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THE RELATIONSHIP OF THE PRODUCTION
OF WHITEFISH,
COREGONUS CLUPEAFORMIS
(MITCHILL) IN THE MICHIGAN WATERS
OF GREEN BAY TO FLUCTUATIONS
IN THE WATER LEVEL

Thesis for the Degree of M. S.
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Allan Hirsch
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This is to certify that the

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THE RELATIONSHIP OF THE PRODUCTION OF
WHITEFISH, COREGONUS CLUPEAFORMIS (MITCHILL)
IN THE MICHIGAN WATERS OF GREEN BAY TO
FLUCTUATIONS IN THE WATER LEVEL

by

Allan Hirsch

A THESIS

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INTRODUCTION

In past years there has been a great deal of concern about the supposedly diminishing supply of whitefish, Coregonus clupeaformis (Mitchill), in Lake Michigan. In fact, there is widespread belief to the effect that the whitefish is "on its way out" as a commercially important species in the Great Lakes. This "decline" has been attributed to several causes, the most often repeated of which is overfishing.

A glance back at the history of the situation will show that this concern is not of recent origin. Reighard in 1894 mentioned anxiety about a decreasing whitefish population in Lake St. Clair. Ward (1896) discussed a scarcity of whitefish in Lake Michigan and a catch figure that had been decreasing since 1880. He concluded that "overcatching" was the cause of this decline. Green (1909) reported a remarkable increase of whitefish in 1907 and 1908 in the "depleted" waters of Lake Ontario. Reighard (1910) suggested that the magnitude of the whitefish catch was controlled by previous overfishing.

The whitefish, however, continues to hold its own even though the catch has been characterized by extreme fluctuations over a period of years (see Plate III). Van Oosten et al (1946) cited a devastating "collapse of the whitefish fishery" in Lake Huron in 1940-42. This same fishery was again producing good catches of whitefish by 1947 (Anonymous

1947, 1948). Overfishing, then, would not seem to hold the complete answer to the question of what cause or causes limit whitefish production in the Great Lakes.

The whitefish population has shown a tremendous capacity to reproduce itself, even when it has seemed to be at its nadir. For example, in 1942 the whitefish stocks in Green Bay were at an extreme low in abundance, yet they produced the 1943 year class which acted to pull the catch some four and five years later to the highest point in many years. If such a small population was capable of producing such tremendous numbers of offspring, it would appear that the size of the brood stock has not been the factor limiting whitefish production. It would seem that the success of the spawning and the survival rate of the young fish were the elements which would decide whether the whitefish catch of future years was to be large or small. This assumption is in accord with a theory concerning fish populations which is held by many biologists.

Doan (1942) states that several of these investigators have associated dominant year classes in fish populations with inquiry about the prevailing conditions at the time of hatching of the class which later became dominant. Doan recognizes the fact that no factor alone is responsible for the success or failure of the survival and growth of a fish population, but he goes on to state that, "A given factor may be so important a control that its variations are reflected in similar variations, in like or opposite phase, in

the size of a fish population."

It was with this possibility in mind that an examination was made of the relationship of the production of whitefish, from Green Bay in Lake Michigan, to the fluctuations in the water level. Some biologists believe that the fluctuations in water levels have a profound effect upon food chain organisms, and therefore upon fish populations. Langlois, Russell, Doan, Chandler, Pearsall, Barnaby, and others have approached this problem, and their works will be discussed in this paper.

This study, then, was made in the hope of better understanding the reasons for the fluctuations in abundance of the whitefish in Lake Michigan.

METHODS

Langlois (1948) lists Green Bay as a "key area" for Lake Michigan, in which the energy cycle culminating in crops of fish begins. J. Van Oosten writes that the majority of the whitefish spawning in the bay occurs in the more northern areas. For these reasons, northern Green Bay was chosen as the area to be studied.

The information on the topography of Green Bay was obtained for the most part from the Department of Land and Water Conservation at Michigan State College, and from the Agricultural Extension Service at the University of Wisconsin.

The data on the fluctuations in lake levels were taken from the United States Lake Survey Hydrograph Catalog No. 1000. W. T. Laidly of the United States Lake Survey states in a written communication that the monthly mean change in lake level is the same for Green Bay as it is for the entire Lake Michigan, as represented on Hydrograph Catalog No. 1000. Data on the flow of the individual rivers flowing into northern Green Bay were not available. Precipitation and evaporation are responsible for most of the changes in lake levels (Doan 1942, Chandler and Weeks, 1945), and consequently lake levels were used in this study as indices to the amount of precipitation and runoff into the lake from year to year.

Much of the information on whitefish, lake herring, and walleye abundances and catches for this particular area was

received from the Great Lakes investigations of the Fish and Wildlife Service at Ann Arbor, Michigan.

A study of the food of the whitefish was made, because many biologists believe food to be the limiting factor in fish production. The results were achieved by a search of the literature and by stomach analyses of whitefish from Green Bay, and From Torch Lake in Antrim County, Michigan.

DESCRIPTION OF GREEN BAY

Green Bay is situated off the northwest corner of Lake Michigan, extending about one hundred miles southwest through the Michigan Peninsula and northeastern Wisconsin. (Plate I illustrates the location of Green Bay.) The northern and southern ends of the basin are shallow, with depths not exceeding thirty feet, in general. Offshore the lake bottom drops to depths of about thirty-five feet, and the basin slopes downward from both the north and south ends to depths of approximately one hundred and twenty feet near the center of the bay.

The rivers that flow into the southern end of the basin drain silt loam and clay loam soils which are heavily farmed. They carry a great deal of sediment into the bay even though Lake Winnebago acts as a settling basin for the upper Fox and lower Wolf rivers. The Menominee River, at the border between Wisconsin and Michigan, drains land that is only partially developed for agriculture. Much of this land is covered by forests and brush. Reservoirs in this river make the stream-flow fairly constant all year round.

Northern Green Bay, with which this study is principally concerned, is bounded by Menominee and Delta Counties, Michigan. The Menominee, Big Cedar, and Ford Rivers, and their tributaries drain nearly the entire Menominee County. About sixty or sixty-five per cent of the county is naturally well drained (Moon et al, 1929). The county is marked by a

high proportion of organic soils and by the dominance among the mineral soils of loams and fine sandy loams derived from very limey glacial drift. Only within the last forty years has agriculture assumed much importance in the county. The 1935 soils map of the United States Soil Conservation Service showed little or no erosion for the county, but some erosion has been reported for the center of the county in recent years.

Delta County is largely forested, the southwestern portion being the only intensively farmed area in the county, and little erosion occurs here. Much of the drainage from this county flows through lands of limey origin. The sand plains in the southwestern portion of the county probably act as a settler for any silts and sands which may be carried down from the uplands (Plate II illustrates the soil composition of Delta and Menominee Counties).

Plate I

Green Bay. Area M-1
illustrates the State of Michigan
waters in Green Bay

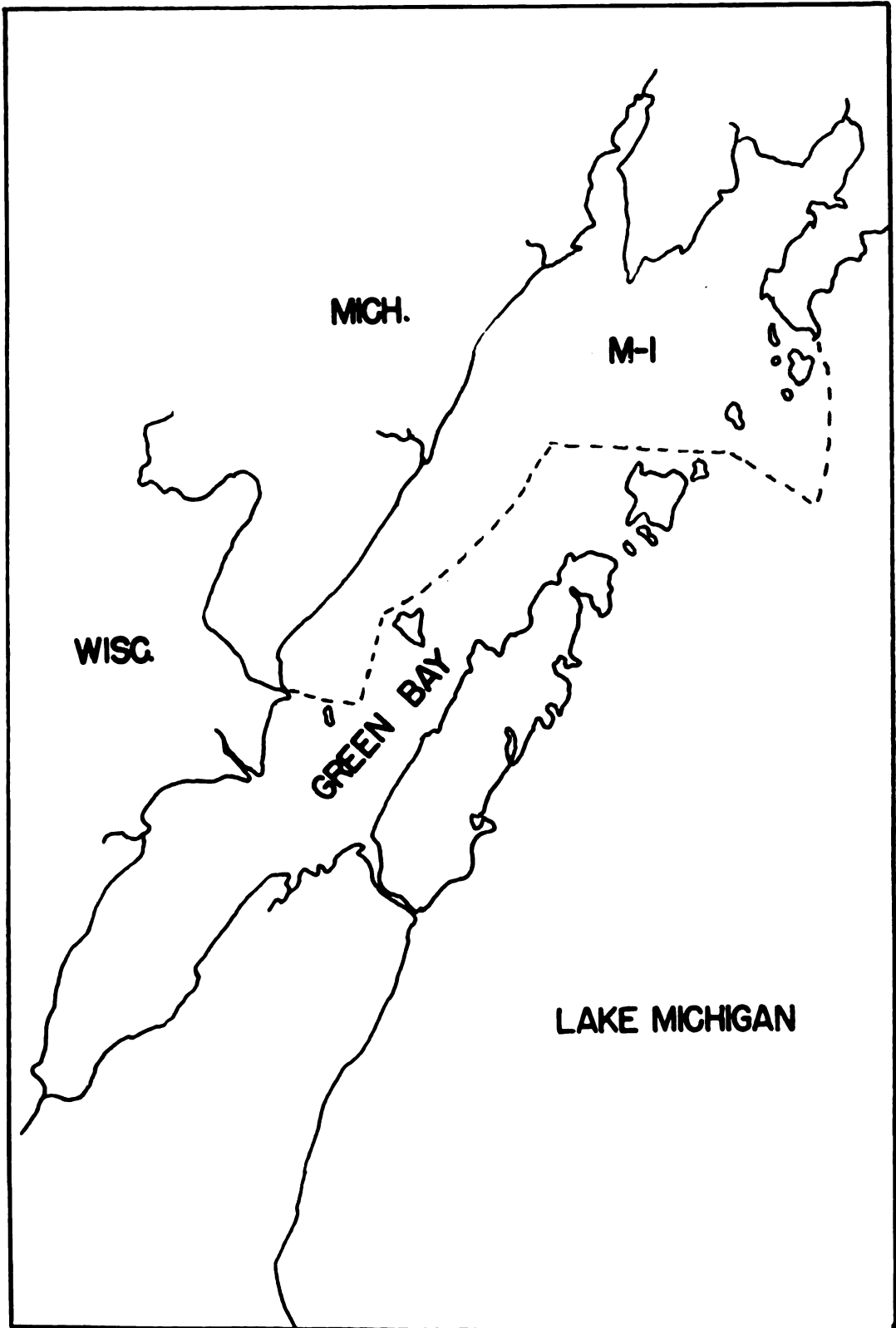
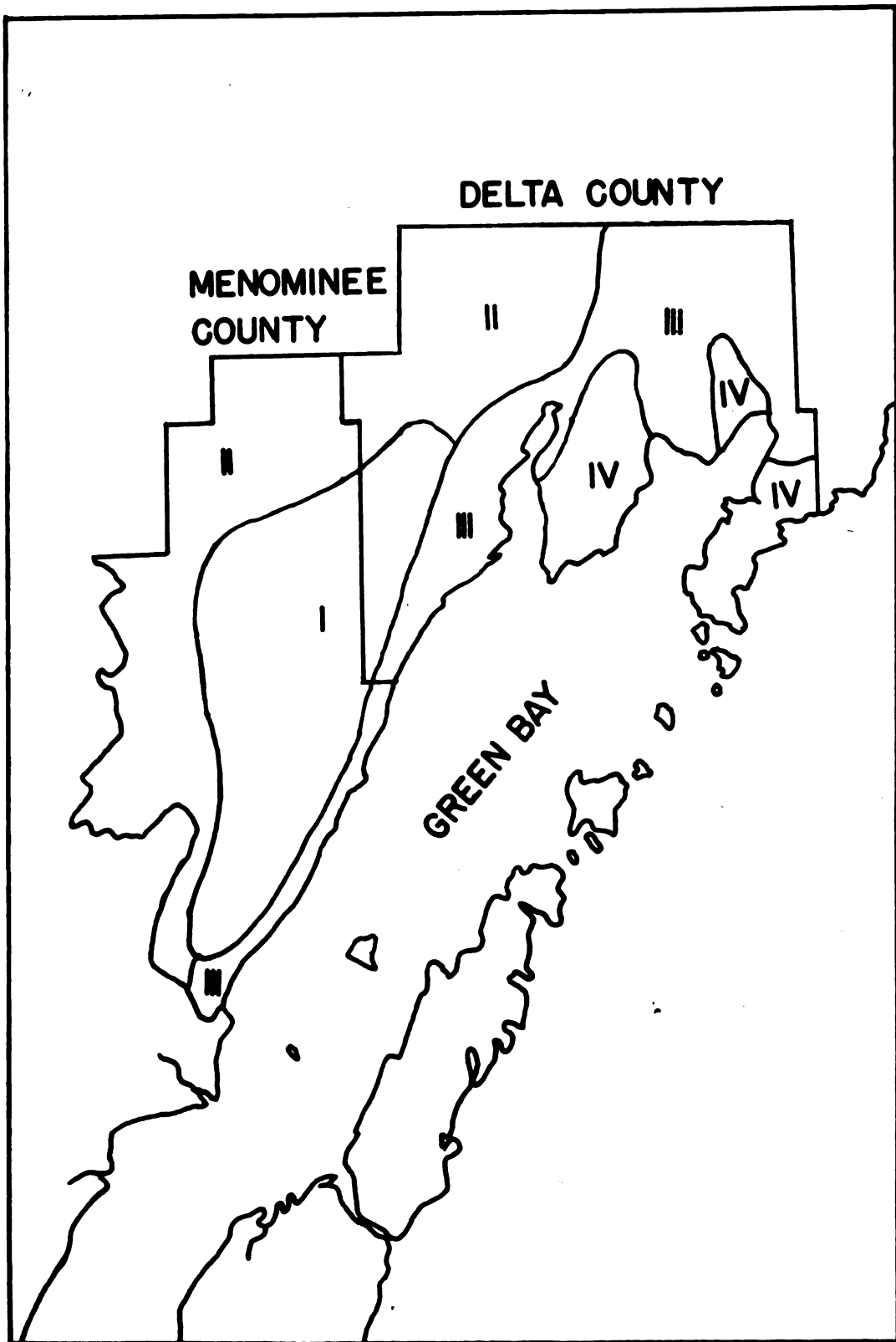


Plate II

Generalized soil map of Delta and Menominee Counties

(Adapted from J. O. Veatch, Generalized Soil and
Land Map of the Upper Peninsula of Michigan)

- I - Mainly loam, silt, and fine sand
underlain by limey clay; level sur-
face; in part excessively wet;
medium to high fertility.
- II - Mainly loams and sandy loams; limey
soils medium to high fertility; in
part excessively stony or excessively
wet; mainly rolling, but in part
hilly.
- III - Mainly sands and peats, low fertil-
ity; in part dry plains and ridges,
in part swamp. Mainly cutover
forest.
- IV - Soils medium to high fertility;
for most part excessively stony;
in large part forested and cut-
over land; mostly level or roll-
ing; in part swamp.



FOOD OF THE WHITEFISH

Summary of the Literature

Forbes (1912) found that the first food of whitefish fry consisted almost wholly of the smallest species of Entomostraca. As the fish grew older they took larger entomostacans.

Ewers (1933) took young whitefish from 10 to 31 millimeters in total length from the open waters of Lake Erie. Crustaceans constituted almost 100 per cent of the food taken by these fish. At least 88.9 per cent of the identifiable food was Copepoda, and at least 7.9 per cent was Cladacera. Sixty-four and nine-tenths per cent of the identifiable food was the copepod, Cyclops.

Hankinson (1914) examined eight whitefish fry from Lake Superior. These fish were from 4.9 to 9 centimeters in length. They contained mainly Entomostraca, principally of the genera Bosmina, Diaptomus, and Cyclops.

Hart (1930) observed that whitefish fry began feeding upon small Entomostraca toward the end of April in the Bay of Quinte. Cladacera, Copepoda, and insects were found to compose the bulk of the food in all cases.

Smallwood (1918) found that the food of 8 to 12 inch whitefish from Lake Clear in the Adirondacks consisted almost entirely of Daphnia and Cyclops.

Rimsky Korsakoff (1929) found whitefish from 10.6 to 17.7 inches to be feeding heavily on molluscs, crustaceans,

and midge larvae. The crustaceans were mostly Amphipoda, but some Cladocera were taken.

Clemens et al (1924) states that young whitefish are plankton eaters, but that they early become bottom feeders. The chief foods of the larger fishes were found to be the crustacean, Pontoporeia hoyi and chironomid larvae, with molluscs and mayfly nymphs ranking next in importance. It was found that the kinds of food varied with the depths at which the fish were taken, and these depths varied from 2 to 300 feet.

Hankinson (1911) studied the food of whitefish 1.5 to 2.5 pounds in weight from Walnut Lake, Michigan. He found that red midge larvae constituted the main food in April and May; but, that in August, the fish taken contained only Entomostraca, chiefly Daphnia. He mentioned the sucker, as did Clemens et al (1923), as a food competitor of the whitefish.

Smith (1874) found the crustaceans, Pontoporeia hoyi and Mysis relicta, molluscs, and insect larvae to be the principle foods of the whitefish in Lake Superior.

Ward (1896) described the food of adult whitefish from Lake Michigan. Crustaceans constituted 63 per cent of the total food, molluscs 26 per cent, and insects 15 per cent at the most and 5 per cent on the average. The insects concerned were chiefly chironomids. He considered the whitefish to be a bottom feeder to a great extent, although the crustacean element was never totally absent from the diet.

Hart (1931b) found the whitefish to be chiefly a bottom feeder, although it occasionally feeds away from the bottom,

and even at the surface. He suggested that the whitefish does not feed very selectively. The food was found to consist chiefly of amphipod crustaceans, molluscs, and insect larvae.

Hart observed that plankton was an important food of the smaller sized whitefish in Shakespeare Island Lake, and that plankton was taken in considerable quantities by fish until they reached the fifth year of age. Daphnia constituted 88 per cent of the total food of second year fish in this lake.

Brunson and Newman (1950) took whitefish from 30 to 100 feet of water in Flathead Lake during July and August. These fish ranged from 37.0 to 51.5 centimeters in length. He found that chironomid larvae were the most important food of these fish, with molluscs ranking next.

Van Oosten and Deason (1939) found an indication that autumn is a season of reduced feeding activities; 85.8 per cent of the stomachs examined were void of food. The fish were taken in a seine so digestion could not have taken place after capture. The food of whitefish from 14.8 to 26.2 inches in total length was found to be 99.1 per cent invertebrate. Ninety-two and one tenth per cent of the stomach contents of these fish were small molluscs, and 6.4 per cent were insects and insect larvae. No crustaceans were found in the twenty fish containing food in this study.

Laboratory Investigations

Thirteen whitefish from 2.25 to 6 pounds in weight were taken in pound nets from Garden Bluff in Big Bay De Noc, Lake Michigan. These fish were caught on October 14, 1949 in approximately thirty feet of water.

The esophagi and stomachs of these fish were examined, and eleven of these were empty. The contents of the other two were:

- Fish no. 1 - 1 Ephemerida nymph
 1 Cladacera
 trace filamentous algae
 (Dichotomosiphon)
- Fish no. 2 - trace filamentous algae
 (Dichotomosiphon)

Thirty-seven adult whitefish were taken in pound nets from Burnt Bluff in Big Bay De Noc on October 18, 1950. These fish were caught in approximately forty feet of water.

The esophagi and stomachs of these fish were examined and all but four of these were empty. The contents of the four esophagi and stomachs containing food were:

- Fish no. 1 - 1 Hexagenia nymph
- Fish no. 2 - 1 Hexagenia nymph
- Fish no. 3 - 1 insect
 1 Amphipoda
 trace filamentous algae
 trace vascular plant
 material
- Fish no. 4 - 1 Ephemerida nymph
 2 Amphipoda

Twelve intestines, from some of the fish with empty

stomachs, were analyzed. Of these, three were devoid of identifiable material, although they did contain organic debris. The contents of the other nine are shown in Table 1.

Table 1

Contents of the intestines of nine adult white-
fish taken from Burnt Bluff in Big Bay De Noc,
Lake Michigan. October 18, 1950.

Organism	Number of intestines in which found	Average number per intestine
<u>Winged Diptera (midges)</u>	1	9
<u>Chironomidae pupae</u>	1	1
<u>Insect remains</u>	3	1.3
<u>Cladacera</u>	3	25 *
<u>Cladacera ephippia</u>	1	2
<u>Amphipoda</u>	1	3
<u>Crustacean remains</u>	3	2
<u>Vascular plant material</u>	4	trace
<u><u>Dichotomosiphon</u></u>	3	trace

* approximately

Some of the Cladacera from these intestines were identified as Daphnia pulex. Microscopic examination of the Dichotomosiphon from one of the intestines revealed small amounts of Desmidium, Epithemia, and Navicula in close association with the filamentous algae.

Thirty-two whitefish, all adult spawners over two pounds in weight, were taken from the eastern side of Torch Lake in Antrim County, Michigan on December 24, 1949. These fish were speared at night in water six to eighteen feet deep. The stomachs and esophagi of these fish were examined, and the results of these examinations are shown in Table 2.

Five whitefish, between two and four pounds in weight, were speared in the eastern side of Torch Lake on the night of December 27, 1950. These fish were in the spent condition. An examination was made of their stomachs and esophagi, and the contents are shown in Table 3.

The Amphipoda taken from these Torch Lake whitefish were found to be Gammarus and Hyallolella. The numbers of Amphipoda were estimated. Even in those cases where there were few of these animals present, the count could not be entirely accurate because many animals were fragmented or partially digested.

Of the 258 Ephemerida nymphs present, 232 were identified as Ephemera, 8 as Hexagenia, 14 as members of the subfamily Baetinae, and 4 remained unidentified.

Those Coleoptera larvae which could be identified were found to be Hydrophilidae.

The Gastropoda and Pelecypoda were all minute. Many of

Table 2

Contents of the esophagi and stomachs of
thirty-two adult whitefish taken from
Torch Lake, Antrim County, Michigan.
December 24, 1949.

Fish no.	Amphi- poda*	Chironom- idae	Hydra- larvae	Pelec- carina	Gastro- poda	Ephemerida nymphs	Whitefish eggs	Miscellaneous
1	300	9	1	4	3	1	-	
2	500	12	11	17	16	9	-	1 Ceratopogonidae larva
3	25	-	-	1	-	1	-	1 fish, approximately 55 mm.
4	250	25	2	14	9	-	-	1 fish, approximately 45 mm.
5	150	27	-	5	11	-	-	
6	35	2	2	1	1	-	-	
7	75	13	-	15	20	2	-	4 <u>Asellus</u>
8	90	1	-	1	-	2	-	7 Coleoptera larvae, 3 Asellus, 1 Ostracoda 12 plant seeds
9	600	3	4	7	6	6	18	
10	35	7	3	8	1	8	4	1 plant seed, <u>Dichotomosiphon</u>

Table 2 (continued)

Fish no.	Amphi- poda*	Chironom- idae	larvae	Hydra- carina	Pelecy- poda	Gastro- poda	Ephemera- nymphs	Whitefish eggs	Miscellaneous
11	300	10	5	7	10	2	-	-	1 Tricoptera case, 1 Ceratopogonidae larva, filamentous algae
12	125	3	1	-	-	-	-	-	
13	20	-	-	-	22	1	-	-	1 plant seed, vascu- lar plant material
14	-	3	-	2	3	113	17	-	2 Coleoptera larvae, vascular plant ma- terial, cedar twigs
15	125	2	1	-	1	10	-	-	Incomplete, esopha- gus and proventri- culus missing
16	10	-	-	1	1	-	-	-	
17	175	8	20	8	1	-	-	-	1 Coleoptera larva, 1 Ceratopogonidae larvae, 1 Pentatom- idae (?) adult, 1 insect remains, 2 plant seeds, cedar twigs
18	-	12	1	2	-	17	68	-	
19	115	17	-	19	41	1	-	-	2 plant seeds

Table 2 (continued)

Fish no.	Amphi-poda*	Chironomidae larvae	Hydra carina	Pelecypoda	Gastro-poda	Ephemerida nymphs	Whitefish eggs	Miscellaneous
20	130	22	1	3	2	10	-	1 fish, approx. 35 mm. 1 Diptera larva, 1 Coleoptera adult, 1 Tricoptera case, cedar twigs
21	75	-	2	-	1	1	-	
22	375	5	-	2	13	6	-	
23	50	10	3	18	5	8	-	1 plant seed 1 insect remains, 1 Gloeotrichia colony
24	75	14	1	13	17	-	-	
25	15	1	-	-	-	-	-	1 fish (Ameluridae?), 2 Oligochaeta eggs, fragment of wood
26	100	1	-	-	1	8	17	
27	900	-	-	-	2	1	-	1 Coleoptera larva 1 Diptera (Tabanidae?) larva
28	75	14	1	8	2	4	-	2 Coleoptera larvae, 1 millepede, 2 Oligochaeta eggs, 1 plant stem, 70 mm., cedar twigs
29	50	1	-	2	1	13	42	

Table 2 (continued)

Fish no.	Amphi- poda*	Chironom- idae larvae	Hydra- carina	Pelecy- poda	Gastro- poda	Ephemera- nymphs	Whitefish eggs	Miscellaneous
30	60	5	-	6	-	2	-	1 plant seed, vasou- lar plant material
31	50	4	15	10	-	3	13	1 plant seed, cedar twigs
32	200	1	1	1	-	4	-	

* numbers estimated

Table 3

Contents of the esophagi and stomachs of
five adult whitefish taken from Torch
Lake, Antrim County, Michigan.
December 27, 1950.

Fish no.	Amphi- poda*	Gastro- poda	Pelecy- poda	Chironom- idae larvae	Hydra- carina	Ephemerida nymphs	Miscellaneous
1	300	91	2	15	8	-	1 Ostracoda, 1 Clada- cera ehippium 2 plant seeds
2	65	-	-	3	-	13	Vascular plant material
3	2	2	1	-	-	9	6 Boleosoma nigrum 41- 67 mm., 10 unidenti- fied fish 25-40 mm., tree bark
4	90	1	4	2	3	-	
5	225	82	51	8	8	3	2 Ostracoda

* numbers estimated

the Pelecypoda could be identified, and these were found to be Pisidium.

Some of the whitefish eggs found in the stomachs had well developed embryos. Hart (1930) assumed that whitefish ingest eggs incidently while respiring.

Vascular plant material was never present in large quantities, nor was algae. Small pebbles were found in approximately one third of the stomachs but they were not included in the stomach analysis tables.

The intestines of almost all the fish from Lake Michigan, and the stomachs and intestines of almost all the fish from Torch Lake were found to be heavily infested by *Acanthocephala*. The parasites taken from the Lake Michigan fish were identified as Echinorhyncus coregoni by H. J. Van Cleave.

The stomachs of many of the fish from Torch Lake were heavily parasitized by Nematoda of the superfamily Spiruroidea. Four immature tapeworms were found in the stomachs of one of these fish.

It will be noted that, while the whitefish does feed heavily on the bottom, Amphipoda constituted an extremely important part of the diet, and were present in the great majority of the stomachs examined.

RELATIONSHIP OF FISH PRODUCTION TO WATER LEVEL FLUCTUATIONS

The total annual catch of whitefish in Lake Michigan from 1889 to 1948 was plotted against the highest annual water levels in the Lake (Plate III). The figure used for the highest annual water level was actually the highest monthly mean water level of the year. Although the time at which the highest water level occurs varies from year to year, it was assumed that a year with a high extreme would also have a high average.

The annual abundances of whitefish, lake herring (Leucichthys artedii), and walleye (Stizostedion vitreum) in the state of Michigan waters of Green Bay from 1929 to 1949 were plotted against the highest annual water levels in Green Bay (Plates IV, V, and VI). The abundances of these species of fish were estimated from the catch per lift of the types of gear accounting for the bulk of the take (See Table 4).

A coefficient of correlation was computed (Snedecor, 1946) for the abundance of each of the three species mentioned above as related to the highest annual water levels of previous years. The length of the lag used depended upon the biology of the species involved; that is, the number of years from the time of hatching until the fish first entered the commercial fishery in any appreciable numbers.

No significant correlation was found for the whitefish

Plate III

Total annual catch of whitefish in
Lake Michigan from 1889 to 1948 as
related to the highest annual water
levels in Lake Michigan.

(Data from Van Oosten, 1946; Fishery
Statistics of the United States,
1940-1946; from Lake Fisheries 1946-
1948.)

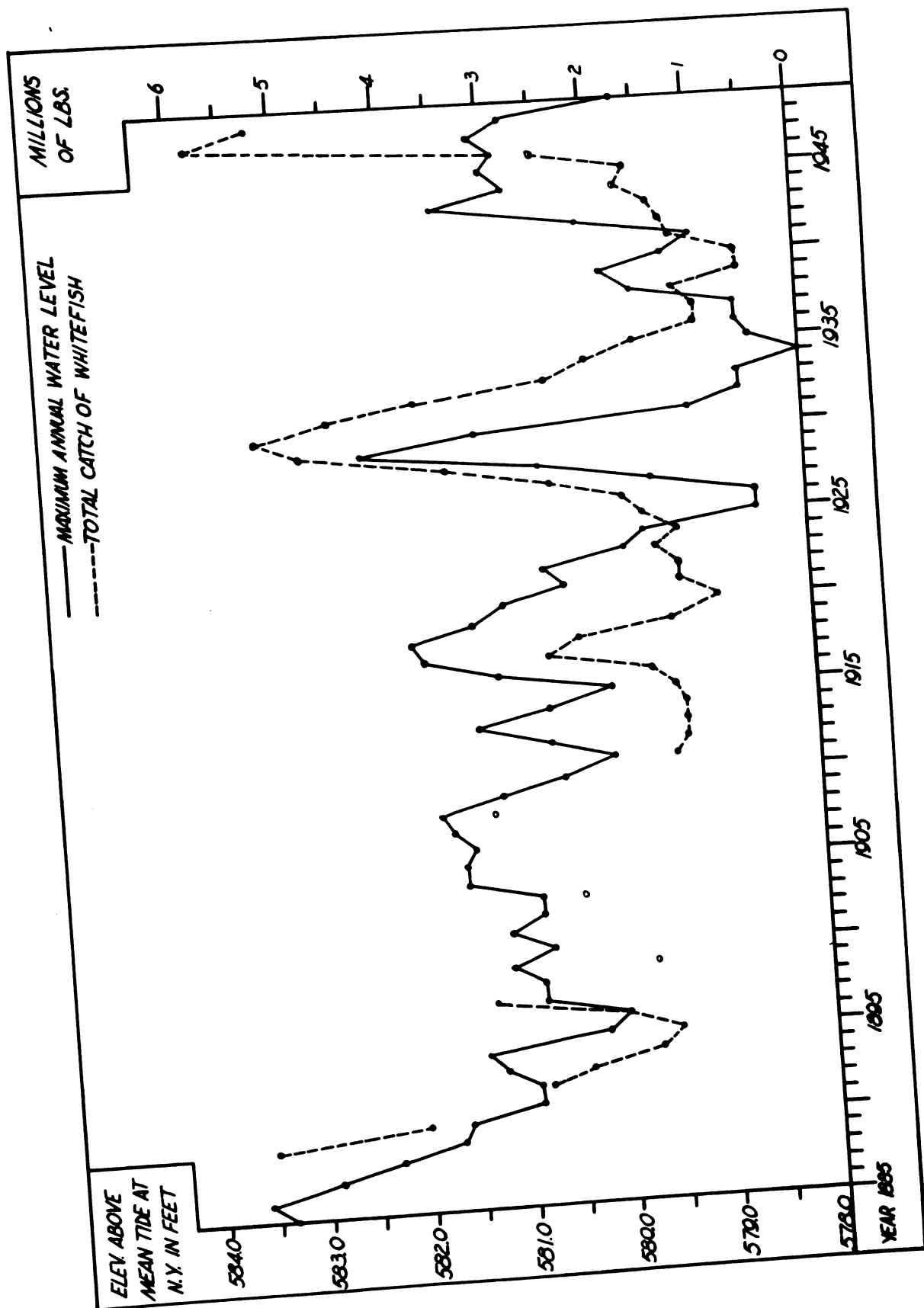


Table 4

Production (thousands of pounds), fishing intensity, and abundance of whitefish, lake herring, and walleye in the State of Michigan waters of Green Bay, 1929-1949. Fishing intensities and abundances are given as percentages of the 1929-1943 means.

(Data from the Fish and Wildlife Service at Ann Arbor, Michigan.)

Year	Whitefish			Lake herring			Walleye		
	A	B	C	A	B	C	A	B	C
1929	1140	180	180	396	78	76	27	54	104
1930	1076	145	211	484	83	88	27	57	98
1931	1195	143	238	521	91	85	41	83	102
1932	910	120	215	170	58	44	85	121	144
1933	238	66	102	160	57	42	108	198	111
1934	263	91	82	916	197	70	108	171	129
1935	175	89	56	1054	170	92	57	106	108
1936	90	75	34	1271	153	124	74	115	127
1937	105	65	46	1834	138	197	59	105	112
1938	354	104	97	1552	105	220	38	57	132
1939	238	86	78	697	96	108	30	54	112
1940	123	74	47	668	104	96	28	86	64
1941	116	90	37	297	54	82	26	108	48
1942	93	80	33	285	51	84	16	66	48
1943	141	92	44	402	65	92	36	119	61
1944	232	114	58	419	82	76	43	152	56
1945	234	100	66	2193	306	107	21	89	47
1946	514	148	99	2367	367	96	72	136	105
1947	2427	275	250	1881	247	113	262	220	236
1948	3066	221	395	2668	203	195	572	282	403
1949	2263	158	407	2230	228	145	1063	344	615

A = Production
 B = Fishing intensity
 C = Abundance

Plate IV

Abundance of whitefish in the State of Michigan waters of Green Bay from 1929 to 1949 as related to the highest annual water levels in Green Bay.

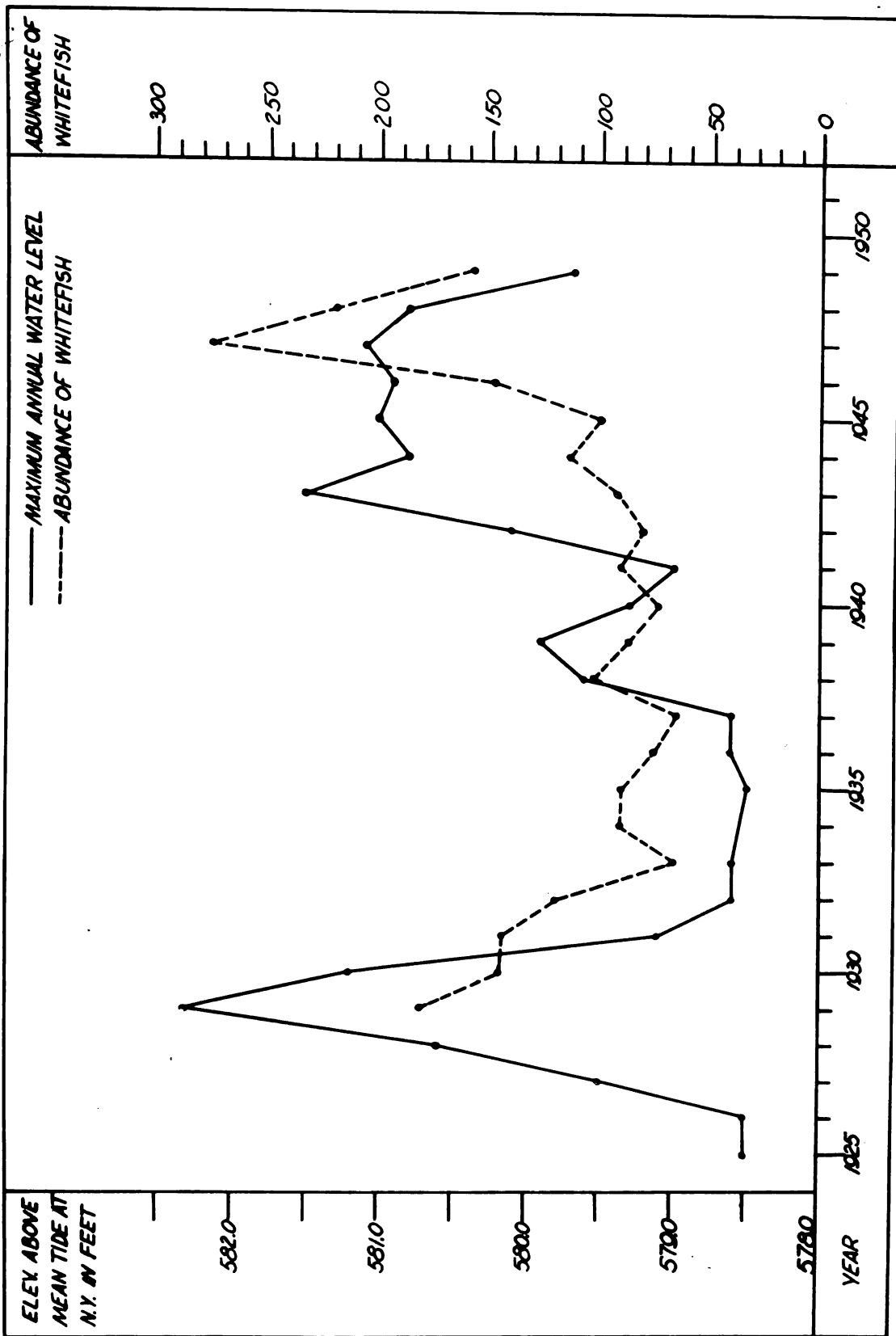


Plate V

Abundance of lake herring in the State of
Michigan waters of Green Bay from 1929 to
1949 as related to the highest annual water
levels in Green Bay.

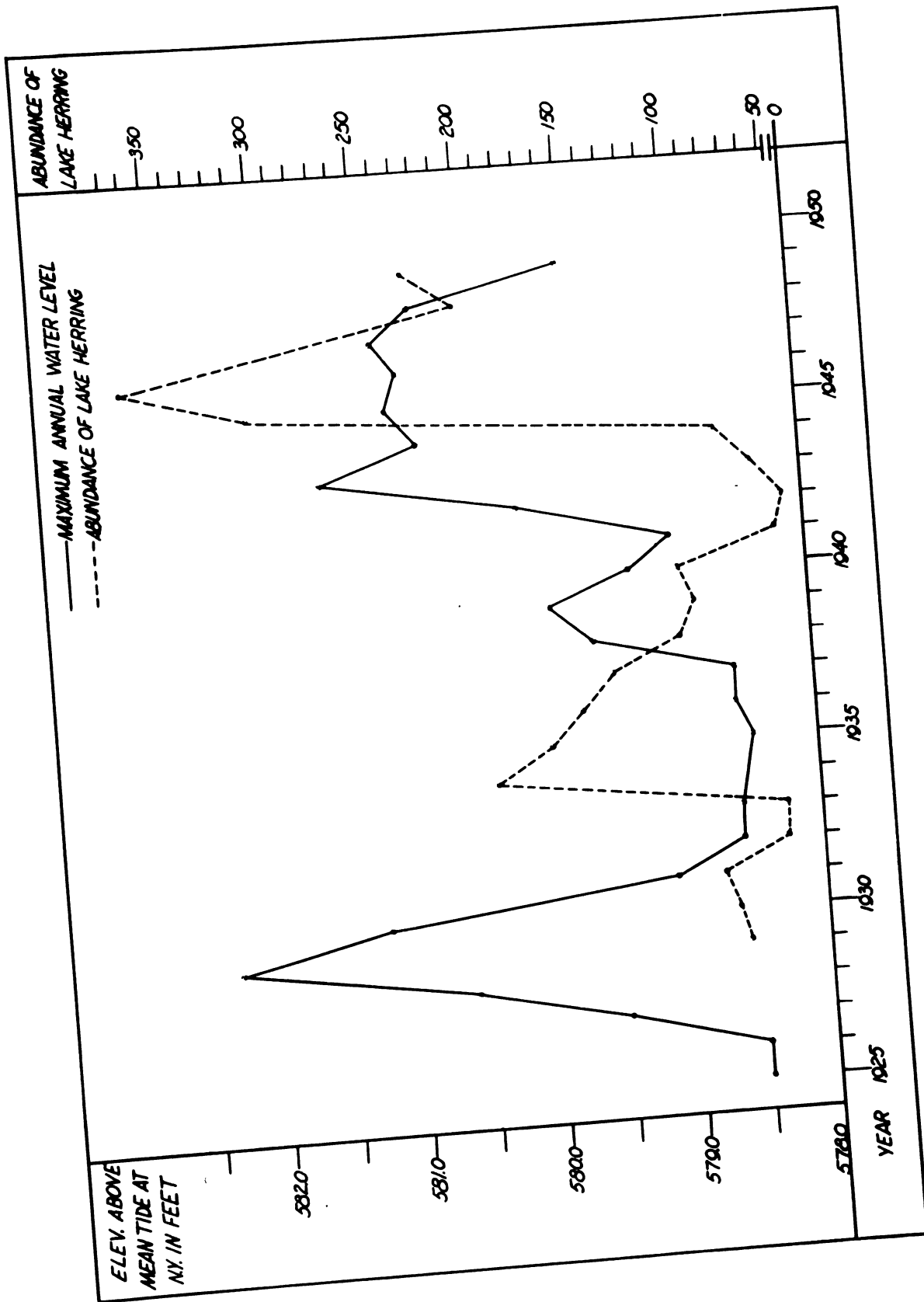
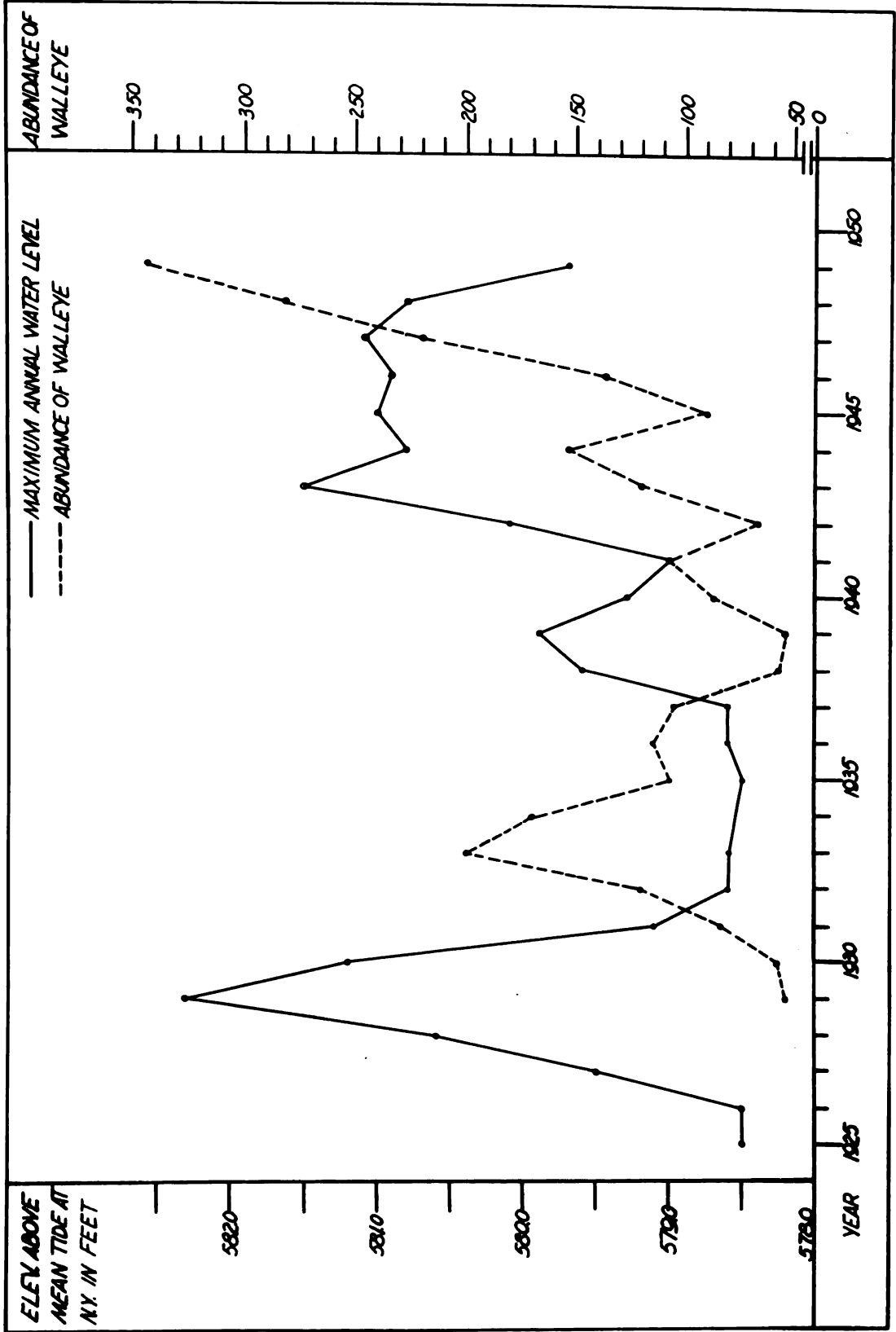


Plate VI

Abundance of walleye in the State of Michigan
waters of Green Bay from 1929 to 1949 as re-
lated to the highest annual water levels in
Green Bay



or the lake herring when a fixed lag in years was used. An examination of Plates III and IV will show, however, that there appears to be some relationship between the water level fluctuations and whitefish abundance. Periods of high catches or high abundance seem to be somewhat coincidental to periods of high water level, although the time relationship between the two elements is not constant.

The coefficient of correlation for walleye abundance from 1929 to 1949 as related to the highest annual water level four years previous was + .76, which is statistically significant at the one per cent level. This would indicate that 57 per cent of the variability in the abundance of walleyes could be explained in terms of relationship with water levels four years before the fish were caught.

The coefficient of correlation for the same walleye abundance, with the water levels used being five years previous, was + .69, which is also significant at the one per cent level. This figure would indicate that 48 per cent of the variability in the abundance of walleyes could be explained in terms of relationship with the water level five years before the fish were caught.

A limitation to the use of the correlation coefficient in relating catches to water levels of previous years is that fish hatched in one year may contribute heavily to the catches of several years. For example, the whitefish year class of 1943 in Big Bay De Noc contributed in high proportion to the catches of 1948 and 1949, and was important in

the catch of 1950 (Caraway, MS). A refinement of method and more complete data concerning the age composition of the catch would be necessary in order to relate the contribution of any one year class to the fishery with the conditions at the time at which that particular year class was produced.

DISCUSSION

Insufficient data were obtained in the course of this study to allow the drawing of any definite conclusions. However, a possible hypothesis to explain the relationship of water level fluctuations to fish production in Green Bay will be compounded from the findings and theories of many investigators. It is axiomatic that biological conditions vary widely with the locality, environment, and species concerned; but some general laws do exist which may be applied, or at least considered for a wide variety of circumstances.

Frequent note has been made in the literature of the fluctuations in the abundance of fishes. Dymond (1948) states that some of the outstanding discoveries of European fisheries biologists have been that some year classes are fifty or sixty times as abundant as others, and that such wide fluctuations are characteristic of most of the commercially important species of fishes. Langlois (1948) notes that vast differences are known to occur in the numbers of larvae of any particular year class, and that tremendous fluctuations in the abundance of fishes occur which are not attributable to depletion by the fishery. Burkenroad (1948) states that, "It is well known that great periodic fluctuations in the abundance of various marine animals do occur, which appear to be entirely independent of human activities; and which may in some cases even be possible to predict empirically, long in advance."

The situation may be summarized by a quotation from Huntsman (1944): "So long as the annual take corresponds with expectation based on past experience, the situation tends to be accepted without remark. Natural fluctuations in the abundance of the stock, which are largely of unknown origin, are quite usual and affect the take. When an increased take has continued for a number of years, it results in expectations of indefinite continuance. Then, a decrease in the take causes general complaint and an explanation is sought. Before attributing decreased annual productivity to overfishing, the possibility of natural fluctuation in the stock being the cause should be excluded, which may be very difficult. Misinterpretation may lead to application of the wrong remedy."

Baranoff (1916) suggests that there are two factors which may affect the abundance of young fish: the quantity of eggs deposited, and the mortality among eggs and fry. The influence of the fishery is limited solely to the decrease in the number of eggs deposited annually due to the removal of spawners. Two factors govern the quantity of the young that will survive:

- (1) The possibility that there will survive to grow to a later stage some definite percentage of all eggs laid, independent of numbers. In this case, the abundance of the young would be proportional to the number of eggs laid, and thus removal of adult fish would be reflected in the abundance of the young.

- (2) The possibility that the total abundance

of surviving young is dependent upon some constant factor, and therefore the absolute abundance of young could not exceed a certain maximum, no matter what the number of eggs laid was. In that case, the abundance of surviving young would not be affected by the intensity of the fishery except in extremes of depopulation where the number of eggs would not exceed a certain minimum.

Many investigators offer evidence which supports the latter theory. Herrington (1944) gives convincing evidence to the effect that the cycles in the size of the haddock population were related to the periodic success of reproduction and survival of the young. It has been shown in the study of the haddock that the largest spawning stocks almost invariably have yielded the smallest year classes, while the poor spawning stocks have done much better, although the very small adult spawning stocks have been less successful than the intermediate ones. It seems obvious that the largest stocks produced the largest numbers of eggs, so the later scarcities must have been due to greater mortality. Langlois (1941) points out that the occurrence in the Great Lakes of dominant year classes of such species as the yellow pickerel leads to years when there are mature spawning individuals in abundance, but the stocks are not increased by them. Peak production years have been followed by low production years, and peak production years always come from seasons when the brood stock is at a minimum. Huntsman (1933) states that the high reproductive powers of

most fishes make it unlikely that many spawning individuals are needed to produce all the young that will be able to find conditions for survival. Burkenroad (1948) attributes the increase in the Pacific halibut to causes other than an increase in egg production. Merriman and Warfel (1948) state that an interesting question is posed by the fact that dominant year classes sometimes occur when the adult stock is at a relatively low level. Ricker (1946) believes that the efficiency of reproduction and the survival rate of young fish tends to increase as the number of spawners decreases. Barnaby (1944) gives an example of overcrowding of fish on their spawning grounds resulting in a very poor return of pink salmon.

Hjort (1914) reports, concerning an extraordinarily abundant production of fry that, "it is impossible to associate this circumstance with especially profuse egg production." He gives an example showing that a year with a small spawning can produce a relatively large quantity of fry. Hjort found it possible to conclude that the cause of the poor production of young in ordinary years lies in a, "frightful destruction of the fry." Russell (1932) states that poor spawning years have often been good brood years, and that there is no necessary connection between the number of eggs produced in a spawning season, and the numbers of young which survive. The critical period of great mortality in the life of the young fish is generally thought to fall in the first few days or weeks after the eggs hatch. Sette (1943) found it prob-

able that the success or failure of year classes is determined during the early life of the fish. Barnaby (1944) showed a red salmon mortality of over 99 per cent in the egg and fry stages. Foerster and Ricker (1942) found it evident that a loss of roughly 96 per cent of young sockeye salmon could be anticipated, even after the fry have hatched and left the spawning beds.

It is realized that productivity varies widely among different species of fishes, but there is evidence which indicates that the biology of the whitefish is such that it would support Baranoff's second theory, as do the examples from the literature given above.

Einsele (as quoted by Hasler*) showed that fertility of coregonid fishes in nature is great, and that mortality after hatching is also great. Some records show that less than 0.001 per cent of the coregonids hatched in the Bodensee reach the fishermen's nets.

Milner (1874) found that "moderate" sized whitefish produced 11,000 or 12,000 eggs per pound of fish. Hart (1930) found that the whitefish from the Bay of Quinte produced between 4,000 and 6,500 eggs per pound of fish. He found data which indicated that there is a very high percentage of fertilized eggs on the whitefish spawning grounds, and also

* Hasler, A. D. A war time view of European biological stations (an unpublished account of some experiences and information gathered in Europe, 1945).

a heavy mortality upon the eggs which remain on the bottom throughout the winter. Hart suggested that the magnitude of the whitefish catch is not controlled solely by previous overfishing; but that "biological factors" are of great importance.

Ricker (1946), on the other hand, states that in some Canadian lakes reproduction has been curtailed enough by fishing to cause a progressive decline in abundance of whitefish populations. This would not seem to be the case in Lake Michigan, as an examination of Plate III will indicate. It will be seen that small brood stocks in the lake have produced high catches of fish some years later.

Many biologists believe that food is one of the limiting factors, if not the limiting factor, in the survival of the fry, and therefore in fish production. Herrington (1948) states, "in the final analysis it is the amount of food available which provides the over-all limitation on the amount of life which can be supported in a given area. Thus at high population levels intraspecific competition for food should be dominant."

Ricker and Foerster (1948) found that the mortality rate in sockeye salmon is greatest when the fry are small. The prolongation of this period of small size would also prolong the period in which the fry are the most vulnerable to mortality. A prolongation of this critical period would result when the food supply is inadequate for the number of fry that are dependent upon it.

Hjort (1914, 1926) concluded that the fluctuations in the fish stocks have their origins in certain conditions prevailing at a very early period in the life of the fish. Much evidence indicates that the relative abundance of food at the time the fry are hatched is one such condition. Hjort believed that the fry die from lack of food, especially in the spring months. He postulated that whenever a plankton pulse corresponds with a period when the young fish will need food badly, a greater number of fish than average will survive, and a good fish year will occur. A dominant year class, then, would require the contemporary hatching of the fry and the development of the special plants or zooplankters which they will need for nourishment.

Langlois (1937, 1948) found data which suggested that the critical period for young fish is the period after hatching, when they depend upon the plankton for their food. He states, "It is known that the dominant year classes of fish are produced in years when the larvae or post-larval stages are not destroyed or lost, and there is an apparent correlation between ample spring pulses of plankton and the production of dominant year classes of certain species of fish."

Russell (1932) adduced lack of planktonic food as one of the factors probably affecting survival. Smith and Swingle (1939) found a direct relationship between the production of plankton in ponds and the production of fish, in spite of the fact that no definite relationship could be established between zooplankton alone and fish production. Doan (1942)

cites the work of Bullen, who reported a positive correlation between the quantity of zooplankton in the sea and English mackerel catches.

A tremendous supply of plankton is necessary to raise a crop of fish. Foerster (1944) states that big year groups of sockeye salmon may have put heavy drains on the plankton resources of a lake. Ricker (1937) made observations which suggest that a Daphnia population could be depleted by the feeding of sockeye salmon. Ricker (1946) quotes Okul who estimated that 1.7 million tons of plankton were consumed by the plankton eating fishes of the Sea of Azov in one year. Ricker also cites the work of Sushkina who found that fingerling Caspian shad consumed 11 per cent of their body weight daily, chiefly in Cladocera and Copepoda. Manteufel (as quoted by Ricker) has found that the herring of the Barents Sea can and do produce local depletions of the Copepod, Calanus at certain times of the year, while in the restricted bay areas this food may be almost exterminated.

Sette (1943) reports that two seasons with good zooplankton production produced good year classes of mackerel. He cites a case in which survival of mackerel from the time of spawning to the end of the planktonic phase of life was on the order of one to ten fish per million eggs spawned. One of the reasons suggested for this mortality was a general paucity of zooplankton in the spring of 1932. Thus, there is an indication of a correlation between zooplankton abundance and the survival of a mackerel year class.

There is evidence which indicates that these food scarcities may operate under certain conditions as limiting devices in the survival of whitefish fry. Hart (1930) indicated that the food of the fry may be the limiting factor in whitefish abundance. The same author (1931a) showed that slow growth rates may be the result of overcrowding of the young near the spawning grounds. If that is so, there is an indication that food is not always available in abundance. Miller (1947) found that an increase in the growth rate of whitefish and a decrease in the age of spawning whitefish followed an increased fishing intensity in two Alberta lakes. This is another instance where food would appear to be a factor limiting a whitefish population.

Einsele (as quoted by Ricker and Foerster, 1948, and by Hasler) found that Coregonus fry, when first hatched, died in large numbers if they were fed plankton at the density of its occurrence in the lake. When plankton was concentrated and fed to the fry, the increase in survival went up correspondingly with the increase in food. Einsele found that Coregonus fry ate from 50 to 500 times the concentration of plankton found in normal lake water at the season of their hatching. Fish of about 20 millimeters in length ate about 500 plankters a day, and fish 30 millimeters long ate about 1,000 plankters a day. Einsele believed that the efficiency of survival depended somewhat upon the size of the plankton organisms during the critical period in the life of the fry; that is, whether Diaptomus, Cyclops, Bosmina, or Daphnia were

abundant to that time.

If food is the device by which the size of a fish population is controlled in nature, it is necessary to study the conditions that may cause fluctuations in the food supply. The production-increasing effect of fertilization of fresh water ponds is well known (Smith and Swingle, 1939; Ball, 1949; Patriarche and Ball, 1949).

Ricker (1946) states that fertilization of larger bodies of water is not economically feasible in most cases, but that it often occurs incidentally as when domestic sewage empties into a lake or stream and causes tremendous phytoplankton blooms. Chandler and Weeks (1945) found that the highest values for total inorganic nitrogen in Lake Erie follow periods of the greatest discharge from two rivers into the lake. Concentrations of nitrate N in the lake water near the Bass Island region of Lake Erie vary directly as, but not necessarily in proportion to, the river discharge from the southwestern drainage area of western Lake Erie.

Pearsall (1923) stressed the importance of land drainage in the concentration of inorganic compounds in lakes, especially where the drainage basin is predominantly soil covered. He found that the periodicity of diatom blooms seemed to be largely conditioned by floods, since the algae respond to nutrients dissolved in the water. Pearsall also concluded that Daphnia longispina is most abundant when the water contains the most refuse such as organic detritus washed in by floods, since the Cladacera is a refuse feed-

ing organism.

Ricker (1938), on the other hand, noted that the diatom maximum in Cultus Lake came toward the end of the rainy season; but that other considerations left doubt as to the fact that diatom periodicity is caused by influxes of water. He cites exceptional rains in January 1935 followed by extremely meager Melosira and Asterionella pulses. Ricker found characteristic differences in the abundance of zooplankton and phytoplankton from year to year, but he was unable to correlate these fluctuations directly with climatic or other causes.

Barnaby (1944) stated that variations in meteorological conditions result in changes in environmental conditions on the spawning grounds of salmon. He postulated that fluctuations in the supply of salts in the waters of Karluk Lake could affect the growth and survival of the fish in the lake by limiting the primary food organisms. Phosphorus and silicon are the limiting elements on phytoplankton production in Karluk Lake, and these salts are carried into the lake by streams. Presumably the stream flows vary from year to year, and so therefore does the supply of salts, thus causing fluctuations in the abundance of red salmon fingerlings.

Russell (1936, and other papers) found, as a result of extended investigations in the English Channel, that there is parallel between the abundance of young fish and the quantity of phosphates present in the water during the previous winter. He suggested that an inflow of rich water from the

south of Ireland replenishing the supply of phosphorus in the Channel would be necessary before conditions would again be suitable for the survival of young fish. The same author (1947) noted that there was a continued scarcity of plankton in the Channel during the period 1936-46, and that any inflow of rich water into the Channel during those years had been extremely unlikely. In spite of the rest from fishing in the Channel during the war, the numbers of pelagic young of summer spawners showed no increase over those in the years just before the war.

Hjort (1926) quotes Gran as demonstrating after long study the great importance which fresh waters draining into the sea as rivers and melting snow must have upon development of plankton through the salts, especially nitrates and phosphorus, which they add to the sea water. If plankton is the decisive factor in the production of year classes, it would be expected that heavy rain or snow would give a rich year class. Sund (also quoted by Hjort), found to the contrary, that rich year classes of Norwegian cod and years of small snowfall were directly correlated. Hjort gave a possible explanation of Sund's findings in his theorization that the fry might be carried out over the great depths of the Norwegian Sea by the increased currents which might result from a heavier runoff. There they would not be able to return and reach the bottom of the continental shelf to feed before the plankton died out in the upper waters during the autumn months of their

first year of life.

Langlois (1941, 1948) has proposed a theory to account for decreases in cisco, whitefish, and perch populations in Lake Erie. He cites the work of Chandler and Weeks (1945) who have demonstrated a correlation between the annual cycles of fluctuating abundance of the nitrates and phosphates with the runoff from the lands of northwestern Ohio. The amounts of these salts in the lake water increase highly at times of accelerated discharge, and since discharge varies from year to year so do the amounts of salts in the lake. Unfortunately, in Lake Erie, when the inflows of these salts are at a maximum, the inflow of silt is also high. The western areas of the lake become more turbid, and this prevents the photosynthesis which would allow a phytoplankton bloom to develop. Tremendous variations in the numbers of plankton organisms and in their periods of abundance have been noticed in this region. Langlois states that the main problem of maintaining the commercial fishery industry of Lake Erie appears to be one of land use, closely associated with erosion problems.

Langlois also postulated that the seasonal fluctuations in the lake level may flood the breeding grounds or expose them to air, in either case rendering them useless.

Doan (1941, 1942) found a significant positive coefficient of correlation of 0.79 between the mean April-May turbidities in Lake Erie and the Ohio sauger catches three years later. These turbidities were due to silt carried

into the lake by streams, and to the stirring up of the lake bottom by storms. Doan gave three possible explanations of the above correlation:

(a) Turbidity may prevent stickiness in sauger eggs.

(b) Turbidity may protect the fry from predators.

(c) Turbidity may facilitate the feeding of young saugers by concentrating zooplankton near the surface.

Doan found temperature and currents to be of considerable importance in his study. Currents play a major role in the distribution of suspended matter in the lake. There are indications that winds are the dominant determinants of the direction of flow.

Other environmental conditions have been suggested as influencing the survival of young fish. Russell (1932) gave as two of the factors probably affecting survival variations in temperature and variations in normal currents drifting larvae to localities unsuited to their growth and development. Herrington (1948) included unfavorable conditions in respect to temperature, salinity, and currents as a few of the causes for the mortality experienced by eggs and young fish. He states, that within the favorable temperature and salinity ranges of a species, food and predators are much more likely to be important determiners of average survival than are temperature and salinity (Still, it must be kept in mind that these environmental factors affect not only the

fish directly; but, perhaps even more importantly, the fish food organisms).

Chandler (1941) states, "The importance of solar radiation as a factor causing annual variations in phytoplankton production may be considerable, but the present data are too limited to furnish conclusive evidence." Chandler found water temperatures to be intimately related to annual variations in the abundance of phytoplankton. Cooper (1934) observed that three out of four midwinter plankton outbursts studied had followed periods of sunny weather with little wind. Einsele (as quoted by Hasler) has illustrated experimentally a direct effect of light intensity upon the survival of the fry. In experiments with the light concentration at only three lux, coregonid fry starved to death in spite of the presence of adequate food. Mortality was eliminated when the light intensity was increased to 15,000 lux. Einsele stated the possibility that many fry might perish if the winter were long and they were unable to see well enough to feed because of the presence of snow covered ice.

Doan (1942) notes that spring temperature variations influence spawning and fry survival. There is a relation between the May-June temperature and the catch of blue pike two years later. He states that wide daily variation in water temperatures in Lake Erie might result in a greater death rate for eggs and fry. Rounsefell (1930) correlated the success of spawning in the Alaska herring to the air temperatures. He proposed that the correlation was not due

to any direct effect upon the eggs, but rather to the effect upon the plankton which the young fish require for survival. Hart (1930) postulated that temperature alone could not be the factor causing high mortality in whitefish eggs. Doan (1942) cites an attempt to correlate catches of whitefish from the Ohio waters of Lake Erie with mean autumn air temperatures of the same year. No significant correlation was found.

Sette (1943) gave, as a possible reason for poor year classes of mackerel, winds which may have blown the fry from the nursery grounds. Dymond (1948) also mentions the effect of gales which could disturb the sea bottom and produce unfavorable conditions for the survival of the eggs or larvae.

It will be seen that a multiplicity of factors have been described as affecting the survival of fishes in the early stages of life. Hjort (1926) summarizes the problem of understanding these environmental effects by saying, "One might perhaps expect that the conditions which decide the fate of the larvae may in all cases be of a similar general character, but in each case subject to modifications, which will also modify the effect of their influence."

An examination of Plates III and IV will show that some relationship does appear to exist between the fluctuations in whitefish abundance and the fluctuations in water level. The fact that the lag in years between high water levels and high abundance varies may indicate the presence of some other factor or factors which may operate in conjunction with the fluc-

tuating water level. When these factors combine to create optimum conditions for the survival of the young fish, a dominant year class occurs. Evidently the spring of 1943 was marked by such an optimum in Green Bay, since good year classes of whitefish, lake herring, and walleye were all produced simultaneously. Hile (1950) suggests that the increase in all three species may have arisen from peculiarly favorable weather conditions.

The situation that Langlois describes for Lake Erie, in which turbidities prohibit photosynthesis and the utilization of the increased nutrients, does not exist in northern Green Bay. There the lands are largely forested and the soils are not easily eroded by heavy runoffs. An increase in dissolved nutrients in the bay would not be accompanied by the harmful turbidities that occur in Lake Erie, and thus production of plankton would be increased.

The suggested hypothesis, then, is that heavy runoffs from the streams draining into northern Green Bay in combination with some other factor or factors as yet unknown, create favorable conditions for the production of plankton organisms in the bay. The ensuing increased food supply allows more fry to survive and a good year class of whitefish is produced.

Some questions immediately arise upon consideration of this hypothesis. It will be noted that in periods of unusually high water, the levels stay high for several years. The question then comes to mind as to why several consecu-

tive dominant year classes of fish are not produced, if high water level is considered as indicating a favorable condition. Two possible answers to this question are:

1. If another cause (or causes) is associated with heavy runoff to create favorable conditions for survival of the fry, some fluctuation of this unknown factor may result in unfavorable conditions, even though the water level is high. For example, if high water levels due to heavy run-offs combined with high temperatures should provide the ideal conditions for plankton production, the presence of either factor alone might have no effect upon the survival of the young fish. This might explain some of the discrepancies in the lag between high water levels and high fish abundance.

2. The first dominant year class produced may provide enough competition for food to prevent high survival in the fry hatched in following years, even though continued high (or even higher) water levels may result in continued rich plankton crops. Caraway (MS) found that the tremendous 1943 year class of whitefish in Big Bay De Noc was followed by a nearly complete failure of the 1944 year class, and by a small 1945 year class.

Both of the above theories could work in conjunction. Herrington (1944, 1948) offers evidence which would support the second theory by suggesting that when the adult stock is large, the adults compete for food with the young in one or more stages of their development. He found that where both intra-year-class and inter-year-class competition for food

are present, their effects are combined, since both serve to reduce the amount of food available per fish. It will be seen from the section on the food habits of the whitefish that the adults sometimes feed upon plankton Crustaceans, as do the young, thus making inter-year-class food competition possible.

A serious unanswered objection to the hypothesis being presented is the lack of any apparent relationship between lake herring abundance and fluctuations in the water level. (See Plate V). According to Ball (1949), it appears that the closer are the feeding habits of the fish concerned to the base of the food chain, the greater are the effects of fertilization reflected in the weight of the fish produced. If this is so, the plankton feeding herring should reflect the changes in lake level the most decisively of the three species considered in this study. Another disparity that will be seen by a glance at Plate III is the fact that the whitefish catch begins to rise, leading to the peak of 1930 while the annual water levels are descending from a high.

These questions, and others which may present themselves will be answered definitely only after actual observations have been made of the environmental conditions existing in Green Bay, as they relate to fish production. The data and arguments presented here can neither prove nor disprove that the production of whitefish in northern Green Bay is dependent upon water level changes. They do, however, indicate that such a relationship may exist. Examination of this and

other environmental factors in Green Bay must be undertaken before the commercial fisheries of the bay can be completely understood and managed correctly.

SUMMARY

1. Concern about the depletion of whitefish stocks in the Great Lakes has been evidenced for many years, but the fish continue to hold their own despite heavy fishing pressure.
2. The whitefish is a plankton feeder in the early stages of life, and primarily a bottom feeder after maturity.
3. No statistically significant correlation was found between the yearly whitefish and lake herring abundances in the Michigan waters of Green Bay, and the fluctuations in the water levels of previous years. However, there appears to be a general relationship between the two factors in the case of the whitefish.
4. The coefficient of correlation for walleye abundance from 1929 to 1949 as related to the highest annual water level four years earlier was + .76. The coefficient of correlation for the same walleye abundance, with the water levels used being five years earlier was + .69.
5. A hypothesis to account for the apparent relationship of water level fluctuations to whitefish production in northern Green Bay was suggested. It was as follows: Heavy runoffs from the streams draining into northern Green Bay in combination with some other factor or factors, as yet unknown, create favorable conditions

for the production of plankton in the bay. The increase in the food supply that follows allows more fry to survive, and a heavy year class of fish comes into existence.

6. The above hypothesis poses many questions which can only be answered definitely after actual observations have been made of the environmental conditions existing in Green Bay as they relate to fish production.

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