Michigan DNR

STATE OF MICHIGAN
DEPARTMENT OF NATURAL RESOURCES

Number 2024

December 19, 1996

Mechanisms of Recruitment Failure in Bluegill Ponds

James E. Breck

FISHERIES DIVISION
RESEARCH REPORT

MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION

Fisheries Research Report 2024
December 19, 1996

MECHANISMS OF RECRUITMENT FAILURE IN BLUEGILL PONDS

James E. Breck

Printed under authority of Michigan Department of Natural Resources
Total number of copies printed 200 — Total cost $480.12 — Cost per copy $2.40

Michigan Department of Natural Resources
Fisheries Research Report No. 2024, 1996

Mechanisms of Recruitment Failure in Bluegill Ponds

James E. Breck

Michigan Department of Natural Resources
Institute for Fisheries Research
212 Museums Annex Building
Ann Arbor, MI 48109-1084
e-mail: breckj@dnr.state.mi.us

Abstract.–A series of eight experiments was conducted to study the factors influencing year-class failure in high-density bluegill ponds. Ponds were considered to have successful bluegill reproduction if age-1 fish were present at spring pond draining 1 year after stocking. Experiment 1 varied total bluegill stocking density to evaluate its effect on adult relative weight (W_r), gonadosomatic index (GSI), fecundity of females, and on reproduction. Three ponds were stocked at each of three densities: 56 ("low"), 134 ("medium") and 336 ("high") kg/ha; of the specified total, 37 kg/ha was fish >127 mm total length. There was a year-class failure in all three high-density ponds, in one medium-density pond, in two low-density ponds. Of the three successful ponds, two had received the lowest stocking density of fish <51 mm. A total of 469 adult bluegills was sampled by hook and line. The sex ratio among fish 152 mm or greater was 9:1 (males:females). The W_r of males and females was significantly greater at lower stocking densities. For fish sampled in June, the 6-fold range of stocking densities produced a 3-fold range in mean GSI of females, from 3.0% at high density to 9.3% at low density, but there was no significant effect of stocking density on male GSI. The June number of eggs per gram body weight of female varied from 120±11 (mean±SE) at low density, to 83±11 at medium density, to 40±12 at high density. This indicates that fewer eggs are produced per female as density increases. Experiment 2 evaluated the effect on reproduction of age-1 density. The three treatments were 0 (four ponds), 5.6 (two ponds), and 17 (three ponds) kg/ha of age 1, each with 56 kg/ha of small (102-151 mm) adults. Reproduction was successful in all six ponds with 0 and 5.6 kg/ha of age 1s, but failed in all three ponds with age 1s at 17 kg/ha. Experiment 3 further evaluated the effect of age-1 density on reproduction, using age-1 densities of 0, 17, and 50 kg/ha (three ponds at each density); adults were stocked at 56 kg/ha. Most adults came from experiment 2, and were 1 year older and about 25 mm longer. Reproduction was successful in all six ponds at 0 and 17 kg/ha; reproduction failed in two of three ponds at 50 kg/ha. Experiment 4 evaluated the ability of adults in poor condition to reproduce. One pond was stocked with small adults (102-151 mm) with a very low relative weight (64±6.5%, mean±SD); they came from ponds stocked the previous year at 336 kg/ha. Though some nests were observed, no fry were produced; the year class failed. Experiment 5 also tested adults that spent the previous year in ponds stocked at 336 kg/ha. Unexpectedly, not all adults were in poor condition. Whereas for small adults (102-151 mm) the average W_r was 70-75%, the W_r of 203-253 mm fish was 82-87%, and three fish 254-278 mm long had a W_r of 96%. The year class was successful in all three ponds stocked with these fish. Thus, any carry-over effect of previous high density is not sufficient to cause year-class failure if some adults are in good condition. Experiment 6 used a 2×2 cross-classified design to evaluate effects of both adult size and age-1 density. Ponds received either only small (102-151 mm) adults or both small and large (>151 mm) adults, combined with either 0 or 17 kg/ha of age-1 bluegills. Reproduction was successful in 11 of the 12 ponds, failing only in one of three ponds that received small adults and 17 kg/ha of age 1s. Experiment 7 evaluated the effect of age-2 and age-1 density on reproduction. Nine ponds received adults at 56 kg/ha. Three of these ponds were stocked with no juveniles. Two ponds were stocked with age 2s at 78 kg/ha and another received 30 kg/ha. The last three ponds received age-1 bluegills at 17 kg/ha; two of these received age 2s at 78 kg/ha and the other received age 2s at 30 kg/ha (there was a shortage of age 2s at stocking). Reproduction was successful in all ponds except one receiving age 1s at 17 and age 2s at 78 kg/ha. Experiment 8 was similar to experiment 7, testing the effect of age 2s and age 1s on reproduction. Nine ponds received adults at 56 kg/ha. Three of these ponds were stocked with no juveniles, three ponds with age 1s at 17 and age 2s at 28 kg/ha, and three ponds with age 1s at 17 and age 2s at 78 kg/ha. Reproduction was successful in seven of nine ponds, failing in one pond each of the latter two treatments. Year-class failure in bluegill ponds is clearly associated with the presence of juvenile bluegills, that is, age-1 and age-2 bluegills, less than about 100 mm. Of the 61 pond-year occasions in this study, reproduction failed on 16 occasions. For ponds without juveniles, reproduction failed on only 1 of 23 occasions, for a failure rate of 4%; this was the single pond stocked with small adults in very poor condition. For ponds stocked with juveniles, reproduction failed on 16 of 38 occasions, for a failure rate of 39%, not significantly different from the failure rate of 22 of 45 occasions observed by Clark and Lockwood (1990). The mechanism of year-class failure does not appear to be starvation of age 0s after hatching, nor overwinter mortality, nor cannibalism on fry larger than 20 mm. It does not appear to be adult lack of adequate energy for reproduction, except in extreme cases. While not causing failure, these mechanisms can influence year-class strength. This study and experiments by Gray (1991) suggest that predation by juvenile bluegills, on eggs and larvae in the nest and on fry soon after leaving the nest, is the major mechanism producing recruitment failure in high-density bluegill ponds.

Slow-growing bluegill populations are a common problem in southern Michigan lakes. Successful methods for improving growth in these populations are likely to involve reductions in the number of young bluegills surviving their first year of life (Beard 1971; Schneider 1981). Clark and Lockwood (1990), in experiments at the Saline Fisheries Research Station, observed cases of failed recruitment in ponds with stunted bluegill populations whenever the standing crop exceeded 224 kg/ha. Understanding the mechanisms causing recruitment failure in high-density bluegill ponds may suggest improved methods for reducing recruitment in lakes and ponds with stunted bluegill populations.

In Clark & Lockwood's study, nine ponds were followed for five years, and yearlings were missing at the spring pond draining on 22 of 45 occasions (Appendix 1). Recruitment to age 1 failed half the time. At least three ponds produced young each year, and at least three ponds failed to produce young each year, indicating the importance of factors operating within the pond.

Several hypotheses can be advanced to explain the failure of recruitment in high-density bluegill ponds, as was observed by Clark and Lockwood at the Saline Fisheries Research Station. These hypotheses are not mutually exclusive.

H_1: *Not Enough Energy for Successful Reproduction*

H_{1a}: *Females have inadequate energy to develop mature eggs.*–A high density of bluegills might reduce the available food to such low levels that females cannot obtain enough energy to develop mature eggs. In his review of environmental influences on gonadal activity, Lam (1983) said that "a reduced food supply retards or inhibits gonadal development in salmonids (Scott 1962; Baganal 1969), in *P. reticulata* (Hester 1964; Dahlgren 1979), in the winter flounder, *P. americanus* (Tyler and Dunn 1976), and in the roach, *Rutilus rutilus* (Kuznetzov and Khalitov 1978). ... In the stickleback, *G. aculeatus*, food limitation during the breeding season reduces the number and frequency of spawnings per female, and total food deprivation terminates spawning (Wooton 1973, 1977)" (Lam 1983, p. 92).

Delayed bluegill reproduction was noted by Swingle and Smith (1943): "When a pond was badly overcrowded with bluegills during winter and spring, no young were produced before August or even September." Perhaps reproduction would be skipped altogether in a particular year if very little food were available.

The gonadosomatic index (GSI, gonad weight as a percentage of fish weight) gives an indication of readiness to spawn. Swingle and Smith (1943) report that for well-fed bluegills, ovaries began to develop in December; when there was less abundant food, little or no development of the ovaries was discernible until the water warmed in the spring. Morgan (1951) showed that the GSI increased dramatically the first week in May and decreased in August in Buckeye Lake, Ohio. James (1946) found a similar pattern in bluegills from Fork Lake, Illinois.

Perhaps the energy available to an individual female has a larger effect on the number of *yolked* eggs than on the *total* number of eggs in the ovary. If so, then fish standing crop should make a difference in the size-frequency distribution of eggs in females. This possibility was not evaluated.

H_{1b}: *Males have inadequate energy to guard nests.*–Another hypothesis is that males have inadequate energy to remain guarding nests until fry leave the nest. Nesting males have little opportunity to feed, and nest guarding can be a demanding task (Thorp et al. 1989; Hinch and Collins 1991). Hinch and Collins (1991) estimated that the metabolic rate of guarding smallmouth bass *Micropterus dolomieu* was up to 60% greater than that of nonguarding males. If higher population densities reduced individual food consumption, then fewer males would be expected to attempt nesting and fewer would succeed in raising fry.

H_2:*Cannibalism of Age-0 Bluegill by Older Bluegill*

H_{2a}: *Eggs eaten.*–A high density of bluegills could result in intense predation on eggs. Carlander (1977, Volume 2, page 109) indicated that "when food is scarce, bluegills commonly eat their own eggs [Swingle and Smith 1943]." Swingle and Smith (1943) also note that in bass-bluegill ponds "where bluegills were overcrowded, they ate bass eggs. ... The hungry bluegills also ate some of the newly hatched fry, with the result that practically no young bass were produced in these overcrowded ponds." Morgan (1951) studied bluegill in Buckeye Lake, Ohio: "In April, May, June, and July, during the spawning period, bluegills of all sizes eat fish eggs. During these months an average of 16.82 per cent [of all food taken] was recorded. Many stomachs were gorged with pumpkin seed [sic] eggs, eggs of the green sunfish, eggs of the large mouth [sic] bass and the gizzard shad" (p. 50).

H_{2b}: *Larvae or fry eaten.*–A high density of bluegills could result in intense predation on larvae or fry. Krumholz (1946) stocked bluegills in ponds at the Wolf Lake Hatchery. "Examination of the stomachs of 60 adult bluegills from Pond 5 revealed that 27 of them (45 %) contained small bluegills. No bluegills were found in the stomachs of 30 adults recovered from Pond 4. This cannibalism, which is not so frequently noticed among bluegills as among some other hatchery-reared fish (notably the black basses and yellow pikeperch [sic]), reduced the population of young bluegills in Pond 5 to a great extent." Consumption of age-0 bluegills by adult bluegills was observed by Schneider (personal communication) in the fall of 1988 during another study in ponds at Saline. Werner (1977) quantified the time required by different sizes of bluegills to pursue and consume green sunfish fry.

H_3: *Starvation of Age-0 Bluegill*

H_{3a}: *Fry starve after hatching.*–A high density of bluegills might reduce the appropriate zooplankton prey to such low densities that fry starve shortly after hatching. The observations of Toetz (1966a, b) indicated that bluegill fry starved if they were not provided food by 6.5 to 7 days after hatching. DeVries et al. (1991) and Stein et al. (1995) report that age-0 threadfin shad *Dorosoma petenense* and gizzard shad *Dorosoma cepedianum* can reduce the density of zooplankton to very low levels, and that this can cause reduced survival and limited recruitment of other age-0 fishes, including bluegill. In their laboratory experiments, Hart and Werner (1987) found that survival of pumpkinseed larvae after yolk absorption was directly related to zooplankton density.

H_{3b}: *Overwinter mortality of age 0.*–A high density of bluegills is likely to produce slow growth of the age-0 fish, and could result in age 0s entering the winter period with insufficient energy reserves. Experiments on age 0s of other centrarchids have indicated that smaller individuals are more vulnerable to overwinter starvation than larger individuals (Oliver and Holeton 1979; Shuter et al. 1980; Adams et al. 1982). Toneys and Coble (1979) observed an overwinter increase in mean length of age-0 bluegills in one lake, indicating a higher mortality of smaller fish; however, this pattern was not seen in two other bluegill populations. If age-0 bluegills do not attain a sufficient size during the growing season, overwinter mortality could potentially be substantial.

H_4: *Pheromone Prevents Reproduction*

A high density of bluegills could lead to production of sufficiently high pheromone concentrations to inhibit reproduction. Swingle's 1953 abstract, "A repressive factor controlling reproduction in fishes," says that he found evidence that goldfish, common carp, buffalo fish, largemouth bass, "and possibly other species, excrete a substance or substances into the water which specifically retards development of sexual products or prevents laying of eggs." He did not specifically include bluegills in that list of species, but noted that overcrowded bluegills "apparently excrete a material which retards or prevents reproduction by largemouth bass."

Lam (1983) said that "factors associated with crowding have been shown to retard or inhibit spawning in several species (Swingle 1957; Whiteside and Richan 1969; Yu and Perlmutter 1970; Chew 1972; FitzGerald and Keenleyside 1978)." It should be noted that hypotheses 1, 2, and 3 are also "factors associated with crowding," but do not involve pheromones.

The proposed pond experiments are designed to evaluate several mechanisms that could explain recruitment failure in high-density bluegill ponds. By observing the reproductive condition of the adults and watching for the production, survival, and growth of age 0s, it should be possible to determine the relative contribution of hypotheses 1, 2, and 3 toward recruitment failure at high bluegill densities.

This study was conducted to evaluate the effects of bluegill population density on parental condition and reproduction in bluegills ponds. The objective was to measure the effect of bluegill stocking density on condition factor and relative gonad weight of the adults over the growing season in ponds, and on the numbers of age-1 bluegills present the following spring. Additional experiments were conducted to evaluate the influence of (1) bluegill density in the *previous* year, and (2) the density of age-1 and age-2 bluegills on the numbers of age-1 bluegills present the next spring.

Methods

This study was conducted in experimental ponds at the Saline Fisheries Research Station, Saline, Michigan, operated by the Fisheries Division of the Michigan Department of Natural Resources. The ponds, described in Latta and Merna (1977) and Clark and Lockwood (1990), are approximately 0.25 hectare in area, 1 m in average depth, and contain little vegetation. The bluegills used in these experiments were primarily progeny or survivors of fish used in these ponds by Clark and Lockwood (1990), who had netted fish several years earlier from Cedar, Mill and Sugarloaf lakes, Washtenaw County, Michigan. Additional adult bluegills were obtained in spring 1989 from Ford Lake (3.2 kg), Washtenaw County, and Wamplers Lake (5.0 kg), Lenawee County. Table 1 provides a brief guide to the eight experiments of this study. For this study, bluegills in a pond were considered to have reproduced successfully if age-0 fish were produced and survived to be yearlings at pond draining the following spring.

Experiment 1: Effect of bluegill stocking density

The first experiment tested the hypothesis that bluegill reproduction would fail at high stocking densities and would not fail at low or medium stocking densities (Table 1). It was further hypothesized that at high densities there would be inadequate energy for adult bluegills, resulting in lower relative weight and reduced fecundity compared to adult bluegills stocked at lower densities.

Nine ponds were stocked with bluegills in April 1989 at three densities: 56, 134, and 336 kg/ha, hereafter termed low, medium and high densities (Table 2). These densities were chosen based on the experience of Clark and Lockwood (1990) with these ponds. Clark and Lockwood observed recruitment failure in almost all ponds with more than 225 kg/ha, so a density of 336 kg/ha was expected to clearly result in failure. Recruitment was expected to be greatly reduced, but not totally eliminated, at a density of 134 kg/ha. A density of 56 kg/ha was expected to result in nearly maximal recruitment. Over this range of densities, clear differences in the reproductive condition of the adults and the production, survival and growth of age-0 bluegill were expected. This range of densities encompasses the average bluegill standing crop for Michigan lakes with slowly growing bluegills (167 kg/ha, 82% of the total standing crop of fishes: 204 kg/ha; Schneider 1973). The lowest density used was somewhat higher than the average bluegill standing crop in Michigan lakes with normal fish populations, where bluegills averaged 43 kg/ha, 44% of the total 88 kg/ha (Schneider 1973).

Each pond was stocked with 37 kg/ha of bluegills 127 mm total length (TL) or larger, with the remaining biomass in smaller fish (Table 2). Fish were sampled by hook and line approximately every week from late May through early September. Sampled fish were measured to the nearest mm and weighed to the nearest 0.01 g. Gonads and livers were removed and weighed to the nearest 0.0001 g. Ovaries were preserved in modified Gilson's fluid (Snyder 1983); preserved eggs were completely enumerated. Gonadosomatic index (GSI, %) was computed as

$$\mathrm{GSI} = 100\ G/W,$$

where G is gonad weight (g), and W is wet weight (g). Liversomatic index (LSI, %) was computed as

$$\mathrm{LSI} = 100\ V/W,$$

where V is liver weight (g). Relative weight (W_r, %) was computed as

$$W_r = 100\ W/W_s,$$

where W_s (g) is the standard weight for fish of a given length (L, mm) and

$$\log 10\ W_s = -5.374 + 3.316 \log_{10} L$$

(Murphy et al. 1991). The sex ratio was determined for 25.4-mm length groups of fish sampled by hook and line. In some of the smaller fish, the gonad could not be clearly identified as ovary or testis; such individuals were classified as immatures. Ponds were sampled on October 25, 1989, using a 2.5-m seine (mesh size, 1×3 mm) to assess the presence or absence of age-0 bluegills.

Ponds were drained in April 1990. Yearlings (i.e., fish that hatched the summer before) were sorted from older fish based on size (confirmed by checking scale samples), and total weight measured. The total number of yearlings per hectare (Y) was estimated from the total weight of yearlings (*B*, g), the weight (*S*, g) of a counted subsample, and pond area (*A*, ha):

$$Y = \frac{Bn}{SA},$$

where n is the number of yearlings in the subsample. The number of older bluegill was estimated in a similar manner. Yearlings in the subsample were measured to the nearest mm, and mean, standard deviation (SD) and mode of length were determined.

One-way analysis of variance was used to evaluate the influence of stocking density on GSI, relative weight, eggs per gram of female, and LSI by sex and month.

Experiments 2 & 3: Effect of Age-1 Density

Experiments 2 and 3 tested the hypothesis that high levels of age-1 bluegills lead to reduced numbers of age-0 bluegills being produced by adults (Table 1). As in experiment 1, the method used to evaluate this hypothesis was to assess numbers of young present at pond draining the following spring. Additional observations and measurements were made to evaluate some potential mechanisms by which age-1 bluegill might reduce age-0 numbers: interference with adult nesting or spawning, cannibalism of eggs or fry, or competition for zooplankton leading to starvation of fry.

Experiment 2.–In April 1990, nine ponds were stocked with 56 kg/ha of adult bluegills (102-152 mm) from ponds stocked at 56 or 134 kg/ha the previous year. In addition to these adults, different levels of juvenile bluegills (less than 51 mm) were added (Table 3). It was intended that juveniles be stocked into three ponds at 16.8 kg/ha, three ponds at 5.6 kg/ha, and that three ponds receive no juveniles. However, a stocking error was discovered when the ponds were drained in April 1991. Pond 9 was to have been stocked with 16.8 kg/ha of juveniles, but no juveniles were present; the adjacent Pond 8 was to have received 5.6 kg/ha, but had a very large number of juveniles present. I conclude that the juveniles intended for Pond 9 had gone into Pond 8. Therefore, the actual treatments were as follows: one pond (Pond 8) received 23.5 kg/ha of juveniles, two ponds received 16.8 kg/ha, two ponds received 5.6 kg/ha, and four ponds received no juveniles (Table 3).

Adult bluegills were sampled by hook and line every two weeks during the summer of 1990. Measurements were made of fish length, wet weight, gonad weight, liver weight, and weight of the stomach and viscera. Values were computed for W_r, GSI, and LSI. The ponds were observed for bluegill nests from late May through the end of June. Ponds were seined about twice a week during June and once per week during July. A sample of age-0 bluegill was preserved in 95% ethanol, and lengths later measured to 0.1 mm. Ponds were drained in spring 1991. The biomass, mean weight, mean length and density of yearlings and older fish were measured as in experiment 1.

Zooplankton were sampled weekly from May through mid-August as described in Gray (1991). Briefly, vertical tows were made with a 30-cm diameter, 20-μm mesh plankton net. Samples from four fixed sites per pond were pooled, stained with Eosin Y, and preserved in 5% formalin with sucrose (Haney and Hall 1973). Densities were determined for the following taxonomic groups: *Daphnia*, *Diaphanosoma*, *Bosmina*, *Ceriodaphnia*, *Chydorus*, copepod nauplii, juvenile and adult copepods, ostracods, and rotifers. For each pond and date through July 9, length was measured for at least 30 individual zooplankters. Densities were also estimated for the following size groups: large zooplankton (0.8-2 mm), medium zooplankton (0.4-0.8 mm), and total zooplankton (less than 2.0 mm, excluding rotifers).

Experiment 3.–In April 1991, nine ponds were stocked with 56 kg/ha of adult bluegills (≥102 mm). In addition to these adults, different amounts of age-1 bluegills (less than 51 mm) were added. Yearlings were stocked into three ponds at 50 kg/ha, three ponds at 16.8 kg/ha, and three ponds received no yearlings (Table 3). The ponds were examined for bluegill nests and eggs, or were seined for fry, on three days per week for four weeks beginning on May 13, 1991, twice per week to mid July, then about once per week, ending August 16, 1991. A sample of adult bluegills was taken to determine the sex ratio and reproductive condition at pond draining in April 1992. Ponds were drained in spring 1992, and fish were measured as in experiment 1.

Experiments 4 & 5: Effect of Previous Density (Poor Condition)

Experiments 4 and 5 evaluated the hypothesis that adult bluegills in poor condition (low W_r) would have inadequate energy for reproduction and so would not be able to successfully produce young (Table 1). It was assumed that adult bluegills that came from ponds stocked the previous spring at 336 hg/hectare would be in poor condition.

Experiment 4.–In April 1990 one pond was stocked only with adult bluegills (102-152 mm) in poor condition, at a rate of 54.4 kg/ha (Table 3). These fish came from ponds which had been stocked at 336 kg/ha in April 1989. There were not enough surviving 102-152-mm adults from those three high-density ponds to stock the two additional ponds that were planned for this treatment. These fish were in very poor condition at stocking (Table 5). Their relative weight was 64±6.5 % (mean±SD, N = 108), with a maximum W_r of 77 and a minimum W_r of 48 %. Three additional ponds served as controls (Treatment 1 of experiment 2; Tables 1 and 3).

As in experiments 1 and 2, adult bluegills were sampled by hook and line every two weeks during the summer of 1990. Measurements were made of fish length, wet weight, gonad weight, liver weight, and weight of the stomach and viscera. Values were computed for W_r, GSI, and LSI. This pond was drained in spring 1991, and fish were measured as in experiment 1.

Experiment 5.–Because only one pond was able to be used in the 1990 test of the inadequate-energy hypothesis, the test was repeated in 1993. Three ponds were stocked at a biomass density of 56.0 kg/ha with adults (≥102 mm) in poor condition in the spring of 1993; three additional ponds served as controls (Treatment 3 of experiment 6, Table 1, Table 4). The bluegills were taken from ponds which were stocked in the spring of 1992 at a total biomass density of 336 kg/ha. It was expected that these fish would not be able to reproduce successfully in the early summer of 1993 because of inadequate energy stores. One complication was that some of the largest fish used in 1993 did *not* appear to be in poor condition, based on their relative weight at stocking, even though they came from a pond with a high density of bluegills (Table 5). The average fish was in poor condition: the average W_r for the fish stocked into Ponds 2, 12, and 13 was 72, 75, and 76%, respectively. Ponds were drained in spring 1994, and fish were measured as in experiment 1.

Experiment 6: Effect of Adult Size & Age-1 Density

The experiment in 1993 tested the specific hypothesis that 16.8 kg/ha of yearlings is sufficient to prevent successful reproduction of small adults (102-152 mm) but will still allow reproduction by larger adults (greater than 152 mm). Twelve ponds were used in a cross-classified design, three ponds for each of four treatments. Ponds with some large adults or only small adults received either 0 or 16.8 kg/ha of yearlings (Tables 1 and 4). It was expected that there would be successful reproduction in all of these ponds except the combination with small adults and 16.8 kg/ha of yearlings.

Fewer than expected adults were available for stocking, so the stocking density of adults was not the same for all ponds (Tables 1 and 4). Most of the adults used in this experiment were in good condition; for example, adults from Pond 7 and Pond 10 had an average W_r of 87±5.0% (mean±SD), and 95±7.4%, respectively. However, some of the adults taken from Pond 15 were in poorer condition than expected, having an average W_r of 76±10.3%. Adult bluegill from Pond 15 were only stocked into Ponds 8, 9, 14, and 18; each of these four ponds also received adults from Pond 10.

The ponds were monitored for nest construction, spawning, and nest desertion or successful production of fry in order to determine the point at which reproduction fails.

The ponds were examined for bluegill nests almost every day for about two months beginning on May 12, 1993. Ponds were seined for fry once or twice per week from June 3 to August 11, with a final sample taken on September 8. Ponds were drained in spring 1994, and fish were measured as in experiment 1. For ponds where age 1s were present at draining, about 20 adult bluegill were stomach pumped to look for cannibalism.

Experiments 7 & 8: Effect of Age-1 and Age-2 Density

Experiment 7.–The experiment in 1994 attempted to test the specific hypothesis that, in the presence of 78 kg/ha of age-2 fish, 16.8 kg/ha of yearlings is sufficient to prevent successful reproduction (Table 1). Nine ponds were stocked in the spring of 1994 at an adult (≥102 mm) biomass density of 56 kg/ha and different densities of juveniles. Ponds with adults and 78 kg/ha of age 2s received either 0 or 16.8 kg/ha of yearlings; three control ponds received only adults (Tables 1 and 6). Because of an insufficient number of age-2 bluegills at stocking, two ponds received only 30 kg/ha of age 2s instead of 78 kg/ha as intended. It was expected that there would be successful reproduction in all ponds without yearlings, and unsuccessful reproduction in the three ponds with yearlings. Ponds were examined for bluegill nests, spawning, and nest desertion about every other day for about two months beginning on May 23, 1994. Ponds were seined for fry once or twice per week from June 14 to August 10, with final samples taken on October 12 and 18. Ponds were drained in spring 1995, and fish were measured as in experiment 1. For ponds where age 1s were present at draining, about 20 adult bluegill were stomach pumped to look for cannibalism.

Experiment 8.–This experiment was a modification of Experiment 7, conducted to more thoroughly evaluate the effects of 30 and 78 kg/ha of age-2 bluegills on adult reproduction, in the presence of 16.8 kg/ha of yearlings. Nine ponds were stocked in the spring of 1995 at an adult (≥102 mm) biomass density of 56 kg/ha and different densities of juveniles. Ponds with adults and 16.8 kg/ha of yearlings received either 30 or 78 kg/ha of age 2s; three control ponds received only adults (Tables 1 and 6). It was expected that there would be successful reproduction in the control ponds and in ponds with yearlings and 30 kg/ha of age 2s, but that reproduction would fail in the ponds with yearlings and 78 kg/ha of age 2s. Ponds were examined for bluegill nests, spawning, and nest desertion on May 10, 19, 23, 26, and 30, daily during June, and every 2-5 days in July. Ponds were seined for fry once or twice per week from June 12 to August 7, with final samples taken on August 29, 1995. Ponds were drained in spring 1996, and fish were measured as in experiment 1. For ponds where age 1s were present at draining, about 20 adult bluegill were stomach pumped to look for cannibalism.

Results

Experiment 1: Effect of Bluegill Stocking Density

Recruitment.–Recruitment failed in the three ponds with a high stocking density (336 kg/ha). Failure also occurred in three of six ponds with a lower stocking density. When the ponds were seined in October, age-0 bluegill were found in two medium density ponds (ponds 10 and 15) and one low density pond (Pond 18); no age 0s were found in the three high density ponds. This year class was also found in these same ponds at pond draining the following April (Table 7). Of the six low- and medium-density ponds used in this experiment, Pond 18 and Pond 10 were stocked with the lowest density of fish less than 51 mm; Pond 15 received the fifth lowest (Table 2).

Adults.–A total of 469 bluegills was sampled by hook and line during experiment 1. The sex ratio was highly skewed toward males among the larger bluegills sampled. Among fish 152 mm or greater in length, the sex ratio was 9:1 (males:females) (Table 8). The proportions of males, females, and immatures were consistent with a 1:1 sex ratio among fish less than 152 mm in length. The smallest mature female was caught on June 29: a 94-mm bluegill with a GSI of 8.7%. Based on GSI, many bluegills in these ponds are mature at 102 mm.

There was a significant effect of stocking density on the GSI of female bluegills in June, July and August, but not on the GSI of males (Table 9, Figures 1 and 2). For females in June, the 6-fold range of stocking densities produced a 3-fold range in mean GSI, from 3.0% at high density to 9.3% at low density; this effect was highly significant ($P < 0.001$, Table 9). In contrast to the results for females, there was no significant effect of stocking density on male GSI.

The relative weight of males and females was significantly greater at lower stocking densities (Table 10). Stocking density had a highly significant effect on the W_r of females in June, July and August, and a highly significant effect on the W_r of males in June and July (Table 10). The effect of stocking density was less apparent, but still statistically significant, by August. There was also an effect of bluegill size on W_r , most apparent in males from high-density ponds (Figures 3 and 4). Males from about 125 to 150 mm had a low W_r, whereas larger males were generally in much better condition, approaching the W_r of males from medium and low densities. This could be explained by larger bluegills having access to a prey size or type that is not available to smaller fish, so that their food supply is relatively abundant, even in a high-density pond.

The relative size of the liver tends to reflect recent feeding history; larger ration tends to produce a larger liver (Heidinger and Crawford 1977). Stocking density had a detectable influence on the LSI of females in June, but not in July or August (Table 11). Relative liver size was smallest in females in the high density ponds. There was an effect on the LSI of males in August, but not in June or July (Table 11). It is not clear why male LSI in August would be smallest in males from low-density ponds and largest in males from high-density ponds. It is interesting that stocking density had a much greater effect on mean W_r than on mean LSI, suggesting that mean W_r is the more sensitive index of fish condition.

There was great variation in egg number per female (from 0 to 33,300), with egg number varying with female size, ovary wet weight, stocking density, and sampling month. Much of the variation among individuals was reduced by expressing the results per gram of female (Table 12). The grand mean was 62 (2 SE = 12, N = 105) eggs per gram wet weight of female. An effect of stocking density and sampling month is apparent; eggs per gram female declines as stocking density increases and declines from June to August (Table 12). These values are similar to the bluegill fecundity reported by Mayhew (1956) and Ulrey et al. (1938), but are lower than the values reported by Morgan (1951) and Latta and Merna (1977) (Figure 5). Because of the effect of stocking density demonstrated here, those higher fecundities reported could be due to sampling fish from lower density populations or from more productive water bodies.

The variation in egg number among fish was further reduced by expressing the number of eggs per gram of ovary. The grand mean was 922 (2 SE = 116, N = 105) eggs per gram wet weight of ovary tissue, but there was a substantial effect of stocking density and sampling month (Table 13). The number of eggs per gram of ovary was highest in June, decreasing in July and August, and higher for females from the low- and medium-density ponds (Table 13). The June three-fold difference among density treatments in eggs per gram of female (Table 12) is due primarily to the three-fold difference in female GSI (Table 9); there is much less difference in egg number per gram of ovary (Table 13). The information on egg number and GSI suggests that intraspecific competition for food increases with stocking density and results in reduced egg production per female.

Experiment 2: Effect of Age-1 Density

Nests.–Nests were first observed on May 28; none had been apparent 4 d earlier. Periodic observations of the pond margins revealed evidence of bluegill nests in five of the six ponds with 0 or 5.6 kg/ha of juveniles. Fry were later captured in all six of these ponds, so one pond must have had nests in deeper water not visible from the shore. Bluegill nests were observed in two of the three ponds with 16.8-23.5 kg/ha of juveniles (the third pond was very turbid); no fry were found in these three ponds. In one of these ponds (Pond 18), nests that were defended on May 28 and again on May 30 appeared abandoned on May 31; a few guarded nests were observed later, but eggs or fry were never seen in this pond.

Multiple modes in the size-frequency distribution of age-0 bluegills captured by seining indicate that there were two or more spawning periods in six of these ponds. The changes over the summer in the growth rate of the young of the year are summarized in Table 14.

Recruitment.–All six ponds with low densities of juveniles (0 or 5.6 kg/ha) successfully produced young that survived to the following spring. None of the three ponds with high densities of juveniles (17-23.5 kg/ha) produced young (Table 7).

Zooplankton.–The results of the zooplankton sampling and the relationship with growth of the young-of-the-year bluegill are described in Gray (1991) and Gray et al. (1997). The changes over the summer in the mean density of all zooplankton (excluding rotifers) are summarized in Table 14. In brief, zooplankton density increased in the ponds during May and early June. The change in zooplankton dynamics after early June depended on whether age-0 bluegill were produced in the pond. From early June to early July, zooplankton density decreased greatly in ponds with age 0s (with or without age 1s), but was variable (without a prominent decrease) in ponds without age 0s. Thus, the effect of age 0s on zooplankton was greater than the effect of yearlings on zooplankton, at the densities used in this experiment. Age-1 bluegill did not cause a dramatic crash in the zooplankton that might have lead to starvation of age 0s and a year-class failure.

Adults.–A total of 441 bluegills was sampled by hook and line during experiment 2. The sex ratio was slightly skewed toward males among the larger bluegills sampled. Among fish 152 mm or greater in length, the sex ratio was 2.5:1 (males:females) (Table 15). This is much less than the 9:1 ratio observed in experiment 1, and suggests that female survival was greater in experiment 2. As in experiment 1, the proportions of males, females and immatures were consistent with a 1:1 sex ratio among fish less than 152 mm in length.

Juvenile stocking density did not have a significant effect on female GSI during May and June (ANOVA, $P > 0.05$, Table 16). However, there was a significant effect on female GSI during July ($P < 0.001$) and August ($P < 0.01$), due to the larger GSI of females in ponds stocked with juveniles at 17 kg/ha (Table 16). No age-0 bluegills were captured by seining in those ponds, and it is possible that fewer eggs were spawned, causing those females to have a larger GSI.

As in experiment 1, female GSI decreased from May and June through August in ponds with 0 or 5.6 kg/ha of juveniles. Male GSI also decreased from May and June to August and September (Table 16).

Juvenile stocking density had very little effect on male GSI (Table 16). The effect was most apparent in August, when adult males from treatment 3 (juveniles at 17 kg/ha) had a greater average GSI than males from treatments 1 and 2.

Experiment 3: Effect of Age-1 Density

Nests.–Nests were observed on May 13, 1991, the first day of observation; this was 15 d earlier than the first nests were seen in 1990. Eggs were first seen on May 15, and fry were first seen in the nests on May 20 (Table 15). Bluegill fry were first observed in seine hauls on May 21. If fry were found in seine hauls in May or June, 1991, then at least 50,000 yearlings per acre were found at draining in April 1992. In Pond 18, fry were not found until July 12, and only 471 yearlings per acre were found at draining. Fry produced this late in the season could be much more vulnerable to predation because of larger yearling size and a decline in other prey available to yearlings.

On May 24, 1991, cannibalism was observed in a bluegill nest in Pond 5 that was being examined for the presence of eggs with an observation tube (a section of stove pipe with a piece of glass sealed across one end). The defending male left the nest when the observation tube got very close. A yearling bluegill (<50 mm) was seen in the nest eating eggs. Many yearlings were near the nests, and another male was seen chasing away yearlings that were getting too close to his nest. On May 23, 1991, many yearlings were also seen around the nests in Pond 5; 30-40 yearlings were estimated to be around two of the actively defended nests. These observations suggest that predation by juveniles on eggs or small fry has the potential to cause year-class failure, consistent with laboratory predation experiments of Gray (1991). However, because active nests were not observed in the two ponds with year-class failure, the failures in 1991 may have occurred before predation could play a role.

Recruitment.–All three ponds without yearlings successfully produced young of the year (Table 7). (Though no juveniles were intentionally stocked, a small number of juveniles was found in two of these ponds at draining.) In experiment 2 in 1990, none of the three ponds with 17-23.5 kg/ha of yearlings produced young; however, in the summer of 1991, all three ponds with 17 kg/ha of yearlings produced young, though one pond produced only a few (Pond 18, Table 7). Also, one of the ponds with 50 kg/ha of yearlings produced young. This improved reproductive success could be due to the larger size of the adults in 1991. Larger males might be better able to successfully raise a nest of fry.

Adults.–At spring draining in 1992, the GSI was relatively low for both males and females (Table 16). Apparently bluegill gonad size does not increase appreciably by early April. The GSI is expected to be much larger by late May and early June, based on the results from 1989 (Table 9). There were 108 males and 192 females, for an overall sex ratio of 1 male per 1.78 females (36% males) (Table 17). The male:female ratio increased in the larger size groups. Among fish 175 mm and larger, the ratio was 1.88 males per female. This sex ratio, however, is much different than that observed in 1989 among the recent survivors of Clark and Lockwood's (1990) study (19.3 males per female for fish >178 mm; Table 8), suggesting an improved survival of larger females.

At pond draining in April 1992, one adult male bluegill (202 mm, 164.2 g) from Pond 10 had two juvenile bluegills in its stomach, each fish about 50 mm in length. This stimulated examination of adult stomachs at pond draining in subsequent years to look for further evidence of cannibalism by adults.

Experiments 4 & 5: Effect of Adults in Poor Condition

In 1990, nests, but no fry, were observed in the single pond with small (102-151 mm) adults in poor condition. No age-1 bluegill were present at pond draining the next spring (Table 7). These fish were so thin at stocking (W_r = 64%, Table 5) that it is not surprising that they did not reproduce successfully.

In 1993, in contrast, adults reproduced successfully in all three ponds, even though these adults had also come from high-density ponds (Tables 7 and 18). However, some of the larger bluegills were in good condition at stocking in spring 1993 (Table 5). Whereas the average W_r of 102-151 mm fish was 70-75%, the W_r of 203-253 mm fish was 82-87%, and three 254-278 mm fish had a W_r of 96%. The carry-over effect probably reduced the reproductive output of some adults, especially the smaller ones, but there were enough adults in good enough condition to produce successful year classes in all three ponds. The carry-over effect of bluegill density is not sufficient to cause year-class failure if some adults are in good condition.

For both males and females in experiment 4, average GSI in May 1990 was highly significantly lower than corresponding values for adults from experiment 2 (t - test, $P < 0.001$, Table 16). By June, however, both male and female GSI values had increased enough that they were not significantly different from the adults in experiment 2. By July, female (but not male) GSI was again significantly different ($P < 0.001$), because the seasonal decrease for the females in experiment 2 was much greater than that for females of experiment 4. By August, there was no significant difference in female GSI, but male GSI was higher for fish in experiment 4.

Experiment 6: Effect of Adult Size & Age-1 Density

The summer 1993 experiment also evaluated the combined effects of yearling density and adult size on reproduction. It was expected that reproduction would be poorest in the treatment with small adults combined with yearlings at 16.8 kg/ha. This was, in fact, the only treatment where a reproductive failure occurred (Pond 14), though reproduction was successful in the other two ponds of this treatment (Table 18). Reproduction was successful in the other three treatments, i.e., in all ponds containing either some adults over 152 mm in length or no yearlings. Yearlings at 16.8 kg/ha appear to have a larger negative effect on small adults than on large adults.

Successful reproduction occurred in eleven of the twelve ponds. The one pond that failed had been stocked with small adults and 16.8 kg/ha of yearlings.

Reproductive failure occurs early in the season. If young were captured by seining in June, then young in that pond were captured through the summer, in the fall, and were found at pond draining the next spring (Table 18).

Much of the nest abandonment that was observed in 1993 appeared to be related to decreases in water temperature associated with cold fronts. Claussen (1991) found that cooler temperatures during the reproductive season can lead to increased numbers of nest desertions by male bluegills.

Experiment 7: Effect of Age-1 and Age-2 Density

Nests were present in three ponds on May 23 (the first day of observation), in two more ponds by May 31, and probable nests were observed in the turbid water of Pond 18 on June 15 (Table 19). Turbid water prevented confirmation of nests in the other three ponds. Spawning was first observed on June 1 (though some may have occurred before May 23) and bluegill fry were observed in some nests on June 8 and in the seine hauls which began on June 14. In Ponds 2, 9, and 14, fry were caught by seining even though no bluegill nests had been observed.

In the one pond (Pond 2) where no age 0s had been seined in June or July, modest numbers were found in October. Two distinct modes in age-0 length (23.5 and 35 mm) suggest they were produced in two late spawning bouts.

If fry were found in seine hauls in June 1993, then yearlings were found at draining in spring 1994. This was generally true for the 1994 experiment, but not for Pond 16. In that pond one 12.0-mm bluegill was found on July 1, but none from that year class was found at draining in spring 1995.

In the 1994 experiment, some age-0 bluegills were captured in every pond, contrary to expectation, but the relative numbers of age 0s varied with treatment and season. The clearest pattern in numbers of age 0s appeared in early summer, when large numbers of age 0s were seined in all three control ponds, few or no age 0s were caught in ponds with 78 kg/ha of age 2s, and moderate numbers of age 0s were found in ponds with 30 kg/ha of age 2s (Table 19). Thus, in early summer the observed numbers of age 0s were strongly and inversely related to the density of age-2 bluegills. This early summer pattern is consistent with cannibalism by age 2s on eggs and fry. The effect of age-1 bluegills in this experiment was largely masked by the strong negative effect of age 2s.

The pattern was somewhat different by October. Relatively large numbers of age 0s continued to be found in the control ponds.

However, there were changes in the relative numbers in the other ponds (Table 19). In the one pond (Pond 2) where no age 0s had been seined in June or July, modest numbers were found in October; so if age-2 bluegills in this pond had prevented successful fry production in early summer, they did not do so all summer. In the two ponds with 30 kg/ha of age 2s, modest numbers of age 0s were seined in June and July, but only a few were found in October. In two ponds, repeated seining in October found no age 0s.

The relative numbers of age-0 fish changed somewhat by spring (Tables 7 and 19). The biggest change occurred in one control pond (Pond 8): whereas consistently large numbers had been observed in summer and fall, only a small number (2,709 per hectare) were present by spring. It is not clear what caused this reduction in numbers, and whether it is related to the large amount of fathead minnows *Pimepheles promelas* (419 kg/ha) produced in this pond or the small mean weight of surviving adults (55.7 g).

Several new observations were made in this experiment. First, some spawning occurred in late July or later, whereas in previous experiments almost all reproduction occurred in May and June. This late summer spawning produced a substantial year class (56,328 age-1 bluegills per hectare) by spring in a pond in which no age 0s had been observed in seine hauls in June and July. The juveniles that appeared to eliminate age-0 bluegills in June did not eliminate age-0 production later in the season.

The second new observation was the great reduction in age-0 numbers during winter in one control pond. In Pond 8, substantial numbers of age-0 bluegills had been observed by seining all summer and also in October. But relatively few (about 1000) from this age class were present the following spring. This suggests that overwinter mortality may substantially reduce year-class strength in some circumstances.

The third observation was the importance of the density of age-2 bluegills for reproduction. Summer production of age 0s was zero or very low in ponds with 78 kg/ha of age 2s, but was moderate in ponds with only 30 kg/ha of age 2s. Based on this and previous experiments, both age-1 and age-2 bluegills can have substantial negative effects on the number of age-0 bluegills surviving to the following spring, and predation appears to be the major mechanism for the effect.

Experiment 8: Effect of Age-1 and Age-2 Density

Nests.–In 1995 the first nests were observed in two ponds on June 1, and in seven more ponds by June 7 (Table 20). Age-0 bluegill were first caught in seines on June 12; these fish ranged from 4.9 to 7.2 mm.

Recruitment.–Reproduction occurred in all three ponds without juveniles (Treatment 1) and in two of three ponds in each of the other two treatments (Table 7). In Pond 8 of treatment 3 (age 1s at 17 and age 2s at 78 kg/ha), only a few age 0s were caught all summer by seining, and only 1,766 yearlings/hectare were found at spring draining, a very weak year class (Table 20). In Pond 5, where a year class failed, nests were observed on June 7, but no fry were found by seining. This suggests that the failure occurred very early in the season. Pond 18 this year was turbid enough to make it hard to observe nests, and none were observed, no fry were caught in seines, and no young found at pond draining (Table 20); this also suggests that the year-class failure occurred early in the season.

Discussion

Year-class failure in these bluegill ponds is clearly associated with the presence of juvenile bluegills, that is, age-1 and age-2 bluegills, less than about 100 mm. This series of eight experiments involved a total of 61 pond-year combinations, and reproduction failed in 16 of these (Table 7). Of the 23 occasions involving ponds stocked without juveniles, there was only one year-class failure (a failure rate of 4%). That failure was the single pond in experiment 4 that received small adults (102-151 mm) in very poor condition (W_r of 64%; Table 5). Of the 38 occasions involving ponds with juveniles, reproduction failed in 15, for a failure rate of 39%. This was not significantly different from the 49% failure rate observed by Clark and Lockwood (1990): 22 failures out of 45 occasions (Chi-square test, using 22/45 as the expected proportion of failures, $P > 0.1$). However, the observed frequency of failure in ponds without juveniles, 1 failure in 23 occasions, is highly significantly different (Chi-square test, $P < 0.001$).

Year-class failure is not typically caused by overwinter mortality of age 0s. If at least a dozen age-0 bluegill were captured by seining in June or July, then young in that pond were captured through the summer, in the fall, and were found at pond draining the next spring (Tables 15-20). [In the case of Pond 16 in 1994, a single 12.0-mm bluegill was captured on July 1, but no other age 0s were ever seined, and none was found at spring pond draining (Table 19).] Year-class failure occurs earlier in the season.

Clark and Lockwood (1990) suggested the possibility that juvenile bluegills might physically interfere with adults at spawning, and exert some negative social interaction that would prevent completion of the spawning act. I observed one kind of interference with spawning caused by sneakers. Sneakers are small, relatively young, precociously mature males that do not build nests of their own, but dart into the nests of parental males during oviposition (Gross 1984). On many occasions I observed parental (i.e., nest-building) male bluegills interrupt rim-circling behavior or the spawning act to drive away other males that came too close, or to drive away sneakers in the nest when they were discovered. But I never observed such interruptions completely prevent spawning by a female. Sneakers would not be successful in passing on their genes if they prevented spawning, so although this type of interference would affect the paternity of the fry, it would not be expected to completely prevent spawning.

Starvation of fry now appears to be a very unlikely explanation for year-class failure in these bluegill ponds. When age-0 bluegill are present in a pond, growth of the first natal cohort is initially quite rapid, even in ponds with age-1 bluegill present (Gray et al. 1997). The age 0s typically graze the larger zooplankton down to very low densities by midsummer; and then growth slows near the time they switch to feeding on copepods and midge larvae (Gray 1991; Breck 1993; Gray et al. 1997). Although the growth rate of age-0 fish was sometimes very low in late summer, mass mortality due to starvation was not apparent. In this series of experiments, if more than a few fry were observed early in the summer, then young were observed in the fall and at pond draining the following spring.

While overwinter mortality did not typically cause year-class failure in these ponds, overwinter mortality may have had a substantial effect on year-class strength in some cases. For example, in experiment 7 all three ponds of treatment 1 (no juveniles) appeared to have large year classes in the summer and fall of 1994; many age 0s were consistently caught by seining (Table 19). However, by the next spring one pond had only 2,709 age 1s per hectare, whereas the other two had 169,885 and 122,880 per hectare. It is not clear what caused this reduction in numbers, and whether it is related to the large amount of fathead minnows *Pimepheles promelas* (419 kg/ha) produced in this pond or the small mean weight of surviving adults (55.7 g).

Adult bluegills can and do consume some juvenile bluegills in ponds. Figure 8 shows results of pumping stomachs of adult bluegills at spring pond draining. The maximum size consumed is consistent with the estimated gape limit based on predator mouth size and prey maximum body depth (Schneider and Breck 1996). However, except for one pond where only a single individual was found all summer (Table 19), in this series of experiments there were no other cases where a year class was observed in the summer but was missing the following spring. Cannibalism on young larger than about 20 mm is unlikely to cause year-class failure. However, cannibalism on age 0s during winter by adults will contribute to a reduction in year-class strength, which can increase the subsequent growth rate of the survivors. In this way the presence of large adults can have a positive effect on the growth rate of juveniles, which can help perpetuate the presence of large bluegills in the population.

Cannibalism by juvenile bluegills on age-0 bluegills less than 13 mm appears to be the major mechanism causing reduced recruitment and even year-class failure in high-density bluegill ponds. The aquarium studies of Gray (1991) show that the rate of predation by age-1 bluegills on age-0 bluegills is strongly size-dependent, with the highest rates of predation on the smallest prey. Gray (1991) measured a rate of 110±19 prey·predator^{-1}·h^{-1} (mean±2 SE, N = 11) for 32-38-mm bluegill consuming 5.5±0.1 mm bluegill (N = 6), the size at which bluegill fry leave the nest and begin feeding (Toetz 1966). For age-1 bluegill weighing 0.4 g (Table 7), 16.8 kg of age 1s would number 42,000 individuals, or 10,500 fish if stocked at a rate of 16.8 kg/ha in these 0.25-hectare ponds. Feeding at this rate, 10,000 age-1 bluegill could consume 1,100,000 fry in 1 h, and many more in a day, easily capable of having a dramatic effect on year-class strength during the first few days after fry leave the nest.

The rate of predation by 35-mm juveniles declines to very low levels for age 0s larger than about 13 mm (Gray 1991), probably due to gape limitation (Figure 8). The growth rate of the first natal cohort is about 0.6 mm/d (Breck 1993). Starting at 5.5 mm when they leave the nest (Toetz 1966), and growing at 0.6 mm/d, it would take bluegill fry 12.5 d to reach 13 mm. That is a long time to run the gauntlet of predation by age 1s. Cannibalism by juvenile bluegill on age-0 bluegill can readily explain reduced recruitment and year-class failure in these ponds.

In lakes, bluegill fry rapidly move to the pelagic zone after leaving the nest, then return to the littoral zone after growing to 22-25 mm (Werner 1967, 1969). At this size they should be safe from predation by bluegills smaller than about 75 mm, based on gape limitation (Figure 8). Mittelbach and Osenberg (Osenberg et al. 1992; Mittelbach and Osenberg 1993) argue convincingly that juvenile bluegill less than 75mm SL (about 96mm TL) remain in the littoral zone to reduce the risk from predators such as largemouth bass. Perhaps bluegill fry in lakes remain in the pelagic zone until they are large enough to have a low risk of predation from larger juvenile sunfish in the littoral zone.

Claussen (1991) found that cooler temperatures during the reproductive season can lead to increased numbers of nest desertions by parental male bluegills, leading to reduced production of fry in cool years. Cooler temperature delays egg and fry development (Beard 1982) and therefore increases the time that males must guard the nest, increasing the costs of reproduction for the males. Claussen's study demonstrates that nest desertion can affect the total number of fry produced. In the present study, nest desertion following a cold front was observed on several occasions. By extending development time of eggs and larvae and slowing the growth rate of fry after leaving the nest, cooler temperatures would lengthen the time that eggs and fry are vulnerable to predation by larger juveniles.

Juvenile bluegill density influences year-class strength of age-0 bluegill. Figure 6 shows the number of young surviving to spring plotted against total bluegill density at stocking, for different stocking densities of juveniles. The number of yearling recruits declines as juvenile stocking density increases.

In extreme cases, high population density can reduce the condition of adult bluegills to such low levels that they cannot successfully produce young, even when transferred to a low-density pond in spring (Experiment 4). This may explain some year-class failures, particularly in populations with small adults (<152 mm). However, large bluegills can be in good condition and successfully rear young, despite having spent the previous year at high population densities. It appears that larger bluegills (>152 mm) in these ponds can have access to prey items not available to smaller adults, such as juvenile crayfish, so that large bluegills can be in good condition while smaller adults in the same pond are in poor condition. The larger adults, then, have the energy resources to successfully produce young.

Population density clearly influences relative ovary weight (GSI) and fecundity in bluegill ponds (Figure 5). Growth of age-0 bluegill is also density-dependent (Figure 7).

This will influence the vulnerability to predation by larger bluegills (Figure 8) as well as other predators. Density-dependent fecundity and growth (and consequent survival) are likely to be very important in modeling bluegill population dynamics in systems such as these.

This study demonstrated that year-class failure in high-density bluegill ponds is strongly associated with the density of juvenile bluegills. The mechanism of year-class failure does not appear to be starvation of age 0s after hatching (caused by competition with age 1s for zooplankton or other prey), nor overwinter mortality, nor cannibalism on fry larger than 20 mm. It does not appear to be adult lack of adequate energy for reproduction, except in extreme cases. While not causing failure, these mechanisms probably do have an influence on year-class strength. This study and experiments by Gray (1991) suggest that predation by juvenile bluegills, on eggs and larvae in the nest and on fry soon after leaving the nest, is the major mechanism producing recruitment failure in high density bluegill ponds.

Acknowledgments

This study was completed by the combined efforts of management and research sections in the Michigan Department of Natural Resources, Fisheries Division. I thank the personnel in Districts 11, 13, and 14 for help in stocking and draining the ponds; J. Brandao, C. L. Sibert, G. W. Crawford, S. C. Latta, K. Edly, L. J. Kowalewski, W. R. Spaller, C. S. Willett, P. A. Petrusso, L. Winkelbauer, A. J. Schrank, I. I. Pamphilis, and E. Grube for field and lab work; and J. Gapczynski, T. Zorn and A. D. Sutton for their very professional assistance. This study was funded by Federal Aid in Sport Fish Restoration (Dingell-Johnson) Project F-35-R and the Fish and Game Fund of the State of Michigan.

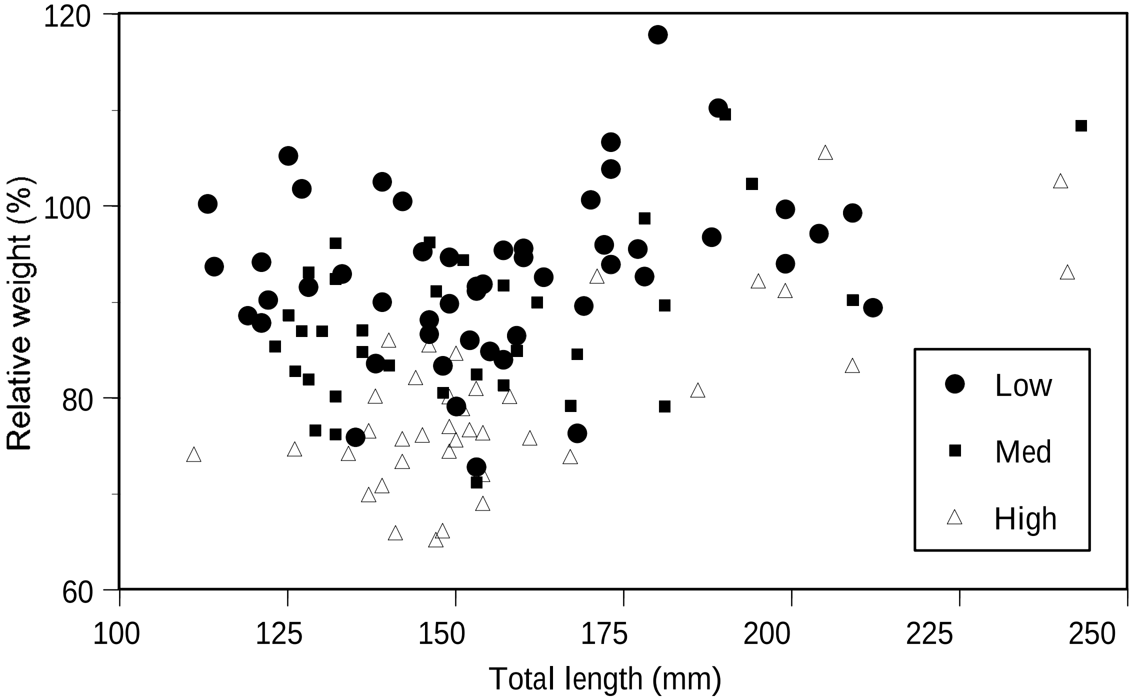

Figure 1.—Relative weight of various sizes of male bluegill sampled by hook and line in June, 1989. Symbols indicate the treatments of experiment 1: “Low” = 56 kg/hectare; “Med” = 134 kg/hectare; “High” = 336 kg/hectare, total bluegill density. In high-density ponds in June, large males were in better condition than small males.

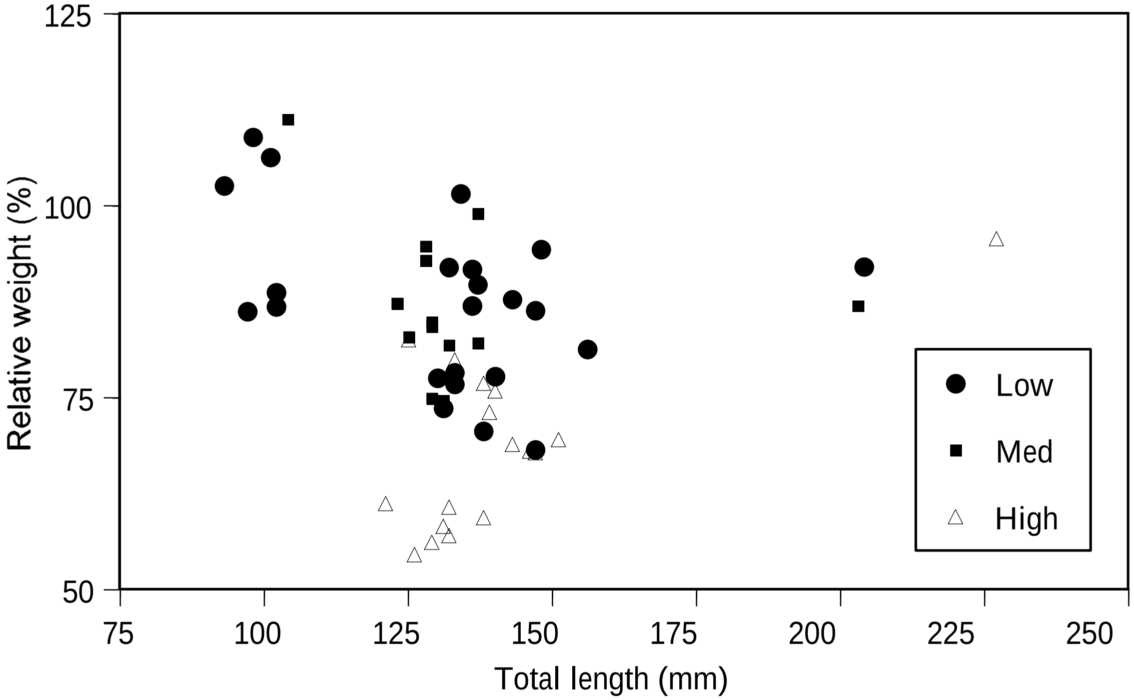

Figure 2.—Relative weight of various sizes of female bluegill sampled by hook and line in June, 1989. Symbols indicate the treatments of experiment 1: "Low" = 56 kg/hectare; "Med" = 134 kg/hectare; "High" = 336 kg/hectare, total bluegill density. In June, females were in poorest condition in high-density ponds.

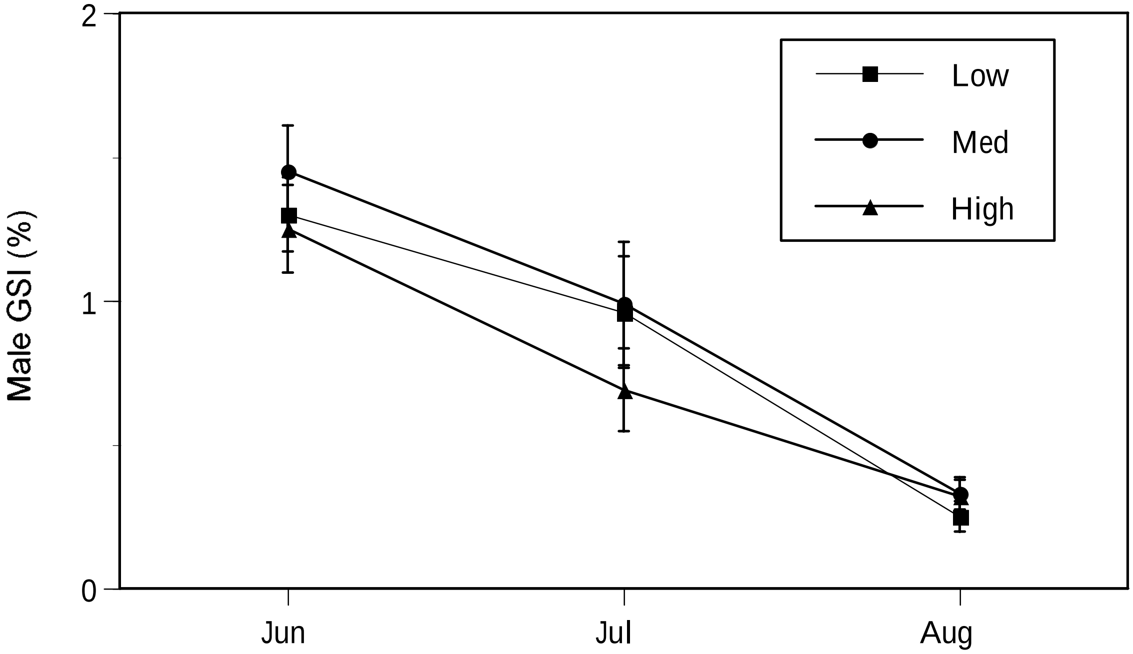

Figure 3.—Male gonadosomatic index (GSI) of bluegill sampled by hook and line in summer, 1989, for three treatments of experiment 1: “Low” = 56 kg/hectare; “Med” = 134 kg/hectare; “High” = 336 kg/hectare, total bluegill density. Male GSI did not vary with density, but declined through the summer.

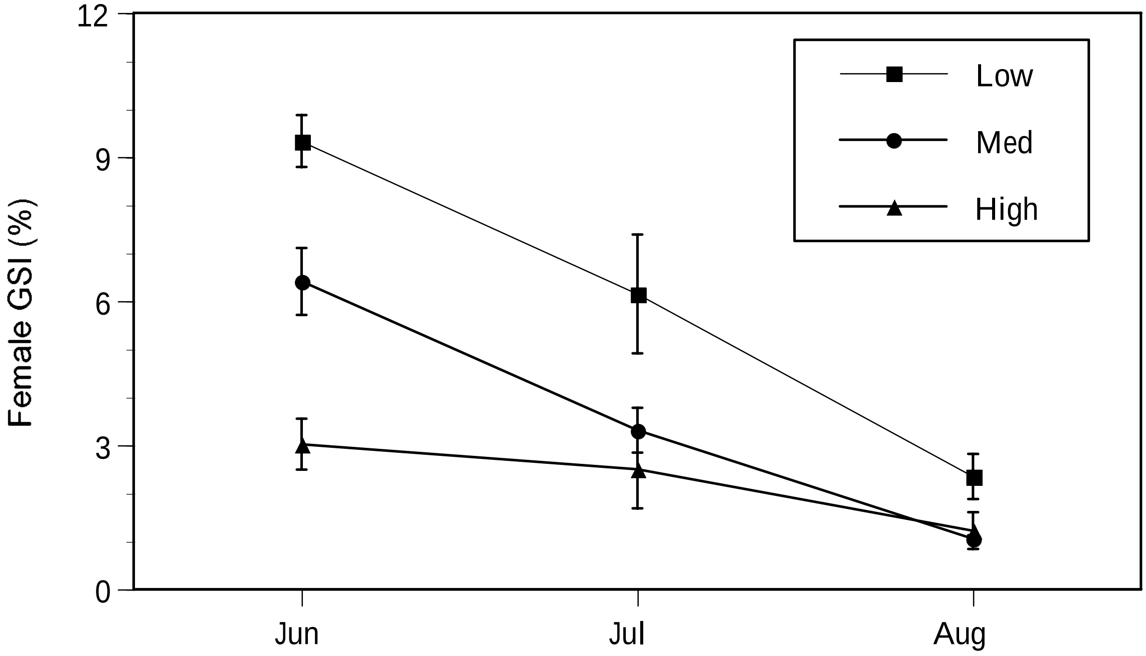

Figure 4.—Female gonadosomatic index (GSI) of bluegill sampled by hook and line in summer, 1989, for three treatments of experiment 1: “Low” = 56 kg/hectare; “Med” = 134 kg/hectare; “High” = 336 kg/hectare, total bluegill density. Female GSI was highest in the low-density ponds and declined through the summer.

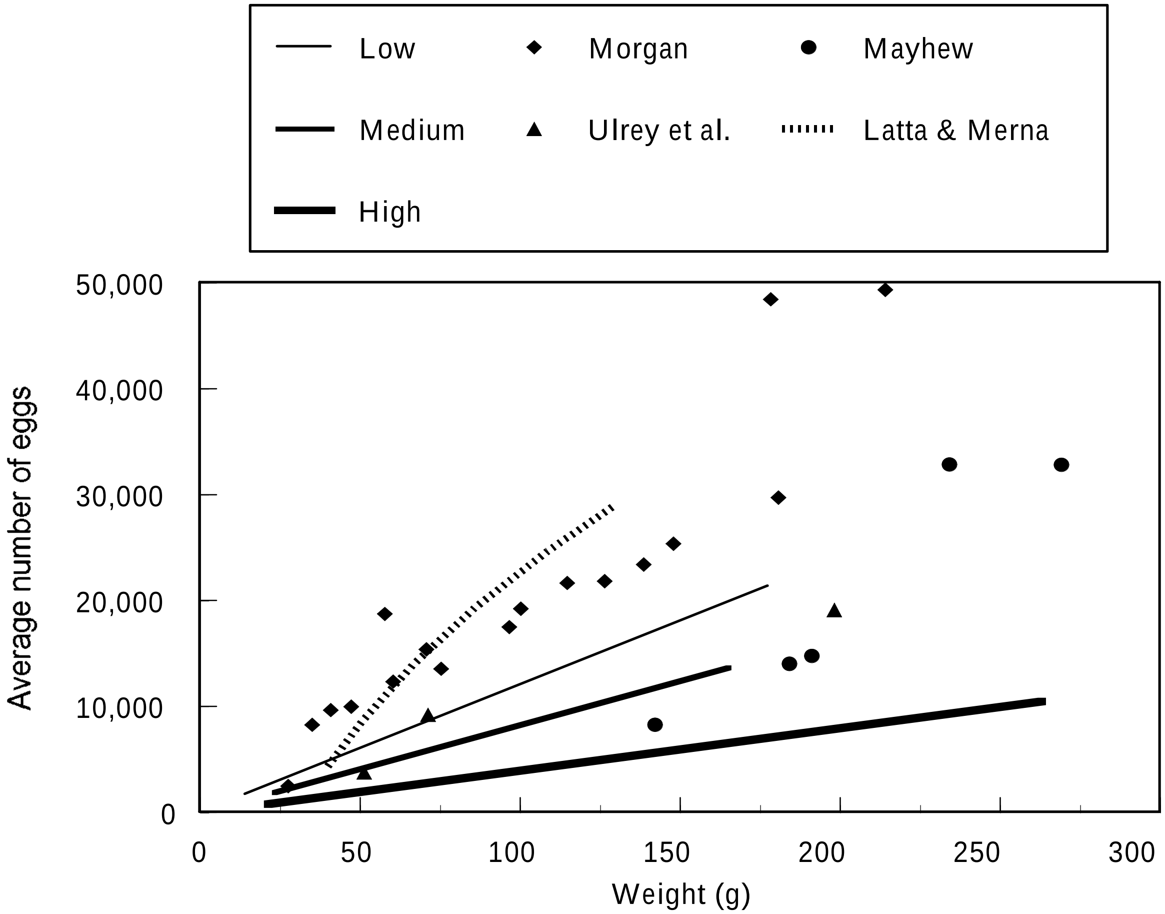

Figure 5.—Bluegill fecundity increases with female size and decreases with stocking density. Solid lines represent 120, 83, or 40 eggs/g female (this study, Table 12). Other values are from Ulrey et al. (1938), Morgan (1951), Mayhew (1956), and Latta and Merna (1977).

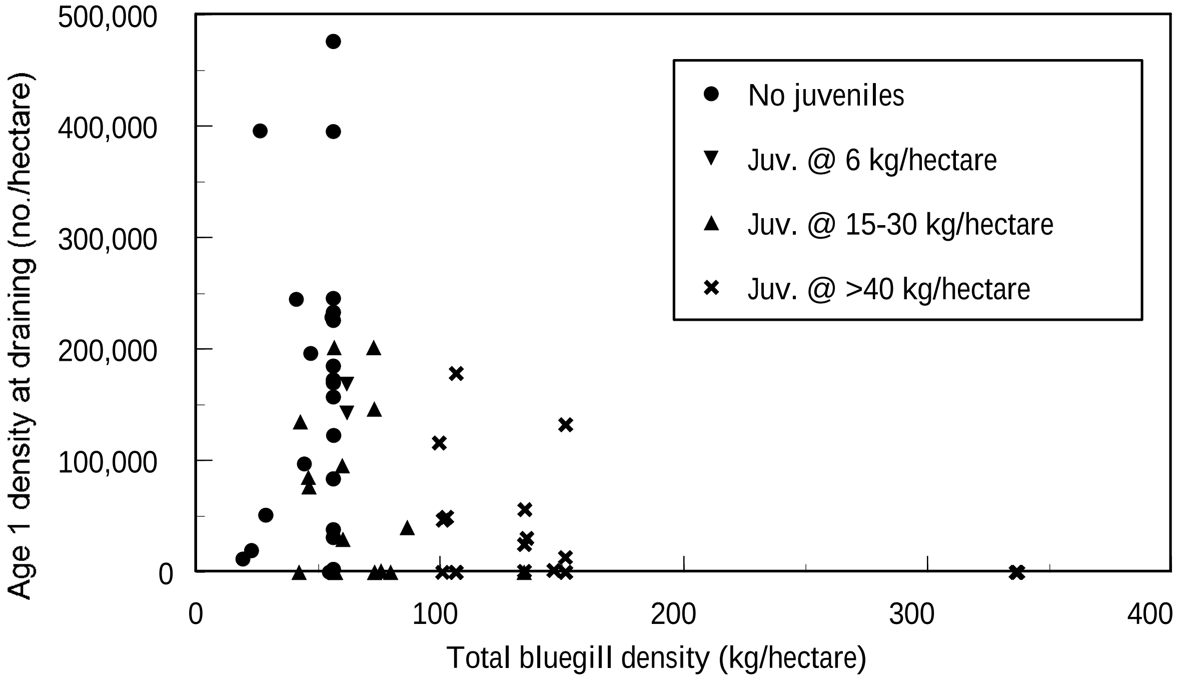

Figure 6.—Density of age-1 bluegill at spring pond draining versus total bluegill biomass at stocking. Symbols indicate the stocking biomass contributed by juveniles (fish < 102 mm).

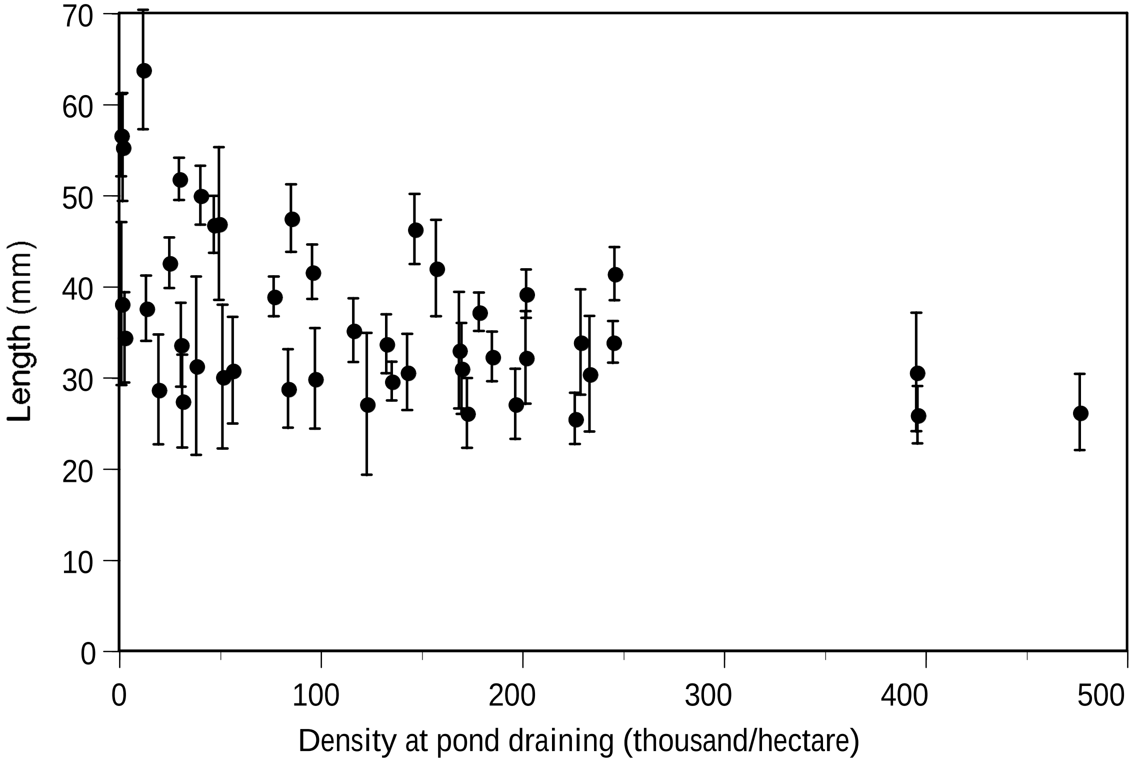

Figure 7.—Length (±1 SD) versus density of age-1 bluegill at spring pond draining. The larger values of mean length tend to occur at lower densities.

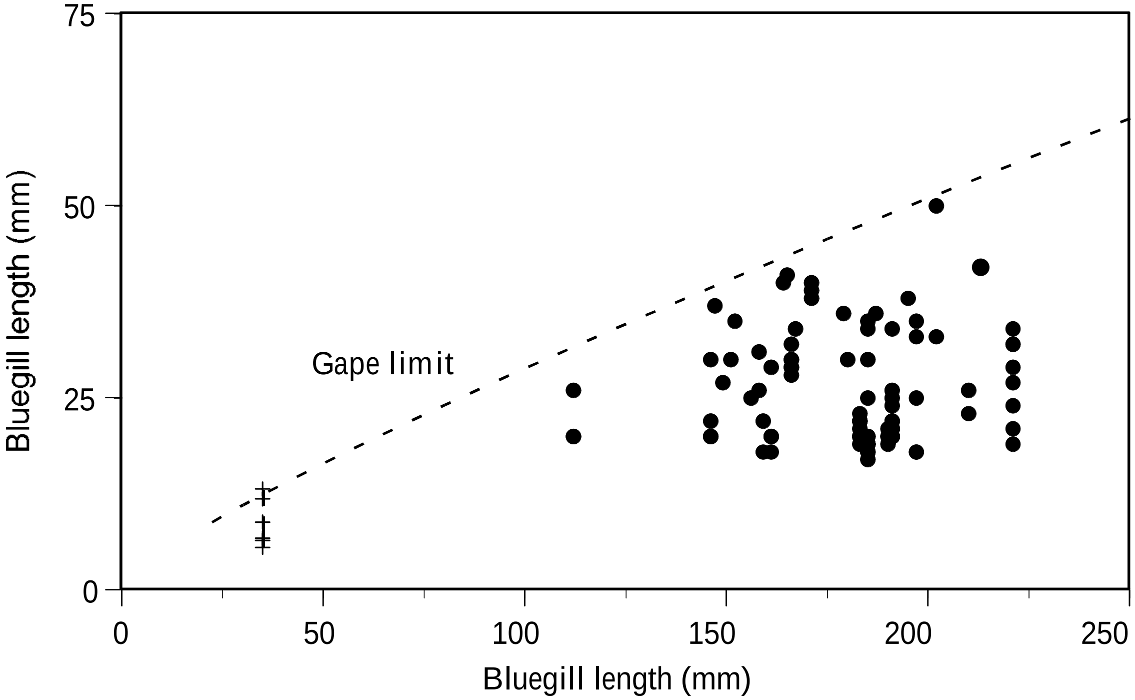

Figure 8.—Sizes of age-1 bluegill found in the stomachs of adult bluegill at spring pond draining. The dashed line is the estimated gape limit for bluegill, based on the mouth gape of the predator and the maximum body depth of the prey (Werner 1974; Breck 1993; Schneider and Breck 1996). The “+” symbols indicate the sizes of age-0 bluegills consumed by age-1 bluegills in the aquarium studies of Gray (1991).

Table 1.–Experimental treatments for eight experiments on bluegill reproduction conducted at the Saline Fisheries Research Station. Number of ponds per treatment is given in parentheses.

Experiment number and description	Year	Treatment (kg/hectare)			
		1	2	3	4
1 Vary total bluegill biomass; constant 37 kg/hectare of fish ≥127 mm.	1989	total: 56 (*N* = 3)	total: 134 (*N* = 3)	total: 336 (*N* = 3)	
2 Vary age-1 biomass; constant 56 kg/hectare of fish 102-151 mm.	1990	0[a] (*N* = 4)	5.6 (*N* = 2)	17[b] (*N* = 3)	
3 Vary age-1 biomass; constant 56 kg/hectare of fish ≥102 mm.	1991	0 (*N* = 3)	17 (*N* = 3)	50 (*N* = 3)	
4 Evaluate adults in poor condition; use fish from ponds stocked at 336 kg/hectare the previous year.	1990	low W_r: 56 (*N* = 3)	controls[a]: 56 (*N* = 3)		
5 Evaluate adults in poor condition; use fish from ponds stocked at 336 kg/hectare the previous year.	1993	low W_r: 56 (*N* = 3)	controls[c]: 56 (*N* = 3)		
6 Vary adult size and age-1 density; total of 56 kg/hectare of fish ≥102 mm.	1993	small adults, no age 1s (*N* = 3)	small adults, age 1s at 17 (*N* = 3)	large adults[c], no age 1s (*N* = 3)	large adults, age 1s at 17 (*N* = 3)
7 Vary age-1 biomass in presence of age 2s at 78 kg/hectare; constant 56 kg/hectare of fish ≥102 mm; treatment 1 is control: no juveniles.	1994	no age 1s, no age 2s, adults at 56 (*N* = 3)	no age 1s, age 2s at 78[d], adults at 56 (*N* = 3)	age 1s at 17, age 2s at 78[d], adults at 56 (*N* = 3)	
8 Vary age-2 biomass in presence of age 1s at 17 kg/hectare; constant 56 kg/hectare of fish ≥102 mm treatment 1 is control: no juveniles.	1995	no age 1s, no age 2s, adults at 56 (*N* = 3)	age 1s at 17, age 2s at 30, adults at 56 (*N* = 3)	age 1s at 17, age 2s at 78, adults at 56 (*N* = 3)	

[a] The control for experiment 4 was treatment 1 of experiment 2, both in 1990.

[b] Pond 8 received fish intended for Pond 9, so Pond 8 received 23.5 kg/hectare of age 1s.

[c] The control for experiment 5 was treatment 3 of experiment 6, both in 1993.

[d] One of the three ponds in each of treatments 2 and 3 of experiment 7 received only 30 kg/hectare of age 2s due to insufficient fish of this age.

Table 2.–Biomass density (kg/hectare) of three size groups of bluegills stocked into ponds in spring 1989 for experiment 1, varying total bluegill biomass.

Pond number	Area (hectares)	Bluegill size <51 mm	Bluegill size 51-126 mm	Bluegill size ≥127 mm	Total
Experiment 1, Treatment 1: 56 kg/hectare					
5	0.30	7.6	11.5	37.5	56.6
14	0.21	10.6	8.5	36.9	55.9
18	0.20	0	19.4	36.9	56.3
Experiment 1, Treatment 2: 134 kg/hectare					
7	0.26	69.4	27.9	36.9	134.2
10	0.25	1.2	97.4	36.8	135.4
15	0.29	36.0	61.5	37.0	134.4
Experiment 1, Treatment 3: 336 kg/hectare					
8	0.25	167.0	132.0	37.2	336.3
9	0.27	36.3	262.6	37.1	336.1
16	0.24	0	299.8	37.0	336.8

Table 3.–Biomass density (kg/hectare) of three age groups of bluegills stocked into ponds in spring for experiment 2 (1990) and experiment 3 (1991), both varying the density of age-1 bluegills, and for experiment 4 (1990), evaluating adults in poor condition.

Pond	Area	Age at stocking			
number	(hectares)	1	2	$^{3}3$	Total
Experiment 2, Treatment 1: No age 1					
5	0.30	0	0	56.0	56.0
9	0.27	0	0	56.0	56.0
11	0.10	0	0	56.0	56.0
15	0.29	0	0	26.0	26.0
Experiment 2, Treatment 2: Age 1 at 5.6 kg/hectare					
10	0.25	5.6	0	56.0	61.6
17	0.24	5.7	0	56.0	61.7
Experiment 2, Treatment 3: Age 1 at 17 kg/hectare					
2	0.16	16.9	0	56.0	72.9
18	0.20	16.9	0	56.0	72.9
8	0.25	23.5[a]	0	56.0	79.5
Experiment 3, Treatment 1: No age 1					
8	0.25	0	0	56.0	56.0
11	0.10	0	0	56.0	56.0
16	0.24	0	0	56.0	56.0
Experiment 3, Treatment 2: Age 1 at 17 kg/hectare					
5	0.30	16.8	0	55.7	72.5
10	0.25	16.8	0	56.0	72.8
18	0.20	16.8	0	58.8	75.6
Experiment 3, Treatment 3: Age 1 at 50 kg/hectare					
9	0.27	49.9	0	56.2	106.2
15	0.29	50.4	0	56.0	106.4
17	0.24	50.4	0	56.0	106.4
Experiment 4, Treatment 1[b]: Adults in poor condition					
3	0.15	0	0	54.4	54.4

[a] Pond 8 received fish intended for Pond 9, so Pond 8 received 23.5 kg/hectare of age 1s.

[b] The control for experiment 4 was treatment 1 of experiment 2, both in 1990.

Table 4.–Biomass density (kg/hectare) of three size groups of bluegills stocked into ponds in spring 1993 for experiment 5, evaluating adults in poor condition, and experiment 6, varying adult size and density of age-1 bluegills.

Pond	Area	Bluegill size range			
number	(hectares)	<51 mm	102-151 mm	³152 mm	Total
Experiment 5[a], Treatment 1: Adults in poor condition					
2	0.16	0	16.6	39.4	56.0
12	0.15	0	7.3	48.7	56.0
13	0.19	0	20.6	34.9	55.5
Experiment 6, Treatment 1: Small adults, no age 1					
6	0.28	0	40.8	0	40.8
16	0.24	0	46.7	0	46.7
17	0.24	0	18.9	0	18.9
Experiment 6, Treatment 2: Small adults, age 1 at 17 kg/hectare					
3	0.15	16.8	42.8	0	59.6
5	0.30	16.8	43.1	0	59.9
14	0.21	16.9	25.0	0	41.9
Experiment 6, Treatment 3[a]: Large & small adults, no age 1					
7	0.26	0	34.5	9.6	44.1
10	0.25	0	18.0	10.3	28.3
18	0.20	0	14.1	8.3	22.4
Experiment 6, Treatment 4: Large & small adults, age 1 at 17 kg/hectare					
8	0.25	16.8	17.1	11.8	45.7
9	0.27	15.1	18.8	12.1	46.0
15	0.29	16.9	15.8	9.7	42.4

[a] The control for experiment 5 was treatment 3 of experiment 6, both in 1993.

Table 5.–Relative weight of bluegills stocked into one pond in spring 1990 (experiment 4) and into three ponds in spring 1993 (experiment 5) to test the inadequate-energy hypothesis for reproductive failure. All fish came from ponds stocked at 336 kg/hectare the previous year.

Size range (mm)	Relative weight (%) Average	SD	*N*	Maximum	Minimum
Experiment 4: Pond 3					
102-126	65	6.8	58	77	50
127-151	63	6.2	50	77	48
Overall	64	6.5	108	77	48
Experiment 5: Pond 2					
102-126	70	7.4	87	84	56
127-151	70	5.9	28	84	58
152-177	70	5.8	33	82	55
178-202	80	5.2	18	91	67
203-228	86	3.8	7	92	81
229-253	94	1.0	4	96	93
Overall	72	8.5	177	96	55
Experiment 5: Pond 12					
102-126	74	8.7	34	94	60
127-151	72	9.0	9	89	60
152-177	73	7.9	17	84	57
178-202	74	10.1	40	98	55
203-228	87	8.3	10	106	76
Overall	75	9.9	110	106	55
Experiment 5: Pond 13					
102-126	75	7.5	137	96	50
127-151	75	8.1	29	93	63
152-177	80	6.3	11	93	69
178-202	84	2.7	5	88	80
203-228	85	8.3	13	104	68
229-253	82	3.7	9	88	77
254-278	96	13.2	3	114	83
Overall	76	8.5	207	114	50
Experiment 5: All three ponds					
Overall	74	9.0	494	114	50

Table 6.–Biomass density (kg/hectare) of three age groups of bluegills stocked into ponds in spring for experiment 7 (1994) and experiment 8 (1995), both varying the density of age-1 and age-2 bluegills.

Pond number	Area (hectares)	Age at stocking			Total
		1	2	≥3	
Experiment 7, Treatment 1: No age 1, no age 2					
8	0.25	0	0	56.0	56.0
10	0.25	0	0	56.0	56.0
14	0.21	0	0	56.1	56.1
Experiment 7, Treatment 2: No age 1, age 2 at 78 kg/hectare[a]					
2	0.16	0	78.4	56.2	134.6
17	0.24	0	78.3	56.1	134.4
18	0.20	0	30.3[a]	56.0	86.3
Experiment 7, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare[a]					
5	0.30	16.8	78.4	56.0	151.2
9	0.27	16.8	29.6[a]	56.0	102.4
16	0.24	16.8	78.4	56.0	151.2
Experiment 8, Treatment 1: No age 1, no age 2					
6	0.28	0	0	56.0	56.0
14	0.21	0	0	56.0	56.0
17	0.24	0	0	56.0	56.0
Experiment 8, Treatment 2: Age 1 at 17, age 2 at 28 kg/hectare					
5	0.30	16.8	28.0	56.0	100.8
15	0.29	15.3	28.1	56.0	99.4
16	0.24	16.9	28.1	56.0	101.0
Experiment 8, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare					
7	0.26	16.9	78.4	56.0	151.3
8	0.25	16.8	73.7	56.0	146.5
18	0.20	16.9	78.4	56.0	151.3

[a] One of the three ponds in each of treatments 2 and 3 received only 30 kg/hectare of age 2s due to insufficient fish of this age.

Table 7.–Density, biomass, mean weight, mean length (±SD, *N*), and mode of length for age-1 bluegills present at spring draining for eight experiments on bluegill reproduction conducted at the Saline Fisheries Research Station.

Pond number	Density (number/hectare)	Biomass (kg/hectare)	Mean weight (g)	Mean length±SD(*N*) (mm)	Length mode (mm)
Experiment 1, Treatment 1: Total bluegills at 56 kg/hectare					
5	0	0	.	.	.
14	0	0	.	.	.
18	201,674	80.8	0.401	32.2±5.1 (220)	35
Experiment 1, Treatment 2: Total bluegills at 134 kg/hectare					
7	0	0	.	.	.
10	30,632	14.8	0.484	33.6±4.6 (223)	35
15	24,894	22.6	0.907	42.6±2.8 (209)	41
Experiment 1, Treatment 3: Total bluegills at 336 kg/hectare					
8	0	0	.	.	.
9	0	0	.	.	.
16	0	0	.	.	.
Experiment 2, Treatment 1: No age 1 [a]					
5	476,499	112.5	0.236	26.2±4.2 (500)	25
9	172,580	40.8	0.236	26.1±3.8 (297)	25
11	31,333	9.0	0.286	27.4±5.1 (286)	25
15	396,081	79.8	0.202	25.9±3.1 (333)	24
Experiment 2, Treatment 2: Age 1 at 5.6 kg/hectare					
10	168,644	84.2	0.500	33.0±6.4 (209)	27
17	142,963	52.6	0.369	30.6±4.2 (252)	27
Experiment 2, Treatment 3: Age 1 at 17 kg/hectare [b]					
2	0	0	.	.	.
18	0	0	.	.	.
8[b]	0	0	.	.	.
Experiment 3, Treatment 1: No age 1					
8	245,768	245.5	1.000	41.4±2.9 (331)	40
11	185,042	83.4	0.450	32.3±2.7 (326)	30
16	395,499	161.0	0.410	30.6±6.5 (324)	24
Experiment 3, Treatment 2: Age 1 at 17 kg/hectare					
5	201,877	151.0	0.750	39.2±2.7 (282)	40
10	146,573	194.5	1.330	46.3±3.8 (169)	43
18	1,163	1.0	0.850	38.1±8.9 (231)	30
Experiment 3, Treatment 3: Age 1 at 50 kg/hectare					
9	0	0	.	.	.
15	178,467	108.5	0.610	37.2±2.1 (456)	35
17	0	0	.	.	.
Experiment 4, Treatment 1: Adults in poor condition [a]					
3	5	0	.	.	.
Experiment 5, Treatment 1: Adults in poor condition [c]					
2	38,272	20.5	0.537	31.3±9.8 (201)	27
12	233,294	99.6	0.427	30.4±6.4 (242)	27
13	228,840	112.4	0.492	33.9±5.8 (213)	30

Table 7.–Continued.

Pond number	Density (number/hectare)	Biomass (kg/hectare)	Mean weight (g)	Mean length±SD(*N*) (mm)	Length mode (mm)
Experiment 6, Treatment 1: Small adults, no age 1					
6	244,978	125.8	0.514	33.9±2.3 (212)	34
16	196,471	56.5	0.288	27.1±3.9 (252)	25
17	11,844	44.2	3.734	63.8±6.6 (190)	55
Experiment 6, Treatment 2: Small adults, age 1 at 17 kg/hectare					
3	95,778	88.4	0.924	41.6±3.0 (236)	42
5	29,721	56.9	1.917	51.8±2.3 (157)	51
14	0	0	.		
Experiment 6, Treatment 3: Large & small adults, no age 1[c]					
7	97,119	35.8	0.369	29.9±5.5 (224)	30
10	51,368	27.8	0.541	30.1±7.9 (239)	24
18	19,533	7.6	0.390	28.7±6.0 (239)	27
Experiment 6, Treatment 4: Large & small adults, age 1 at 17 kg/hectare					
8	85,291	126.3	1.483	47.5±3.7 (214)	50
9	76,741	57.3	0.748	38.9±2.2 (208)	40
15	135,212	41.2	0.305	29.6±2.1 (215)	31
Experiment 7, Treatment 1: No age 1, no age 2					
8	2,709	1.3	0.498	34.4±5.0 (236)	32
10	169,885	63.1	0.372	31.0±5.0 (243)	31
14	122,880	40.6	0.331	27.1±7.8 (240)	21
Experiment 7, Treatment 2: No age 1, age 2 at 78 kg/hectare[d]					
2	56,328	22.4	0.398	30.8±5.9 (239)	24
17	996	2.3	2.340	56.6±4.5 (238)	55
18[d]	40,310	64.2	1.593	50.0±3.2 (240)	53
Experiment 7, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare[d]					
5	13,416	9.5	0.711	37.6±3.6 (240)	37
9[d]	49,497	74.6	1.508	46.9±8.4 (241)	40
16	0	0	.	.	.
Experiment 8, Treatment 1: No age 1, no age 2					
6	83,805	26.3	0.314	28.8±4.3 (240)	30
14	226,120	45.6	0.202	25.5±2.8 (241)	24
17	157,243	155.2	0.988	42.0±5.3 (239)	40
Experiment 8, Treatment 2: Age 1 at 17, age 2 at 28 kg/hectare					
5	0	0	.	.	.
15	116,140	63.1	0.544	35.2±3.5 (240)	31
16	46,958	68.9	1.469	46.8±3.1 (171)	47
Experiment 8, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare					
7	132,509	70.5	0.533	33.7±3.2 (237)	35
8	1,766	4.2	2.355	55.3±5.9 (223)	53
18	0	0	.	.	.

[a] The control for experiment 4 was treatment 1 of experiment 2, both in 1990.

[b] Pond 8 received fish intended for Pond 9, so Pond 8 received 23.5 kg/hectare of age 1s.

[c] The control for experiment 5 was treatment 3 of experiment 6, both in 1993.

[d] One of the three ponds in each of treatments 2 and 3 of experiment 7 received only 30 kg/hectare of age 2s due to insufficient fish of this age.

Table 8.–The percentages of males, females and immatures, by length group, for 469 bluegills sampled by hook and line from late May to early September 1989 (Experiment 1).

Length (mm)	Males		Females		Immatures		Total Number
	Number	Percent	Number	Percent	Number	Percent	
76-101	2	11.8	6	35.3	9	52.9	17
102-126	47	43.5	57	52.8	4	3.7	108
127-151	102	49.8	82	40.0	21	10.2	205
152-177	66	85.7	7	9.1	4	5.2	77
178-202	29	96.7	1	3.3	0	0.	30
203-228	18	90.0	2	10.0	0	0.	20
229-253	10	100.0	0	0.	0	0.	10
254-278	1	100.0	0	0.	0	0.	1
Total:	276	58.8	155	33.1	38	8.1	469

Table 9.–Influence of stocking density on mean gonadosomatic index (GSI, gonad weight as a percentage of body weight), ±1 SE, for female and male bluegills in the months of June, July and August 1989 (Experiment 1). The sample size is given in parentheses below each mean GSI. NS indicates not significant, *P*>0.05; * indicates *P*<0.05; ** indicates *P*<0.01; *** indicates *P*<0.001.

	Stocking density			ANOVA results		
Month	56 kg/hectare	134 kg/hectare	336 kg/hectare	df	*F*	*P*
Females						
June	9.33±0.54 (24)	6.41±0.70 (14)	3.02±0.58 (17)	54	30.285	***
July	6.15±1.24 (14)	3.05±0.44 (30)	2.37±0.73 (9)	52	5.755	**
Aug	1.84±0.38 (12)	1.05±0.07 (16)	1.22±0.39 (10)	37	2.375	NS
Males						
June	1.33±0.13 (51)	1.46±0.16 (35)	1.25±0.15 (39)	124	0.467	NS
July	0.96±0.19 (25)	0.99±0.22 (20)	0.67±0.14 (22)	66	0.892	NS
Aug	0.22±0.04 (19)	0.36±0.05 (19)	0.24±0.04 (16)	53	2.916	NS

Table 10.–Influence of stocking density on mean relative weight (W_r), ±1 SE, for female and male bluegills in the months of June, July and August 1989 (Experiment 1). The sample size is given in parentheses below each mean. NS indicates not significant, *P*>0.05; * indicates *P*<0.05; ** indicates *P*<0.01; *** indicates *P*<0.001.

	Stocking density			ANOVA results		
Month	56 kg/hectare	134 kg/hectare	336 kg/hectare	df	*F*	*P*
Females						
June	89.1±2.9 (24)	86.4±2.8 (14)	68.6±2.7 (17)	54	14.757	***
July	92.2±2.9 (14)	88.7±2.4 (30)	64.8±3.7 (9)	52	15.591	***
Aug	86.2±1.4 (12)	76.9±1.4 (16)	75.3±3.8 (10)	37	7.198	**
Males						
June	93.6±1.3 (52)	89.2±1.9 (35)	79.1±1.5 (39)	125	24.556	***
July	96.0±2.5 (25)	88.9±2.9 (20)	82.1±2.0 (22)	66	8.132	***
Aug	84.8±0.9 (19)	81.2±1.5 (19)	78.5±.2.0 (16)	53	4.501	*

Table 11.–Influence of stocking density on mean liver somatic index (LSI, liver weight as a percentage of body weight), ±1 SE, for female and male bluegills in the months of June, July and August 1989 (Experiment 1). The sample size is given in parentheses below each mean LSI. NS indicates not significant, *P*>0.05; * indicates *P*<0.05; ** indicates *P*<0.01.

	Stocking density			ANOVA results		
Month	56 kg/hectare	134 kg/hectare	336 kg/hectare	df	F	P
Females						
June	2.09±0.17 (11)	1.65±0.11 (4)	1.05±0.18 (2)	16	4.274	*
July	1.76±0.14 (14)	1.49±0.05 (30)	1.28±0.26 (9)	52	3.068	NS
August	1.11±0.07 (12)	1.16±0.06 (16)	1.36±0.22 (10)	37	1.193	NS
Males						
June	1.43±0.08 (9)	1.50±0.17 (9)	1.22±0.07 (12)	29	1.938	NS
July	1.34±0.06 (25)	1.43±0.08 (20)	1.37±0.10 (22)	66	0.311	NS
August	0.90±0.03 (19)	1.01±0.04 (19)	1.12±0.06 (16)	53	5.780	**

Table 12.–Influence of stocking density on mean number of eggs per gram body weight of female, ±1 SE, in the months of June, July and August 1989 (Experiment 1). The sample size is given in parentheses below each mean. NS indicates not significant, *P*>0.05; * indicates *P*<0.05; *** indicates *P*<0.001.

	Stocking density			ANOVA results		
Month	56 kg/hectare	134 kg/hectare	336 kg/hectare	df	*F*	*P*
June	120±11 (22)	83±11 (14)	40±12 (12)	47	11.147	***
July	73±20 (14)	32±8 (30)	16±9 (9)	52	4.067	*
Aug	19±12 (4)	0 (1)	20±18 (3)	7	0.216	NS

Table 13.–Mean number of eggs per gram wet weight of bluegill ovary in June, July, and August, for ponds stocked at three densities of bluegill in April 1989, with two standard errors and sample size (Experiment 1).

Stocking density of yearlings (kg/hectare)	Eggs per gram of ovary								
	June			July			August		
	Mean	2 SE	*N*	Mean	2 SE	*N*	Mean	2 SE	*N*
56	1285	134	22	957	304	14	726	864	4
134	1256	202	14	725	240	27	0	0	1
336	861	389	12	406	322	8	511	721	3

Table 14.–Changes over three time periods in the mean density of all zooplankton (excluding rotifers) and in the growth rate of age-0 bluegill in a reference pond and in ponds with juvenile bluegills or age 0 or both (Experiment 2). All ponds (except the reference pond) were also stocked with 56 kg/hectare of adults. (Modified from Gray 1991.)

Parameter	Reference pond	Ponds with juveniles	Ponds with age 0	Ponds with juveniles and age 0
May to early June				
Zooplankton (number/L)	No change (171)	Increased (242)	Increased (389)	Increased (469)
Age-0 growth (mm/day)	NA	NA	(Before spawning)	(Before spawning)
Early June to early July				
Zooplankton (number/L)	No change (121)	Variable (556)	Decreased (228)	Decreased (297)
Age-0 growth (mm/day)	NA	NA	High (0.56)	High (0.57)
Early July to mid-August				
Zooplankton (number/L)	No change (138)	Variable (593)	No change (20)	No change (47)
Age-0 growth (mm/day)	NA	NA	Low (0.11)	Low (0.15)

Table 15.–The percentages of males, females and immatures, by length group, for 441 bluegills sampled by hook and line from May to September 1990 (Experiments 2 and 4).

Length (mm)	Males		Females		Immatures		Total
	Number	Percent	Number	Percent	Number	Percent	Number
76-101	3	60.0	1	20.0	1	20.0	5
102-126	29	48.3	31	51.7	0	0.0	60
127-151	139	44.1	176	55.9	0	0.0	315
152-177	40	69.0	17	29.3	1	1.7	58
178-202	3	100.0	0	0.0	0	0.0	3

Table 16.–Influence of juvenile stocking density (Experiment 2) and low relative weight (W_r) at stocking (Experiment 4) on mean gonadosomatic index (GSI, gonad weight as a percentage of body weight), ±1 SE, for female and male bluegills in the months of May, June, July, August, and September 1990. The sample size is given in parentheses below each mean GSI. The ANOVA tests treatments within experiment 2; the *t*-test compares experiment 4 with (pooled) experiment 2. NS indicates not significant, $P>0.05$; * indicates $P<0.05$; ** indicates $P<0.01$; *** indicates $P<0.001$.

Month	Expt. 2 0 kg/hectare	 5.6 kg/hectare	 17 kg/hectare	Expt. 4 Low W_r	Total df	ANOVA *F*	*P*	*t*-test
Females								
May	11.11±1.06 (8)	8.67±2.11 (5)	7.58±1.15 (8)	5.35±0.07 (2)	20	2.054	NS	***
Jun	8.68±0.80 (36)	7.68±1.01 (16)	8.61±0.53 (22)	7.38±1.30 (6)	73	0.363	NS	NS
Jul	3.06±0.37 (32)	2.76±0.45 (15)	6.72±0.67 (16)	6.33±0.10 (2)	62	17.818	***	***
Aug	1.12±0.06 (31)	0.96±0.10 (9)	1.60±0.20 (14)	2.01±0.78 (2)	53	6.806	**	NS
Males								
May	1.87±0.22 (16)	1.18±0.33 (7)	2.46±0.40 (11)	0.71±0.31 (4)	33	3.217	0.054	**
Jun	1.39±0.29 (18)	1.23±0.21 (7)	1.20±0.21 (20)	1.52±0.45 (6)	44	0.171	NS	NS
Jul	1.01±0.11 (16)	0.91±0.18 (9)	1.39±0.18 (21)	1.48±0.26 (10)	45	2.437	NS	NS
Aug	0.28±0.03 (17)	0.29±0.05 (9)	0.61±0.10 (18)	1.16±0.31 (10)	43	6.041	**	*
Sep	(0)	0.13±0.01 (6)	0.38±0.12 (7)	(0)	12	3.640	NS	

Table 17.–Dates of the first observation of bluegill nests, nests with eggs, nests with fry, and fry in seine hauls, in ponds stocked in April 1991 with 0, 17, or 50 kg/hectare of age-1 juveniles (<51 mm) (Experiment 3). All ponds were also stocked with 56 kg/hectare of adult bluegills (≥102 mm). The density (number/hectare) of yearling bluegills measured at pond draining in April 1992 is also shown. N.O. indicates "not observed." A question mark indicates a possible nest.

Pond	First nests	First eggs	First fry in nests	First fry in seine	Density at draining (number/acre)
Experiment 3, Treatment 1: No age 1					
8	5/13/91	5/15/91	N.O.	5/27/91	245,768
11	5/15/91	5/15/91	5/20/91	5/23/91	185,042
16	5/13/91	5/17/91	5/22/91	5/27/91	395,499
Experiment 3, Treatment 2: Age 1 at 17 kg/hectare					
5	5/13/91	5/15/91	5/20/91	5/28/91	201,877
10	5/13/91? 5/22/91	N.O.	N.O.	5/21/91	146,573
18	5/31/91? 6/6/91	N.O.	N.O.	7/12/91	1,163
Experiment 3, Treatment 3: Age 1 at 50 kg/hectare					
9	5/13/91?	N.O.	N.O.	N.O.	0
15	N.O.	N.O.	N.O.	6/10/91	178,467
17	N.O.	N.O.	N.O.	N.O.	0

Table 18.–Bluegill average gonad weight as a percentage of body weight (gonadosomatic index, GSI) and sample size (*N*) in three ponds at draining in April 1992 (Experiment 3).

Pond		Males		Females	
number	Treatment	GSI (%)	*N*	GSI (%)	*N*
11	1: No age 1	0.45	9	1.41	21
10	2: Age 1 at 17 kg/hectare	0.34	21	1.36	30
9	3: Age 1 at 50 kg/hectare	0.42	23	1.51	27
Total		0.39	53	1.43	78

Table 19.–Percentages of adult male and female bluegill by 25-mm size groups in three ponds at draining in April 1992 (Experiment 3).

Size group (mm)	Males		Females	
	Percent	Number	Percent	Number
Pond 11, Treatment 1: No age 1				
100-124	0	0	0	0
125-149	0	0	100	1
150-174	18	13	82	58
175-199	65	17	35	9
200-224	0	0	0	0
225-249	0	0	0	0
Total	31	30	69	68
Pond 10, Treatment 2: Age 1 at 17 kg/hectare				
100-124	0	0	0	0
125-149	0	0	100	2
150-174	16	8	84	41
175-199	51	21	49	20
200-224	100	8	0	0
225-249	0	0	0	0
Total	37	37	63	63
Pond 9, Treatment 3: Age 1 at 50 kg/hectare				
100-124	100	1	0	0
125-149	40	12	60	18
150-174	24	12	76	39
175-199	86	12	14	2
200-224	50	2	50	2
225-249	100	2	0	0
Total	40	41	60	61
All three ponds				
100-124	100	1	0	0
125-149	36	12	64	21
150-174	19	33	81	138
175-199	62	50	38	31
200-224	83	10	17	2
225-249	100	2	0	0
Total	36	108	64	192

Table 20.–Dates of first observation of bluegill nests, total nests observed, dates of first collection of age-0 bluegill in seines, length range at first collection, and density at pond draining the next spring, for experiments 5 and 6 (1993) in the Saline ponds.

Pond number	First nests	Total nests	First age 0 in seines	Length range (mm)	Density at draining (number/hectare)
Experiment 5, Treatment 1: Adults in poor condition, no age 1					
2	May 26	49	June 21	5.8-9.1	38,272
12	May 21	12	June 8	7.0-9.3	233,294
13	May 29	84	June 14	7.8-8.5	228,840
Experiment 6, Treatment 1: Small adults, no age 1					
6	May 12	161	July 14	16.7-20.1	244,978
16	May 10	167	June 14	7.2-10.2	196,471
17	---[a]	0	June 21	7.3-13.1	11,844
Experiment 6, Treatment 2: Small adults, age 1 at 16.8 kg/hectare					
3	May 13	55	June 29	11.1-14.0	95,778
5	June 10	85	July 9	16.3	29,721
14	---[a]	0	---	---	0
Experiment 6, Treatment 3: Large & small adults, no age 1					
7	May 12	237	June 17	7.0-9.4	97,119
10	May 31	104	June 21	6.9-12.8	51,368
18	June 17	11	June 24	7.2-11.2	19,533
Experiment 6, Treatment 4: Large & small adults, age 1 at 17 kg/hectare					
8	June 11	13	June 29	7.0-11.5	85,291
9	May 12	1	June 21	6.9-7.3	76,741
15	---[a]	0	June 29	12.4-15.1	135,212

[a] No nests observed from May 12 to July 2.

Table 21.–Dates of first observation of bluegill nests, total nests observed, dates of first collection of age-0 bluegill in seines, length range at first collection, and qualitative estimates of age-0 density in June-July and October 1994 in the Saline ponds (Experiment 7). Observing for nests began on May 23, and seining began on June 14, 1994.

Pond number	First nests	Total nests	First age 0 in seines	Length range (mm)	Relative density		Density at draining (number/hectare)
					June-July	October	
Experiment 7, Treatment 1: No age 1, no age 2							
8	May 23	49	June 14	8.0-14.1	+++	+++	2,709
10	May 23	45	June 14	10.2-16.0	+++	+++	169,885
14	---[a]	---	June 17	5.4-11.6	+++	+++	122,880
Experiment 7, Treatment 2: No age 1, age 2 at 78 kg/hectare							
2	---[a, b]	---	August 3	8.1-21.7	0	++	56,328
17	May 31	>9[b]	June 24	18.9	+[c]	0	996
18	June 15?[b]	---	June 24	13.1-26.6	++	+	40,310
Experiment 7, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare							
5	May 26	11	July 21	17.0-19.4	+[d]	++	13,416
9	---[a, b]	---	June 24	11.1-25.0	++	+	49,497
16	May 23	33	July 1	12.0	+[e]	0	0

[a] No nests observed from May 23 to August 3.

[b] Generally too turbid to detect nests.

[c] In seining from June 14 to August 10, 1994, only six age-0 bluegill were captured in pond 17; one was 18.9 mm on June 24; five ranged from 18.5-25.5 mm on July 27.

[d] In seining from June 14 to August 10, 1994, only seven age-0 bluegill were captured in pond 5; four ranged from 17.0-19.4 mm on July 21; three ranged from 22.1-25.7 mm on July 27.

[e] In seining from June 14 to August 10, 1994, only one age-0 bluegill was captured in pond 16; it was 12.0 mm on July 1.

Table 22.–Dates of first observation of bluegill nests, total nests observed, dates of first collection of age-0 bluegill in seines, length range at first collection, and qualitative estimates of age-0 density in June-July and August 1995 in the Saline ponds (Experiment 8). Observing for nests began on May 10, and seining began on June 12, 1995, and ended August 29, 1995. N.O. indicates "not observed," N.C. indicates "not counted," a question mark indicates possible nests, and "tr" indicates that very few were captured.

Pond number	First nests	Total nests	First age 0 in seines	Length range (mm)	Relative density June-July	Relative density August	Density at draining (number/hectare)
Experiment 8, Treatment 1: No age 1, no age 2							
6	6/2/95[a]	>105	6/14/95	5.3-7.2	+++	++	83,805
14	6/5/95	12	6/12/95	4.9-7.2	+++	+++	226,120
17	6/7/95?	N.C.	6/16/95	12.1-14.3	++	++	157,243
Experiment 8, Treatment 2: Age 1 at 17, age 2 at 28 kg/hectare							
5	6/5/95	N.C.	N.O.	N.O.	0	0	0
15	6/1/95	>30	6/30/95	13.0-18.4	++	++	116,140
16	6/1/95	>9	7/7/95	19.0-21.8	+	+	46,958
Experiment 8, Treatment 3: Age 1 at 17, age 2 at 78 kg/hectare							
7	6/7/95	N.C.	7/3/95	15.3-18.2	++	++	132,509
8	6/7/95	N.C.	7/10/95	12.7-19.3	tr[b]	tr	1,766
18	N.O.	N.O.	N.O.	N.O.	0	0	0

[a] Spawning observed in pond 6 on June 6, 8, 14, 15, 16, and 20, 1995.

[b] In seining from July 13 to August 7, a total of only 16 more age-0 bluegill were captured in pond 8, ranging from 18-37 mm.

References

Adams, S. M., R. B. McLean, and M. M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Canadian Journal of Fisheries and Aquatic Sciences 39:1175-1184.

Baganal, T. B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. Journal of Fish Biology 1:167-182.

Beard, T. D. 1971. Panfish literature review. Wisconsin Department of Natural Resources, Research Report 71, Madison.

Beard, T. D. 1982. Population dynamics of young-of-the-year bluegill. Wisconsin Department of Natural Resources, Technical Bulletin No. 127, Madison.

Beckman, W. C. 1946. The rate of growth and sex ratio for seven Michigan fishes. Transactions of the American Fisheries Society 76:63-81.

Bohlin, T., C. Dellefors, and U. Faremo. 1994. Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta*) depends on condition factor 1 yr in advance. Canadian Journal of Fisheries and Aquatic Sciences 51:1920-1926.

Breck, J. E. 1993. Hurry up and wait: growth of young bluegills in ponds and in simulations with an individual-based model. Transactions of the American Fisheries Society 122:467-480.

Carlander, K. D. 1977. Handbook of freshwater fishery biology. Volume two. Life history data on centrarchid fishes of the United States and Canada. The Iowa State University Press, Ames.

Chew, R. L. 1972. The failure of largemouth bass, *Micropterus salmoides floridanus* (Le Sneur), to spawn in eutrophic, overcrowded environments. Proceedings Southeastern Association of Game and Fish Commissioners 26:1-28.

Clark, R. D., Jr., and R. N. Lockwood. 1990. Population dynamics of bluegills subjected to harvest within the 5.0- to 6.9-inch size range. Michigan Department of Natural Resources, Fisheries Research Report 1961, Ann Arbor.

Claussen, J. 1991. Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. Masters Thesis. Department of Zoology, University of Toronto, Ontario.

Dahlgren, B. T. 1979. The effects of population density on fecundity and fertility in the guppy *Poecilia reticulata* (Peters). Journal of Fish Biology 15:71-91.

Deacon, L. I., and J. A. Keast. 1987. Patterns of reproduction in two populations of pumpkinseed sunfish, *Lepomis gibbosus*, with differing food resources. Environmental Biology of Fishes 19:281-296.

DeVries, D. R., R. A. Stein, J. G. Miner, and G. G. Mittelbach. 1991. Stocking threadfin shad: consequences for young-of-year fishes. Transactions of the American Fisheries Society 120:368-381.

Dutil, J.D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 1986:945-955.

FitzGerald, G. J., and M. H. A. Keenleyside. 1978. The effects of numerical density of adult fish on reproduction and parental behaviour in the convict cichlid fish *Cichlasoma nigrofasciatum* (Gunther). Canadian Journal of Zoology 56:1367-1371.

Gray, T. R. 1991. The competitive and predatory effects of juvenile bluegill on bluegill year-class strength. Masters Thesis. School of Natural Resources, University of Michigan, Ann Arbor.

Gray, T. R., J. E. Breck, and P. W. Webb. 1997. Effects of age-1 bluegill on large zooplankton and age-0 bluegill growth and recruitment. Michigan Department of Natural Resources, Fisheries Research Report No. 1990, Ann Arbor.

Gross, M. R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. Pages 55-75 *in* G. W. Potts and R. J. Wooton, editors. Fish reproduction: strategies and tactics. Academic Press, London.

Haney, J. F., and D. J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnology and Oceanography 18:331-333.

Hart, T. F., Jr., and R. G. Werner. 1987. Effects of prey density on growth and survival of white sucker, *Catostomus commersoni*, and pumpkinseed, *Lepomis gibbosus*, larvae. Environmental Biology of Fishes 18:41-50.

Heidinger, R. C., and S. D. Crawford. 1977. Effect of temperature and feeding rate on the liver-somatic index of the largemouth bass, *Micropterus salmoides*. Journal of the Fisheries Research Board of Canada 34:633-638.

Hester, F. J. 1964. Effects of food supply on fecundity in the female guppy *Lebistes reticulatus* (Peters). Journal of the Fisheries Research Board of Canada 21:757-764.

Hinch, S. G., and N. C. Collins. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observation. Transactions of the American Fisheries Society 120:657-663.

James, M. F. 1946. Histology of gonadal changes in the bluegill, *Lepomis macrochirus* Rafinesque, and the largemouth bass, *Huro salmoides* (Lacepede). Journal of Morphology 79:63-91.

Krumholz, L. A. 1946. Rates of survival and growth of bluegill yolk fry stocked at different intensities in hatchery ponds. Transactions of the American Fisheries Society 76:190-203.

Kuznetzov, V. A., and N. Kh. Khalitov. 1978. Alterations in the fecundity and egg quality of the roach, *Rutilus*, in connection with different feeding conditions. Journal of Ichthyology 18:63-70.

Lam, T. J. 1983. Environmental influences on gonadal activity in fish. Pages 65-116 *in* W. S. Hoar, D. J. Randall, and E. M. Donaldson (eds.), Fish Physiology, Volume IX. Reproduction. Part B. Behavior and fertility control. Academic Press, New York.

Mayhew, J. 1956. The bluegill, *Lepomis macrochirus* (Rafinesque) *in* West Okoboji Lake, Iowa. Proceedings of the Iowa Academy of Science 63:705-713.

Mittelbach, G. G., and C. W. Osenberg. 1992. Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology 74:2381-2394.

Morgan, G. D. 1951. The life history of the bluegill sunfish, *Lepomis macrochirus*, of Buckeye Lake (Ohio). Journal of the Scientific Laboratories, Denison University Bulletin 42:21-59.

Murphy, B. R., D. W. Willis, and T. A. Springer. 1991. The relative weight index in fisheries management: status and needs. Fisheries (Bethesda) 16(2):30-38.

Oliver, J. D., and G. F. Holeton. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1993. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology 73:255-267.

Schmittou, H. R. 1967. Sex ratios of bluegill in four populations. Transactions of the American Fisheries Society 96:420-421.

Schneider, J. C. 1973. The standing crop of fish in Michigan lakes. Michigan Department of Natural Resources, Fisheries Research Report No. 1794, Ann Arbor.

Schneider, J. C. 1981. Differences between good and poor bluegill lakes. Final Report, Project F-35-R-7 (Study Group 2), Study 244. Michigan Department of Natural Resources, Institute for Fisheries Research, Ann Arbor.

Schneider, J. C., and J. E. Breck. 1996. Overwinter consumption of bluegill by walleye and yellow perch. Michigan Department of Natural Resources, Fisheries Research Report No. 1992, Ann Arbor.

Scott, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 19:715-730.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Snyder, D. E. 1983. Fish eggs and larvae. Chapter 9. Pages 165-197 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Stein, R. A., D. R. DeVries, and J. M. Dehmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52:2518-2526.

Swingle, H. S. 1953. A repressive factor controlling reproduction in fishes. Pages 118-119 *in* Abstracts presented to the Eighth Pacific Science Congress, Quezon City, Philippines.

Swingle, H. S. 1957. A repressive factor controlling reproduction in fishes. Pages 865-871 *in* Proceedings of the Eighth Pacific Science Congress 1953, Volume 3a.

Swingle, H. S., and E. V. Smith. 1943 (reprinted 1950). Factors affecting the reproduction of bluegill bream and largemouth black bass in ponds. Alabama Polytechnic Institute, Agricultural Experiment Station, Circular No. 87.

Thorp, J. H., L. D. Goldsmith, J. A. Polgreen, and L. M. Meyer. 1989. Foraging patterns of nesting and nonnesting sunfish (Centrarchidae: *Lepomis auritus* and *L. gibbosus*). Can. J. Fish. Aquat. Sci. 46:1342-1346.

Toetz, D. W. 1966a. Factors affecting the survival of bluegill sunfish larvae. Doctoral dissertation. Department of Zoology, Indiana University, Bloomington.

Toetz, D. W. 1966b. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. Investigations of Indiana Lakes and Streams 7:115-146.

Tomcko, C. M., and R. B. Pierce. 1993. The relation of male bluegill reproductive strategies to exploitation and population size structure in twelve Minnesota lakes. Minnesota Department of Natural Resources, Fisheries Investigational Report 432, St. Paul.

Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.

Tyler, A. V., and R. S. Dunn. 1976. Ration, growth, measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding populations homeostasis. Journal of the Fisheries Research Board of Canada 33:63-75.

Ulrey, L., C. Risk, and W. Scott. 1938. The number of eggs produced by some of our common fresh-water fishes. Investigations of Indiana Lakes and Streams No. 6:73-77.

Wege, G. J., and R. O. Anderson. 1978. Relative weight (W_r): a new index of condition for largemouth bass. Pages 79-91 *in* G. Novinger and J. Dillard, eds. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, MD.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. Journal of the Fisheries Research Board of Canada 31:1531-1536.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfish species. American Naturalist 111:553-578.

Werner, R. G. 1967. Intralacustrine movements of bluegill fry in Crane Lake, Indiana. Transactions of the American Fisheries Society 96:416-420.

Werner, R. G. 1969. Ecology of limnetic bluegill (*Lepomis macrochirus*) fry in Crane Lake, Indiana. American Midland Naturalist 81:164-181.

Whiteside, B. G., and F. J. Richan. 1969. Regressive factors controlling reproduction in goldfish. Progressive Fish-Culturist 31:165.

Wooton, R. J. 1973. Fecundity of the three-spined stickleback, *Gasterosteus aculeatus* (L.). Journal of Fish Biology 9:683-688.

Wooton, R. J. 1977. Effect of food limitation during the breeding season on the size, body content and egg production of female sticklebacks (*Gasterosteus aculeatus*). Journal of Animal Ecology 46:823-834.

Yu, M. L., and A. Perlmutter. 1970. Growth inhibiting factors in the zebrafish (*Brachydanio rerio*) and the blue gourami (*Trichogaster trichopterus*). Growth 34:153-175.

Approved by Richard D. Clark, Jr.
Alan D. Sutton, Graphics
Kathryn L. Champagne, DTP

Appendix 1.–Ponds and years with successful (+) or unsuccessful (0) bluegill reproduction at the Saline Fisheries Station (Clark and Lockwood 1990).

Pond number	Year				
	1984	1985	1986	1987	1988
9	0	0	0	+	+
15	+	+	0	+	0
18	0	0	0	+	+
5	+	0	+	+	+
10	0	0	0	+	0
16	+	0	+	0	0
6	+	+	+	0	+
17	0	0	0	+	+
14	+	+	0	0	+