71-4582

CLADY, Michael David, 1942-
REGULATION OF FISH POPULATIONS IN THREE LIGHTLY EXPLOITED LAKES IN NORTHERN MICHIGAN.

The University of Michigan, Ph.D., 1970
Ecology

University Microfilms, Inc., Ann Arbor, Michigan

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

REGULATION OF FISH POPULATIONS IN THREE LIGHTLY EXPLOITED LAKES IN NORTHERN MICHIGAN

by

Michael D. Clady

A dissertation submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy in

The University of Michigan

1970

Doctoral Committee:
Professor James T. McFadden, Chairman
Professor Frank F. Hooper
Professor Alexander H. Smith
Research Associate William C. Latta

ABSTRACT

REGULATION OF FISH POPULATIONS IN THREE LIGHTLY EXPLOITED LAKES IN NORTHERN MICHIGAN

by

Michael D. Clady

Chairman: James T. McFadden

Selective harvest of predatory fish was used to study the mechanisms of population regulation of the unique lightly exploited fish communities in three unproductive lakes in the Sylvania Tract of northern Michigan. It was theorized that fish production was limited by the large standing crop of large, old predatory bass and that compensatory mechanisms would allow some sport harvest of bass without significantly altering the populations.

One lake was designated as a control while the bass in the other two were experimentally harvested at rates of approximately 20% in 1967 and 1968. Any population parameter which was altered in the experimental populations but not in the control population was considered responsive to density changes.

The survivorship curves of the several populations of perch and bass varied considerably and there was no consistent evidence that mortality was density-regulated. Growth was

density-independent and regulated by the amount of food available during a season. The total reproductive potential of the populations varied considerably from year to year due to fluctuations in year-class strength and due to increases in size-specific fecundity resulting from increased growth. There was no consistent evidence that density limited the amount of spawning. Egg predators apparently removed a large percentage of the egg potential from the bass nests. Year-class strength of bass in these lakes was directly related to temperature during the first year of life. In addition, there was a positive correlation between the maximum length attained by individuals and year-class size at the end of the first summer.

Since mortality, growth, reproduction, and year-class recruitment of bass were not density-regulated there was a fairly constant direct relationship between the biomass present and production during any year. The biomass harvested was only replaced by a chance improvement in growth. One yellow perch population was largely predator-controlled and showed an inverse relation between standing crop and production.

It was concluded that catch-and-release management is the only method likely to maintain the unique fish populations now present in Sylvania.

ACKNOWLEDGMENTS

This study was supported by the Institute for Fisheries Research, Michigan Department of Natural Resources. The U.S. Forest Service provided me with office space and special access to the research lakes. I am especially indebted to Mr. Clinton Harris of Monterey, Virginia, and Mr. Bernard Otterpohl of Land O' Lakes, Wisconsin, for their generous assistance in the field studies. I also wish to thank the members of my doctoral committee. Dr. James McFadden, Chairman, and Dr. W. C. Latta supervised the research and the preparation of the manuscript. Dr. Frank Hooper originally suggested Sylvania as a research area and he and Dr. Alexander Smith also edited the manuscript. Every permanent employee of the Institute during 1967-70 provided either field or clerical assistance or critical advice. Special thanks go to my summer field aides, Mr. Thomas Cannon and Mr. Joseph Kowalis. Daniel Vokovich drafted the figures.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES	iv
LIST OF FIGURES	vi
INTRODUCTION	1
History of Sylvania Recreation Area	2
Description of Research Lakes	3
Katherine Lake	3
Cub Lake	6
Marsh Lake	10
Experimental Design	13
METHODS	16
RESULTS AND DISCUSSION	25
Population Estimates and Harvest	25
Mortality	33
Growth	38
Reproduction	41
Year Class Recruitment	55
Standing Crop and Production	74
Management Implications	81
LITERATURE CITED	83

LIST OF TABLES

Table		Page
1	Estimated number of smallmouth bass and average total length in inches for each age group in Marsh Lake, 1967-69	26
2	Estimated number of smallmouth bass, number harvested, and average total length in inches, for each age group in Katherine Lake, 1967-69	27
3	Estimated number of largemouth bass, number harvested, and average total length in inches, for each age group in Cub Lake, 1967-69	28
4	Estimated number of yellow perch and average total length in inches, for each age group in Cub Lake, 1967-69	29
5	Estimated number of smallmouth bass and average total length in inches, for each age group in Cub Lake, 1967-69	30
6	Average 95% confidence limits for total population estimates for three years as a percentage ± of the point estimate	31
7	Percent survival from egg to fall fingerling and intermediate life history stages for smallmouth bass in Katherine Lake, 1967-69	42
8	Number of eggs and fry found in nests of smallmouth bass in Katherine Lake, 1967-69	46
9	Percent survival from egg to fall fingerling and intermediate life history stages for largemouth bass in Cub Lake, 1967-69	53
10	Number of eggs and fry found in nests of largemouth bass in Cub Lake, 1967-69	54

Table		Page
11	Arbitrary rank of numerical strength of year classes for three populations of bass in Sylvania lakes in 1967	57
12	Monthly deviations in air temperature (° F) from the long-term mean for the western Upper Peninsula, 1959-1969	58
13	Average total length in inches, for the first year of life of each year class of bass in three Sylvania lakes	69
14	Biomass, harvest, and production in pounds of fish in three Sylvania lakes, 1967-69	75

LIST OF FIGURES

Figure		Page
1	Map of Katherine Lake	5
2	Map of Cub Lake	8
3	Map of Marsh Lake	12
4	Survivorship curves, starting with the first fall of life, for four species of fish in lakes of the Sylvania tract.	35
5	Fecundity of smallmouth bass in Katherine Lake	45
6	Fecundity of largemouth bass in Cub Lake	51
7	Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for smallmouth bass in Katherine Lake	60
8	Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for smallmouth bass in Marsh Lake	62
9	Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for largemouth bass in Cub Lake	64
10	Relation between algebraic sums of the deviations from monthly mean air temperatures for June through August to year class strength for three populations	67
11	Relation between maximum length and numbers of young-of-the-year in two populations of smallmouth bass	72

INTRODUCTION

As human populations increase there is increased demand on fishery resources for food and sport. In most areas of the world, especially in heavily settled areas like the midwest United States, relatively unexploited fish populations are becoming rare. The opportunity to do research on an unexploited lake is exciting because of the possibility of using selective manipulation to study methods of intrinsic population regulation which have been altered, perhaps permanently, in populations already heavily fished by man. It is also likely that such a population will exhibit unique qualities such as catchability, size of fish, or stability which are attractive to sport fishermen and which may be worthy of preservation. This paper is largely a study of the regulatory mechanisms of three lightly exploited fish populations. Also, I attempt to use these insights to predict how these populations can be utilized by man without significantly altering their unique structure.

History of Sylvania Recreation Area

The Sylvania Tract is in Gogebic County in the extreme western end of Michigan's Upper Peninsula, the southern end of the area forming part of the Michigan-Wisconsin boundary. The 14,000-acre tract is geologically unique, being on the continental divide between the St. Lawrence and Mississippi river drainages. None of the 36 named lakes and 19 ponds on the area have any significant inlet, and only three have outlet streams which form part of the Ontonagon River headwaters. Virtually untouched forests of hemlock, maple, birch and associated species cover the upland areas while many of the lower areas are acid bogs.

Until 1966, the tract was in private ownership and used as a hunting and fishing preserve by a succession of owners without significantly exploiting the fish populations. In that year the federal government purchased the area and placed it in the surrounding Ottawa National Forest of the U.S. Forest Service where, since 1967, the tract has been managed as a semi-wilderness area with restrictions on access, motorized travel and other public usage.

Preliminary fish surveys in 1966 revealed very significant populations of large predatory fish in many of the lakes on the property. In keeping with overall management goals, strict season, size, method and bag restrictions were drawn up by the Forest Service and Michigan Department of Natural Resources and only

trophy and catch-and-release fishing was allowed in Sylvania. Three of the smaller lakes were closed to the public for the years 1967 through 1969 and set aside for this research.

Reighard (1929) stated that the lakes of the Sylvania area were left as water-filled depressions by retreating glaciers, and that the populations of smallmouth bass he studied were stocked in the lakes around the turn of the century. Virtually all fish stocks on the property, including walleyes, lake trout, bass, and even ciscoes can apparently be traced to plantings made during the years of private ownership. Of course, this does not necessarily mean that these species were not naturally present before stocking, but there is strong evidence that many of the Sylvania lakes were naturally fishless because of virtual isolation from stream drainage and the resultant post-glacial reinvasion routes for fishes.

Description of Research Lakes

Katherine Lake

Katherine Lake is a darkly stained seepage lake of 48 acres and has a maximum depth of 56 feet (Fig. 1). It contains only about 3 ppm of methyl orange alkalinity and has a pH of 5.7. The bottom is mostly organic detritus, but has some areas of sand, gravel and rock off windswept points of land. The lake is surrounded mainly by wooded upland, but there are a few encroaching mats. The bog flora is typically acid, consisting of Sphagnum moss, leatherleaf

Figure 1.--Map of Katherine Lake.

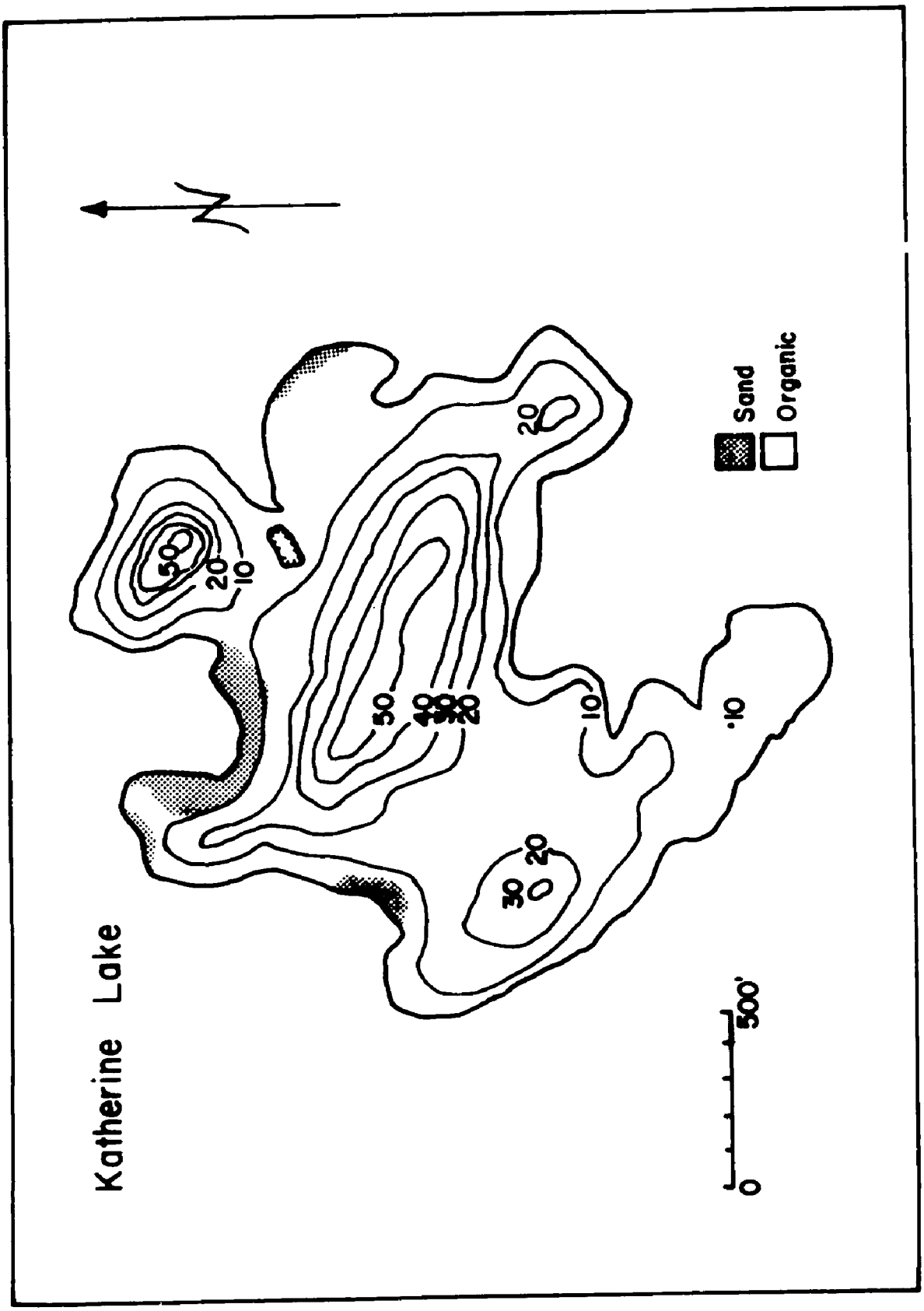


Figure 1

(Chamaedaphne calyculata), Ledum groenlandicum, blue flag (Iris), pitcher plant (Sarracenia flava), and Calla palustris. True aquatic plants are very scarce both qualitatively and quantitatively, and there are only sparse stands of Nuphar, Sparganium, and Eriocaulon. Marginal aquatics are Acorus calamus, Eleocharis, Carex, and Dulichium arundinaceum.

Bottom organisms collected with an Ekman dredge included Chaoborus, Hexagenia, Limnephilus, Caenis, Sialis, Amphipoda, Odonata, and Chironomidae. Freshwater sponge (Spongilla) became very abundant during the summer. Copepods, cladocerans, water mites (Hydracarina) and Chaoborus were abundant in plankton net hauls. Oxygen profiles in late July showed at least 3.5 ppm to the bottom in 1967 and 1968, while there was only about 1 ppm near the bottom in 50 feet of water in 1969.

The smallmouth bass (Micropterus dolomieui) and the mudminnow (Umbra limi) are the only fish species in the lake. Several lodges are maintained on Katherine Lake by beaver (Castor canadensis) while the only possible fish predators seem to be loons (Gavia immer) and very large snapping turtles (Chelydra serpentina).

Cub Lake

Cub Lake is 28 acres in area but has a maximum depth of only 20 feet, most of the lake being less than 15 feet deep (Fig. 2). A number of rocky "reefs" extend out into the lake, and much more

Figure 2.--Map of Cub Lake.

Figure 2

of the bottom consists of sand, gravel and rock than is shown in Figure 2. Most of the lake shore is forested and has burned over areas of spruce, aspen and white birch. There is no inlet or outlet. The water contains about 7-10 ppm total alkalinity and has a pH of 6.7. Encroaching mats containing sundew (Drosera) in addition to those mat species found in Katherine Lake are also present. True aquatic plants are fairly numerous and consist of Sparganium, Nuphar, Utricularia, Lemna minor, Eriocaulon and several species of Potamogeton. Marginal plants include Sagittaria, Acorus calamus, Dulichium, Carex, Bidens, Veronica, Leersia, Calla palustris, Polygonum and Cyperus.

Benthic animals collected were Tendipes, Chaoborus, Caenis, various Trichoptera and Odonata, leeches, snails and fingernail clams. Plankton net hauls captured copepods, small cladocerans, water mites, Chironomidae, Leptodera and Chaoborus. The algae Gleotrichia echinulata bloomed annually during late summer and early fall. The colonial free-floating form became so abundant at times that visibility in the water was greatly reduced. This lake did not stratify significantly in the summer.

Fish species are smallmouth bass, largemouth bass (Micropterus salmoides), yellow perch (Perca flavescens), white sucker (Catostomus commersoni), Iowa darter (Etheostoma exile) and mudminnow. Beaver, loons, and snapping turtles are present. I often observed bald eagles (Haliaeetus leucocephalus) near this lake as well as one otter (Lutra canadensis) in 1969.

Marsh Lake

Marsh Lake is 65 acres in area and 40 feet deep and has an apparent outlet which quickly disappears into a marsh. The water is very darkly stained and has about 2-6 ppm of total alkalinity and a pH of 5.8. Most of the bottom is sand and rock and organic deposits occur only in the deeper areas (Fig. 3). Part of the shore is covered with pine forest, but the most striking feature is the extensive bog area surrounding the lake. Not all of this is encroaching on the lake and there are numerous shallow sandy shoals separating bog mat and lake proper.

The bog flora is quite complex and includes Sphagnum, Chamaedaphne, Ledum, Potentilla, Andromeda, Menyanthes, Iris, and Sarracenia. Aquatic plants that become abundant in summer are Sparganium, Nuphar, Utricularia, Brasenia schreberi, Eriocaulon, and several species of Potamogeton. Cyperus, Polygonum, Acorus, Veronica, Calla palustris, Eleocharis, Dulichium, Leersia and Carex comprise most of the higher aquatics around the margin of the lake.

Chaoborus, Hexagenia, Limnephilid caddis, and Tendipes and other Chironomidae were abundant in bottom samples. Chaoborus were also abundant in plankton samples along with water mites, copepods, Polyphemus and other cladocerans. Oxygen depletions in Marsh Lake were greater than in the other two lakes. Readings at depths below 16 feet were fairly low in July of 1967 (<3.0 ppm) and 1968 (<4.3 ppm) and less than 1.3 ppm in July of 1969. In all

Figure 3.--Map of Marsh Lake.

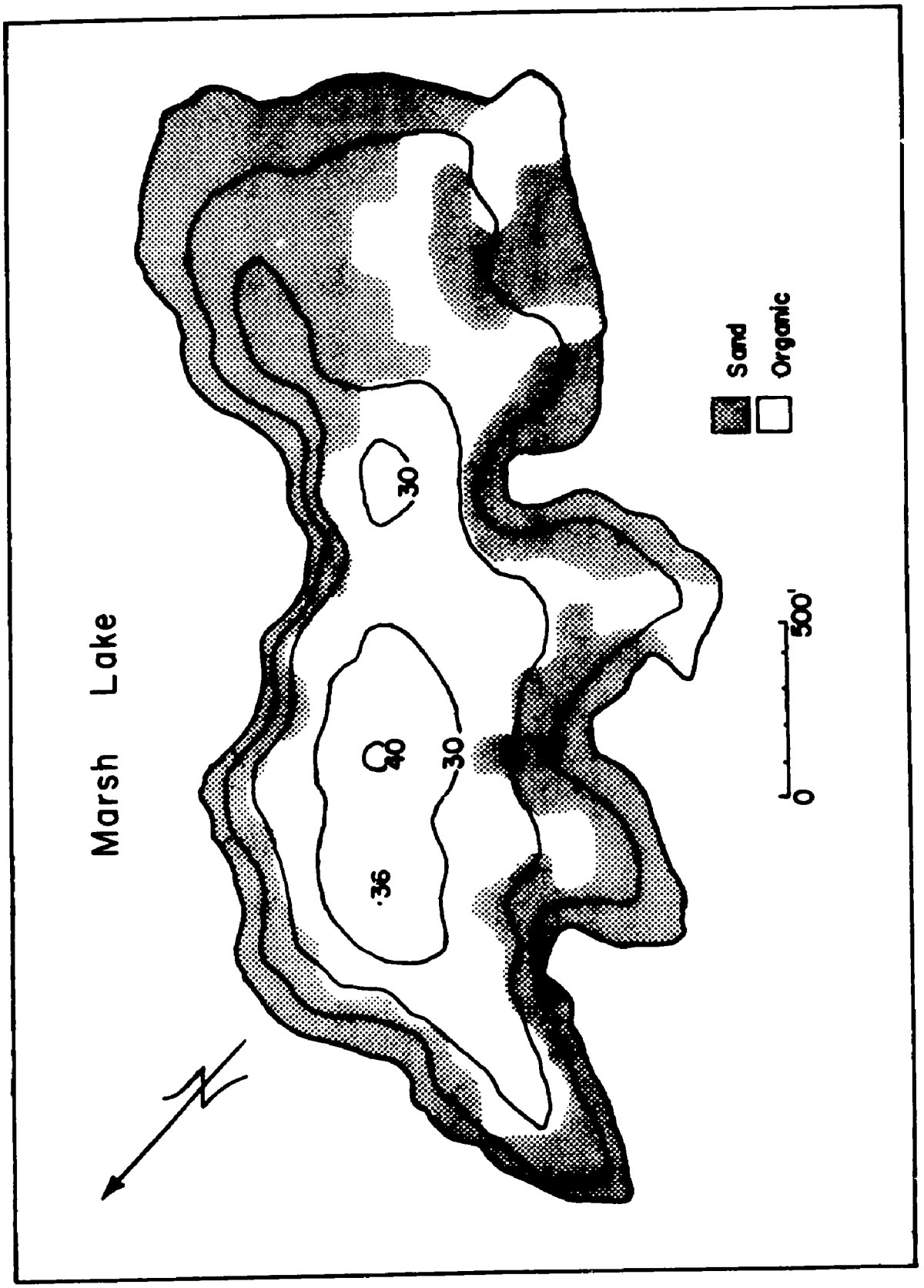


Figure 3

three years, there was little or no oxygen left near the bottom in July.

Smallmouth bass, mudminnows, and white suckers are the only fish species and, again, loons and extremely large snapping turtles frequent the lake. A large great blue heron (Ardea herodias) rookery is near Marsh Lake and these birds commonly fish on the lake, as do several families of bald eagles which nest nearby. I observed one family of otters in Marsh Lake in 1969.

Experimental Design

Backiel and LeCren (1967) conclude the equilibrium state for many fish species in temperate waters is one of a dense slow-growing population with a low production-to-standing-crop ratio. I hypothesized that production in these lightly exploited Sylvania lakes was limited by a high population of large, old, predatory game fish. If this were true, removal of some segment of this biomass would alter density-dependent population controls which should be measurable. As McFadden, Alexander and Shetter (1967) have pointed out, causes of stability can be uncovered only if the population varies somewhat.

This hypothesis on changes in production encompassed a number of sub-hypotheses. Production estimates, of course, include both direct mortality and growth estimates. However, density controls on reproduction and fecundity should also be

important in determining the magnitude of production. I drew up the following sub-hypotheses on the populations and the effect of a harvest before the beginning of field work in 1967 and will treat each one separately. They are:

1. The mortality of large, old, predatory fish would be low and would remain unchanged.
2. The mortality of small, young fish would be high and would be lowered because of reduced predation on and competition from bigger fish.
3. The growth of large fish would be slow and would increase due to reduced competition.
4. Fecundity of individual fish would be low and might increase, but the reproductive capacity of the entire population would not change because it is closely adjusted to the environment.
5. The percentage of the reproductive potential used in a given year would be low and would increase due to loosening of competition at spawning time.

At the end of this paper I will bring all these parameters together, ascertain their effect on production, and test my basic hypotheses.

My experimental and temporal design was very simple. In 1967, I studied several aspects of the fish populations such as mortality, growth and reproduction, and then harvested a segment of the adult standing crop of bass. I again measured these parameters in 1968 and 1969, and also exploited the bass populations again in 1968.

Katherine and Cub were designated experimental lakes and Marsh Lake a control where the fish populations were not manipulated. Any parameter which varied in 1968-69 in the experimental populations and not in a similar manner in the control lake was considered a reaction to the harvest and should elucidate a density-regulatory mechanism in some way. The purpose of the control lake was to dissect out any variation due to density-independent factors such as weather which should affect all the lakes the same.

METHODS

Population estimates of adult fish were made during May and June by using the formula of Schumacher and Eschmeyer (1943). Fish were captured in trap nets similar to those described by Crowe (1950). In 1967, netting sites were chosen by placing a numbered grid over the lake map and using a table of random numbers (Cooper and Latta, 1954). All nets were moved each day. In 1968 and 1969, nets were moved almost daily between areas that produced fish, a net being allowed to remain more than one day only if it was very successful in that spot. Fish were marked by clipping a fin and released in an area where they would not move directly into a net lead.

The smallmouth bass in Cub and Marsh lakes were so difficult to catch in trap nets in May that the data for fish of all inch groups had to be combined to get a reasonable number of recaptures. Only one estimate, that of the total adult population, was calculated. Otherwise, estimates with trap nets were done on individual inch groups. Because of trap-net selectivity, Latta (1959) emphasized doing estimates of each inch group. The failure to do this resulted in the inconsistencies in age structure seen later in smallmouth in Marsh Lake.

Ricker (1958, p. 86) lists six conditions that must be met to validly make this type of mark-and-recapture population estimate. The spring estimates of largemouth in Cub Lake and smallmouth in

Katherine Lake met all of these conditions, especially since the fish were not growing yet and the cold weather and water made handling mortality minimal.

In August and September, Schumacher-Eschmeyer estimates of numbers of small fish were made by electrofishing with a boom from a 14-foot fiberglass boat. Fish were marked by clipping a fin. The conductivity of the lakes is so low (23.8 to 32.9 mhos/cm at 21 C) that conventional shocking gear with an output of 230 volts alternating current or direct current did not work satisfactorily because of insufficient current flow. Mr. Clinton Harris designed and built a special variable voltage transformer control unit with an output of up to 560 volts running on three split phases working in sequence. Input was supplied by a 3-phase, 230-volt a-c, 2500-watt gasoline generator.

Use of this gear involved several problems. The very high a-c voltage potential (300-560 v) combined with low current (<2 amp) severely tetanized and damaged the spinal column of a few fish, especially suckers and the heavy bodied smallmouth bass in Cub Lake. Suckers were the only fish directly killed in this way. Damaged bass held in cages did not die but the injury hindered their swimming. I believe that small fish damaged by electrofishing were more vulnerable to predation, and did not conform to Ricker's (1958) first condition that marked and unmarked fish suffer the same mortality. The resultant population estimates for these fish might be high.

Another problem, especially in Katherine and Marsh lakes, was that only the relatively narrow, shoal areas could be sampled by electrofishing. If some fish remained in deeper water the entire population was not being sampled, violating Ricker's fourth condition. Further, if fish captured and released in shallow water tended to remain there, marked fish would be more vulnerable to fishing than unmarked, violating condition two of Ricker. Klein (1967) found similar problems in estimating trout populations by electrofishing in Parvin Lake, Colorado. The failure to satisfy either or both of these conditions would lead to an underestimation of population size. The magnitudes of the above errors are not known. Any overestimates caused by higher mortality of marked fish would be offset somewhat by underestimates caused by the latter problems.

Population estimates of inch groups of bass and perch were converted into estimates of age groups by first aging scales from a representative sample of fish from each inch group. Then a corresponding portion of the population was assigned to each age group. All smallmouth taken in Cub and Marsh lakes were aged, while suckers in Marsh and Cub lakes were not aged. Scale impressions in cellulose acetate were made by use of a roller press (Smith, 1954) and studied on a microprojection machine (Moffett, 1952), using a magnification of 53. When aging older, slow-growing bass captured during the summer, it was often difficult to determine if the narrow margin of growth beyond the last annulus was the previous year's

increment or that of the present growing season. This problem caused the vast majority of incorrect age assessments in this study. However, making population estimates in spring before the initiation of growth and in fall after most growth was completed, minimized this error.

In calculating electrofishing estimates of smaller fish, it was common for all fish of several consecutive inch groups of a species to be the same age. Here I pooled the data for several inch groups and did one combined estimate, not because it was necessary for lack of recaptures, but because it allowed me to put confidence limits directly on age groups by simply transferring from the pooled estimate for the size groups in that age. Of the 14 instances where I did this, the deviations of the combined estimate for several inch groups from the estimate obtained by adding the separate estimates of each inch group were 0 to 12.5%, with a mean of only 3.6%. Ten of the 14 deviations were 2.8% or less. Obviously, pooling data in this way is a legitimate procedure when doing thorough estimates of small fish with electrofishing gear in lakes.

With few exceptions, bass of ages 0-III were estimated by fall shocking and IV and older fish by spring trap netting. For the interval from III to IV, the time elapsed was only 8 months, running roughly between September (as III) and May (as IV). Otherwise, the time elapsed between the estimates of a year class at a given age and that estimate of the same year class at the next older age the following year was one year.

Body-scale relationships calculated for smallmouth are similar to those found by other authors (Latta, 1963) and consist of two regression lines. The formulae are of the form $L = a + bS$, where L is total length of fish in inches, a is the ordinal intercept in inches, and S is the anterior scale radius in millimeters x 53. The regressions for 477 Marsh Lake smallmouth are $L = 0.66 + 0.082S$ and $L = 3.00 + 0.046S$ with the intersect of the two lines at 5.9 inches. For 700 Katherine Lake smallmouth the formulae are $L = 0.92 + 0.071S$ and $L = 3.51 + 0.044S$ with an intersect of 6.8 inches. Back-calculations of growth were made with the regressions as explained by Latta (1963), using the formula

$$L_1 = C + \frac{S_1}{S} (L - C),$$

where L_1 = average length of fish when annulus x was formed; L = average length of fish at the time scale samples were taken; S_1 = average length of scale radius to annulus x ; S = average length of total scale radius; and C = correction factor consisting of the ordinal intercept. The body-scale relationship for 663 Cub Lake largemouth is a straight-line regression with the formula $L = 1.34 + 0.047S$. The above formula was also used for back-calculations in this species.

Fish captured at times other than during the population estimates were taken by seines, gill nets, and hook and line as well as with trap nets and the boom shocker. Food habits were determined by preserving either whole small fish or the stomachs

of larger fish in formalin and identifying the contents later. The frequency of occurrence, numbers, and volumes of each food organism in each stomach were recorded. I determined fecundity of female fish by preserving the ovaries in formalin and later weighing them and counting the number of clear, large eggs (the "maturing" eggs described by Bagenal, 1967) in several subsamples. A ratio was then used to obtain the number of eggs in the entire ovary. Total egg potential for a given year was obtained by multiplying the average fecundity, for that year only, of mature inch groups (usually 10 inches and larger) by one-half the spring population estimate for that inch group. Sex ratio was considered to be 1:1 for the entire population. Other writers working with smallmouth have found a 1:1 ratio to be generally true (see Latta, 1963).

I observed bass nests with a water telescope. Collections of eggs and fry from nests were made with a glass tube siphon (Carbine, 1939). I continued siphoning a nest until no more eggs or fry could be seen or collected, a process which at times approached the 4 1/2-hour maximum time given by Carbine (1939). Collections were strained, preserved in formalin and counted later. All eggs and fry of smallmouth bass were counted. A random subsample of about one-ninth of the total sample of largemouth eggs and fry were counted and a ratio was used to estimate the total nest contents. Total eggs deposited and total black fry emerging were obtained by multiplying the number of nests by average numbers of eggs and fry collected from a sample of nests.

I accepted Ricker's (1958) definition of production as the total increase in weight of fish during the year including growth in the part of the population which dies before the year is finished. I used his formula 1.37 where production equals $g\overline{W}$ and $\overline{W} = \frac{W_o (e^{g-i} - 1)}{g - i}$, the average biomass of the fish during the interval of calculation. The value of W_o is the initial weight of the fish being considered, while g and i are the instantaneous rates of growth and mortality (the natural logarithms of the ratios of final weight to initial weight and of final numbers to initial numbers).

I had planned to calculate separate production values for about four periods during the growing season. I took scale samples at 1- to 1 1/2-month intervals and calculated age-specific growth curves for most age groups, with the objective of apportioning a fraction of annual mortality during the interval corresponding to the fraction of annual growth attained during the interval. To determine if mortality did, in reality, occur during the growing season, I made additional trap net population estimates in the fall of 1969 for adult smallmouth in Katherine Lake and largemouth in Cub Lake. There were 164 adult smallmouth in Katherine Lake in June, and 131 in September. I removed 31 fish during this period, so there was a net natural mortality of 3 fish. Cub Lake contained 396 adult largemouth in June, and 385 in September. I harvested 33 fish during this interval, so there was no natural mortality in this population. Thus the above procedure was not necessarily valid

for older fish. This does not agree with Patriarche (1968) who found that 81% of natural mortality of bluegills occurred in the summer.

Chapman (1967) points out the fallacies involved in trying to calculate production for short intervals when survivorship data are obtained at much longer intervals, and concludes that perhaps estimates should be confined to intervals no shorter than those between population estimates. On the other hand, mortality can only vary between 0 and 100% while potential variation in growth is infinite. Thus, changes in the instantaneous mortality rate may be insignificant in comparison to changes in the instantaneous growth rate and it would be desirable to interpolate mortality at shorter intervals even if the basis for this distribution has not been proven. For the youngest age groups there is little doubt that most of the mortality occurred early in the season and most of the growth late in the season. By assuming that mortality was exponential, I calculated production at shorter intervals using empirical growth data. This did not increase or decrease the production estimates by a consistent fraction. The greatest value of my production estimates is for comparative purposes within this study. Since the most important precaution is that the method of production estimation remained constant for all intervals, I will present only annual production.

Standing crops were also calculated for the three years by multiplying the number of fish in each age group by their average

empirical weight. Standing crops of suckers were obtained by multiplying the number of fish in each inch group by the average empirical weight for that inch group.

RESULTS AND DISCUSSION

Population Estimates and Harvest

Point population estimates for all game fish in 1967-69 and harvest figures for smallmouth in Katherine Lake and largemouth in Cub Lake are given in Tables 1 to 5. A summary of the asymmetrical confidence limits for the Schumacher-Eschmeyer estimates calculated for $\frac{1}{N}$ as suggested by Ricker (1958, p. 102) is given in Table 6. Most of the confidence intervals for individual inch groups are much narrower than the summary shows. The limits of the sizes of fish near the limits of efficiency of the gear (less than 10 inches for largemouth and less than 8 inches for smallmouth in trap nets, and greater than 8 inches for electrofishing) widen the average confidence intervals. For example, confidence limits of trap net estimates of 8-inch smallmouth in Katherine Lake averaged -27.2% and +60.5% of the point estimate for the three years, while for 11-inch fish they averaged only -16.2% and +2[illegible].4%.

The harvest of largemouth in Cub Lake and smallmouth in Katherine Lake was graduated, the removal rate being greater in the larger size groups. The legal minimum size limit for bass in Michigan is 10 inches. The majority of fish harvested were larger than 10 inches, so that the exploitation would simulate angler harvest under state-wide regulations.

Table 1.--Estimated number of smallmouth bass and average total length in inches for each age group in Marsh Lake 1967-69

Age group	Year of capture					
	1967		1968		1969	
	Number	Total length	Number	Total length	Number	Total length
0	6,092	2.7	3,878	2.3	7,836	2.7
I	113	5.8	110	5.3	2	4.0
II	-	-	68	8.0	5	8.6
III	2	10.6	3	9.6	26	8.7
IV	82	11.2	11	11.3	4	9.5
V	32	12.1	37	12.3	24	12.5
VI	58	13.3	48	13.4	53	13.2
VII	30	14.2	43	14.7	51	14.2
VIII	14	14.5	13	15.6	26	14.8
IX	12	14.6	13	15.7	11	15.3
X	9	15.3	6	16.1	11	15.5
XI	-	-	-	-	6	16.6
XII	-	-	-	-	2	17.1
Combined trap-net estimate of adults	238		174		214	

Table 2. --Estimated number of smallmouth bass, number harvested, and average total length in inches for each age group in Katherine Lake, 1967-69

Age group	Year of capture							
	1967			1968			1969	
	Number		Total length	Number		Total length	Number	Total length
	Esti-mated	Har-vested		Esti-mated	Har-vested		esti-mated	
0	2,871	-	2.4	1,708	-	2.5	4,174	2.7
I	1,144	-	5.3	886	-	4.8	396	5.0
II	108	4	7.7	966	38	7.4	244	7.0
III	41	5	8.7	22	2	9.4	355	9.4
IV	429	53	9.4	34	5	10.5	11	9.9
V	64	10	10.6	147	13	11.2	31	11.4
VI	61	11	11.5	37	10	12.2	83	12.2
VII	31	8	12.2	17	3	13.4	13	13.4
VIII	40	13	13.4	13	3	14.4	10	13.8
IX	9	5	13.9	6	-	14.3	9	14.7
X	4	1	15.8	2	-	15.9	5	15.7
XI	-	-	-	1	-	16.2	2	16.5

Table 3. --Estimated number of largemouth bass, number harvested, and average total length in inches for each age group in Cub Lake, 1967-69

Age group	Year of capture							
	1967			1968			1969	
	Number		Total length	Number		Total length	Number	Total length
	Estimated	Harvested		Estimated	Harvested		estimated	
0	-	-	-	11,709	-	1.9	12,760	1.9
I	3,603	-	4.8	116	-	4.2	1,434	4.5
II	206	4	7.8	1,050	49	6.7	42	6.6
III	128	19	9.0	131	11	8.6	312	8.3
IV	180	47	10.5	108	34	10.9	93	10.3
V	228	40	11.7	181	45	11.9	121	12.0
VI	222	24	12.6	191	21	12.8	125	12.8
VII	44	6	13.0	50	11	13.5	42	13.2
VIII	21	6	13.5	13	3	14.0	10	13.7
IX	5	6	13.6	1	1	14.2	1	14.3
X	-	-	13.6	1	-	14.4	4	14.4
XI	-	-	-	1	1	14.9	-	-

Table 4.--Estimated number of yellow perch and average total length in inches for each age group in Cub Lake, 1967-69

Age group	Year of capture					
	1967		1968		1969	
	Number	Total length	Number	Total length	Number	Total length
0	-	-	48,115	2.1	8,974	2.1
I	6,736	4.3	962	4.0	2,381	4.2
II	24	6.5	1,053	5.9	718	6.4
III	30	8.1	30	8.7	913	8.3
IV	-	9.7	-	8.3	13	9.5

Table 5. --Estimated number of smallmouth bass and average total length in inches for each age group in Cub Lake, 1967-69

Age group	Year of capture					
	1967		1968		1969	
	Number	Total length	Number	Total length	Number	Total length
0	-	-	-	-	206	2.1
II	2	6.7	-	-	-	-
III	27	10.4	15	8.9	1	9.9
IV	7	12.7	18	12.5	4	11.2
V	7	14.1	7	13.8	1	13.5
VI	2	15.1	6	15.7	3	15.8
VII	-	-	2	16.8	1	17.0
VIII	4	16.3	-	-	-	-
Combined trap-net estimate of adults	49		48		10	

Table 6.--Average 95% confidence limits for total population estimates for three years as a percentage ± of the point estimate

Species and lake	Method of capture					
	Trap netting		Electrofishing			
	Adults		Juveniles		Fry	
	-	+	-	+	-	+
Smallmouth bass						
Cub Lake	37.6	208.5	-	-	-	-
Katherine Lake	22.2	64.6	39.2	99.8	23.4	50.5
Marsh Lake	20.8	39.2	39.6	72.1	22.7	82.5
Largemouth bass						
Cub Lake	20.2	38.7	34.8	92.0	23.8	48.9
Yellow perch						
Cub Lake	28.6	42.9	38.4	274.5	21.7	41.2
White sucker						
Cub Lake	30.2	77.6	-	-	-	-
Marsh Lake	19.6	55.8	-	-	-	-

In 1967, 18.1% (18.4% by number) of the total weight of largemouth in Cub Lake of ages IV-IX was harvested with the rate varying from 10.5% for age VI to 100% for age IX. In 1968, the overall rate was 21.8% of weight (21.2% by number) and varied from 10.3% for age VI to 100% for ages IX and XI. For the smallmouth in Katherine Lake, 19.5% of the biomass (15.8% by number) of ages IV-X was removed in 1967, with an additional harvest of 17.0% (13.2% by number) in 1968. Age-specific harvests ran from 12.7% (age V) to 60.7% (age IX) in 1967, and from 8.5% (age V) to 29.4% (age VI) in 1968. For smallmouth, Latta (1963) gives actual angling mortality rates of 22% by number in Lake Michigan, while Forney (1961) reports exploitation rates for three years of 5, 18, and 21% by number. Bennett (1962) gives fishing mortality for largemouth bass of 20 to 30% by number.

These two species were chosen for experimental manipulation because they were desirable game fish which dominated the fish communities in 1967. Except for minimal removals of yellow perch and smallmouth in Cub Lake for fecundity and food habit studies, other fish species in the experimental lakes were not harvested. Rather their populations were monitored for responses to the bass harvests.

Mortality

Total annual mortality (a) was derived directly from successive population estimates in Tables 1 to 4, and annual rate of exploitation (u) was calculated from the harvest during the year. Subtracting u from a gives v, the annual expectation of natural death. Survivorship curves for the smallmouth bass in Katherine and Marsh lakes and largemouth bass and yellow perch in Cub Lake are given in Figure 4. The curves were calculated from the mean annual expectations of natural death starting with a year class in the first fall of life of 100,000. General conclusions emerging from the curves are that early mortality was high and that there was a tendency for mortality to level off somewhere near the mid-point of the life span and then increase again. This resulted in an accumulation of moderately old fish. There were 49 large smallmouth bass in Cub Lake in 1967, and 48 in 1968, but only 10 in 1969 (Table 5). Because of this unexplained disappearance of most of the Cub Lake smallmouth between 1968 and 1969, I made no mortality analysis of this population.

Ricker (1949) gives natural annual mortality of 8% to 79% for older age groups in three little exploited fish populations. There are few published reports of mortality of juvenile warmwater fish in natural lake situations. Mraz (1968) gives second year survival of 19 to 81% for walleyes in a Wisconsin lake. I assumed that mortality in the younger age groups would be high, but that once a

Figure 4. --Survivorship curves, starting with the first fall of life, for four species of fish in lakes of the Sylvania tract.

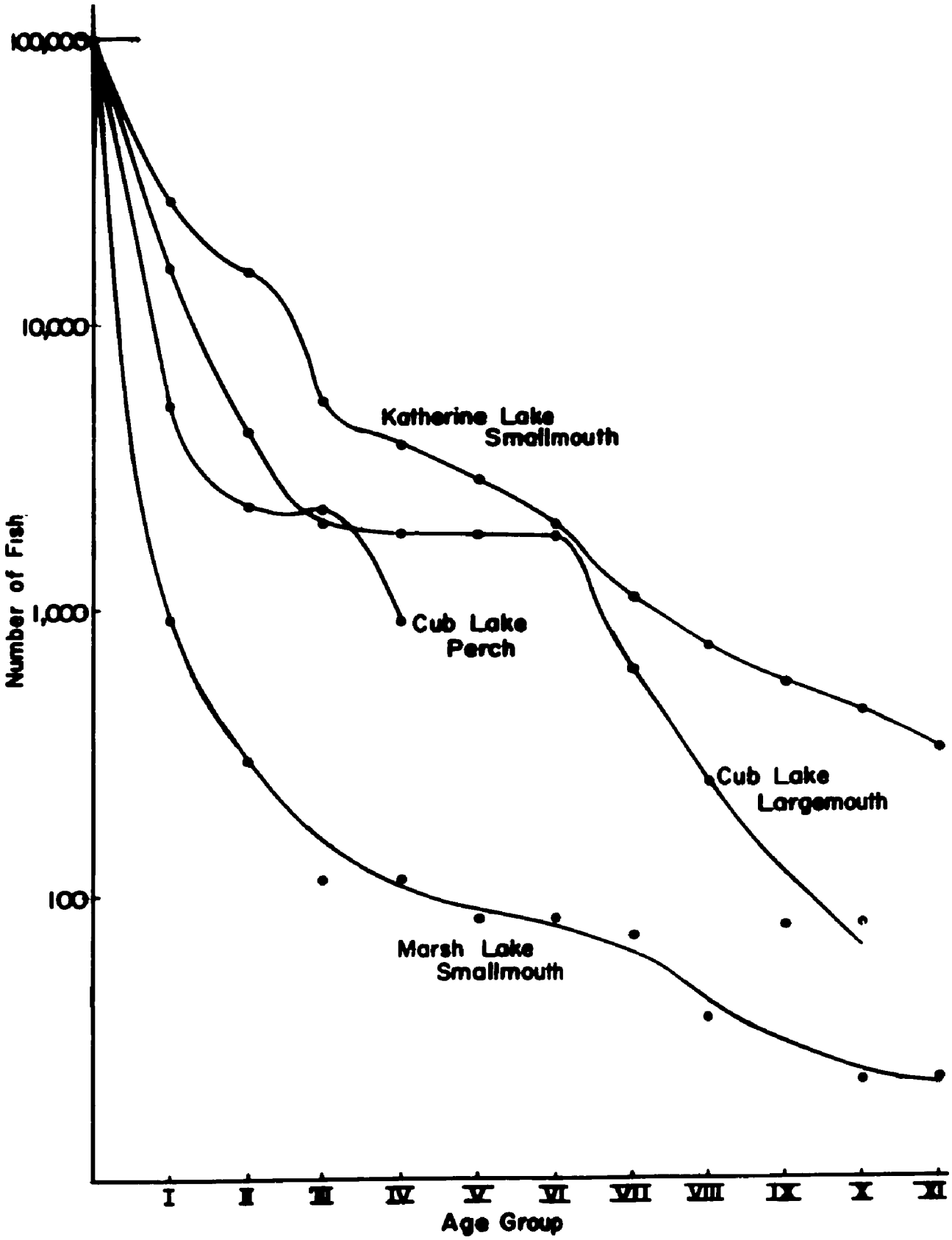

100,000
10,000
1,000
100
Number of Fish
Katherine Lake
Smallmouth
Cub Lake
Perch
Cub Lake
Largemouth
Marsh Lake
Smallmouth
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
Age Group

Figure 4

fish had lived past a critical size, its chances of growing to an old age would be very good in the absence of human predation. Mortality of the smallmouth population in Marsh Lake followed this pattern, being very high from ages 0 to III (especially between young-of-the-year and yearling estimates) and low thereafter. If numbers of fish in the adult ages IV-XI are combined and compared with V-XII fish the following year, mortality was 32.5% in 1967-68, but zero in 1968-69. Zero mortality is not realistic, but certainly mortality was minimal for the adult fish in 1968-69.

Mortality of the smallmouth in Katherine Lake was somewhat different. Natural mortality was again high up to age III, although the second year rate (0-I) was much less than for Marsh Lake. After age III, with some exceptions, natural mortality was quite constant during any given year. Expectation of natural death for combined adult fish (IV-XI) for the two periods (49.2% in 1967-68 and 46.3% in 1968-69) indicated that fishing mortality had little effect on natural mortality, affecting only the total annual rate. Total mortality and expectation of natural death of adult smallmouth were similar to the 36% natural and 58% total mortalities found by Latta (1963) in Lake Michigan, and also to the 13, 34, and 37% natural mortalities given by Forney (1961) for smallmouth in Oneida Lake. The shapes of the two curves for smallmouth are similar, but the magnitudes are different. The extreme second-year mortality in Marsh Lake quickly reduced numbers to somewhere near carrying capacity

and resulted in high survival thereafter. In Katherine Lake this die-off was more gradual and extended even into the adult years.

Mortality of largemouth bass in Cub Lake was high early in life, but then dropped very low for ages III to VI, and then increased markedly during the next three years. The response of the largemouth to harvest was different than that of the smallmouth. In 1968-69, the natural mortality of the exploited age groups of adults apparently decreased in response to harvest, being only 23.3% or about one-half the 44.2% mortality of 1967-68. Considering the drop of natural mortality for these ages from 32.5% to near zero in the control smallmouth population, this so-called response must be viewed with reservation, however. Both Bennett (1962) and Emig (1966a) give largemouth bass mortalities calculated mostly from studies using fish 10 inches and over. Most vary from 20 to 50% for natural mortality and 35 to 80% for total mortality. The $\underline{a}$ and $\underline{v}$ values for adult largemouth in Cub Lake fall in these ranges.

Except for the interval between ages II and III, the high mortality of yellow perch in Cub Lake reflected, in part at least, heavy predation by bass, as also did the short life span of the perch in this lake. There were a few perch older than IV, but not enough to make estimates of their abundance.

There is no consistent evidence that mortality adjusted to harvest. Miller (1950) found that the total natural mortality in an unfished cisco population could exceed total mortality (both natural

and fishing) in a lightly fished lake, and that fishing mortality influenced the total mortality rate by decreasing natural mortality. This response, shown by the largemouth in Cub Lake, but not by smallmouth in Katherine Lake, is not necessarily one of density-dependence. It is one of competing risks where fishing is removing fish which would have died a natural death anyway during that time. Beverton and Holt (1957) conclude that there is no good evidence to indicate that adult fish mortality is density-dependent. Backiel and Le Cren (1967) think that mortality will be density regulated at extremes of density. It is probable that harvest rates much greater than 20% would be needed to elicit a pronounced density response in mortality in these sterile Sylvania lakes.

Growth

The average empirical total lengths of all age groups when population estimates were made of the various species in 1967-69 are given in Tables 4 to 5. The lengths of the perch in Cub Lake, after the second year of life, were 1-2 inches above the Michigan state average (Beckman, 1949). The lengths of the sparse smallmouth population in Cub Lake were below average for the first six years but then caught up to the state average. During their entire lifespan the other three populations all grew at rates far below the Michigan average, lengths of age groups of adults (older than III) falling 2-4 inches below it. These slow growth rates are the result of the very

short growing season for bass at Upper Peninsula latitudes. Juvenile and sub-adult bass generally formed their annulus early in June, but growth in older adults usually did not get underway until late in July. In some years in Marsh Lake the growing season of older fish apparently was no longer than the month of August. Gerking (1966) found that populations of bluegills with the shorter growing seasons also had the slower annual growth.

Backiel and Le Cren (1967) concluded that in most populations inverse changes in growth should accompany major changes in density. I hypothesized that lowered competition would elicit such a growth response in this study also. The average lengths of IV and older bass in the experimental lakes increased considerably from 1967 to 1968 and then remained about the same in 1969, while the size of III and younger fish decreased from 1967 to 1968 and then also remained stationary in 1969 (Tables 2 and 3). This was not a density response, for growth in the control smallmouth population (Table 1) showed the same changes for these years.

The yellow perch of all sizes seemed to be in direct competition with largemouth bass in Cub Lake, especially with the younger bass. Common food items included Chironomidae, small Trichoptera, small Ephemeroptera, Odonata, Leptodera, leeches and bass fry. If the perch were more proficient at obtaining food organisms pursued by both species, it would have been an important inhibitor of any density response by largemouth.

Backiel and Le Cren (1967) state that growth may be so slow in dystrophic waters with extremely stunted fish populations that a small growth increase after population reduction would go undetected. Patriarche (1968) did not find an improvement of growth in slow-growing bluegills after thinning the population (44-75% of various age groups). While this explanation could apply to the older fish in the Sylvania lakes, it does not seem true for the younger exploited age groups which were still growing at significant rates of 1 to 2 inches per year. The 3-year duration of this study was admittedly short, and there is the possibility, also emphasized by Backiel and Le Cren (1967), that there might be considerable lag in growth response to population reduction in unproductive waters.

From the data available, however, I believe that the growth of juvenile and adult bass in these Sylvania lakes is not regulated by competition for food or space, but by the limited ability of individuals of the species to exploit their unproductive environment. Within natural limits of population density for these lakes, individual fish may continue to utilize the available food resources at about the same rate regardless of the number of other fish present. Weather conditions and their effect on the amount of food available will then determine growth during any given season.

Reproduction

Numerous authors have described the spawning behavior and nests of the smallmouth bass (see Latta, 1963). The smallmouth in Katherine Lake began spawning when water temperatures reached about 60 F, and on several occasions, a drop in the temperature below 60 F caused nest desertion by males. Most bass spawned during the last week of May and the first two weeks of June. Spawning grounds in Katherine Lake were chiefly in 3 to 6 feet of water on rock, sand, and gravel areas, particularly off windswept points. Suitable nesting substrate did not seem to be limiting. There were substantial areas with similar bottom that were not utilized completely.

Summaries of the early life history of the experimental smallmouth population in Katherine Lake for 1967-69 are given in Table 7. Survival between egg deposition and fry emergence was constant for all three years, ranging between 25.8% and 32.5%. Data of Latta (1963) give a comparable survival of 27.6% for Lake Michigan smallmouth, while Pflieger (1966) reports an average of 94.1% survival for the same interval in a Missouri stream. My hypothesis that the reproductive potential of the population would remain constant is disproved but exploitation did not elicit the change. The variation in egg potential between years can be attributed to the very strong 1963 year class (Table 2), which matured for the first time at age V in 1968.

Table 7. --Percent survival from egg to fall fingerling and intermediate life history stages for smallmouth bass in Katherine Lake, 1967-69

Life history stage	Year of observation					
	1967		1968		1969	
	Number	Percent survival	Number	Percent survival	Number	Percent survival
Egg potential	491,479		559,202		761,555	
		15.4		30.9		34.9
Egg deposition	75,820		172,710		265,501	
		25.8		32.5		27.6
Black fry	19,550		56,070		73,292	
		14.7		3.0		5.7
Fall fingerling	2,871		1,708		4,174	
Egg potential to black fry		4.0		10.0		9.6
Egg potential to fall fingerling		0.6		0.3		0.6

This large year class contained 51.3% of the total egg potential in 1968 and 47.7% in 1969. The age and size at maturity of the majority of female smallmouth in Katherine Lake were V and about 10.5 inches. Fecundities for the smallmouth in Katherine Lake for three years are shown in a scatter diagram (Fig. 5). The fecundities are similar to those for fish of similar size from other populations (Emig, 1966b).

McFadden, Cooper, and Andersen (1965) and Scott (1962) show that food reduction or infertile environments can lead to lowered fecundity. I hypothesized that fecundity of fish in these slow growing Sylvania populations might be density controlled at some low level and could be increased through exploitation if more food were available to the remaining fish. No trend toward increase in fecundity in fish of similar size is apparent in Figure 5, however. In Katherine Lake the environment did not influence reproductive potential through the size-specific fecundity of females, but rather through variable recruitment of year classes.

The reason for the low percentage of egg potential that was deposited on nests is not clear. The counts of nests given in Table 8 are total counts, including some nests that were not successful. Egg deposition and black fry in Table 7 are probably overestimated since the averages obtained from counts of eggs and fry of successful nests were multiplied by total nests. Inclement weather and poor visibility in this darkly stained lake prevented accurate determination of nest

Figure 5. --Fecundity of smallmouth bass in Katherine Lake.

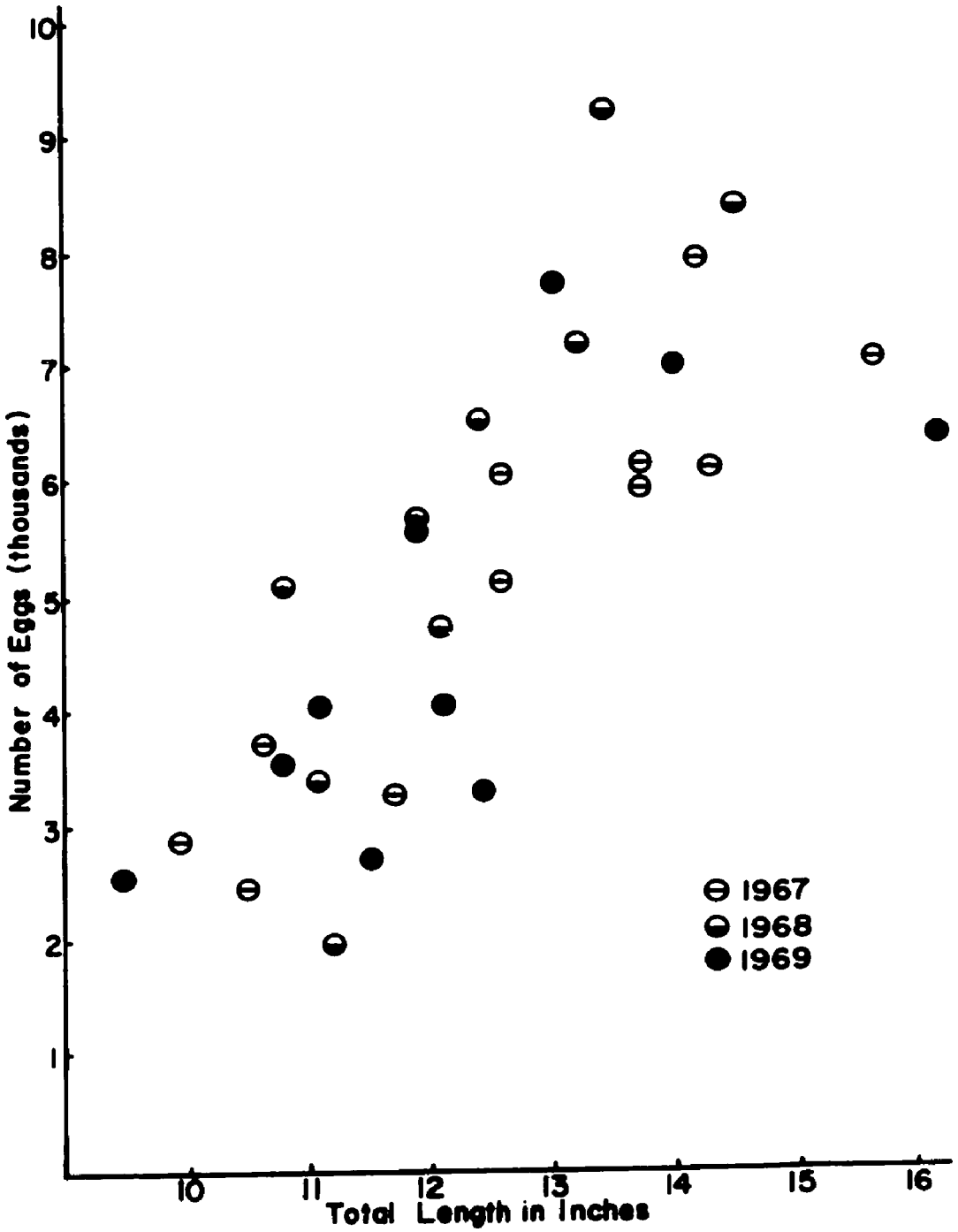

Number of Eggs (thousands)
10
9
8
7
6
5
4
3
2
1
10
11
12
13
14
15
16
Total Length in Inches
1967
1968
1969

Figure 5

Table 8. --Number of eggs and fry found in nests of smallmouth bass in Katherine Lake, 1967-69

Life history stage	Year of collection		
	1967	1968	1969
Eggs per nest	1,481	2,185	2,832
	960	1,907	2,370
	708	1,447	3,012
	453	3,099	5,858
	860	956	4,111
Mean	892	1,919	3,637
Fry per nest	230	103	2,608
	-	996	744
	-	826	489
	-	344	175
	-	845	-
Mean	230	623	1,004
Total number of nests	85	90	73
Number of adult bass age IV and older	209	223	153
Ratio nests to adults	0.407	0.404	0.477

success. Pflieger (1966) lists nest failures of 11% and 18% for two spawning periods while Latta (1963) cites failures between 20% and 56%. Thus, survival rates for egg potential to eggs deposited, fry to year class, and egg potential to fry are maximum estimates (Table 7).

Except for the 1969 egg counts, the average counts of eggs and fry given in Table 8 are at or below the lower limits of ranges summarized by Latta (1963), i.e., 2,000-10,000 eggs and 2,000-3,000 fry. Most of the mature fish spawned, since the ratios of nests to adults (both males and females) were 0.407, 0.404, and 0.477 for the three years (Table 8). There are three possible explanations for the low deposition of eggs. One is that females deposited only part of their complement of eggs in one nest and retained and resorbed the remainder without depositing them later in another nest. More than one female centrarchid will spawn in a given nest. The low egg counts compared to fecundities indicate this is not common in Katherine Lake, however. How a population of fish which routinely spawns only a portion of its complement of eggs could evolve through natural selection is difficult to explain. Nevertheless, unspawned eggs are not energy lost but are resorbed by the individual. It is conceivable, at least, that this retained energy could bestow a long-term selective advantage on such individuals in these very unproductive lakes.

A more reasonable explanation is the rapid removal of eggs from the nest shortly after deposition. I propose that eggs on

smallmouth nests in Katherine Lake have survival similar to that for fish fry after emergence, i.e., a critical initial period during which mortality can be extremely high followed by periods of leveling off and comparatively low mortality. The egg predator I suspect is the red water mite (Hydracarina), a predacious arachnoid. I did not observe mites to directly kill or devour eggs, but mites were clinging to live eggs in preserved material. Concentrations of mites were not found in empty nests, but their numbers usually exceeded the number of eggs in active nests. Perhaps newly deposited eggs were much more susceptible to the predators and the more developed eggs and fry which I usually collected underwent little predation from the mites, resulting in the constant egg-to-fry survival for all years. Then yearly variations in egg deposition were due to variation in mite predation on the very early egg stages, perhaps reflecting water temperature and the resultant developmental rate of the eggs. A Kruskal-Wallis one-way analysis of variance shows a significant difference between years in nest egg counts ($H = 9.6$, $p<0.009$). Fry counts were not significantly different.

The third possibility is that the eggs rapdily died due to some unknown factor soon after deposition and that the large numbers of mites were scavengers. Pennak (1953), however, states that the great majority of water mites are carnivorous or parasitic, and even in some cases cannibalistic. He says that sluggish species may feed on dead animals. The species in Katherine Lake was a good swimmer

and was common in plankton net hauls made near the surface. There were large numbers of dead eggs collected with mites from nests containing live eggs in all years. Mites were also collected from active nests not containing dead eggs, however.

For smallmouth in a stream, Pflieger (1966) found 0.15% survival from fry dispersal to September of the first year, which is much lower than the 14.7%, 3.0%, and 5.7% I calculated for this interval. Since Pflieger reported 94.1% survival from egg to fry on the nest, perhaps survival during the two periods is compensatory, i.e., bass fry with high survival on the nest die more rapidly after dispersal, and visa versa.

The spawning of largemouth bass is well known (Mraz, Kmiotek, and Frankenberger, 1961; Carbine, 1939; Kramer and Smith, 1960). In Cub Lake the largemouth spawned at generally the same depths, time and temperature as smallmouth in Katherine Lake. The main difference is that the largemouth built less defined nests and spawned on all bottom types, thus utilizing the entire shoal area of the lake. The age and size at maturity were also similar to the smallmouth in Katherine Lake (V and 10 inches), although more IV largemouth were mature.

There was no definite density response in fecundity in this species (Fig. 6). As for the smallmouth (Fig. 5), however, many of the highest counts were made in 1968 and might hint to a response to increased fish size in 1968. The range of fecundity was between 7,000 and 29,000.

Figure 6. --Fecundity of largemouth bass in Cub Lake.

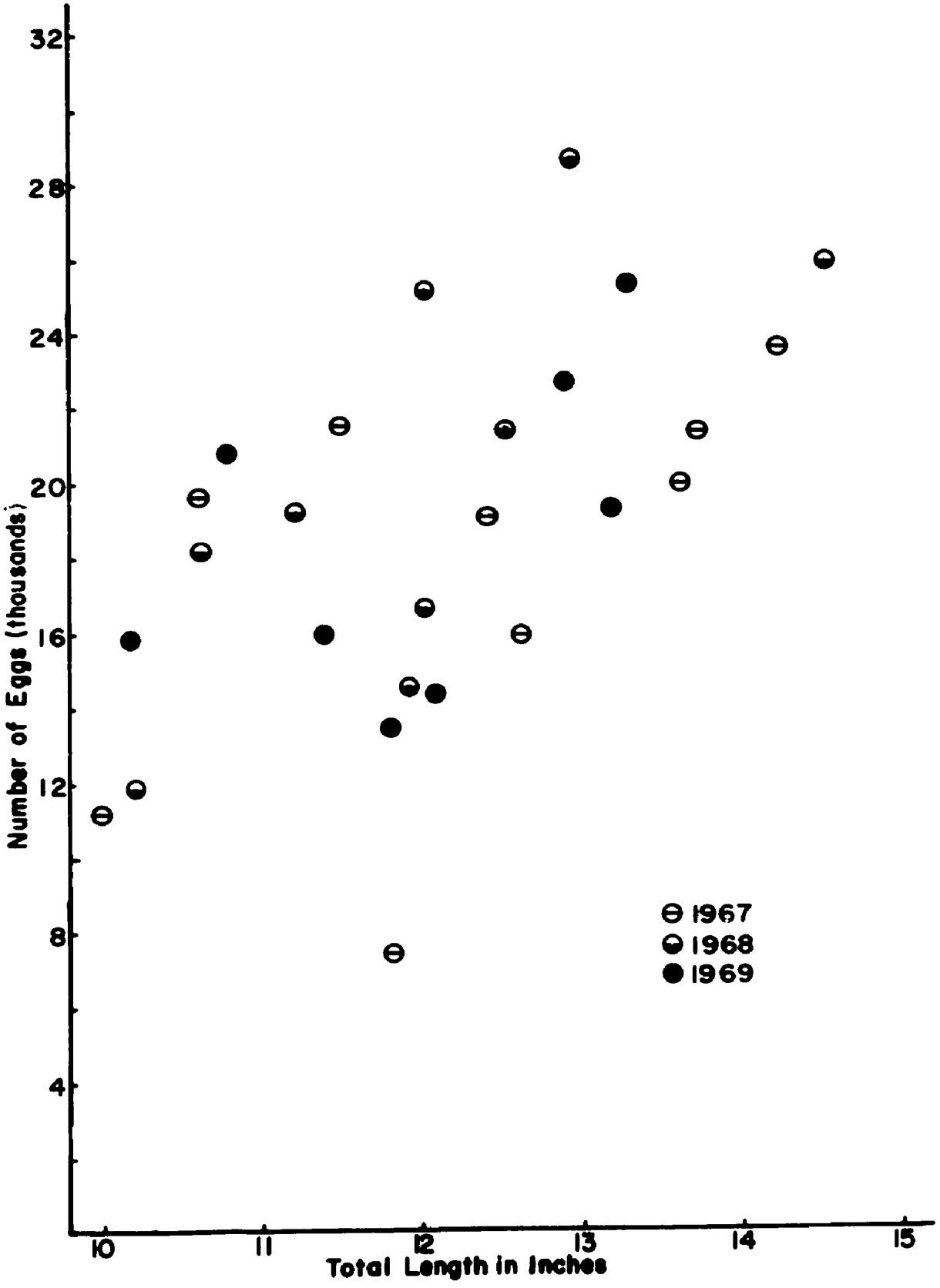

32
28
24
20
16
12
8
4
Number of Eggs (thousands)
10
11
12
13
14
15
Total Length in Inches
1967
1968
1969

Figure 6

A limited summary of the early life history of the largemouth in Cub Lake is presented in Table 9. This population also showed considerable fluctuation in egg potential, but this fluctuation was not due to variable recruitment of year classes. The distribution of egg potential by age was very constant. For the three years an average of 18.4% (range, 15.4-22.4%) of total egg potential was in the IV age group, 32.0% (30.8-33.1%) in age V, 37.2% (34.7-38.8%) in age VI, 7.8% (6.0-9.8%) in age VII, 3.3% (2.6-3.7%) in age VIII, and 1.2% (0.6-2.0%) in ages VIII+. The high 1968 egg potential was, in fact, due to higher egg counts for fish of a given size in that year. I believe this was a response to the accelerated growth between the 1967 and 1968 adult population estimates (Table 3). This growth change was not related to the population reduction.

Data for largemouth nests in Cub Lake are given in Table 10. The two high egg counts in 1968 were probably multiple spawnings in one nest. The counts of eggs in nests are similar to the 5,000 figure given by Mraz et al. (1961) and to the 5,000 to 35,000 range given by Kramer and Smith (1960). Carbine (1939) found an average of about 5,000 fry (range 751-11,457) produced per nest in a Michigan lake while Kramer and Smith (1960) give a range of 500 to 12,715 fry per nest. The limited 1969 fry counts in Cub Lake seem low. The nest per adult ratio of 0.267 in 1967 compared to 0.449 and 0.470 in 1968 and 1969 indicates that pre-harvest competition probably prevented a significant portion of the population from spawning.

Table 9. --Percent survival from egg to fall fingerling and intermediate life history stages for largemouth bass in Cub Lake, 1967-69

Life history stage	Year of observation					
	1967		1968		1969	
	Number	Percent survival	Number	Percent survival	Number	Percent survival
Egg potential	5,671,771		10,922,615		6,315,046	
		18.3		32.5		9.9
Egg deposition	1,037,850		3,552,500		624,030	
		-		-		66.6
Fry	-		-		415,338	
		-		-		3.1
Fall fingerling	-		11,709		12,760	
Egg potential to fall fingerling		-		0.1		0.2

Table 10.--Number of eggs and fry found in nests of largemouth bass in Cub Lake, 1967-69

Life history stage	Year of collection		
	1967	1968	1969
Eggs per nest	7,500	6,200	1,050
	7,400	22,300	5,550
	4,100	7,600	3,450
	3,200	21,900	-
Mean	5,550	14,500	3,350
Fry per nest	-	-	933
	-	-	2,250
	-	-	3,516
Mean			2,233
Total number of nests	187	245	186
Number of adult bass age IV and older	700	546	396
Ratio nests to adults	0.267	0.449	0.470

The factors causing such a low percentage of the egg potential to be recovered from the nests were probably the same in both lakes.

Year Class Recruitment

I have already presented data which show considerable variation in the numerical strength of year classes at the end of their first summer (Tables 1-5). I calculated the ratios of numbers of young-of-the-year in 1968 and 1969 to numbers of young-of-the-year in 1967 in both the experimental and control smallmouth populations. The decline in year-class size in 1968 can be attributed to density-independent factors, since the 1968/1967 ratio is virtually identical in both exploited (0.59) and non-exploited situations (0.64). The same is essentially true for the ratio 1969/1967, except there is more discrepancy in the two ratios (1.45 and 1.18, respectively). Perhaps a small part of the 1969 increase in year class in Katherine Lake was a density response to population alteration.

Fry and Watt (1957) and Watt (1959) extensively studied the factors governing year-class size in smallmouth bass in northern Lake Huron at a latitude close to that of the Sylvania lakes. They found density-independent influences dominant here at the northern limit of the species' range. Fry and Watt (1957) showed that nearby air temperatures were highly correlated with water temperatures and that year-class yield was directly related to the algebraic sum of the monthly deviations from the mean air temperatures from July through

October during the first year of life. Since there was no fishery in the present study I have no yield figures. To evaluate the comparative strength of past year classes, I arbitrarily assigned rank numbers to all year classes present when I first estimated the populations in 1967 (Tables 1-3). If year-class recruitment were constant the number of fish should decline consistently in progressively older age groups of an age-frequency distribution. Year classes with unusually high or low numbers of individuals were given the extreme ranks. The rankings are given in Table 11. There can be argument about the values assigned to the average or mediocre year classes ranked 3 to 6. There is no question, however, that the 1964 and 1965 year classes were the poorest numerically in all three populations and that the 1963 and 1966 year classes were very strong in Katherine Lake. The monthly deviations from the long-term mean air temperature for the western Upper Peninsula as recorded by the U.S. Weather Bureau for 1959-69 are given in Table 12. I included June in my analysis since bass fry hatch early in this month in the Sylvania lakes. In Figures 7-9 rank of year classes was plotted against the summed monthly deviations from July to October (Fry and Watt, 1957).

A strong correlation existed between the two variables for smallmouth in Katherine Lake (Fig. 7). The strong 1959, 1963 and 1966 year classes were hatched in the only three years that had positive summed deviations, while the very poor 1964 and 1965

Table 11.--Arbitrary rank of numerical strength of year classes for three populations of bass in Sylvania lakes in 1967

Year class	Lake and species		
	Katherine Smallmouth bass	Marsh Smallmouth bass	Cub Largemouth bass
1966	2	5	3
1965	7	8	8
1964	8	7	7
1963	1	1	4
1962	6	4	2
1961	5	2	1
1960	4	3	5
1959	3	6	6

Table 12. --Monthly deviations in air temperature (° F) from the long-term mean for the western Upper Peninsula, 1959-1969

Year	Month					Algebraic sum	
	June	July	Aug.	Sept.	Oct.	June-Oct.	June-Aug.
1969	-6.7	-2.3	+2.9	+0.3	-	-5.8	-6.1
1968	-1.8	-1.7	-1.5	+1.4	+2.6	-1.0	-5.0
1967	-0.6	-3.1	-3.6	-0.1	-2.7	-10.1	-7.3
1966	+1.8	+2.8	-2.3	-0.1	-1.8	+0.4	-
1965	-2.0	-4.3	-2.9	-5.1	+0.4	-13.9	-
1964	-1.0	+1.2	-4.0	-1.4	-1.6	-6.8	-
1963	+0.7	+0.9	-2.0	+0.3	+9.2	+9.1	-
1962	-2.0	-4.0	-1.1	-3.0	+0.8	-9.3	-
1961	-1.9	-0.2	-2.0	+0.6	+0.6	-2.9	-
1960	-2.3	-2.5	+0.8	+1.0	+0.3	-2.7	-
1959	+1.4	+0.4	+3.1	+1.6	-4.5	+2.0	-

Figure 7. --Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for smallmouth bass in Katherine Lake.

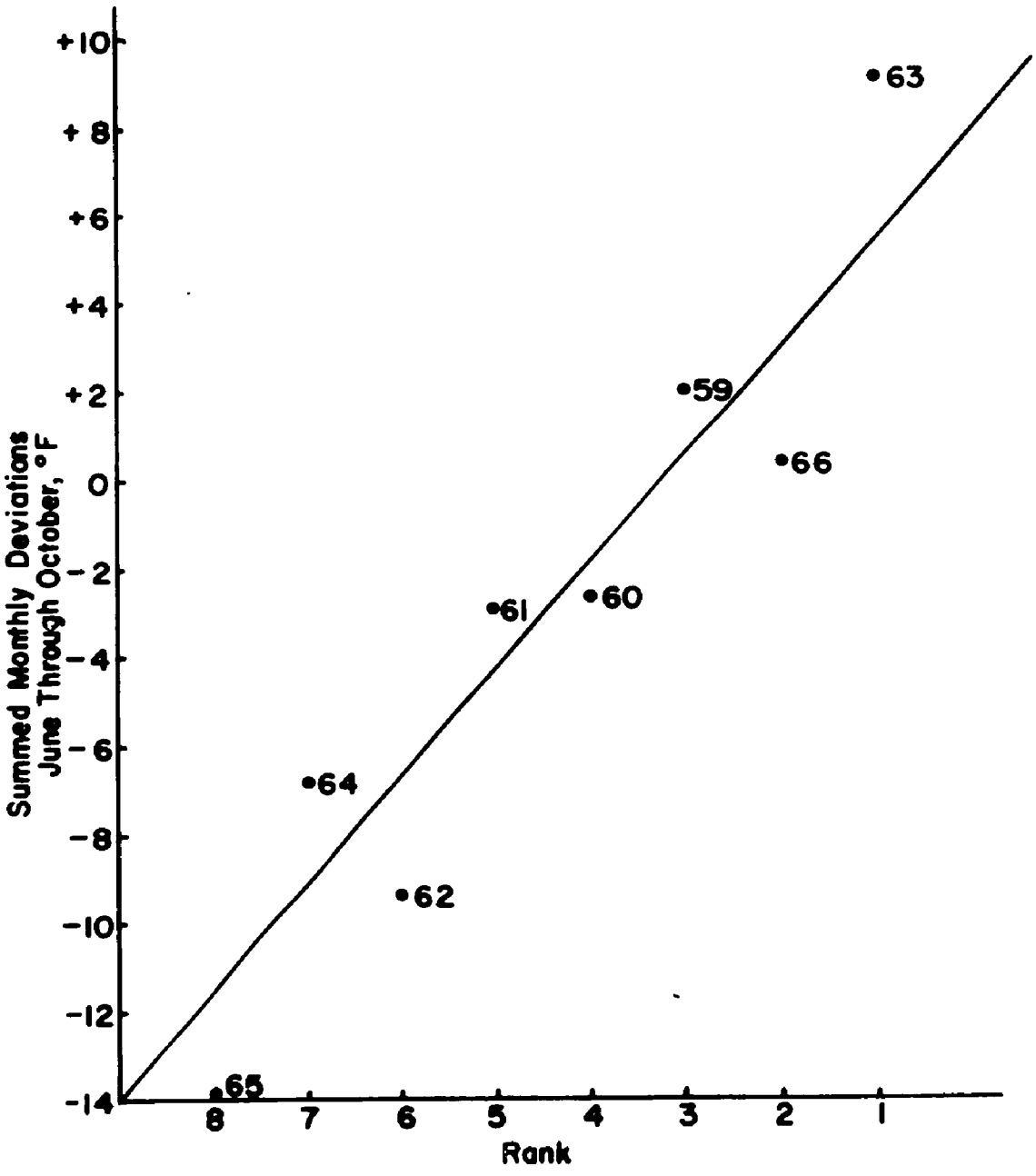

+10
+8
+6
+4
+2
0
-2
-4
-6
-8
-10
-12
-14
Summed Monthly Deviations
June Through October, °F
63
59
66
61
60
64
62
65
8
7
6
5
4
3
2
1
Rank

Figure 7

Figure 8. --Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for smallmouth bass in Marsh Lake.

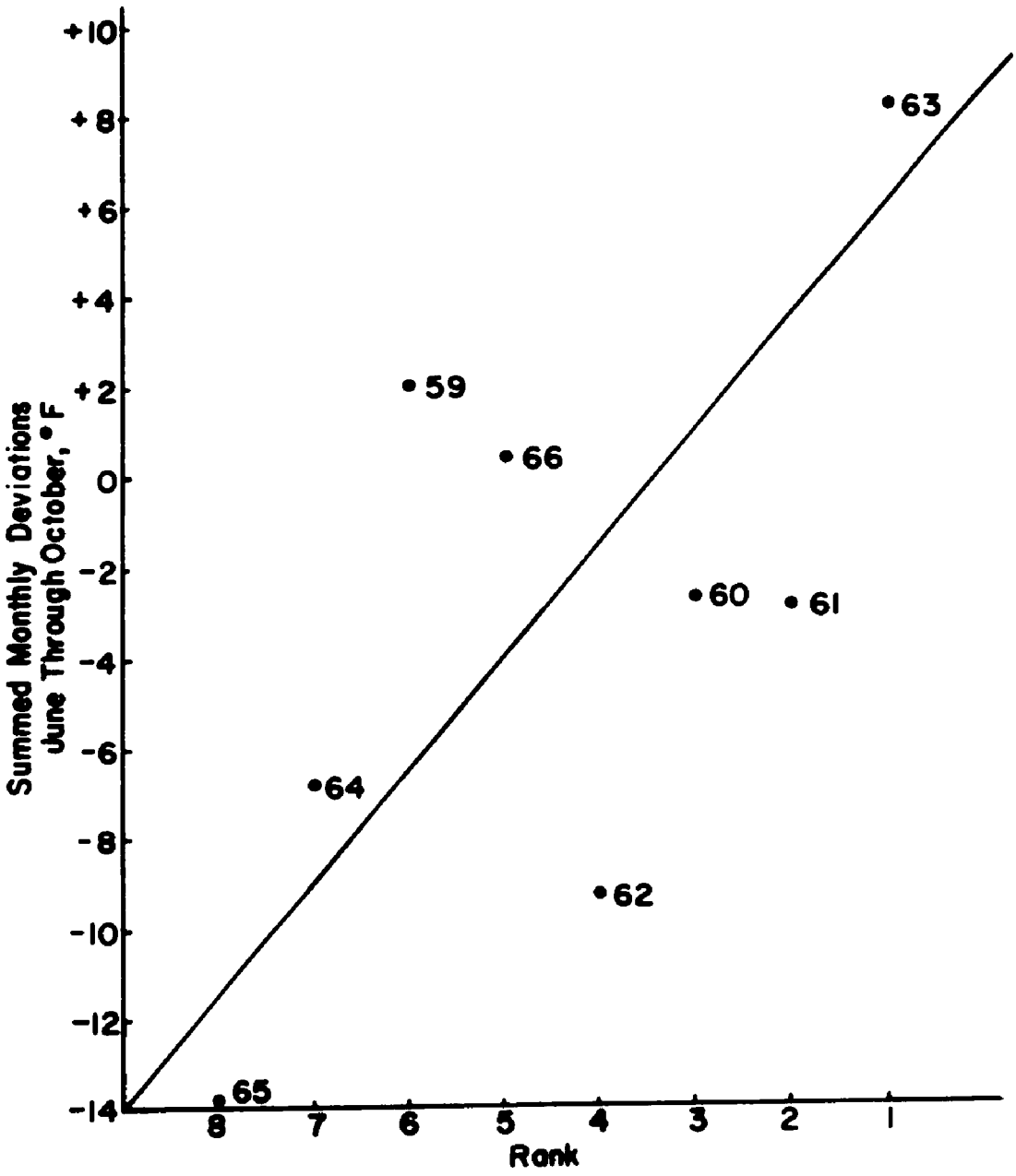

+10
+8
+6
+4
+2
0
-2
-4
-6
-8
-10
-12
-14
Summed Monthly Deviations
June Through October, °F
63
59
66
60
61
64
62
65
8
7
6
5
4
3
2
1
Rank

Figure 8

Figure 9.--Relation between algebraic sums of the deviations from monthly mean air temperatures for June through October to rank of year class strength for largemouth bass in Cub Lake.

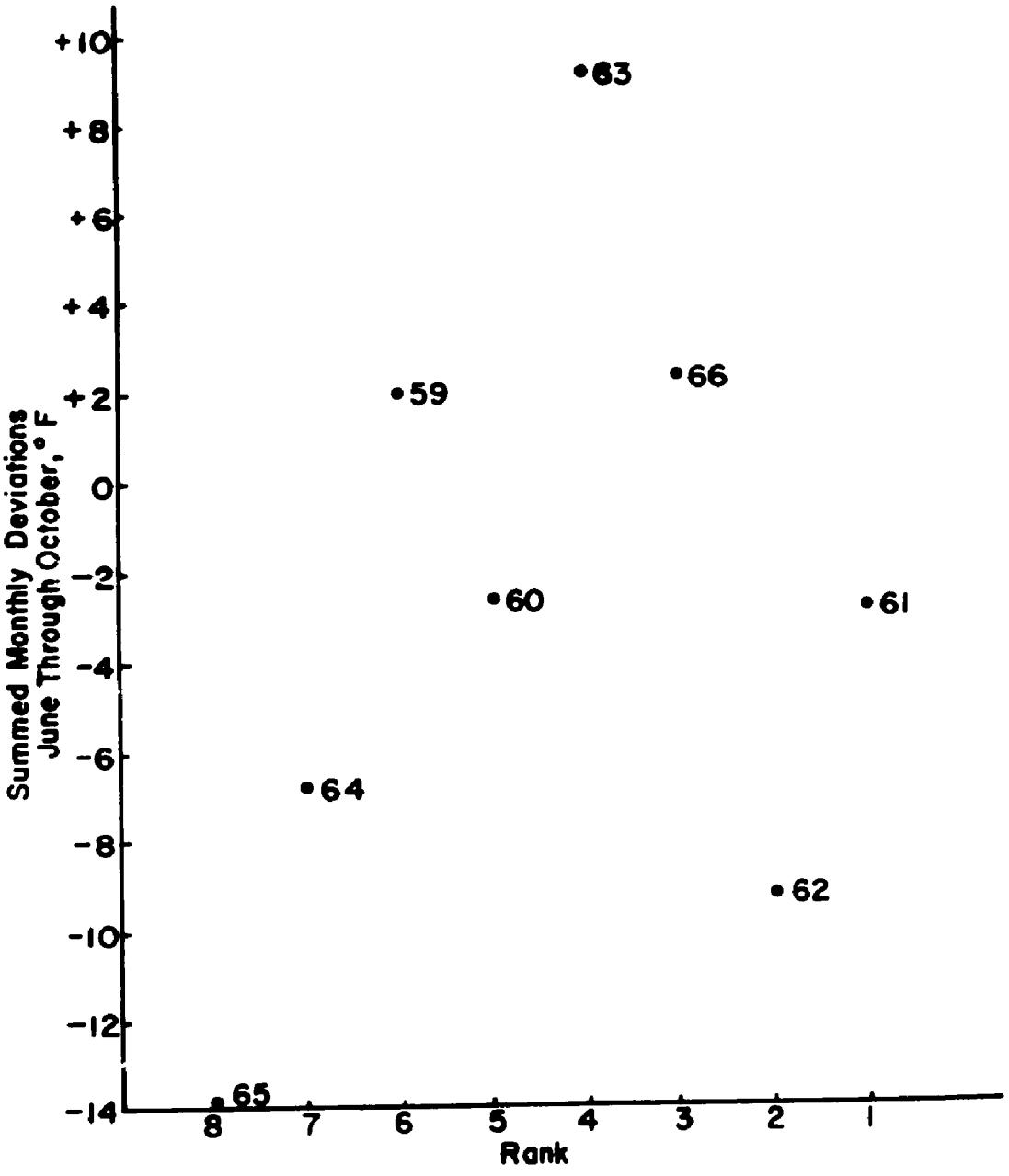

+10
+8
+6
+4
+2
0
-2
-4
-6
-8
-10
-12
-14
Summed Monthly Deviations
June Through October, °F
63
66
59
60
61
64
62
65
8
7
6
5
4
3
2
1
Rank

Figure 9

year classes were hatched in years with two of the three lowest negative values (Table 12). The importance of warm weather in the early life history of young-of-the-year is apparent. The three top-ranked year classes (1966, 1963, and 1959) all had positive values in both June and July. For the five lesser year classes, there was a total of only one positive value during these months (July in 1964). Nevertheless, the very warm 1963 October probably also contributed to the dominance of the 1963 year class. Similar correlations for the smallmouth in Marsh Lake and largemouth in Cub Lake were not as strong (Figs. 8 and 9), although the 1964 and 1965 year classes were again the poorest of all, and 1963 was strong again in Marsh Lake.

The numbers of fry in the 1967, 1968 and 1969 year classes were estimated in late August and early September. To determine if there was any relationship between summer temperatures (June-August) and year-class strength immediately thereafter, I calculated the last column in Table 12 and plotted the data in Figure 10. While this graph does not show any correlations, it does point out by its very lack of relationships a possibility not evident in previous analyses. This is the importance of summer and fall weather, through its influence on growth, in determining survival after the first growing season. Year classes with a considerable number of individuals underwent very high mortality in the second year of life (1967 and 1968 year classes in Marsh Lake). It is possible that year classes containing

Figure 10. --Relation between algebraic sums of the deviations from monthly mean air temperatures for June through August to year class strength for three populations.

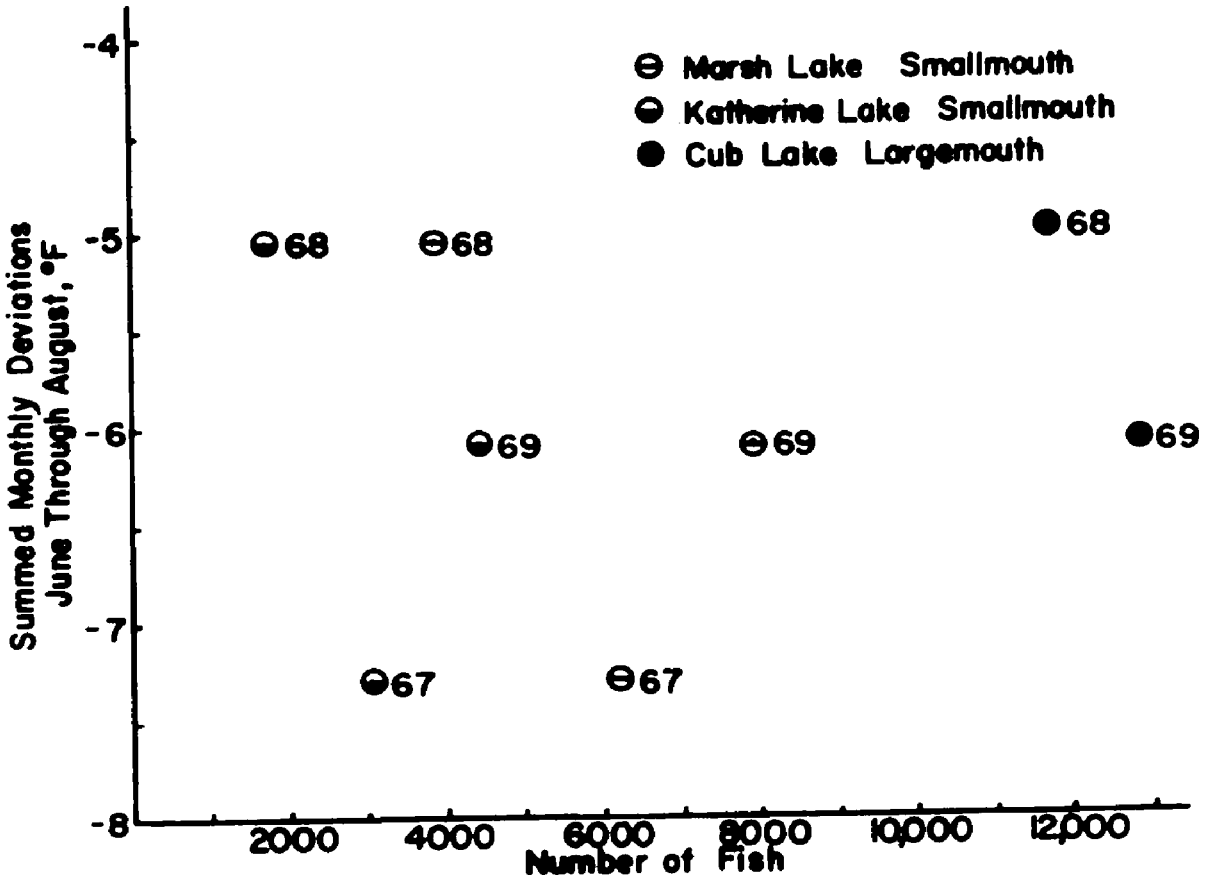

Marsh Lake Smallmouth
Katherine Lake Smallmouth
Cub Lake Largemouth
Summed Monthly Deviations June Through August, °F
-4
-5
-6
-7
-8
68
68
68
69
69
69
67
67
2000
4000
6000
8000
10,000
12,000
Number of Fish

Figure 10

young-of-the-year of small relative size were more susceptible to this die-off. Then year classes such as the 1963 and 1966 classes in Katherine Lake should have had exceptional first-year growth.

To test this proposal I back-calculated the growth of all year classes in the 1967 population and the first-year growth is presented in Table 13. The results are inconclusive and do not substantiate that numbers of fish in a year class after the first year of life are related to first-year growth when the fish were captured later in life (year classes 1959-1966) or at the end of their first summer (year classes 1967-1969). In the smallmouth populations, the strong 1963 year class had only average first-year growth, while the strong 1966 year class was below average. The very poor 1964 year class was also below average in both lakes, while the poor 1965 year class was below average in Katherine Lake and above average in Marsh Lake. For the empirical 1967-69 data in Katherine Lake the most abundant year class (4, 174 in 1969) was greatest in average length, but the average length of the poor 1968 year class (1, 708) exceeded that of the intermediate 1967 year class (2, 871). For Marsh Lake, the poor 1968 class (3, 878) had the smallest average length, but the average length of the intermediate 1967 class (6, 092) equaled that of the most abundant 1969 class (7, 836).

The data for the largemouth population in Table 13 show little variation and are equally inconclusive, although the slowest

Table 13.--Average total length in inches for the first year of life of each year class of bass in three Sylvania lakes. (Maximum length in parentheses.)

Year class	Lake and species		
	Katherine	Marsh	Cub
	Smallmouth bass	Smallmouth bass	Largemouth bass
1969 [a]	2.7 (4.0)	2.7 (4.4)	1.9
1968 [a]	2.5 (2.9)	2.3 (2.9)	1.9
1967 [a]	2.4 (3.1)	2.7 (3.9)	-
1966	3.5	2.7	2.9
1965	3.6	3.3	2.7
1964	3.6	3.0	3.1
1963	3.8	3.1	2.9
1962	3.8	3.1	2.9
1961	4.1	3.0	2.9
1960	3.8	3.1	2.9
1959	4.1	3.3	2.8
Mean 1959-66	3.8	3.1	2.9

[a] For year classes 1967-69 the data are empirical lengths at time of population estimate; for all other year classes the lengths were back-calculated.

growth did occur in 1965, the year with the poorest year-class recruitment. There were year classes with similar numbers in 1968 and 1969 (11,709 and 12,760, respectively) and the empirical average length was identical.

It was evident from handling young-of-the year during the fall population estimates that the size of individual fry at that time was related to the strength of the fall year class. The maximum sizes attained by individuals given in Table 13 and plotted in Figure 11, along with year class numbers, support this. The individuals of the numerically strong 1969 year class were very large, many of those in Marsh Lake exceeding 4 inches and weighing up to 20 grams. The year before, no individuals of the approximately one-half as abundant 1968 year class exceeded 2.9 inches and 7 grams in either Marsh or Katherine lakes. This 1968 year class practically disappeared in Marsh Lake (Table 1). The numerically intermediate 1967 year class showed intermediate maximum sizes. Numbers of fish in the 1967 year class of largemouth in Cub Lake were not estimated as young-of-the-year, not only because the fry were too sparse, but also because they were so small that handling mortality was excessive. I believe this strong positive correlation between year-class size and empirical length of fry in 1967-69 cannot be discounted, even though back-calculated growth did not show such a clear-cut relationship between the two parameters.

Figure 11. --Relation between maximum length and numbers of young-of-the-year in two populations of smallmouth bass.

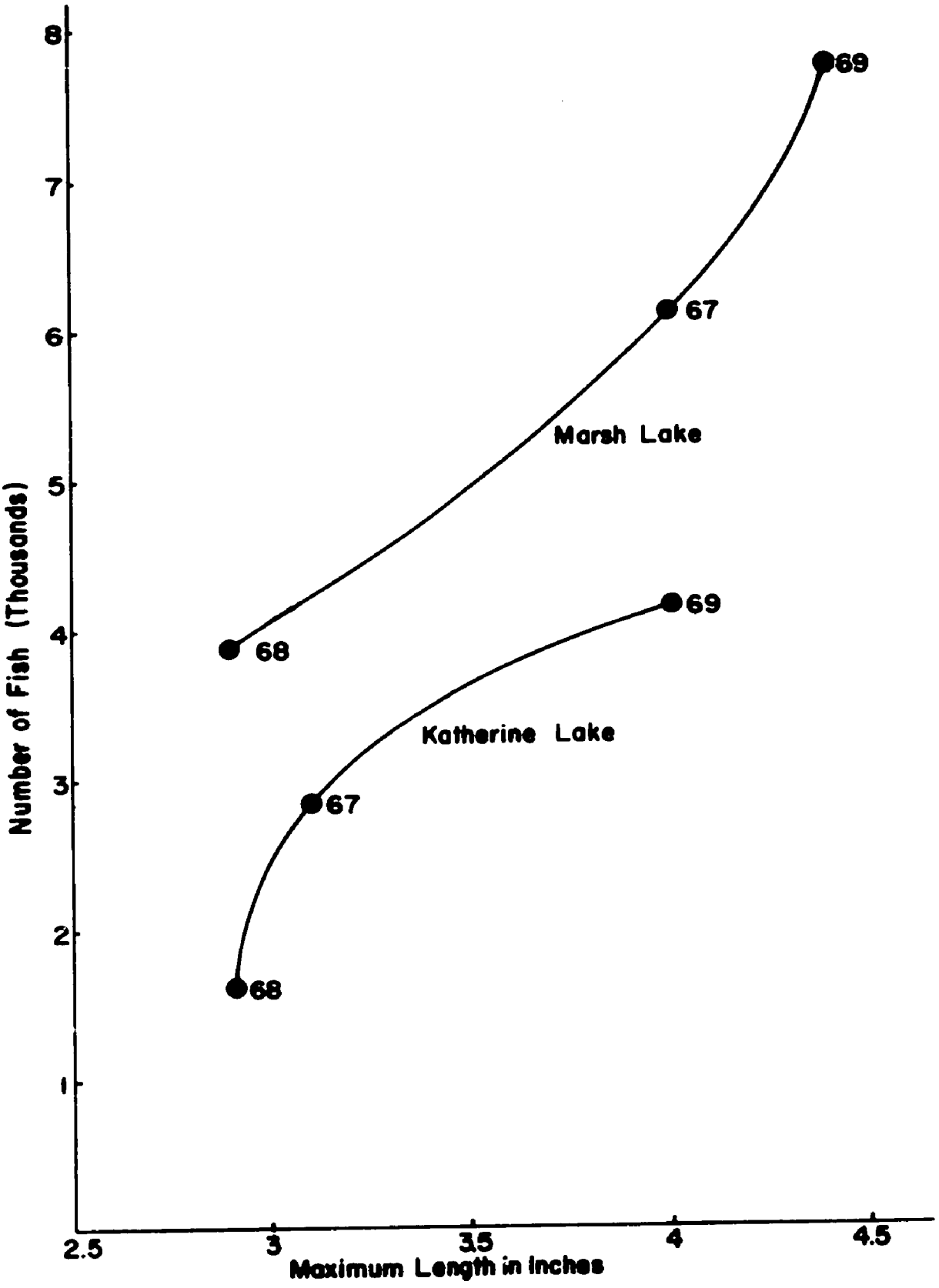

8
7
6
5
4
3
2
1
Number of Fish (Thousands)
69
67
Marsh Lake
68
69
Katherine Lake
67
68
2.5
3
3.5
4
4.5
Maximum Length in Inches

Figure 11

In summary, year-class strength of bass in these lakes near the northern limit of their range was directly related to temperature during the first year of life. Temperature was probably most important in determining the food supply available to fry, but could also significantly influence mortality by its effect on developmental rates and the feeding behavior of fry, especially that during the critical transition from internal to external feeding (Braum, 1967). Temperature was probably not directly responsible for the death of smallmouth bass eggs (Webster, 1948). The maximum size attained by individuals was positively correlated with year class size at the end of the first summer (Fig. 11), but there was no strong relation between year-class strength and average back-calculated first-year growth (Table 13). It is not clear whether strong year classes with these large individuals had better survival later in life, or whether their numerical dominance was established mainly by the end of the first year. Regardless, the large and small individuals of the same year class apparently underwent the same rate of mortality after the first year, since back-calculated first-year growth of fish captured at older ages did not indicate better survival of large individuals (Table 13).

Standing Crop and Production

Standing crops, weight harvest, and production are summarized in Table 14. In the production calculations, a first-year survival rate of 2% for yellow perch from fry to fall is used. Also, a survival of 25% from egg to fry on the nest was used to calculate the initial number of largemouth fry of the 1968 year class. This is the approximate survival of smallmouth in Katherine Lake for the same interval during this year. Second-year survival of the 1967 year classes of perch and largemouth was assumed to be the same as second-year survival of the 1966 year classes for these species.

Cub Lake contained a standing crop of 62.0 pounds per acre of fish in 1967, one-half the average of 125 to 150 pounds per acre given for warmwater lakes by Carlander (1955). Marsh Lake, with two species, contained 51.4 pounds per acre, of which 46.8 pounds were suckers. Katherine Lake, with only smallmouth bass, contained 9.7 pounds per acre. This supports Carlander's (1955) statement that standing crop per acre increases as the number of species increases.

The 1967 standing crop of 28.8 pounds per acre of largemouth bass in Cub Lake was within ranges published of standing crops for this species in natural lakes (Emig, 1966a; Carlander, 1955), but most of these studies included only fish over 10 inches. There was a standing crop of 9.8 pounds per acre of yellow perch in Cub Lake.

Table 14.--Biomass, harvest, and production in pounds of fish in three Sylvania lakes, 1967-69

Year	Lake and species								
	Cub					Katherine	Marsh		
	Yellow perch	White sucker	Large-mouth bass	Small-mouth bass	Total	Small-mouth bass	Small-mouth bass	White sucker	Total
1967 Biomass	275	611	806	45	1,737	464	298	3,045	3,343
1967 Harvest	-	-	120	-	120	60	-	-	-
1968 Biomass	267	253	705	48	1,273	451	242	2,401	2,643
1968 Harvest	-	-	107	-	107	34	-	-	-
1969 Biomass	369	316	548	14	1,247	383	285	2,426	2,711
1967-68 Production	660	-	428	18	-	339	179	-	-
1968-69 Production	481	-	440	-	-	297	121	-	-
Ratio 1967-68 production to 1967 biomass	2.40	-	0.53	0.39	-	0.73	0.60	-	-
Ratio 1968-69 production to 1968 biomass	1.75	-	0.62	-	-	0.66	0.50	-	-

Carlander (1955) gives a mean of 9.1 pounds per acre of perch for lakes from Iowa to Nova Scotia. There were 1.6, 4.6, and 9.7 pounds per acre of smallmouth bass in Cub, Marsh, and Katherine lakes, respectively. These standing crops of the one species are inversely proportional to the total number of species in each lake. Carlander (1955) gives a range of 0.04 to 11.8, with a mean of 4.2 pounds per acre for this species. Annual production in pounds per acre for the 1967-68 period was 15.3 for the largemouth in Cub Lake, 23.6 for the perch in Cub Lake, 0.6 for the smallmouth in Cub Lake, 2.8 for the smallmouth in Marsh Lake, and 7.1 for the smallmouth in Katherine Lake.

The ratios of total 1967-68 production of bass to total 1967 standing crop of bass in Table 14 seem to support my original hypothesis that production was limited by a large biomass of old, slow growing fish. These ratios range from 0.4 for smallmouth in Cub Lake to 0.7 for smallmouth in Katherine Lake. Studying only older fish, Patriarche (1968) found total production averaged 34% to 48% of standing crop in the slow growing bluegill populations of several unproductive lakes and cites three other studies which report production to biomass ratios of approximately 0.5 for warmwater fish. Age-specific production to standing crop ratios for Sylvania IV+ bass ranged from 0.02 to 0.48 and averaged 0.27 for smallmouth in Katherine Lake and 0.13 for largemouth in Cub Lake. Age-specific ratios for III and younger bass ranged from

0.34 to 2.14 and averaged 0.99 and 1.28 for the two populations respectively. The relation between production and standing crop of young and adult fish seemed to be compensatory. The population with greater relative production early in its life cycle had poorer relative production later on, and visa versa.

The continued low values for the ratio of 1968-69 production over 1968 standing crop in Table 14 indicate that these ratios were largely a function of the unproductive environment. Similar declines in the ratio from 1967-68 to 1968-69 were found in both the experimental and control populations of smallmouth. The ratio for the second interval increased slightly in the exploited largemouth population. This was due exclusively to increased production in unexploited age groups, however. Adult (IV+) production in 1967-68 was 114 pounds but only 59 pounds in 1968-69. There is a fairly constant direct relationship between the biomass present and production during any year. This is logical since the growth and mortality components showed no density response in these populations. Watt (1959) concluded that productivity could only be increased by exploitation if intraspecific competition were present in the unfished population. Patriarche (1968) found that reduction in population density of bluegills did not improve the relationship between production and standing crop for his older age groups.

There was little change in standing crop biomass in response to harvest (Table 14). Of the 120 pounds of largemouth harvested from Cub Lake in 1967, 19 pounds were replaced by 1968. Of the 60 pounds of smallmouth harvested in Katherine Lake in 1967, 47 pounds were replaced by 1968. These gains were undoubtedly the result of improved density-independent growth (Tables 2 and 3). During the poorer growth period of 1968-69 the harvested biomass was not only not replaced, but there were additional losses in standing crop of 50 pounds of largemouth and 34 pounds of smallmouth.

The yellow perch population in Cub Lake presented more "normal" standing crop–production relationships (Table 14). The 1967-68 production to standing crop ratio was 2.4, which falls within the range of 1.2 to 2.5 given for six studies summarized by Chapman (1967). The standing crop of perch increased by 34% from 1967 to 1969, mainly because of the abundant 1966 year class (Table 4). Perhaps this was a result of my harvest of largemouth bass. Even if it was, this does not necessarily prove that perch were better competitors, since the standing crop of bass in Katherine Lake did not recover in 1968-69 in the absence of competitors. The increase in biomass of perch was accompanied by a decrease in production, both in absolute pounds of production and production/standing crop ratio. If 1968-69 production is placed over 1969 standing crop, the ratio falls to 1.3. This inverse correlation between biomass and

production has been found by other authors (Ricker and Foerster, 1948; Hunt, 1966) and is what I erroneously expected in the experimental Sylvania bass populations. Probably more of the available food is used for maintenance at higher biomass levels, and more for growth at lower standing crops. If so, then the instantaneous growth rate is inversely related to biomass (Chapman, 1967).

Why did the perch population have such a high turnover rate compared to bass? I believe the perch was largely a forage species in Cub Lake and its population was predator-controlled. Perch up to 10 inches in length were the staple diet of largemouth in Cub Lake and the number of individuals living more than 4 years was very small (Table 4). Beckman (1949) found considerable numbers of perch to live up to age X in other Michigan lakes. To test this theory, I have calculated a trophic level production efficiency, which, as given by Chapman (1967) and Gerking (1962) equals the ratio of production of predator to production of prey.

For three years in Cub Lake, the average percentage of the total food volume of adult largemouth that consisted of perch and unidentified fish was 68.1% (90.7% in 1969, 50.8% in 1968, and 62.7% in 1967). For juveniles the average was 45.3% (52.9% in 1969, 28.9% in 1968, and 54.1% in 1967). Adult (IV+) production in 1967-68 was 114 pounds and juvenile production was 215 pounds. Windell (1967) showed that all natural food organisms are digested by bluegills at approximately the same rate, regardless of the

chemical composition of the body. Therefore, to obtain the production of largemouth derived from perch, I simply multiplied 114 by 0.681 and 215 by 0.453. The sum of the two is 175 pounds and gives a trophic level production efficiency of 175/660 or 0.27 if I assume that largemouths were the only predators on perch. Production of adult largemouth in 1968-69 was 59 pounds and production of juveniles was 210 pounds. I calculated that 135.3 pounds of largemouth production was derived from perch by again multiplying by the appropriate ratios. The trophic level production efficiency for this interval is 135.3/481 or 0.28.

Some perch were removed by predators other than largemouth bass. Of eight stomach samples of smallmouth bass taken in Cub Lake in 1967, all contained perch and this species comprised 99.6% of the total volume of food. Thus the numerator of the ratio is too great. A small percentage of the unidentified fish in the largemouth stomachs was probably not perch, so the denominator is also overestimated. The two sources of error should cancel each other somewhat. Phillipson (1966) states that the few ecological efficiencies measured for natural systems range from 5% to 30%. Gerking (1962) gives summer trophic level production efficiency values for bluegills of 0.23 and 0.19 based on protein and live weight, respectively. While it is not necessarily true that the energy value of perch is higher than that of the invertebrates consumed by bluegills (Warren and Davis,

1967; Table 1), it is generally assumed that there is increased efficiency in higher consumer groups (Lindeman, 1942) and I would expect the efficiency of the largemouth in the present study to be greater than that found by Gerking (1962) for bluegills. There is strong evidence that most of the production of perch ends up as production of largemouth bass in Cub Lake. Since few perch are dying from other causes, predation by bass may be a significant control on the perch population.

Management Implications

It is apparent that the Sylvania lakes present a unique and harsh environmental challenge to bass. It is also apparent that only a 20% harvest of adult fish in two consecutive years can lead to substantial declines in the total production and standing crop of bass without giving rise to any compensatory responses in the internal population structure.

For any significant exploitation to be replaced by the next season, three conditions would have to be met:

1. There must be appropriate numbers of fish in critical size and age groups from which the harvested fish must be replaced. This condition is necessary because of the irregular year-class recruitment in these populations.

2. Weather must be very favorable (warm) and allow these fish to rapidly grow to the same size as the harvested fish.

3. There probably must be a minimum of competition from more dynamic fish populations. This study has not definitely shown a relationship between the perch or sucker populations and the inability of the bass to produce a density response to harvest. Nevertheless, it is likely that the less selective perch which is capable of living at a somewhat lower trophic level may have a competitive advantage over the bass in these unproductive lakes.

The present-day fishery manager cannot assure that the first two conditions are met during any given fishing season. He cannot constantly monitor the size and age structure of the populations, and he certainly cannot predict the weather. If he is fortunate he may be able to accomplish panfish and rough fish control through the use of chemical toxicants, but studies have shown any gain is usually only temporary. To assure maintenance of the Sylvania bass populations at present levels, there is no alternative other than management where all fish caught are returned to the water. Opening of any segment of the bass population to exploitation could quickly, or slowly, depending on the harvest rate and weather and the resultant growth potential, reduce the catchable population to very low levels.

LITERATURE CITED

Backiel, T., and E. D. Le Cren. 1967. Some density relationships for fish population parameters, p. 261-293. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.

Bagenal, T. B. 1967. A short review of fish fecundity, p. 89-111. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.

Beckman, W. C. 1949. The rate of growth and sex ratio for seven Michigan fishes. Trans. Amer. Fish. Soc., 76(1946): 63-81.

Bennett, G. W. 1962. Management of artificial lakes and ponds. Reinhold Publ. Corp., New York, 283 p.

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Invest., Lond. (II), 19: 1-533.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply, p. 113-131. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.

Carbine, W. F. 1939. Observations on the spawning habits of centrarchid fishes in Deep Lake, Oakland County, Michigan. Trans. 4th Ann. N. Amer. Wildl. Conf.: 275-287.

Carlander, K. D. 1955. The standing crop of fish in lakes. J. Fish. Res. Bd. Canada, 12(4): 543-570.

Chapman, D. W. 1967. Production in fish populations, p. 1-29. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.

Cooper, G. P., and W. C. Latta. 1954. Further studies on the fish population and exploitation by angling in Sugarloaf Lake, Washtenaw County, Michigan. Pap. Mich. Acad. Sci., 39(1953): 209-223.

Crowe, W. R. 1950. Construction and use of small trap nets. Prog. Fish-Cult., 12(4): 185-192.

Emig, J. W. 1966a. Largemouth bass, p. 332-353. In Calhoun, A. (ed.), Inland Fisheries Management, Calif. Dept. Fish and Game.

Emig, J. W. 1966b. Smallmouth bass, p. 354-366. In Calhoun, A. (ed.), Inland Fisheries Management, Calif. Dept. Fish and Game.

Forney, J. L. 1961. Growth, movements and survival of smallmouth bass (Micropterus dolomieui) in Oneida Lake, New York. N. Y. Fish Game J., 8(2): 88-105.

Fry, F. E. J., and K. E. F. Watt. 1957. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Trans. Amer. Fish. Soc., 85(1955): 135-143.

Gerking, S. D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr., 32: 31-78.

Gerking, S. D. 1966. Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. J. Fish. Res. Bd. Canada, 23(12): 1923-1956.

Hunt, R. L. 1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wisc. Cons. Dept., Tech. Bull. No. 35, 52 p.

Klein, W. D. 1967. Evaluation of a pulsating direct-current shocking device for obtaining trout from a lake for population estimates. Prog. Fish-Cult., 29(3): 140-149.

Kramer, R. H., and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, Micropterus salmoides (Lacépède), and some related ecological factors. Trans. Amer. Fish. Soc., 89(2): 222-233.

Latta, W. C. 1959. Significance of trap-net selectivity in estimating fish population statistics. Pap. Mich. Acad. Sci., 44(1958): 123-138.

Latta, W. C. 1963. The life history of the smallmouth bass, Micropterus d. dolomieui, at Waugoshance Point, Lake Michigan, Mich. Dept. Cons., Inst. Fish. Res. Bull. No. 5, 56 p.

Lindeman, R. L. 1941. The trophic-dynamic aspect of ecology. Ecology, 23: 399-418.

McFadden, J. T., E. L. Cooper, and J. K. Andersen. 1965. Some effects of environment on egg production in brown trout (Salmo trutta). Limnol. Oceanogr., 10(1): 88-95.

McFadden, J. T., G. R. Alexander, and D. S. Shetter. 1967. Numerical changes and population regulation in brook trout Salvelinus fontinalis. J. Fish. Res. Bd. Canada, 24(7): 1425-1459.

Miller, R. B. 1950. Observations on mortality rates in fished and unfished cisco populations. Trans. Amer. Fish. Soc., 79(1949): 180-186.

Moffett, J. W. 1952. The study and interpretation of fish scales. The Science Counselor, 15(2): 40-42.

Mraz, D. 1968. Recruitment, growth, exploitation and management of walleyes in a southeastern Wisconsin lake. Wisc. Dept. Nat. Res. Tech. Bull. No. 40, 38 p.

Mraz, D., S. Kmiotek, and L. Frankenberger. 1961. The largemouth bass. Its life history, ecology and management. Wisc. Cons. Dept. Publ. 232, 13 p.

Patriarche, M. H. 1968. Production and theoretical yields for the bluegill (Lepomis macrochirus) in two Michigan lakes. Trans. Amer. Fish. Soc., 97(3): 242-251.

Pennak, R. W. 1953. Fresh-water invertebrates of the United States. The Ronald Press Co., New York, 769 p.

Pflieger, W. L. 1966. Reproduction of the smallmouth bass (Micropterus dolomieui) in a small Ozark stream. Amer. Midl. Nat., 76(2): 410-418.

Phillipson, J. 1966. Ecological energetics. Edward Arnold, Ltd., London, 57 p.

Reighard, J. 1929. A biological examination of Loon Lake, Gogebic County, Michigan, with suggestions for increasing its yield of smallmouth bass (Micropterus dolomieu). Pap. Mich. Acad. Sci., 10(1928): 589-612.

Ricker, W. E. 1949. Mortality rates in some little-exploited populations of fresh-water fishes. Trans. Amer. Fish. Soc., 77(1947): 114-128.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada No. 119, 300 p.

Ricker, W. E., and R. E. Foerster. 1948. Computation of fish production. Bull. Bingham Oceanogr., Coll., II: 173-211.

Schumacher, F. X., and R. W. Eschmeyer. 1943. The estimate of fish population in lakes or ponds. J. Tenn. Acad. Sci., 18: 228-249.

Scott, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, Salmo gairdneri. J. Fish. Res. Bd. Canada, 19(4): 715-731.

Smith, S. H. 1954. Method of producing plastic impressions of fish scales without using heat. Prog. Fish-Cult., 16(2): 75-78.

Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish, p. 175-214. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.

Watt, K. E. F. 1959. Studies on population productivity. II. Factors governing productivity in a population of smallmouth bass. Ecol. Monogr., 29: 367-392.

Webster, D. A. 1948. Relation of temperature to survival and incubation of the eggs of smallmouth bass (Micropterus dolomieu). Trans. Amer. Fish. Soc., 75(1945): 43-47.

Windell, J. T. 1967. Rates of digestion in fishes, p. 151-173. In Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, Inc., New York.