER CHEMISTRY OF THOSE SITES.

Michigan State University, Ph.D., 1973
Ecology

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A STUDY OF THE FEEDING HABITS OF FOUR SPECIES OF FISH, *Alosa pseudoharengus*, *Coregonus hoyi*, *Perca flavescens*, AND *Osmerus mordax*, AT THREE SITES ON LAKE MICHIGAN, AS COMPARED TO THE ZOOPLANKTON, PHYTOPLANKTON AND WATER CHEMISTRY OF THOSE SITES.

By

Glen Allan Rasmussen

A THESIS

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ABSTRACT

A STUDY OF THE FEEDING HABITS OF FOUR SPECIES OF FISH, Alosa pseudoharengus, Coregonus hoyi, Perca flavescens, AND Osmerus mordax, AT THREE SITES ON LAKE MICHIGAN, AS COMPARED TO THE ZOOPLANKTON, PHYTOPLANKTON AND WATER CHEMISTRY OF THOSE SITES.

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Four species of fish, *Alosa pseudoharengus*, *Coregonus hoyi*, *Perca flavescens* and *Osmerus mordax*, were studied at three sites on Lake Michigan in terms of age and growth characteristics, depth selection and food preferences. All four species showed repeatable depth selection patterns on a yearly basis and all showed overlap in their food selection. All four species are selective zooplankton predators in the sense of Brooks and Dodson (1965) but the alewife, *Alosa* is the most efficient of the four in terms of ability to acquire this food source. Large smelt and perch over six inches in length tend to piscivory.

Zooplankton and phytoplankton numbers were also followed at the three study sites as well as basic chemical parameters. All showed fluctuations over time. It is hypothesized that selective predation influences zooplankton numbers which in turn influences phytoplankton abundance.

ACKNOWLEDGMENTS

I would like very much to thank the following people without whom this thesis would have been impossible; Dr. James Braddock, who persevered with me for four years and who gave invaluable help, Dr. Eugene Roelofs, who was my English consultant, Dr. Clarence McNabb, who gave me both philosophical and scholarly help, and Dr. Peter Tack, who gave me access to data and provided critical evaluation of the manuscript. I would also like to thank Dr. Charles Liston and crew and The Consumers Power Company for the data collected at the Ludington site during 1972. And special thanks goes to my wife Susan who helped in all ways to get the project done.

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INTRODUCTION

On the basis of current patterns and submarine ridges, Lake Michigan can be divided into two major basins, herein designated as north and south. In these studies, the southern basin was considered to be that area south of a line connecting Muskegon, Michigan and Milwaukee, Wisconsin, while the northern basin included everything north of this line excluding Green Bay and the Mackinac Straits area (Figure 1). Each of these basins shows considerable internal mixing as well as mixing between basins (Ayers et al., 1958). Three study sites were chosen, one in the southern basin - three to five miles north of the Kalamazoo River, Allegan County, Michigan (1970-1972), and two in the northern basin - one off Big Sable Point, Mason County, Michigan (1970-1971) and another four miles south of Ludington, Mason County, Michigan (1972). Latitudes and longitudes for these sites are given in Figures 2-4. These sites were chosen on the assumption that the internal mixing characteristics of the basins would create different physical and chemical effects at the different sites, thus affecting phytoplankton, zooplankton, and fish characteristics. The purpose of these studies was thus severalfold:

(1) To determine if the internal mixing was great enough and the inter-basin mixing small enough to affect zooplankton food stocks in such a manner as to change the eating habits of the fish at the Saugatuck site versus the Ludington-Big Sable Point sites.

(2) To determine if the selective feeding hypothesis of Brooks and Dodson (1965) could be substantiated by stomach analyses of fish from Lake Michigan.

(3) To determine if this selective feeding could alter zooplankton numbers.

(4) To see if fluctuations in zooplankton numbers and species would cause fluctuations in the numbers and species of phytoplankton.

(5) To determine the effect of temperature, sex, and age on the distribution and feeding habits of certain fish species in Lake Michigan. Of particular interest were the alewife, Alosa pseudoharengus, the bloater, Coregonus hoyi, the yellow perch, Perca flavescens, and the smelt, Osmerus mordax. An effort was made to examine these four species in the lake in terms of: food preferences, depth distribution throughout the year, and inter- and intra-specific competition for food and for spawning sites.

(6) To determine food acquisition ability and selectivity of feeding under controlled conditions.

(7) To determine, by analysis of alewives washed up on the beach, whether these fish were statistically identical in terms of size, sex, age, and whether reproduction had been completed as compared to the general population in the lake.

Background Material

The alewife, Alosa pseudoharengus (Wilson), was introduced into Lake Michigan via the Erie and Welland Canals. It has apparently been allowed to succeed because of the lack of predation by such large piscivorous species as the lake trout, Salvelinus namaycush (Walbaum); the walleye, Stizostedion vitreum vitreum (Mitchell); and the burbot, Lota lota (Linnaeus), species whose numbers were depleted by the sea lamprey, Petromyzon marinus (Linnaeus), and also by fishing pressure. An account of this can be found in Smith (1968a and 1968b). Since the alewife's first sighting in Lake Michigan in 1949, it increased in numbers until 1967, when 42,000,000 pounds were taken in commercial trawls. Since that time the species has decreased in numbers and appears to be continuing to decline.

The smelt, Osmerus mordax (Mitchill), was introduced into Crystal Lake in Benzie County, Michigan in 1906 (Van Oosten, 1937). It reached Lake Michigan through a channel connecting the two lakes and proliferated, becoming a factor in the fisheries around 1930. 4.8 million pounds were captured in 1940, but disease struck the population and reduced its numbers drastically (Van Oosten, 1947). The catch again climbed to 9.1 million pounds in 1958, but the current level is approximately 1/8 of that maximum. Competition with the alewife is a probable reason for this decline.

The bloater, Coregonus hoyi (Gill), (Leucicthys hoyi by Smith, 1968a), is one of seven species of "Chubs" or "Ciscos" of the family Salmonidae subfamily Coregoninae, that inhabits Lake Michigan:

Coregonus nigripinnis (Gill) - blackfin cisco
C. johannae (Wagner) - deepwater cisco
C. alpenae (Koeltz) - longjaw cisco
C. kiyi (Koeltz) - kiyi
C. reighardi (Koeltz) - shortnose cisco
C. zenithicus (Jordon and Evermann) - shortjaw cisco
C. hoyi (Gill) - bloater

Of these seven species, the bloater now constitutes about 98% of all the chub stock (Smith, 1968a) and about 97% of all chubs taken during these studies. This is down slightly from 1964, when this species constituted 99.2% of all chubs taken (Wells, 1966). According to Wells (1966) lamprey predation, fishing pressure, and alewife competition appears to have been the major factors in the demise of these seven species. Figure 5 graphically shows some of these relationships. It is interesting to note that the bloater, in the absence of the other six chub species, increased both in size and numbers before competition from the alewife and a certain amount of fishing pressure caused its numbers to lessen (Smith, 1968).

The yellow perch, Perca flavescens (Mitchell), is larger than the alewife, smelt, or chub, attaining lengths of 15 - 18 inches in the Great Lakes. As such, perch represent a valuable fishery, 5.8 million pounds being harvested in 1964. Although the species is planktivorous when young, older individuals tend to piscivory and, in the absence of the lake trout, the perch was the major predator in the lake. The 1964 catch level of 5.8 million pounds represents an increase over previous figures. This is presumably associated with two factors - a decrease in predation on young perch because of the decrease in the lake trout population and the exploitation of a new food source - the burgeoning alewife population. However, as the alewife was reaching its peak in 1967 the perch population was showing a significant decline (600,000 pounds caught in 1968). It is my assumption and that of Smith (1968a) that the concentration of alewives inshore during the spawning and hatching period of the perch caused a decrease in the recruitment of the perch species. From current data, the perch are making a significant comeback and should again make up a significant part of the fisheries.

Figure 1 - Lake Michigan showing dividing line between the North and South Basin based on current patterns and submarine ridges. The numbers 1-6, 7-11, and 12-17 represent locations of study sites set up in 1970-72. Figures 2-4 show further detail of the study sites. Latitude and Longitude given horizontal and vertical axes.

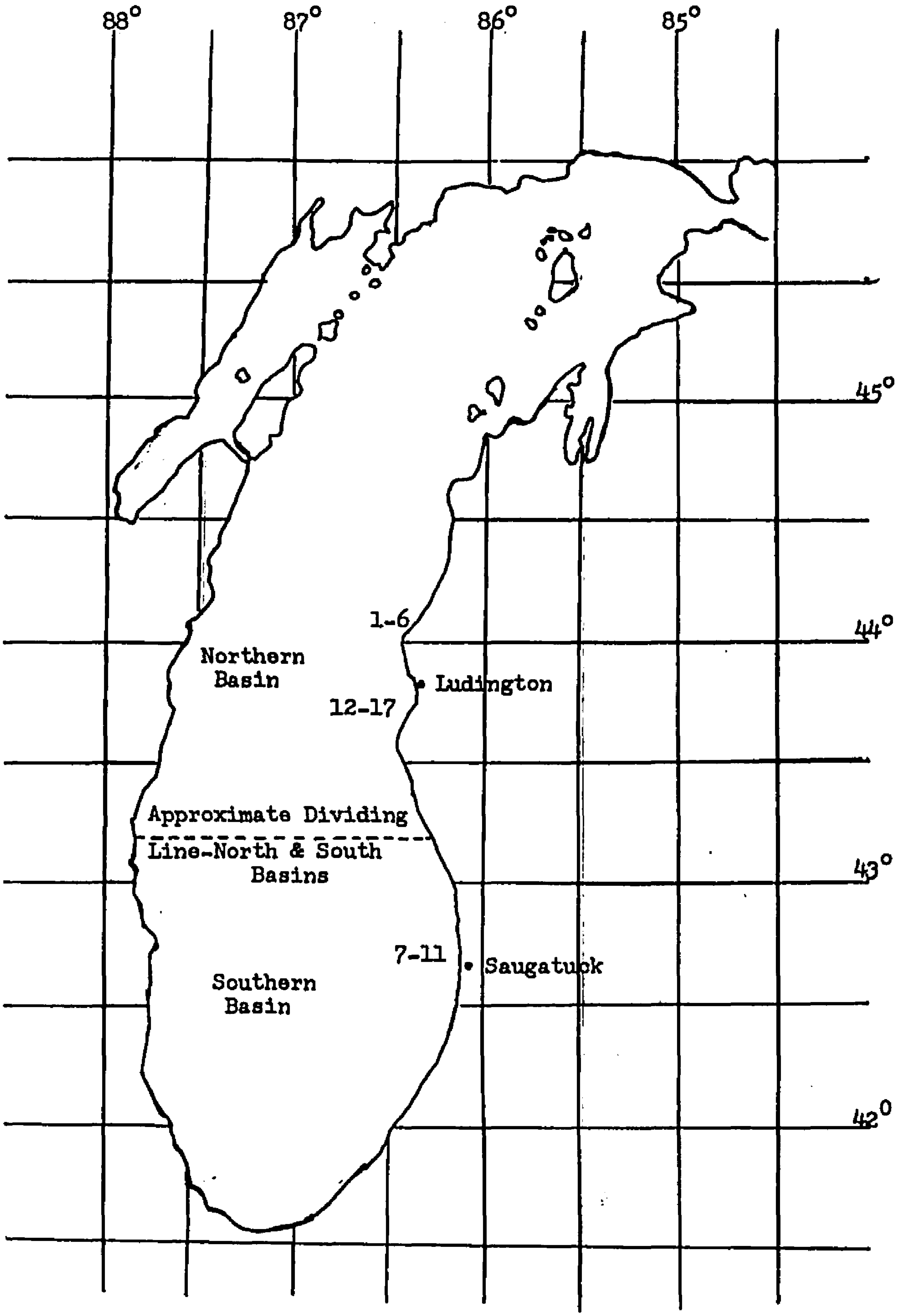
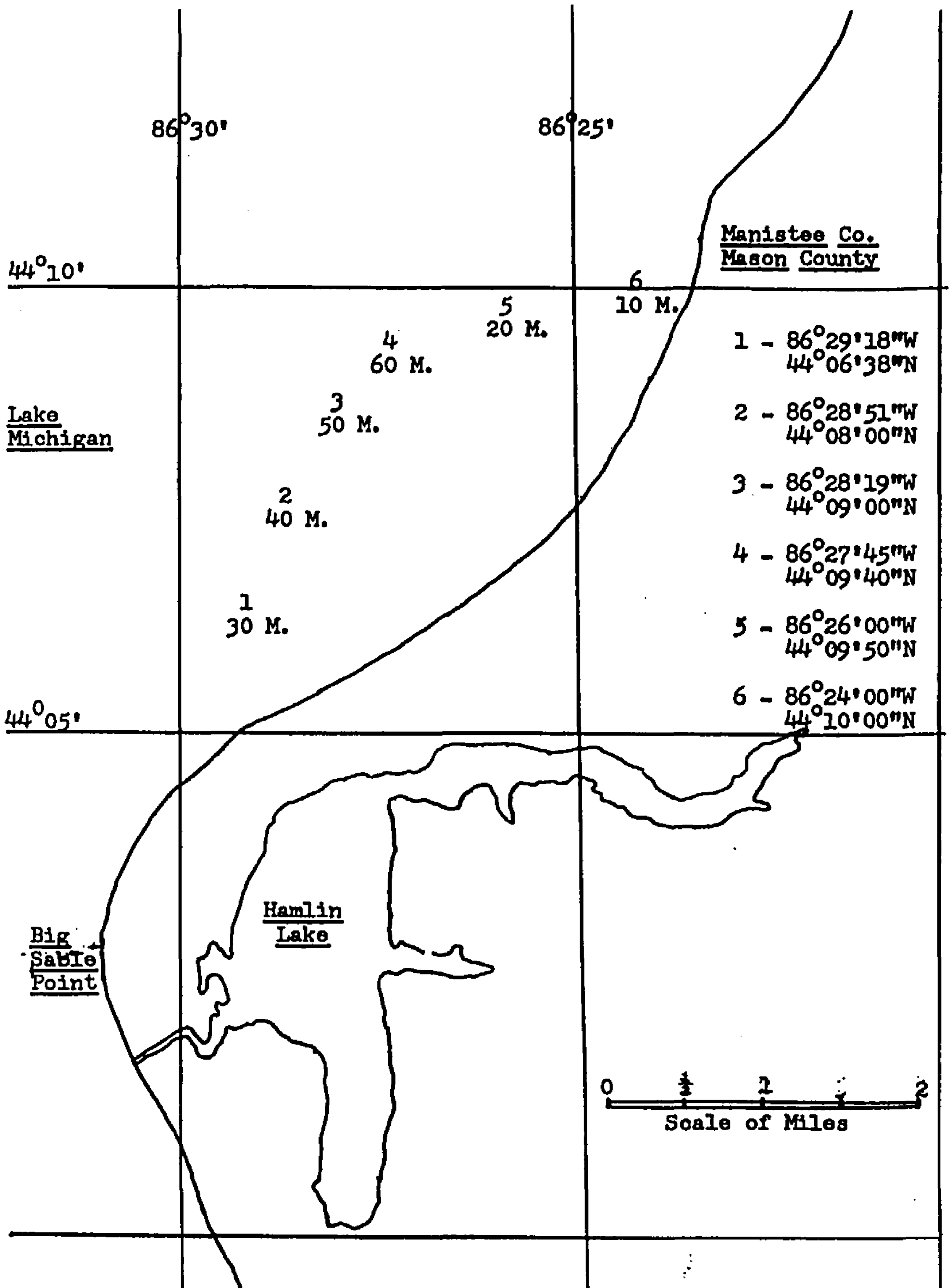

88°
87°
86°
85°
45°
44°
43°
42°
1-6
Ludington
12-17
Northern
Basin
Approximate Dividing
Line-North & South
Basins
7-11
Saugatuck
Southern
Basin

Figure 2 - North Basin Big Sable Point. Location of study sites 1-6 shown including maximum depth at those sites. Latitude and Longitude of sites given at right of map. (Adapted from U.S. Geological Survey Map, Mason County, Michigan.)



86°30'
86°25'
44°10'
44°05'
Manistee Co.
Mason County
Lake
Michigan
1
30 M.
2
40 M.
3
50 M.
4
60 M.
5
20 M.
6
10 M.
1 - 86°29'18"W
44°06'38"N
2 - 86°28'51"W
44°08'00"N
3 - 86°28'19"W
44°09'00"N
4 - 86°27'45"W
44°09'40"N
5 - 86°26'00"W
44°09'50"N
6 - 86°24'00"W
44°10'00"N
Hamlin
Lake
Big
Sable
Point
0
2
Scale of Miles

Figure 3 - South Basin. Location of Study Sites 7-11 including maximum depths at each site. Study conducted 1970-1972. Latitude and Logitude given at right. Adapted from U.S. Geological Survey Map, Allegan County, Michigan.

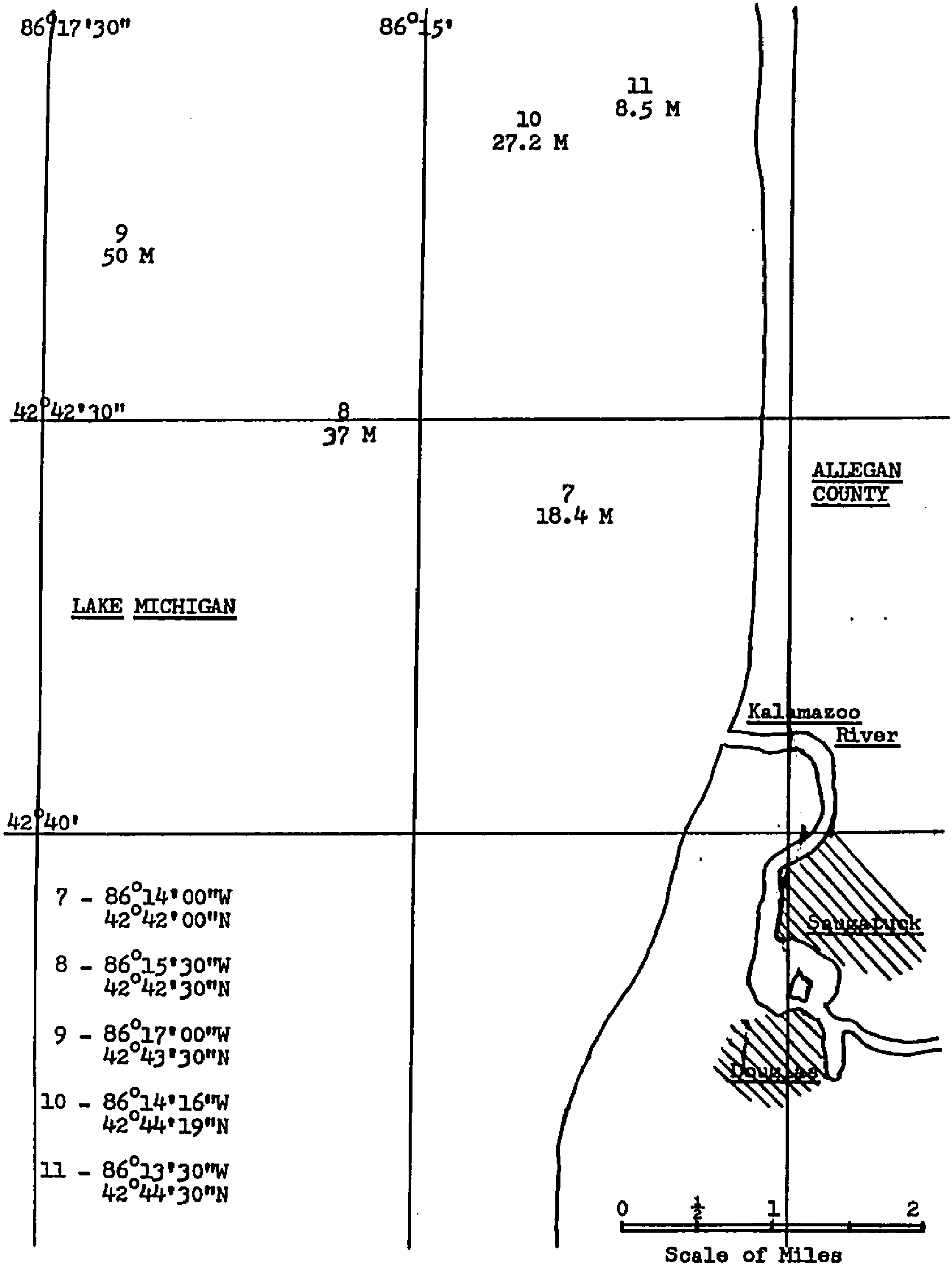

86°17'30"
86°15'
11
8.5 M
10
27.2 M
9
50 M
42°42'30"
8
37 M
ALLEGAN
COUNTY
7
18.4 M
LAKE MICHIGAN
Kalamazoo
River
42°40'
Saugatuck
7 - 86°14'00"W
42°42'00"N
8 - 86°15'30"W
42°42'30"N
9 - 86°17'00"W
42°43'30"N
10 - 86°14'16"W
42°44'19"N
11 - 86°13'30"W
42°44'30"N
0 ½ 1 2
Scale of Miles

Figure 4 - Ludington Power Project site of Consumers Power Company. Study Sites 12-17 shown, including maximum depths at each site. Latitudes and Longitudes given at right. (Adapted from Liston and Tack, 1972)

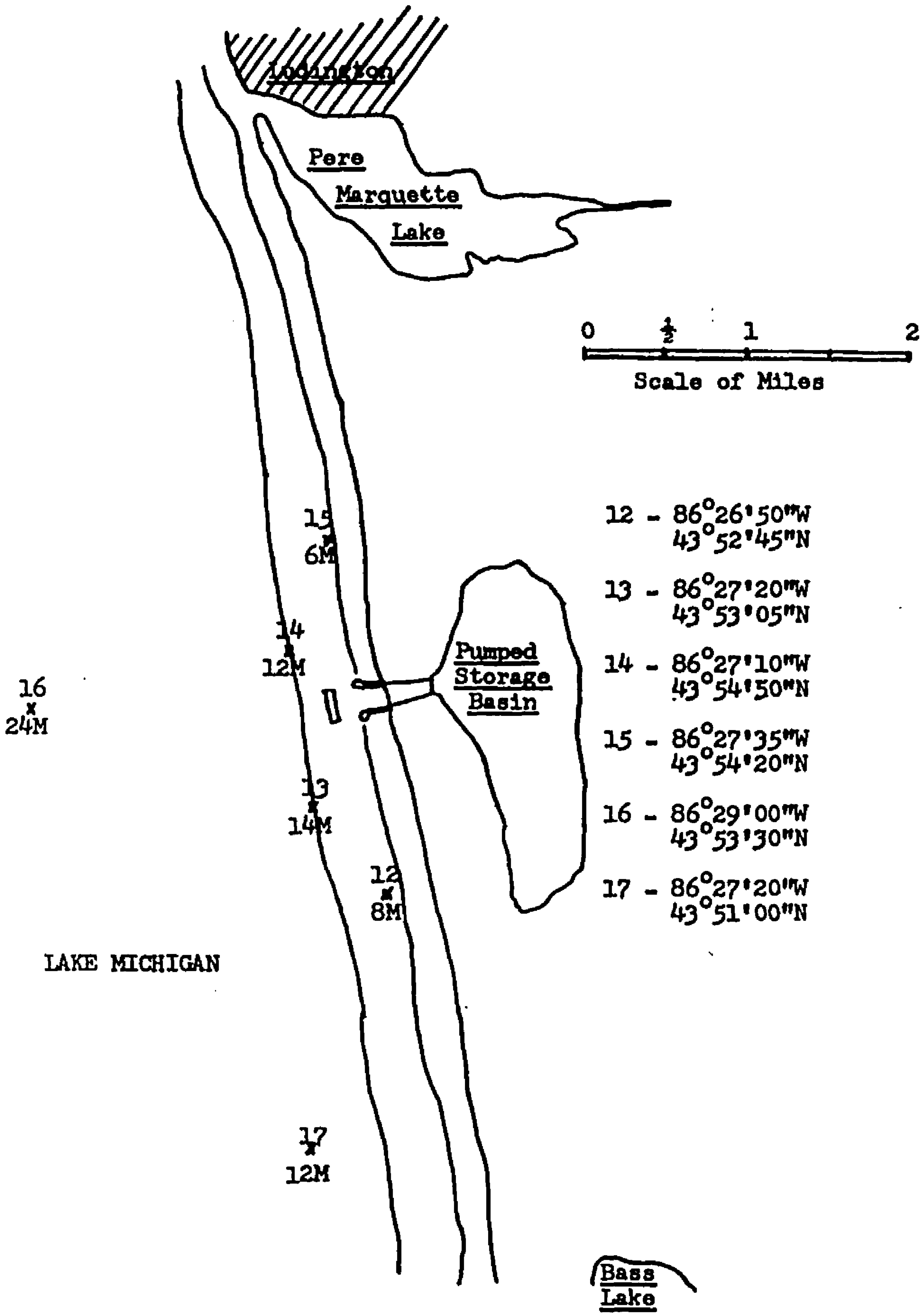

Pere
Marquette
Lake
0 ½ 1 2
Scale of Miles
12 - 86°26'50"W 43°52'45"N
13 - 86°27'20"W 43°53'05"N
14 - 86°27'10"W 43°54'50"N
15 - 86°27'35"W 43°54'20"N
16 - 86°29'00"W 43°53'30"N
17 - 86°27'20"W 43°51'00"N
15 x 6M
14 x 12M
16 x 24M
Pumped
Storage
Basin
13 x 14M
12 x 8M
LAKE MICHIGAN
17 x 12M
Bass
Lake

Figure 5

Possible factors which may explain the current status of the fisheries in Lake Michigan. Data includes the factors of predation, competition and fisheries pressure. Explanation for the symbols is given below:

C = Competition
P = Predation
R = Recruitment

LTA = Lake Trout Adults
LTY = Lake Trout Young
LT = Lake Trout (Adults and Young)

LCA = Large Chubs - Adults - Includes Coregonus kiyi
C. nigripinnis
C. zenithicus
C. alpenae
C. reighardi
C. johannae

LCY = Large Chubs - Young

CS = Small Chubs (Bloater - Coregonus hoyi)

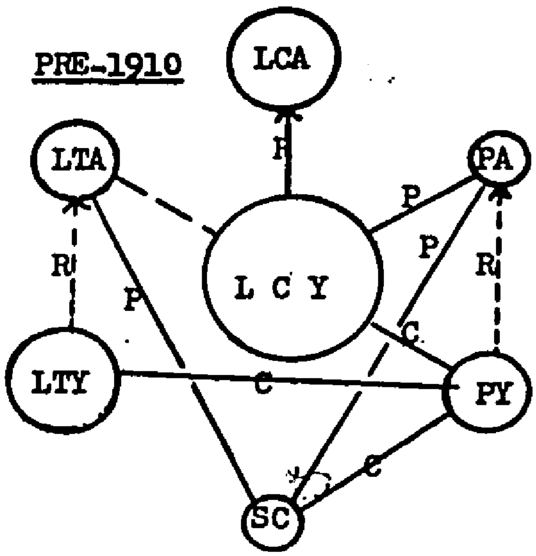
PA = Perch Adults
PY = Perch Young

S = Smelt

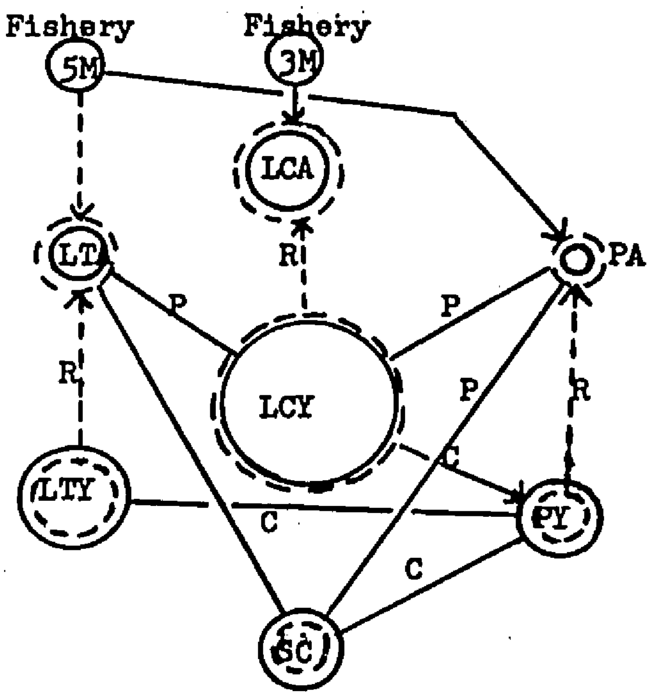
MC = Medium Chubs - the remnants of the populations of large chubs from before 1950 - includes the following species
C. zenithicus
C. alpenae
C. reighardi
C. kiyi

Adapted from Wells (1966) and Smith (1968a), Great Lakes Fisheries Catch Statistics.

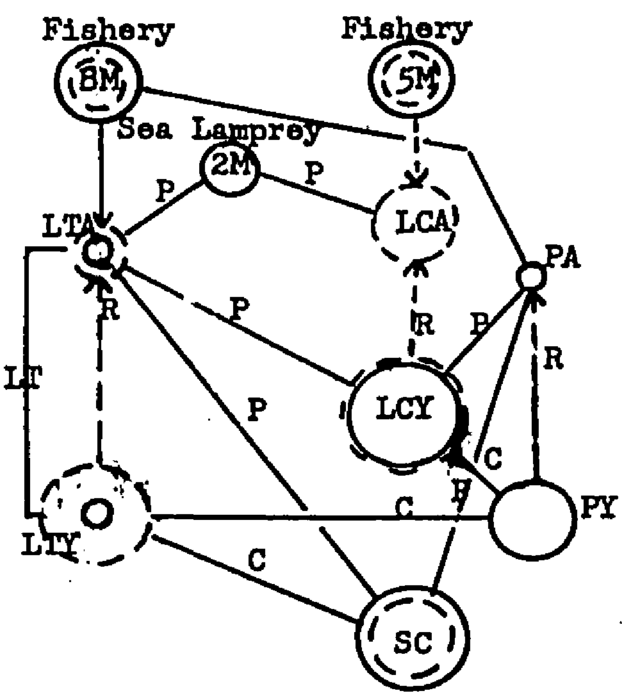
PRE-1910



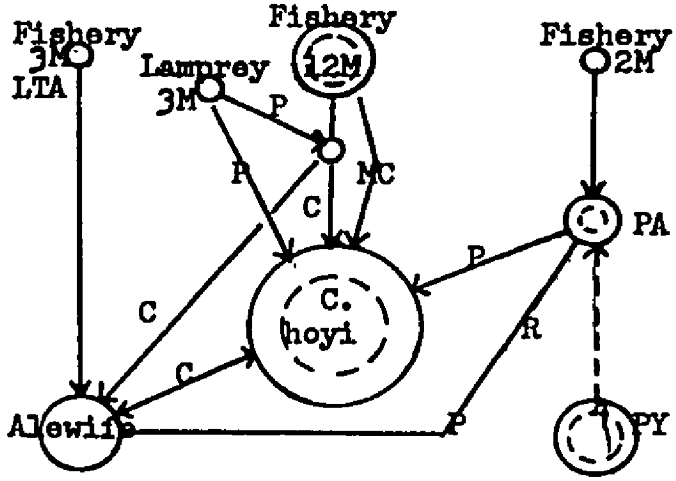
1910-1940



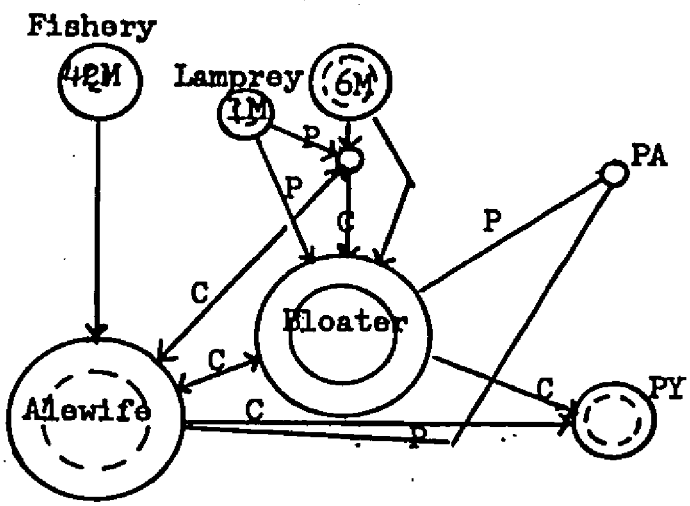
1940-1950



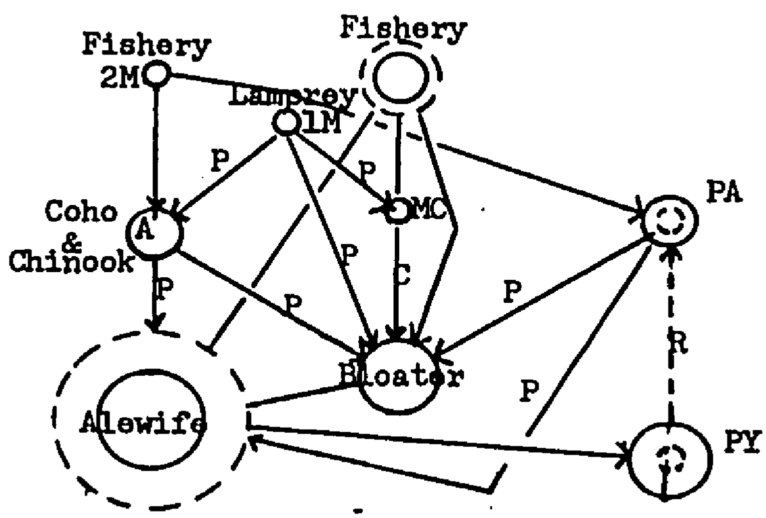
1960



1967



1972



METHODS AND MATERIALS

Fish Collections

Using the system of Horak and Tanner (1960), fish were caught in 1-inch, 2-inch, and 2½-inch mesh gill nets, each net either 12 feet by 50 feet or 6 feet by 50 feet. The nets were set at each station for a 24-hour period at each of three depths (surface, 4-5 meters, and near the bottom). Nets were set in blocks of three so that a panel of each mesh size was present at each station and at each depth. Although it was not always possible to get out on the lake on the same dates each year due to inclement weather, lifts did take place each year during specified periods of days.

After the nets were set for 24 hours, they were brought on board and the fish were immediately measured, weighed and sexed (where possible). Scales were taken to determine age and, where determination of sex was a problem, the fish were placed on ice and taken ashore for examination. Although total number and weight of each of the species of interest was obtained, not all fish were examined in detail because of the large numbers involved. Fish within each species were taken at random for more complete examination. In all, 2598 perch, 1232 smelt, 2520 alewives, and 1870 bloaters were examined in detail.

Zooplankton

Zooplankton were taken at the same time and sites as the fish, phytoplankton and chemical studies. A meter plankton net (180 mesh) was towed at approximately 2-3 miles/hour for 100 meters at depths of 0-1 meter, 4-5 meters, and near the bottom. Samples were fixed in concentrated formalin (a 38% aqueous solution of formaldehyde) for one week and then two aliquot portions were taken and counted. Species were enumerated and expressed as number/m^3.

Physical and Chemical Studies

The following parameters were studied - temperature profile, transparency, pH, alkalinity, dissolved oxygen and carbon dioxide, and dissolved solids. Turbidity was measured at the Ludington stations but at no others.

Water temperatures were measured at each station using a thermistor as gill nets were being lowered. Temperatures were taken at two-meter intervals at all stations. Water transparency was measured at the same time using a Secchi disk. Standard chemical analytical methods were used to measure D.O., CO_2, alkalinity, and dissolved solids. A pH meter (made by Beckman), calibrated before each outing against a 0.008695M KH_2PO_4 + 0.0304M Na_2HPO_4 solution with a pH of 7.413 (at 25°C), was used in all pH calculations, all values being temperature corrected using the system of Bates (1962). All tests were run on samples taken on a bi-weekly basis using a 1-liter modified Kemmerer sampler from depths of 0-1 meter, 4-5 meters, and 1 meter from the bottom. If the site was greater than 40 meters in depth, a fourth sample was often taken at 20 meters.

Phytoplankton

Phytoplankton were enumerated using the technique of McNabb (1960); 400-ml samples were taken, in duplicate, from water taken from the surface, 4-5 meters, 1 meter from the bottom, and from 20 meters where available. These 400-ml samples were fixed with 16 ml of concentrated formalin and 50 ml of the sample was filtered through a .45u millipore filter. The filter was dried for 24 hours and then cleared with emersion oil. A cover glass was placed on the slide and 30 fields were scanned at 450 X. Concentration was expressed as numbers per milliliter of lake water.

Controlled Feeding Experiment

A collateral experiment to determine feeding preferences was attempted using the following system: fish of all four species were caught using a 1-inch mesh trawl net during the months of April, June, and August. These fish were placed in holding tanks (½ of an unused 500-gallon oil-fuel tank) for 24 hours to insure that they had not eaten for at least that period of time. They were then introduced into a pool (15 feet in diameter by 4 feet in depth) into which Lake Michigan water had been placed. The fish were placed in the pool in single species groups of 5, or 10, or mixed species groups of ten individuals (for example - 5 perch, 5 smelt, or 2 perch, 2 smelt, 3 alewives, 3 bloaters). The fish were allowed to remain in the pool for 30 minutes to feed on known concentrations of zooplankton. Undisturbed fish would begin feeding within 15 minutes of introduction. Only fish less than or equal to 6.0 inches in length (15 cm) were used. After each test, the pool was sampled to determine remaining zooplankton concentration and the fish were cut open to determine stomach contents. In all, 120 fish of each species were sampled.

As all feeding experiments were conducted in a closed shed with a red light source, the zooplankton and large crustaceans were distributed fairly uniformly through the water mass. The fish were acclimated for the 24 hour period in this light to eliminate as many depth cues as possible. Ample oxygen was pumped through the system and constant numbers and concentrations of food organisms were used throughout April, June and August.

Stomach Analyses

On the 8220 fish whose stomach contents were examined in detail, the following system was used:

(1) The fish to be sampled were brought back to the laboratory on ice to slow decomposition of any material in the stomach.

(2) The stomach was quickly removed along with a one inch section (2.5 cm) of gut on either end of the stomach.

(3) The contents of the entire segment was placed in a small vial containing 72% ethanol and set aside for examination.

(4) The material was examined at 10X, with higher magnification being used for some closer identification of the smaller zooplankton forms. Following the system of Wells and Beeton (1963), small numbers of plankters were counted while larger numbers were estimated. No attempt was made to key clams and ostracods to species. Zooplankton were divided only into Cladocerans and Copepods with numbers expressed both in terms of percentage frequency of occurence and percent volume.

RESULTS

Depth Distribution of Fish

Depth distributions vary from species to species with time of the year. Within some species, depth distribution varies with sex and age, but average depth is given in Figure 6.

Bloaters (Coregonus hoyi) were seldom caught in depths less than 20 meters and even more seldom caught in nets set more than 10 meters off the bottom. Young bloaters (up to 2 years) were caught in midwater ranges (20-40 meters in depth) but after 2 years joined the adults in a yearly migratory trend from deeper water (greater than 60 meters) in the winter to shallower water (20± meters) by mid-summer. After this time the population began a progressive movement back toward deeper water, regaining 60 meters by late August or early September. Both sexes were caught together and there seem to have been no depth-sex interactions.

Alewives (Alosa pseudoharengus) show movement from depths greater than 60 meters in early May to depths of about 3 meters by late May. They remain between 3 and 10 meters until late August, and then move toward the depths. Young alewives (1-2 years) inhabit the same midwater pelagic zone occupied by the bloater and utilize the same food sources. Data significant at the $p < .05$ level indicate the following:

(1) Large alewives of the 1-2 year class inhabit the 0-20 meter zone in the spring, but seem to be displaced off-shore as the larger, older individuals come up from greater depths.

(2) The largest members of the older age classes (3 years and older) seem to move into shallow water before smaller individuals of those same age classes. As the temperature rises in the summer, the larger

individuals are again the first to move, to 20 meters in early August and to greater than 50 meters by early September.

Smelt (<u>Osmerus mordax</u>) occupy a zone about 40-50 meters in depth during the winter and then move inshore very early in the spring to complete breeding. They remain in shallow water (less than 10 meters) until early June and then gradually move deeper, reaching 40 meters by late October. Available data indicate that all breeding smelt move inshore en masse, with none of the size differences shown by alewives. There does not appear to be a depth difference related to size or sex.

Perch (<u>Perca flavescens</u>) inhabit a wide zone of 0-40 meters in depth all year round, concentrating their activities in waters less than 25 meters deep. They move into shallow water (less than 10 meters) in mid-June, returning to their wintering depth by the end of September. At the $p < .05$ level, the data suggest the following:

(1) The largest individuals of age groups I and II are found in shallow water in the summer and in deeper water in the fall, a pattern also exhibited by the population in general, although these younger fish are not involved in breeding. The inshore movement is probably keyed to food acquisition.

(2) Male perch move into the shallow water breeding and feeding areas sooner than do the females, and remain there longer.

(3) More females were caught in mid-water nets than were males, while more males were caught in nets set on the bottom than were females, strongly suggesting that perch show differences in feeding habits and locales based on sex. This is borne out by stomach analyses (p. 49).

(4) Male perch prefer shallower water (5-15 meters) on a year round basis while females are distributed uniformly over all depths at all

seasons (0-40 meters). This is probably keyed to food acquisition, males being primarily bottom feeders, females being primarily pelagic feeders. This in turn affects their food habits (see p. 40-41).

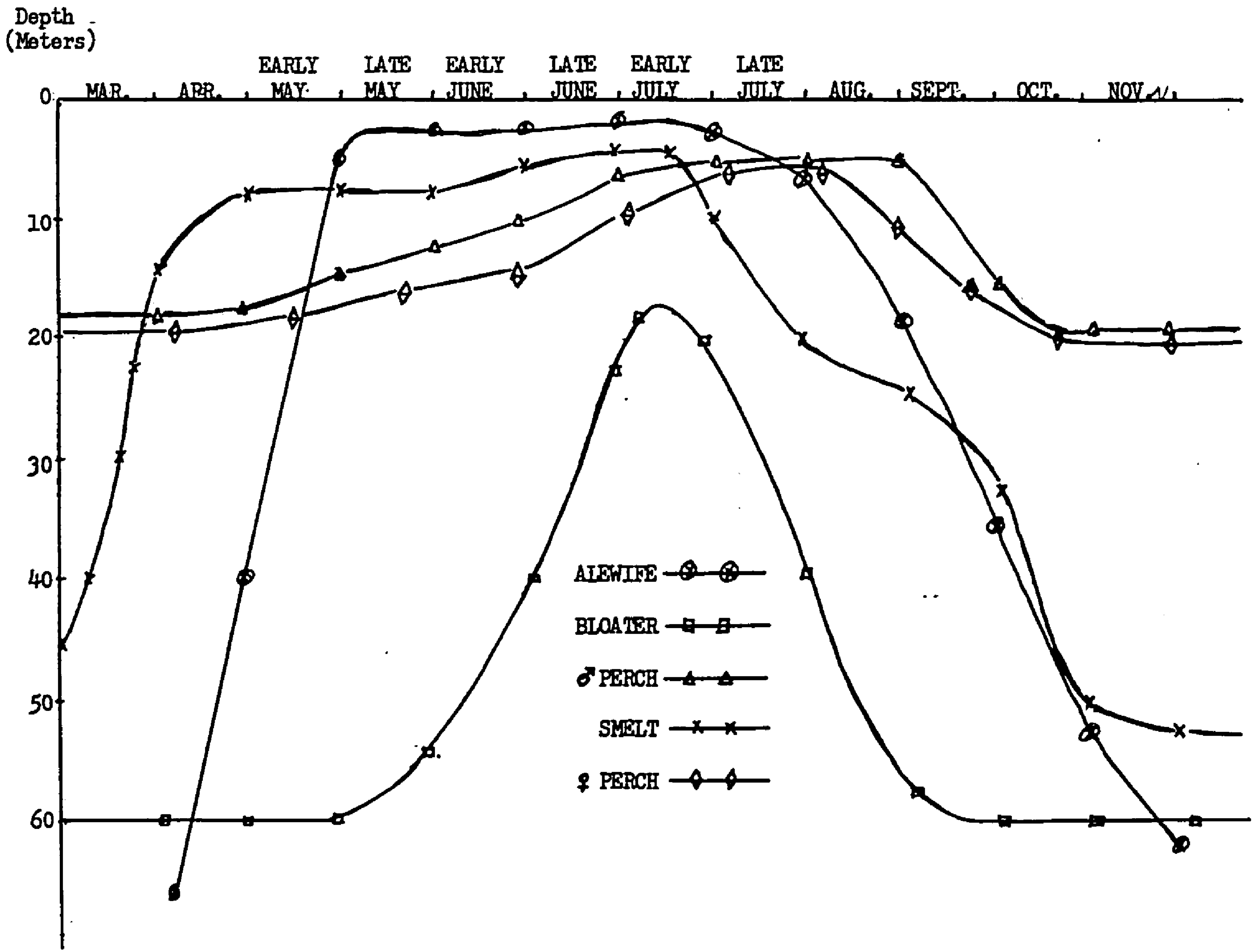
There were no significant differences in terms of length, weight or sex composition of populations of alewives, smelt, perch, or chubs captured at Saugatuck, Ludington, or Big Sable Point. It was expected that there might be differences based on differences in zooplankton and phytoplankton concentrations and on water chemistry variations between the three sites, but no differences significant at the $p < .05$ level were detected.

Overall Food Habits

Although quantities of various food organisms consumed changes throughout the year on the basis of age, depth, season, location, and sex in some species, it would still seem valid, given the large number of individuals sampled, to compare overall percentages of food. This has been done for four species, both as a percentage of the fish that utilize that food source, and as the percentage of dry weight that this food source makes up on a yearly basis (Tables 1a-5a and 1b-5b).

Definite competition for food sources appears to exist. Alewives and bloaters use the same major food sources, large zooplankton and crustacean stocks, but smelt feed on ostracods and insect larvae to a far greater degree than any of the other three species, and perch consume fish as a major percentage (31% overall, but 48.8% in the largest fish) of their diet, though not to the exclusion of other food organisms. Female perch took a greater percentage of fish than did male perch, suggesting differential feeding habits related to location. Indeed a greater

Figure 6 - Yearly depth selection by alewives, smelt, perch and bloaters in Lake Michigan (1970-1972) from Ludington, Big Sable Point and Saugatuck.


Depth
(Meters)
EARLY
LATE
EARLY
LATE
EARLY
LATE
MAR.
APR.
MAY
MAY
JUNE
JUNE
JULY
JULY
AUG.
SEPT.
OCT.
NOV.
0
10
20
30
40
50
60
ALEWIFE
BLOATER
♂ PERCH
SMELT
♀ PERCH

percentage of females than males were captured both inshore and in pelagic waters, while a greater percentage of males were captured in nets set on the bottom in deeper waters. Alewives, bloaters, and smelt seem not to show this differential feeding response related to sex. Bloaters showed a sex ratio very much in favor of females among those greater than 7 inches long (almost 30:1 in the largest specimens). The young bloaters showed a greater percentage of females than males but not to as great an extent. This sex ratio had no effect on the types of foods utilized.

Feeding response changed for all fish species from month to month, particularly among the zooplankton feeders as the numbers of particular species of zooplankton (ex. Cyclops, Daphnia) rose and fell. Since these changes could be followed for three years and since they could be lumped in blocks, the months March, April, and May were combined as Spring data; June, July, and August as Summer data; and September, October, and November as Fall data. Trends were similar enough during each of these 3-month blocks that no statistical significance was lost. Indeed, significance was gained because of the greater numbers of individuals in each block.

Food Habits of the Bloater

Bloaters were collected at all depths (0-60 M) during spring, summer and fall. Stomachs of 2265 fish were examined of which 1870 contained identifiable food, 203 were empty, and 192 contained food which was unidentifiable. References here are made only to those 1870 individuals with identifiable food.

Of the 133 bloaters less than 6 inches in length which contained food, 98 came from the zone between 10 and 40 meters in depth. The

Overall Food Habits of Four Fish Species in the Lake as Measured by Stomach Analysis

Table 1a. Percent Frequency of Occurrence of Various Food Organisms

Species	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Bloater	1870	44.1	42.2	33.9	17.6	22.6	2.8	7.4	1.5	5.2
Alewife	2520	63.4	34.6	73.4	63.0	1.1	12.5	1.2	1.8	8.9
Smelt	1232	27.3	23.2	72.1	68.1	0.6	11.8	8.8	21.9	64.0
Perch	2598	57.0	45.0	40.5	36.8	7.3	37.4	44.6	44.4	18.1
Average		47.95	36.25	54.9	46.38	7.9	16.12	15.5	17.15	24.1

Table 1b. Percent Volume of Various Food Organisms

Species	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Bloater	1870	35.6	30.0	18.5	8.4	1.6	1.0	3.5	0.6	1.1
Alewife	2520	34.4	24.6	21.2	17.1	0.2	1.5	0.3	0.3	0.6
Smelt	1232	8.5	7.6	28.5	23.9	0.2	3.4	2.7	5.5	20.1
Perch	2598	13.5	12.8	15.0	13.7	1.6	31.0	5.2	4.6	4.0
Average		23.0	18.75	20.8	15.78	0.9	9.23	2.93	2.75	6.45

remaining 35 fish were caught at depths greater than 40 meters. Zooplankton made up the entire diet of the fish caught in the mid-depth ranges, and 72% (volume basis) of the diet of bottom feeders at greater than 40 meters. Zooplankton species of greatest importance were Cyclops bicuspidatus, Diaptomus sp., and Daphnia galeata. The percentages of zooplankton identified in stomach analysis changed over the three year period in close correlation with the changes measured in the zooplankton stocks. (Coefficient = .87). Midge larvae also constituted a relatively large proportion of the food of bottom feeding individuals (12.1%).

Fish 6.0 to 6.9 inches long fell into age classes I and II and tended to show a mid-depth preference. Zooplankton was the most important food for both mid-depth and bottom feeders, although Pontoporeia and Mysis were consumed to a fairly high degree by the bottom feeders. No other organisms constituted a significant percentage of the food at this age. A tendency found in the 1-2 age class but reversed in older fish is that Mysis is a more important food organism than Pontoporeia.

As in the study by Wells and Beeton (1963), Pontoporeia was the most important food of bloaters greater than 7 inches in length, followed by Mysis and large zooplankton species. Some stomachs contained over 200 Pontoporeia, particularly in the large bloaters feeding on the bottom in shallow water (10-40 meters). Of the zooplankton eaten, Cyclops, Diaptomus, and Daphnia were found to predominate in terms of numbers consumed, number of fish consuming these organisms, and percentage dry weight. This correlates well with a selective feeding hypothesis based on size and number of organisms available.

Table 2a. Percent Frequency of Occurrence of Various Food Items in the Stomach of the Bloater, *Coregonus hoyi*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	133	4.4	5.6	87.0	49.6	0.0	0.0	18.6	1.0	2.0
6.0- 6.9	666	27.0	57.0	41.6	17.5	2.5	0.5	2.7	2.3	3.1
7.0- 7.9	454	43.2	51.0	21.3	10.6	21.6	1.3	2.6	2.7	4.5
8.0- 9.9	316	65.6	51.4	16.5	5.4	38.5	4.2	6.5	0.9	6.7
10.0-11.9	301	80.3	46.0	3.0	3.0	51.5	8.3	6.7	0.8	9.8
Weighted Average		47.2	49.2	29.4	13.9	20.9	2.5	5.2	1.8	4.7
Season										
Spring	851	54.1	28.3	30.8	5.3	26.3	5.1	7.1	1.3	3.3
Summer	556	38.1	47.2	46.5	17.2	16.2	1.2	7.1	1.5	5.2
Fall	463	40.1	51.1	34.5	30.3	25.4	2.1	8.0	1.7	7.1
Weighted Average		45.8	39.5	36.3	15.0	23.1	3.2	7.3	1.5	4.8
Depth(m)										
0-20 m	113	10.0	13.0	3.3	14.4	24.9	1.1	9.6	2.6	2.3
20-50 m	1047	51.2	41.3	67.4	24.4	27.4	2.0	7.5	1.4	4.7
> 50 m	610	71.2	72.3	31.0	14.1	15.5	5.3	5.1	0.5	8.6
Weighted Average		56.3	51.4	49.7	19.9	22.7	3.2	6.7	1.1	6.0

Table 2a. Percent Volume of Various Food Items in the Stomach of the Bloater, *Coregonus hoyi*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	133	5.0	7.5	49.0	23.0	0.0	0.0	12.1	1.0	2.3
6.0- 6.9	666	24.0	35.5	26.3	8.8	1.4	0.3	2.1	0.8	2.0
7.0- 7.9	454	30.0	49.0	11.0	6.0	1.5	1.2	1.0	0.3	0.1
8.0- 9.9	316	47.0	38.0	5.0	4.0	1.7	1.5	1.1	0.5	0.8
10.0-11.9	301	72.0	20.0	1.0	0.3	3.2	2.1	1.3	0.3	0.3
Weighted Average		35.7	34.7	16.5	6.6	1.6	1.0	2.2	0.6	1.0
Season										
Spring	851	48.2	23.6	16.1	4.1	1.0	2.1	3.8	0.6	1.1
Summer	556	32.3	34.3	22.8	8.0	1.1	0.9	4.2	0.5	1.0
Fall	463	26.3	42.1	16.6	13.1	2.7	0.0	2.5	0.7	1.2
Weighted Average		38.1	31.3	18.2	7.5	1.5	1.2	3.6	0.6	1.1
Depth(m)										
0-20 m	113	15.7	15.7	24.4	8.3	1.2	0.0	3.5	0.6	1.3
20-50 m	1047	58.5	31.3	15.7	10.7	2.6	1.0	6.1	0.6	1.3
<50 m	610	32.7	53.1	15.4	6.2	1.0	2.0	0.9	0.5	0.7
Weighted Average		44.0	35.4	15.3	8.5	1.8	1.2	3.9	0.5	1.0

Food Habits of the Alewife

Stomachs were examined from 3110 fish, of which 2520 contained identifiable food organisms, 396 were empty, and the remainder (214) had unidentifiable stomach contents. Frequencies of occurrence and percent dry weight were calculated, Tables 3a and 3b.

Food of Alewives < 6.0 Inches Long

Fish from 1.7 to 5.9 inches were sampled. Nearly all (95%) had zooplankton in their stomachs and zooplankton constituted 76.5 percent of the dry weight of the contents. No preference could be shown for particular zooplankton in specimens less than 4 inches long. From 4.0 to 5.9 inches the alewife started demonstrating specificity towards the larger forms of zooplankton (*Cyclops bicuspidatus*, *Mesocyclops edax*, *Daphnia galeata mendota*, *D. retrocurva*, *Epischura lacustris*, and *Diaptomus sicilis*). A certain number of the largest forms (*Leptodora kindii*, *Limnocalamus macrurus*, *Pontoporeia affinis*, and *Mysis relicta*) were also found, but these are not as important as in larger fish, probably for two reasons. Fish of this size are usually pelagic and the largest crustaceans are found very near the bottom, and the small fish may not be able to handle the larger forms of crustaceans. This hypothesis is given support by the fact that the young alewives seldom consume fry of their own or other species, presumably because of an inability to handle organisms of this size.

Food of Alewives 6.0 Inches and Greater

As alewives approach lengths of 6 inches or greater, they leave the pelagic mid-depth zone which they have inhabited up to that time and begin to show vertical migration with the seasons. It is also about this time, when the alewives are about 3 years old, that they first begin to show pronounced inshore movements during the breeding season, June through August. This has a marked influence on the amount and types of food they eat. Although zooplankton were still found in a high percentage of stomachs in 6-inch fish (average 79% vs 95% in less than 6 inches), the percent dry weight begins to show a decrease at this time (from 77.5% for fish less than 6 inches to 59.0% in 6.0-6.9 inch fish). This trend increases in older fish, where zooplankton forms an increasingly smaller portion of the diet. On the other hand, Mysis and Pontoporeia become increasingly more important with increase in size. Pontoporeia makes up greater than 4 times the percent dry weight of the stomach contents of a 7.0+ inch fish as it does in an alewife less than 6 inches in length. There also seems to be a seasonal and depth variability in food acquisition. For example, alewives in the spring and fall were found to have higher concentrations of Mysis than in the summer. From Figure 6, alewives at these two seasons were at greater depths, where Mysis appears in greater concentration (Beeton, 1960). Pontoporeia, on the other hand, show a tendency to have their highest numbers in water less than 50 meters in depth (Wells and Beeton, 1963), a trend reflected in the percent dry weight of this species in the stomachs of alewives caught in shallower water. The zooplankton show a similar distribution pattern to Pontoporeia and thus were found in greater concentration in alewife stomachs from less than 50 meters in depth.

Fish eggs and fry, as expected, show their greatest occurrence in alewife stomachs during summer and early fall in the shallower depths, with the larger alewives consuming the greatest percentages of this food.

Other food sources show no definite statistical trends but are included to show comparison. It is interesting to note that fingernail clams, midges, and other insects form a far greater part of the diet of bloaters than of the alewives (about 4½ times as great). Since a far greater percentage of bloaters eat clams (22.6% vs 1.1% for the alewives), this could be a factor in the survival of the bloater in competition with the alewife. Another factor which may be of importance is the amount of time the two species, alewife and bloater, spend in the same depth zone of the lake (2 months), thus minimizing direct competition to this 2 month period.

Food Habits of the Smelt

Smelt in Lake Michigan apparently arose from an introduced stock from Crystal Lake, Michigan (Creaser, 1926, Van Oosten, 1953), which in turn came from Green Lake, Maine (Kendall, 1927). Sex ratios in Lake Michigan seem to be approximately 60% female; 40% male, data consistent with Beckman (1964) who found a 61%:39% ratio in Crystal Lake, and Barley (1964) who found a 68%:32% ratio. This ratio of females to males tends to increase with age, a fact substantiated by Beckman, Bailey, and McKenzie (1964). However this differential sex ratio does not appear to have a significant effect on the type of food utilized, so sexes are combined in Tables 4a and 4b.

In Gull Lake, Michigan, Burbidge (1969) found a tendency toward eating zooplankton in the spring and fall and <u>Chaoborus</u> and tendipedids during the summer, suggesting a change in food availability habits through the year. No such change was found in Lake Michigan smelt. Perhaps the decrease in various zooplankton forms which occur in Lake Michigan occurs

Table 3a.

Percent Frequency of Occurrence of Various Food Items in the Stomach of the Alewife, *Alosa pseudoharengus*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	316	41.0	12.0	91.0	93.0	<1	3.0	<1	<1	6.0
6.0- 6.9	956	51.0	18.0	85.0	72.0	<1	11.5	<1	1.3	7.0
7.0- 7.9	907	78.0	45.0	82.0	68.0	1.0	15.0	1.0	1.0	8.5
8.0- 9.0	308	71.0	41.0	64.0	48.0	1.6	17.5	1.7	2.3	9.8
>9.0 in.	43	76.0	48.0	45.0	34.0	2.0	19.0	2.5	4.0	13.1
Weighted Average		62.29	30.24	81.43	69.62	1.1	6.0	1.1	1.3	7.86
Season										
Spring	307	66.0	41.0	61.0	73.0	1.3	2.0	1.3	3.0	9.8
Summer	1602	58.0	25.0	83.0	68.0	<1	24.0	<1	1.0	11.0
Fall	611	76.0	38.0	76.0	48.0	1.6	15.0	1.5	1.4	6.9
Weighted Average		55.9	30.0	78.3	63.5	1.3	19.1	1.3	1.4	9.8
Depth										
0-20 m	762	36.0	24.0	81.0	68.0	1.0	3.3	1.8	3.4	11.1
20-50 m	1239	85.0	33.0	88.0	83.0	1.8	31.0	1.3	2.0	13.2
>50 m	519	69.0	47.0	51.0	38.0	0.5	4.2	0.4	0.0	2.4
Weighted Average		66.6	33.8	77.95	68.5	1.1	17.0	1.2	2.0	10.4

Table 3b.

Percent Volume of Various Food Items in the Stomach of the Alewife, *Alosa pseudoharengus*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	316	12.1	10.0	41.8	35.7	0.0	0.1	0.3	0.3	0.7
6.0- 6.9	956	19.6	18.5	31.6	27.4	0.1	1.3	0.4	0.5	0.6
7.0- 7.9	907	41.0	31.0	15.3	9.8	0.1	1.2	0.5	0.5	0.6
8.0- 8.9	308	48.0	31.5	9.0	8.0	0.2	2.1	0.1	0.3	0.8
>9.0 in.	43	51.2	32.6	8.2	4.5	0.4	3.0	0.0	0.0	0.1
Weighted Average		30.3	20.8	20.0	19.4	0.1	1.3	0.4	0.4	0.6
Season										
Spring	307	34.4	26.6	17.2	20.7	0.3	0.0	0.3	0.4	0.4
Summer	1602	35.8	21.7	22.5	15.6	0.3	2.4	0.4	0.6	0.7
Fall	611	33.3	26.1	21.9	15.2	0.1	2.0	0.4	0.2	0.6
Weighted Average		34.8	23.27	21.6	16.6	0.3	1.8	0.4	0.5	0.6
Depth										
0-20 m	762	37.6	15.5	26.4	20.6	0.2	1.9	0.4	0.6	0.3
20-50 m	1239	42.2	26.7	28.2	22.7	0.2	2.3	0.3	0.3	0.8
>50 m	519	23.4	31.6	7.0	8.0	0.1	0.2	0.1	0.0	0.6
Weighted Average		36.8	24.2	23.2	18.9	0.2	1.9	0.3	0.4	0.5

to a greater extent in Gull Lake, necessitating a change to larval food sources. Lackey (1969), working on a Maine Lake, did not find that zooplankton totally disappeared from the diet, as did Burbidge, but zooplankton numbers did decrease and insects and isopods made up a greater percentage of the food. In Lake Michigan, the juvenile smelt (up to about 6 inches in length) fed mainly on copepods, cladocerans, and ostracods. These data agree substantially with those of Kendall (1927), Greene (1930), and Gordon (1961). Adult smelt were found to consume <u>Mysis</u>, <u>Pontoporeia</u>, insects, and fish (primarily young-often of their own species) in addition to the copepods, cladocerans, and ostracods. This agrees with data of Schneberger (1937), Baldwin (1950), and Ferguson (1965). The diet of the smelt does vary seasonally in the Great Lakes, and this variation follows the variation in food stock populations, suggesting that smelt pick the most abundant fauna available. Smelt abundance also seems to be keyed to depth but mainly because smelt were only rarely caught below 50 meters, and then only very early in the spring. Of the 1712 smelt caught, 1232 contained food in a identifiable state, 266 were empty, and 314 contained unidentifiable food. The data are presented in Tables 4a and 4b.

Food Habits of the Perch

Lake Michigan perch attain greater lengths and weights than any of the other 3 species of fish studied. Individuals sampled during the 3 years ranged from 2.5 to 16.1 inches in length. Of the 3462 perch sampled, 2598 of these contained identifiable food, 488 contained unidentifiable food and 376 contained no food at all. As with the other 3 species, average contents varied over both station and depth, but ample numbers allowed closer approximations than is available in most studies. Tharratt

Table 4a.
Percent Frequency of Occurrence of Various Food Items in the Stomach of the Smelt, *Osmerus mordax*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
6.0 in.	106	18.0	9.0	97.0	95.0	0.0	0.0	1.0	16.0	92.0
6.0- 6.9	407	26.0	27.0	83.5	77.8	0.3	6.4	8.2	18.5	73.2
7.0- 7.9	385	25.5	31.5	74.4	66.5	0.6	12.6	10.4	18.0	61.8
8.0- 8.9	242	33.0	37.6	60.8	61.0	0.8	13.8	10.7	27.6	45.6
9.0	92	34.0	41.0	44.9	40.2	1.1	24.0	13.6	29.5	47.4
Weighted Average		27.2	30.1	74.6	69.8	0.5	10.6	9.2	20.8	64.1
Season										
Spring	665	26.5	27.3	97.0	79.6	0.7	6.1	11.5	16.1	74.3
Summer	346	28.3	17.9	58.2	51.6	1.1	14.7	10.6	25.6	47.6
Fall	221	27.1	25.4	61.2	73.1	0.0	14.6	4.3	24.0	70.1
Weighted Average		27.1	25.4	79.8	70.7	0.7	10.1	9.9	20.2	66.2
Depth										
0-20 m	438	31.3	12.1	96.1	85.6	0.8	15.6	14.3	22.6	75.4
20-50 m	718	36.4	31.7	84.3	80.2	1.0	17.2	10.8	27.6	68.6
50 m	76	13.3	25.8	36.0	48.5	0.0	2.6	1.3	15.5	48.0
Weighted Average		33.3	24.4	85.6	80.2	0.8	15.8	11.5	25.1	69.8

Table 4b.
Percent Volume of Various Food Items in the Stomach of the Smelt, *Osmerus mordax*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	106	1.1	1.7	37.0	32.1	0.0	0.0	0.2	3.6	24.3
6.0- 6.9	407	3.5	2.6	34.0	30.5	0.1	0.6	1.6	3.5	24.6
7.0- 7.9	381	7.3	11.4	26.2	21.7	0.2	3.4	3.7	4.8	21.3
8.0- 8.9	242	11.8	10.1	24.7	19.5	0.3	4.6	3.8	6.7	16.5
>9.0	93	18.6	12.4	20.5	15.6	0.4	0.5	4.3	6.9	13.9
Weighted Average		7.1	7.4	28.9	24.6	0.2	2.7	2.7	4.8	21.1
Season										
Spring	665	12.5	8.4	30.2	28.2	0.1	4.8	2.4	3.8	11.0
Summer	343	4.2	6.2	19.9	19.3	0.3	5.1	3.6	9.4	32.0
Fall	221	8.8	8.2	35.4	23.3	0.2	1.3	0.3	3.3	17.3
Weighted Average		9.5	7.7	28.2	24.8	0.2	4.0	2.3	5.3	18.0
Depth										
0-20 m	428	9.1	4.8	30.6	23.3	0.2	6.4	3.3	5.2	15.0
20-50 m	727	8.1	5.1	32.7	26.1	0.3	3.5	3.2	6.3	17.6
> 50 m	74	8.0	12.9	22.2	18.5	0.1	0.3	1.6	5.0	30.7
Weighted Average		8.4	5.5	31.3	24.6	0.2	4.3	3.1	5.8	17.5

(1959) studied perch from Saginaw Bay, as did El-Zarka (1959) but large variance and small sample sizes in their studies made meaningful analysis difficult.

Eschmeyer (1938), Weller (1938), Jobes (1952), and others have suggested that yellow perch school by sexes. Although the data as presented in Table 5a and 5b do not show this, the suggestion appears to have some validity in perch greater than 6 inches in length. These older perch (2+ years) appeared to choose different food organisms, females taking a greater percentage of fish and males taking a higher percentage of midges and large crustaceans.

In perch less than 6.0 inches long, zooplankton and insect larvae were of the greatest importance. Tharratt (1959) found insect larvae to compose the greatest fraction in his studies, but all his stations were in shallow water (6-21 meters in depth) and all sampling was done with bottom trawls. In the present studies, zooplankton, both copepods and cladocerans, were found to be of the greatest importance, particularly in fish less than 4.0 inches in length. In fish 4.0 to 6.0 inches in length, other organisms (Mysis, Pontoporeia, Gammarus, clams, snails, ostracods, and small fish) began to be found in increasing numbers, although cladocerans and copepods still formed a large portion of the diet. In perch greater than 6.0 inches in length, zooplankton become a less important factor in the diet, with the exception of some Limnocalanus and Leptodora. Mysis and Pontoporeia become more important, especially to the males; and fish, particularly minnows, young alewives, young smelt, and young perch, increase in importance in the female fish. The minnows referred to here include the emerald shiner, Notropis athernordis, in 132 perch stomachs; spottail shiner, Notropis hudsonius, in 168 perch stomachs;

nine spine stickleback, _Pungitius pungitius_, in 334 perch stomachs; and some unidentifiable fish in 85 perch stomachs. Most identifiable fish remains however were either young smelt (primarily in late summer, in 456 perch stomachs), young alewives (mainly in late summer, in 353 perch stomachs), and young perch (chiefly in summer and fall, in 412 stomachs). Of stomachs containing remains which were identifiably fish in origin (971), 654 were from females and 317 were from males,. about 2:1, even though males outnumbered females approximately 1.5:1. Conversely, midges, _Pontoporeia_, _Gammarus_, and _Mysis_ were present in greater percentage in males than in females (57% of all males vs. 31% of all females). This agrees in principle, with the findings of Tharratt (1959). The evidence suggests that older female perch feed in both open water and on the bottom while male perch tend to feed mainly on the bottom. This difference in feeding habits could also explain differences in numbers found at inshore stations, where females often predominated, if this movement was keyed to movement of a food source (minnows or smelt for example).

Laboratory Feeding Experiment

Four hundred and eighty fish, 120 of each of the four species of interest, were given food stocks taken from Lake Michigan on which to feed to determine if feeding in the lake was based on selection of a particular food source or merely availability.

Results agree fairly closely with those of fish sampled in the lake, with the exception that _Pontoporeia_ and _Mysis_ make up a slightly larger percentage under the test conditions than in the lake for all species tested, implying a possible lack of availability of this food source, at least for fish of this size, in the lake. Secondly, ostracods make up a

Table 5a.

Percent Frequency of Occurrence of Various Food Items in the Stomachs of the Perch, *Perca flavescens*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	316	23.0	18.0	95.0	91.0	2.0	14.6	65.0	61.0	15.0
6.0- 6.9	665	61.0	52.0	48.0	43.0	5.5	34.5	49.0	53.0	22.6
7.0- 7.9	753	68.0	53.0	32.0	26.0	8.6	37.6	43.0	44.0	19.5
8.0- 9.9	642	63.0	53.5	15.0	12.0	9.0	46.8	34.0	36.0	18.5
>10.0 in	222	69.0	48.2	12.0	8.0	10.4	53.0	32.0	28.0	17.6
Weighted Average		59.6	48.2	37.8	34.5	16.9	30.2	44.0	45.0	24.5
Season										
Spring	473	68.5	61.6	43.7	46.1	6.0	31.4	31.5	48.8	21.4
Summer	1561	46.3	17.4	34.8	29.2	11.4	48.3	64.3	47.9	16.5
Fall	564	56.2	55.0	43.0	35.1	4.5	32.5	37.0	36.5	17.9
Weighted Average		52.5	31.8	38.2	33.5	8.9	37.6	52.4	45.6	19.0
Depth										
0-20 m	1795	48.3	18.8	55.2	49.2	11.8	36.3	60.5	61.8	23.8
20-50 m	635	60.2	48.6	51.6	41.8	7.6	41.7	51.2	50.3	18.9
> 50m	168	62.5	66.6	19.7	16.4	2.5	44.2	22.1	21.1	13.1
Weighted Average		52.1	29.2	51.7	46.0	10.7	31.5	55.7	56.4	21.9

Table 5b.

Percent Volume of Various Food Items in the Stomach of the Perch, *Perca flavescens*.

Item	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Fish Eggs and Fry	Midges	Other Insects	Ostracods
Length										
<6.0 in.	316	4.0	3.0	38.0	35.0	0.5	4.8	6.0	5.7	3.0
6.0- 6.9	665	10.4	9.6	18.6	16.4	1.3	27.6	6.6	5.0	4.5
7.0- 7.9	753	14.8	13.9	10.6	9.5	1.7	33.7	5.8	4.6	4.5
8.0- 9.9	642	17.9	16.9	5.0	4.4	1.8	40.2	5.4	4.0	4.3
>10.0 in	222	20.3	18.7	3.0	3.2	2.6	48.8	5.2	4.0	4.3
Weighted Average		13.6	12.6	13.9	12.6	1.6	31.5	5.9	4.6	4.3
Season										
Spring	473	13.6	13.4	16.5	14.3	2.3	26.2	5.7	4.0	3.8
Summer	1561	13.4	11.6	13.2	12.7	1.1	36.8	5.5	4.6	4.2
Fall	564	13.5	12.2	15.3	14.1	1.4	30.0	5.5	5.2	4.0
Weighted Average		13.5	12.1	14.3	13.3	1.4	33.4	5.5	4.6	4.1
Depth										
0-20 m	1795	10.1	7.9	17.5	17.5	2.2	28.7	6.8	6.3	4.0
20-50 m	635	15.2	11.8	18.6	15.1	1.3	28.2	5.0	4.0	2.9
>50 m	168	15.2	17.5	8.9	8.5	1.3	36.1	4.0	3.5	5.1
Weighted Average		11.7	9.5	17.2	16.3	1.9	29.1	6.2	5.6	3.8

smaller volume in smelt stomachs under experimental conditions than in the lake. This may or may not be significant. The percent volume in perch stomachs differed in lab and lake data but this could be due to the lack of small fish fry as an alternative food source.

In the absence of fish eggs and fry in this experiment, some organisms may have been preyed on more heavily than otherwise, but this food source does not appear to be very important in fish less than 6.0 inches in length, as determined in natural populations, and should not have created too great a discrepancy. The results of the experiment are listed in Tables 6a and 6b.

In terms of efficiency of acquiring these foods, the alewife is more efficient than the other three species as shown by a comparison of the amount of food consumed per unit time. These data are presented in Table 6c.

Given the conditions of the experiment, alewives were more efficient predators on zooplankton and the large crustaceans Mysis and Pontoporeia than were the other species. The alewife also took greater proportions of the major copepods and cladocerans. Bloaters took the greatest volume of midge larvae in the study, smelt the greatest portion of ostracods, and perch, given these conditions, were generalists in their food gathering. Given a different age group and different initial food source, the percentages are certain to be different, but this experiment gives some idea of the food preferences for this age and size group and shows where competition could exist.

Selective predation on zooplankton by the alewife has been proposed by Brooks and Dodson (1965) and Smith (1970). These investigators inferred selective predation on the basis of numbers of various zooplankton

Table 6a. Percent Frequency of Occurrence of Various Food Items in the Stomachs of Four Fish Species.

Species	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Midges	Other Insects	Ostracods
Bloater	120	8.0	9.3	93.0	86.0	1.0	21.2	4.6	3.8
Alewife	120	46.0	14.7	97.0	92.0	1.0	4.2	4.0	6.0
Smelt	120	23.0	12.0	97.0	95.3	0.0	4.6	3.5	92.0
Perch	120	26.0	23.0	95.0	89.5	3.4	61.0	58.3	37.0

Table 6b. Percent Volume of Various Food Items in the Stomachs of Four Fish Species.

Species	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Midges	Other Insects	Ostracods
Bloater	120	7.5	8.2	46.0	22.8	<1	12.2	1.0	2.4
Alewife	120	12.9	10.6	39.5	34.1	<1	0.6	0.5	1.5
Smelt	120	5.9	4.6	34.4	32.0	0.0	3.6	3.2	16.3
Perch	120	7.8	6.1	34.0	31.6	1.1	6.8	6.4	8.2

Table 6c. Percentage of Total Volume of all Stomachs (480) Sampled Containing a Particular Food Source.

Species	# of Fish	Pontoporeia	Mysis	Copepods	Cladocerans	Clams	Midges	Other Insects	Ostracods	Total
Bloater	120	1.6	2.0	10.1	5.6	<0.1	3.3	0.25	0.6	23.6
Alewife	120	4.0	3.4	12.3	8.7	<0.1	1.0	0.1	1.2	30.8
Smelt	120	1.0	1.1	7.4	7.0	0.0	1.0	1.0	4.0	23.5
Perch	120	1.2	1.5	7.4	7.1	0.25	1.3	1.4	2.7	22.9

forms before introduction of the alewife. The current set of studies tend to indicate, on the basis of stomach analyses as compared to zooplankton counts in the lake, that not only alewives, but also bloaters, perch and smelt are selective zooplankton predators, both in the laboratory and in the lake.

The justification for this statement lies in the following: Average numbers/m^3 of 15 zooplankton and limnetic crustacea species were tabulated from Table 11 and the average volume/individual (in mm^3) was found by two methods, idealized calculations based on integration of body length and diameter and by water displacement. The average volume is given in column A of Table 7.

In the second column of Table 7 is a figure representing the average number of individuals of each species per m^3 on a yearly basis. This figure fluctuates to a great degree on a monthly basis but column B gives the average/m^3/yr.

Column C of Table 7 is the product of columns A times column B and represents the average density in mm^3/m^3/yr that any one species occupies in the lake.

On the basis of column C, zooplankton on a yearly basis represents approximately 2432 mm^3/m^3/yr, whereas Mysis and Pontoporeia represent only 80.4 mm^3/m^3/yr, a ratio of approximately 30:1. However, in actual stomach analyses, Mysis and Pontoporeia compose 2.4 times the volume of zooplankton in the bloater, 1.5 times as much in the alewife, 92% as much in the smelt, and 30% as much in the perch. Even in the perch, the large limnetic crustacea compose 10 times as much volume as would be expected by random chance alone. On this basis then, selective predation on particular food items can be inferred and the hypothesis of Brooks and Dodson (1965), and Smith (1970), seems valid.

Table 7. Food sources in Lake Michigan - Zooplankton and Limnetic Crustacea: Average Volume per individual, Average Number of Individuals Per Cubic Meter of Lake Water, Average Volume of Each Species Per Cubic Meter of Water On A Yearly Basis.

	Ave. Volume (mm^3)	Ave. $\#/m^3$ On A Yearly Basis	Density-Volume Units Ave. Vol./m^3 On A Yearly Basis
Daphnia galeata	1.8	125.0	225.0
D. retrocurua	1.8	141.0	253.8
D. longiremis	1.3	1.5	2.0
Epischura lacustris	0.5	21.0	10.5
Diaptomus sicilis	0.82	443.0	363.3
D. ashlandi	0.25	101.0	25.3
Polyphemus pediculus	0.15	9.2	1.38
Cyclops bicuspidatus	1.1	607.0	667.7
Mesocyclops edax	1.4	72.5	101.5
Diaphenosoma brachyurum	0.82	1.8	1.5
Leptodora kindtii	3.92	6.5	25.5
Limnocalanus macrurus	2.0	375.0	750.0
Mysis relicta	34.5	23.3	80.4
Pontoporeia affinis	34.5	23.3	80.4
Bosmina longirostris	0.05	93.0	4.6

Total Zooplankton = 2432 Vol./m^3/yr.

Total Mysis & Pontoporeia = 80.385 Vol./m^3/yr.

Zooplankton

History

Very few papers have been published on limnetic crustacea in Lake Michigan. Early works (Birge 1882, 1894; Forbes 1882; March 1895) mainly consist of brief accounts of certain species. Not until the papers of Eddy (1927) was any thorough analysis attempted. This work stood almost alone until Well's studies were published in 1960 and 1968, studies which provide much of the background for this paper.

Results and Discussion

Table 11 gives zooplankton concentration in numbers/meter^3 for 15 species of zooplankton in Lake Michigan (numbers/10 meters^3 for *Pontoporeia affinis* and *Mysis relicta*). Although in different families, *Pontoporeia* and *Mysis* show similar distribution patterns (Beeton, 1957) and are lumped in Table 11. These numbers are averages over all depths and stations and do not reflect the true distribution at time of capture. Since Well's 1960 paper goes into detail on depth distribution, I omitted these data here. Of the 35 species identified (Table 8), 19 showed vertical migration on a diel basis, further complicating distribution patterns. The 15 species shown in Table 11 show changes consistent with those found by Wells in terms of numbers/meter^3 during the various months of the year. They also show changes in frequency on a year to year basis (Table 11). Forms that declined sharply from 1954 to 1966 (Wells 1970), and are now increasing in numbers, are the largest cladocerans (*Leptodora kindtii*, *Daphnia galeata*, and *Daphnia retrocurva*), the largest calanoid copepods (*Limnocalanus macrurus*, *Epischura lacustris*, and *Diaptomus sicilis*), the largest cyclopoid copepod (*Mesocyclops edax*), the mysid *Mysis relicta*, and

Table 8. Zooplankton and Limnetic Crustacea from Lake Michigan 1970-1972 (Saugatuck, Ludington, and Big Sable Point)

	Mean Length (mm)	Range of Lengths (mm)
Cyclopoid Copepods		
Cyclops bicuspidatus	0.91	0.60- 1.20
Cyclops vernalis	0.91	0.66- 1.13
Mesocyclops edax	1.15	0.87- 1.30
Tropolycyclops parasinus	*	*
Eucyclops agilis	*	*
Calanoid Copepods		
Diaptomus ashlandii	0.85	0.68- 0.96
Diaptomus minutus	0.83	0.65- 0.92
Diaptomus oregonensis	1.08	0.95- 1.17
Diaptomus sicilis	1.25	1.07- 1.40
Limnocalnus macrurus	2.45	2.00- 2.65
Eurytemera affinis	1.07	0.92- 1.18
Epischura lacustris	1.70	0.87- 1.98
Senecella calanoides	2.89	2.00- 3.26
Cladocera		
Bosmina longirostris	0.45	0.27- 0.56
Bosmina coregonia	0.48	0.27- 0.69
Daphnia galeata mendotae	1.13	0.65- 1.87
Daphnia retrocurva	1.13	0.60- 1.85
Daphnia longiremis	0.85	0.50- 1.61
Diaphanosoma brachyurum	0.85	0.38- 1.06
Diaphanosoma leuchtenbergianum	0.84	0.42- 1.00
Ceriodaphnia quadrangula	0.55	0.37- 0.70
Ceriodaphnia lacustris	0.60	0.40- 0.75
Eurycercus lamellatus	*	*
Holopedium gibberum	0.70	0.45- 1.00
Polyphemus pediculus	0.56	0.45- 0.96
Leptodora kindtii	5.00	2.36- 5.80
Chydorus sphaericus	*	*
Sida crystallina	*	*
Amphipoda		
Pontoporeia affinis	≈11.70	7.00-13.00
Mysidacea		
Mysis relicta	≈12.40	8.00-14.00
Very rare species		
Daphnia schodleri	*	*
Daphnia ambigua	*	*
Scapholebris aurita	*	*
Simnocephalis sp.	*	*
Moina micrura	*	*

* Too few captured for adequate estimation of mean length or range.

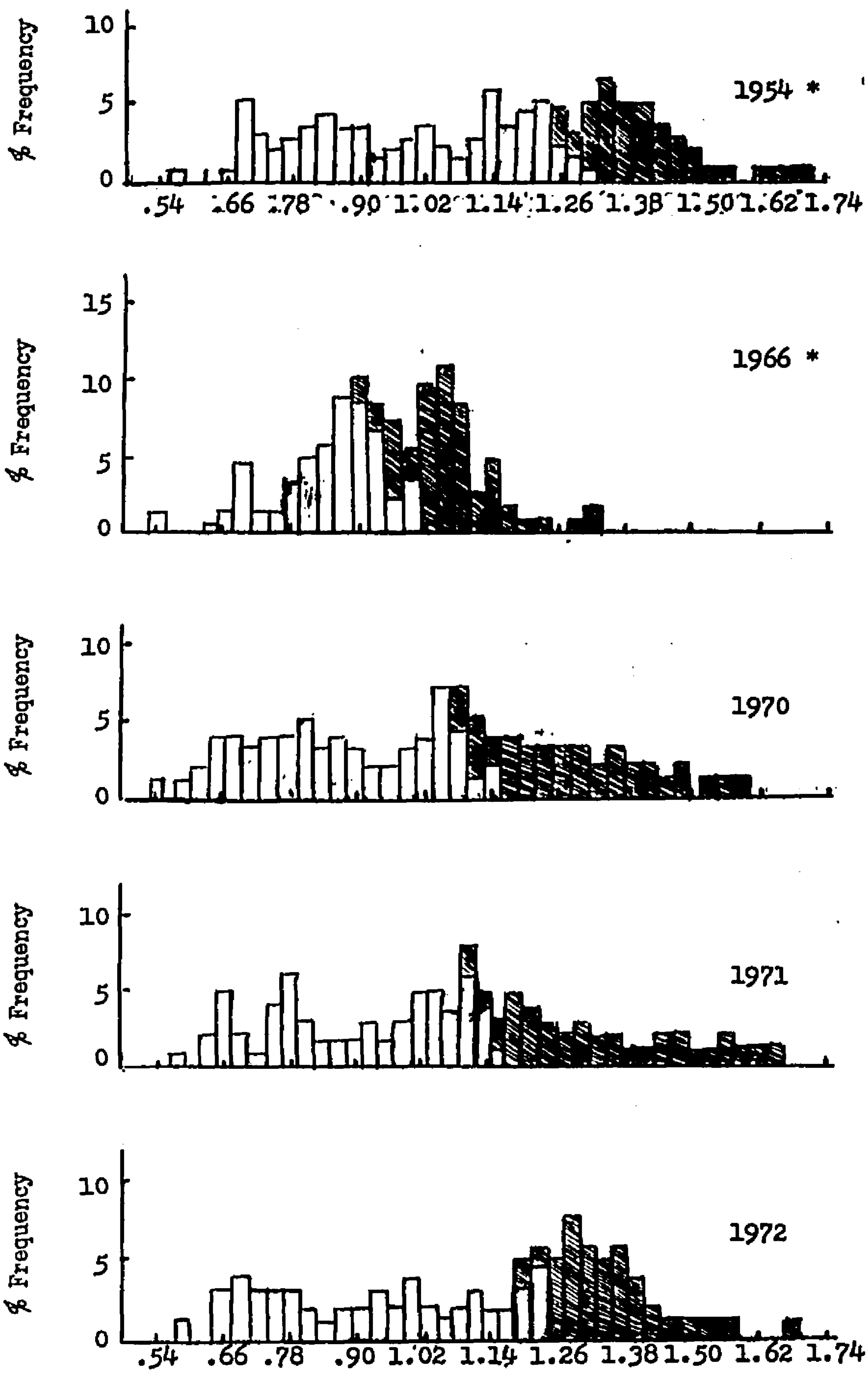
the amphipod Pontoporeia affinis. Of these Daphnia galeata and Mesocyclops edax became extremely rare by 1966, but are now present in numbers equal to the 1954 population size. Some of the medium and small species, which increased in numbers from 1954 to 1966, and which are now on the decline, are the cladocerans Daphnia longiremis, Polyphemus pediculus, and Bosmina longirostris, and the copepods Cyclops bicuspidatus and Diaptomus ashlandi. Some of the middle sized forms show the same pattern as the larger forms, but on a smaller scale (i.e. Disphanosoma brachyurum). The zooplankton composition of 1972 has shifted back towards that of 1954.

Figure 7 shows another facet of this change. The average size, and size at onset of maturity, of Daphnia retrocurva has also changed through the years. The 1972 population of this species has shifted from that of 1966 to resemble more closely that of 1954.

Phytoplankton

Of all species of phytoplankton identified from Lake Michigan, (Table 9) over 99% were diatoms. During the three-year counting period, 2471 diatom slides were made and enumerated. Because of the large numbers of slides involved, a direct count of frustules/ml was impossible. Consequently the method of McNabb (1960) was used, with the following change; since this method cannot estimate the number of frustules for chain-forming diatoms such as Fragilaria and Tabellaria or the numbers in a "composite" diatom such as Asterionella, I multiplied the number of diatoms determined by McNabb's method by the average number of composite parts, or average chain length to obtain an average for number of frustules. This is in close agreement (.05 level of significance) with actual

Figure 7. Length distribution of female <u>Daphnia</u> <u>retrocurva</u> from samples in 1954, 1966, 1970, 1971, and 1972. (Darkly shaded portions represent mature individuals.)



* Data obtained from Wells (1970)

frustule counts. Average numbers are given in Table 9. The seasonal abundance of 12 species by season and depth is graphically shown in Figures 8A-H.

Cyclotella bodanica and Cyclotella comta are both listed on one graph as a sum of the two species on the basis of size, shape, and similarity of trends. Both species are found in highly oligotrophic conditions (Holland, 1968), as the smaller Cyclotella species, Kutzingiana and michiganiana, both of which are also listed on one graph. Skvortzow (1937) reported that Cyclotella bodanica was common among diatoms from the Chicago city mains in January 1936, along with C. comta, C. michiganiana, and C. ocellata. These forms, though still present in the southern basin, have given way to other forms (Stoermer and Yang, 1970). C. michiganiana, a form endemic to Lake Michigan, is approximately twice as common in the northern basin as in the southern (Holland, 1969). As the graphs show, all of these species reach greater numbers in the northern basin than in the southern, indicating cleaner waters to the north. The graphs also indicate summer maxima slightly later in the northern basin. Another trend, not shown here is a tendency for the numbers of oligotrophic forms to increase in numbers as one moved further offshore or further from a "polluting" source (i.e. - the Kalamazoo River).

In contrast to these highly oligotrophic forms, one also finds many eurytopic species, some eutrophic, and some which are found in hypereutrophic habitats. Among the eurytopic species are Melosira islandica, Fragilaria crotonensis Kitton. var. crotonensis, Asterionella formosa Hass. var. formosa, Tabellaria fenestrata (Lyngb.) Kutz. var. fenestrata, Tabellaria flocculosa (Roth) Kutz. var. flocculosa, Synedra acus Kutz. var. acus, and Synedra nana Meist.. Each of these will be discussed.

Melosira islandica is a eurytopic species which is the usual spring dominant form and has been so for many years (Ahlstrom, 1936). This species is abundant in oligotrophic lakes in the mountain and northern regions of Europe (Stoermer and Yang, 1970), and appears to be favored by low levels of enrichment, as it is reduced around polluted harbors in Lake Michigan and in Green Bay (Stoermer and Yang, 1970). M. islandica peaked in late April-early May at Saugatuck and in mid-May at Ludington, decreasing to less than 10 organisms/ml by late June in both areas.

Melosira islandica is replaced as the dominant form in the early summer by Fragilaria crotonensis and Asterionella formosa. F. crotonensis also peaks at the beginning of May, but does not dwindle to less than 100 frustules/ml until about the end of September. It is the most consistent major dominant in the lake and is reduced only adjacent to polluted harbors (Stoermer and Yang, 1970).

Asterionella formosa, the other summer dominant, shows an odd distribution pattern. In the southern basin of Lake Michigan, it is one of the dominant forms in May and June, but only at shallow depths (less than 5 meters). The species then virtually disappears until late September. By contrast, data from Big Sable Point and the Ludington Project show a uniform depth distribution with the highest levels occurring in late June through September, data which agree with those of Stoermer and Yang (1970), but disagrees with those of Cholnoky (1968) who, in smaller lakes, found patterns more consistent with those found in the southern basin. This would appear to relate to thermal stratification and availability of nutrients.

Tabellaria fenestrata and Tabellaria flocculosa are grouped together in Figure 8 because of their close affinity. Indeed, because of their similar distribution pattern, the two species are often considered two expressions or forms of the same genotype (Knudson, 1952). Their peaks in Lake Michigan's two major basins coincide quite closely but approximately 1½ times as many frustules were counted at the peak near Saugatuck, again stressing the more advanced eutrophication of that area.

Synedra acus and Synedra nana were grouped for convenience. Their numbers peaked during the summer (June-August) and seldom during the counting period dropped below 100 frustules/ml, except at the closer inshore Ludington stations. Numbers averaged 600/ml at the Saugatuck stations in midsummer, 400/ml in the Ludington area.

One form, Melosira granulata, shows significant differences between the two basins. This form, though not dominant in Lake Michigan, is often dominant in eutrophic, alkaline lakes in northern Europe and North America (Cleve-Euler, 1951; Huber-Pestalozzi, 1942; Stoermer and Yang, 1970). It reaches peaks of greater than twice as many individuals at Saugatuck and reaches these peaks a month to a month and a half earlier than the smaller peak at Ludington. As it is not yet a dominant, it seems to imply that Lake Michigan is, as yet, relatively oligotrophic or mesotrophic.

This implication is further strengthened by the low-level presence of Stephanodiscus tenuis, a form associated with disturbed habitats (Stoermer and Yang, 1970). This species has been reported in sampling from Lake Ontario (Nalewajko, 1960), Lake Erie (Hohn, 1969) and Green Bay and other parts of Lake Michigan (Holland, 1969). It has long been present in Lake Michigan but reached levels of 1% of all phytoplankton only recently (Stoermer and Yang, 1970). According to Stoermer and Yang, its abundance is restricted as yet to near shore areas and harbors. This is borne out in this set of studies, the inshore zones contributing the greatest numbers of individuals, with the zone just north of the Kalamazoo River contributing the highest numbers of all in these studies, (525 frustules/ml in early June in 1971). Stoermer and Yang (1970) project an increase in the numbers of this species as pollution increases.

The average numbers of some of the large forms (greater than 15u in size) of phytoplankton such as Asterionella formosa, Synedra ulna, Melosira islandica and Cyclotella bodanica have shown decreases over the three year period. This decrease was accompanied by an increase in the numbers of some of the smaller Cyclotella forms and the small Stephanodiscus forms. There has been no concommitant decrease or increase in the size of any of the species. Colleagues associate this decrease in large forms with decreasing levels of phosphate, nitrate, and silicate in the lake, an association without adequate statistical backing. I believe the decrease to be associated with increasing numbers of large zooplankters since 1967, when the alewife, a selective predator on large zooplankton forms (Brooks and Dodson, 1965; Wells, 1970), reached it's peak and started to decline, allowing the large zooplankton to increase in numbers. This rise in numbers could have effected the decrease in numbers of large phytoplankton in two ways (1) large zooplankton consume a greater quantity of phytoplankton/body volume and (2) large zooplankton are the only ones that can handle larger (greater than 15 u) phytoplankton.

Physical and Chemical Studies

Temperatures ranged from .2°C to 22.3°C over the three year period. On most dates, except in shallow water, temperatures were slightly lower at the bottom depths. Thermal stratification was observed during the

Table 9
Phytoplankton Species

Species	Location North or South Basin	# Frustules/ Chain or Complex
Achnanthes clevei	both	1.0
Amphipleura pellucida	"	1.0
Amphiporora ornata	"	1.0
Amphora ovalis	"	1.0
Amphora perpusilla	"	1.0
Ceratoneis arcus	"	1.0
*Cyclotella bodanica	Mainly North	1.0
*Cyclotella comta	" "	1.1
*Cyclotella glomerata	"	4.0
*Cyclotella kutzingiana	Mainly North	3.0
Cyclotella meneghiniana	Mainly South	1.5
*Cyclotella michiganiana	Mainly North	2.3
Cyclotella ocellata	both	2.1
*Cyclotella stelligera	"	2.0
Cymatopleura solea	"	1.0
Cymbella turgida	"	1.0
*Diatoma tenue v. elongatum	"	1.7
Diatoma vulgare	"	1.5
Eucocconeis flexella	Mainly North	1.1
Fragilaria capucinea	both	6.0
Fragilaria construens	"	6.3
*Fragilaria crotenensis	"	7.2
Fragilaria intermedia	"	4.2
*Fragilaria pinnata	"	4.5
Fragilaria virescens	"	4.0
Gomphonema olivaceum	"	1.0
*Melosira ambigua	"	5.0
Melosira binderana	Mainly South	6.8
Melosira distans	both	5.0
*Melosira granulata	"	5.4
*Melosira islandica	"	3.9
Melosira varians	"	3.8
Meridion circulare	"	5.6
Navicula anglica	"	1.0
Navicula radiosa	"	1.0
Navicula reinhardtii	"	1.0
Navicula scutelloides	"	1.0
Nitzschia acicularis	"	1.0
Opephora martyi	"	1.0
Rhoicosphenia curvata	"	1.0
Rhizosolenia eriensis	"	1.0
*Stephanodiscus astraea	"	1.6
*Stephanodiscus niagarae	"	1.1
*Stephanodiscus tenuis	Mainly South	4.0
Surirella angusta	both	1.0
Surirella tenera	"	1.4
*Synedra acus	"	1.4

Table 9 (contimued)

Species	Location North or South Basin	# Frustules/ Chain or Complex
*Synedra nana	both	1.0
*Synedra ulna	"	1.0
Synedra vaucheriae	"	1.0
*Tabellaria fenestrata	"	12.4
*Tabellaria flocculosa	"	10.1
Cocconeis interruptus	"	1.7
*Asterionella formosa	"	5.8

* Principal species

Figure 8A-8H. Phytoplankton trends in Lake Michigan 1970-1972.

Figure 84A

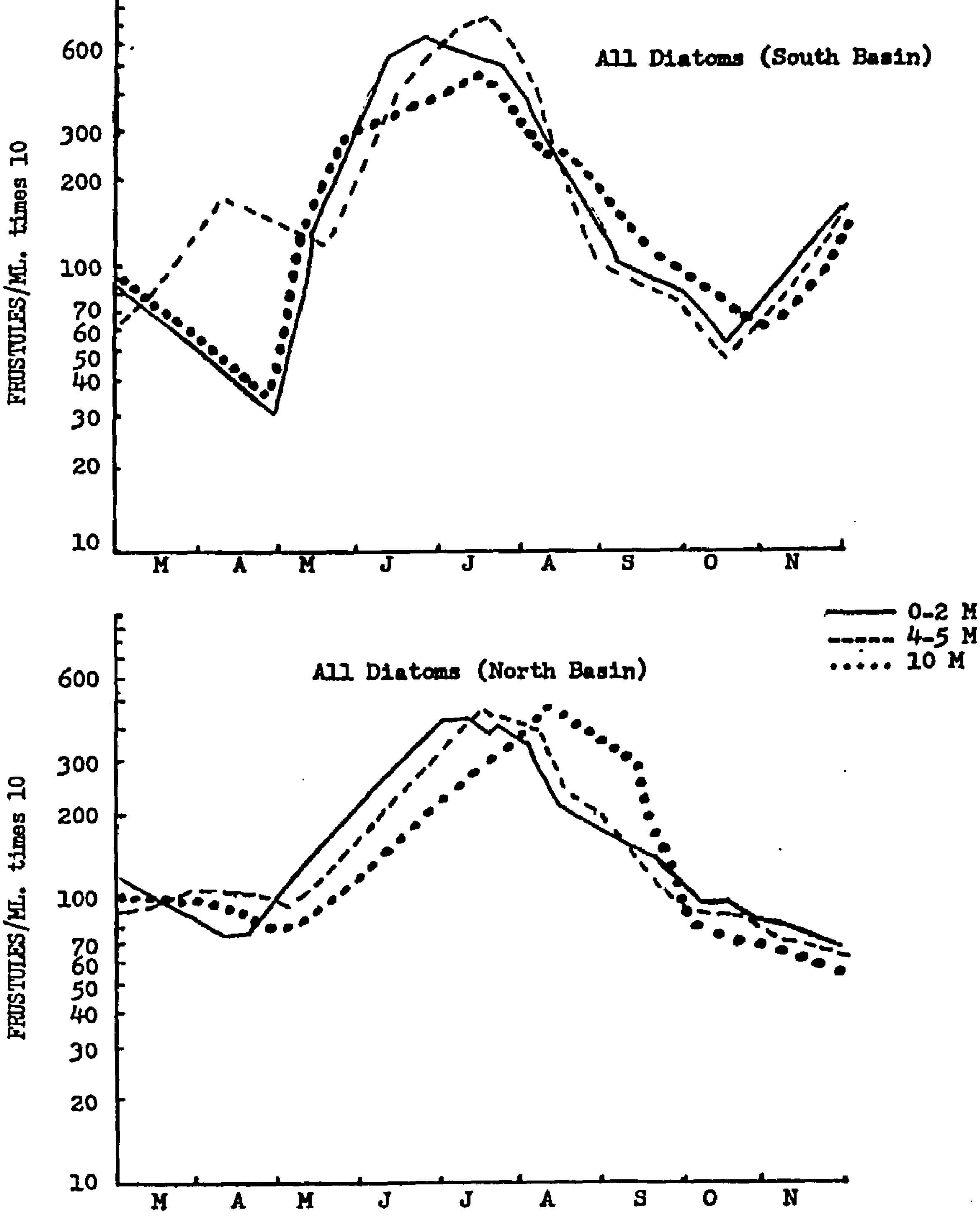

All Diatoms (South Basin)
FRUSTULES/ML. times 10
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N
0-2 M
4-5 M
10 M
All Diatoms (North Basin)
FRUSTULES/ML. times 10
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N

Figure 8-B

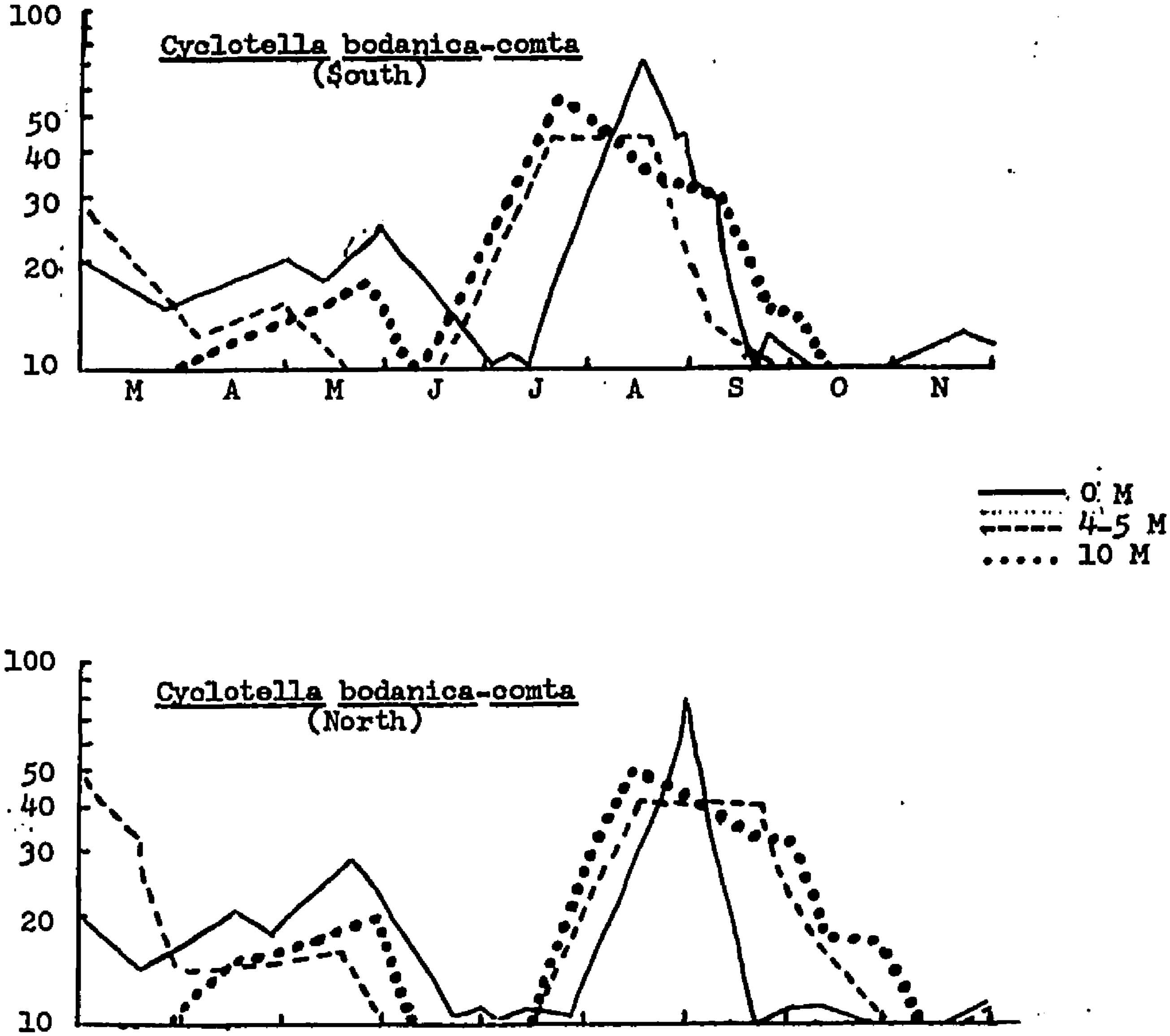

Cyclotella bodanica-comta
(South)
100
50
40
30
20
10
M
A
M
J
J
A
S
O
N
0 M
4-5 M
10 M
Cyclotella bodanica-comta
(North)
100
50
40
30
20
10
M
A
M
J
J
A
S
O
N

Figure 8-B (continued)

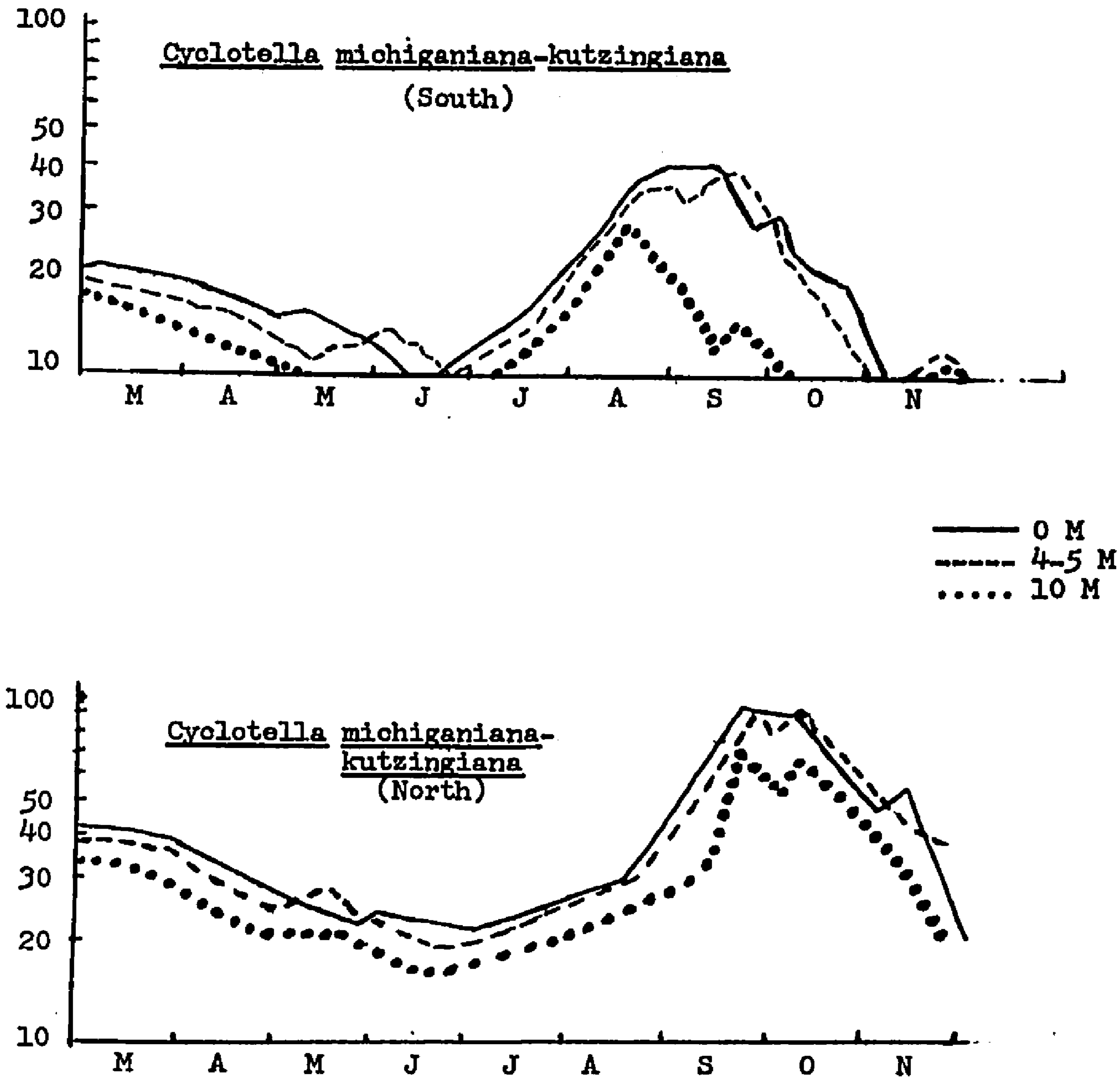


Figure 8-C

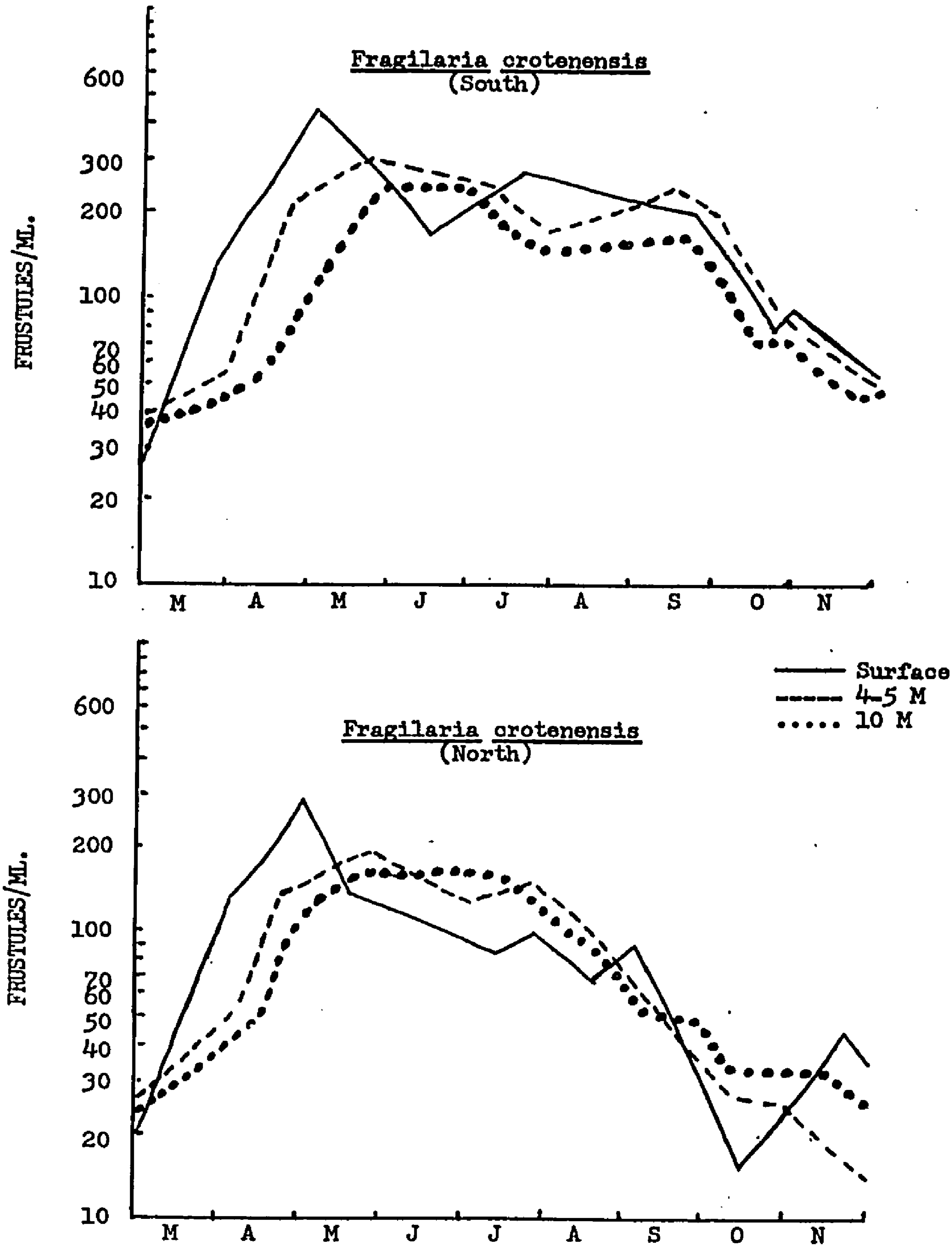
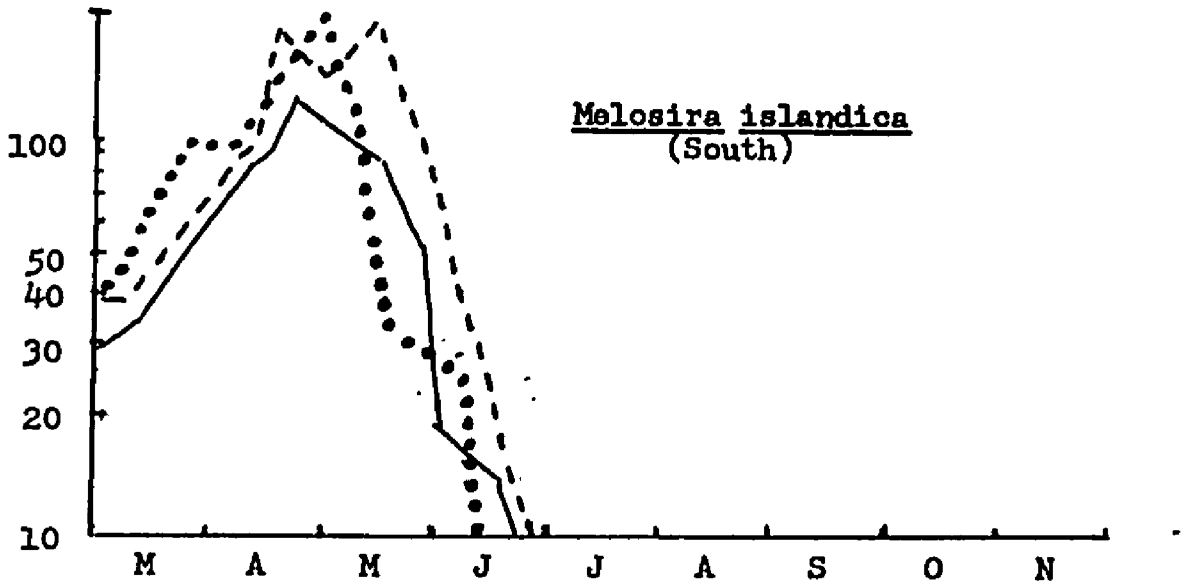

Fragilaria crotenensis
(South)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N
Surface
4-5 M
10 M
Fragilaria crotenensis
(North)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N

Figure 8-D


Melosira islandica
(South)
100
50
40
30
20
10
M
A
M
J
J
A
S
O
N

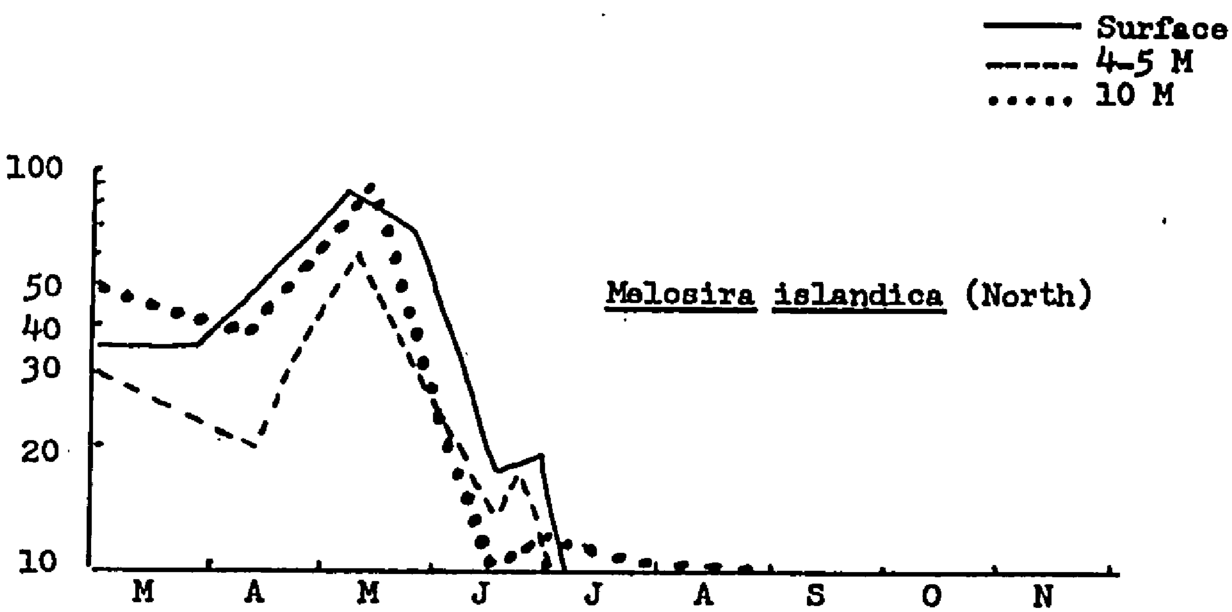
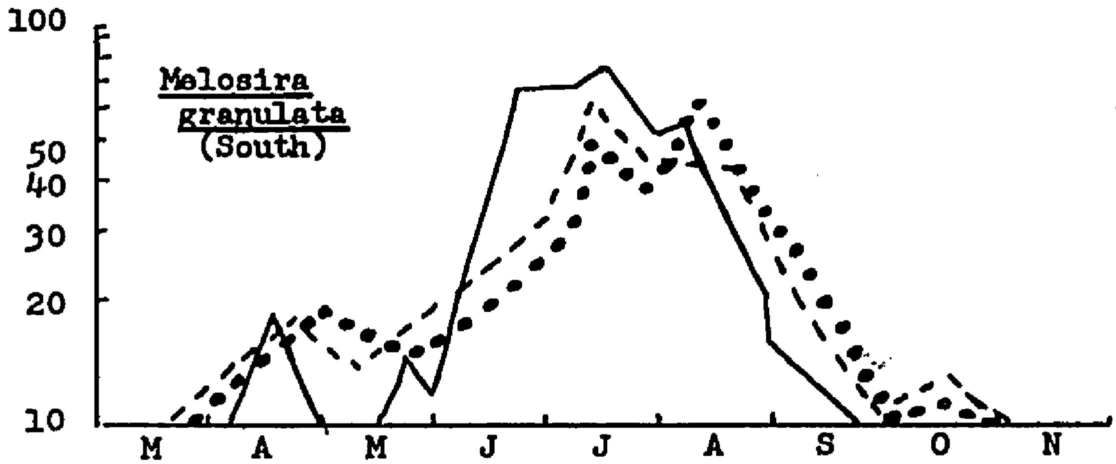

Surface
4-5 M
10 M
Melosira islandica (North)
100
50
40
30
20
10
M
A
M
J
J
A
S
O
N

Figure 8-D (continued)



——— Surface
----- 4-5 M
..... 10 M

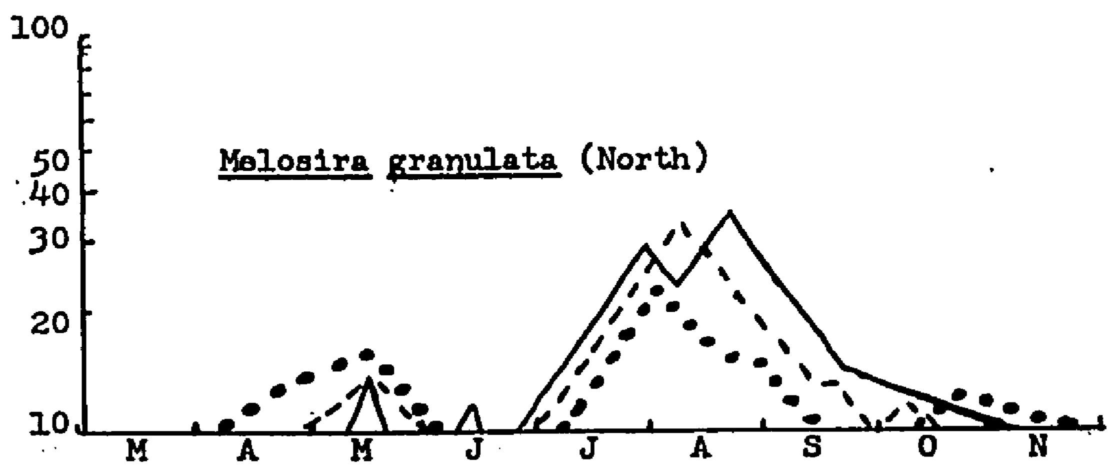
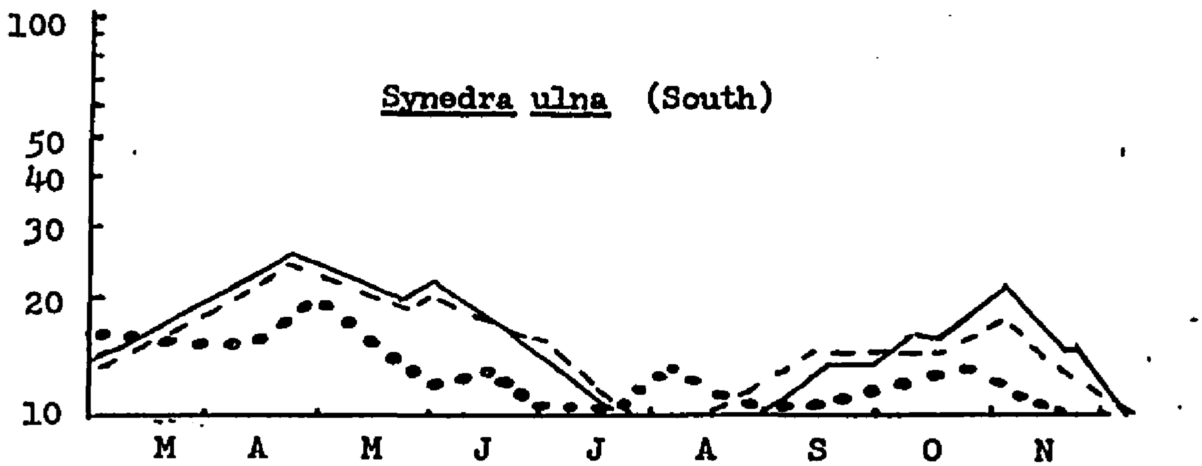


Figure 8-E


100
50
40
30
20
10
Synedra ulna (South)
M
A
M
J
J
A
S
O
N

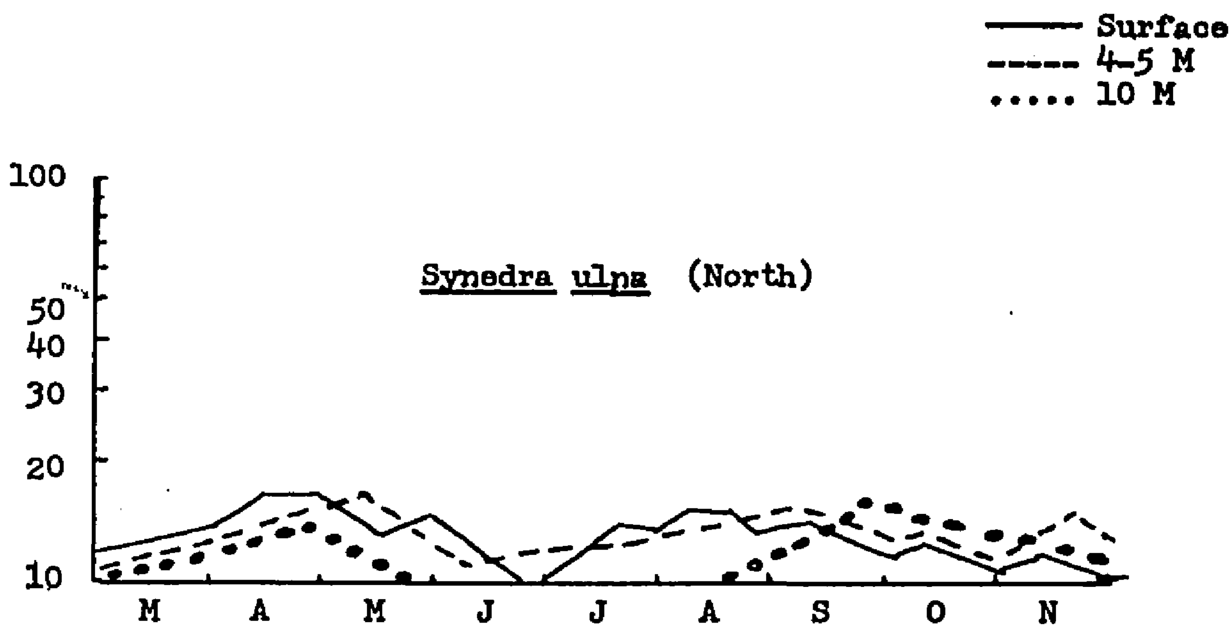

Surface
4-5 M
10 M
100
50
40
30
20
10
Synedra ulna (North)
M
A
M
J
J
A
S
O
N

Figure 8-E (continued)

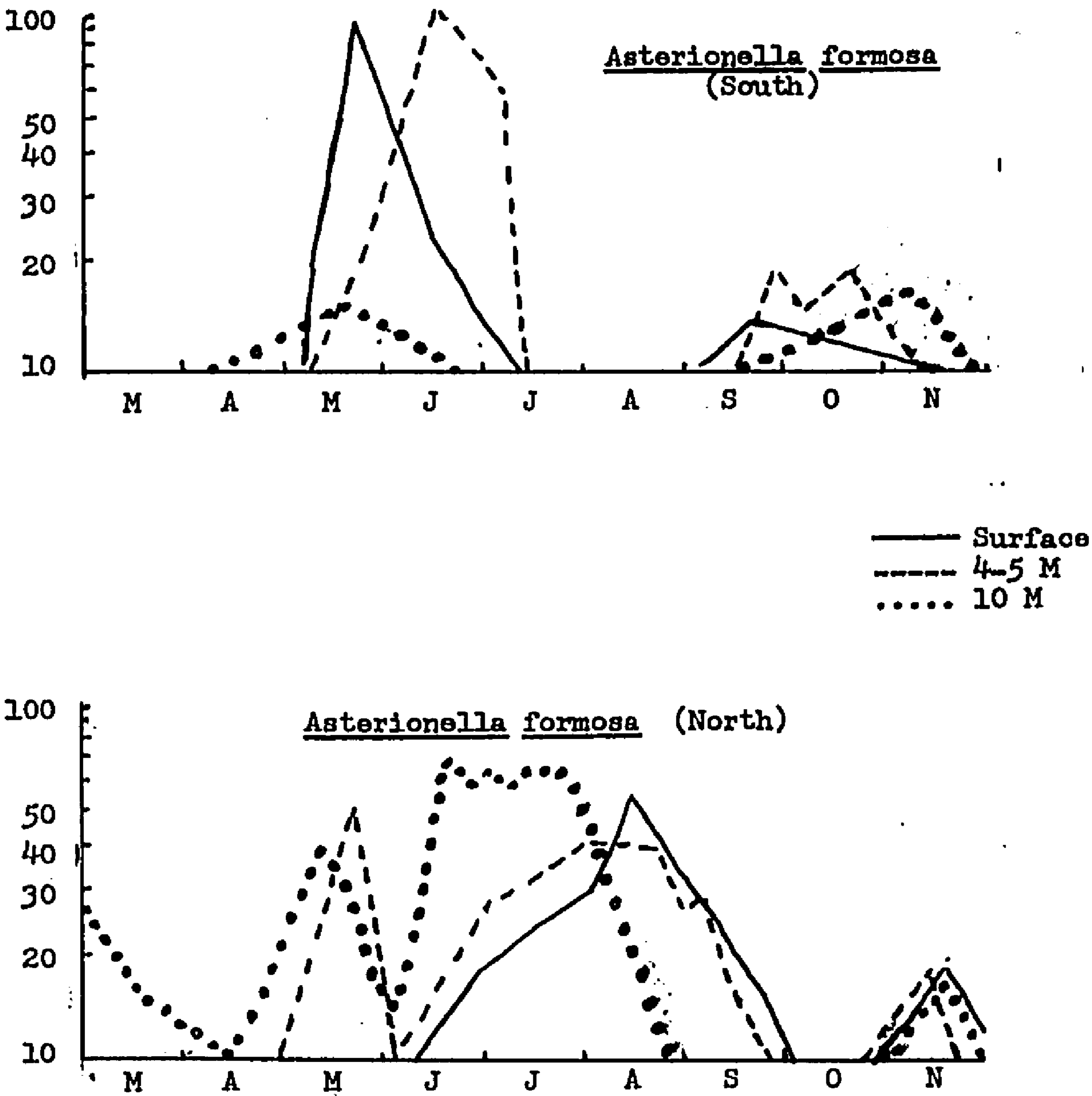
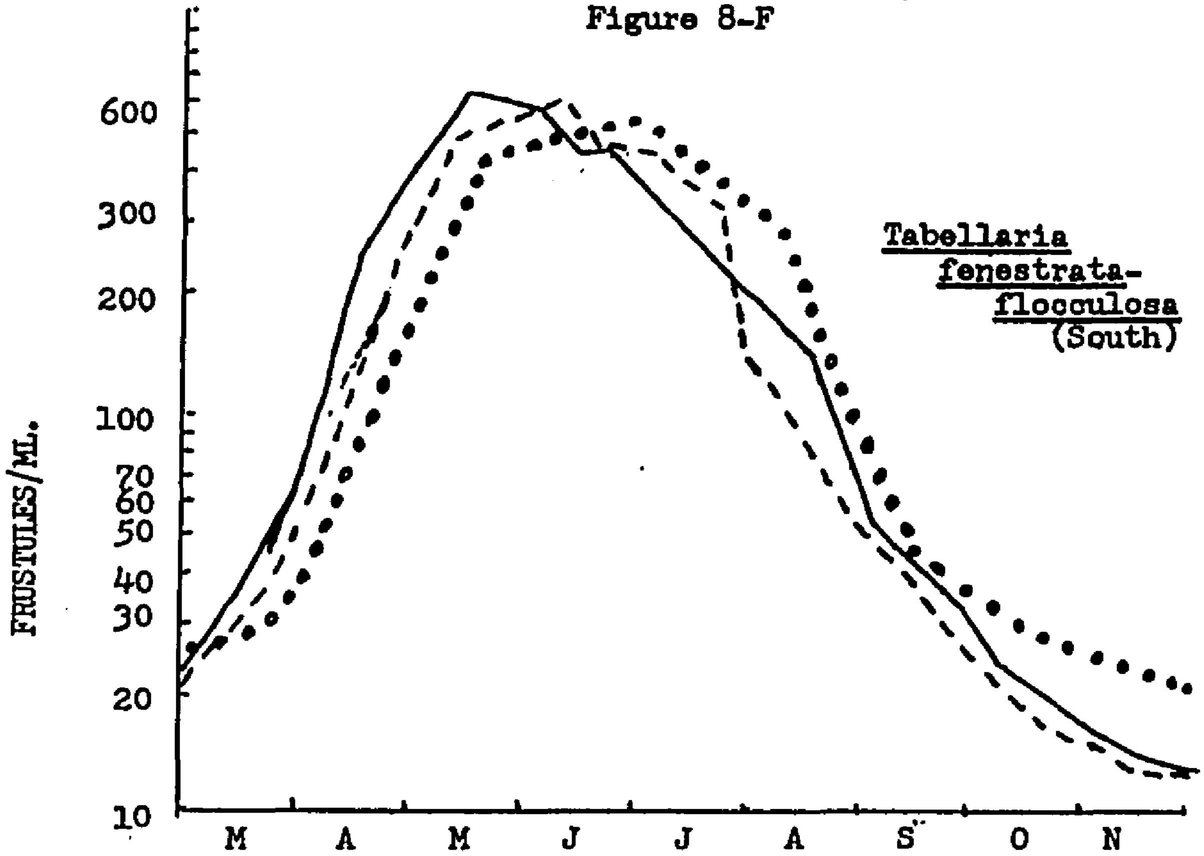


Figure 8-F


Tabellaria fenestrata-flocculosa (South)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M A M J J A S O N

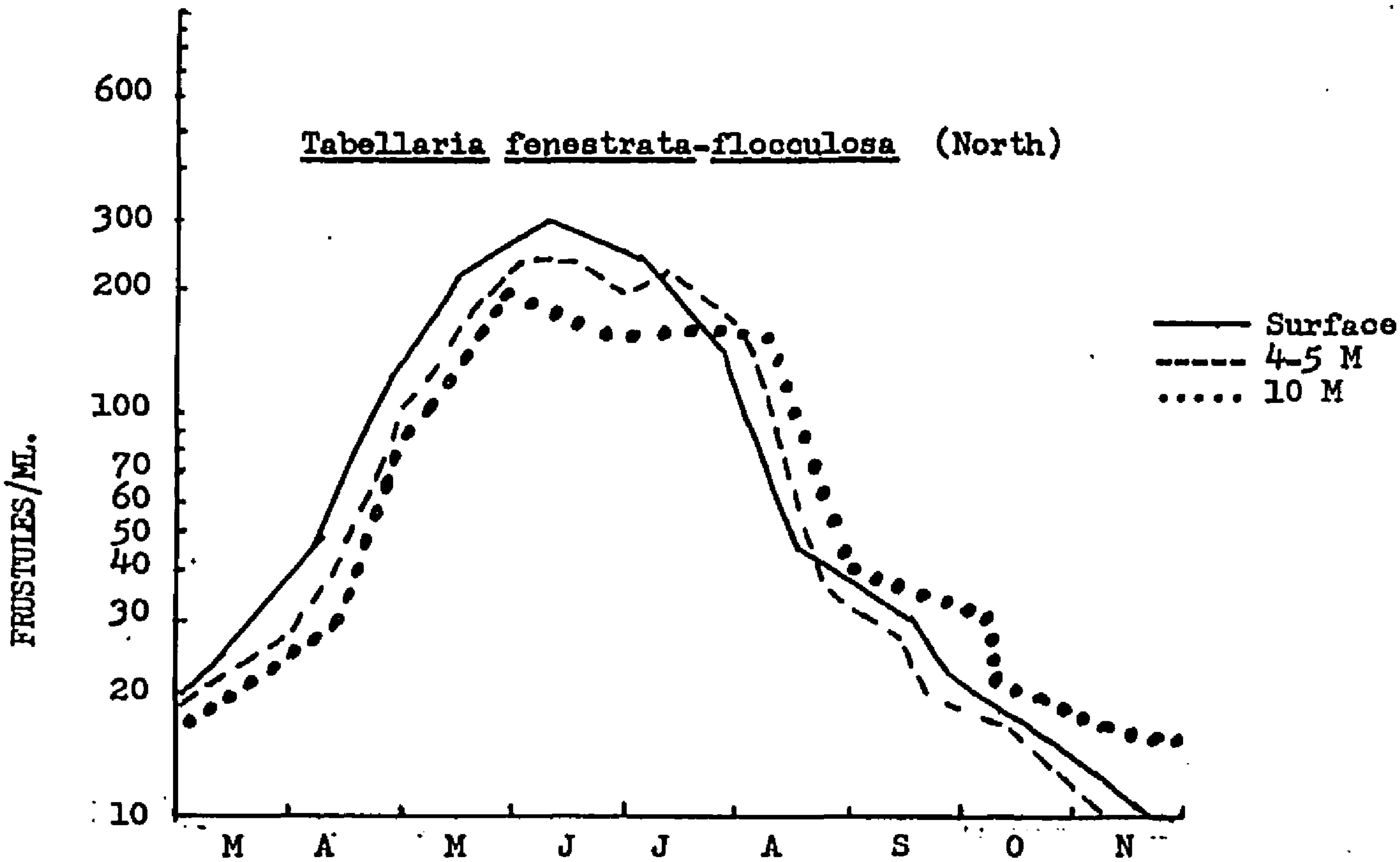
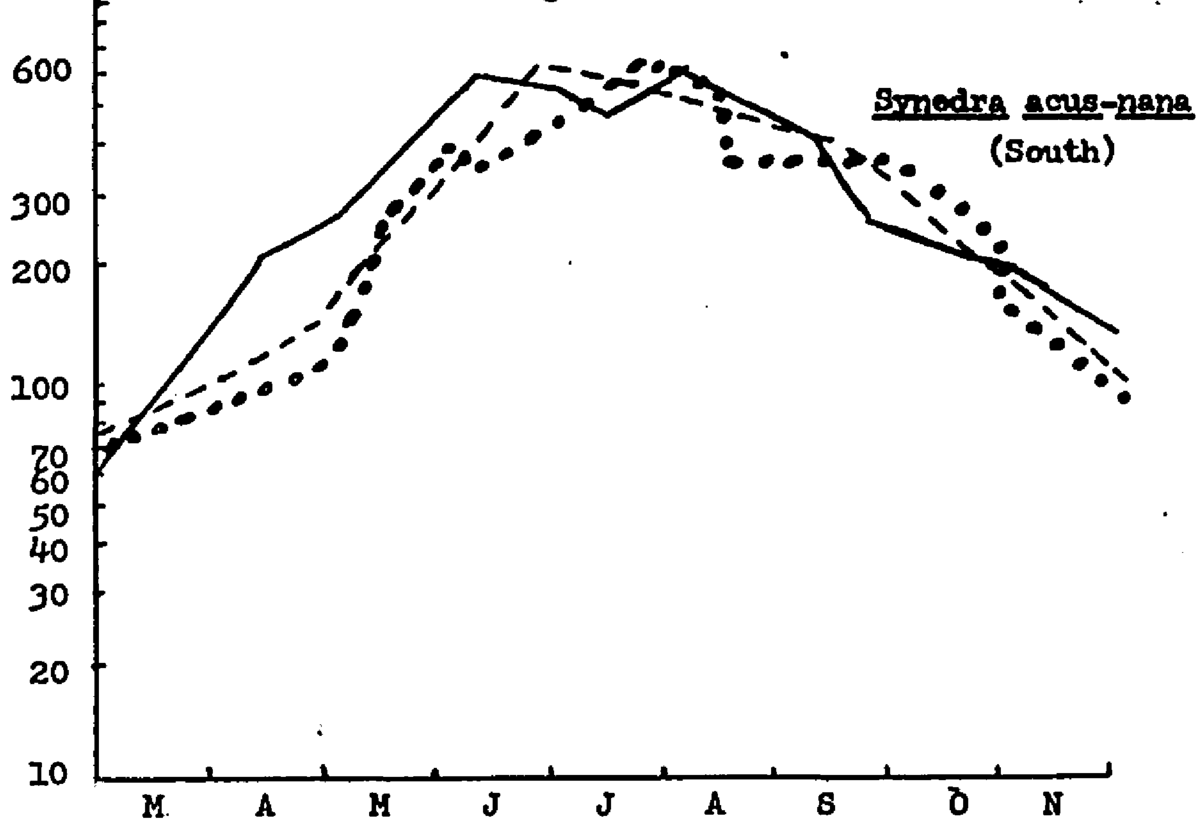

Tabellaria fenestrata-flocculosa (North)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M A M J J A S O N
Surface
4-5 M
10 M

Figure 8-G


Synedra acus-nana
(South)
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N

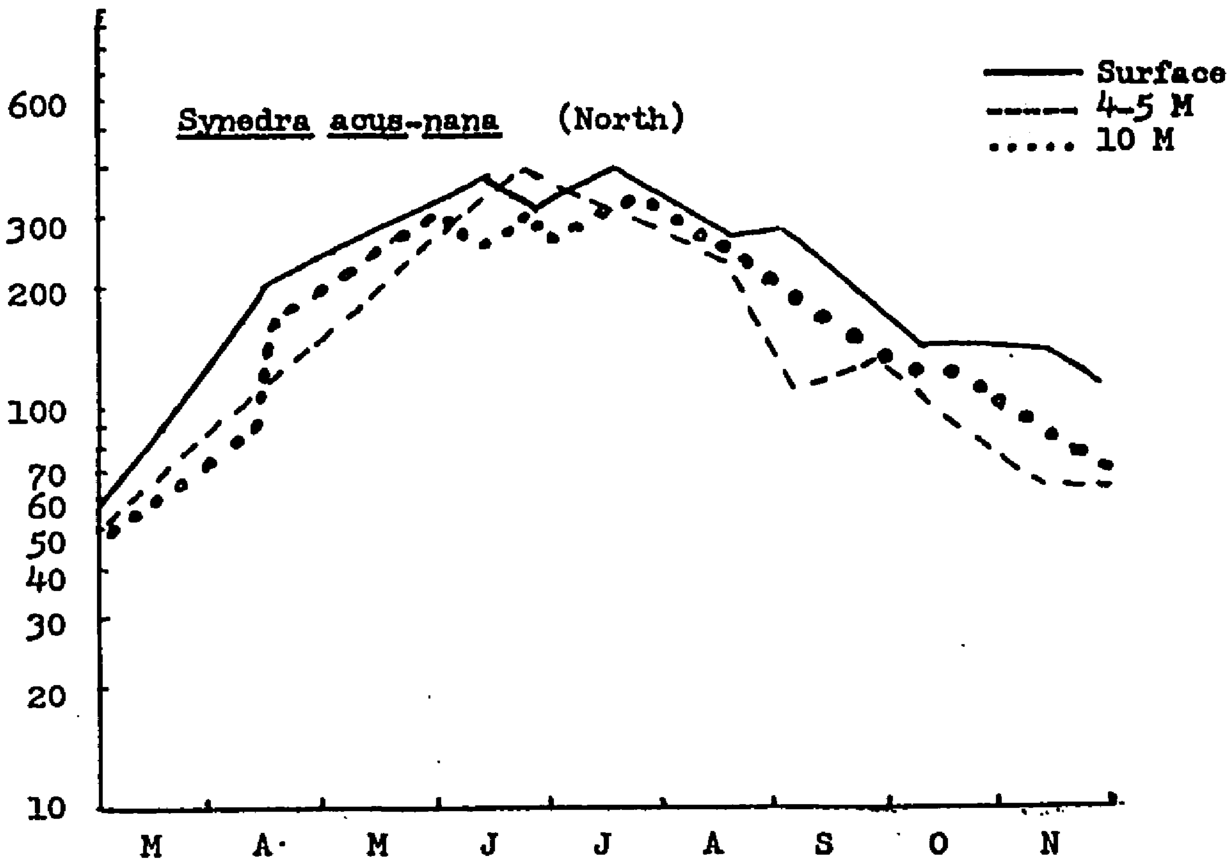
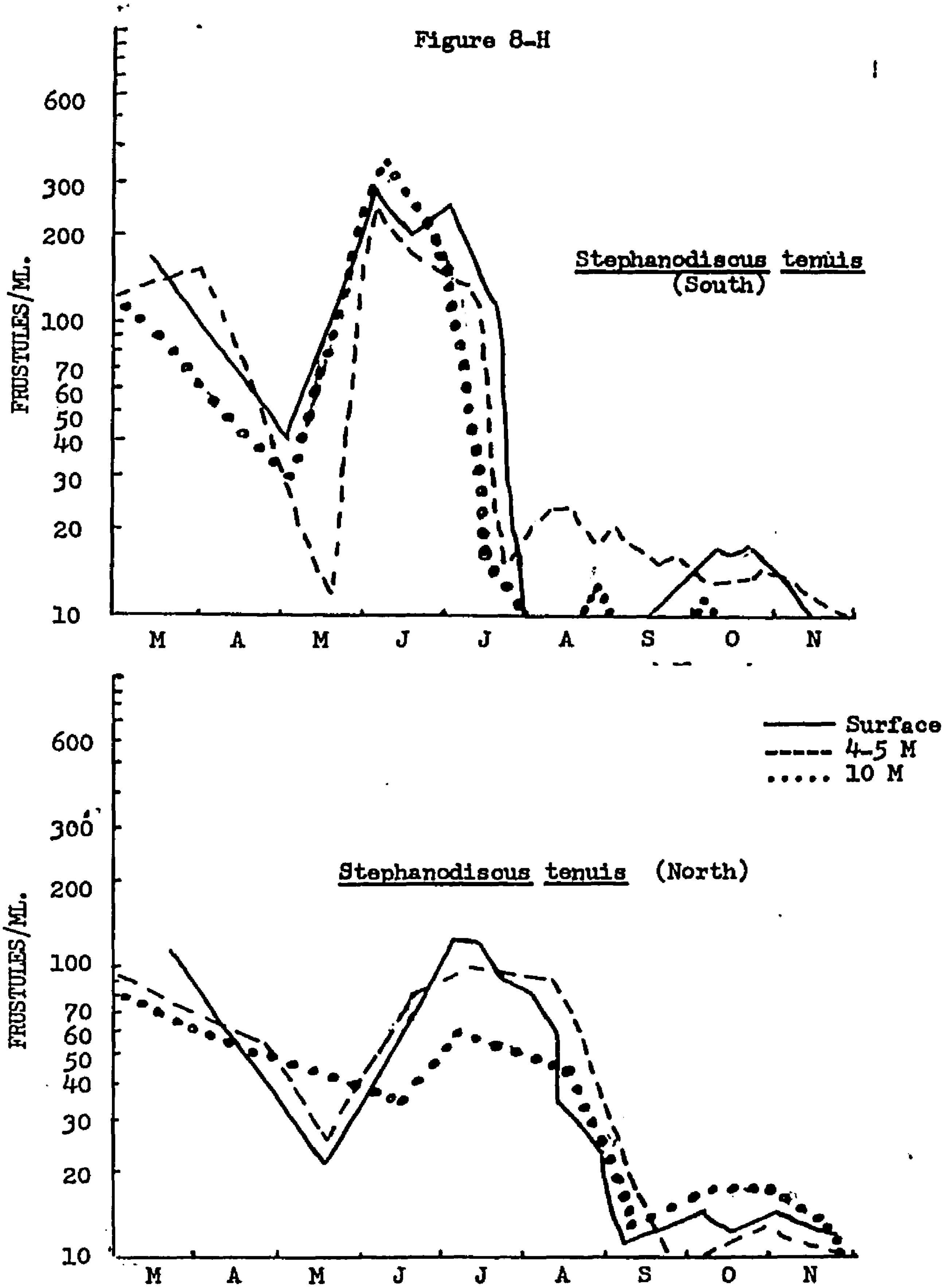

Surface
4-5 M
10 M
Synedra acus-nana (North)
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N

Figure 8-H


Stephanodiscous tenuis
(South)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N
Surface
4-5 M
10 M
Stephanodiscous tenuis (North)
FRUSTULES/ML.
600
300
200
100
70
60
50
40
30
20
10
M
A
M
J
J
A
S
O
N

summer at Big Sable Point Stations 2, 3, and 4; Saugatuck station 9 and Ludington station 16. These are the deep-water stations and stratification is to be expected here. During stratification, temperature differences of up to 13°C were observed between the surface and bottom values.

Although turnover and initial warming occurred at different times over a three-year period, a gradual warming trend is apparent which affects the closer inshore waters sooner than the waters further offshore. This warming trend shows wide fluctuations due to winds and upwelling currents. Northerly winds, as expected, tend to lower the temperatures while southerly winds tend to increase temperatures in short (24 hour) periods of time. These changes are particularly evident during June, July, and August when surface water normally at temperatures around 15°C can be lowered up to 8.5°C in one 24-hour period. In the shallower depths, bottom temperatures tend to follow the same curves as the surface water. Nevertheless, temperatures did show a constant warming trend and reached maximum temperatures of 17.8°C at Big Sable Point (station 6), 18.2°C at Ludington (station 16), and 22.3°C at Saugatuck (station 7) during this study. The warming trend begins earlier in the southern basin than in the northern, and higher maximum temperatures are reached in the southern basin. Minimum temperatures for this study were 2.2± 2°C for all three locations over all three years. These lows were recorded in March and April and again in late October and November for all depths. In March and April there is often ice on the lake, but all sample sites were out beyond this drift ice, thus yielding the slightly warmer temperatures than might be expected otherwise.

Water transparency as determined by Secchi disk is shown in Table 10. The greatest transparency was recorded in April at the Big Sable Point stations 3, 4, and 5. This transparency level of 11 meters is in substantial agreement with the study of Ayers et al. (1958) who found water of this clarity off Frankfort during June. Low Secchi disk readings at Big Sable Point and at Ludington were generally preceded by high wind and wave conditions which stirred up silt and clay from the bottom. Low transparency readings for the Saugatuck stations, were most often associated with a wind from the south which caused the plume of the Kalamazoo River to turn northward. The Kalamazoo carries a high load of suspended solids (silt and organics mainly) which dramatically lower the transparency of the water. The stations further offshore (station 9) and further north (numbers 10 and 11) were less affected by this weather condition. The southern basin tends to have a greater load of suspended solids and supports a greater phytoplankton growth (see phytoplankton) and thus showed lower overall transparency levels than the northern basin over the course of the three year study period.

Other data from chemical determinations are shown in Table . All the data are in the form of ranges and means for depths of 0-1 meters, 4-5 meters, and at the bottom. Although data are available for some dates and stations at 20 meters, those data are statistically identical (.05 level) with the bottom data and are excluded for the sake of clarity.

pH increased from about 7.0 (Saugatuck #7) or 7.8 (Ludington and Grand Sable Point) to around 8.5 to 8.6 during the month of June at all stations, with the exceptions of Grand Sable Point stations 4 and 5, which showed a slower rate of change at depths of 50-60 meters. The change is attributed to phytoplankton growth and photosynthesis, which changes the free CO_2 balance, and hence pH (Ruttner, 1969). It is of note that the greater initial reserves of CO_2 in the southern basin were used up at approximately the same time as those in the northern basin, implying that photosynthesis began sooner, or at a greater rate in the southern basin. This is consistent with earlier warming of the surface layers in the southern end of the lake. It is also of note that both the northern and southern basins reach the same pH endpoint, stressing the fact that the waters of the two areas show considerable mixing and probably have a large bicarbonate buffering capacity.

CO_2 levels, in connection with pH changes mentioned above, changed from 3.6 - 4.0 ppm to 0.0 ppm by the first weeks in July at all stations. As above, the levels began dropping sooner in the southern basin than in the northern, with inshore levels being the first to drop. Free CO_2 was again found at Grand Sable Point stations 2, 3, and 4, at Ludington station 16, and at Saugatuck station 9 at the beginning of August. Concentration varied for the three stations over the course of the three years, but free CO_2 did appear in quantity during August. After this time, quantities of free CO_2 fluctuated in the surface and deeper waters as the effects of wind mixing, temperature, rate of photosynthetic activity, and upwelling currents were felt, but at no time did the level drop to 0.0 ppm again.

Dissolved oxygen ranged from 10-15 ppm at Grand Sable Point, from 10-14 ppm at Ludington, and 6-14 ppm at Saugatuck. The high levels were found early and late in the year, when O_2 levels were constant throughout the water column. Levels dropped after this time, particularly at Saugatuck where levels dropped to 6 ppm at station 7 during July, probably due to a large influx of decomposing organic matter from the Kalamazoo River. This is substantiated by high dissolved solid levels at this time. Deep water O_2 levels decreased under the summer thermocline on calm days.

Measurements taken after storms with force 4 winds (about 8 ft. waves) showed dissolved oxygen levels to be equal throughout the water column implying wind-generated turnover of the water column. None of these readings are low enough to prevent utilization of the water column by any of the fish species inhabiting the lake, but some of the trout and salmon species tend to avoid the lower levels of O_2 exhibited around Saugatuck if other, higher levels were available (Frey, 1960).

Alkalinity levels were lower at the southern basin sites than at the northern sites (.01 level of significance). This is related both to CO_2 and to pH levels and was to be expected. A discussion of CO_2, pH, and alkalinity is found in Ruttner (1969) and Reid (1961).

Dissolved solids were significantly higher in the southern basin than in the northern. This can apparently be attributed to a complex of factors:

(1) The Kalamazoo River, which carries a high load of sediment and organics, enters Lake Michigan near the study sites. Indeed when the wind was from the south the amount of dissolved solids went up.

(2) The Saugatuck site receives a greater nutrient load, as measured by concentration of dissolved solids (Table 10) than do either of the northern basin sites. Internal current systems as measured by Ayer et al (1958) maintain these materials within the two basins, although some mixing does occur. The higher nutrient levels at the Saugatuck site should support a greater zooplankton and benthos crop than at Ludington or Big Sable Point.

Table 10
Water chemistry and transparency: ranges and means from surface, middle and bottom waters, 1970 and 1971, Big Sable Point (#1-3)

	Station 1			Station 2			Station 3		
Depth (meters)	1	5	30	1	5	40	1	5	50
Dissolved oxygen (ppm)									
range	10-15	10-15	10-15	10-15	10-15	10-15	10-15	10-15	9-15
mean	13	13	13	13	13	13	13	13	12.5
CO_2 (ppm)									
range	0.0-3.8	0.0-3.8	0.0-3.8	0.0-3.9	0.0-3.9	0.0-3.9	0.0-4.0	0.0-3.5	0.0-3.5
pH									
range	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5
mean	8.3	8.3	8.2	8.3	8.3	8.3	8.3	8.3	8.2
Alkalinity (ppm)									
range	126-140	126-140	126-140	126-140	126-140	126-140	128-144	128-144	128-144
mean	132	132	132	132	132	132	134	134	134
Dissolved solids (ppm)									
range	170-181	169-181	166-178	169-177	168-177	164-177	169-176	166-175	164-170
mean	175	175	172	174	174	166	173	171	166
Secchi Disk Reading (M)									
range		4.0-8.0			4.4-8.0			4.7-11.0	
mean		5.6			5.8			6.1	

Table 10 (continued)
Water chemistry and transparency: ranges and means from surface, middle and bottom waters, 1970 and 1971, Big Sable Point (#4-6)

	Station 4			Station 5			Station 6		
Depth (meters)	1	5	60	1	5	20	1	5	10
Dissolved oxygen (ppm)									
range	10-15	10-15	8-15	10-15	10-15	10-15	10-15	10-15	9-15
mean	13	13	12.3	13	13	13	13	13	13
CO_2									
range	0.0-4.0	0.0-3.8	0.0-3.8	0.0-4.0	0.0-3.8	0.0-3.6	0.0-3.1	0.0-3.4	0.0-3.6
mean									
pH									
range	7.9-8.6	7.8-8.5	7.9-8.6						
mean	8.3	8.3	8.2	8.3	8.3	8.3	8.3	8.3	8.3
Alkalinity (ppm)									
range	128-144	128-144	128-144	128-144	128-144	128-144	126-140	126-140	126-140
mean	135	135	135	134	134	135	133	134	133
Dissolved solids (ppm)									
range	169-176	164-172	160-165	168-177	166-177	160-171	172-190	172-189	170-188
mean	172	168	162	174	173	164	180	180	178
Secchi Disk Reading (M)									
range		4.8-11.0			4.8-11.0			4.2-8.7	
mean		7.2			7.2			5.9	

Table 10 (continued)
Water chemistry and transparency: ranges and means from surface, middle and bottom waters, 1970, 1971, and 1972 (#7-9)

	Station 7			Station 8			Station 9		
Depth (meters)	1	5	7.5	1	5	20	1	5	46
Dissolved oxygen (ppm)									
range	6-13	6-13	7-13	8-13	8-13	8-12	10-14	9-14	8-12
mean	12	12	11	12	12	11	13	13	12
CO_2									
range (ppm)	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6
pH									
range	7.0-8.4	7.0-8.4	7.0-8.4	7.1-8.3	7.2-8.3	7.2-8,4	7.2-8.4	7.2-8.4	7.3-8.4
mean	7.5	7.5	7.7	7.7	7.7	7.8	7.7	7.8	7.8
Alkalinity (ppm)									
range	17-94	17-94	17-94	26-72	28-72	28-94	28-94	28-94	37-94
mean	61	61	61	56	56	60	56	54	54
Dissolved solids (ppm)									
range	155-285	155-280	155-260	160-230	155-200	125-135	114-180	116-170	114-130
mean	200	198	195	202	180	130	135	130	118
Secchi Disk Reading (M)									
range		0.9-4.0			1.2-5.0			3.0-6.0	
mean		2.2			3.2			4.5	

Table 10 (continued)
Water chemistry and transparency: ranges and means from surface, middle and bottom waters, 1970, 1971 and 1972, Saugatuck (#10-11)

	Station 10			Station 11		
Depth (meters)	1	5	20	1	5	8.5
Dissolved oxygen (ppm)						
range	8-13	8-13	8-12	7-13	7-13	7-12
mean	13	12	12	12	12	11
CO_2 (ppm)						
range	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6	0.0-3.6
pH						
range	7.3-8.3	7.3-8.3	7.3-8.4	7.2-8.3	7.2-8.3	7.2-8.3
mean	7.7	7.7	7.7	7.6	7.7	7.7
Alkalinity (ppm)						
range	37-72	37-72	37-94	28-72	28-72	28-72
mean	56	56	58	60	61	61
Dissolved solids (ppm)						
range	155-200	135-160	118-138	155-230	155-230	150-230
mean	158	140	125	160	160	152
Secchi Disk Reading (M)						
range		2.5-5.0			2.5-4.0	
mean		3.6			3.1	

Table 10 (continued)
Water chemistry and transparency; ranges and means from surface and bottom depths, 1972 Ludington (#12-14)

	Station 12		Station 13		Station 14	
Depth (meters)	1	8	1	14	1	12
Dissolved oxygen (ppm)						
range	10-13	10-13	10-13	10-13	10-13	10-13
mean	12	12	12	12	12	12
CO_2 (ppm)						
range	0.0-2.8	0.0-3.5	0.0-3.5	0.0-3.5	0.0-3.5	0.0-3.5
pH						
range	7.9-8,5	7.8-8.6	7.8-8.6	7.9-8.6	7.8-8.5	7.8-8.6
mean	8.3	8.3	8.3	8.3	8.3	8.3
Alkalinity (ppm)						
range	116-120	114-120	116-118	114-118	116-120	116-118
mean	118	117	117	117	117	117
Dissolved solids (ppm)						
range	172-188	172-190	172-185	172-184	174-181	175-188
mean	179	180	179	179	178	179

Table 10 (continued)
Water chemistry and transparency: ranges and means from surface, and bottom depths, 1972 Ludington (#12-14)

	Station 15		Station 16		Station 17	
Depth (meters)	1	6	1	24	1	12
Dissolved oxygen (ppm)						
range	11-12	10-14	11-13	9-13	10-13	10-13
mean	12	12	13	12	12	11
CO_2 (ppm)						
range	0.0-3.7	0.0-3.5	0.0-3.5	0.0-3.5	0.0-3.3	0.0-3.5
pH						
range	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5	7.8-8.5
mean	8.3	8.3	8.3	8.1	8.3	8.3
Alkalinity (ppm)						
range	114-120	116-122	114-118	116-120	108-124	114-120
mean	118	118	117	118	116	116
Dissolved solids (ppm)						
range	175-184	175-181	170-181	169-179	172-180	173-180
mean	180	179	175	174	176	177

Table 11
Fluctuation in Zooplankton Numbers Over Time.

Month	1970 Saugatuck	1970 Ludington	1971 Saugatuck	1971 Ludington	1972 Saugatuck	1972 Ludington
Daphnia galeata mendota - 1.15 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	1	0	0	0	1	1
Early June	0	1.	1.	1.	2.5	1.8
Late June	20	10	37	17	150	31
Early July	120	32	125	32	210	70
Late July	120	38	288	100	720	125
August	35	108	765	117	1350	210
September	15	152	188	480	220	502
October	8	297	108	708	115	810
November	8	169	14	165	26	185
Daphnia retrocurva - 1.15 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	1	0
Late May	0	0	0	0	0	1
Early June	0	1	0	0	0	0
Late June	7	1	15	1.5	140	1
Early July	25	4	210	15	310	15
Late July	30	5.5	1400	47	1500	68
August	88	47	1410	85	1500	68
September	30	108	785	135	880	154
October	0	137	82	220	75	20
November	0	52	0	100	0	81
Daphnia longiremis - 0.85 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	2	0	1	1	0	0
Late May	3	1.2	0	1	1	0
Early June	6	1.5	4.2	0	0	1
Late June	6.5	3.2	4	1.1	0	1
Early July	6	3.7	4	1	1	1
Late July	2	3.5	2	0	5	1.5
August	10	8.4	1.5	0	0	1
September	8	5.5	2	0	0	0
October	0	1	0	0	0	1
November	0	0	0	0	0	0

Table 11 (continued)
Fluctuation in Zooplankton Numbers Over Time

Month	1970 Saugatuck	1970 Ludington	1971 Saugatuck	1971 Ludington	1972 Saugatuck	1972 Ludington
Epischura lacustris - 1.66 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	0	1	0	1	1	0
Early June	1	1	1	1.1	3.3	3
Late June	11	8	11	8	18	11
Early July	17	18	42	37	68	47
Late July	88	65	95	90	106	85
August	32	43	36	68	55	66
September	18	33	32	30	47	45
October	18	28	16	18	25	23
November	4	6	3	10	10	17
Diaptomus sicilis - 1.28 mm						
March	785	892	808	977	1176	1300
April	780	880	895	1000	1008	1500
Early May	755	800	816	1000	892	1100
Late May	430	475	514	525	542	550
Early June	88	109	95	157	190	208
Late June	85	77	78	80	92	88
Early July	66	45	75	75	85	62
Late July	15	21	52	12	25	14
August	14	13	9	10	13	5
September	16	11	9	1	14	5
October	175	186	115	200	188	197
November	888	950	1100	1350	2100	2000
Diaptomus ashlandi - 0.85 mm						
March	25	16	16	13	15	12
April	28	16	17	11	14	12
Early May	37	37	24	31	17	14
Late May	38	32	28	26	17	14
Early June	49	43	32	38	26	46
Late June	127	88	92	87	150	49
Early July	302	287	251	284	199	200
Late July	300	296	284	275	208	209
August	215	202	186	152	147	118
September	67	88	55	65	45	42
October	18	20	26	17	17	12
November	208	244	190	212	208	217

Table 11 (continued)
Fluctuations in Zooplankton Numbers Over Time

Month	1970 Saugatuck	1970 Ludington	1971 Saugatuck	1971 Ludington	1972 Saugatuck	1972 Ludington
Bosmina longirostris - 0.45 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	2	1	0	0	0	0
Early June	31	29	30	19	3	16
Late June	245	210	210	210	245	190
Early July	288	267	222	210	45	195
Late July	613	395	188	304	41	320
August	168	308	139	288	28	85
September	160	201	102	150	34	35
October	142	120	88	107	62	65
November	32	15	17	15	24	12
Diaphanosoma brachyurum - 0.85 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	0	0	0	0	0	0
Early June	0	0	0	0	0	0
Late June	0	0	0	0	3.6	0
Early July	0	0	0	0	7.4	1
Late July	0	0	2.1	1	2.8	2.1
August	1.1	0	2	2	2.6	0
September	2	1	3.5	3.9	10	11
October	2.4	1.8	3.8	13	18	24
November	0	0	0	0	8.7	12
Leptodora kindtii - ≈5 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	0	0	0	0	0	1
Early June	0	0	0	1	1.2	1.5
Late June	1.2	0	3.8	4.6	193	15.5
Early July	7.8	6.7	16.8	14.6	28.9	28
Late July	10	6.4	22	15.8	29	18
August	16.5	6	28	8	36.4	10.2
September	6	1.4	6.8	6	10.2	11.7
October	2	1	4	6	1.1	14.4
November	1	0	1	1.8	1	4.7

Table 11 (continued)
Fluctuations in Zooplankton Numbers Over Time.

	1970		1971		1972	
Month	Saugatuck	Ludington	Saugatuck	Ludington	Saugatuck	Ludington
Polyphemus pediculus - 0.56 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	0	0	0	0	0	0
Early June	0	0	0	0	0	0
Late June	4	4	4	3	4.5	1.6
Early July	5.8	16	6.2	15	3.8	12.2
Late July	60	168	25	142	18	84
August	12	18	15	15	10	15
September	0	0	0	0	4	5
October	0	0	0	0	0	0
November	0	0	0	0	0	0
Cyclops bicuspidatus - 0.91 mm						
March	64	88	64	67	52	66
April	128	155	122	167	123	188
Early May	500	490	600	388	605	295
Late May	762	867	750	802	710	895
Early June	900	901	800	1030	880	1100
Late June	950	1410	902	1400	620	1200
Early July	1100	1500	900	1310	625	1100
Late July	987	1008	865	986	700	833
August	800	870	633	808	302	677
September	780	800	400	546	180	342
October	405	622	298	436	165	205
November	302	308	256	244	200	200
Mesocyclops edax - 1.15 mm						
March	0	0	0	0	0	0
April	0	0	0	0	0	0
Early May	0	0	0	0	0	0
Late May	0	0	0	0	0	0
Early June	0	0	0	0	0	0
Late June	15	11	26	33	55	65
Early July	108	88	151	119	205	208
Late July	206	161	149	174	485	255
August	180	158	222	182	214	226
September	117	47	188	106	200	187
October	26	14	48	49	105	144
November	0	0	0	0	5	12

Table 11 (continued)
Fluctuations in Zooplankton Numbers Over Time.

	1970		1971		1972	
Month	Saugatuck	Ludington	Saugatuck	Ludington	Saugatuck	Ludington
Limnocalanus macrurus - 2.50 mm						
March	12	0	38	31	46	48
April	241	202	276	225	500	247
Early May	502	701	980	801	1700	1100
Late May	488	641	1012	866	1800	1350
Early June	118	109	223	412	500	600
Late June	33	108	226	201	470	325
Early July	10.8	15	96	43	130	68
Late July	6.8	11	92	16	90	32
August	34	88	157	89	280	131
September	54	65	198	90	285	107
October	332	231	607	402	720	562
November	391	466	981	890	1100	1000
Mysis relicta and Pontoporeia affinis - ea. 12 mm #/10 cu meters						
March	0	0	0	2	0	0
April	0	0	2	3.2	12	10
Early May	20	20	224	34	30	52
Late May	176	24	220	84	30	106
Early June	20	84	22.6	106	32	135
Late June	88	18	9.6	22	13.2	27
Early July	1.2	8	2.4	17.2	6	26.4
Late July	0.8	8.4	2	10.6	8	13
August	0.8	7.6	3.2	9.4	7.6	11
September	2.2	12.2	3.6	15.8	13.6	20
October	5	13.6	8	25	20	33
November	8	5.6	13.6	18	32	135

SUMMARY

A study was undertaken at three sites on Lake Michigan to study the feeding habits of four species of fish, Alosa pseudoharengus, Coregonus hoyi, Perca flavescens, and Osmerus mordax, and to determine if these species were selective feeders in the sense of Brooks and Dodson (1965). To accomplish this, stomach analyses were performed on 2520 alewives, 1870 bloaters, 2598 yellow perch and 1232 american smelt. Fish were collected three of the four seasons of the year at depths from 0 to 60 meters.

Small individuals of all four species preyed primarily on small Cledocerans and Copepods as well as the larger limnetic crustacea Pontoporeia affinis and Mysis relicta. Larger individuals also consumed these organisms but added other food items. Adult perch fed heavily on fish eggs and young and the smelt consumed large quantities of ostracods. Approximately three times as many female perch as males were found to contain fish, suggesting schooling by sex in this species as related to food acquisition. This differential schooling is confirmed by statistical evaluation of catch location. Neither alewives, bloaters nor smelt showed similar schooling or feeding differences based on sex. Feeding differences were found for all four species based on depth, time of the year, and availability of various food sources.

A laboratory experiment using 120 fish of each of the four species was also performed to determine if particular species of zooplankton were consumed in greater numbers and would be expected if the fish were eating at random. All four species consumed greater proportions of the large limnetic crustacea Pontoporeia and Mysis than would be expected on a random feeding basis. This selective feeding is also found in fish taken from the lake itself. Zooplankton counts were made over a three year period and

compared to data from stomach analyses. The larger limnetic crustacea and zooplankton were found to contribute a greater percentage in stomach analyses than their volume in the lake would suggest. The hypothesis of Brooks and Dodson (1965) thus seems to be upheld for these four species.

Phytoplankton studies were also undertaken as well as chemical and physical studies to determine if fish from the three sites were affected by these parameters. Although differences were detected in parameters, no major differences in size, age composition or sex composition could be found in the four fish species stocks that could be correlated with changing physical and chemical parameters or changing phytoplankton stocks.

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