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[1]**A contribution from Dingell-Johnson Project F-35-R, Michigan.**

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Abstract.— We conducted a nine-pond experiment to test the effects of exploiting bluegills *Lepomis macrochirus* under a slotted size limit. For 5 years, bluegills from 5.0 to 6.9 inches were harvested annually via pond draining at three rates (0%, 25%, and 55%), in three ponds each. The 0% harvest rate was considered the experimental control. Density, size structure, growth, mortality, harvest, and reproduction of bluegills were monitored in each pond to help describe specific details of the population dynamics. The mean standing crop (weight/area) of bluegills larger than 7 inches was significantly greater ($P < 0.05$) in 25%-harvest ponds than in 0%- or 55%-harvest ponds, but we think this might have been due to chance differences in initial stocking rates. Even after 5 years, all fish over 7 inches in the ponds were survivors from the initial stocking. No significant differences were found between harvest rates for mean standing crops of bluegills 5.0 to 6.9 inches or less than 5.0 inches. From the standpoint of fishery potential, bluegill size structures that developed in all experimental ponds would be classified as stunted. Bluegills smaller than 6.0 inches made up over 99% of the populations by number and 93% to 97% by weight. Natural mortality of bluegills was density independent, but individual growth rate and population reproductive success were density dependent. Reproductive success was highly variable and not related to harvest rate. Reproduction failed in 22 of 45 year/pond combinations. Stepwise multiple-linear regression showed that reproductive success was negatively correlated with density of 1.0- to 3.9-inch bluegills (possibly representing predators or competitors of newborn fish), positively correlated with density of 5.0- to 5.9-inch bluegills (possibly representing the majority of sexually mature females), and positively correlated with density of 9.0-inch-plus bluegills (possibly representing the majority of reproductively fit males). In conclusion, bluegills possessed two qualities which made their populations unstable and which led to size structures unsuitable for good fishing: 1) 1.0- to 3.9-inch fish had the ability to avoid starvation and survive at high densities for several years while growing slowly; and 2) 4.0-inch-plus fish had the ability to reproduce large year classes whenever density of small fish was low. Normal sportfishing cannot directly affect either one of these things. Hence, we believe special fishing regulations, if applied directly to bluegills, could not be effective in correcting or preventing overpopulation and stunting. Rather, special fishing regulations should be designed to maintain high densities of predators which might be able to reduce survival and abundance of 1.0- to 3.9-inch bluegills and prevent stunting.

Stunted bluegills *Lepomis macrochirus* are a common problem in small lakes and ponds of the Great Lakes Region. Bluegills tend to overpopulate these environments, leading to a reduction in food and growth for individuals. The most common management approach is to thin or eradicate bluegill populations with fish toxicants such as rotenone or antimycin. Toxicants can be an effective solution, but the benefits are often only temporary. Hooper et al. (1964) reviewed the success of toxicant applications in Michigan's warmwater lakes from 1955 to 1963. They rated success of applications in 30 warmwater lakes as good in 40%, fair in 33%, and poor in 27% of the cases. In lakes rated good and fair, the average duration of success was only 4.7 years.

Despite the popularity of bluegills among anglers, the difficulties experienced in controlling bluegill populations have resulted in them being classified as undesirable fishes for stocking in Michigan ponds by the Cooperative Extension Service, Michigan State University (Schrouder et al. 1989). Even in larger bodies of water, the dynamics of exploited bluegill populations are little understood and, in particular, the effects of angling have been controversial (Coble 1988). Fisheries managers need to develop a better understanding of the dynamics of bluegill stunting so that new, more effective methods of population control might be developed.

We conducted a study of bluegill populations in nine ponds at Saline Fisheries Research Station, Saline, Michigan. Our study expanded upon a series of earlier studies that began in the early 1960s (Beyerle and Williams 1972; Beyerle 1977; Latta and Merna 1977). The general objective of these studies was to determine if good bluegill populations could be maintained by reducing abundance of fish in various size groups through annual thinning or harvest. Thinning or harvest was accomplished by draining ponds and removing fish and was meant to simulate harvest by fishermen, manual removal by managers, or feeding by predators.

Beyerle and Williams (1972) used three experimental ponds to study population-level effects of removing large numbers of young-of-the-year bluegills. They removed 60% and 90% of each new year class, but still could not maintain desirable bluegill populations. Ironically, it seemed that removal of large numbers of young served to stimulate the birth and survival of even more young. Reproductive success was obviously density-dependent.

In another study, Beyerle (1977) tried to produce an optimal number of large bluegills by maintaining a constant level of annual recruitment and a prescribed total standing crop of 90 pounds per acre. He concluded that the optimum sustained production of large bluegills could be achieved by restricting annual production of young to about 2000 fall fingerlings per acre and maintaining a total annual mortality of 50% on the adult stock. Of course, this is not an easy task on a natural lake, but at least it provides a general target for managers.

Latta and Merna (1977) studied factors influencing the size of bluegill year classes. They placed various numbers of adult bluegills in ponds, allowed them to reproduce, and then estimated the abundance and mean length of the young they produced. They were successful in quantifying a relationship between year class strength, parent stock abundance, and primary productivity. However, they were dealing with bluegills at low densities, below the densities occurring in most natural lakes and ponds.

Recently, there has been interest in trying to maintain balanced populations through special fishing regulations, such as slotted or inverted size limits. Our study grew from this interest and was designed to determine if desirable bluegill populations could be maintained by fishing under a slotted size limit. We thought that overharvest of larger bluegills (7 inches and over) and underharvest of medium-size bluegills (5 to 7 inches) by fishermen could be contributing to the stunting problem. For example, unfished or lightly-fished populations often contain relatively good growth and high densities of large bluegills. Possibly, the presence of larger bluegills reduces recruitment and overpopulation via cannibalism or some other mechanism.

The specific hypothesis for our experiment was that annual harvest of 5.0- to 6.9-inch bluegills and the protection of bluegills 7.0 inches and larger would prevent overpopulation and stunting; that thinning abundance of 5.0- to 6.9-inch fish would maintain good individual growth in the population and protecting fish 7.0 inches and larger would prevent excessive recruitment.

Methods

Harvest of 5.0- to 6.9-inch (total length) bluegills was accomplished by draining ponds and removing fish. We use the term "harvest" because the removal of fish was meant to simulate harvest by anglers. Treatments for the experiment were different annual harvest rates and the response variables were weight harvested and the standing crops of bluegills smaller than 5.0 inches, from 5.0 to 6.9 inches, and 7.0 inches and larger.

Nine ponds at the Saline Fisheries Research Station (Figure 1) were stocked with bluegills netted from Cedar, Mill, and Sugarloaf Lakes in Washtenaw County, Michigan. None of the source lakes contained stunted populations. Each pond was stocked with 50 pounds of bluegills per acre to begin the experiment, of which 35% (17.5 pounds per acre) were less than 5.0 inches long, 45% (22.5 pounds per acre) were from 5.0 to 6.9 inches long, and 20% (10 pounds per acre) were 7.0 inches or longer. Three annual harvest rates were randomly assigned to three ponds each and applied to bluegills in the 5.0- to 6.9-inch size range. Fifty-five percent by weight was harvested from ponds numbered 9, 15, and 18 (surface areas of 0.66 acre, 0.71 acre, and 0.49 acre, respectively), 25% percent by weight was harvested from ponds numbered 5, 10, and 16 (surface areas of 0.74 acre, 0.62 acre, and 0.59 acre, respectively), and 0% was harvested from ponds numbered 6, 14, and 17 (surface areas of 0.70 acre, 0.53 acre, and 0.59 acre, respectively). The latter three ponds were included as controls to help gauge the effects of pond draining or other systematic errors.

Ponds were drained annually between early-April and early-May, which is about 2 to 4 weeks before bluegills normally spawn in lower Michigan. The appropriate weight (55% or 25%) of 5.0- to 6.9-inch bluegills was removed at draining time. Also, any other fishes (such as green sunfish *Lepomis cyanellus* or fathead minnows *Pimephales promelas*) that contaminated the ponds during the year were removed. All other bluegills were temporarily transferred to oxygenated tanks, where samples were taken to estimate annual mortality, growth, and reproduction. Ponds were refilled as bluegills were being processed, and fish were returned to their respective ponds as soon as possible. The entire draining and harvest procedure for each pond took from 5 to 10 hours and was completed in a single working day. Mortality due to draining and handling was assumed to be insignificant.

Annual sampling of the bluegill populations included weighing the entire population in each pond and taking length measurements and scale samples from subsamples of fish in different size categories. Total weight of bluegills was measured in each of four size categories: 0.0 to 2.9 inches, 3.0 to 4.9 inches, 5.0 to 6.9 inches, and 7.0 inches and over. Within each size category a subsample of up to 50 fish was randomly selected. The individuals were measured for length and then weighed as a group. The size structure determined for the subsamples (proportion of fish in each inch group) was assumed to be representative of the broader size categories. Scales were collected from 10 individuals in each inch group in each pond. Later, bluegills were aged from scale samples and length-age keys were developed, indicating the proportion of fish in each inch group belonging to the various age groups. These proportions were then applied to the total number per inch group to estimate the number per age group. Mean lengths were calculated as weighted averages of numbers per inch per age.

We determined reproductive success for a year t based on the density of age-1 fish found at pond draining in the following year $t+1$. We used stepwise multiple linear regression to determine if relationships existed between reproductive success of bluegills and other intrinsic population variables, such as size of parent stock and abundance of bluegills in various size categories. We also investigated effects of some extrinsic variables, such as spring temperatures. Average monthly air temperatures for Ann Arbor were used as reported by the National Oceanic and Atmospheric Administration, Climatic Data Center, Asheville, North Carolina. The Ann Arbor weather station is 10 miles from the experimental ponds.

More specifically, we constructed regression models of the form,

$$Y = f(X_1, X_2, X_3, \ldots),$$

where Y was the number/acre of age-1 bluegills found at draining time in year $t+1$ and X_1, X_2, X_3, ... were one or more independent variables that might affect production of age-1 bluegills during year t. A full list of models and independent variables tested appears in Appendix A. Basically, the stepwise regression analysis identifies subsets of variables that, for the sample, are good predictors of the dependent variable (Neter and Wasserman 1974). The procedure often results in development of several statistically acceptable models, and it is left up to the investigators to choose the "best" model based on biological interpretations, or other criteria. This was the case for our bluegill data, as we will show later.

Results and Discussion

The original standing crops of 50 pounds of bluegills per acre increased rapidly in all ponds after the initial planting. Plots of population biomass trajectories indicated that the bluegill carrying capacity of the ponds (K) was about 350 pounds per acre (Figure 2). Exploitation did not appear to affect the biomass trajectories. The maximum standing crops produced in individual ponds ranged from 317 pounds per acre in Pond 16 in 1988 (25% harvest) to 449 pounds per acre in Pond 18 in 1985 (55% harvest). Ponds 6 (unexploited), 10 (25% harvest), and 17 (unexploited) also produced standing crops of 400 pounds per acre of bluegills at some time during the study. Standing crops and size structures of populations by pond and year are listed in Appendix B.

Effects of Harvest

The mean weight per acre of bluegills larger than 7 inches was significantly greater ($P < 0.05$) in 25%-harvest ponds than in 0%- or 55%-harvest ponds. Mean spring standing crops of bluegills larger than 7 inches were 10.1 pounds/acre for 0% harvest, 18.3 pounds/acre for 25% harvest, and 10.1 pounds/acre for 55% harvest. This result suggested a hypothesis that 25% harvest might be near the optimum for balancing the opposing effects of growth and mortality for fish entering and growing through the 5.0-6.9 inch size range. However, this hypothesis was not supported by bluegill abundance and growth information, and we believe it should be rejected. For the hypothesis to be correct, it would be necessary for density-dependent growth to be occurring within the harvest slot. One would expect to find 0%-harvest ponds with largest standing crops and slowest growth within the slot, 25%-harvest ponds with medium standing crops and medium growth, and 55%-harvest ponds with smallest standing crops and fastest growth. But we found no significant difference in the standing crops of 5.0- to 6.9-inch bluegills between harvest rates. Nor could we find evidence that growth rate was related to harvest rate. Growth was density dependent for bluegills born in the ponds (see *Individual Growth* section below), but it is important to note that during the 5-year study, few bluegills born in the ponds achieved 5 inches in length. Given the growth rates observed, the majority of bluegills would not have recruited into the 5.0- to 6.9-inch range until 6 or 7 years of age.

Thus, for the 5-year term of the study, nearly all bluegills over 5 inches were fish from the original seed stock, and we believe the best explanation for the observed differences in standing crops of large bluegills was slight variations in the numbers and sizes of bluegills stocked. Sizes of bluegills stocked were recorded within rather broad size categories (less than 5.0 inches, from 5.0 to 6.9 inches, and 7.0 inches and larger). Within these categories bluegills were selected randomly for stocking, so there is potential for slight variation in size structure.

The mean weights per acre of bluegills less than 5.0 inches were not significantly different between harvest rates. Bluegills smaller than 5.0 inches averaged 90% of the total biomass of fish in all ponds (Appendix B), regardless of harvest level. Harvest did not directly affect these small fish, and indirect effects were either insignificant or did not emerge within the 5-year period of study.

Population Size Structure

From the standpoint of fishery potential, size structures of bluegill populations in all our experimental ponds would be classified as "stunted", "unbalanced" (Novinger and Legler 1978), or poor (Schneider 1981). Bluegills smaller than 6.0 inches made up over 99% of the populations by number and 93% to 97% by weight (Appendix B).

Population Age Structure and Mortality

Population age structures and natural mortality rates were difficult to analyze because year class strength was highly variable in all ponds (see section below on reproduction). Too many year classes were absent to make any meaningful comparisons between ponds with different harvest rates.

However, it was possible to compute natural mortality rates for 11 cohorts of bluegills born in the ponds, and for these cohorts, natural mortality was density independent. Percent annual mortality between ages 1 and 2 averaged 57%, and the cohorts with the lowest (2,800 fish per acre) and highest (53,700 fish per acre) densities exhibited the same mortality rates (52%). Percent mortality averaged 63% between ages 2 and 3 and 69% between ages 3 and 4, and again, no relationship was found between mortality and density.

Individual Growth

Individual growth of bluegills born in Saline ponds was slow (Figure 3). Mean lengths at age were well below Michigan state averages reported by Laarman et al. (1981), and differences became progressively greater with age. Saline pond fish were 0.7 inches smaller at age 1 and 1.7 inches smaller at age 4.

Individual growth of bluegills born in Saline ponds was inversely density dependent (Figure 4). Mean lengths at ages 3 and 4 could be calculated for nine and seven cohorts, respectively. Least squares regressions of mean length versus initial density were significant for both age groups ($P < 0.05$). The slopes were negative, meaning there was a significant decline in growth as density increased.

Reproduction

Reproductive success of bluegills was highly variable and not related to harvest rate. Year class strength varied from 0 to 140,000 age-1 fish per acre. Typically, bluegills produced a strong year class in one year, and then reproduction failed for the next 1 to 4 years. Strong year classes (more than 2,000 yearlings/acre) were observed in 17 of 45 year/pond combinations (9 ponds times 5 years), weak year classes (100-2,000 yearlings/acre) in 6 combinations, and no year classes (0 yearlings/acre) in 22 combinations.

Bluegills are generally regarded as being prolific and able to produce successful year classes consistently, regardless of population size structure (Coble 1988). The erratic reproductive success we found, including total failure of reproduction in nearly half of the observations, was unexpected and one of the most interesting aspects of the study. Other investigators have observed failure of fish reproduction under crowded conditions, and several alternative hypotheses have been advanced to explain the phenomenon. The two leading hypotheses appear to be the *energetics hypothesis* and the *repressive factor hypothesis*, both of which seem to have originated from the Alabama pond studies of H. S. Swingle. Swingle and Smith (1950) reported that bluegills and bass failed to spawn in Alabama ponds when overcrowded. They first proposed an energetics-based hypothesis, suggesting that eggs of bluegills did not mature within the female when insufficient food was available:

> The time of year at which spawning occurred varied widely, depending on the food available for the adult fish. Where bluegills and bass were in proper balance, bluegills in ponds at Auburn, Alabama, spawned at irregular intervals each month from April to October. If the pond became overcrowded with bluegills after the first spawning in the spring, no more young were produced until fall; if the bass feeding on the young bluegills kept them thinned down sufficiently, egg-laying occurred each month until frost. When a pond was badly overcrowded with bluegills during the winter and spring, no young were produced before August or even September.

It seems doubtful that young bluegills spawned in August would survive the winters in Michigan. We found no evidence that bluegills spawned successfully during late summer in our ponds. That is, bluegill year classes did not display the bimodal length frequencies that might be expected from late-season spawning, and we did not see any fish spawning in the ponds in July or August. However, it is possible that fish spawned in deep water where we could not see them. Beard (1982) observed bluegills spawning as late as August in northern Wisconsin, where winters are harsher than in the Saline area of southern Michigan. But Beard correlated late spawning with weak year class strength, and he hypothesized that reproduction occurring after the first week in July did not significantly contribute to bluegill year classes.

The repressive factor hypothesis was formulated later when experiments suggested that some fishes might excrete a chemical substance which inhibits reproduction under crowded conditions. Bailey and Dean (1975) studied the reproductive failure of largemouth bass in a Texas reservoir and produced a literature review on the subject of reproductive failures under crowded conditions. They documented and gave evidence supporting Swingle's repressive factor hypothesis:

> Swingle (1954 and 1956) showed an apparent excretion of a repressive factor prevents reproduction of goldfish, carp and buffalo under crowded conditions. However, spawning was induced, sometimes within 24 hours, by placing them in fresh water. He stated it was apparent the repressive factor inhibits only the final stages of spawning and not gonad maturation. Whiteside and Richan (1969) had similar results in hatchery ponds crowded with goldfish. When these ponds were flushed with fresh water, goldfish spawned within approximately 24 hours. These authors attributed lack of reproduction to a hormone-like repressive factor or to an accumulation of metabolic waste products. Swingle (1956) suspected a repressive factor was widespread

among fishes. He stated bluegill may excrete a repressive factor that prevents largemouth bass reproduction. Rapidly growing largemouth bass did not spawn in the presence of large numbers of bluegill, but spawned when moved to fresh water. Pfuderer et al. (1974) partially isolated the "crowding factor" for goldfish and carp by observing heart rate depression. They related the compound to phthalate esters or a complex between a natural phthalate and another lipid constituent produced by liver tissue.

Bailey and Dean (1975) also described and provided evidence supporting other alternative hypotheses for explaining reproductive failure under crowded conditions:

> Greene (1968) found crowding appeared to affect spawning activity rather than maturation of gametes. Barwick and Holcomb (1974) found no largemouth bass reproduction in a pond crowded with sunfishes. They suggested this was associated with a physical factor such as harassment of these bass by sunfishes. Bennett (1954) reported largemouth bass reproduction was inversely correlated to number of bluegill present and related this to predation of bass eggs and fry by bluegill.

Whichever hypothesis is correct, it seems obvious that reproductive failure (or success) under crowded conditions is a powerful mechanism regulating population size of bluegills, and we tried to determine what factors were related to reproductive success in our ponds through the multiple regression analysis. There was no obvious choice for "best" model among the ones we tested in Appendix A.

Models 1 through 8 were attempts to define stock-recruit relationships, although they were not formulated as traditional stock-recruit models. At best, these models displayed only weak relationships. Models 2 and 7 were best of the group. They were highly significant ($P < 0.01$), but had coefficients of determination of only 0.21 and 0.24, respectively. Both defined parent stock as pounds per acre of bluegills larger than 4.0 inches.

Several of the other models tested described better relationships than those in the stock-recruit group. Model 9 was highly significant ($P < 0.01$), had a good coefficient of determination (0.54), and was mathematically simple because it did not contain squares or transformations of variables. Model 11 was also highly significant ($P < 0.01$) and had the best coefficient of determination (0.75) among all models tested. Model 16 was highly significant ($P < 0.01$), had a good coefficient of determination (0.40), and was simple because it contained only 2 independent variables, as opposed to 5 and 7 variables in models 9 and 11, respectively.

Residual analysis showed that these models did not significantly violate regression assumptions, but error variances on predicted values were too large to make them useful in predicting year class strength of bluegills. For example, an error of 10,000 yearling bluegills/acre does not seem important when observed values are in the range of 140,000/acre, but when observed values are in the range of 2,000/acre the predictions become useless. Unfortunately, in most practical situations (or in modeling of practical situations), it is this lower end of the scale (100 to 10,000 per acre) where good predictions are needed. The poor predictability of our models was probably due to important independent variables being missed. Variables we did not measure, such as food abundance, were probably important.

Despite poor predictability, a number of strong relationships which seem biologically valid emerged consistently in the regressions. First, the presence of small bluegills appeared to inhibit or reduce successful reproduction. Regression coefficients associated with bluegills smaller than 4.0 inches were consistently negative. For example, coefficients in Model 9 were -474.9 for 1.0- to 1.9-inch fish, -81.3 for 2.0- to 2.9-inch fish, and -62.7 for 3.0- to 3.9-inch fish. Similar relationships emerged in other Models (10, 11, 12, 14, and 16) using pounds/acre of small bluegills as independent variables. All the coefficients carried a negative sign, and, based on their relative numerical size, the presence of 1.0- to 1.9-inch fish had a greater depressing effect than 2.0- to 2.9-inch fish, and 2.0- to 2.9-inch fish had a greater depressing effect than 3.0- to 3.9-inch fish. Reproduction was never successful when 11 pounds/acre of 1.0- to 1.9-inch bluegills were present in a pond (Figure 5).

One or more of the following hypotheses could explain these empirical results:

1. *Energetics hypothesis*: As Swingle and Smith (1950) suggested, eggs of bluegills might not mature when insufficient food is available. Or, adult females might require more than one year to regain energy lost from spawning when food is scarce.

2. *Repressive factor hypothesis*: As Swingle (1956) suggested, a hormone-like repressive factor might be excreted, or the accumulation of metabolic waste products could inhibit reproduction under crowded conditions.

3. *Interference hypothesis*: Small bluegills might reduce reproductive success by physically interfering with adults at spawning time, that is, they could exert some negative social interaction preventing adults from going through the spawning act.

4. *Predation hypothesis*: Small bluegills might reduce reproductive success by eating newborn bluegills in the egg or fry stage.

5. *Competition hypothesis*: Small bluegills might reduce reproductive success by competing for food and/or space with newborn bluegills.

Further experimentation is required to determine which, if any, of these hypotheses is correct.

The second relationship which emerged from the regression analysis was a consistent, positive correlation between production of yearling bluegills and the pounds/acre of 5.0- to 5.9-inch fish in the pond. This relationship appeared in all models in which pounds/acre of 5.0- to 5.9-inch fish was used as an independent variable (Models 9, 10, 11, 12, 13, and 15).

We suggest that the reason pounds/acre of 5-inch fish was positively correlated with year class strength was that most of the egg-producing females were in that size range. At the end of our study, sex ratios and sexual maturity information were collected from bluegills in our ponds as part of another study. These data showed that the male/female ratio increased with size (Breck 1990). For example, about 50% of bluegills smaller than 6.0 inches were females, while only 7% of fish 6.0 inches or larger were females. Some females were sexually mature at sizes as small as 3.7 inches, and more than 80% of the 5.0- to 5.9-inch females were mature. Five-inch females also carried more eggs per individual than 4-inch females. Thus, it appears that the 5.0- to 5.9-inch segment of the bluegill population could have had the highest reproductive value with respect to females.

Finally, the presence of very large bluegills appeared to improve success of reproduction. There was a strong, positive relationship between production of yearling bluegills and the pounds/acre of bluegills 9.0-inches and larger. This relationship appeared in most models in which pounds/acre of 9.0-inch-plus bluegills was used as an independent variable (Models 9, 10, 11, and 12). Furthermore, more of the variation in year class strength is explained by the 9-inch-plus-fish variable than any of the others, 24% of 54% in Models 9 and 11 and 32% of 75% in Models 10 and 12.

We propose that pounds/acre of 9-inch-plus fish was positively correlated with year class strength because all bluegills in this size range were reproductively-fit males. The sex-ratio data mentioned earlier showed that 100% of bluegills over 9 inches were males (Breck 1990). Perhaps males of this large size were the only ones capable of successful reproduction in the crowded ponds. Larger males would probably be more effective both in attracting mature females and in guarding nests from potential predators.

Conclusions

Harvesting bluegills under the slotted size limit did not prevent overpopulation and stunting, so we reject our hypothesis. Thinning abundance of 5.0- to 6.9-inch bluegills had no significant effect on growth, and protecting fish 7.0 inches and larger did not prevent excessive recruitment. In fact, our regression analysis suggested that fishing regulations protecting large bluegills will enhance bluegill recruitment, not inhibit it, and will encourage overpopulation, not retard it.

Coble (1988) suggested four factors which tended to cause persistent overpopulation and stunting of bluegill populations: consistent recruitment of young of the year, density-dependent natural mortality, size-selective exploitation, and density-dependent growth. We learned in this study that consistent reproduction and density-dependent natural mortality were not characteristics of bluegill populations in ponds, and that size-selective exploitation had no effect on stunting. Density-dependent growth and density-dependent reproductive success were the primary mechanisms controlling bluegill population size and structure in our experimental ponds. Density-dependent mortality was not observed. Year class strength was set by age 1, after which, natural mortality was constant and growth and reproduction adjusted according to density.

Bluegills possessed two qualities which made their populations unstable and which led to size structures unsuitable for good fishing: 1) 1.0- to 3.9-inch fish had the ability to avoid starvation and survive for several years at high densities while growing slowly; and 2) 4.0-inch-plus fish had the ability to reproduce large year classes whenever density of small fish was low. Normal, sportfishing cannot directly affect either one of these things.

Hence, we believe special fishing regulations, if applied directly to bluegills, would not be effective in correcting or preventing overpopulation and stunting. Rather, special fishing regulations should be designed to maintain high densities of the predators of 1.0- to 3.9-inch bluegills. This type of predator management might make it possible to maintain higher mortality, lower abundance, and faster growth of 1.0- to 3.9-inch bluegills and could lead to bluegill size structures which are more suitable for fishing. However, high predator abundance would have to be maintained continuously, because reducing abundance of 1.0- to 3.9-inch bluegills would also have the effect of enhancing bluegill reproductive success. Bluegill adults would be capable of producing enough young in any given year to send the population into a cycle of slow growth and intermittent reproduction.

Acknowledgments

Research biologist Percy W. Laarman designed this study and guided the field work from 1982 to 1984. We assumed responsibility for the study in 1984 after Laarman's untimely death. The study was completed by the combined efforts of management and research sections in Michigan Department of Natural Resources, Fisheries Division. Many people employed by these two sections played important roles in the study, but we would especially like to thank management biologists Ken Dodge and Ron Spitler; management technicians Tom Adams, Torre Anderson, and Gloria Torello; and research technicians Jim Gapczynski, Al Sutton, and Troy Zorn.

The study was funded by fishermen through their tax dollars paid into the Federal Aid in Fish Restoration (Dingell-Johnson) Project F-35-R (75%) and their fishing license fees paid into the Fish and Game Fund of the State of Michigan (25%).

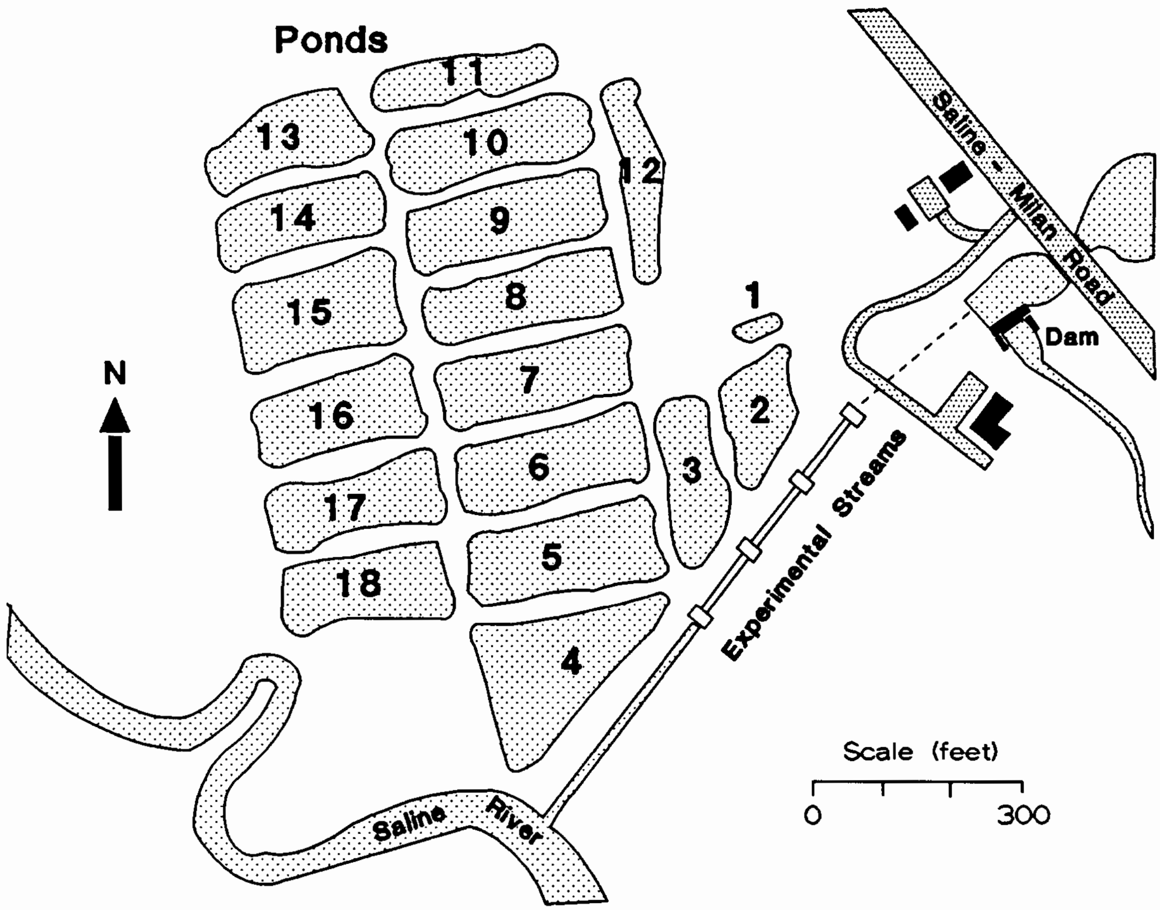

Figure 1.—Experimental ponds at Saline Fisheries Research Station, Saline, Michigan.

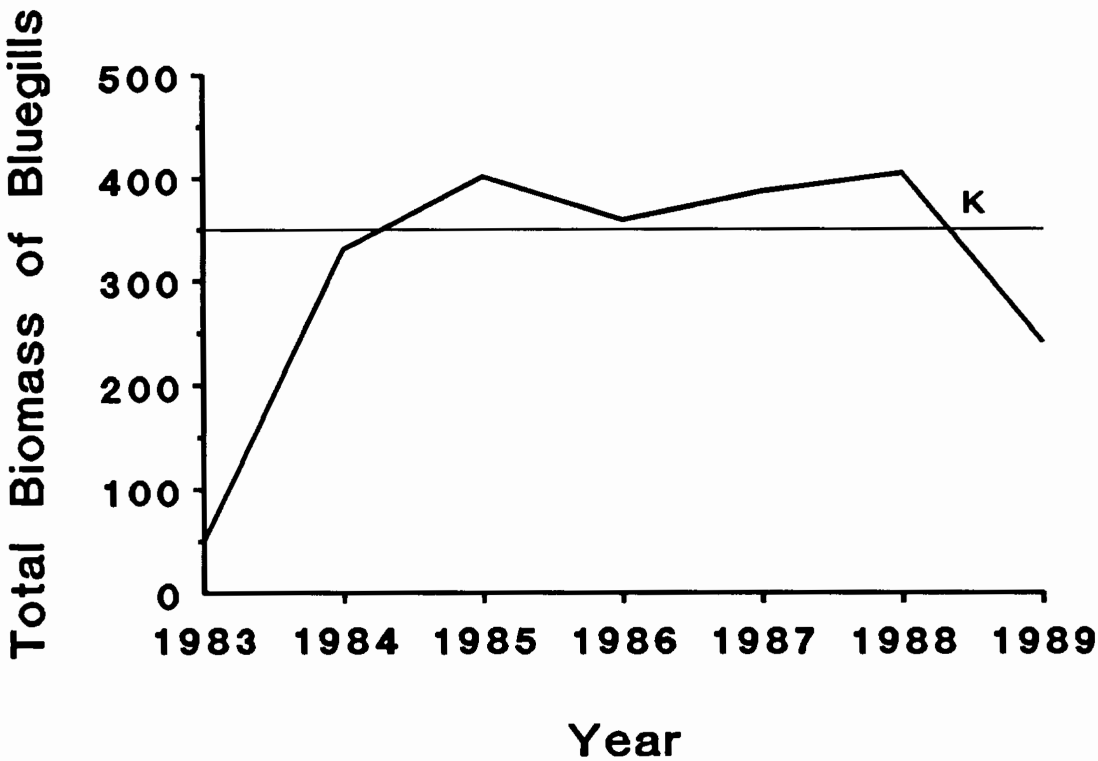

Figure 2.—Population biomass trajectory for bluegills in Pond 10. The carrying capacity (*K*) was estimated by eye and appeared to be about 350 pounds/acre. Biomass trajectories and carrying capacities were similar for the other ponds.

Figure 3.—Mean lengths at age for bluegills in experimental ponds compared to average lengths at age for bluegills in Michigan lakes.

Figure 4.—The relationship between the number of bluegills in a cohort at age 1 and the mean lengths of fish in that cohort at age 3 (dashed line, solid markers) and age 4 (solid line, open markers). The lines are least squares regressions fitted to data for respective ages. For age 3, $Y = 3.906 - 0.017 X$, $n = 9$, $R^2 = 0.59$. For age 4, $Y = 4.734 - 0.023 X$, $n = 7$, $R^2 = 0.67$.

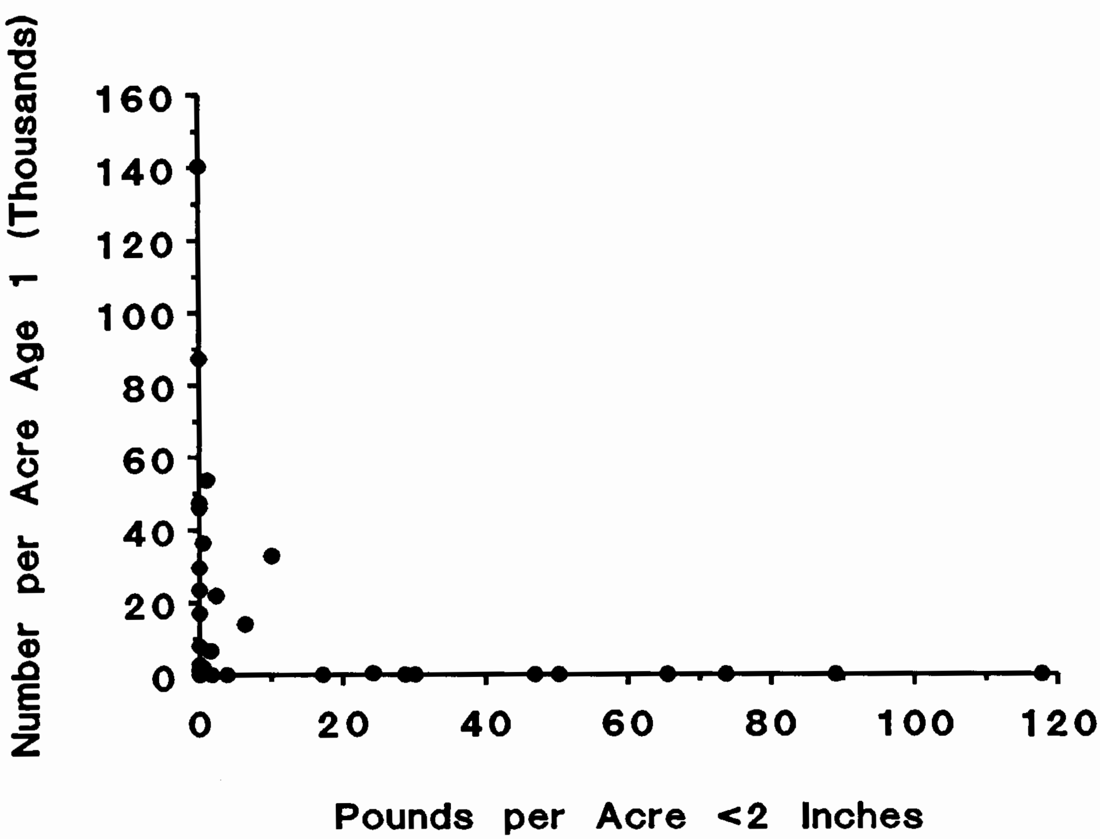

Figure 5.—Pounds/acre of bluegills <2 inches found in a pond in a given year (t=0) versus the number/acre of age-1 bluegills found in the same pond the next year (t=1).

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Appendix A.—List of linear regression models used to derive relationships between success of bluegill reproduction and intrinsic and extrinsic variables in the experiment. For Models 1 through 14, the dependent variable (Y) in regressions was the number/acre of age-1 bluegills found in year $t+1$. For Models 15 and 16, Y was the natural logarithm of number/acre of age-1 bluegills found in year $t+1$. When number/acre was 0, 1/acre was substituted, because the natural logarithm of 0 is undefined. Coefficients of determination (R^2) and significance levels (P) for each model are listed in parentheses. Sample sizes for all models was 43 year/pond combinations (1984 and 1985 data for Pond 14 were not used). For multiple regressions, "best" equations derived by stepwise approach are presented with variables in the order of their entry into the equation.

Models Using One Independent Variable

Model 1. X_1 = pounds/acre of total bluegill population in year t,

$Y = 35193.5 - 108.4\ X_1$,

($R^2 = 0.16$, $P < 0.01$).

Model 2. X_1 = pounds/acre of parent stock defined as bluegills larger than 4 inches in year t,

$Y = -2749.4 + 142.4\ X_1$,

($R^2 = 0.21$, $P < 0.01$).

Model 3. X_1 = pounds/acre of parent stock defined as bluegills larger than 5 inches in year t,

$Y = 1504.1 + 361.5\ X_1$,

($R^2 = 0.12$, $P = 0.02$).

Model 4. X_1 = pounds/acre of parent stock defined as bluegills larger than 6 inches in year t,

$Y = 11349.2 + 103.1\,X_1$,

($R^2 < 0.01$, $P = 0.83$).

Model 5. X_1 = pounds/acre of parent stock defined as bluegills larger than 7 inches in year t,

$Y = 16286.8 + 202.5\,X_1$,

($R^2 < 0.01$, $P = 0.75$).

Models Using Multiple Independent Variables

Transformations not performed on dependent variable

Model 6. Variable X_1 (defined as in Model 1) and X_1^2,

$Y = 39033.9 - 159.0\,X_1 + 0.1\,X_1^2$,

($R^2 = 0.17$, $P = 0.03$).

Model 7. Variable X_1 (defined as in Model 2) and X_1^2,

$Y = 6653.5 - 77.5\,X_1 + 0.8\,X_1^2$,

($R^2 = 0.24$, $P < 0.01$).

Appendix A.—(Continued):

Model 8. Variable X_1 (defined as in Model 3) and X_1^2,

$$Y = -135.1 - 446.6\,X_1 + 0.7\,X_1^2,$$

$$(R^2 = 0.12,\ P = 0.08).$$

Model 9. X_1 = pounds/acre of 1.0- to 1.9-inch bluegills in year t,

X_2 = pounds/acre of 2.0- to 2.9-inch bluegills in year t,

X_3 = pounds/acre of 3.0- to 3.9-inch bluegills in year t,

X_4 = pounds/acre of 4.0- to 4.9-inch bluegills in year t,

X_5 = pounds/acre of 5.0- to 5.9-inch bluegills in year t,

X_6 = pounds/acre of 6.0- to 6.9-inch bluegills in year t,

X_7 = pounds/acre of 7.0- to 7.9-inch bluegills in year t,

X_8 = pounds/acre of 8.0- to 8.9-inch bluegills in year t,

X_9 = pounds/acre of 9.0+ inch bluegills in year t.

Best equation: $Y = 9068.5 + 4754.6\,X_9 - 474.9\,X_1$

$$+ 245.7\,X_5 - 62.7\,X_3 - 81.3\,X_2,$$

$$(R^2 = 0.54,\ P < 0.01).$$

Appendix A.—(Continued):

Model 10. All independent variables included in Model 9 and:

X_{10} = average May air temperature in year t,

X_{11} = average June air temperature in year t,

X_{12} = average July air temperature in year t,

X_{13} = pounds/acre of other fish (minnows, suckers, bass, and so on) contaminating pond in year t.

Best equation: Same as Model 9. The air temperature and other-fish variables did not enter the equation.

Model 11. All independent variables included in Model 9 and their squares (that is, X_1^2, X_2^2, and so on).

Best equation: $Y = 33107.1 + 1142.2\,X_9^2 - 8.2\,X_1^2$

$+ 284.4\,X_5 - 7393.5\,X_9 - 0.3\,X_3^2$

$- 0.6\,X_2^2 - 0.3\,X_4^2$,

($R^2 = 0.75$, $P < 0.01$).

Appendix A.—(Continued):

Model 12. All independent variables included in Model 10 and their squares (that is, X_1^2, X_2^2, and so on).

Best equation: Same as Model 11. The air temperature and other-fish variables did not enter the equation.

Model 13. The natural logarithms of all independent variables in Model 9 (that is, $\ln(X_1)$, $\ln(X_2)$, and so on).

Best equation: $Y = 2124.7 + 6365.8 \ln(X_5)$

$+ 1387.6 \ln(X_4)$,

($R^2 = 0.20$, $P = 0.01$).

Model 14. The natural logarithms of the following variables:

X_1 = pounds/acre of 1.0- to 3.9-inch bluegills in year t,

X_2 = pounds/acre of 4.0- to 6.9-inch bluegills in year t,

X_3 = pounds/acre of 7.0- to 8.9-inch bluegills in year t,

X_4 = pounds/acre of 9.0+ inch bluegills in year t,

Appendix A.—(Continued):

$$\text{Best equation: } Y = 60548.2 - 10032.7 \ln(X_1)\ ,$$

$$(R^2 = 0.22,\ P < 0.01).$$

Natural logarithm transformation performed on dependent variable

Model 15. All independent variables included in Model 13.

$$\text{Best equation: } \ln(Y) = 2.5 + 0.4 \ln(X_4) + 1.0 \ln(X_5)\ ,$$

$$(R^2 = 0.25,\ P < 0.01).$$

Model 16. All independent variables included in Model 14.

$$\text{Best equation: } \ln(Y) = 9.4 - 1.7 \ln(X_1) + 0.8 \ln(X_2)\ ,$$

$$(R^2 = 0.40,\ P < 0.01).$$

Appendix B.—Pounds per acre of bluegills by inch group (number per acre in parentheses) recovered at draining for each year and pond in study. Pounds per acre harvested (number per acre in parentheses) were removed from 5.0- to 6.9-inch totals, and the remaining fish were returned to their respective ponds. Inch group 1 ranges from 1.0 to 1.9 inches, inch group 2 ranges from 2.0 to 2.9 inches, and so on. Ponds were drained in April or early May. Percent exploitation appears in parentheses after pond number.

Pond 9 (55%)

Inch group	Year 1984	1985	1986	1987	1988
1	1.7 (724)	0.0 (0)	0.0 (0)	0.0 (0)	<0.1 (17)
2	215.4 (35,464)	136.0 (13,300)	0.0 (0)	0.0 (0)	1.3 (167)
3	0.0 (0)	99.0 (6,259)	255.5 (12,198)	269.0 (10,865)	104.9 (4,185)
4	0.0 (0)	0.0 (0)	24.0 (507)	59.5 (1,768)	144.8 (4,017)
5	11.8 (124)	4.0 (39)	1.3 (17)	1.6 (18)	2.5 (27)
6	12.3 (83)	7.1 (47)	2.5 (17)	1.2 (8)	1.3 (9)
7	6.6 (27)	11.6 (41)	8.0 (27)	4.2 (17)	2.8 (9)
8	2.9 (8)	5.6 (14)	10.2 (21)	6.6 (17)	5.1 (12)
9+	0.8 (2)	2.5 (5)	3.5 (6)	3.6 (6)	1.8 (3)
Total standing crop	251.5 (36,432)	265.8 (19,705)	305.0 (12,793)	345.7 (12,699)	264.5 (8,446)
Harvested	13.9 (114)	6.1 (47)	2.1 (34)	1.5 (14)	2.1 (20)

Appendix B.—(Continued):

Pond 15 (55%)

Inch group	Year 1984	1985	1986	1987	1988
1	0.0 (0)	1.1 (1,286)	89.1 (52,589)	0.0 (0)	28.8 (17,102)
2	0.0 (0)	0.0 (0)	18.4 (1,073)	151.8 (26,839)	125.4 (11,968)
3	61.1 (1,952)	0.0 (0)	35.8 (1,363)	15.9 (1,118)	122.1 (8,666)
4	87.1 (1,952)	133.5 (3,341)	50.4 (909)	0.0 (0)	0.0 (0)
5	13.3 (145)	7.3 (100)	60.6 (687)	18.0 (210)	3.8 (54)
6	11.6 (69)	8.6 (23)	3.8 (28)	17.5 (118)	1.8 (14)
7	4.5 (18)	3.3 (13)	1.4 (4)	5.7 (18)	4.7 (18)
8	3.9 (9)	1.6 (4)	1.3 (3)	1.3 (3)	2.2 (6)
9+	3.0 (6)	5.3 (8)	4.3 (6)	5.3 (7)	2.7 (16)
Total standing crop	184.5 (4,151)	160.7 (8,926)	265.1 (56,662)	215.5 (28,313)	291.5 (37,844)
Harvested	13.7 (118)	8.7 (68)	32.0 (393)	19.4 (180)	3.1 (37)

Appendix B.—(Continued):

Pond 18 (55%)

Inch group	Year 1984	1985	1986	1987	1988
1	30.1 (9,151)	0.0 (0)	0.0 (0)	0.0 (0)	0.5 (306)
2	27.7 (4,159)	6.9 (714)	0.0 (0)	0.0 (0)	2.6 (204)
3	152.0 (6,655)	262.7 (12,869)	258.8 (9,461)	40.4[1] (1,014)	17.1 (1,169)
4	39.2 (833)	159.4 (4,290)	115.3 (2,988)	344.5[1] (6,231)	47.4 (847)
5	0.7 (6)	5.5 (69)	1.1 (20)	1.9 (16)	92.5 (1,200)
6	4.7 (27)	0.4 (2)	0.0 (0)	1.4 (8)	2.9 (25)
7	17.0 (63)	7.8 (31)	3.5 (12)	1.2 (4)	1.2 (4)
8	3.7 (10)	5.0 (14)	3.4 (8)	3.2 (6)	1.0 (2)
9+	2.2 (4)	0.9 (2)	2.4 (4)	2.7 (4)	5.8 (8)
Total standing crop	277.3 (20,908)	448.6 (17,991)	384.5 (12,493)	395.3[1] (19,776)	171.0 (3,765)
Harvested	3.0 (18)	3.3 (39)	0.6 (11)	1.8 (13)	52.4 (674)

[1]An estimated 193 pounds fish died from these groups due to draining stress when an oxygen tank failed.

Appendix B.—(Continued):

Pond 5 (25%)

Inch group	Year 1984	1985	1986	1987	1988
1	1.5 (2,838)	3.8 (1,774)	0.0 (0)	0.5 (135)	0.0 (0)
2	26.3 (2,838)	37.7 (5,916)	0.0 (0)	4.5 (849)	15.6 (1,464)
3	90.5 (6,149)	63.2 (2,958)	117.3 (4,650)	17.9 (566)	17.4 (815)
4	0.0 (0)	132.1 (4,141)	226.6 (5,458)	260.8 (5,657)	98.0 (1,789)
5	5.7 (50)	1.3 (16)	0.8 (11)	8.3 (114)	155.2 (2,054)
6	18.7 (118)	6.7 (49)	1.2 (10)	1.3 (10)	0.0 (0)
7	20.0 (72)	8.6 (34)	3.8 (14)	2.3 (7)	3.3 (12)
8	7.9 (20)	7.8 (22)	5.9 (15)	1.4 (3)	1.1 (3)
9+	4.1 (8)	2.5 (5)	3.8 (7)	7.5 (11)	9.1 (12)
Total standing crop	174.7 (12,093)	263.7 (14,915)	359.4 (10,165)	304.5 (7,352)	299.7 (6,149)
Harvested	6.1 (42)	2.0 (16)	0.5 (5)	2.4 (31)	38.8 (514)

Appendix B.—(Continued):

Pond 10 (25%)

Inch group	Year 1984	1985	1986	1987	1988
1	50.3 (15,531)	0.0 (0)	0.0 (0)	0.0 (0)	117.4 (140,250)
2	99.1 (15,531)	166.3 (25,423)	107.5 (10,719)	0.0 (0)	0.0 (0)
3	147.1 (5,916)	207.6 (11,965)	224.8 (14,802)	57.5 (1,882)	0.0 (0)
4	0.0 (0)	0.0 (0)	0.0 (0)	281.2 (7,531)	250.5 (7,368)
5	0.6 (7)	3.4 (42)	5.6 (55)	15.9 (179)	8.1 (116)
6	11.0 (68)	4.2 (26)	1.6 (10)	10.0 (69)	5.9 (29)
7	15.7 (58)	12.0 (45)	6.6 (23)	3.9 (13)	5.0 (18)
8	2.4 (7)	5.4 (15)	9.8 (23)	5.2 (11)	3.4 (8)
9+	4.8 (8)	3.0 (5)	3.8 (7)	13.2 (21)	13.9 (22)
Total standing crop	331.0 (37,126)	401.9 (37,521)	359.7 (25,639)	386.9 (9,706)	404.7 (14,7811)
Harvested	2.9 (19)	1.9 (17)	1.8 (16)	6.5 (62)	3.5 (36)

Appendix B.—(Continued):

Pond 16 (25%)

Inch group	Year 1984	1985	1986	1987	1988
1	0.0 (0)	75.1 (46,084)	10.1 (8,075)	65.2 (32,712)	0.0 (0)
2	0.0 (0)	0.0 (0)	57.5 (25,570)	14.3 (1,242)	208.3 (25,714)
3	1.5 (46)	0.0 (0)	0.0 (0)	125.8 (6,525)	61.3 (2,922)
4	125.8 (2,214)	0.0 (0)	0.3 (7)	0.0 (0)	22.2 (585)
5	28.1 (327)	110.1 (1,196)	29.3 (346)	1.2 (12)	1.1 (20)
6	29.5 (154)	33.5 (227)	6.7 (56)	4.4 (29)	3.7 (20)
7	5.8 (20)	6.3 (22)	5.7 (19)	10.0 (34)	6.4 (20)
8	2.8 (7)	1.4 (3)	1.7 (3)	10.0 (22)	9.1 (20)
9+	1.1 (2)	4.3 (5)	2.3 (3)	0.0 (0)	4.7 (9)
Total standing crop	194.6 (2,770)	230.7 (47,537)	113.6 (34,079)	231.4 (40,576)	316.8 (29,310)
Harvested	14.4 (120)	35.9 (356)	9.0 (101)	1.4 (10)	1.2 (10)

Appendix B.—(Continued):

Pond 6 (0%)

Inch group	Year 1984	1985	1986	1987	1988
1	2.3 (657)	24.2 (21,869)	0.0 (0)	46.9 (23,429)	0.0 (0)
2	3.7 (376)	0.0 (0)	41.3 (3,556)	1.7 (177)	0.0 (0)
3	68.0 (3,004)	0.0 (0)	163.1 (9,141)	147.8 (7,413)	151.2 (6,350)
4	29.1 (657)	179.7 (3,560)	101.1 (1,734)	44.6 (1,236)	176.5 (3,891)
5	7.5 (87)	22.1 (280)	66.7 (1,116)	34.5 (490)	20.1 (247)
6	3.1 (19)	2.5 (19)	28.5 (47)	1.5 (10)	4.6 (9)
7	4.6 (14)	0.9 (3)	2.3 (9)	3.7 (14)	6.1 (20)
8	13.8 (31)	6.2 (14)	0.0 (0)	1.7 (4)	4.9 (11)
9+	1.5 (3)	0.9 (3)	4.1 (7)	3.2 (4)	3.3 (4)
Total standing crop	133.6 (4,848)	236.5 (25,748)	407.1 (15,610)	285.6 (32,777)	366.7 (10,532)
Harvested	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)

Appendix B.—(Continued):

Pond 14[1]

Inch group	Year 1986	1987	1988
1	0.0 (0)	0.0 (0)	0.0 (0)
2	84.2 (7,702)	2.8 (257)	0.0 (0)
3	90.3 (4,781)	235.2 (12,043)	117.5 (3,804)
4	38.0 (796)	18.2 (513)	243.9 (5,706)
5	8.6 (94)	8.3 (102)	8.0 (109)
6	7.8 (53)	7.0 (47)	11.4 (51)
7	5.9 (21)	2.3 (8)	5.2 17)
8	3.9 (9)	5.2 (11)	2.8 (6)
9+	3.4 (6)	2.3 (4)	3.5 (6)
Total standing crop	242.1 (13,462)	281.3 (12,985)	392.3 (9,699)
Harvested	0.0 (0)	0.0 (0)	0.0 (0)

[1]Complete draining of Pond 14 was impeded by thick filamentous algae in 1984 and 1985. Pond was treated with copper sulfate and the fish data for those years were not used in the analysis.

Appendix B.—(Continued):

Pond 17 (0%)

Inch group	Year 1984	1985	1986	1987	1988
1	17.2 (6,558)	0.0 (0)	0.0 (0)	0.0 (0)	6.4 (6,356)
2	179.6 (20,271)	125.9 (11,570)	0.0 (0)	0.0 (0)	13.4 (1,648)
3	41.7 (2,983)	242.2 (14,725)	363.6 (21,985)	265.1 (12,186)	120.7 (4,736)
4	0.0 (0)	0.0 (0)	48.1 (915)	8.5 (249)	133.4 (3,910)
5	2.7 (29)	3.1 (36)	2.6 (34)	2.6 (29)	0.7 (9)
6	1.5 (9)	1.6 (10)	1.6 (14)	1.6 (12)	1.7 (10)
7	20.8 (68)	6.4 (22)	2.3 (9)	1.5 (5)	3.1 (12)
8	13.1 (32)	8.9 (22)	4.3 (12)	1.6 (3)	2.0 (5)
9+	3.6 (7)	0.3 (2)	1.7 (3)	5.2 (9)	3.0 (5)
Total standing crop	280.2 (29,957)	388.4 (26,387)	424.7 (22,972)	286.1 (12,493)	284.4 (16,691)
Harvested	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)