A CONTRIBUTION TO THE POPULATION DYNAMICS AND HOMING BEHAVIOR OF NORTHERN WISCONSIN LAKE FISHES

BY

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A thesis submitted to the Graduate School of the University of Wisconsin in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

by

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Date August 3, 1956

To Professors: Hasler

Fraser

Curtis

This thesis having been approved in respect to form and mechanical execution is referred to you for judgment upon its substantial merit.

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Approved as satisfying in substance the doctoral thesis requirement of the University of Wisconsin.

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Date 8 Aug., 1956

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SOME EFFECTS OF "THINNING" ON A POPULATION OF FISHES

INTRODUCTION

Purpose and scope

Many workers have concluded that the growth of individual members of a fish population is inversely proportional to the density. This is in support of the results of Walter (1934) in his extensive analysis of the factors which influence the growth of carp in ponds, and his efforts were among the earliest that placed fish production on a scientific basis. Church (1927) and Shaw (1929), as cited by Schneberger (1935), studied the effect of crowding on the growth of the tropical fish Platypoecilus maculatus rubra and found that the least number of fish per unit of volume grew at the fastest rate.

Ricker and Foerster (1948) report that the average weight of sockeye salmon Oncorhynchus nerka belonging to year classes with few individuals is higher than that of sockeye of year classes with many individuals. This also has been shown for rainbow trout Salmo gairdneri in small lakes of northern Wisconsin (Johnson and Hasler 1954).

Bardach (1951), on the basis of historical reports, believed that a severe reduction in the numbers was followed by an increase in the average length and weight of yellow perch Perca flavescens (Mitchill) in Lake Mendota, Wisconsin. Churchill (1949) was unable to show an increase in rate of growth in length of perch in Curtis Lake, Wisconsin, after netting had removed 62.3 pounds per acre over a four-year period; however, the fish were heavier at a given length than before removal. Dymond (1926) and Schneberger (op. cit.) state that the size of perch taken in Lake Nipigon, Ontario, and Nebish, Silver, and Weber Lakes,

Wisconsin, respectively, attain lengths which are correlated negatively with relative abundance based upon frequency of capture in nets. Eschmeyer (1937, 1938) has obtained similar results, as did Alm (1946) who transplanted perch Perca fluviatilis Linnaeus to non-perch waters. On the other hand, removal of most of the perch in Lake Windermere, England, failed to produce a significant change in rate of growth (LeCren 1949).

In Alabama ponds, the addition of more bluegills (Lepomis macrochirus macrochirus Rafinesque) without increasing the food supply decreased the average size of the fish surviving (Swingle and Smith 1939). Swingle has focused attention on the relationship between production and pounds of predator and prey fish. He points out that, in general, a ratio of the weights of forage to carnivorous species of from 3.0 to 6.0 is most desirable (Swingle 1950).

King (1953) described an unsuccessful attempt to increase the growth of fishes in Lake Hiwassee, Oklahoma, by eliminating part of the population with rotenone. One- and two-year old largemouth bass Micropterus salmoides (Lacépède) showed a slight increase, but older fish did not. Shoreline spraying killed many bluegills without affecting the growth of the remainder.

Following reduction of population densities by winterkill, Beckman (1950) observed an increased rate of growth for bluegills, yellow perch, and pumpkinseeds (Lepomis gibbosus Linnaeus), and a very small increase for largemouth bass. These advantageous growth rates were sustained for only a few years. Beckman (1941, 1943) previously had reported a marked positive change in the growth rate of rock bass Ambloplites rupestris rupestris (Rafinesque) after approximately one-half of Standard Lake, Michigan, was poisoned with powdered derris root.

Two years after the stocking of a new pond with bluegills, over-

population from natural spawn caused stunting (Bennett 1943). Stunted breeder bluegills taken from Homewood Lake and placed in Fork Lake, Illinois, grew as much during the succeeding 15 months as they did during the past two to five years (Bennett, Thompson, and Parr 1940). A growth stimulus produced by severe thinning of the bluegill population in Ridge Lake, Illinois, has been noted by Bennett (1954).

In 1952, a study was begun by Johnson, et al. (1953) which had as its objective the determination of the effects of removal of excess roughfish and stunted panfish on the growth and survival of largemouth bass. The work was continued through 1956 by me and was enlarged to include the effects on other species. Many of the early workers performed their thinning experiments in the laboratory or in artificial ponds which could be drained periodically. A need for more quantitative data on the growth-density relationship in small natural lakes is foremost among the reasons which prompted this study. In addition, the varied methods which have been used in the past to analyze growth after a reduction in numbers seem to lack the precision necessary for adequate appraisal, and pre-treatment estimates of the population size often were omitted. Throughout the following discussion of the results of this five-year program, emphasis has been placed on the application of a consistent, analytical approach.

Description of Flora Lake

Flora Lake, the site of this study, lies in a kettle of the "pitted outwash" of Vilas County, Wisconsin. The outwash is composed of nearly all horizontally bedded sand with scattered pebbles and boulders, and the underlying bed rock is of a crystalline nature (Thwaites 1929). Maximum depth of the lake is about 30 feet, and the irregular surface covers an area of 102 acres.

The brown stain of the water is typical of many lakes in the vicinity, and it is thought to be owing to the accumulation of humic colloids. As a result, most of the penetrating light is absorbed in the upper two meters, and mid-summer limnological observations show an absence of light and oxygen below six meters. Water temperatures are relatively warm throughout, but a distinct thermocline is evident. As would be expected in lakes of this type, there are few carbonates (under 10 p.p.m.) and the pH is below 6.0 (figure 1).

Included among the more common larger aquatic plants are Nymphaea odorata, Nuphar advena, Brasenia Schreberi, Dulichium arundinaceum, Utricularia sp., Ceratophyllum demersum, and several species of Potamogeton. Isoetes Braunii is plentiful, as is the moss Fontinalis. The plankton of some lakes in this region has been discussed by Johnson (1954).

One hybrid and seven species of fish were netted consistently, namely, largemouth bass, bluegill, pumpkinseed, bluegill x pumpkinseed hybrid, rock bass, yellow perch, white sucker Catostomus commersonnii commersonnii (Lacépède), and golden shiner Notemigonus crysoleucas auratus (Rafinesque). Burbot Lota lota maculosa (LeSueur), yellow pikeperch Stizostedion vitreum vitreum (Mitchill), and northern black bullhead Ameiurus melas melas (Rafinesque) were taken rarely.

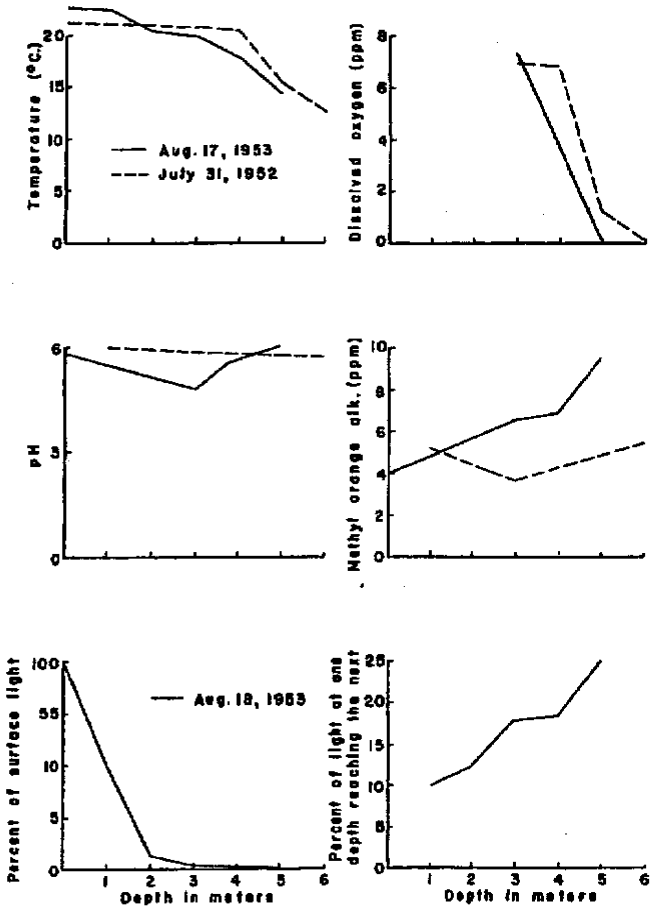

Figure 1. Some limnological observations on Flora Lake, Wisconsin, in 1952 and 1953

METHODS

Population estimates

At the beginning of every summer during the period 1953-1956, the populations of important species of fish were estimated by mark and recapture methods (table 1). Estimations were made according to Petersen (1896) in most instances; however, the Schnabel method (Schnabel 1938) was applied to largemouth bass and my own modification of Petersen's method (Parker 1955) was utilized for a population composed of bluegills, pumpkinseeds, and hybrids of these two. Grouping of species in a single estimate has been shown to be inadvisable (Ricker 1948), but rapid handling made separate treatments impractical. It is questionable whether the few pumpkinseeds and hybrids in the threefold combination would greatly influence the overall estimate in this case. Estimates by least-squares-analysis were not used for the remaining species, since there were few recaptures and a high degree of variability in the required ratio of marked returns to the total number sampled. It is my opinion that the standard method employed yielded results which were slightly high.

My regression-estimate was developed originally for extremely stunted populations in which the large number of new recruits could not be recognized from lengths alone. A further verification of the accuracy of this method was obtained by applying it to a population of beans in which the initial number of individuals, both marked and unmarked, was known. The members were subjected to a fixed absolute rate of recruitment and mortality which produced nearly the same relative, numerical change as occurred in the 1953 natural population. Results from the above model were compared with the corresponding Petersen estimates,

A Method for Removing the Effect of Recruitment on Petersen-type Population Estimates[1,2]

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ABSTRACT

A regression analysis, which is based on time changes in the ratio of the number of marked fish in the daily catch to the total daily catch, was used to estimate initial population size. This method eliminates overestimation caused by recruitment.

PROCEDURE

Many Petersen-type estimates of fish populations based on seasonal recovery of marked individuals are found to be too high. This is due in part to recruitment to the catchable population during the period being considered. Methods which have been used in the past to eliminate or correct for recruitment have been reviewed by Ricker (1948).

Under suitable assumptions, namely (1) equal rates of catchability and natural mortality at any one time for both marked and unmarked individuals, (2) random dispersal of marked fish, and (3) constant absolute rate of recruitment to the catchable portion of the population, it is possible to estimate the initial population by plotting the ratio of the number of marked fish in the daily catch to the total daily catch against the number of days after marking has ceased. Effects of this ratio's non-normality may be partially removed by applying a transformation such as the arcsin (Bartlett, 1936) or the more common logarithmic. The former has been used here. The slope of the best fitting linear regression line will be negative, corresponding to a decrease in the computed ratio as time passes. Number of fish marked divided by the Y-intercept gives the initial population estimate.

EXAMPLE

This method has been applied to marking data collected in 1953 from a population of bluegills, common sunfish, and hybrids between the two in Flora Lake, Vilas County, Wisconsin. Although this type of grouping has been shown to be inadvisable (Ricker, 1948), identification difficulties preclude separate treatments.

The fish were caught in fyke nets and were marked by removal of left pelvic fins, between the dates July 2 and July 6. Subsequent catches were made in the same nets, and all fish netted were killed. These samples were taken between July 9 and October 18. The data are presented in Table I.

[1]Received for publication November 15, 1954.
[2]Data used were taken from a study supported in part by a grant from the Wisconsin Alumni Research Foundation.

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TABLE I. Data used in making a marked fish regression analysis of a population of bluegills, common sunfish, and hybrids between the two.

Date	Days after end of marking	Fish in sample	Marked fish in sample / Total fish in sample	Arc-sin of $\sqrt{\text{ratio}}$	Marked fish removed by netting	Estimated nat. mort. of marked fish	No. of marked fish remaining at day's end
July 6	...	...	...	...	...	9[a]	3,230
9	3	86	0.1279	20.96	11	15	3,191
10	4	733	0.0559	13.69	41	5	3,145
11	5	648	0.0525	16.61	51	5	3,092
12	6	708	0.0708	16.11	54	5	3,033
13	7	673	0.1352	21.81	93	5	2,935
14	8	915	0.1298	21.13	123	4	2,808
15	9	241	0.0664	15.24	24	4	2,780
16	12	225	0.1156	19.91	26	13	2,741
19	13	622	0.1495	22.70	93	4	2,644
20	14	540	0.1481	22.30	78	4	2,562
21	15	659	0.1518	23.11	100	4	2,458
22	16	907	0.1246	20.79	113	4	2,341
23	17	252	0.0675	15.12	17	4	2,320
24	18	1010	0.1100	19.46	113	1	2,203
25	19	540	0.0674	17.10	18	3	2,152
26	20	567	0.1376	21.81	78	3	2,071
27	21	438	0.1027	18.72	45	3	2,023
28	22	181	0.0608	11.48	11	3	2,009
29	24	537	0.1117	19.55	60	3	1,946
30	24	98	0.0714	15.15	7	3	1,936
31	25	765	0.0889	18.15	77	3	1,856
Aug. 2	27	387	0.0388	11.39	15	6	1,835
3	28	215	0.1070	18.72	24	3	1,808
5	30	270	0.1593	23.33	29	6	1,782
6	31	135	0.1704	19.10	47	3	1,732
8	33	500	0.1052	18.91	61	5	1,666
13	38	128	0.1055	15.12	13	11	1,610
14	39	151	0.0464	12.39	7	2	1,601
15	40	305	0.1836	25.10	56	2	1,543
16	41	56	0.1071	26.13	7	2	1,534
20	45	91	0.1209	20.56	11	9	1,514
21	46	1025	0.1005	12.62	58	2	1,454
22	47	308	0.0584	12.23	11	2	1,441
24	49	305	0.0558	12.23	11	1	1,427
27	52	51	0.0980	18.21	5	7	1,415
30	55	78	0.0641	14.65	5	6	1,404
31	56	193	0.0518	13.18	10	2	1,392
Sept. 2	58	240	0.1333	21.47	30	8	1,346
27	83	71	0.0704	15.79	4	51	1,291
Oct. 18	101	142	0.0634	14.24	5	41	1,245
Totals		16,950			1,701	280	

[a]During marking.

TABLE II. Comparison of conventional and modified Petersen estimates.

	Conventional	Modified	
Population estimate	32,138	28,238a	28,150b
95% confidence interval			
Lower limit	30,725	24,139	24,394
Upper limit	33,628	31,778	31,681

a Natural mortality during marking period ignored.
b Natural mortality during marking period estimated.

TABLE III. Estimation of recruitment to the catchable portion of the population for the period July 6, 1951 to October 18, 1951.

(1) Estimated population as of July 6	28,150
(2) Estimated population as of October 18	21,168a
(3) Removal	16,930
(4) Estimated natural mortality	3,457
(5) (3) + (4)	20,387
(6) (1) − (5)	7,772
(7) (2) − (6) = recruitment	16,676

a N = 128 (Table I) divided by 0.00605 (using fin-rays after 108 days).

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and in three experiments, there was a marked overestimation by the Petersen method (table 2). This same relationship was thought to hold when both types were compared for the bluegills, pumpkinseeds, and hybrids of Flora Lake in 1953, 1954, and 1955.

The total weight of the catchable population of each species in Flora Lake at the time of estimation was based on the numerical estimates and on the average weight of fish removed during the week immediately following the marking period (table 3).

No population estimates were made in 1952 except that of largemouth bass. Under the assumption that the lake was in or near a state of equilibrium as far as the fish population was concerned, the total numbers present were approximated by adding the number removed in 1952 to the estimated number in 1953.

Removal

Fyke nets of 3/8-inch and 1-inch bar mesh were employed almost exclusively to remove bluegills, pumpkinseeds, hybrids, rock bass, yellow perch, white suckers, and golden shiners, while largemouth bass taken were returned to the water. A few large perch traps of wire mesh were used with little success in 1953, and in 1954 a large bay was blocked off with a seine and poisoned with rotenone. Total numbers and pounds removed are summarized in table 4.

The percentage of the weight of all species present before removal operations began each summer which was subsequently taken from the lake ranged from 10.2 in 1956 to 52.6 in 1953 (table 5). The 1956 total quantity of fish removed obviously had no influence on the rates of growth measured here, since it was merely those fish which were removed in making the necessary final population estimates. The percentage removed may have been considerably more in 1955, when an unreliable

Table 2. A comparison of two methods of estimating the size of a bass population composed of 5000 individuals of which 500 were marked*, based on 40 samples

Experiment number	Ave. "daily" sample size	Petersen estimate	95% conf. int.	Parker estimate	95% conf. int.
I	46.7	3921	3386 4658	2792	2179 3723
II	47.4	4218	3628 5042	3459	2712 4586
III	49.3	4022	3480 4762	2654	2321 3081
Mean of estimates		4054		2968	

* The population was subjected to an absolute "daily" mortality rate of 9 individuals and an absolute recruitment rate of 43 individuals.

Table 3. Average weight in pounds of each species of fish removed from Flora Lake, Wisconsin, during the week following the period of marking in 1952 - 1956

Year	Bluegill Pumpkinseed Hybrid	Rock bass	Yellow perch	White sucker	Golden shiner
1952*	0.0982**	0.1908	0.0435	0.4608	0.1000**
1953	0.0982	0.2146	0.0344	0.8592	0.1000
1954	0.0793	0.2068	0.0506	0.8256	0.0342
1955	0.0622	0.1361	0.0419	0.3493	0.0864
1956	0.0274	0.1062	0.0362	0.6795	0.0800

* July and August
** Figures from 1953

Table 4. Numbers and pounds of each species of fish removed from Flora Lake, Wisconsin, during the summers of 1952 - 1956

		Year					
		1952	1953	1954		1955	1956
No. of fyke net days		123	286	405	Poison*	490	41
Bluegill Pumpkinseed Hybrid	No.	5,055	16,943	13,276	879	6,159	3,027
	Wt.	502.6	1588.6	928.2	61.4	242.2	83.1
Rock bass	No.	131	310	694	44	376	48
	Wt.	25.0	60.4	104.3	6.6	45.0	5.1
Yellow perch	No.	131	1,956	7,094	1,297	1,292	177
	Wt.	5.7	107.3	288.9	52.8	47.7	6.4
White sucker	No.	222	734	708	182	929	122
	Wt.	102.3	708.1	314.0	80.8	506.5	82.9
Golden shiner	No.	0	317	1,627	360	487	15
	Wt.	0.0	17.0	65.0	14.4	40.2	1.2

* Estimates were made before poisoning of a large bay which was blocked off with a seine.

Table 5. Percentage of the estimated total weight in pounds of each species present in Flora Lake, Wisconsin, at the time of population estimation which was subsequently removed during the summers of 1952 - 1956

Year		Species					
		Bluegill Pumpkinseed Hybrid	Rock bass	Yellow perch	White sucker	Golden shiner	All species
1952	Est. total	3268.7	232.1	473.3	728.5	174.4	4877.0
	Removed	502.6	25.0	5.7	102.3	0.0	655.6
	Percent	15.4	10.8	1.2	14.0	0.0	13.0
1953	Est. total	2772.4	232.9	370.2	1167.6	174.4	4717.5
	Removed	1588.6	60.4	107.3	708.1	17.0	2481.4
	Percent	57.3	25.9	29.0	60.6	9.7	52.6
1954	Est. total	1018.6	313.7	856.6	1296.3	222.6	3707.8
	Removed	989.6	110.9	341.7	394.8	79.4	1916.4
	Percent	97.2	35.4	39.9	30.5	35.7	51.7
1955	Est. total	242.3	301.1	537.1	658.4	1004.1	2743.0
	Removed	242.2	45.0	47.7	506.5	40.2	881.6
	Percent	100.0	14.9	8.9	76.9	4.0	32.1
1956	Est. total	593.5	42.5	369.1	663.2	79.2	1747.5
	Removed	83.1	5.1	6.4	82.9	1.2	178.7
	Percent	14.0	12.0	1.7	12.5	1.5	10.2

estimate of golden shiners was very high and indicated that they made up over 35 percent of the grand total.

Scale and weight analyses

Scale samples were collected periodically during the five years of the study to determine whether an increased rate of growth would be in evidence on them. These were removed from the left side of the fish on an imaginary line from the front of the dorsal fin to the base of the pectoral fin. The scales were easily read dry because of their usually small and flexible nature. Mounting between two glass slides and projecting with a Bioscope at a magnification of 50 diameters proved to be satisfactory. Focus, annuli, and edge were marked on a strip of paper, from which back calculations of total length at each annulus were made from nomographs similar to those described by Carlander and Smith (1944) and Hile (1950). A linear relationship between anterior scale radius and total length was found to give a sufficient prediction of length at the time of scale formation for all species (table 6). A curvilinear regression may have given a slightly better correlation, but the small increase in the degree of accuracy does not seem to warrant the additional labor in calculation. Least-squares-approximations have been used for consistency with the work of other writers; however, the methods of Wald (1940) and Bartlett (1949) which fit straight lines when both variables are subject to error might yield more realistic results.

In order to decide on whether there had been an increase or decrease in the rate of linear growth following removal, it was necessary to find a method which would permit one to decide if a down- or upswing in growth was a "normal" fluctuation. To do this, a second-degree polynomial regression of calculated total length at each annulus on year of life was fitted to the data on the growth which took place before 1952 (table 7).

Table 6. Linear regression of total length (mm.) on anterior scale radius (mm. x 50) for one hybrid and seven species of fish taken from Flora Lake, Wisconsin, during the period 1952 - 1955

Species	n	Intercept	Slope	Correlation coefficient	Error sum of squares
Largemouth bass	479	22.8	1.4496	0.974	193389
Bluegill	1119	32.6	0.9799	0.959	115068
Pumpkinseed	119	30.4	0.7750	0.853	12875
B x P hybrid	276	31.4	0.7908	0.891	43552
Rock bass	255	35.5	0.7495	0.946	50503
Yellow perch	342	47.8	1.4112	0.920	54251
White sucker	285	70.2	1.3830	0.976	55432
Golden shiner	184	63.7	1.1459	0.826	47188

Table 7. Second-degree polynomial regression of calculated total length (mm.) at each annulus formed in or before 1952 on year of life for fish collected from Flora Lake, Wisconsin, in 1952 - 1956

Species	n	Intercept	b_1	b_2	$s_{L \cdot A}$
Largemouth bass	556	39.2	73.98	- 3.542	22.34
Bluegill	3403	31.7	21.47	- 0.659	6.58
Pumpkinseed	309	25.2	28.88	- 0.783	8.80
B x P hybrid	585	27.5	25.64	- 0.570	11.38
Rock bass	729	32.7	22.18	- 0.205	10.27
Yellow perch	455	61.5	21.64	0.755	9.10
White sucker	265	64.4	86.98	- 3.573	26.46
Golden shiner	48	54.7	35.82	- 0.237	20.45

Hile (1943) reviewed the early works of Ritter (1920), Ford (1933), and Wagler (1936, 1937) on length-age functions, and he related the length of rock bass to age by an equation which assumed that the ratio of the relative growth rates in successive years was constant. It is clear that the least-squares-analysis utilized here only covers the period from age one to age n, and does not pass through zero at age zero. A 95 percent confidence interval for the mean length at a given age was set about the regression, and it was agreed to call all means of calculated total lengths at annuli formed after 1952 which fell outside of this interval an increase (or decrease) resulting from removal. Since the choice of a growth curve is arbitrary, confidence limits for other possible functions likely would differ point for point from those used in this study; however, the areas enclosed probably would agree closely. The confidence limits are inexact when the error distributions of the lengths at successive annuli of equi-aged fish are partially dependent, as was found in some of the faster growing species. In addition, we must assume that the same length-scale relationship holds for all years considered, that the rare occurrence of Lee's phenomenon does not reduce appreciably the precision of the computations, and that no "abnormal" fluctuations in growth rate would have occurred had no thinning been done. Because of these reasons, one should attach little significance to borderline changes in the rate of growth as identified with the above procedure.

The soundness of the scale method is based on three assumptions (Van Oosten 1929): (1) that the scales remain constant in number and retain their identity throughout the life of the fish, (2) that the annual increment in the size of the scale remains functionally related to the annual increment in body length, and (3) that annuli are formed

yearly and at the same time each year. In Flora Lake, annuli were formed in all years during the period from mid-May to mid-June, with older fish being the last to lay down an annulus. Aging was not difficult, but largemouth bass and yellow perch had occasional check marks or false annuli. The ages assigned were correct for most age groups, less so for the older fish.

The other possible change in rate of growth following thinning is that in the weight of an individual at a given length. Schuck (1942) has used the covariance technique to analyze the differences between the "fatness" of tagged and untagged trout. Similar methods have been employed here on equal sized, randomly selected samples of fish collected in 1952 and in 1956. In making the analysis, if the slopes of the two logarithmic weight-length regressions differed significantly, the error sum of squares used in testing for a difference between adjusted means was computed in the manner of Mood (1950). It should be pointed out that the covariance technique as applied to weight-length data gives only approximate results, since neither variable can be measured without error.

RESULTS

Largemouth bass

Growth. Previous to the initiation of removal operations in 1952, the linear growth rate of largemouth bass in Flora Lake was similar to that of bass in other lakes of northern Wisconsin as given by Bennett (1937). A comparison of the average calculated total lengths in inches at each annulus is made below.

Age	Northern Wisconsin	Flora Lake
1	2.8	4.2
2	6.5	6.8
3	9.7	9.1
4	11.7	11.2
5	13.2	12.4
6	13.9	13.6
7	15.2	15.0
8	16.7	15.9
9	17.7	17.2
10	18.5	18.5

It appears that the Flora Lake bass grow faster during the first two years of life, but this may be due to the fact that Bennett probably assumed direct proportionality of growth to scale radius with a zero intercept, whereas an intercept of 22.8 millimeters has been used here. It is likely that the bass in Flora Lake grow at a rate which is slightly behind the northern Wisconsin average throughout life.

Table 8 and figure 2 give the mean calculated length at each age before removal as determined from the actual totals and as estimated from the quadratic equation in table 7. The quantities estimated agree well with the actual ones, thus confirming the validity of the estimation method. Large differences are found only in ages 9 and 10, where few fish were represented. Using the appropriate intervals from table 8, the growth of the bass after 1952 was examined with the hope of finding a marked increase. Changes were decided on as agreed earlier, and (+),

Table 8. Total length (mm.) of Flora Lake largemouth bass at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with appropriate confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
1	139	107.5	109.7	98.2 - 121.2
2	130	174.2	173.0	166.1 - 179.9
3	115	231.5	229.2	227.0 - 231.4
4	72	283.5	278.4	272.9 - 283.9
5	45	315.0	320.5	308.0 - 333.0
6	28	348.1	355.5	335.1 - 375.9
7	13	379.1	383.4	354.1 - 412.7
8	10	402.6	404.3	365.4 - 443.2
9	5	437.0	418.1	368.7 - 467.5
10	1	470.0	424.8	364.0 - 485.6

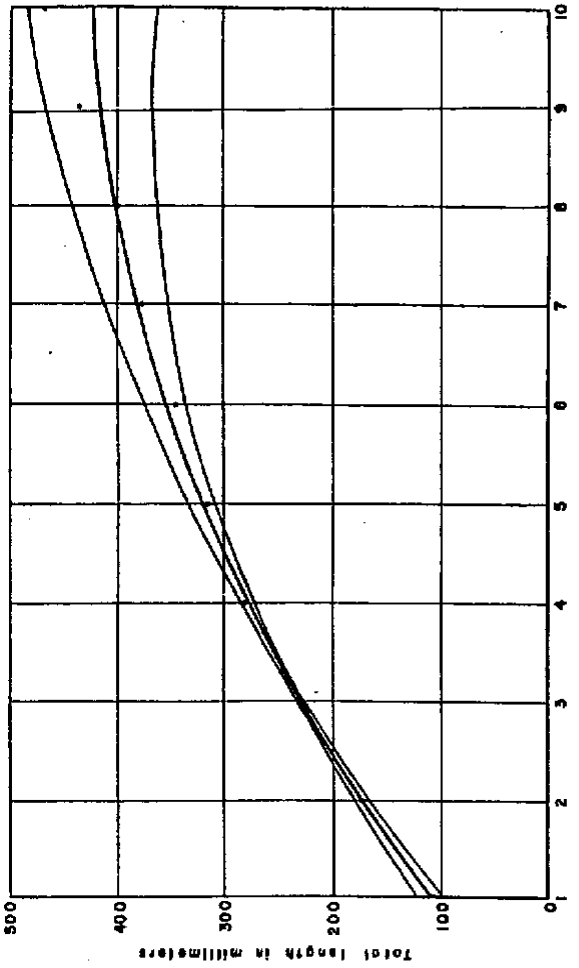

Figure 2. Pre-treatment theoretical growth curve for largemouth bass from Flora Lake, Wisconsin, with 95 percent confidence interval and actual means shown

(-), or (0) were used to identify them in table 9. In 1953, the year after the first reduction, only four- and five-year old bass showed an increase. These two year classes maintained the increase during succeeding years. The 1950 year class exhibited a negative change, while increases were shown by the 1951 year class. The following year class was below expectation in 1955, but had gained enough to overcome the deficit by 1956. During the first year of life, every year class was within the normal range except that of 1954, which fell far below. This is probably the result of a very successful year class which could have caused stunting within the age group due to crowding. In considering the bass as a whole, one must conclude that there has been no significant change in the linear rate of growth (figure 3).

Lee's phenomenon, that is, an apparent decrease in the calculated lengths as determined from successively older groups of fish, could be demonstrated only for the 1953 and 1954 year classes. Averages for 1953 yearlings were computed as 108, 103, and 91 millimeters, based on 77, 104, and 26 fish collected in 1954, 1955, and 1956, respectively. The 1954 yearlings averaged 81 and 74 millimeters according to 72 and 117 scale samples examined in 1955 and 1956, respectively.

A somewhat better picture is obtained when the "plumpness" of bass taken in 1952 is compared with that of those taken in 1956 (table 10). Although there was a significantly smaller slope of the logarithmic regression of weight on length in 1956 when compared with that in 1952, the adjusted, mean logarithmic weight in 1956 was higher than it was in 1952. In this case, as with all of the other species to be discussed, the adjusted mean weight was computed at the mean of the logarithmic lengths of both years combined.

Table 9. Calculated total lengths (mm.) at annuli formed in successive years by each year class of largemouth bass taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 indicated by + or - and no change indicated by o

	Year class													
Year	'41	'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55
1942	101 1*													
1943	166 1													
1944	235 1	81 4												
1945	275 1	144 4	93 5											
1946	320 1	211 4	159 5	108 3										
1947	357 1	259 4	218 5	167 3	91 15									
1948	393 1	300 4	260 5	222 3	157 15	101 17								
1949	419 1	342 4	294 5	269 3	210 15	175 17	106 27							
1950	445 1	384 4	332 5	303 3	260 15	232 17	182 27	115 41						
1951	470 1	410 4	366 5	351 3	310 15	286 17	254 27	178 41	130 17					
1952	490 1	436 4	393 5	390 3	348 15	331 17	305 27	229 41	181 17	105 9				
1953							335+ 5	317* 3	224- 3	171° 9	102° 47			
1954							405* 1	352* 3	258- 2	233+ 6	178° 25	103° 207		
1955								382* 1	281- 1	282° 5	217- 18	172° 150	77- 189	
1956										345+ 1	291* 1	221- 26	170° 14	104° 14

* Number of fish

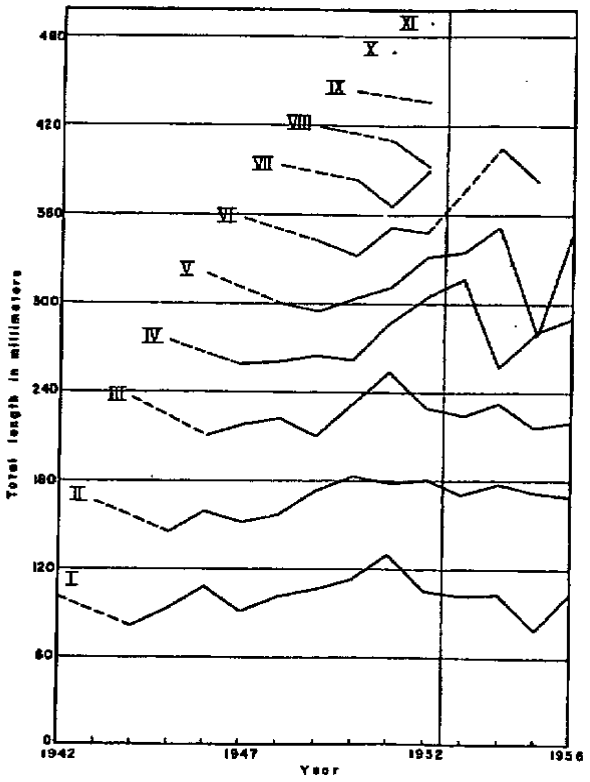

Figure 5. Fluctuations in the mean, calculated total lengths of Flora Lake largemouth bass in each age group

Table 10. Covariance analysis of natural logarithms of weights (g.) and total lengths (mm.) of largemouth bass taken from Flora Lake, Wisconsin, in 1952 and 1956

Year	Adjusted mean weight	n	Log a	Slope
1952	5.00665	119	-12.60039	3.22203
1956	5.08912	119	-11.76539	3.08432

Errors of estimate

Source	d.f.	Sum of squares	Mean square
Ave. within years	235	1.39460	
Deviations from ind. year regressions	234	1.34453	0.00575
Diff. between slopes	1		0.05007**
Diff. between adjusted means	1		0.18707**

Yield. Creel records were difficult to obtain on the voluntary basis employed, but examination of the completed cards and a record book of Dairyman's Country Club, on whose property Flora Lake is located, gave reasonably accurate returns except for the first part of 1952. There has been a definite increase in the yield of largemouth bass to fishermen (table 11), and this is correlated negatively with the size of the bluegill population (tables 1 and 5). The same situation has been encountered by Bennett (1954). Although data on angling-effort were lacking, the presence of the same number of boats kept at the landing (3) and my daily observations convinced me that the effort was nearly constant.

Survival and total population. Bennett, in his Ridge Lake study (1954), states that there is no apparent relationship between the number of spawning adults and the number of bass fry produced. In an earlier work (1945), he mentions that a heavily overfished population of bass was able to reproduce enough young to replace those individuals caught. He also points out that the number of bass fry observed in Ridge Lake is related negatively to the number of bluegills present in the lake, and in some years all of the bass fry were eliminated by the bluegills. The latter condition has been shown to exist in some southern ponds (Swingle and Smith 1943).

In Flora Lake, there has been a decided yearly rise in the number of bass between 130 and 300 millimeters (5.1 - 11.8 in.) in length since 1952 (table 1). The estimated total weight in this group at the time of population estimation in 1952 to 1956 was 49.8, 22.8, 30.7, 65.5, and 81.0 pounds, respectively. After 1952, it was almost impossible to catch largemouth bass over 300 millimeters (11.8 in.) with fyke nets. For this reason

Table 11. Summary of the numbers and lengths in inches of largemouth bass taken from Flora Lake, Wisconsin, by anglers during the years 1952 - 1955

Period	1952		1953		1954		1955	
	No.	Ave. length	No.	Ave. length	No.	Ave. length	No.	Ave. length
6/20-7/4		?	12	14.4	3	14.5	5	15.8
7/5 -7/19		?	2	13.0	7	14.9	19	15.2
7/20-8/4		?	3	15.0	21	14.5	16	13.8
8/5 -8/19	1	13.0	1	12.0	11	15.1	20	15.2
8/20-9/4	16	15.1	10	15.6	13	15.4	29	15.0
9/5 -9/19	5	13.7			3	16.5	1	12.0
9/20-10/4							1	12.0
Total	22	14.7	28	14.7	58	15.0	91	14.9
Est. wt. (lbs.)		33.9		43.2		93.2		143.3

and also because bass under 130 millimeters (5.1 in.) were subject to a possibly higher mortality after marking, the number and weight of fish within these limits was used as an index of the magnitude of the total population.

During the first summer of the experiment, an estimation of bass over 300 millimeters (11.8 in.) was made. An analysis indicated a population of 235 fish which weighed 333.6 pounds or 87.0 percent of the total weight of bass over 130 millimeters (5.1 in.). If this same relationship is maintained through 1956, the total weight will have risen to 623.6 pounds (6.1 pounds per acre). In 1952 and 1956, the bass constituted 7.3 percent and 26.3 percent, respectively, of the total weight of all species; however, this striking increase is partially the result of a reduction in the total weight of all species per acre from 51.4 pounds in 1952 to 23.2 pounds in 1956.

The net change in the total weight of bass is a measure of the increase or decrease in the standing crop after losses from angling and natural mortality have taken place. The greatest change occurred between 1954 and 1955, namely a 375-pound addition (table 12). Presumably, the removal efforts had their most pronounced effect on the growth of the population during the growing season of 1954, two years after their initiation. Up until 1954, 30.5 pounds per acre had been removed, and in 1954, 18.7 pounds per acre were removed.

Bluegills, pumpkinseeds, and bluegill x pumpkinseed hybrids

The growth of bluegills prior to the onset of netting in 1952 was very slow, with annual increments being less than one inch. Some indication of their stunted condition can be had by comparing their average length at a given age, say five, with the corresponding length of the

Table 12. Changes in the estimated total weight in pounds of largemouth bass in Flora Lake, Wisconsin, during 1952 - 1956

Year	130 - 300 mm. 5.1 - 11.8 in.	Over 300 mm. 11.8 in.	Total	Net change	Removed by anglers
1952	49.8	333.6	383.4		33.9 (?)
1953	22.8	152.8	175.6	- 173.9	43.2
1954	30.7	205.5	236.2	+ 103.8	93.2
1955	65.5	452.5	518.0	+ 375.0	145.3
1956	81.0	542.6	623.6	+ 250.9	

bluegills in other areas. Kuehn (1949) gives an average of 7.1 inches for fish from Minnesota lakes, whereas those from Flora Lake were only 4.9 inches (table 13). Specimens from Third Sister Lake, Michigan, averaged 7.4 inches (Brown and Ball 1943), while bluegills taken from Onized Lake, Illinois, 500 miles to the south, already had reached 7.4 inches at age four (Bennett 1945).

Agreement between actual and estimated, mean, calculated lengths is excellent (table 7); consequently, the polynomial provides a good fit to the length-age data. Examination of the calculated total lengths after 1952 shows that a definite increase is not apparent until 1956, when all year classes except 1955 are higher than if a normal fluctuation had occurred (table 14 and figure 4). Even though members of the 1954 year class were below expectation as yearlings, they reached a greater length as two-year olds than any like-aged group in the past. The increase in the two- and the three-year olds was of high significance, since these fish made up 75.4 and 23.3 percent, respectively, of the total catchable population in 1956.

Bluegills are dominant among the three sunfishes considered here. Samples netted in 1953 and 1956 yielded the following composition expressed as percentages.

	Bluegill	Pumpkinseed	Hybrid
1953	88.5	4.5	7.0
1956	86.0	0.6	13.4

The increase in the population of bluegills between 1955 and 1956 (table 1) was the result of the recruitment of a large 1954 year class which previously had been unavailable to the nets. It would seem that the lower density of the population has enabled a higher percentage of the bluegill-hatch to survive. Swingle and Smith (1943) claim that

Table 13. Total length (mm.) of Flora Lake bluegills, pumpkinseeds, and bluegill x pumpkinseed hybrids at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with appropriate confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
Bluegills				
1	876	52.9	52.6	51.2 - 54.0
2	836	72.2	72.0	71.2 - 72.8
3	772	88.2	90.3	89.9 - 90.7
4	387	110.0	107.4	106.5 - 108.3
5	269	123.9	123.0	121.0 - 125.0
6	131	137.6	137.5	134.4 - 140.6
7	73	148.8	150.6	146.2 - 155.0
8	32	165.1	162.5	156.7 - 168.3
9	5	169.4	173.1	165.8 - 180.4
10	2	175.5	182.5	173.5 - 191.5
Pumpkinseeds				
1	84	53.6	53.3	43.7 - 62.9
2	84	79.2	79.9	75.7 - 84.1
3	70	105.7	104.8	102.0 - 107.6
4	50	127.6	128.2	117.5 - 138.9
5	20	150.6	150.0	130.1 - 169.9
6	1	171.0	170.3	140.0 - 200.6
Bluegill x pumpkinseed hybrids				
1	152	53.1	52.5	44.7 - 60.3
2	146	75.7	76.5	72.7 - 80.3
3	140	98.8	99.3	97.6 - 101.0
4	99	121.5	121.0	113.4 - 128.6
5	39	143.8	141.5	126.9 - 156.1
6	7	153.9	160.9	138.4 - 183.4
7	2	173.0	179.1	147.7 - 210.5

Table 14. Calculated total lengths (mm.) at annuli formed in successive years by each year class of bluegills taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change indicated by o.

	Year class													
Year	'42	'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55
1943	50 2*													
1944	68 2	52 3												
1945	88 2	68 3	52 27											
1946	104 2	86 3	70 27	54 41										
1947	118 2	103 3	86 27	74 41	53 58									
1948	133 2	117 3	103 27	92 41	73 58	53 158								
1949	145 2	132 3	119 27	109 41	91 58	77 158	54 98							
1950	156 2	141 3	133 27	125 41	109 58	97 158	77 98	52 585						
1951	168 2	151 3	145 27	139 41	125 58	112 158	95 98	69 385	53 64					
1952	176 2	164 3	165 27	152 41	139 58	124 158	110 98	82 385	73 64	57 40				
1953	184 1	168⁻ 1	168° 7	160° 12	151° 29	135° 100	123° 61	99⁻ 370	91⁺ 65	77⁺ 39	51⁻ 73			
1954	193 1		182° 3	170° 1	159° 7	153° 52	140° 23	120⁻ 239	104⁻ 12	88⁻ 20	72° 67	47⁻ 174		
1955						158° 3	151° 7	137° 50	124° 8	112⁺ 12	96⁺ 52	72° 174	48⁻ 309	
1956							170⁺ 1	165⁺ 1	160⁺ 1		137⁺ 1	107⁺ 72	80⁺ 235	50⁻ 20

* Number of fish

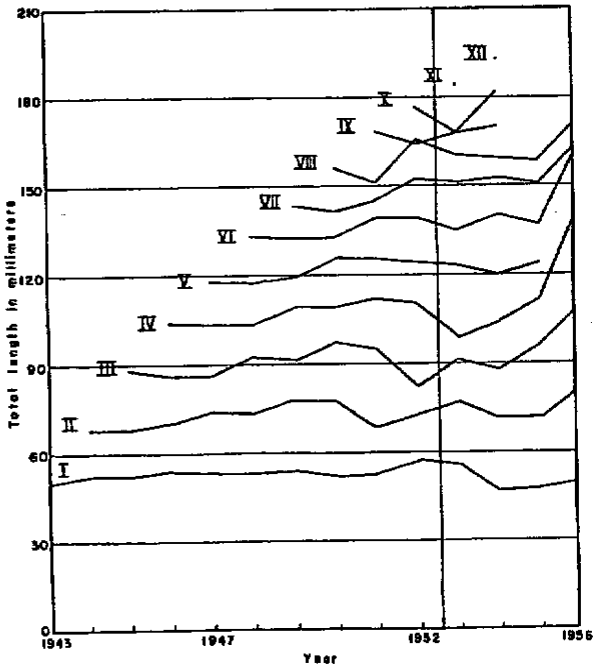

Figure 4. Fluctuations in the mean, calculated total lengths of Flora Lake bluegills in each age group

bluegills, when overpopulated, will eat many or all of their own eggs. The thinning process in Flora Lake apparently has reduced the numbers to a point where cannibalism is of no consequence, and a dominant year class erupted.

Although the bluegills captured in 1956 had shown an increase in rate of linear growth, they were considerably thinner than those in the 1952 sample (table 15). The difference between the adjusted logarithmic means may be explained in part by the fact that the average length of fish in 1956 was less than in 1952, and it is often true that there is a normal difference between small and large individuals (Beckman 1948).

Analysis of the sexual composition of the 1956 sample yielded a ratio of 104 males for every 100 females, with females predominating above age two. The growth rates of the two sexes belonging to recent year classes are nearly identical (table 16).

Lee's phenomenon could not be identified positively in any of the year classes of bluegills, pumpkinseeds, or hybrids, except possibly in the 1949 year class of bluegills (table 17).

Pumpkinseeds grew at a faster rate before 1952 than did the bluegills or hybrids (table 13). Carbine and Applegate (1948) described a similar occurrence in Deep Lake, Michigan, from which the entire population was removed by poisoning. In their study, bluegills were found to grow faster than the other two, in contrast with the situation here. Hubbs and Hubbs (1931, 1933) have observed that some hybrid centrarchids outgrow both of the parent species in tanks under laboratory conditions.

In Flora Lake, pumpkinseeds belonging to the 1953 year class increased significantly in linear rate of growth during their second and

Table 15. Covariance analysis of the natural logarithms of weights (g.) and total lengths (mm.) of bluegills, pumpkinseeds, and bluegill x pumpkinseed hybrids taken from Flora Lake, Wisconsin, in 1952 and 1956

Bluegills

Year	Adjusted mean weight	n	Log a	Slope
1952	3.22555	191	-10.95669	2.98833
1956	3.04166	191	-12.06153	3.18268

Source	Errors of estimate d.f.	Sum of squares	Mean square
Ave. within years	379	5.31642	
Deviations from ind. year regressions	378	5.22145	0.01386
Diff. between slopes	1		0.09497**
Diff. between adjusted means	1		1.61777**

Pumpkinseeds

Year	Adjusted mean weight	n	Log a	Slope
1952	3.89496	17	-11.49256	3.12343
1956	4.02139	17	-25.05247	5.90165

Source	Errors of estimate d.f.	Sum of squares	Mean square
Ave. within years	31	1.04378	
Deviations from ind. year regressions	30	0.54622	0.01821
Diff. between slopes	1		0.49756**
Diff. between adjusted means	1		0.12095*

Bluegill x pumpkinseed hybrids

Year	Adjusted mean weight	n	Log a	Slope
1952	3.46265	71	-11.76449	3.17696
1956	3.46572	71	-12.91231	3.41708

Source	Errors of estimate d.f.	Sum of squares	Mean square
Ave. within years	139	1.51422	
Deviations from ind. year regressions	138	1.45877	0.01057
Diff. between slopes	1		0.05545*
Diff. between adjusted means	1		0.00005

Table 16. Calculated total length at each annulus for male and female bluegills of recent year classes netted from Flora Lake, Wisconsin, in 1956

Year class	No. of fish	Sex	Ave. length at capture (mm.)	Ave. weight at capture (g.)	Length at annulus I	II	III
1955	5	Male	58	2.8	55		
	5	Female	54	1.6	51		
1954	130	Male	88	9.0	48	80	
	104	Female	88	9.2	48	80	
1953	28	Male	117	22.1	47	72	108
	44	Female	115	21.3	47	73	107

Table 17. Calculated total length at each annulus of the 1949 year class of bluegills collected from Flora Lake in 1952 - 1956 with sexes combined

		Length (mm.) at annulus						
Year	n	I	II	III	IV	V	VI	VII
1952	15	60	81	97				
1953	131	54	70	83	100			
1954	189	51	67	80	98	120		
1955	49	55	69	82	98	118	136	
1956	1	56	72	91	110	129	151	163

third years of life. Generally, however, there was a decrease in the growth of the older fish netted before 1956 and little or no change in the younger fish (table 18, figure 5). Pumpkinseeds in 1956 had a distinct advantage in adjusted mean weight when compared with the 1952 specimens (table 15). Although no difference between the rates of linear growth by sex could be detected, females were slightly heavier than males at a given length.

Attention should be called to the marked reduction in the percentages listed above of pumpkinseeds taken in 1953 and in 1956. During the latter year, only 17 pumpkinseeds were among the 3027 members of the triple combination removed. Of these, one was two years old, 15 were three years old, and one was four years old. Could this small population have become predaceous on the numerous young of their near relatives, thereby moving from a normal last to first place in growth among the three?

The theoretical pre-treatment growth curve of the bluegill x pumpkinseed hybrids was midway between those of the parents (tables 7 and 13). Important gains in the rate of linear growth were registered by the 1951 year class in 1954, by the 1953 year class in 1955 and in 1956, and by the 1954 year class as of age two (table 19, figure 6). In contrast with the parent species, hybrid females of recent year classes apparently grew faster linearly than did the males (table 20).

The adjusted mean of the logarithmic weights in 1952 did not differ significantly from that in 1956; however, the slope of the 1956 regression was much higher than the slope in 1952 (table 15).

As shown earlier, a decided increase has occurred in the relative number of hybrids present among their parents. Ripe male and female

Table 18. Calculated total lengths (mm.) at annuli formed in successive years by each year class of pumpkinseeds taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change is indicated by o.

	Year class							
Year	'45	'47	'48	'49	'50	'52	'53	'54
1946	45 1*							
1947	62 1							
1948	93 1	52 19						
1949	119 1	80 19	52 30					
1950	142 1	108 19	80 30	56 20				
1951	171 1	131 19	106 30	81 20	56 14			
1952	181 1	151 19	126 30	104 20	76 14			
1953			129^{-} 1	108^{-} 2	94^{-} 14	53^{o} 1		
1954			136^{o} 1	121^{-} 2	110^{-} 11	77^{o} 1	54^{o} 19	
1955					126^{-} 1	101^{-} 1	90^{+} 19	53^{o} 1
1956						138^{o} 1	129^{+} 15	95^{+} 1

* Number of fish

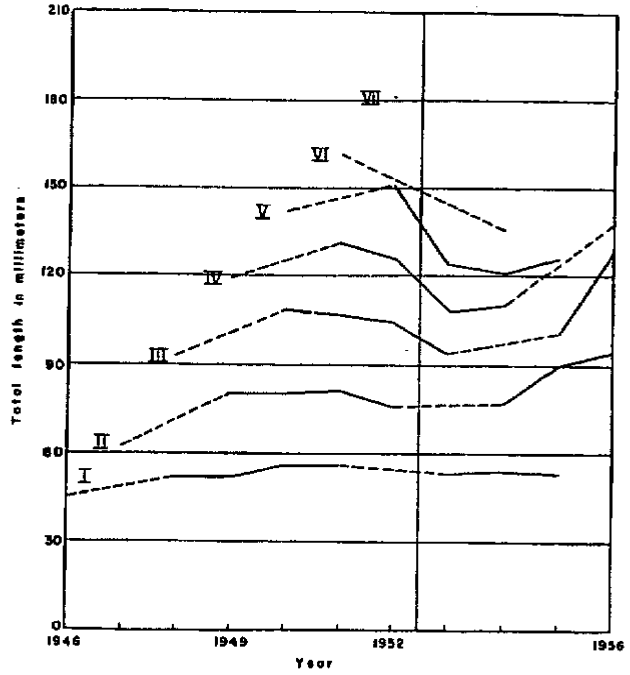

Figure 5. Fluctuations in the mean, calculated total lengths of Flora Lake pumpkinseeds in each age group

Table 19. Calculated total lengths (mm.) at annuli formed in successive years by each year class of bluegill x pumpkinseed hybrids taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change is indicated by o.

	Year class										
Year	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55
1946	59 2*										
1947	88 2	57 5									
1948	113 2	81 5	54 32								
1949	136 2	105 5	78 32	53 60							
1950	153 2	121 5	105 32	77 60	53 41						
1951	164 2	137 5	127 32	100 60	73 41	48 6					
1952	173 2	150 5	144 32	118 60	91 41	62 6	52 6				
1953		156° 3	144° 8	135° 27	107⁻ 31	83⁻ 6	80° 6	49° 26			
1954		163 1	161° 6	154° 16	126⁻ 22	100⁻ 5	102⁺ 5	73° 26	53° 112		
1955				151° 1	144° 4		125° 4	97⁻ 18	84⁺ 87	49° 82	
1956					156° 5			122° 10	124⁺ 19	82⁺ 64	57° 4

* Number of fish

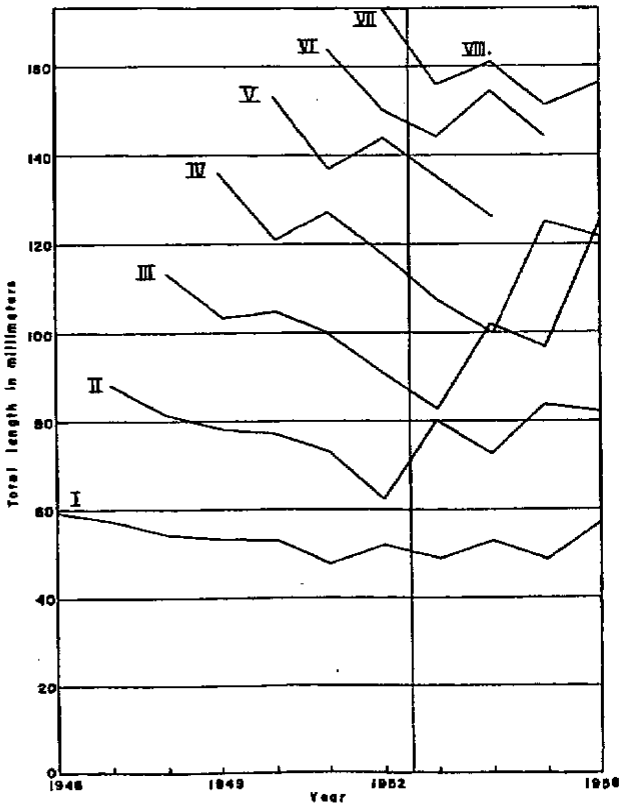

Figure 6. Fluctuations in the mean, calculated total lengths of Flora Lake bluegill x pumpkinseed hybrids in each age group

Table 20. Calculated total length at each annulus for male and female bluegill x pumpkinseed hybrids of recent year classes netted from Flora Lake, Wisconsin, in 1956

Year class	No. of fish	Sex	Ave. length at capture (mm.)	Ave. weight at capture (g.)	Length at annulus I	II	III	IV
1954	48	Male	91	12.8	48	81		
	16	Female	94	14.4	50	85		
1953	4	Male	124	35.2	47	73	114	
	15	Female	130	42.1	53	85	126	
1952	2	Male	112	25.5	48	74	86	108
	8	Female	128	41.0	46	66	95	125

hybrids were caught in 1956, suggesting that this rise, along with the drop in the number of pumpkinseeds, may be explained on the basis of successful reproduction by the hybrids and the inability of the rare pumpkinseeds to find mates of their own species.

It should be emphasized that significant increases in the rate of linear growth occurred in the 1953 and 1954 year classes of bluegills, pumpkinseeds, and hybrids, thereby indicating that the three react similarly to the stimulus provided by the thinning operations.

Rock bass

The earliest recorded study on the growth of rock bass in lakes of the immediate vacinity (Trout and Muskellunge) was that of Wright (1929). He used direct proportionality between body and scale lengths, and as a result, his growth records are not directly comparable with those of rock bass in Flora Lake. Hile (1941, 1942) analyzed the growth rates of rock bass in Silver, Allequash, and Nebish Lakes, in addition to the two lakes mentioned above. His attempts to relate fluctuations in growth to air temperature and amount of precipitation met with some success. Although his data are presented in terms of calculated standard length at each annulus, the rate of growth was quite similar to that of Flora Lake rock bass.

It has been known for some time that rock bass respond favorably to a severe reduction in population density (Beckman 1941, 1943). Significant deviations from the estimated pre-treatment means (table 21) appeared in over half of the year classes by 1954. In 1956, three-year old fish were 20 millimeters longer than the upper limit of the normal expected value, and four-year old fish averaged 25 millimeters above the upper bound (table 22, figure 7). Even though the fish showed an

Table 21. Total length (mm.) of Flora Lake rock bass at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
1	160	56.4	54.7	49.9 - 59.5
2	157	75.0	76.3	73.2 - 79.4
3	147	95.3	97.4	96.3 - 98.5
4	109	118.4	118.1	115.8 - 120.4
5	85	139.0	138.5	134.0 - 143.0
6	32	164.6	158.4	150.9 - 165.9
7	21	182.2	177.8	166.9 - 188.7
8	11	194.3	197.0	182.4 - 211.6
9	6	208.3	215.7	197.0 - 234.4
10	3	220.7	234.0	210.9 - 257.1

Table 22. Calculated total lengths (mm.) at annuli formed in successive years by each year class of rock bass taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change is indicated by o.

	Year class													
Year	'42	'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55
1943	61 3*													
1944	83 3	57 3												
1945	99 3	74 3	57 5											
1946	119 3	92 3	77 5	57 10										
1947	137 3	108 3	97 5	75 10	57 11									
1948	154 3	127 3	115 5	97 10	78 11	56 51								
1949	171 3	150 3	138 5	120 10	101 11	76 51	57 26							
1950	189 3	173 3	161 5	143 10	123 11	97 51	76 26	56 38						
1951	208 3	192 3	181 5	166 10	148 11	118 51	99 26	72 38	55 10					
1952	221 3	209 3	199 5	189 10	172 11	137 51	119 26	88 38	71 10	52 3				
1953			189⁻ 1	212⁺ 2	204⁺ 2	157° 21	139° 16	107⁻ 35	91⁻ 10	72⁻ 3	56° 52			
1954			210⁻ 1	234° 2	222⁺ 1	178° 11	172⁺ 12	150⁺ 28	125⁺ 8	99⁺ 3	79° 52	56° 62		
1955						172⁻ 1	189⁺ 2	167⁺ 4	156⁺ 5	114⁻ 1	109⁺ 20	81⁺ 50	52° 32	
1956							209° 1	193⁺ 3	171⁺ 2	140° 1	146⁺ 4	119⁺ 23	76° 17	52° 1

* Number of fish

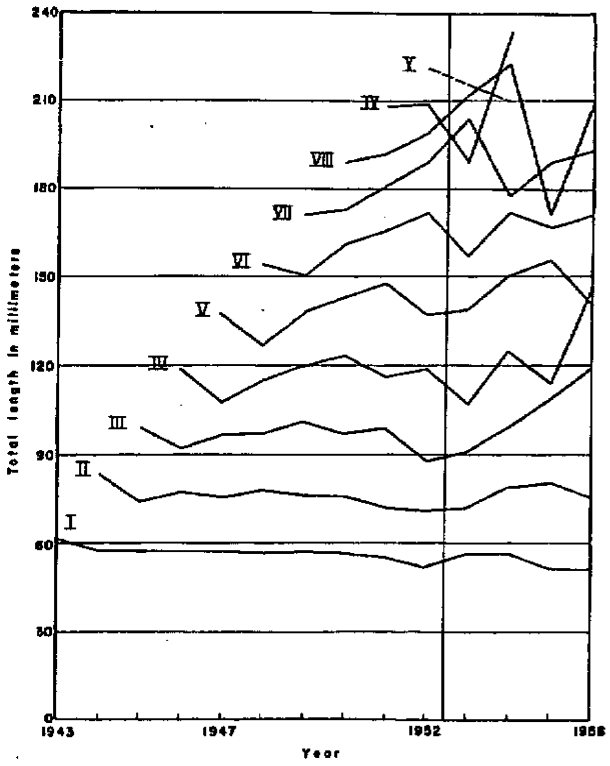

Figure 7. Fluctuations in the mean, calculated total lengths of Flora Lake rock bass in each age group

increase in linear rate of growth, a comparison of the adjusted mean logarithmic weights yielded no real difference between individuals collected in 1952 and individuals collected in 1956 (table 23).

The relatively small numbers of rock bass in Flora Lake are highly piscivorous, and apparently do not associate with other species except to feed. Why these fish respond so quickly and positively in their rate of growth to a lower total population density is an open question which bears need of future investigation. In addition, analysis of the growth-response is complicated by the fact that there was a general increase in the numbers of rock bass from 1952 through 1955 (table 1).

Sample sizes were usually insufficient to demonstrate the occurrence of Lee's phenomenon, although some evidence was found among members of the 1947 year class (table 24). As was the case with all species, no pre-treatment sex-composition data were obtained by Johnson, et al.; consequently, comparisons could not be made. In 1956, little difference was noted between the growth rate of sexes during the first three years of life; however, Hile's studies established that males grow distinctly better than females in later years.

Yellow perch

The perch in Flora Lake ranked second in numbers during most of the period 1952 - 1956 (tables 1 and 4), and they grow much more slowly than do perch in neighboring Hobish, Weber, and Silver Lakes (Solmeberger op. cit.) and in Curtis Lake (Churchill op. cit.). Their computed growth curve was the only one having a positive coefficient for the squared term of the polynomial (table 7), that is, the curve was concave upwards. This may indicate that the few larger perch have

Table 23. Covariance analysis of natural logarithms of weights (g.) and total lengths (mm.) of rock bass taken from Flora Lake, Wisconsin, in 1952 and 1956

Year	Adjusted mean weight	n	Log a	Slope
1952	3.81370	52	-11.24900	3.05464
1956	3.81638	52	- 8.50133	2.49797

Errors of estimate

Source	d.f.	Sum of squares	Mean square
Ave. within years	101	8.10311	
Deviations from ind. year regressions	100	7.51544	0.07515
Diff. between slopes	1		0.58767**
Diff. between adjusted means	1		0.00774

Table 24. Calculated total length at each annulus of the 1947 year class of rock bass collected from Flora Lake in 1952 - 1955 with sexes combined

		Length (mm.) at annulus							
Year	n	I	II	III	IV	V	VI	VII	VIII
1952	30	57	76	98	119	138			
1953	10	57	78	101	123	144	169		
1954	10	55	72	92	111	130	147	160	
1955	1	54	70	88	104	116	127	138	172

reached a length where they were able to prey upon their numerous kin, thereby increasing their rate of growth. Estimated means are very near to the actual values (table 25), except for age six where there is a discrepancy of 10.5 millimeters. After examining the mean calculated lengths for growth following 1952 (table 26, figure 8), one necessarily concludes that there has been no increase in the rate of growth, but rather a decrease. More than likely, this is due to the presence of large, recent year classes, while the total perch population has remained relatively stable (table 1). Furthermore, individuals are thinner now than they were in 1952 (table 27).

Subsequent to severe winterkill, the growth of perch in Duck Lake and Green Lake, Michigan, rose to 61 and 35 percent, respectively, above the normal mean (Beckman 1950). This suggests that the perch in Flora Lake may have grown faster if more of them would have been removed, that is, more than 40 percent of the standing crop (table 5).

Schneberger (op. cit.) concluded that male and female perch grow at approximately the same rate. The same conclusion has been reached for Flora Lake perch, at least among the younger individuals (table 28). Males were scarce among the older age groups, as was also noted by Eschmeyer (1937).

White suckers

The pre-treatment growth rate of the white suckers in Flora Lake (table 29) was considerably better than the growth rate of suckers in nearby Muskellunge Lake (Spoor 1939), with Flora Lake fish attaining a length of 148 millimeters in one year. After 1952, the suckers, which ranked second in total weight (table 5), began to grow more rapidly (table 30, figure 9). This increase is of considerable interest,

Table 25. Total length (mm.) of Flora Lake yellow perch at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with 95 percent confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
1	212	85.5	85.9	79.8 - 88.0
2	154	109.4	107.8	106.9 - 108.7
3	59	131.2	133.2	127.6 - 138.8
4	19	158.9	160.2	148.3 - 172.1
5	8	188.5	183.6	169.4 - 207.8
6	2	229.0	216.5	191.0 - 246.0
7	1	249.0	250.0	233.2 - 286.8

Table 26. Calculated total lengths (mm.) at annuli formed in successive years by each year class of yellow perch taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change is indicated by o.

	Year class										
Year	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55
1946	107 1*										
1947	136 1	89 1									
1948	156 1	112 1	82 6								
1949	183 1	145 1	110 6	82 11							
1950	212 1	168 1	132 6	108 11	83 40						
1951	238 1	196 1	155 6	134 11	108 40	84 95					
1952	249 1	220 1	183 6	158 11	129 40	110 95	82 58				
1953		243° 1	208° 5	179° 7	151° 24	131° 62	109+ 51	84° 61			
1954		261 1	228° 4	201° 3	178° 7	148- 19	125- 23	109+ 51	79- 151		
1955			204 1		174- 2	166- 2	151° 2	124- 23	101- 128	77- 11	
1956							173° 2	142- 9	122- 70	108° 11	83° 21

* Number of fish

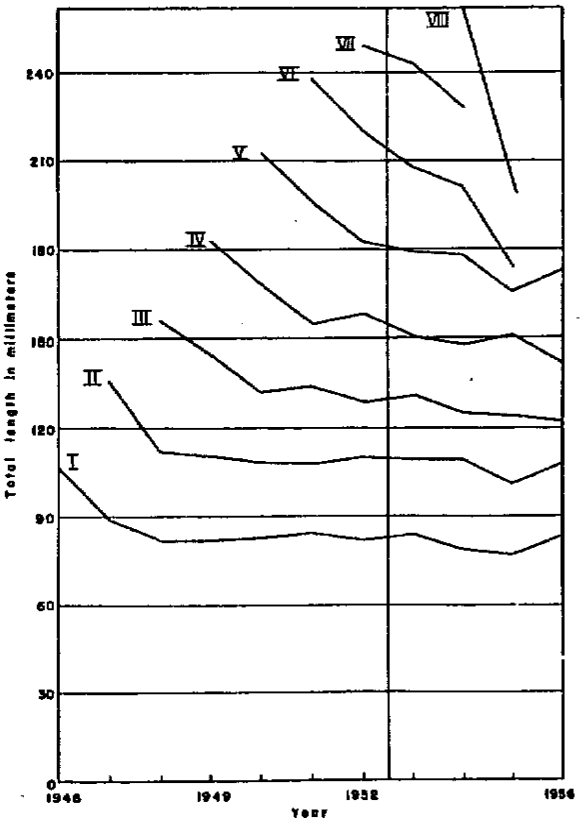

Figure 8. Fluctuations in the mean, calculated total lengths of Flora Lake yellow perch in each age group

Table 27. Covariance analysis of natural logarithms of weights (g.) and total lengths (mm.) of yellow perch taken from Flora Lake, Wisconsin, in 1952 and 1956

Year	Adjusted mean weight	n	Log a	Slope
1952	2.77284	62	-12.28443	3.12003
1956	2.69485	62	-10.62066	2.75912

Errors of estimate

Source	d.f.	Sum of squares	Mean square
Ave. within years	121	1.88171	
Deviations from ind. year regressions	120	1.77559	0.01480
Diff. between slopes	1		0.10612**
Diff. between adjusted means	1		0.13648**

Table 28. Calculated total length at each annulus for male and female yellow perch of recent year classes netted from Flora Lake, Wisconsin, in 1956

Year class	No. of fish	Sex	Ave. length at capture (mm.)	Ave. weight at capture (g.)	Length at annulus I	II	III
1955	12	Male	88	5.9	83		
	9	Female	88	5.9	83		
1954	7	Male	110	9.7	75	108	
	4	Female	112	10.0	80	110	
1953	28	Male	122	14.4	81	101	120
	42	Female	127	15.8	79	101	123

Table 29. Total length (mm.) of Flora Lake white suckers at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with 95 percent confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
1	130	147.9	147.8	128.0 - 167.6
2	78	224.6	224.1	220.3 - 227.9
3	40	289.6	293.1	264.0 - 322.2
4	12	366.0	355.1	293.6 - 416.6
5	5	402.0	410.0	310.6 - 509.4

Table 30. Calculated total lengths (mm.) at annuli formed in successive years by each year class of white suckers taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are indicated by + or - and no change is indicated by o.

	Year class								
Year	'47	'48	'49	'50	'51	'52	'53	'54	'55
1948	161 5*								
1949	244 5	170 7							
1950	304 5	246 7	126 28						
1951	361 5	314 7	206 28	162 38					
1952	402 5	370 7	281 28	232 38	145 52				
1953	442 2	435° 1	378° 3	330+ 10	244+ 42	178+ 23			
1954			426° 2	439+ 1	324+ 3	286+ 16	148° 87		
1955					364° 1	357+ 4	238+ 54	162° 120	
1956						455+ 1	340+ 12	274+ 67	194+ 20

* Number of fish

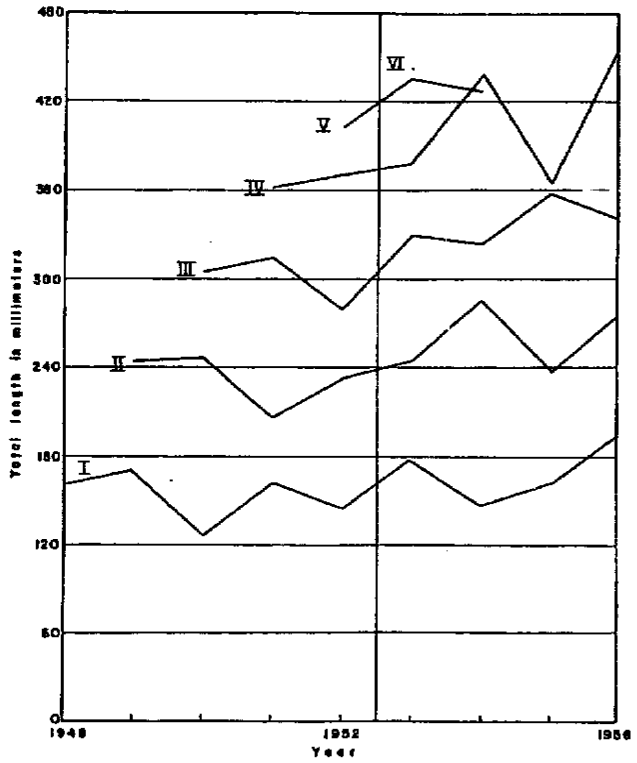

Figure 9. Fluctuations in the mean, calculated total lengths of Flora Lake white suckers in each age group

since the fish were not stunted before the start of removal operations, but still had an inherent ability to grow faster. In addition, as with the rock bass, there was an increase in numbers to a peak in 1955 (table 1). In contrast with the rock bass, however, the suckers taken in 1956 were "fatter" than individuals netted in 1952 (table 31).

The separation of calculated lengths according to sex failed to show a real difference between males and females (table 32), at least through age three.

Golden shiners

The relatively few golden shiners available for the computation of a theoretical pre-1952 growth curve caused very wide confidence intervals (table 33). As a consequence, no significant change in the rate of linear growth could be detected (table 34, figure 10); however, fish sampled in 1956 were lighter than those taken in 1952 (table 35).

Although the population estimates give large numbers for golden shiners (table 1), their low frequency of capture in fyke nets lends support to the belief that the high estimates were the result of a greater mortality among the marked individuals, possibly owing to handling. It is questionable whether more than 2000 catchable golden shiners have been present in Flora Lake at any time during the past five years.

Table 31. Covariance analysis of natural logarithms of weights (g.) and total lengths (mm.) of white suckers from Flora Lake, Wisconsin, in 1952 and 1956

Year	Adjusted mean weight	n	Log a	Slope
1952	5.55440	73	-11.01745	2.91365
1956	5.65338	73	-11.65834	3.04022

Errors of estimate

Source	d.f.	Sum of squares	Mean square
Ave. within years	143	0.65018	
Deviations from ind. year regressions	142	0.61013	0.00430
Diff. between slopes	1		0.02005*
Diff. between adjusted means	1		0.34952**

Table 32. Calculated total length (mm.) at each annulus for male and female white suckers of recent year classes netted from Flora Lake, Wisconsin, in 1956

Year class	No. of fish	Sex	Ave. length at capture (mm.)	Ave. weight at capture (g.)	Length at annulus I	II	III
1955	15	Male	221	122.9	196		
	5	Female	215	111.0	190		
1954	51	Male	296	292.6	159	274	
	16	Female	298	306.6	157	273	
1953	2	Male	354	514.5	136	230	330
	10	Female	361	520.3	137	220	342

Table 33. Total length (mm.) of Flora Lake golden shiners at each annulus formed in or before 1952 as estimated from the second-degree equation given in table 7, with 95 percent confidence intervals

Age	n	Actual mean	Estimated mean	95% confidence int.
1	22	89.6	90.3	34.5 - 146.1
2	18	126.9	125.4	106.6 - 144.2
3	8	158.5	160.0	47.2 - 272.8

Table 34. Calculated total lengths (mm.) at annuli formed in successive years by each year class of golden shiners taken from Flora Lake, Wisconsin, in 1952 - 1956 with sexes combined; significant changes in growth rate after 1952 are identified by + or - and no change is indicated by o.

Year	Year class '49	'50	'51	'52	'53	'54
1950	84 8*					
1951	130 8	92 10				
1952	159 8	125 10	91 4			
1953		155° 10	130° 4	94° 67		
1954		170 3	152° 4	124° 49	88° 106	
1955		178 2	168 3	142° 32	118° 66	88° 3
1956				167 6	152° 10	

* Number of fish

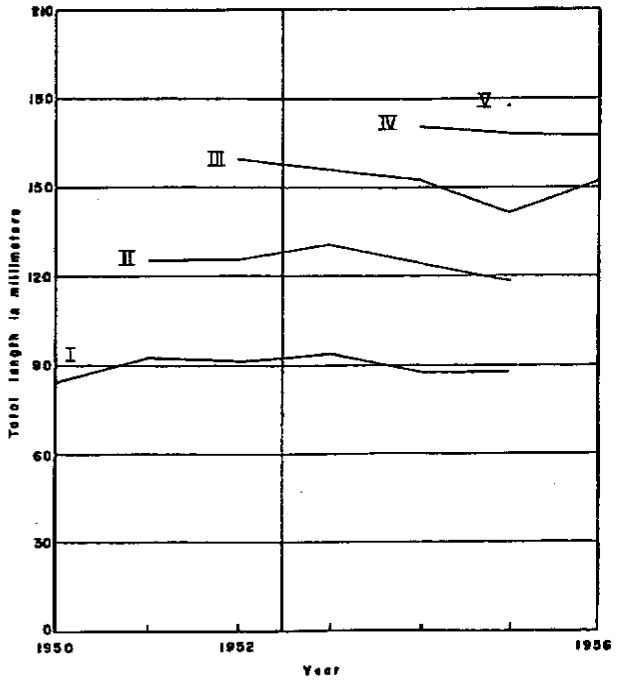

Figure 10. Fluctuations in the mean, calculated total lengths of Flora Lake golden shiners in each age group

Table 33. Covariance analysis of natural logarithms of weights (g.) and total lengths (mm.) of golden shiners taken from Flora Lake, Wisconsin, in 1952 and 1956

Year	Adjusted mean weight	n	Log a	Slope
1952	3.98394	8	- 4.04647	1.56825
1956	3.78428	8	-13.54188	3.34461

Errors of estimate

Source	d.f.	Sum of squares	Mean square
Ave. within years	13	0.07478	
Deviations from ind. year regressions	12	0.04285	0.00357
Diff. between slopes	1		0.03193*
Diff. between adjusted means	1		0.07177**

SIGNIFICANCE

The rather inconsistant growth-responses observed here for different species, presumably resulting from the reduction in the density of the population, is rather remarkable. For example, although the rock bass and the yellow perch were thinned similarly (table 5), the growth rate of the former changed favorably while that of the latter decreased. The largemouth bass, on the other hand, apparently did not benefit from the removal operations except for a slight increase in weight at a given length.

At the present time, I do not know of any thorough thinning studies which have shown definitely that the growth rate of the largemouth bass is density dependent, but one intuitively feels that it must be. In July 1954, largemouth bass from Dadek Lake, which were stunted when compared with those from Flora Lake (tables 9 and 36), were transferred to Corrine Lake, Wisconsin. The latter body of water had a bass-density of less than one-fourth of that in Dadek Lake. A preliminary analysis of data collected in September 1954 and June 1956 shows that an initial spurt in growth occurred among one- and two-year old fish during the same summer as the stocking; however, the increased rate of growth soon subsided. As a result, the bass were no longer in 1956 than would have been expected had they remained in Dadek Lake (table 36, figure 11). Before one is able to draw a valid conclusion here, it is necessary to investigate the effect of reducing the bass population itself. Perhaps some information could be had by continuing the elimination of bass from Dadek Lake, with an eye toward evaluating the growth of the remaining bass. In spite of the fact that the bass in Dadek and Flora

Table 36. Summary of the mean calculated total lengths and annual increments in lengths of Dadek Lake largemouth bass collected in 1954, with sexes combined*

Year class	No. of fish	Calculated length at annulus							
		I	II	III	IV	V	VI	VII	VIII
1953	40	68							
1952	47	64	127						
1951	25	60	120	172					
1950	14	59	118	165	198				
1949	20	64	117	159	193	220			
1948	18	63	121	166	194	216	238		
1947	5	64	116	156	183	204	227	249	
1946	3	70	123	157	186	214	237	260	278
Grand average									
Total lengths									
Millimeters		64	122	165	193	216	236	254	278
Inches		2.5	4.8	6.5	7.6	8.5	9.3	10.0	10.9
Annual increments									
Millimeters		64	58	43	28	23	20	18	24
Inches		2.5	2.3	1.7	1.1	0.9	0.8	0.7	0.9
Number of fish		172	132	85	60	46	26	8	3

* Calculated lengths are based on a linear length-scale relationship with an intercept of 18.4 millimeters.

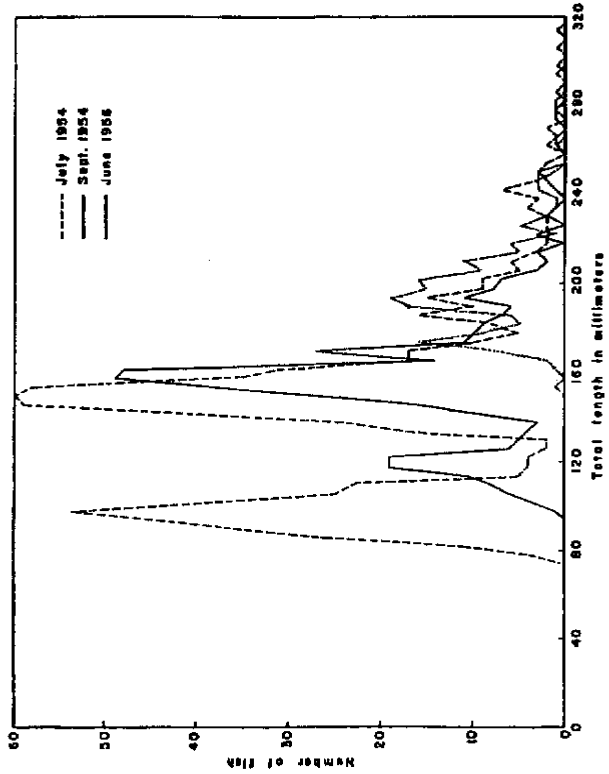

Figure 11. Length-frequency distributions of largemouth bass in Corrine Lake following treatment with rotenone, based on four-millimeter length groups

Lakes have different rates of growth, a common physiological ancestry may dictate that neither will grow faster under conditions of reduced density, and the introduction of members of this species from both lakes into another might shed some light on the possible hereditary background of the two groups.

As mentioned previously, perch in Sweden and in England (Lake Windermere) reacted differently after an intra-specific decrease in numbers; however, these contrasting results are not directly comparable because Alm (op. cit.) moved individuals to other waters while LeCren (op. cit.) described a perch population which was reduced in situ. Furthermore, in other experiments Alm was unable to secure a favorable response under conditions similar to those in Lake Windermere, but in very small lakes. The yellow perch, which is closely related to the European species, showed a positive change in growth rate subsequent to a partial winterkill of unknown relative intensity in Duck and Green Lakes, Michigan (Beckman 1950), indicating that if the perch of Flora Lake had been thinned to a greater degree, there may have been an effect opposite to that demonstrated.

As for the rock bass, these studies confirm those of other workers in that this species is nearly always the first to grow faster following a reduction in density. This result, coupled with the erratic changes exhibited by the other species involved, leads one to speculate on some possible explanations. The answer may lie in the genetics of different species, quite probably in the genic control of the hormonal complex which governs most of the bodily processes. Future studies of the type executed here might well be pointed toward an evaluation of the physiological mechanisms correlated with changing rates of growth.

It is obvious from the statistics on removal (table 5), that the

differential rates of removal play but a small role in determining what the response of a particular species will be. There is some likelihood that a careful examination of the behavior traits of different species will reveal an influence on the rate of growth after some of the co-inhabitants have been destroyed.

Competition, as defined in the very liberal sense of Nicholson (1933), may actually be the controlling factor. Larkin (1956) reviewed briefly the voluminous literature concerning the intricacies of competition between species, and made special reference to works concerning fishes. In Flora Lake, any attempt to analyze the interrelationships which affect the growth of so many species likely would prove futile, particularly since other variables known to be of some importance were not measured (e.g., food supply). It may be that future efforts may resolve the problem by identifying a density-threshhold not reached in these experiments which must be exceeded before the growth of species unaffected here is stimulated.

SUMMARY

1. Flora Lake, a 102-acre body of water in northern Wisconsin, was the site of a five-year program in which the density of fishes was reduced in an attempt to increase the growth rates of important fish species.

2. Fyke nets were utilized yearly in removing large numbers of a hybrid and six species of fish. The total quantity removed ranged up to 2481 pounds, or 52.6 percent of the catchable standing crop at the time of population estimation in the early summer.

3. Scale samples, which were collected periodically, were used in the back-calculation of the total length at each annulus according to the nomograph method. A linear function was employed for every species to describe the relationship between the radius of the anterior part of the scale and the total length of the fish.

4. A second-degree polynomial was fitted to the data on the calculated total length at each annulus formed in or before 1952, in other words, a pre-treatment growth curve was formulated as were appropriate confidence limits for the means. It was agreed that fluctuations in the mean, calculated total lengths after 1952 which fell outside of the confidence interval would be termed significant changes in the rate of growth.

5. The covariance technique was used to analyze the differences between adjusted, mean, logarithmic weights of specimens collected in 1952 and of those collected in 1956.

6. No important changes occurred in the linear growth rate of largemouth bass; however, in 1956, individuals were heavier at a given length than in 1952. In addition, the total weight of bass over 5.1 inches (130 mm.) in length increased from 3.8 to 6.1 pounds per acre, and the angling-yield

rose from 34 pounds in 1952 to 145 pounds in 1955, although the effort remained nearly constant.

7. Bluegills, pumpkinseeds, and hybrids of these two species belonging to recent year classes (1953 and 1954) responded favorably in linear rate of growth after the reduction in their numbers, but only the bluegills and pumpkinseeds were "fatter" in 1956 than in 1952. Presumably due to the virtual elimination of cannibalism, the 1954 year class was highly successful, and the catchable population erupted from a low of 3900 in 1955 to 21,600 in 1956.

8. Rock bass in Flora Lake have exhibited a marked increase in their linear growth rate, particularly by members of the 1949, 1950, 1952, and 1953 year classes, even though the total number of rock bass present reached a peak in 1955. A difference could not be demonstrated between adjusted, mean, logarithmic weights in 1952 and in 1956.

9. Yellow perch were thinner and grew more slowly after the initiation of removal operations than they did before. This is attributed to: a) no real change in the total numbers of perch during the study, and b) possible intra-year class stunting in a population currently composed primarily of young fish.

10. A relatively fast growing group of white suckers was able to respond to the lower overall density in a positive manner, in spite of a continued rise in their own numbers through 1955.

11. The golden shiners in Flora Lake did not change in linear growth rate, but as among the perch, individuals were lighter at a given length. An overestimation of their population size was thought to be due to a higher mortality of marked fish.

12. Genetic background, rates of reduction during the experiment,

and competition are discussed briefly as possible reasons for the inconsistant effects of lower population density on the growth of individuals of different species.

THE RETURN OF DISPLACED CENTRARCHIDS TO A "HOME" TERRITORY

INTRODUCTION

It was our object to study further the degree of faithfulness of "homing" in captured largemouth bass, bluegills, and pumpkinseeds after being displaced to a central release point. Other workers have observed this behavior in centrarchid fishes (Larimore 1952, Shoemaker 1952, Cooper 1953, Hasler and Wisby 1955), but more evidence is needed to determine how widespread homing is among the individuals of a population and the mechanism used by the fish in finding their way. Moreover, to learn to what extent this peculiarity of behavior influences the statistical estimation of population size in summer periods where the statistics are based upon random movement of marked fish.

In 1955, an experiment was planned to find the relationship between the proportion of fish marked at one station ("home") which were recaptured at another station and the shortest water distance from home. It must be kept in mind that one is dealing here with an untrained and undomesticated animal, hence not comparable with the "return to a loft" behavior seen in passenger pigeons. It implies, if proved to exist, the ability to orient in space without landmarks and to return to familiar territory nearby which might be recognized as learned from previous experience.

METHODS AND RESULTS

Flora Lake

Eight areas were established in Flora Lake, and combinations of two fin-clips indicated the area designated as home. The central location in the lake to which fish were displaced after capture in fyke nets is shown in figure 12, together with the mid-points of the home areas. All marked largemouth bass, bluegills, pumpkinseeds, and hybrids of the latter two were adult fish, but they could not be separated as to sex. The last three groups were considered as one, since positive identification was uncertain in rapid handling.

Recaptures were recorded for station of marking and station of recapture, and the distance between stations was measured in 10-foot units (table 37). In this lake, no effort was made to distinguish multiple recaptures and the time between successive captures. A regression analysis was performed to obtain a function which would relate the proportion mentioned above with distance. This was done in terms of natural logarithms because the use of a quadratic form did not give as good a correlation. To avoid the difficulty caused by the appearance of zeros, distance plus one and one minus the proportion were taken as variables. Regression components are summarized in table 38, and the non-logarithmic equations are graphed in figure 13. These equations give the approximate relative distribution of marked fish after release, and the area under a curve can be used to estimate the fraction of individuals marked at a given station which will be found within a certain radius of that station.

It is of interest to note that the displaced bluegills, pumpkinseeds, and hybrids returned to the site of original capture in greater propor-

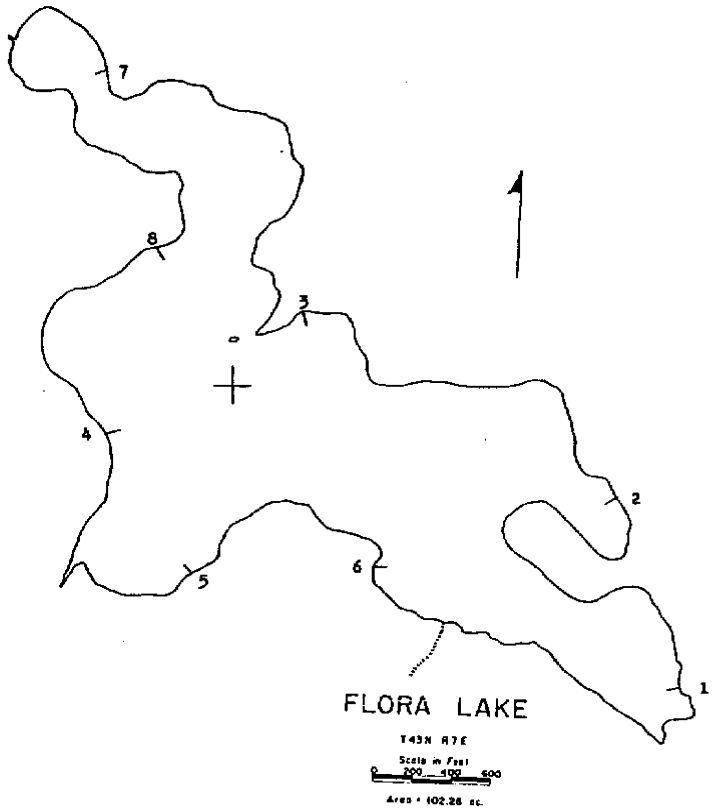

Figure 12. Map of Flora Lake showing mid-points of home areas and central release point

Table 37. Summary of the numbers of recaptured largemouth bass*, bluegills, pumpkinseeds, and hybrids** taken in Flora Lake during 1955 and the shortest water distances between stations in 10-foot units***

Marking station	Station of recapture							
	1	2	3	4	5	6	7	8
1	11*	5	4	12	3	6	3	1
	4**	1	2	2	0	2	0	0
	0***	201	284	325	298	176	456	361
2	7	21	35	22	7	9	8	4
	13	70	37	13	10	35	15	24
	201	0	189	258	235	131	366	270
3	11	27	113	60	25	33	22	23
	3	26	90	18	20	21	30	44
	284	189	0	120	152	141	194	98
4	14	8	38	111	25	16	17	39
	1	6	2	18	2	2	5	3
	325	258	120	0	80	160	217	104
5	3	7	9	16	20	12	4	7
	0	3	5	7	14	5	3	5
	298	235	152	80	0	134	282	172
6	4	5	10	9	5	15	1	3
	14	42	37	17	11	115	14	26
	176	131	141	160	134	0	302	205
7	8	5	32	33	6	20	64	32
	7	0	0	1	0	0	6	0
	456	366	194	217	282	302	0	119
8	2	8	10	24	4	5	25	19
	0	7	8	6	5	5	33	63
	361	270	98	104	172	205	119	0

Table 38. Summary of regression analyses of marked fish distribution data collected from Flora and Dadek Lakes during 1955 (natural logarithms)

Regression	Errors of estimate Sum of squares	d.f.	Intercept	Slope	r
Dadek Lake Largemouth bass	1.08462	55	- 0.45204	0.076827	0.679
Flora Lake Largemouth bass	0.38526	55	- 0.34729	0.044938	0.721
Flora Lake Bluegills Pumpkinseeds Hybrids	0.75021	55	- 0.49453	0.075142	0.780

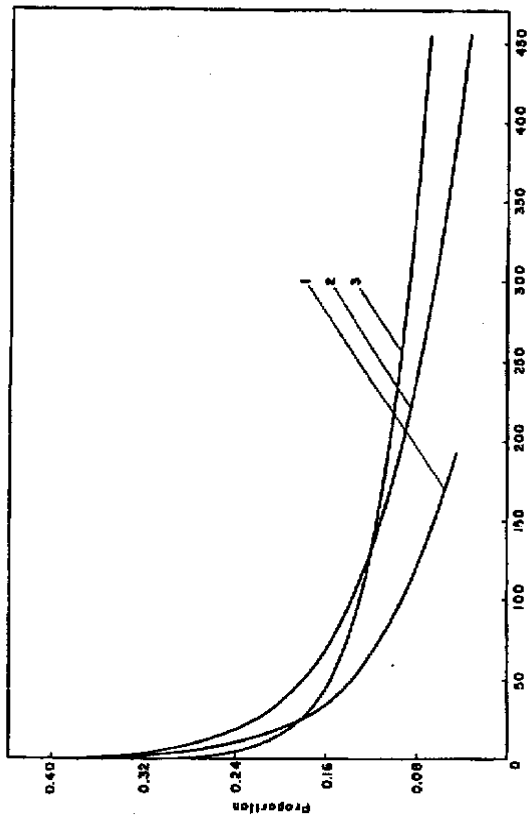

Figure 13. Theoretical relative distribution during 1955 of some marked (1) largemouth bass in Dadek Lake, (2) bluegills, pumpkinseeds, and bluegill x pumpkinseed hybrids in Flora Lake, and (3) largemouth bass in Flora Lake

tion than did the largemouth bass; 38.9 and 32.0 percent, respectively. This result establishes the fact that these fishes, like the green sunfish (Hasler and Wisby op. cit.) and the bass, will return to a "home" territory. If the return of the marked individuals were explained on the basis of random movement (roulette fashion), only about 12.5 percent would have been expected to return to the site of initial capture.

Dadek Lake

Eight permanent fyke netting stations were established in Dadek Lake, and all largemouth bass taken were marked with Petersen tags and released at the same central location (figure 14). The recaptures were treated in the same manner as those netted in Flora Lake (tables 38 and 39, figure 13), and the percentage homing was 38.9. The latter figure is the same as that of bluegills, pumpkinseeds, and hybrids in Flora Lake.

Since all fish captured were marked with numbered tags, multiple recaptures could be recognized and the length of time between marking and successive recaptures could be determined. One might assume that there would be a difference in the success of individuals in finding home after being at large for different periods between marking and initial recapture. Of 151 initially recaptured bass, 42 were caught at some point during the first week after marking, 35 during the second week, and 74 during the next nine weeks. The percentages reaching the original site were 38.1, 40.0, and 39.2, respectively; consequently no real difference is evident.

One further possibility of differential success in homing might be with respect to the direction from the point of release to the point of capture. Stations 8, 1, 2, and 3 lie in a segment of $57^{\circ}45'$ with a mean direction of $N81^{\circ}49'E$, and stations 4, 5, 6, and 7 lie in a segment

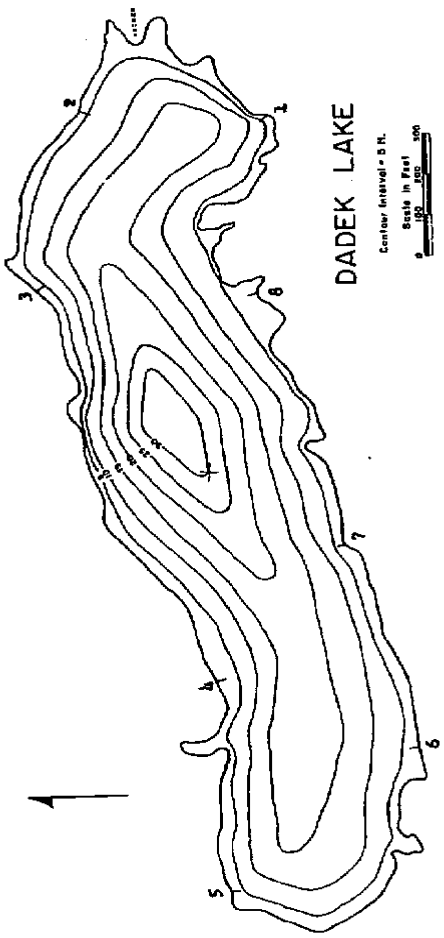

Figure 14. Map of Dadek Lake showing netting stations and central release point

Table 39. Summary of the numbers of recaptured largemouth bass* taken from Dadsk Lake during 1955 and shortest water distances between stations in 10-foot units** (including multiple recaptures)

Marking station	Station of recapture 1	2	3	4	5	6	7	8
1	1*	0	2	1	1	0	0	4
	0**	46	71	146	196	171	118	56
2	4	15	5	4	4	4	2	6
	46	0	45	144	196	176	124	62
3	3	2	19	3	2	2	3	6
	71	45	0	106	158	144	96	53
4	0	1	1	4	2	2	1	2
	146	144	106	0	51	50	46	98
5	1	0	2	2	8	10	0	2
	196	196	158	51	0	58	90	149
6	0	0	1	4	3	16	7	4
	171	176	144	50	58	0	53	119
7	0	1	0	3	0	4	3	7
	118	124	96	46	90	53	0	67
8	1	1	3	0	1	3	5	18
	56	62	53	98	149	119	67	0

of 58°15' with a mean direction of S65°W. The northeast group of recaptures (80) was 40.0 percent successful, and the southwest group (71) exhibited 38.0 percent success; again no significant difference.

SIGNIFICANCE

Examination of the data from both lakes leads one to inquire into the possibility of having two separate populations, one that homes and one that moves about at random. An analysis which excludes homing individuals confirms the plausibility of this proposal (table 40), and the means of the percentages of homing and non-homing fish in each of the lakes are presented in table 41. In every case, the homing portion is quite small; however, the question of how these individuals find home cannot be overlooked. The waters of Dadek and Flora Lakes are deeply stained, and light penetration is reduced greatly. This fact, coupled with the depth at the release point, renders unlikely the use of bottom contours as an immediate guide. Furthermore, the fish were too far from shore to utilize the treeline as a mark. Certainly, a searching process which involves the preceding methods should not be ruled out. Fish can be trained to use an artificial sun for orientation purposes (Hasler 1956), and it may be that the fish in these lakes have a "sun compass" mechanism similar to that found in homing pigeons and starlings by Kramer (1952).

In table 41, a comparison of the mean percentages of homing and non-homing individuals gives interesting information on the approximate size of the two groups. It would appear, for example, that 25 percent of the largemouth bass in Dadek Lake return home directly, whereas 75 percent either move at random or make errors enroute and are captured at another station. This points up the need for a method to determine the direction of "take off" when a fish has been displaced. The fish could be fairly well oriented toward home, an area of considerable yardage along shore, but he may be caught in one of the nets before reaching

Table 40. Analysis of errors of estimate of marked fish distribution data collected from Flora and Dadek Lakes during 1955 with home stations omitted (natural logarithms)

Source of variation	d.f.	Dadek Lake Largemouth bass SS	MS	Flora Lake Largemouth bass SS	MS	Flora Lake Sunfishes SS	MS
Dev. from mean	48	0.81054		0.35072		0.70062	
Dev. from regression	47	0.79927	0.01701	0.34715	0.00739	0.69894	0.01487
Reduction	1		0.01127		0.00357		0.00168

Table 41. Mean percentages of fish marked at one station in Flora and Dadek Lakes which did and did not "home", including multiple recaptures

Lake and species	Returning home	Mean percentage Non-homing (each of 7 sta.)	Homing segment of population
Dadek Largemouth bass	34.3	9.4	24.9
Flora Largemouth bass	28.3	10.2	18.1
Flora Bluegills Pumpkinseeds Hybrids	39.7	8.6	31.1

the exact net of initial capture or he may avoid nets owing to an unpleasant experience. We are now attempting to solve this problem by direct tracing of released individuals and may have an answer to better explain the results reported here.

SUMMARY

1. During the summer of 1955, largemouth bass from Dadek Lake and Flora Lake, Wisconsin, and bluegills, pumpkinseeds, and bluegill x pumpkinseed hybrids from Flora Lake were caught in fyke nets, marked as to the area of initial capture, and released at a central point.

2. Data on the numbers of fish marked at one station which were recaptured at any other station and the shortest distance via water between stations as measured in 10-foot units were utilized in a regression analysis which yielded a theoretical curve of the relative distribution of marked individuals with respect to their "home" territory.

3. Further analyses confirmed the possible existence of two groups in the population, one that "homes" and one that moves about at random. The "homing" segment was estimated to be about 31 percent of the bluegills, pumpkinseeds, and hybrids in Flora Lake, 18 percent of the bass in Flora Lake, and 25 percent of the bass in Dadek Lake.

4. Some aspects of the mechanisms which displaced fish may employ in returning to a preferred area are discussed.

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TITLE OF THESIS A CONTRIBUTION TO THE POPULATION DYNAMICS AND HABITAT PREFERENCE OF NORTHERN WISCONSIN LAKE PERCH

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