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## CHARACTERISTICS OF A POPULATION OF WARM-WATER FISH IN A SOUTHERN MICHIGAN LAKE, 1964-1969<sup>1</sup>

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### Abstract

The fish populations of Mill Lake were observed during the 5-year period from October 1964 to October 1969; during this period, public fishing was not allowed. The size of the fish populations was estimated each spring by means of mark-and-recapture techniques. Data on growth and food habits were also collected. Age structure, year class strength, and natural mortality rates of the fish populations were determined. Descriptive models of "typical" year classes were developed.

Large changes occurred in the size and age structures of the bluegill, pumpkinseed and yellow perch populations; smaller changes occurred in the black crappie, largemouth bass and northern pike populations. These changes were caused mainly, if not entirely, by natural fluctuations in year class strength.

Fluctuations in recruitment seemed to be density independent, except perhaps at high densities of fish. Growth of pike and bass, and to a lesser extent, of perch and crappies, was density related. Natural mortality was not density dependent for most species. Evidence is presented that bluegill, perch, bass and pike populations are food limited.

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## Introduction

Problems in management of warmwater lake fisheries continue to plague biologists. Fishing quality varies greatly between lakes and also from one year to the next. Fishing quality is related apparently to abundance of fish of desirable size, and to vulnerability of the fish to angling methods. The former is primarily a function of growth, mortality, recruitment, and productivity of the lake in terms of amount of energy flowing into yield; the latter is related primarily to intrinsic or learned aggressiveness, to food habits, to physical characteristics of the environment such as depth and weeds, and of course, to methods of angling, legal restrictions on angling, and the ability of the angler to catch fish. The biological factors are influenced by water chemistry, climate, and the abundance of the same and other species in the lake. Our knowledge about these factors and processes varies greatly; very little is known about death and productivity, but relatively much is known about growth, food habits, and angling characteristics.

At least three approaches may be used to study biological factors in fish populations: ( 1) experimental, (2) observational studies comparing a number of lakes and their populations, and ( 3) observational studies on changes in one population through time. The study at Mill Lake is of the third approach.

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### Description of Mill Lake

Mill Lake is in the Waterloo Recreation Area of southern Michigan (Washtenaw County, T. 2 S., R. 3 E., Secs. 4 and 5). Land within the Recreation Area is of low fertility. It is largely abandoned farms acquired by the State of Michigan several decades ago. The drainage basin of Mill Lake is 1. 8 square miles; it consists mainly of abandoned fields, marsh and swamp. Human development on the basin is minimal. It consists of about  $1/4$  mile of county highway, a small park with a privy, and perhaps 30 cottages which are at the edge of the basin and high above the water table. These developments are at the extreme upper end of the basin and probably have little effect on the ecology of the lake. A boat launching site and a state-owned camp are located at the outlet of Mill Lake. They are the only developments on the lake itself and likewise should have little effect.

Mill Lake is fed by an intermittent stream from Doyle Lake. The intermittent outlet is the source of Mill Creek, a tributary of the Huron River. Passage of fish to and from Mill Lake occurs to a limited extent as evidenced by the recovery in Doyle Lake of two pike captured, tagged and released in Mill Lake. However I feel that pike are more migratory than the other species, and I consider the fish population virtually closed. Species of fish are (in order of abundance) bluegill (Lepomis macrochirus), pumpkinseed (Lepomis gibbosus),

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yellow perch (Perea flavescens), largemouth bass (Micropterus salmoides), black crappie (Pomoxis nigromaculatus), rock bass (Ambloplites rupestris), brown bullhead (Ictalurus nebulosus), yellow bullhead (Ictalurus natalis), black bullhead (Ictalurus melas), warmouth (Chaenobryttus gulosus), lake chubsucker (Erimyzon sucetta), northern pike (Esox lucius), bowfin (Amia calva) and a few white suckers (Catostomus commersoni). The bluntnose minnow is common.

Mill Lake is moderately productive in terms of morphology and biota, like many lakes in this region. Of the total surface area of 136 acres, 57% is less than 5 feet deep, 25% is 5 to 10 feet deep, and the remainder of the lake is 10 to 25 feet deep. The deeper areas are ringed by dense stands of Potamogeton spp and Ceratophyllum demersum. Chara, Nuphar, and several other genera of emergent and submergent plants are common. Higher plants are abundant enough to discourage water skiing and are some hindrance to fishing. Muck substrates predominate, but sand is common. Lack of spawning habitat probably does not limit recruitment or abundance of any of the fish species except, perhaps, northern pike which may benefit from higher levels of water in the marshes.

The reputation of Mill Lake for angling has varied. It was reputed to be a good lake for northern pike in the 1930's, and a good fishing lake for most species until the mid-1950's. In June 1957, as a special management procedure, 85-90% of the fish were killed with rotenone because they were growing slowly. Growth of survivors and

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angling quality were good for 3-4 years (Hooper et al., 1964). From 1962 until October 1964, when the lake was closed to angling, growth was poor, while angling was good for largemouth bass and average for other species.

The fish population and catch were not measured prior to the closure in 1964. However, an intensive creel census and population study were conducted earlier at Sugarloaf Lake, which is in the same area and is very similar physically, chemically and biologically to Mill Lake. Data of Cooper ( 1953) and Cooper and Latta ( 1954) on the fish and fishery at Sugarloaf Lake are presented in Table 1. Fishing pressure averaged 107 angler hours per acre. Figures are limited to largemouth bass 10 inches and larger, pike 14 inches plus, and panfish 6 inches plus. Total catch and fishing pressure may be less at Mill Lake because the lake is slightly smaller ( 136 vs 180 acres) and is not ringed by cottages; however, exploitation rates and characteristics of the fish population should be very comparable. Cooper and Latta (1954) made mortality estimates of Sugarloaf Lake fishes from age-frequency distributions, a method which assumes that the recruitment is constant from year to year.

#### Methods

A variety of methods were used to capture Mill Lake fish. Trap nets with pots 3 feet by 5 feet by 8 feet of 1 1/ 2-inch stretched mesh (Crowe, 1950) were used throughout the study and were the

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most efficient gear. They retained relatively unbiased samples of crappies and perch larger than 7 inches, of other centrarchids larger than 6 inches, of bass larger than 10 inches, and of pike larger than 20 inches. These sizes will be considered to be the minimum sizes desired by anglers.

Trap nets of the same size but only 30 inches deep and with 3/4-inch stretched mesh were used in 1968 and 1969. They retained bluegills as small as **2 1** / 2 inches, but caught few small fish and fewer larger fish than the traps with larger mesh.

Electrofishing gear was used in 1964-1967 to obtain mark-andrecapture estimates of fish too small to trap, and to obtain relatively unbiased samples of small fish for age determinations in all years. The gear consisted of a large, wooden, square-end boat with booms supporting electrodes of flexible conduit. A 3-phase, a-c, d-c generator, through a control box, supplied 220-volt current at 7-10 amperes, to three electrical fields formed by five electrodes. Four electrodes were arranged in a square, 8 feet on a side; the fifth electrode was in the center. Flood lamps powered by 110-volt d-c illuminated the water at the bow. Collecting was usually done from sunset to about midnight. Fish did not show galvanotaxis; consequently the gear was only effective to a depth of about 3 feet. Thus, large areas of the lake could not be sampled, and the accuracy of the mark-andrecapture estimates made by electrofishing rests on the dubious assumption that marked fish distribute themselves randomly. Because

of homing tendencies of larger fish, the assumption is probably not met. Estimates in which electrofishing gear was used to capture fish both during the first or marking run, and during the second or recapture run, were usually less than estimates made with trap nets or with both gears. For this reason electrofishing estimates were not made in 1968 and 1969, and those made previously were not used if alternative data were available or if they seemed unreasonable.

A large seine 800 feet by 20 feet, pulled by a winch, was used in the fall of 1964. It was not used again because sufficient manpower was not available and only a small fraction of the area could be seined, resulting in a sampling bias.

Mark-and-recapture population estimates were made in the fall of 1964 (September-November) and in the spring each year of 1965-1969 (March-June). Additional fall estimates were not made because fish were difficult to catch. Furthermore, estimates in the fall of 1964 were not consistent with estimates obtained in the spring of 1965. Consequently, the fall data will not be presented. Where the same gear was fished repeatedly, as for example the trap net, the Schumacher-Eschmeyer method of estimation was used ( Ricker, 1958). When one gear was used on the marking run, and another gear on the recovery run, the Bailey modification of the Petersen formula was used (Ricker, 1958). Estimates were stratified by species and inch group to reduce bias caused by gear selectivity. Sometimes data for several inch groups (of the same species) were pooled so that an estimate could be made.

Scale samples were removed for age determinations, from bluegills, pumpkinseeds, yellow perch, black crappies, northern pike,

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warmouth, largemouth bass and rock bass. Most fish were growing slowly and were difficult to age. Bullheads, bowfins, and suckers were not aged. When large numbers of fish were caught, scale samples were stratified by taking 30 from each inch group of each species. The frequency of an age group within a size group was used to apportion estimates by size groups into estimates by age groups. For example, if  $50\%$  of the scale samples collected from  $6.0$ - to  $6.9$ -inch bluegills were age VI, then the estimated number of age VI bluegills would be 50% of the estimated number of 6-inch bluegills plus similar estimates of the number of age VI fish in other size groups.

Random collections of scale samples, or stratified collections which had been weighted by abundance estimates, were used to compute average lengths of age groups by simply averaging the total lengths of fish at capture. Spring collections were made before, during, or slightly after annulus formation.

Average lengths were converted to average weights by means of length-weight curves. Data for the curves were collected in the spring of 1966, the spring of 1968, and in the fall of 1966. Since no difference was found among the data from these dates, they were pooled into one regression for each species. Perch and pike distended with eggs were excluded.

Instantaneous growth rate, g , was calculated on an annual basis for each age group. It was the natural logarithm of the ratio of final weight to initial weight (Ricker, 1958).

Up to five estimates were made of some year classes during the study. Estimates of bluegill, pumpkinseed, perch, pike and largemouth

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bass were plotted on semi-logarithmic graph paper and a line or curve was fitted by eye. Smoothed estimates were read from the graphs. These were used in subsequent calculations of annual mortality, standing crop, and production. The smoothing procedure reduced sampling variation inherent in the original estimates but may have obscured real year-to-year differences in mortality which were present in the data. Estimates of crappies appeared reasonably precise and were not smoothed.

Since angling was prohibited during the study, all fish mortality was due to either natural causes or to biological sampling. Fish (mostly bluegills) were removed for studies of growth hormone, pathology and food habits. However, the numbers removed were an inconsequential part of the total population and can be ignored. Thus, total mortality equals natural mortality. Some pike less than 20 inches long were gilled in trap nets during population estimates. Because the pike population was small, these losses were of some importance and the estimates were adjusted somewhat by deducting deaths of marked pike from the running summary. As far as is known, loss of marked fish of other species was negligible.

Up to four estimates of annual mortality were calculated for those year classes which had been estimated five consecutive times. Since only natural mortality was occurring at Mill Lake and since estimates were made yearly, total annual mortality (a), annual natural mortality (n), and the expectation of death from natural causes (v) are equal. These fractional mortality rates are simply the number of

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deaths during the year divided by the population present at the beginning of the year (Ricker, 1958). The instantaneous mortality rate ( $i = q$ ) is equal to the natural logarithm (with sign changed) of the complement of the annual mortality rate  $(a = n)$ .

Standing crop of a year class in the spring was simply the estimated number in the spring times their average weight. Production was calculated from standing crop (W), instantaneous mortality (i), and instantaneous growth ( g) with the equations and tables of Ricker ( 1958). Calculations were made on an annual basis because seasonal changes in mortality and growth were not measured. Production estimates will be in error to the extent that growth and mortality do not vary in parallel fashion (Ricker, 1958). However Patriarche ( 1968) found over-winter mortality of bluegills in Jewett Lake to be less than over-summer mortality- -a seasonal pattern roughly similar to growth. Thus errors in production estimates may be minor.

In summary, estimates of abundance by size and age have been made for several species of fishes inhabiting Mill Lake. These have been used to compute annual mortality rates and provide a means of comparing the relative strength of several year classes. Data on average length of each year class during the 5-year study have been converted to weight from length-weight curves, and were used to calculate annual growth (g). From these data were calculated standing crop and production. All symbols and calculations follow Ricker ( 1958).

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Confidence limits on the estimates vary by species and size, but as a whole, they are broad- -especially those on fish of small size. For large crappies and bluegills, which trap readily, the 95% confidence limits were sometimes within 5% of the point estimate. However, close limits should not be equated with precision of the estimate. In field studies like this one, there is a high risk of sampling a subpopulation of fish instead of the whole, as, for example, subpopulations which move about in such a manner as to make them more vulnerable to fishing gear than other fish. These systematic sampling errors are not reflected in, and overshadow, the random statistical errors. Some insight into sampling problems was gained by comparing the catch from different gears and by following the consistency of the estimates through time as the fish grew and their vulnerability to the fishing gear changed.

Confidence limits on the size estimates are included in this report but those on age could not be calculated. The Schumacher- Eschmeyer equations yield a variance of  $1/\hat{N}$  which is asymmetrical. This variance cannot be combined with other variances when computing estimates by age groups. If limits on age estimates could be calculated, it is apparent that they would be broad--even those derived from size estimates with tight limits. Confidence limits become even broader by the time standing crop and production estimates are calculated.

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### Results and discussion

## Length-weight relationships

A straight line was fitted by eye to a graph of  $\log_{10}$  weight (grams) against  $\log_{10}$  length (inches) yielding a regression of the type:

$$
\log W = \log a + b \log L
$$

where a and b are empirically determined constants. These constants are given in Table 2.

The regression for the rock bass is similar to that made by Beckman ( 1948) from state-wide collections. Bluegill, pumpkinseed and yellow perch from Mill Lake were comparatively light in weight, whereas largemouth bass and pike were relatively heavy. All species were growing more slowly than their respective state averages.

## Status and changes in

## species population

Because of the large quantity of information which has been collected, it will be presented in two parts. In the first part, data for each species will be summarized, discussed, and compared to the literature under the following topics: food habits, growth,

abundance, mortality, standing crop, and production. These will be followed by a brief discussion of the characteristics of a typical year class and the dynamics of that species. Note that pertinent literature will not be reviewed in a "discussion" section but will be inserted among the results. This was done to facilitate comparisons, and to reduce repetition and fragmentation in the manuscript. In the second part, the species will be reviewed collectively and the interaction between species will be considered in greater detail.

#### Bluegill

The bluegill was the most abundant species of fish in Mill Lake, both in numbers and in weight.

Food habits of bluegill. -- Stomach contents for a small sample of bluegills are summarized in Table 3. A more extensive seasonal analysis for larger bluegills, by P. W. Laarman (unpublished data), is in Table 4. All samples were taken with electrofishing gear, usually just after sunset.

Bluegills within the entire size range (from the 1-inch group to the largest size) ate similar kinds of foods; however larger fish ate more large-sized organisms such as Hexagenia nymphs and insects, and they ate slightly larger individuals of small-sized species (Table 3). Zooplankters, amphipods, chironomids, and the small mayfly Caenis were important items in the diet of small fish. Caddis, molluscs and odonates were important to intermediate sizes. The diet of the

largest bluegills was more diverse, but 53 to 96% (by weight) was aquatic or terrestrial insects (Table 4).

The seasonal analysis (Table 4) shows that bluegill stomachs were fullest during June, July and September. However, the September collection should be discounted because it was biased by the freak occurrence of a hatch of winged ants. Aquatic insects predominated in the other collections.

Growth of bluegill. - Growth of the bluegill was slow (Table 5). On the average, a length of 6 inches was attained during the sixth growing season; however fast-growing fish reached 6 inches in 4 years. Four years is the state average (Laarman, 1963). In Mill Lake most of the deviation from average occurred during the first 2 years of life when growth was very slow. Growth rate improved when a length of 5-6 inches was reached; however, only one fish larger than 9 inches was observed during the study. Bluegills grew as slowly in 1965-1969, as in 1957 when the population was thinned. As pointed out earlier, thinning improved growth for about 3 years.

Seasonal periodicity of growth was studied by P. Laarman (unpublished data). In 1965 he found that most adult bluegills formed annuli in mid-May, and 85% of the annual growth (in length) was completed by August 1. Almost all growth was completed by September 1. By contrast, bluegills reared in ponds 30 miles from Mill Lake completed only 76% of their annual growth by August 1

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(Laarman, 1970). For northern Indiana lakes, Gerking ( 1966) reported that bluegills complete 90% of their growth by mid-September, and that fast-growing populations had a longer growing season than did slow-growing populations. It is evident that the growing season for bluegills in Mill Lake is very short.

There is good agreement between the growth periodicity and seasonal food habit studies by Laarman. At temperatures of 70-75 F ( typical of early summer) the maintenance ration of bluegills is about 0. 8% of their body weight per day (Anderson, 1959). Therefore a 6-inch bluegill weighing 60 g must consume 480 mg of food per day just to maintain its tissues. Using the equation and digestion rate given by Seaburg and Moyle ( 1964), an average of approximately 200 mg of food will be present in the stomach of a 6-inch bluegill on a maintenance diet. At higher temperatures there would be slightly less food present because digestion rate would probably increase more than maintenance ration would increase (based on unpublished data for yellow perch). At lower temperatures, more food would be present because digestion rate would probably decrease more than maintenance ration would decrease. Referring back to Table 4, the average weight of food in Mill Lake bluegills exceeded the maintenance level only in June, July, and probably also late May (the September collection was excluded earlier)--the months when almost all of the annual growth took place.

Growth varied little among years or year classes despite large fluctuations in abundance, It will be shown later that year class

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strength varied 10-fold and that standing crop also varied from year to year. This suggests that, within wide ranges, individual growth is not limited by population density. Evidence presented above suggests that a longer growing season would probably improve growth.

At Mill Lake the growing season is clearly not limited by temperature, since summer temperatures are not especially hot (the surface temperature exceeded 80 F for only 20 days in 1966) and fall temperatures are comparable to those in spring when growth is good. The data on food habits, and field observations, lead me to believe that food availability restricts growth to May, June and July. Gerking ( 1962) made a similar observation at Wyland Lake, Indiana. During these months there are large hatches of insects, and for this brief time, food is unlimited and growth is independent of bluegill density. During the rest of the year, food items are small, perhaps largely unavailable, and all food is required for maintenance of body tissues. Only at extremely low population densities (levels comparable to that in 1957 when the standing crop was reduced to 75% of carrying capacity) will sufficient food be available after July for individual growth to continue. Unfortunately, seasonal growth data at very low bluegill densities are not available to test this hypothesis.

Abundance of bluegill. - - Population estimates, by inch groups, are summarized in Table 6. They show that large changes occurred in the size structure of the population. The number of small bluegills decreased between 1965 and 1967, and observations in the field suggest they were also low in 1968 and 1969. The number of large bluegills

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(longer than 6. 0 inches) increased during the study from 6, 000 in 1965 to over 28,000 in 1969.

Abundance of large bluegills in Mill Lake ranged from 44 to 209 per acre. Other lakes in southern Michigan have populations of the same magnitude: Sugarloaf Lake averaged 82 per acre (Table 1); Whitmore Lake, 42 per acre (Cooper and Schafer, 1954); and Third Sister Lake had 156 per acre (Brown and Ball, 1942). Big Portage Lake, which has a marl bottom, had only 7 per acre (unpublished data of IFR). In the northern part of the Lower Peninsula, the unstable bluegill population in Big Bear Lake ranged from 1 to 8 per acre (Crowe, 1953); Fife Lake had 98 per acre in 1950 (Cooper, 1952), and 28 per acre in 1958 (Christensen, 1960); North Twin Lake had about 11 per acre ( Crowe, 1947); Jewett Lake had from 100 to 178 per acre (over 3 years); and Lodge Lake had 35 and 72 per acre in consecutive years (Patriarche, 1968). Each of these estimates was made with trap nets or seines during the spring or summer, except that for Third Sister Lake. The latter estimate was a count of fish removed by angling, plus fish recovered after poisoning; and, depending on the number of fish which were not picked up, it may underestimate the true population by as much as a factor of two times. All populations were being exploited except those in Mill and Third Sister lakes.

Changes in the size structure of the bluegill population during 1965-1969 were the result of recruitment of weak and strong year• classes. This may be seen by examining the population estimates of

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the 1957-1964 year classes (Table 7 and Fig. 1). Smoothed estimates of each age group were read from the lines fitted, by eye, to Figure 1 (Table 8).

The 1960 to 1963 year classes were about ten times stronger than the 1957, 1958, 1959 and 1964 year classes. Observations during electrofishing suggest that the 1965 to 1968 year classes were also weak, but their numbers were not estimated. Since 5 to 6 years were required to reach a length of 6 inches, the increase in numbers of large bluegills during the study is clearly due to the presence of the strong year classes. Any stockpiling caused by protection from fishing was completely obscured by these natural fluctuations. Similarly, abundance should decrease after 1969 because the 1964 to 1968 year classes were weak.

Natural mortality. - - Natural mortality rates calculated from the data in Table 8 are given in Table 9. Mortality was highest among the young and the old fish. Mortality during the third year of life, when the bluegills were 2  $1/2$  to 3  $1/2$  inches long, averaged 0.781. Mortality during ages III-V was very low (about  $25\%)$ ; it increased to  $81\%$  by age VIII.

Although mortality of each year class increased after age III, the stronger year classes of 1960-1963 had a lower percentage mortality than the weak year classes (Table 9). Thus mortality of adult bluegills, as Ricker ( 1954) predicted for most adult fish stocks, is non-compensatory, and differences in year-class strength are maintained during this phase of life. Compensation, if it occurs at all in the bluegill, must occur

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before age III; probably it occurs during the first months of life.

There was also some evidence that mortality, especially during age VI, differed among the four strong year classes (Tables 9 and 10). Mortality was highest in the 1960 year class, it declined in succeeding year classes, and it was probably lowest in the 1963 year class. This progressive change in mortality was probably caused by the build-up of the bluegill population. In effect, the agents of death became swamped not only by the large numbers of bluegills in each age group, as pointed out above, but also by the large number of bluegills in other age groups. This can readily be explained since (1) ages overlapped in size, (2) in general, predators are size selective, and (3) competition for food among bluegills (as evidenced by food habits) must exist over a rather broad range of size and age.

Re-examination of the data in an attempt to pin-point the cause of death, indicates that the number of deaths each year was not constant. More bluegills died out of strong year classes than out of weak ones, but not in proportion to numbers; consequently mortality (rate) decreased as abundance increased. For example, the 1963 year class was three times as abundant as the 1964 year class and their mortality rates during the third year of life were 71. 8% and 84. 4%, respectively. However, 2. 5 times as many of the 1963 year class died  $(63, 000$  versus  $24, 000$ ) in comparison with the 1964 year class. Similar relationships may be seen in the older bluegills: a 10-fold increase in abundance of age-VI

bluegills between 1959 (a weak year class) and 1960 (a strong year class) resulted in a 5-fold increase in the number of deaths but a decrease in death rate (Table 10).

It will be shown later in this paper that production by piscivorous fishes was relatively stable. Other predators, such as the great blue heron, were seen on the lake occasionally, but their catch of bluegills was probably small and probably varied little from year to year. Thus the number of deaths caused by predators of all types was relatively constant. It is possible that some shifting of food habits of predators may have occurred in response to uneven recruitment of prey fishes; however, this alone will not explain the higher loss of bluegills in strong year classes. Many of these deaths may have resulted, simply, from senility or physiological malfunction, and may be conceptualized as the elimination of unfit genotypes which occur with a certain frequency, irrespective of population size. Thus the number of deaths would increase with population density; but total mortality, made up of at least two components--a relatively constant numerical loss to predators and a relatively constant fractional loss to physiological malfunction- -would not be density dependent.

Comparable mortality estimates for unfished bluegill populations are available for only the sublegal population in Wyland Lake, Indiana ( Gerking, 1962). There, total mortality (a) of bluegills age II-IV, 3. 7-5. 0 inches in total length, was O. 56 (Table 11). Mill Lake bluegills of comparable size, but of slightly older age (IV -V), died at a rate of

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only 0. 23-0. 26 (Table 9). Exploited bluegills in Wyland Lake, 5.0-6. 5 inches, age III-V, had a total mortality of 0. 80, and a calculated natural mortality (n) of 0. 75--a rate comparable to bluegills of 7 to 8 inches, age VIII, in Mill Lake. Differences in mortality are reflected in longevity: V at Wyland Lake, IX at Mill Lake. The difference between lakes is even more striking because Wyland Lake had no large predacious fish, whereas Mill Lake has a substantial population of large pike and bass.

Annual expectation of death from natural causes (v), and natural mortality rate (n) measured when fishing mortality was concurrent, have been estimated for several other populations of adult bluegills (Table 11). Except for Wyland Lake, where natural mortality is unusually high, these estimates are remarkably similar. They range from 0. 47 to 0. 66, with a mean of 0. 56. In Mill Lake, the n for age-VI and older bluegills ranged from 0. 858 to 0. 369, depending on population density ( Table 9). Mortality would be close to 0. 54 if recruitment were stable (Table 14).

Standing crop of bluegills. - - Standing crop is the result of interaction between recruitment, growth and mortality. Biomass estimates for several year classes of bluegills are summarized in Table **12.** Variations in recruitment are evident by comparing crops of different year classes at the same age (diagonal, upper left to lower right). The strong classes of 1960-1963 ranged from 828 to 893 kg at

age VI; the weak 1959 class was only 95 kg. At age VII, the 1958 class was stronger than the 1959, but much weaker than the 1960- 1963 year classes. The 1964 class was much weaker than the 1963 and 1962 at comparable age.

Age-to-age changes in the biomass of the 1963 year class were typical of strong classes. By age II its biomass had reached 435 kg. Mortality exceeded growth during that age so that biomass was lower at age III. Growth exceeded mortality until age VI or older when the peak crop was reached. Thereafter, mortality exceeded growth. Biomass of the weak 1964 year class also declined between ages II and III but is expected to increase in similar fasion.

Changes in biomass during the life of a year class were related to strength of the year class because mortality was higher for weak classes than strong ones. The strong year classes peaked at ages V to VII; data for the weak 1959 and 1964 classes suggest they peak at a younger age. Similarly, among the strong year classes, the class with the lowest mortality (1962) peaked at age VII (or older) and the class with the highest mortality (1960) peaked at age V (or younger).

The totals at the bottom of Table 12 suggest that there was a very slight increase in total standing crop of bluegills during the study. This change becomes more pronounced if small additions are made for young bluegills in weak year classes which were not censused in 1967, 1968 and 1969. In general, however, one must be impressed by the relative stability of total biomass during major changes in the

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size and age distribution of the population. In 1965, only 293 kg, or about  $10\%$ , were age VI or older. In 1969, 2,744 kg  $(44 \text{ lb/acre})$ , or almost all of the biomass was old enough and large enough to interest anglers. The relatively small change in biomass from year to year, coupled with the dramatic change in size structure, reinforces the concept of a finite carrying capacity and verifies the hypothesis, suggested by the food habit study, that there is a high degree of competition among bluegills of all sizes beyond the first year of life.

Production. - - Annual production by bluegills was roughly one-half of the spring standing crop (Tables 12 and 13). For ages up to V, the production-to-biomass ratio was 1 to less than 2; for ages older than V, the ratio was 1 to more than 2.

Production by age IV and older bluegills in Jewett Lake and Lodge Lake was 44-48% and 34%, respectively, of the spring standing crops (Patriarche, 1968). Production by age II and older (larger than 3. 6 inches) bluegills in Wyland Lake was 38% of the early summer standing crop (calculated from data of Gerking, 1962). The ratio was about 50% in another Indiana lake (Gerking, 1954).

In other respects variations in production were closely linked to variations in biomass; again due to the inflexibility of growth. Strong year classes had higher production. Production by strong year classes was generally highest before or at ages where biomass was highest.

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Total production, like biomass, was relatively constant from year to year. Allowing for some small production by the 1964 and younger classes which was not estimated, total production ranged between **1,** 100 and 1, 500 kg. Like biomass, most of the production was by small, young bluegills in 1965, but by 1969 most of the production was by large, old bluegills.

Discussion of bluegill. -- Due to large fluctuations in yearclass strength, the age structure and size structure of the bluegill population were not stable during this study. It is of theoretical and practical interest to examine the characteristics of a "typical" year class; that is, one during steady state conditions. These characteristics constitute a model of the population which may serve as a guide for managing this bluegill population and others with similar attributes.

Because growth and standing crop were relatively stable, the data just presented can be used to compute a "typical" year class. Age-specific growth rates are in Table 5, and standing crop of age II and older bluegills was about 2, 700 kg. Age-specific natural mortality rates were also needed. They varied with abundance, however, and since the observed year classes were very atypical, the mean rates at the bottom of Table 9 were used. These are probably too low in the intermediate ages, where data from only strong year classes were available. Mortality rates were converted to age-specific survival rates relative to age II, and the following equation was solved to determine the number of bluegills at age II  $(N_{\text{II}})$ :

 $-24-$ 

Total standing crop = 
$$
Age IX
$$
 (avg. weight per fish) (No. fish)

$$
2,700,000 g = 3.4 N_{II} + 11 (0.2190 N_{II}) + 25 (0.1695 N_{II})
$$

$$
+ 45 (0.1303 N_{II}) + 72 (0.0964 N_{II}) +
$$

$$
97 (0.0568 N_{II}) + 111 (0.0195 N_{II}) +
$$

$$
150 (0.0037 N_{II})
$$

The number of bluegills in ages III through IX could then be calculated from the survival rates.

Population characteristics of the "typical" year class, from ages II to IX, are in Table 14. Total production of this class, 1, 273 kg, checks with data in Table 13. With this stable age structure, the number of bluegills over 6 inches long would be 279 per hectare ( 113 per acre). This is a good population of bluegills by Michigan standards. Few would reach 8 inches long or 10 years old.

The critical size, where growth equals mortality and where biomass is maximal (Ricker, 1958), occurs during age V when the bluegills are about 6 inches long. Ideally, all bluegills should be harvested then, for losses of biomass to natural mortality will exceed gains from growth at older ages. The critical size of a faster growing population of bluegills in Muskellunge Lake, Indiana, was also about 6 inches (from data of Ricker, 1958, p. 214). For the slow-growing population in Jewett Lake, Michigan, the critical size was about 5 inches (from data of Patriarche, 1968). However, since sport fishermen are not able to

fully harvest bluegills right at the critical size, harvest should begin at a smaller size and continue through life (Ricker, 1958). In a subsequent paper I will explore the relationships among yield, size limit, exploitation rate, and population size and structure, to develop a predictive model for bluegill management.

Returning to the information gathered at Mill Lake, the stability of standing crop and production from 1965 to 1969, despite large fluctuations in year class strength, suggests that the bluegill population is regulated to "fit" a fixed portion of the lake ecosystem. Whether by intra- or inter-specific mechanisms, regulation is apparently effected on recruitment prior to age II, since growth and mortality of older bluegills were essentially density independent. The pattern of year class strengths- -two very weak, four very strong, two (or more) very weak--suggests extrinsic factors, such as weather, may be involved which can over-ride or modify intrinsic regulation. These other factors would explain why the 1958 and 1959 year classes were weak rather than strong (as would be predicted after standing crop was reduced by partial poisoning in 1957), and why there were four strong year classes in a row of about equal abundance rather than of diminishing abundance. These and other arguments will be explored later on in this report.

### Pumpkinseed sunfish

The common sunfish was the second most abundant pan fish in Mill Lake. Characteristics of its population were very similar to those of the bluegill in many respects.

Food habits of pumpkinseed. - - Stomach contents of sunfish are summarized in Table 15. Due to small sample size, the data were not stratified by size groups. As with the bluegill, the large sunfish ate larger organisms than did the small sunfish. Food habits of sunfish were similar to those of bluegills, except sunfish ate relatively fewer zooplankters and insects, and relatively more snails and clams. Small differences in food habits must have been significant, however, because growth (Table 16) and condition (Table 2) of the sunfish were considerably better.

Growth of pumpkinseed. - - Pumpkinseeds grew to a length of 6 inches in 5 years (Table 16), which is about average growth in Michigan (Laarman, 1963). Growth was well below average early in life, and well above average late in life. Several specimens were 9. 0 inches long; many reached age IX.

The growth pattern of sunfish--relatively slow when young, relatively fast when old- -was like that of the bluegill. Sunfish reached 6 inches in length a full year earlier, however, and, considering their plumpness and the relatively high numbers of large specimens, the sunfish population was "better" than the bluegill population. This may

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be related to the fact that large areas of the lake (57% of the total) are less than 5 feet deep and are rather barren of vegetation.

There were no consistent year-to-year differences in growth of pumpkinseeds during the study period despite large fluctuations in year class strength. Like the bluegill, fluctuations in year class strength were 10-fold. Unfortunately, the data on seasonal growth and seasonal food habits were not adequate to conjecture that sunfish growth was also food limited and the effect of thinning the population by 75% in 1957 cannot be assessed because scale samples were not taken before and after poisoning. Growth in 1961 and 1962, 4 and 5 years later, was the same as in the period 1965 to 1969.

Abundance of pumpkinseeds. -- Population estimates of sunfish are summarized in Table 17. The number of large pumpkinseeds (larger than  $6.0$  inches) increased two-fold, i.e., from 2, 142 (16 per acre) in 1965, to 4, 232 ( 31 per acre) in 1968. The number of large fish declined in 1969, and this decline will continue until a strong year class is recruited. The number of very large sunfish (larger than 8. 0 inches) increased dramatically, from 45 in 1965 to 597 in 1969.

Changes in the size structure can be explained after population estimates by size groups are converted to estimates by age groups (Table 18, Fig. 2, and Table 19). Like the bluegill, these changes were due to uneven recruitment. Weak year classes were hatched in 1958 and 1959, strong ones in 1960, 1961, 1962 and 1963. Some members of the 1960 year class reached 6 inches by 1965, and some

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reached 8 inches by 1967. The decline in sunfish larger than 6. 0 inches in 1969 occurred because losses to natural mortality among strong classes exceeded gains from the very weak 1964 year class. Strength of succeeding year classes is not known.

Oddly, the pattern of weak and strong year classes of sunfish from 1958 to 1964 was identical to that of the bluegill. Even the magnitude of the fluctuation was the same, i.e., 10-fold. This correlation will be explored in the last section of this paper.

Natural populations of sunfish have been estimated in several other lakes. In Sugarloaf Lake the 3-year average of pumpkinseeds larger than 6.0 inches was 4 per acre (Table 1); which is  $1/4$  to  $1/7$ the number in Mill Lake. Populations were small in other southern Michigan lakes: Whitmore Lake had 2 per acre (Cooper and Schafer, 1954); Big Portage Lake had less than 1 per acre (unpublished data of Institute for Fisheries Research); and Third Sister Lake had 3 per acre (Brown and Ball, 1942). In northern Michigan, Fife Lake had 25 per acre (Cooper, 1952); Big Bear Lake had 3 to 11 per acre (Crowe, 1953); and Lodge Lake ranged from less than 1 to 11 per acre (Patriarche, 1963, and unpublished data).

Mortality of pumpkinseeds. - -The smoothed estimates of Table 19 were used to compute the rates of annual natural mortality given in Table 20. Mortality was high during the third year of life, very low in the fourth, and steadily increased thereafter. This pattern was very similar to that of the bluegill. Mortality of sunfish

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was higher during their prime years, however, 0. 312 compared to 0. 226 during age III, for example. The single observation on mortality of sunfish during age II suggests it may be slightly less than bluegills. This is plausible because the sunfish were larger and, therefore, less vulnerable to predation.

An inverse relationship between year class strength and mortality, which was true for the bluegill, cannot be confirmed or rejected for the sunfish. Mortality of age VI fish in the weak 1959 year class was higher than comparable fish in the strong 1960 year class; but, during ages VII and VIII, mortality of the 1959 class was lower. However, data for the 1959 year class may not be typical or accurate because the number of fish was small and the likelihood of sampling error was large.

Looking at the data another way, mortality of age V and older sunfish was the same in 1965 when their abundance was low (2, 459) as in 1966-1968 when their abundance was high (4, 922-5, 515). Mortality only varied from 0. 55 to 0. 59 during this two-fold fluctuation in abundance. Unlike the bluegill, there was no evidence of a reduction in mortality within successive strong year classes caused by the build-up of the sunfish population. Thus mortality of both the pumpkinseed and the bluegill would be classified as non-compensatory; i.e., mortality rate did not increase as population density increased.

An estimate of natural mortality, concurrent with fishing mortality, was made for one other sunfish population. For sunfish 6. 0 inches and larger in Sugarloaf Lake, n averaged 52% (Table 1).

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This is close to the estimate of 55-59% obtained at Mill Lake. At Muskellunge Lake, Indiana, total mortality (natural plus fishing) was very high- -about 80% between ages II and III (Ricker, 1945).

Standing crop of pumpkinseeds. - - Uneven recruitment caused by varying year class strength was reflected in standing crop (Table **21).**  Thus the strong classes, 1960-1963, developed four or more times the biomass at a given age than did the weak classes, 1957-1959 and 1964.

Changes in biomass of a year class during its life span were the net result of growth and mortality. Growth exceeded mortality early in life resulting in a rapid accumulation of biomass so that by age II the 1963 year class had reached 100 pounds, which was half its maximum. The 1963 year class accumulated little during the following two growing seasons but expanded rapidly during age IV. The maximum biomass of the strong year classes occurred at about age V but adjacent ages were nearly equal; the age at which weak year classes achieved their maximum biomass is not known. Mortality exceeded growth for the remainder of life.

The total standing crop of large sunfish ( age V and older) was lowest in 1965 and highest in 1968, and reflected the passage of weak and strong year classes. The change was nearly three-fold. Considering all sizes of sunfish, however, probably little change occurred. The 1964 through 1967 year classes are believed to be weak, and consequently, would add little to the data in Table 21. It is probable then that total standing crop varied only between 650 and 850 kg during the 5 years.

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Recall that total bluegill biomass was also relatively stable despite large changes in the size and age structure of the population.

Production of pumpkinseeds. --Production was closely related to standing crop ( Tables 21 and 22). Production was highest during age III or IV, and as a result the biomass was at a maximum the following spring.

Ratios of production to spring standing crop decreased during the life of a year class. The ratio was 1:1 for age II, 1:2 for ages IV-V and about 1:7 at age VIII. Ratios for the bluegill were very similar.

Total annual production by age groups II and older was probably highest in 1965 when 466 kg were produced. Standing crop was much higher in 1968, but most of it was comprised of older fish which had a low production to biomass ratio. In 1965 most of the biomass was comprised of younger sunfish which had a high production to biomass ratio.

Discussion of pumpkinseeds. - -Like the bluegill, the sunfish year classes observed during this study were either very weak or very strong. However, the age distribution of a "typical" year class, one which would exist if recruitment were uniform, can be constructed from the data at hand.

Growth, mortality, and total standing crop were stable characteristics of the sunfish population in Mill Lake. Therefore the averages of Tables 16 and 20 were assumed for growth and natural mortality, respectively, and biomass of age II and older sunfish was set at 725 kg. Statistics of the "typical" year class, ages II to IX, were computed from these data (Table 23).

Total production of the typical year class was 371 kg, which falls within the range actually observed during the study. The number of sunfish longer than 6 inches was 53 per ha **(21** per acre). By comparison, the number of bluegills longer than 6 inches was 279 per ha ( 113 per acre). Thus a sunfish fishery would be much smaller than a bluegill fishery.

The critical size, where growth (g) equals natural mortality (q), occurred during age V at a length of about 6. 5 inches. This is the ideal size for harvest, if the sunfish are being exploited intensively. The critical size for the slower-growing bluegill was less, about 6 inches. In a fishery containing both species, where it would be convenient to manage both the same way, there would be only a small loss in sunfish yield if they were managed the same as bluegills.

In summary, dynamics of the sunfish in Mill Lake were remarkably like that of the bluegill. Standing crop, and to a lesser extent production, were rather constant, even though recruitment was very irregular. These and other data presented suggest that: ( 1) the total sunfish population is constrained to a fixed portion of the lake ecosystem; (2) the old and large, and the young and small sunfish are ecologically equivalent on a weight basis; and (3) that population regulation is effected through recruitment of the young, rather than through mortality of the old sunfish.

#### Yellow perch

Perch were abundant in Mill Lake but few reached large size.

Food habits of perch. -- Like the bluegill and pumpkinseed, perch ate a large variety of foods; however, quantity of food per perch was low (Table 24). Small and large perch ate many of the same kinds of invertebrates but larger fish tended to ear larger items. Zooplankters, amphipods, Caenis and chironomids were frequent in small perch, but large items such as odonates made up the bulk of the diet. Large mayflies, fish and crayfish became more frequent as the perch became longer.

Growth of perch. --On the average, perch attained a length of 7. 7 inches at age V, but some fast-growing perch exceeded this length at age III and some slow growers had not reached it by age VII. Average length usually increased with age; however, the average length of old perch in two year classes declined (Table 25). This may have been due to better survival of slow-growing fish or, what is more likely, to errors in sampling or scale reading.

Growth of Mill Lake perch was, as a whole, slower than the state average (Laarman, 1963). There were significant differences among year classes, however. The 1961 year class grew slower than any other, requiring an additional year to reach 7 inches. The 1960 and 1962 year classes also grew slowly, a half year behind the others, Typically, perch grew slowly early in life, but about at state average from age IV on.

Growth of different year classes was inversely correlated with their numerical strength. The 1961 year class was the strongest and grew the slowest; the 1963, 1964 and 1965 were the weakest and grew the fastest; and the 1960 and 1962 were of intermediate strength and growth (Tables 25 and 28). This relationship will be quantified in the section on standing crop.

The strong year classes of bluegills and pumpkinseeds in 1960-1963 apparently had no beneficial effect on the growth of perch. Large numbers of these centrarchids, small enough to be readily eaten by larger perch, were present in the lake during 1960-1965. And with this food abundant, the size of perch in 1965 was less than in later years. On the other hand, growth of perch was apparently not hindered by competition with bluegills and sunfish. Although the strong year classes of slow-growing perch in 1960, 1961 and 1962 coincided with strong classes of bluegills and sunfish, the class of 1963 also grew up with strong classes of bluegills and sunfish, but was of average abundance and average growth. Also, growth of the 1964 year class, which was of average abundance, was average even though the other species had weak year classes. Thus the competitive effect of bluegill and sunfish can be factored out, and I conclude that growth of perch is primarily a function of perch density; i.e., intraspecific competition.

Growth of perch from 1965 to 1969 was comparable **to** prethinning levels in 1957. It was better in 1961, the first sample taken after treatment, but just as poor in 1962.

Abundance of perch. - -Numbers of large perch ( 7. 0 inches and larger) declined during the study ( Table 26). In 1965, there were **11.** 8 per acre; by 1969, only 1. 7 per acre. Perch may have been more abundant in the early 1960 's when the lake was reputed to have a fair perch fishery.

The decline among larger perch was due to uneven recruitment. The strong year classes hatched in 1959 to 1962 dominated the population during the first half of the study, and as they died out, they were replaced by the weak year classes of 1963, 1964 and 1965 (Tables 27 and 28, and Fig. 3). Because of slow growth and short life span, any one year class dominated the population for only a short time. As a result, fluctuations in recruitment were not tempered much, and they had a pronounced effect on numbers of large perch. Accordingly, a fishery would have to be very flexible to make optimum use of the perch population.

The abundance of the 1959 to 1965 year classes can be compared at age V (Fig. 3). The 1961 year class was strongest, with 1,000 survivors; the 1959, 1960 and 1962 year classes had about 550; the class of 1963 had 170; and the 1964 year class had 60 survivors. Judging from the estimates made at age II, the 1965 year class was
only half as abundant as the 1964. Thus in 6 years the year class strength varied from 30 to **1,** 000, a factor of 33.

Comparable estimates have been made at several other Michigan lakes, but unfortunately each population was either very unstable or of poor quality (from a sport fishing point of view). In an experiment at Cassidy Lake, where perch were the only game fish present, large perch (7. 0 inches and longer) became as dense as 21 per acre (Shaffer, 1968). In a similar experiment at Jewett Lake, the population reached 89 per acre (unpublished data of author). Neither population was being exploited and both were unstable. In another single-species lake, Ford Lake, there were only **1** to 2 large perch per acre (Eschmeyer, 1938). A fast-growing but short-lived unexploited population in Cub Lake ranged between **1** and 33 per acre over 3 years (Clady, 1970). The following unpublished estimates for several exploited populations in the Rifle River Recreation Area of Michigan, have been supplied by M. Patriarche: 3. 6 and **11.** 3 per acre in two different years for Jewett Lake; 7. 4 and 33. 6 per acre for Lodge Lake; 5. **1** per acre at Scaup Lake; and up to **17.** 5 per acre at Grebe Lake. The perch fisheries in these lakes were small and incidental to those for other species. As in Mill Lake, the size of the perch population varied greatly from year to year.

Population estimates have not been made in" good" perch lakes. However, estimates of catch by anglers are available from the U.S. waters of Lake St. Clair, one of the best perch fisheries in

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Michigan. The average catch for 1966 and 1967 was about 35 per acre (J. Ryckman, personal communication}. It is likely that the perch population was two to three times greater, and obviously much denser than populations in the inland lakes mentioned above. The yield from Sugarloaf Lake, which had a fair perch fishery amounting to 40% (by number} of all fish caught (Christensen, 1953}, was 52 per acre, a 5-year average (Cooper, 1953}. This estimate includes some perch smaller than 7 inches; however, the population is still much denser than other inland lakes which have been studied.

Mortality of perch. - -Mortality of perch was very high during age I, decreased and remained relatively constant from ages II to VI or VII, then increased as the year classes disappeared at ages VII to IX (Table 29). This pattern differed from that of bluegills and sunfish, in that mortality of perch was constant over many ages, whereas mortality of the other species increased gradually every year beyond age III. Note also that mortality of perch was higher--a mean of 70% during age III compared to  $23\%$  for bluegills and  $31\%$  for sunfish.

Mortality differed among year classes (Table 29). This may be readily seen in Figure 3 where, from ages III to VI, the slopes of the regressions are not parallel. A correlation between year class strength and mortality was destroyed because mortality of the weak class of 1964 was nearly as high as mortality in the strong class of 1961. Table 30 shows that there is clearly no relationship between

abundance of age IV and older perch in the spring and their mortality in the **12** months following. From a high in 1965, the population progressively declined to a low in 1969. A 21-fold change in abundance took place, yet mortality only ranged between O. 69 and O. 77. The number of deaths decreased correspondingly from 3, 794 to 459. This change cannot be attributed to predation because, first, there were few predators (pike and bass) large enough to take perch this size, and second, the number of large predators remained constant, or even increased during the study. On the contrary, because the number of prey fishes of other species was low in the latter years of the study, predation on large perch should have increased. Apparently, most large perch died from intrinsic causes which occurred with a constant frequency.

Two comparable mortality estimates for Cassidy Lake perch can be made from data given by Shaffer (1968). From the spring of 1965 to the spring of 1966, 48% of the age II and older perch died. The following year, 37% of the age III and older perch died. In Cub Lake, mortality of perch, of age II and older, was on the order of 15 to 45% (from data of Clady, 1970). These rates are significantly less than those observed at Mill Lake.

Standing crop of perch. -- The standing crop of perch fluctuated because of uneven recruitment ( Table 31). On an age-specific basis, biomass at age V, for instance, ranged from 58 kg (for the 1961 year class) to 6 kg (for the 1964 year class)- -a 10-fold difference. Since

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there was a 17-fold difference in numerical abundance of these two year classes at that age (Table 28), growth has compensated for abundance and dampened fluctuations in standing crop to some extent. Uneven recruitment also caused a decline in biomass of older (and larger) perch from 60 kg in 1965 to 26 kg in 1969.

A year class achieved its greatest bulk at an early age because mortality was high and growth poor later in life. Thus for the 1965 year class, biomass at age I was a couple times greater than at age II, and judging from the pattern of other classes, would have been greater at age I than any other age (Table 31). Undoubtedly, biomass of other year classes also peaked at age I because their growth was no better and their mortality was as high.

Standing crop of all age groups was 369 kg in the spring of 1966. The crop in 1965 was larger, probably over 600 kg when allowance is made for age-I fish which were not estimated. Total standing crops in other years cannot be accurately estimated because the relative strength of the 1966 to 1968 classes is unknown. It is likely, however, that they were weak and that total biomass in 1968 and 1969 was less than in other years. Even so, total biomass probably varied by a factor of only two to three times, suggesting that, like the bluegill and pumpkinseed, total biomass is a more stable population characteristic than numerical abundance or size-age structure. For perch, however, compensation occurs through growth as well as recruitment.

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Several different ways of expressing growth and abundance were graphed and examined. Each way, except one, indicated an inverse relationship: when abundance increased, growth decreased. The exception, which showed no relationship, was a series of graphs, by age group, of spring standing crop versus instantaneous growth (g) during the following year. However, I feel that g is not an appropriate measure of growth for this comparison because it is relative to initial size of the fish. Thus, if fish in two year classes differ in average weight initially and their relative growth  $(g)$  is the same, the larger fish are actually growing comparatively better because g usually declines with size. Also, the two classes will continue to diverge in absolute size.

Another way of expressing growth, which is the result of cumulative effects of population density (principally year class size), is the average weight of a year class at an age. When mean weight at age V was graphed against standing crop at age V, a linear regression was obtained in which a 10-fold increase in biomass resulted in a 2-fold decrease in average weight. Slopes of comparable regressions made when perch were ages IV or III were, progressively, not as steep and by age II size of perch showed no relationship at all to biomass at age II. This suggests that growth of perch in a year class is independent of their density up to age II (within the range of 28 to 81 kg) and that growth becomes increasingly density dependent with age. Similar conclusions were reached when numerical abundance was

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used instead of standing crop. The quantitative relationship differed, however, due to growth compensation. At age V, for example, a 16-fold increase in numerical abundance resulted in a 2-fold decrease in mean weight. As mentioned earlier, when abundance was expressed as standing crop, only a 10-fold change had the same effect on size.

Production by perch. - -Production by perch was small compared to that of bluegill and pumpkinseed. During the 1966 growing season, perch of age I and older produced only **161** kg- -about one-ninth and one-third of the production by bluegills and sunfish, respectively ( Table 32). If production by age-0 perch had been estimated, this total would have been considerably larger. In fact, production during the first year of life must have exceeded production during any other age because it was the only age in which growth exceeded mortality. As a direct result, biomass of a year class was greatest the following spring (Table 31).

The ratio of production to standing crop declined during the life of a year class, from about O. 8 during age I to O. **1** during age VII, but was rather constant at 0.3-0.4 over a wider range of intermediate ages because growth and mortality were relatively constant. For the fast growing perch in Cub Lake, Clady ( 1970) computed ratios of **1.** 75 and **2.** 40 **(2** years); however his calculation included the first year of life.

Uneven year class strength resulted in fluctuations in production which paralleled those in standing crop in direction and magnitude. Thus the strong year classes produced more at a given age than weak year classes even though they grew more slowly. Uneven recruitment also resulted in declining production of larger perch between 1965 and 1969.

Discussion of perch. --Because growth was density dependent, the dynamics of the perch population was more complex than the dynamics of the bluegill and pumpkinseed. Recruitment of perch was very irregular and not clearly related to perch abundance or to other population characteristics. Natural mortality was high and relatively constant ( on a percentage basis) after the first 2 years of life and was not related to numerical abundance or standing crop. Thus whenever a strong year class appeared, it retained numerical abundance throughout life. Growth, however was closely related to standing crop and, to a lesser extent, numerical abundance of perch but was not correlated with abundance of other panfish. Thus perch in weak year classes grew faster. Growth was inversely related to density but was not proportional; i.e., a large change in standing crop produced a small change in growth. This density feedback was weaker among young perch than among old perch, suggesting that competition among older (and larger) perch was more severe. Density effects were cumulative: by age V a perch which grew up when the biomass of its generation and that of preceding generations was high was one-half the weight of a perch which grew up when perch biomass was one-third as great. The interaction of constant mortality and density dependent, but non-proportional, growth was such that strong classes had larger standing crops and produced more than weak

classes. However, because of growth compensation, standing crop and production were more stable population characteristics than numerical abundance or size-age distribution.

A "typical" (average) year class of perch was constructed by a slightly different method than that used for the bluegill and pumpkinseed. For the sunfishes, an average value of total standing crop was selected from within the range observed, and the structure of the population was computed from mortality and growth data. This was not a good approach with the perch, however, because total biomass was only measured in 1966, a year when the young, most productive age groups were occupied by weak year classes, and, consequently, total biomass was less than usual. Instead, abundance of the "typical" class at age III was set at 3, 000 perch, which is a level of abundance commensurate with the average growth data at the bottom of Table 25. Abundance of other age groups was then calculated by means of the average mortality data in Table 29. Characteristics of the typical year class so generated are summarized in Table 33.

The spring standing crop of the typical year class was 844 kg of which more than half, or 484 kg, was of age I. By contrast, a biomass of 369 kg was present in 1966, of which only 80 kg was contributed by age I perch of the weak 1965 year class. Annual production by the typical year class was also higher than observed production during 1966--636 kg versus 161 kg--due again, to the weak year class at age I. This additional production by the typical year class could have been attained because growth is insensitive to population density early in life.

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Another characteristic of the typical year class was that mortality exceeded growth after the first summer of life. Thus the critical size, where growth equals mortality, and the size at which the perch harvest would be a maximum, is less than 3 inches--a size uninteresting to anglers. However it is a size useful to the piscivorous fishes, bass and pike, and it is likely that much perch production was diverted into these predators. In fact, optimum use of the perch in Mill Lake would be attained by managing them primarily as a forage species which should be preyed upon at the critical size, and only secondarily as a directly harvestable resource.

It is evident from the model that few individuals live long enough and grow big enough to interest anglers. Only about 11 perch per hectare  $(4.5/\text{acre}; 0.9 \text{ kg/ha})$  would reach 7 inches long; too low a density for a good fishery. Reducing natural mortality (if possible) would not enlarge the fishable stock much, because growth would decrease, length of time required to reach 7 inches would increase, and natural mortality would be operative longer. On the other hand, an intensive fishery which removed all perch when they reach 7 inches long would not stimulate growth of smaller perch much, because the food habits of large and small perch are slightly different. The strong relationship between growth of large perch and standing crop of large perch is evidence that their abundance was primarily limited by their food supply, and consequently manipulation of the perch population itself would not enlarge the fishable stock.

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Presuming that it is possible for man or another predator to efficiently harvest perch at the critical size of 3 inches, an estimate is needed of the number of fish which should be allowed to spawn so that the typical year class can replace itself. Only a rough estimate can be made since, for as LeCren ( 1965) has pointed out (for the European perch, Perea fluviatilis), recruitment is only poorly correlated with the size of the adult stock, and year-to-year variations in recruitment seem to be linked to environmental factors. Recruitment of yellow perch in Cassidy Lake was also independent of the size of the adult stock (Shaffer, 1968). At Cassidy Lake, under extremely favorable environmental conditions, the number of perch surviving to age I was equal to 10% of the number of eggs carried by the parental stock. If survival was as high as 10% in Mill Lake, which may be possible at low perch densities caused by an intensive harvest, then almost all perch could be harvested in their second year of life without reducing recruitment. To be on the safe side, however, let us assume that survival is 1%. Then 13 million eggs are needed to replace the typical year class which begins with 127, 700 age-I recruits. Perch in age groups I, II and III alone would produce 16 million eggs.  $^1$ Mortality of perch, then, can be increased by an intensive harvest to include most of the males and all perch of age **IV** and older ( roughly, those larger than 6 3/4 inches).

<sup>1</sup> Calculated from the population estimates in Table 28, length data in Table 25, and unpublished data on maturity and fecundity of Cassidy Lake perch.

If the typical year class was not harvested at all, it would produce 23 million eggs annually. Of these, 127, 700 would reach age I, for an average survival of 0. 56%. By contrast, an unusually large population of perch in Mill Lake produced 35 million eggs in 1965. However, the resulting 1965 year class was unusually weak, only onesixth the size of a typical year class. Survival from egg to Age I was only 0. 06%. This should not be construed to mean, however, that the 1965 year class would have been smaller, or larger, if its parental stock had been smaller, or larger, but simply points out the extent to which environmental factors may influence recruitment.

In summary, the perch will sustain only a small fishery because the food supply of Mill Lake restricts abundance of large perch (larger than 7. 0 inches) to an average of 11 per hectare (4. 5 per acre). Because of slow growth and high mortality, the critical size of perch is about 3 inches long. Consequently, an intensive, virtually unrestricted fishery by man or another predator should be encouraged to increase yield.

## Black crappie

Crappies were not abundant in Mill Lake but many were of good size. They were readily taken in trap nets, and excellent population estimates were obtained.

Food habits of crappies. -- Due to difficulty in capturing crappies with electrofishing gear, the stomach contents of only a few specimens (mostly small) were examined (Table 34). The diet of small

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and large crappies was similar and, like the bluegill, sunfish and perch, their food was diverse. There were, however, significant differences between crappies and these other species; namely, the presence of Chaoborus, which was frequent in larger crappies, and the greater importance of fish in the diet of small specimens.

Some of the prey fish had yolk sacs and, judging from the time of year the crappies were collected (June 5), were probably newly hatched centrarchids. Perch and cyprinids were among the larger prey fish. Many of the insect prey were in pupal or adult stages rather than larval stages. This observation, coupled with the importance of other planktonic forms in the diet, suggests that the crappies were more pelagic than were other fish.

Growth of crappies. -- Mill Lake crappies averaged 7. 3 inches long at age III (Table 35). This is slightly less than the state average of 7. 5-7. 7 inches (Laarman, 1963). At age IV, however, they exceeded the state average and they continued to grow well until death. Thus, like the other panfishes, growth was relatively poor early in life and relatively fast late in life. The largest crappie collected was 13. 6 inches long.

There was remarkably little difference in the growth of crappies in different year classes in spite of large fluctuations in year class strength. At age V, for example, there was a 15-fold difference in class strength but only a 0. 5-inch difference in average length. However, the few very large specimens which were collected belonged to the weakest year classes.

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The effect of the partial poisoning of Mill Lake in 1957 on the growth of crappies cannot be assessed because scale samples were not collected until 4 years later. At that time, in the fall of 1961 and the fall of 1962, they were growing at the 1965-1969 average, and it is apparent that any beneficial effects of thinning on growth were shortlived. However, growth of crappies should have been good in the early 1960's for another reason; forage fish were abundant because the strong year classes of bluegill, sunfish and perch were hatched then. No explanation for the non-response of crappie growth is offered.

Abundance of crappies. --The size structure of the crappie population in Mill Lake from 1965 to 1969 is summarized in Table 36. Crappies smaller than 6 inches were hard to catch and, consequently, were not estimated. Estimates of crappies larger than 7 inches are believed to be highly accurate.

The number of crappies 7 inches and longer averaged 1, 619 ( 29 per ha) and varied little from year to year ( range, 1, 473 to 1, 87 5). There was a change in size structure however. In 1965, there were only 29 crappies between 10 and 12 inches; by 1969 there were 688. This increase resulted from unusually high survival of the 1962 and 1963 year classes. Reasons for the exceptionally good survival of these two year classes (and not others) are obscure but do not seem to be related to protection from angling.

Estimates of the age and year class distribution of crappies are in Figure 4 and Table 37. They have not been smoothed because

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sampling errors were small, as evidenced by the progressive decline of each year class with age.

The occurrence of uneven year class strength is evident from Figure 4. The 1961 year class was the strongest up to age VI, when it was surpassed by the 1962 and 1963 year classes which had better survival. The 1959 and 1960 year classes were the weakest.  $^2$ The most extreme difference in class strength occurred at age VI: only two crappies survived from the 1959 year class, whereas there were 462 survivors from the 1963 year class. At age III, perhaps the best age for comparison, the difference in year class strength was 3 to 4-fold.

The average number of crappies larger than 6 inches was about 32 per hectare--a denser population than most other lakes in Michigan where comparable estimates have been made. Sugarloaf Lake averaged 4 per hectare (Table 1); Whitmore Lake had 2 per hectare (Cooper and Schafer, 1954); Big Portage Lake had 1 per hectare (unpublished data, Institute for Fisheries Research); and Fife Lake had 59 per hectare in 1950 (Cooper, 1952) but only 16 per hectare in 1958 (Christensen, 1960). In the Rifle River Recreation Area, Devoe Lake had less than 3 per hectare; there were 85 per hectare (2-year average) larger than 7 inches in Lodge Lake; and an experimental population in Grebe Lake reached densities as high as 96 per hectare (unpublished data of M. Patriarche).

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This is not a strictly valid comparison because the 1959 year class could have been reduced by fishing prior to age VI, whereas few of the 1963 year class were vulnerable to angling before fishing was prohibited.

Mortality of crappies. - -Annual natural mortality rates (n) calculated from the population data in Table 37 are given in Table 38. Mill Lake crappies were not long-lived; none were older than age VIII.

Mortality was relatively low early in life, and relatively high late in life. An average mortality rate could be calculated for each age group but it would have little utility because there were large differences in mortality among the year classes. For example, death rate during age V was  $0.178$  for one year class, but  $0.729$  for another year class. Like the bluegill, there were consistent differences in mortality rates among the year classes of crappies. This may be seen by comparing the slopes of the survival curves in Figure 4. The 1964 year class experienced a lower mortality than did any other year class (based on only one observation); the 1963 year class had the second lowest mortality; and the 1962 had the third lowest rate of mortality. Unlike the bluegill, however, these differences were not clearly correlated (negatively) with year class strength, and I cannot explain them.

Shapes of the survival curves for crappies also differed among year classes (Fig. 4). The survival curve of the strong 1961 year class had a strong deflection at age V, and survival was relatively linear thereafter. By contrast, the strong 1963 year class and the average 1962 year class had a flat survival curve until age VI (or older) and, if these classes are going to die out at around 8 years, as the other classes did, then their survival would have to decrease tremendously during ages VII and VIII.

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Since the crappie survival curves were not smoothed, it is possible to look at year-to-year fluctuations in mortality ( Table 39). Mortality of age IV and older fish was much higher in 1966 than during any other year, due primarily to the just mentioned die-off in the 1961 year class. The reasons for this die-off cannot be resolved with the data at hand. However, I suspect that every abundant year class of crappies experiences an abrupt change in mortality sometime between age V and VII. Death is probably caused by physiological aging (senility) and is triggered by stresses induced by crowding and by unknown environmental factors. Using the same line of reasoning, mortality of the 1962 and 1963 year classes was unusually low because these stresses were unusually low. Overall, the data in Table 39 indicate that there was little relationship between number of deaths, or between mortality rate of adult crappies, and their standing crop. Few of these deaths could have been caused by predacious fishes because crappies of age IV and older averaged more than 8 inches long ( Table 35).

In the 12 months between the spring of 1965 and the spring of 1966, 33% of all crappies of age III and older died from natural causes. Comparable estimates in two other 12-month periods were 39 and 30%. These estimates from Mill Lake are lower than others reported in the literature. At Sugarloaf Lake, crappies of ages II through V experienced a total mortality of 81%, of which 53% was assigned to natural causes (Table 1). Natural mortality of crappies in Spear Lake, Indiana, was reported by Ricker (1955) to be about 60%. A similar estimate--61%--

was calculated by Ricker ( 1945) for black crappies in Foots Pond, Indiana.

Standing crop of crappies. --Because growth was essentially non-variable, fluctuations in standing crop (biomass) paralleled those in numerical abundance (Table 40). Thus at age III or IV there was about a 4-fold difference in biomass between the very strong 1961 year class and the weak 1966 year class. The 1959 and 1960 year classes were probably even weaker, but a comparison is difficult because they were exploited before the study began.

A year class usually reached its greatest biomass at the beginning of age IV, and losses to mortality exceeded gains from growth thereafter. However, the standing crops of the 1962, 1963 and 1964 year classes were about as large at age V and VI because their survival was unusually high. For the same reason there was nearly a 2-fold increase in the cumulative biomass of age III and older crappies, from 193 kg in 1965 to 354 kg in 1969. All of the increase went into large, relatively old crappies with a short life expectancy. A rough calculation rules out the possibility that the increase in biomass of age III and older crappies was balanced by a decrease in biomass of age I and II crappies. The biomass at age I and II is typically about 25 to 35 kg--much less than the 160 kg gained by the older fish. During this same 5-year interval bluegill and sunfish standing crops were relatively stable, whereas perch biomass declined.

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Production by crappies. --Annual production by the 1960 through 1965 year classes is summarized in Table 41. Variations in production were closely linked to variations in standing crop, again due to the inflexibility of growth. As a result, production-tobiomass ratios were unrelated to year class strength, and strong year classes produced more than weak year classes.

Productivity of crappies, like the other panfish, changed with age. Production was greater during age III (the youngest age sampled) than at any other age; as a result, standing crop was highest the following spring. Average ratios of production to spring biomass were 0. 69 at age III, and 0. 29 at age IV; they declined steadily to 0. 14 by age VII. The large decrease in the ratio, between age III and age IV, is primarily due to the marked decrease in relative growth rate which is characteristic of this (and most other) crappie populations.

Year-to-year changes in production by age III and older crappies followed the increasing trend of standing crop, but were much smaller. Production increased from 81 kg in 1965-1966 to 105 kg in 1968-1969, a 30% gain. Standing crop increased from 193 kg to 354 kg, or 82%, during the same period. The greater stability of production as compared to biomass does not have special significance. It was the result of shifts in the age distribution of the population caused by low mortality among the large, old crappies, which were low in productivity, and the recruitment of weak year classes into the young, productive age groups. Productionto-biomass ratios for age III and older crappies changed correspondingly from o. 42 in 1965 to o. 32 in 1968.

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Discussion of crappies. --The salient features of the black crappie population in Mill Lake may be summarized as follows. Growth was rapid until about age IV and essentially independent of the density of crappies in the ages studied (age III and older). Mortality was much more variable but seemed to be low through middle age and to increase abruptly late in life. Obscuring this general pattern were pronounced differences in mortality among year classes, a sudden die-off in one year class, and unexpectedly good survival by old crappies in two year classes. None of these deviations from the general pattern were clearly related to population density or other factors. Variations in recruitment caused by weak and strong year classes were not so great as occurred in the bluegill, sunfish or perch, being only 3- or 4-fold at age III. The strongest year classes were the 1961 and 1963; the weakest was the 1966. The classes of 1959 and 1960 probably also were weak. The interaction of growth, mortality and recruitment during the 5 years of the study resulted in the following: no change in the number of crappies larger than 7 inches, an increase in the proportion of old and large crappies, a nearly 2-fold increase in spring standing crop, and a small increase in annual production.

The observations that standing crop was not very stable and that recruitment, growth and mortality were not correlated with crappie density, suggest two things: that the crappie population was not so closely or predictably regulated; and that, to a greater extent, regulation was affected by extraspecific factors rather than intraspecific, density-feedback

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mechanisms. Since crappies are piscivorous, and since huge fluctuations in year-class strength of bluegills, sunfish and perch occurred during the study, it is possible that the food resources and, hence, the carrying capacity did increase, thereby enabling the biomass of crappies to increase. I am unable, however, to see any relationship between crappie growth, recruitment, or mortality, on the one hand, and year class strength of bluegills or sunfish, on the other hand. There is however, a suggestive negative correlation between crappie and perch biomass. During the years when crappie biomass was increasing by 160 kg, biomass of perch of age IV and older was decreasing by about the same amount. Although it is unlikely that a decline in adult perch (which I earlier ascribed to poor recruitment) would stimulate an identical increase in adult crappies, there was probably enough overlap in their food habits to explain part of the increase.

In order to develop a model of the crappie population which would exist if recruitment was uniform, I assumed that growth and mortality were density independent within the range observed at Mill Lake. The average lengths and weights at the bottom of Table 35 were used for growth of the typical population and an average standing crop of age III and older crappies of 5. 24 kg per ha was calculated from the data in Table 40. It was very difficult to objectively select age-specific mortality rates for the model because of the great differences in mortality among the year classes which were studied. The following estimates of natural mortality seem reasonable: age III, 0. 30; age IV, o. 26; age V, 0. 45; age VI, 0. 62;

age VII, O. 78; and age VIII, 1. O. The first four estimates are averages from Table 38, and the last two were selected because they were logical extensions of the curve formed by the averages. The assumed curve is intermediate in shape between the type (e.g., 1962 year class) where survival was good until age VII, and presumably, very low thereafter, and the type (e.g., 1961 year class) where survival decreased greatly during age V and was uniform thereafter.

Population characteristics of the typical, unexploited, crappie year class generated by the model are summarized in Table 42. The model begins at age III and continues through age VIII, which is about the maximum life span of crappies in Mill Lake. The growth, standing crop and production data for age VII may be inflated because the average weight is biased by a few very large specimens. However, crappies this old were not abundant, and these errors are relatively unimportant. Total production by the typical year class was 1. 81 kg per ha per year, which falls within the range of 1. 4 to **1.** 9 which was observed in Mill Lake. Standing crop was highest during ages IV to V. Production was highest during age III, then relatively constant for 2 or 3 years, and then fell off rapidly.

Since the average length of the crappies in age group III was 7. 3 inches, virtually all ( 30. 6 per ha) of the crappies included in the model were large enough to interest anglers, and a population of that size would support a modest fishery. The ideal length for intensive harvest, i.e., the critical size, was 8. 5-9. 0 inches. It was reached

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at the beginning of age IV. Since a sport fishery cannot harvest the entire population right at this size, harvest should begin at a smaller size and continue through life. At high levels of exploitation, however, imposition of a size limit close to the critical size may increase yield, because if anglers are unrestricted, they will keep crappies much smaller than the critical size. In this respect there is a greater danger of over-exploiting crappies (i.e., wasting potential yield) than overexploiting bluegills or sunfish, because the critical sizes of the latter are closer to the minimum sizes which anglers will keep. Only 28% of the crappies in Sugarloaf Lake were harvested (Table 1); exploitation rates in three Indiana lakes as reported by Ricker (1945 and 1955), were even less.

## Largemouth bass

Largemouth bass were the most abundant game fish in Mill Lake. The population supported a good fishery prior to prohibition of angling.

Food habits of largemouth bass. - -Samples of bass up to 12. 2 inches long were secured by electrofishing on August 3, 1966, October 26, 1966, and June 5, 1969. The contents of their stomachs were examined and tabulated according to three size groups (Table 43). No small bass, i.e., 2. 1-4. 9 inches, were collected in June.

The food of the largemouth bass in Mill Lake was not unusual. Relatively large food items predominated in both large and small bass.

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Naturally, large bass could and did eat larger sized organisms. Fish, especially perch and minnows (cyprinids), comprised the bulk of the stomach contents and occurred more frequently than any other type of food. Insects, mainly juvenile and adult odonates, were common. Crayfish were frequently found in larger bass.

Growth of largemouth bass. - -Bass grew slowly in Mill Lake. At age I they were 0. 9 inch shorter than the state average, and most did not reach a length of 10 inches until age IV (Table 44). The typical Michigan bass reaches 10 inches during age III (Laarman, 1963). Unlike some other species of fish in Mill Lake, growth of bass did not improve much ( relative to the state average) as they became older (and larger). However, a few old individuals did exceed 20 inches.

There were small differences among year classes in the average lengths and weights of bass. In the 1962, 1963 and 1964 year classes, growth was slowest. For example, at age V the 1962-1964 bass were about 25% lighter than age V bass in earlier year classes. Growth of the 1966 year class was slightly better than growth of year classes adjacent to it. The 1958 year class, which hatched just prior to the rotenone treatment in the summer of the same year, had the fastest growth of all. At age VII they were 1. 4 times heavier than bass in the slow growing 1962 year class.

A negative correlation between the abundance of a year class and its growth suggests that growth is compensatory. The 1962 and 1963 year classes were the strongest and grew most slowly; the 1957-1959

and 1961 year classes were among the weakest and had the fastest growth. This may not be the entire explanation, however, as small samples collected by seine in 1961 and 1962 indicate that the length of bass in these weaker year classes was little better than average. Apparently growth improved between 1962 and 1965, while these classes were middle-aged, and may have been the result of ( **1)** becoming large enough to feed readily on the strong year classes of panfish which were brought off in the early  $1960$ 's, or (2) a compensation for angling mortality which took place before fishing was prohibited. Point (1) may explain why the 1960 year class grew better than the 1962 year class, even though they were equally abundant. Point (2) may apply to the 1957-1961 year classes because they exceeded the 10-inch minimum size limit before the lake was closed to fishing in 1965.

The relationships between growth, standing crop and production, and the evidence for year-to-year fluctuations in growth, are discussed in later sections.

Abundance of largemouth bass. - - The estimated numbers of bass in various size (inch) groups are summarized in Table 45. Estimates are not so precise as those for crappies, because bass were harder to catch and because there were only small numbers of bass in certain size groups. There is some evidence that reliable estimates were not consistently obtained until bass were longer than **11** inches and of age **V** and older.

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The number of bass 11 inches and larger ranged only from 645 to 693 between 1965 and 1968. In 1969, the number jumped to 1, 339 due to an increase in 11- and 12-inch bass. The increase can be traced to the entry of the strong 1964 year class (Tables 44 and 46). The number of bass 10 inches and larger ranged from approximately 1, 040 (18. 9 per ha) to 1, 958 (35. 6 per ha) and averaged 1, 281 (23. 2 per ha).

The year class composition of the bass population was determined from the size group estimates and the frequency of various classes in the scale sample collections (Table 45). Successive estimates were graphed and survival curves were fitted by eye (Fig. 5). Smoothed estimates (Table 47) were read off the graph. Estimates of the 1963 and 1964 year classes at age IV were not graphed because they were less than estimates at age V; I believe that estimates of the larger bass are more reliable.

Recruitment of bass was less variable than recruitment of panfishes. The 1957 and 1958 year classes were the weakest, and the 1962, 1963 and 1964 were the strongest; however, the difference between them was only 2-3 fold. It was pointed out earlier that the abundance of the 1961 and preceding year classes may have been reduced by fishing prior to 1965. Since these classes were relatively weak, fluctuations in recruitment, due to natural causes alone, would have been even smaller than actually observed.

Estimates of largemouth bass 10 inches and larger have been made for several other Michigan lakes. Two of these were unexploited.

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In Third Sister Lake there were 12 bass per acre (Brown and Ball, 1942), and in Cub Lake, there were 25 per acre (Clady, 1970). A comparable average for Mill Lake was 9. 4 per acre ( range 7. 6 to 14 per acre). Among the exploited lakes in southern Michigan, Sugarloaf averaged 2. 5 bass per acre (Table 1), Whitmore about 6 per acre (Cooper and Schafer, 1954), and Big Portage 1 per acre (unpublished data of Institute for Fisheries Research). Among the exploited lakes in northern Michigan, Fife Lake had 3 largemouth per acre in 1950 (Cooper, 1952) and 5. 5 per acre in 1958 (Christensen, 1960); and Lodge and Jewett lakes averaged about 1 and 15 per acre, respectively ( unpublished data of M. Patriarche). The unfished lakes generally had larger populations of largemouth bass than did the exploited lakes.

Mortality of largemouth bass. - - Annual natural mortality rates computed from the smoothed population estimates are given in Table 48. Mortality averaged 33% during ages IV and V and gradually increased to 59% during age VIII. The data suggest that mortality may decrease during very old age; however the number of fish was small and the estimates may not be accurate.

There was no relationship between the strength of a year class and its mortality rate. At the beginning of age V the 1961 and 1963 year classes were the strongest. During that age the 1963 year class had the lowest mortality, i.e., 9. 9%; and the 1961 year class had the highest, i.e., 52. 6% or more. Weaker year classes had intermediate

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mortality rates of about 33%. At other ages there was surprisingly little difference in mortality among the year classes; however, there was only a 2-fold variation in year class strength.

The extraordinarily high survival within the 1963 year class during age V warrants additional comment. In the year 1968 the empirical data for the 1962 year class deviate by 120 fish from the smoothed data. This is the largest deviation in the bass estimates. If the empirical data are more accurate than the smoothed data (and the large deviation is not a sampling error), the survival of this class was also very good in 1968 (and, consequently, very low in 1967). Survival of the 1961 year class during 1968 may also have been slightly underestimated by smoothing. Taken together, these observations suggest that mortality of adult bass was probably above average in 1967 and below average in 1968. Mortality of crappies also showed a year-toyear fluctuation; however, for them a high number of deaths occurred in 1966. I am unable to explain fluctuations in mortality for either species.

An average figure, representing the yearly natural mortality of legal bass (10. 0 inches and larger, approximately age IV and older) was obtained as follows. Empirical estimates of age IV and older bass in the spring of 1965 and 1966 appeared to be reliable, and their mortality was simply the number of age IV and older bass in the spring of year  $1$  (1965 or 1966) minus the number of age V and older survivors in the spring of year 2 ( 1966 or 1967) divided by the number of age IV

and older bass in year 1. The yearly mortality rates so derived were 35% for 1965-1966 and 45% for 1966-1967. Empirical estimates of age IV bass in 1967 and 1968 do not appear to be reliable and a similar computation was begun at age V. Mortality of age V and older bass was very high  $(71\%)$  in 1967 and very low  $(14\%)$  in 1968. I have reservations about the precision of the empirical estimates underlying these extreme values of 14 and 71%; however the average of all four estimates (41%) looks reasonable.

In Sugarloaf Lake annual expectation of death from natural causes of legal bass averaged 35% over a 5-year period, and there was a concurrent exploitation rate of 35% (Table 1). From the agefrequency data given by Brown and Ball ( 1942), I calculated that the total mortality of age III+ (legal size) bass was 46%. Since exploitation was very light, natural mortality alone was roughly 43%, which is in excellent agreement with the Mill Lake data. At Whitmore Lake total mortality was 42% (Cooper and Schafer, 1954), and I computed the expectation of death from natural causes to be 32%. In Cub Lake the expectation of death from natural causes of adult bass was 44% one year and 23% the next (Clady, 1970). Clady points out that the decrease could have been a compensatory response to increased fishing, but that it was probably a natural, year-to-year, fluctuation (like those observed in Mill Lake), since a control population of smallmouth bass changed in like manner. Unfortunately, comparable estimates of natural mortality with and without fishing have not been made in the same lake. In any event,

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there is little doubt that an increase in fishing mortality is only partially compensated for by a decrease in natural mortality and, consequently, the bass population will decline.

Standing crop of largemouth bass. - -Strong year classes developed larger standing crops than did weak year classes (Table 49); however, the difference in biomass among year classes at the same age was not quite so great as their numerical difference, due to some growth compensation. For the same reason, the 2-fold increase in numbers of bass larger than 11 inches between 1965 and 1969 resulted in only a 1. 4-fold increase in their biomass. Thus standing crop was a more stable characteristic of this bass population than was numerical abundance.

Although biomass of large bass (age V and older) increased during the study from 426 kg to 579 kg (Table 49), total biomass (all ages) may not have changed much. Biomass of small bass (younger than age IV) must have been relatively high in 1965 due to the strong year classes of 1962-1964. Field observations suggest that the biomass of small bass was relatively low in 1969; however the strength of their year classes was not measured. If the biomass of small bass was less in 1969 than in 1965, then the standing crop of all bass was relatively stable from year to year.

Typically the biomass of a year class increased up to age IV, V or VI (lengths of 9 to 14 inches) and then declined as mortality exceeded growth. The 1960 year class achieved its greatest biomass

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at ages V-VI; the 1961 year class at V; the 1962 at IV (or younger); and the 1963 at VI. With the exception of the 1963 year class, which is atypical because it experienced very high survival during age V, the faster growing, usually weaker, year classes peaked at an older age than the slower growing, usually stronger, year classes. This occurred because mortality did not vary with abundance.

Production by largemouth bass. --In general production increased as standing crop increased (Tables 49 and 50). The correlation was not very strong, however, because of year-to-year variations in growth which were unrelated to standing crop. For example, the standing crop of age V and older bass was the same at the beginning of 1965, 1966 and 1967; however production during these years ranged from 65 to 187 kg due to fairly good growth in 1965, poor growth in 1966 and very good growth in 1967. Growth was very poor in 1968, when the spring biomass was higher than any other year. As a result, production was fairly high but was less than during the preceding year when biomass was low but growth was good.

Year-to-year variations in growth were likely due to extraspecific factors such as availability of food or length of the growing season. It is interesting, however, that good growth occurred in 1967 when mortality was probably high and poor growth occurred in 1968 when mortality was low. Further discussion will be reserved to the end of this report.

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Production to standing crop ratios were calculated from the data in Tables 49 and 50. There was considerable variation in the ratios due to the year-to-year variations in growth which were just mentioned. The ratios are of the same magnitude as those of the other species of fish in Mill Lake and they, also, declined with age. These averages were obtained for ages IV through X, respectively: 0. 45, 0. 38, 0. 29, o. 23, 0. 24, o. 04, and 0. 18. These are higher than the average ratio of 0. 13 cited by Clady ( 1970) for Cub Lake largemouth because old bass grew much better in Mill Lake than in Cub Lake.

Discussion of largemouth bass. -- The dynamics of bass were complicated and cannot be entirely explained, but there is evidence that the population was fairly closely regulated. The population was denser than those in other Michigan lakes which have been studied, but growth was slower than the state average. Year class strength only varied by a factor of 2 to 3, much less than for the panfishes. An increase in the number and standing crop of legal-sized bass during the study was attributed to growth of a series of strong year classes (1962-1964) and also, possibly, to elimination of fishing mortality. Despite this shift in population structure it is likely that the standing crop of all bass was stable or increased only slightly due to a reduction in growth and to a suspected reduction in recruitment.

Growth was compensatory but not proportional; i.e., a year class which was twice as strong as another grew more slowly, but more than half as fast. As a result, strong year classes developed

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higher standing crops and produced more than did weak year classes. There were also density-independent year-to-year fluctuations in growth and natural mortality which could not be explained.

A model was constructed of a typical year class of largemouth bass for ages IV to XI. Given the average growth in Table 44, average mortality in Table 48, and an average standing crop of age V and older bass equal to  $475 \text{ kg}$  (Table  $49$ ), the structure of the year class was computed using the method outlined in the bluegill section of this report. Statistics of the typical, unexploited, bass population are summarized in Table 51.

Production by age V and older bass was 150 kg which falls within the range actually observed (Table 50). According to this model there would be 19 legal length bass per hectare ( 8 per acre) weighing 9. 4 kg (8. 4 lb. per acre) each spring. Only 5 or 6 bass would live long enough to reach 20 inches.

In the model, growth  $(g)$  balanced natural mortality  $(g)$  at about age V, when the year class averaged **11.** 6 inches long. In terms of yield this would be the ideal time for intensive harvest. For the largemouth bass population in Cub Lake, which had very good survival until age VI, the critical size is somewhat higher, 12. 5-13. 0 inches (from data of Clady, 1970). Age-specific natural mortality rates are not available from Sugarloaf Lake; however, if they were similar to those for Mill Lake bass (which is very likely because the total mortality of legal bass was very similar), then the critical size of Sugarloaf Lake bass would be higher, about 12. 0-12. 5 inches, because of faster growth.

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## Northern pike

Prior to this study Mill Lake supported a modest, mostly winter, pike fishery. Many years ago the lake acquired a reputation for good pike fishing which has hung on even though modern population levels and fishing quality are no better than average. Due to the small size of the population, no pike were sacrificed for a food habit study.

Growth of pike. --Growth of pike in Mill Lake (Table 52) was comparable to that of pike in other waters in Michigan (Laarman, 1963). On the average, the legal length of 20 inches was reached at the beginning of age III; however some slow growers required two more growing seasons, whereas some fast growers reached 20 inches during age II. The largest specimen collected was 34. 2 inches long.

Growth was correlated with the abundance of pike of age II and older, and with the abundance of forage fish. In the first correlation, growth of most year classes, and especially the 1965 and 1966, was below average in 1967 and 1968, when the density of age II and older pike was high. In the second correlation, pike born in years of strong year classes of panfish (1960-1963) generally grew better than did pike hatched in years of weak panfish year classes ( 1964-1966). Observations during electrofishing indicate that another forage fish, the lake chubsucker, also declined about the time that pike growth deteriorated. Together these observations suggest that the growth and abundance of the pike population was food limited.

Abundance of pike. --Pike were not abundant in Mill Lake (Table 53). The sub-population of legal size ( 20. 0 inches and larger) averaged only 3. 1 per hectare (1. 2 per acre); and it was quite stable, ranging only between 2. 3 and 4. 1 per hectare. It was apparent that current levels of exploitation had little effect on population size, as the number of pike at the end of the study was no greater than at the beginning.

The pike populations in other southern Michigan lakes- - Sugarloaf, Whitmore and Big Portage--averaged 1.1 (Table 1), 0. 8 (Cooper and Schafer, 1954), and 0. 6 per acre (unpublished data of Institute for Fisheries Research), respectively. Since these estimates include pike as small as 14 inches, the Mill Lake population is somewhat larger. In northern Michigan there were 6. 4 per acre (14. 0 inches and larger) in Fife Lake (Christensen, 1960), and 10 per acre (13. 0 inches and larger) in a stabilized experimental population in Grebe Lake (unpublished data of M. Patriarche). About half of the Grebe Lake pike exceeded 20 inches. Populations as dense as 41 per acre are reported for Wisconsin (Threinen et al., 1966).

The age distribution and year class composition of the Mill Lake pike population are summarized in Tables 54 and 55 and Figure 6. Recruitment was more stable than anticipated, with most of the variation caused by the 1965 year class. At age III the number of pike in six year classes ranged from 60 to 144; the very strong class of 1965 was unique, with 382. The 1962 year class was slightly

stronger than average, and the 1963 and 1966 year classes were slightly weaker than average.

Although the 1965 year class was strong, an increase in the number of legal-sized pike in the total population did not occur, for two reasons. First, they grew so much more slowly that only half of them reached 20 inches by age IV, whereas most of the fish in older classes were legal at age III. During that extra year natural mortality reduced the number of pike entering the fishable stock to a near-average level. Secondly, the 1966 year class was weak and grew slowly. As a result it added fewer recruits to the legal stock than did an average year class.

Mortality of pike. --Natural mortality rates (Table 56) were calculated from the smoothed estimates of Table 55. Straight lines fit the empirical estimates quite well, indicating that mortality was constant from ages II to VIII (Fig. 6). Much of the scatter in the data points can be attributed to difficulties in sampling the very small numbers of fish which reach old age; however data for the 1963 year class may be an exception. If high survival really did occur during ages IV and V, I am unable to explain why.

Natural mortality of pike was about 55%, irrespective of age and size (Table 56). A similar figure (56%) was calculated from the data of Groebner (1964) for a Minnesota lake. Unpublished data of M. Patriarche for Grebe Lake show that n increased from 16% during age II to 76%

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during age V. Because growth was poor, legal size pike were dying at the rate of 62% per year.

There was some indication in the Mill Lake data that mortality was slightly higher for stronger year classes ( 1962 and 1965); however it was no higher in 1968 when the population of age II and older pike was about three times that for preceding years. Groebner ( 1964) cited two Minnesota lakes where natural mortality was high in years of high population density.

Standing crop of pike. - -Irregularities in year class strength were reflected in standing crop (Table 57). The very strong year class of 1965 weighed 275 kg at age III. By comparison, the weak 1966 year class weighed only 43 kg. However because of declining growth in 1967 and 1968, year-to-year fluctuations in total biomass (age III and older pike) were not so great as those in numerical abundance. A 3-fold numerical increase resulted in a 2-fold increase in biomass. Fluctuations in the biomass of legal sized pike were even smaller, ranging from 3. 5 to 5. 3 kg per ha (3. 1 to 4. 8 pounds per acre); the average was 4. 5 kg per ha (4. 0 pounds per acre). Thus, as for the other species of fish in Mill Lake, biomass was a relatively stable characteristic of the pike population.

A year class of pike achieved its highest biomass at age II when its members were 16 to 19 inches long. Thereafter, losses of biomass to natural mortality exceeded gains from growth, so that by the time the class reached legal size its biomass was two-thirds or less of its maximum.

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Production by pike. --Pike were among the least productive fish in the lake ( Table 58). In 1965, age III and older pike produced about 65 kg. Production in other years was probably somewhat less. Because of poorer growth the very strong year class of 1965 produced less during age III, than did the 1962 year class (33 versus 45 kg per ha). Negative values of production in 1967 and 1968 resulted from an apparent decrease in average length of pike in two year classes. Several explanations are possible, but the most likely two are sampling errors and better survival by slower-growing fish.

Ratios of production to biomass were low, typically about 0. 25 for the age groups which were estimated. The highest ratio probably occurred during age I, when a year class was still accumulating biomass through rapid growth.

Discussion of pike. --The dynamics of the Mill Lake pike population were relatively uncomplicated. Recruitment was remarkably even, except for one very strong year class, the 1965, which I will show later was correlated with a density independent factor. The 1966 year class was slightly weaker than average. Pike grew at the average rate (State) until about 1967 when growth slowed. At that time pike abundance increased as a result of the strong year class, and forage fish diminished as a result of weak year classes of panfish and possibly because of predation by pike. Since under slow growth it took a year longer to reach 20 inches, natural mortality dampened the effect of the

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strong year class. As a result the stock of legal-sized pike (both numbers and biomass) was relatively stable. Natural mortality was constant at 55%, from age II to age VIII. It was slightly higher for the stronger year classes, suggesting a compensatory relationship. All these observations indicate the pike population was fairly closely regulated and that it was kept at a low level by a limited food supply. Apparently the dense, slow growing, populations of perch and bluegills were not good forage.

A typical year class of pike was constructed with the following input: (1) standing crop of age III and older pike of 286 kg, (2) growth as in the averages at the bottom of Table 52, and (3) an annual natural mortality (n) of 0. 55 for ages **II-VIII.** The number of pike in each age group was then estimated from an equation similar to that used for the bluegill ( see bluegill discussion section). These estimates and other characteristics of the typical year class are summarized in Table 59. The standing crop of pike 20. 0 inches and larger was about 236 kg, which is close to the observed average of 248 kg. Production by age III and older pike was 69 kg, compared to an observed production of 65 kg.

According to the model a few pike would live to age VIII and exceed 30 inches in length. Slightly more than half of the age III pike would exceed 20 inches in the spring. The legal sized population would be about two pike per ha (0. 8 per acre) weighing about 4. 2 kg per ha  $(3.7$  pounds per acre). They would produce about 1 kg, and the ratio of standing crop to production would be about o. 25. Highest production

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would occur during age I (not estimated), and the critical size probably occurs just before age II at a length of roughly 16-17 inches.

#### Other species of fish

Limited data were collected for some of the other species of fish which were either of minor importance, not abundant, or could not be sampled adequately.

Bullheads. - -Three species of bullheads were present. The brown and yellow bullheads were common and they were readily trapped and estimated (Tables 60 and 61). Only a few black bullheads were captured. No attempt was made to age bullheads.

The number of brown bullheads 9 inches and longer averaged 15. 6 per ha (6. 3 per acre) over the 5 years. There was no indication of a long-term change in overall abundance, but minor changes within the size structure suggest that some natural fluctuations in recruitment or growth took place.

The number of yellow bullheads 7 inches and longer averaged 6. 4 per ha (2. 6 per acre). Their abundance gradually increased during the study, no doubt due to natural causes. So large an increase cannot be attributed to protection from angling, because bullheads were only lightly fished.

Rock bass. --Rock bass grew faster in Mill Lake than the state average given by Laarman ( 1963). The following lengths (inches) for ages I through X, respectively, were obtained by averaging the mean

lengths of as many as five year classes: 2. 0, 3. 4, 5. 5, 7. 0, 8.1, 8.8, 9.3, 9.7, 10.2 and 10.7. No difference in growth among year classes or years was evident. Presence of fish as old as age X indicated that natural mortality was relatively low. The number of rock bass longer than 6. 0 inches averaged 4. 1 per ha ( **1.** 7 per acre) (Table 62). It increased 2-fold between 1965 and 1969, perhaps due to protection from anglers. Stomachs of seven specimens collected on June 5, 1969, contained mayflies, dragonflies, caddisflies, crayfish and terrestrial insects.

Warmouth bass. --Warmouth grew more slowly than the state average. The following lengths (inches) for ages I through VIII were obtained by averaging the mean lengths of up to five year classes: 1. 7, 3. 0, 3. 6, 4. 4, 5. 5, 5. 9, 6. 5 and 7. 0. Each year class grew at the same rate. Growth of all ages was above average during 1968. Abundance estimates show that few warmouths grew large enough to interest anglers ( Table 62). In the 3 years during which estimates were made, there was an average of 4. **1** warmouth per ha ( **1.** 6 per acre) longer than 6 inches; however the population was declining. Stomachs of eight specimens collected on June 5, 1969, contained mayflies, dragonflies, midges and crayfish.

Bowfin. --Bowfins as long as 27 inches were captured. Their population fluctuated between 1. 4 and 3. 8 per ha, and averaged 2. 1 per ha (0. 9 per acre)--a level similar to that of northern pike.

Suckers. - -Two kinds of suckers occurred in Mill Lake. There were only a few white suckers present, 9 or less (Table 62). They probably entered the lake via the outlet and apparently did not spawn successfully in the lake itself. Lake chub suckers were abundant in 1965 and 1966, when they averaged 29 per ha ( 12 per acre). Estimates were not made in 1967-1969, but the population appeared to be very low.

### Summary and conclusions

In preceding sections of this report, observations on the autecology of many of the fish species have been presented. The purpose of this section is to integrate these observations, give a historical overview of the changes which occurred in Mill Lake, and point out correlations which may explain why these changes took place.

The six major species may be divided into three groups on the basis of their ecological characteristics. The bluegill and pumpkinseed sunfishes were mostly non-piscivorous, their strong year classes were synchronized, and their growth and mortality were noncompensatory (actually bluegill mortality appeared to be inversely density dependent). Perch and crappies were semi-piscivorous, their growth was density related, and the standing crops of large perch and large crappies were inversely related. Largemouth bass and northern pike were highly piscivorous, had relatively small fluctuations in year class strength, their growth was density dependent, and both experienced slower growth in the late 1960's.

The outstanding feature of every species, and especially the panfishes, was variation in year class strength. Uneven recruitment was responsible for major shifts in the structure of the populations. How did weak and strong year classes originate? Were they correlated with the fish populations or with other factors such as weather?

The history of the six major species of fish, since Mill Lake was partially poisoned in 1957, is summarized in general terms in Table 63. Year class strength was ranked as weak (W), average (A) or strong (S); the numbers of juvenile and adult fish were ranked as low (L), average (A) or high (H). "Juveniles" were bluegills, pumpkinseeds and perch in ages I and II, and crappies, bass and pike in age I. "Adults" were all fish older than juveniles. This separation was made to explore the possibility that year class strength was related to one component of the population, and not to the other.

In spite of the partial rotenone treatment on June 25, 1957, the bluegill produced an average sized year class in 1957. Contrary to expectations, no species produced a strong year class the following year- -as usually happens when warmwater fish populations are thinned. Only the perch produced a strong year class in 1959. The years 1960- 1963 were banner years for most species; only the crappie (in 1960) and pike (in 1963) had weak year classes. Only bass were strong in 1964 and only pike in 1965. Classes in 1966 and the years following were probably weak.

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The bluegill and pumpkinseed year classes were highly correlated with each other but with little else. The series of strong broods was followed by a series of weak ones at a time when adult sunfish density was high. This drop in recruitment served to stabilize total standing crop and was probably a compensatory response. Apparently a powerful density independent factor( s) prevented a strong year class until 1960 and caused one in 1963 even though panfish had become moderately dense.

There was a slight negative correlation between year class size of crappie and perch and the density of adults. Large broods of crappies were hatched in 1961 (which was a good year for all panfish), and in 1963. Crappie density was low in these years, but perch density was high in one of them. A weak year class originated in 1966 when adult crappies and other fish were abundant. Strong broods of perch came off (4 years in a row) at a time when adult density was low; weak classes occurred when perch and crappie adults were abundant. As with the sunfishes, the question of why strong classes of perch and crappie did not occur sooner, after chemical treatment, remains unanswered.

Year class fluctuations of bass and pike were relatively small and no correlations were evident. The three strongest year classes of bass were back to back, beginning in 1962, and were not related to the status of the bass population. They developed in some of the years that panfish were abundant, but not in others. Conversely they occurred despite high densities of juvenile panfish which could have been predators

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or competitors. The strong year class of pike came off in 1965 when panfish classes were weak and juvenile perch were scarce. Paucity of prey fish was reflected in slow growth. Weakness of the following year class, the 1966, may have been in part a density response.

In summary, the year class strength of Mill Lake fishes cannot be satisfactorily explained in relation to the fish populations themselves. Most panfish had a series of strong year classes in the early 1960's, and strong classes of largemouth bass followed a couple of years later. Succeeding year classes were weak, and since they occurred at a time when adult densities were high, they probably represent a density feedback response. However some of the most interesting aspects of year class strength remain unexplained; namely, why strong broods were not brought off sooner, why all panfish were strong in 1961, and why bluegill and pumpkinseed classes were either weak or very strong. There is a possibility that there was insufficient brood stock in the late 1950's to produce strong classes (except perch); however this does not seem plausible since the kill was only partial and warmwater fish are very fecund. Apparently much irregularity in recruitment was caused by density independent factors.

Pike year classes were correlated with a density independent factor- -water level- -as measured by the discharge rate of Mill Creek at a point 11 miles below the lake. In the period 1961-1966, for which U.S. Geological Survey records are available, the highest February to April discharge was in 1965 (very strong year class of pike), the second

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highest in 1962 (strong class) and the lowest in 1964 (average class) and 1966 (weak class). Carbine (1944) and Johnson (1957) also observed a positive correlation between year class strength of pike and water level.

U.S. Weather Bureau records on deviations of air temperature from the long term monthly means were examined. Year class strength was not correlated with monthly, seasonal or annual temperature. For example, temperature at the spawning time of the centrarchids in May and June was 7 degrees below average (the most extreme observed) in 1958 when weak year classes were produced, but it was also 7 degrees below average in 1961 when strong year classes were produced.

Temperature was also examined in relation to irregularities in the growth of bass. Bass growth was good in 1967, fair in 1965, poor in 1966, and very poor in 1968. Only a weak and illogical correlation was evident: growth was better in the years when summer temperatures were below normal.

In conclusion, much of the irregularity in recruitment and growth of Mill Lake fish was not explained by density dependent factors such as population density or structure or by density independent factors like temperature. Presumably density independent factors were dominant until the mid 1960's when fish biomass became high. Even at high fish densities the feedback mechanisms of compensatory growth and mortality were rather weak. Reduction of recruitment seemed to be the primary mode of regulation for the panfishes. Compensatory growth by the more

piscivorous species, perch, crappie, bass and pike indicates they were more closely regulated than the bluegill and pumpkinseed.

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INSTITUTE FOR FISHERIES RESEARCH

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Table 1. --Population estimates (mark-and-recapture techniques) and annual expectations of death of fish in Sugarloaf Lake. Data from Cooper, 1952, and Cooper and Latta, 1954.







Table 3.--Analysis of food types in stomachs of bluegills collected August 3, 1966, October 26, 1966 and June 5, 1969 including frequency of occurrence, size of food, number and weight per fish and per cent of total food weight.<br>(N = number of stomachs examined)

(continued)



 $1$  tr = trace

		May	June		July		Aug			Sep	Oct		Nov	
Food types	mg	$\overline{\mathcal{N}}_0$	mg	$\overline{\%}$	mg	$\overline{\mathcal{C}}$	mg	$\%$	mg	$\overline{\%}$	mg	$\overline{\phi_{0}}$	mg	$\overline{\phi_0}$
	per	of	per	of	per	of	per	of	per	of	per	of	per	of
		fish total		fish total	fish total		fish total			fish total		fish total		fish total
Crustacea	14	13	$\,6\,$	$\mathbf{1}$	80	41	$\mathrm{tr}^1$	tr	tr	tr	3	$\overline{2}$	30	34
Insecta	73	69	482	96	103	53	82	74	205	86	100	68	48	54
Mollusca	3	3	$\overline{4}$	$\mathbf{1}$	$\mathbf{3}$	$\boldsymbol{2}$	tr	tr	tr	tr	$\mathbf{3}$	$\overline{2}$	6	$\overline{7}$
Plant	$\mathbf 7$	$6\phantom{1}6$	$\overline{4}$	$\mathbf{1}$	$\overline{5}$	$\overline{2}$	16	15	30	13	40	27	$\overline{4}$	$\overline{4}$
Other	8	8	8	$\mathbf{2}$	$\mathbf{3}$	$\mathbf{1}$	11	10	$\overline{4}$	$\mathbf{2}$	$\mathbf{2}$	$\mathbf{1}$	$\overline{2}$	$\overline{2}$
Total	105 100			504 100		194 100		110 100	239	100	148	100	89	100
Number of fish		58		104		100		101	100			61		60

Table 4. --Weight of food per fish and percent of total food for food types found in stomachs of 5. 5- to 6. 5-inch bluegills collected monthly during 1965 (unpublished data of Percy W. Laarman)

 $^{\rm l}$  tr = trace



Table 5. - -Mean length and estimated mean weight of bluegills in the 1957 -1968 year classes

Size	Year of estimate									
group (inches)	1965	1966	1967	1968c	1969c					
$2.0 - 2.9$	78, 843 <sup>a</sup> $(46, 294 -$ 265, 538)	$30,346^{\rm a}$ $(18, 429 -$ 85, 886)								
$3.0 - 3.9$	25,908 <sup>a</sup> $(18, 026 -$ 46, 038)	$22,585^a$ $(18, 263 -$ 29, 585)	$3,068^{\rm a}$ $(2, 537 -$ 3,879)							
$4.0 - 4.9$	$23,609^{\rm a}$ $(16, 324 -$ 42, 638)	$7,687^{\textcolor{red}{\mathtt{a}}}$ $(5, 635 -$ 12,088)	$20,650^{\rm b}$ $(210 - \infty)$							
$5.0 - 5.9$	$24,888^{\rm b}$ $(18, 704 -$ 41, 446)	$15, 261^{\circ}$ $(9, 945 -$ 32,791)	$18,433^b$ $(11, 586 -$ 45, 289)	4,335 $(3, 769 -$ 5, 103)	3,089 $(2, 453 -$ 4, 172)					
$6.0 - 6.9$	$5, 211^b$ $(3, 940 -$ 8, 509	$11,081^{\circ}$ $(9,657-$ 12,998)	$11,902^{\circ}$ $(11, 464-$ 12, 375)	15,837 $(14, 843 -$ 16, 975)	13,989 $(11, 521 -$ 17, 857)					
$7.0 - 7.9$	$730^{\mathrm{b}}$ $(586 -$ 1,010)	$2,928^{\circ}$ $(2, 541 -$ 3,456	4, $140^{\circ}$ $(3,689-$ 4,737)	6,485 $(6, 043 -$ 6,996)	11,355 $(10, 616 -$ 12, 225)					
$8.0 - 8.9$	45 <sup>b</sup> $(27 - 63)$	39 <sup>c</sup> $(24-100)$	$109^\mathsf{c}$ $(73 - 213)$	415 $(379 - 459)$	2,923 $(2, 793 -$ 3,067					
Total $6.0 - 8.9$	5,987	14,048	16, 151	22, 737	28, 267					

Table 6. - -Spring estimates of the number of bluegills present in 1965-1969 (95% confidence limits are in parentheses)

a Schumacher type estimate. Fish were captured by electrofishing.

b Petersen type estimate. Fish were marked during trap netting; recaptured during electrofishing.

C Schumacher type estimate. Fish were captured in trap nets.

Year			Year of estimate		
$\mathtt{class}$	1965	1966	1967	1968	1969
1957	380	$\mathbf 0$	0	0	0
1958	1,781	135	0	$\mathbf 0$	$\mathbf{0}$
1959	1,169	366	143	22	$\overline{0}$
1960	19,627		7,385	2,379	2,377
1961	19,721		12,378	7,791	4,639
1962	27,807		13,747	11,788	10, 105
1963	88,748	24,025	20, 373		12,397
1964		27,823	4,322		

1965-1969

to the 1957-1964 year classes surviving to the years

Table 7. --Estimated number of bluegills belonging



Table 8. - -Smoothed estimates, from Figure 1, of the number of bluegills belonging to the 1957-1964 year classes surviving to ages II-IX

Year				Age group			
class	$II$ -III	$III - IV$	$IV - V$	V-VI	VI-VII	VII-VIII VIII-IX	
1957							1.000
1958						0.924	1,000
1959					0.714	0.706	0.710
1960				0.385	0.383	0.527	0.528
1961			0.215	0, 210	0.290	0.466	
1962		0.252	0.253	0.247	0.254		
1963	0.718	0, 200	0.225	0.200			
1964	0.844						
Mean	0.781	0.226	0.231	0, 260	0.410	0.656	0.810

Table 9. --Age-specific annual natural mortality rates (n) of several year classes of bluegill







# Table **11.** --Summary of studies on bluegill mortality

 $\ast$ Calculated from data given by the author.



Table 12. - -Standing crop (kilograms) of several year classes of bluegills in the spring of 1965-1969

# Table 13. - -Annual production (kilograms) by several year classes of bluegills during 1965-1969



			Spring statistics		Annual statistics					
Age		Fish Mean Mean		Standing		Growth Natural	Natural	Produc-		
group	per		length weight	crop			mortality mortality	tion		
	ha	(mm)	(g)	(kg/ha)	(g)	(n)	(q)	(kg/ha)		
$\rm II$	1,580	64	3.4	5.37	1.174	0.781	1.52	5.33		
III	346	91	11.0	3.80	0.820	0.226	0.26	4.18		
IV	267	117	25.0	6.69	0.588	0.231	0, 26	4.66		
V	206	140	45.0	9.27	0.470	0.260	0.30	4.74		
VI	152	163	72.0	10.97	0.298	0.410	0.53	2.91		
VII	90	178	97.0	8.72	0.135	0.656	1.07	0.76		
VIII	31		185 111.0	3.43	0.301	0.810	1.66	0.57		
IX		203 6	150.0	0.88						

Table 14. - -Population statistics of a" typical", unexploited, year class of blue gills

Table 15. - -Analysis of food types in the stomachs of 25 pumpkinseeds collected August 3, 1966 and June 5, 1969, including frequency of occurrence, size of food and number per fish





Table 16. --Mean length and estimated mean weight of pumpkinseeds in the 1956-1967 year classes



Table 17. - -Spring estimates of the number of pumpkinseeds present in 1965-1969. (95% confidence limits are in parentheses)

a Schumacher type estimate. Fish were captured by electrofishing.

b Petersen type estimate. Fish were marked during trap netting; recaptured during electrofishing.

C Schumacher type estimate. Fish were captured in trap nets.

d Average of estimates a and b.

Year		Year of estimate							
$_{\rm class}$	1965	1966	1967	1968	1969				
1957	35	$\boldsymbol{0}$	0	0	$\overline{0}$				
1958	54	$\overline{0}$	$\overline{0}$	$\overline{0}$	$\overline{0}$				
1959	147	68	34	23	$\mathbf 0$				
1960	2,219	1,362	847	289	116				
1961	5,747	3,539	2,074	1,156	543				
1962	7,269	4,576	2,427	1,248	951				
1963	16, 207	5,767	3,750	1,523	1,393				
1964					590				

to the 1957-1964 year classes surviving to the years 1965-

1969

Table 18. --Estimated number of pumpkinseeds belonging

Table 19. --Smoothed estimates from Figure 2, of the number of pumpkinseeds belonging to the 1959-1965 year classes surviving to ages II-IX

Year		Age group							
class	п	III	$\overline{\text{IV}}$	V	VI	VII	VIII	IX	
1957						∽	35	$\boldsymbol{0}$	
1958						54	$\boldsymbol{0}$	$\boldsymbol{0}$	
1959					150	72	35	17	
1960				2,220	1,350	800	290	110	
1961			5,700	3,500	2,070	1,200	540		
1962		7,300	4,500	2,610	1,540	900			
1963	16,200	5,800	3,600	2,220	1,400				
1964				590					



 $\cdot$ 

year classes of purnpkinseed

Table 20. --Age-specific annual natural mortality rates (n) of several








			Spring statistics		Annual statistics					
Age		Fish Mean		Mean Standing		Growth Natural	Natural	Produc-		
group			per length weight	crop			mortality mortality	tion		
	ha	(mm)	(g)	(kg/ha)	(g)	(n)	(q)	(kg/ha)		
П	225	71	6, 3	1.42	1.228	0.642	1.03	1.94		
Ш	81	104	21.5	1.74	0.693	0.312	0.38	1.43		
IV	55	130	43.0	2.38	0.568	0.396	0.51	1.40		
$\mathbf v$	34	155	76.0	2,55	0.457	0.395	0.51	1.14		
VI	20		178 120.0	2.44	0.256	0.441	0.60	0.54		
VII	11		193 155.0	1,75	0.177	0.676	1.13	0, 21		
<b>VIII</b>	4	203	185.0	0.67	0.195	0.712	1.25	0.09		
IX		1	216 225.0	0, 25						

Table 23. --Population statistics of a "typical", unexploited, year class of pumpkinseeds



Table 24.--Analysis of food types in stomachs of yellow perch collected August 3, 1966, October 26, 1966 and June 5, 1969 including frequency of occurrence, size of food, number and weight per fish and per cent of total food weight. (N = number of stomachs examined)

(continued)



 $1$  tr = trace



Table 25. --Mean length and estimated mean weight of yellow perch in the 1958-1967 year classes



Table 26. --Spring estimates of the number of yellow perch present in 1965-1969. (95% confidence limits are in parentheses)

a Schumacher type estimate. Fish were captured by electrofishing.

b Schumacher type estimate. Fish were captured in trap nets.

 $\degree$  Schumacher type estimate. Fish were captured by trap netting and electrofishing.



Table 27. - -Estimated number of yellow perch belonging to the 1959-1965 year classes surviving to the years 1965-



Table 28. --Smoothed estimates from Figure 3, of the number of yellow perch belonging to the 1959-1965 year classes surviving to ages I-VIII







 $\mathcal{A}^{\mathcal{A}}$ 

Table 30. --Abundance of age IV and older yellow perch in the spring of the years 1965-1969, number of deaths during the following 12-month period, and annual mortality rate (n)



$\texttt{Year}$				Year of estimate						
$_{\rm class}$	1965	1966	1967	1968	1969					
1959	23	3	0	0	0					
1960	36	12	0	0	0					
1961	147	58	20	8	$\mathbf{1}$					
1962	154	86	36	21	9					
1963	68	50	29	16	9					
1964		81	31		6					
1965		80	28							
$\operatorname{\textsf{Total}}$ Age V+	59	73	56	45	25					

Table 31. --Standing crop (kilograms) of several year classes of yellow perch in the spring of 1965-1969







			Spring statistics			Annual statistics				
Age	Fish		Mean Mean	Standing		Growth Natural	Natural	Produc-		
group	per		length weight	crop			mortality mortality	tion		
	ha	(mm)	(g)	(kg/ha)	(g)	(n)	(q)	(kg/ha)		
	12319.5	76	3.8	8.81	1.437	0.910	2.41	8.73		
II	208.8	119	16.0	3.34	0.724	0.739	1.34	1.86		
Ш	54.5	150	33.0	1,80	0.415	0.699	1.20	0.54		
ΊV	16.4	170	50.0	0.82	0.445	0.710	1.24	0, 26		
V	4.8	196	78.0	0.37	0.472	0.733	1.32	0.12		
VI	1,3		226 125.0	0, 16	0.215	0.826	1.75	0.02		
VII	0.2		241 155.0	0.03	0.149	0.920	2.53			
VIII	0.1		$254$ 180.0							

Table 33. - -Population statistics of a "typical", unexploited, year class of yellow perch



Table 34. - -Analysis of food types in stomachs of black crappies collected August 3, 1966, October 26, 1966 and June 5, 1969, including frequency of occurrence, size of food and number







Table 36. --Spring estimates of the number of black crappies present in 1965-1969. (95% confidence limits are in parentheses)

a Schumacher type estimate. Fish were captured in trap nets.

 $^{\rm b}$  Petersen type estimate. Fish were marked during trapnetting; recaptured during electrofishing.

Year		Year of estimate						
class	1965	1966	1967	1968	1969			
1959	$\boldsymbol{2}$	1	0	$\overline{0}$	$\boldsymbol{0}$			
1960	43	17	$\mathbf 2$	0	$\boldsymbol{0}$			
1961	961	617	176	42	9			
1962	536	398	301	211	131			
1963		911	698	562	462			
1964				382	342			
1965				767	436			
1966					316			

Table 37. - -Estimated number of black crappies belonging to the 1959-1966 year classes surviving to the years 1965-

1969

Table 38. - -Age-specific annual natural mortality rates (n) of several









Table 40. - -Standing crop (kilograms) of several year classes of black crappies in the spring of 1965-1969



## Table 41-- Annual production (kilograms) by

several year classes of black crappies during

$1965 -$ 1966	$1966 -$ 1967	$1967 -$	$1968 -$
		1968	1969
1	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
3	$\mathbf 2$	$\overline{0}$	0
46	20	3	$\mathbf 2$
32	14	22	$\overline{4}$
	56	37	31
			20
			49
			105
	81	92	

1965-1969



	Spring statistics						Annual statistics	
Age group	Fish per ha	Mean (mm)	length weight (g)	Mean Standing crop (kg/ha)	Growth (g)	(n)	Natural Natural mortality mortality (q)	Produc- tion (kg/ha)
Ш	11.6	185	85	0.99	0.662	0.30	0.36	0.77
IV	8.1	226	165	1.34	0.268	0.26	0.30	0.35
V	6.0	246	215	1.30	0.300	0.45	0.60	0.34
VI	3.3	269	290	0.96	0.417	0.62	0.97	0.31
VII	1.3	305	440	0.55	0.160	0.78	1.52	0.05
VIII	0.3	292	375	0.10		1,00		

of black crappies



 $1$  tr = trace



Table 44. - -Mean length and estimated mean weight of largemouth bass in the 1956-1968 year classes



Table 45. --Spring estimates of the number of largemouth bass present in 1965-1969. (95% confidence limits are in parentheses)

a Schumacher type estimate. Fish were captured by trapnetting and electrofishing.

 $^{\rm b}$  Schumacher type estimate. Fish were captured in trap nets.

Table 46. --Estimated number of largemouth bass belonging to the 1953-1965 year classes surviving



to the years 1965-1969

Table 47. --Smoothed estimates, from Figure 5, of the number of largemouth bass belonging to the 1957-1965 year classes surviving to ages IV -XI

Age group Year								
class	$\overline{\text{IV}}$	$\overline{\text{v}}$	$\overline{\text{VI}}$	VII	VIII	IX	$\overline{\mathbf{X}}$	XI
1957					$30\,$	11	$\overline{4}$	3
1958				66	28	15	11	8
1959			185	110	54	19	$\overline{\mathbf{4}}$	
1960		390	270	140	52	${\bf 20}$		
1961	350	280	180	86	45			
1962	1,100	570	270	135				
1963		616	555					
1964		678						
1965	545							

Year	Age group								
class	$IV - V$	$V - VI$	VI-VII		VII-VIII VIII-IX	IX-X	X-XI		
1957					0.633	0.636	0.250		
1958				0.576	0.464	0.267	0.273		
1959			0.405	0.509	0.648	0.789			
1960		0.308	0.481	0.628	0.615				
1961	0, 200	0.357	0.522	0.477					
1962	0.482	0.526	0.500						
1963		0.099							
Mean	0.341	0.323	0.477	0.548	0.590	0.564	0.261		

Table  $4^8$ . --Age-specific annual natural mortality rates (n) of several year classes of largemouth bass







1965-1969

several year classes of largemouth bass during

Table 50. - -Annual production (kilograms) by

			Spring statistics		Annual statistics				
Age		Fish Mean		Mean Standing	Growth	Natural Natural		Produc-	
group	per		length weight	crop			mortality mortality	tion	
	ha	(mm)	(g)	(kg/ha)	(g)	(n)	(q)	(kg/ha)	
IV	9.56	257	218	2.08	0.428	0.341	0.42	0.89	
V	6.30	295	335	2.11	0.476	0.323	0.39	1.05	
VI	4.26	340	540	2.30	0.428	0.477	0.65	0.88	
VII	2.23	389	830	1.85	0.351	0.548	0.79	0.52	
VIII	1.01	432	1,180	1.19	0.252	0.590	0.89	0.22	
IX	0.41	472	1,520	0.62	0.020	0.564	0.83	0.01	
Х	0.18	478	1,550	0.28	0.255	0, 261	0, 30	0.07	
ΧI	0.13	513	2,000	0.26					

Table 51. - -Population statistics of a "typical," unexploited, year class of largemouth bass







Table 53. --Spring estimates of the number of northern pike present in 1965-1969. ( 95% confidence limits are in parentheses) **1** 

1 All estimates were made by the Schumacher method. Fish were caught in trap nets.

Table 54. --Estimated number of northern pike belonging to the 1958-1966 year classes surviving to the years

Year				Year of estimate						
class	1965	1966	1967	1968	1969					
1958-										
1959	6	8	0	$\overline{0}$	$\overline{0}$					
1960	20	15	4	$\overline{2}$	$\boldsymbol{0}$					
1961	41	19	4	$\overline{0}$	$\overline{4}$					
1962	144	50	16	7	10					
1963	119	71	34	32	34					
1964			94	41	21					
1965				382	161					
1966					60					

1965-1969

Table 55. --Smoothed estimates, from Figure 6, of the number of northern pike belonging to the 1960-1966 year classes surviving to

Year	Age group								
class	п	III	$\overline{\text{IV}}$	V	$\overline{\mathtt{VI}}$	$\overline{\text{VII}}$	VIII		
1960				$20\,$	9	$\overline{4}$	$\bf{2}$		
1961			42	20	9	$\overline{4}$	$\overline{\mathbf{4}}$		
1962		144	52	19	7	7			
1963	140	$70\,$	34	34	34				
1964		$9\sqrt{2}$	44	21					
1965		382	161						
1966		60							

ages II-VIII


year classes of northern pike

Table 56. --Age-specific annual natural mortality rates (n) of several

1 Zeros not included in the mean.

Table 57. - -Standing crop (kilograms) of several year classes of northern pike in the spring of 1965-1969



Table 58. - -Annual production (kilograms) by several year classes of northern pike during





				Annual statistics							
							Natural Produc-				
per		crop					tion				
							(kg/ha)				
							1,31				
	528	910	2.15		0.55	0.80	0.66				
							0.31				
			0.78		0.55	0.80	0.21				
							0.03				
						0.80	0.04				
		3050	0.13		1.00						
	ha	Fish Mean (mm) 439 5.25 2.36 1.06 0.48 0, 22 0.10 0.04	(g) 535 599 1320 648 1630 726 2280 749 2470 803	Spring statistics Mean Standing length weight (kg/ha) 2.81 1.40 0.49 0.24	(g)	Growth Natural (n) 0, 55 0.531 0.372 0.285 0.55 0.334 0.55 0.079 0.211 0, 55	mortality mortality (q) 0.80 0.80 0, 80				

Table 59. --Population statistics of a "typical", unexploited, year class of northern pike





a Schumacher type estimate. Fish were captured in trap nets.

b Schumacher type estimate. Fish were captured by electrofishing.

Size	Year of estimate										
group (inches)	1965	1966	1967	1968	1969						
$7.0 - 8.9$	160 $(131 - 207)$	126 $(115 - 140)$	67 $(61 - 74)$	62 $(52 - 76)$	130 $(109 - 161)$						
85 $9.0 - 9.9$ $(72 - 104)$		182 $(163 - 207)$	109 $(106-113)$	93 $(86-102)$	73 $(66 - 82)$						
$10.0 - 10.9$	24 $(16-43)$	74 $(65 - 85)$	92 $(90 - 95)$	113 $(76 - 221)$	109 $(105 - 113)$						
7 $11,0-12,9$ $(5-9)$		26 $(24-28)$	32 $(30 - 34)$	97 $(90 - 105)$	136 $(131 - 142)$						
Total $7.0 - 12.9$	276	408	300	365	448						

Table 61. --Spring estimates of the number of yellow bullheads present in 1965-1969. (95% confidence limits are in parentheses)<sup>1</sup>

 $^{\rm 1}$  All estimates were made by the Schumacher method. Fish were caught in trap nets.



Table 62. --Spring estimates of the fish species of minor importance present



a Schumacher type estimate. Fish were captured in trap nets.

b Schumacher type estimates. Fish were captured by electrofishing.

C Petersen type estimate. Fish were marked during trapnetting; recaptured during electrofishing.

A	Α	W	S	S	S	S	W	W?		?	?	?
$\mathbf L$	$\mathbf L$	$\boldsymbol{A}$	$\boldsymbol{A}$	$\boldsymbol{A}$	$\mathbf H$	$\rm H$	$\mathbf H$	$\mathbf{A}$	$\mathbf L$	$\mathbf L$	L?	$\ddot{\phantom{0}}$
L	L	$\mathbf{L}$	$\mathbf{L}$	A	$\boldsymbol{A}$	$\boldsymbol{A}$	H	H	H	$H_{\rm}$	H	H
?	W	W	$\rm S$	$\rm S$	$\rm S$	S	W	W?		?	?	?
$\mathbf L$	L	$\mathbf L$	$\mathbf{L}$	$\boldsymbol{\mathrm{A}}$	$\rm H$	$H_{\rm}$	H	A	L	L	L?	?
L	$\mathbf L$	$\mathbf L$	$\mathbf{L}$	$\mathbf L$	$\mathbf{L}$	A	H	H	H	H	H	H
?	?	S	$\rm S$	$\rm S$	$\rm S$	A	W	W		?	¿	?
$\mathbf L$	$\mathbf L$	$\ddot{\phantom{0}}$	$\boldsymbol{\rm{A}}$	$\mathbf H$	$\rm H$	$H_{\rm}$	$\mathbf A$	$\mathbf L$	L	$\mathbf L$	$\cdot$	$\boldsymbol{?}$
L	$\mathbf L$	$\mathbf L$	$\mathbf{L}$	$\mathbf{L}$	$\mathbf A$	H	H	H	$\boldsymbol{A}$	$\mathbf L$	$\mathbf L$	$\mathbf{L}$
?	?	W	W	$\mathbf S$	$\boldsymbol{A}$	$\rm S$	$\boldsymbol{A}$	$\boldsymbol{A}$	W	?	?	?
L	$\boldsymbol{?}$	$\mathbf{P}$	$\mathbf L$	$\mathbf L$	$H_{\rm}$	$\boldsymbol{A}$	H	$\mathbf{A}$	$\mathbf{A}$	$\mathbf L$	$\ddot{\mathcal{E}}$	$\ddot{\phantom{0}}$
$\mathbf L$	$\mathbf L$	$\mathbf L$	L?	L?	$\mathbf L$	$\mathbf L$	$\boldsymbol{\mathsf{A}}$	$\boldsymbol{\mathrm{A}}$	$\rm H$	$\rm H$	H	H
		A	$\boldsymbol{A}$	A	S	S	$\rm S$	$\boldsymbol{A}$			?	?
L			$\mathbf A$	$\boldsymbol{\mathrm{A}}$	$\boldsymbol{A}$	$\rm H$		$\rm H$	A		A?	$\ddot{?}$
L	L	$\mathbf{L}$	$\mathbf{L}$	L	$\mathbf{L}$	A	$\boldsymbol{\mathsf{A}}$	$\boldsymbol{A}$	$\rm H$	$H_{\rm}$	$\rm H$	$\rm H$
?	?	A	A	Α	A	W	A	S	W	?	?	?
L	?	?		$\boldsymbol{\mathsf{A}}$	$\boldsymbol{\mathrm{A}}$	$\boldsymbol{\mathrm{A}}$	L		$H_{\rm}$	L		$\ddot{?}$
L			$\ddot{?}$	?	$\boldsymbol{A}$			$\boldsymbol{A}$				H
		$W$ ? $\mathbf{L}$	W? L? $\mathbf{L}$	L? $\boldsymbol{\rm{A}}$			$\mathbf A$	$\overline{\text{Year}}$ $\mathbf H$ $\boldsymbol{A}$	$\boldsymbol{A}$	$\boldsymbol{\rm{A}}$	W? W? W? W? $\rm H$	1957 1958 1959 1960 1961 1962 1963 1964 1965 1966 1967 1968 1969 A? L? $\ddot{\phantom{0}}$ $\mathbf H$

Table 63. - -Relative numbers of juvenile and adult fish of six species, from 1957-1969, as reconstructed from the relative strength of their year classes<sup>1</sup>

 $1$  The letter H connotates high abundance; L, low abundance; A, average abundance or year class strength; W, weak year class; s, strong year class; and ? connotates unknown year class strength or relative abundance.









Figure 2.--Survival curves for the 1959-1963 year classes of pumpkinseeds. The last digit of the year class is used for data points.<br>(The graph has been divided into two parts to improve clarity.)

**The allows** 



Figure 3.--Survival curves for the 1961-1965 year classes of yellow perch. The last digit of the year class is used for data points. (The graph has been divided into two parts to improve clarity.)



Figure 4.--Survival curves for the 1960-1965 year classes of black crappies. The last digit of the year class is used for data points. (The graph has been divided into two parts to improve clarity.)



Figure 5.--Survival curves for the 1957-1963 year classes of largemouth<br>bass. The last digit of the year class is used for data points.<br>(The graph has been divided into two parts to improve clarity.)



Figure 6.--Survival curves for the 1960-1965 year classes of northern pike.<br>The last digit of the year class is used for data points.<br>(The graph has been divided into two parts to improve clarity.)

 $\mathcal{L}_{\mathcal{A}}$  $\sim$   $\sim$