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QUALITY MANAGEMENT OF BLUEGILL: FACTORS AFFECTING POPULATION SIZE STRUCTURE

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Division of Fisheries
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Table of Contents

Executive Summary

Bluegill *Lepomis macrochirus* are a key component of Illinois sport fisheries, serving both as an important prey species and providing anglers with harvestable size fish. The prevention or improvement of poor size structure, often referred to as stunting, in bluegill populations is a major management focus for many agencies. Four hypotheses have been proposed to explain what causes and/or maintains stunting in bluegill populations: adult overharvest, cuckolder overproduction, density-dependent growth limitation, and socially influenced early maturation. Initial surveys were performed on 60 lakes to identify the status of bluegill population size structure in Illinois. These surveys indicated that bluegill populations ranged from quality populations with high abundance of larger fish, to stunted populations with few harvestable size fish. We developed a number of approaches including pond experiments to examine factors responsible for stunting in bluegill populations, field sampling of bluegill populations in order to examine factors influencing growth and maturation, and a management experiment to examine potential strategies for changing bluegill size structure. The management experiment utilized 32 experimental lakes divided into four treatments; an 8-inch minimum size, ten fish bag limit experimental regulation, a largemouth bass *Micropterus salmoides* predator stocking, a combination of stocking and regulation, and a control. We hope to identify important factors influencing bluegill population size structure as well as potential methods for managing these populations.

In Job 101.1, we analyzed creel surveys that were conducted on 32 lakes identified for use in the intensive management experiment. Creels were conducted on each study lake prior to the implementation of the management experiment (1988 – 2000) and again at the conclusion of the experiment (2003 – 2005). Angler catch per unit effort and catch per unit area showed no change for any experimental treatment from the pre experiment to post experiment creels. Mean total length (mm) of angled bluegill was also estimated from creel surveys before and after the application of study treatments and there was no change in mean total length due to treatment effects across the experiment. No significant correlation existed between changes in CPUE or CPUA and changes in mean TL from pre-treatment and post-treatment surveys. These results indicate no changes in size-selective angler efficiency that may have affected interpretation of the effects of study treatments. Percent of bluegill over 170 mm was calculated for each experimental lake and there was also no change in PQBG.170 due to treatment effects across the experiment. Overall, no significant changes in creel data existed throughout the duration of the management experiment.

Electrofishing data was compiled from fall standardized sampling conducted by Department of Natural Resources biologists using the Fisheries Analysis System (FAS). This data was compared to INHS fall electrofishing CPUE for all bluegill, bluegill larger than 150 mm, and bluegill larger than 200 mm. There were significant differences in catch rates between FAS and INHS sampling for total bluegill and bluegill larger than 150 mm, but catch rates were similar for bluegill larger than 200 mm. Differences in catch rates of smaller bluegill are likely due to FAS sampling not specifically targeting bluegill. As a result, INHS electrofishing data was used for all analyses in this report because it targeted bluegill and provided a better representation of bluegill size structure.

In Job 101.2 we examined biotic and abiotic factors that influence growth of bluegill. To do this, we performed two separate analyses that each utilized different metrics of growth; age specific and size specific growth. The age specific growth analysis was based on bluegill size at age 4 from 23 reservoirs. For the size specific growth analysis, we calculated the size specific growth rate of bluegill at 50, 100, and 150 mm TL. These size specific growth rates were based on back calculating the growth of fish from 16 reservoirs using saggital otoliths. For both analyses, we analyzed the effect that temperature, secchi depth, zooplankton density, benthic invertebrate density, angler harvest of bluegill and the average age of maturation of male bluegill have on growth rates using an AIC analysis. In addition, for the size specific growth analysis we assessed the effect of largemouth bass, bluegill, and gizzard shad electrofishing catch per unit effort. The results for the age specific growth analysis suggest that temperature and secchi depth (turbidity) have the greatest influence on the size of bluegill at age 4. The results from the size specific growth analysis show that gizzard shad abundance has a strong, negative influence on the growth of all sizes of bluegill. For bluegill that were 50 and 100 mm TL, gizzard shad influenced size specific growth of bluegill by increasing water turbidity, and reducing the foraging efficiency and growth of these smaller bluegill. At 150 mm TL, it appears that gizzard shad also influence the size specific growth of bluegill through direct competition for forage. The average age of maturation of male bluegill also had a negative influence on the size specific growth of bluegill, but this effect was only significant at 50 mm TL. Results suggest management actions that reduce the abundance of gizzard shad, decrease the amount of turbidity, and increase age at maturation should promote good bluegill growth.

As part of this job, we also conducted pond experiments to examine the influence of age of maturation, social structure, and food resources on bluegill size structure. First, we examined the relative strength of genetic (population source, stunted v. quality) and environmental (population social structure, presence v. absence of large mature males) factors on variation in growth and timing of maturation for juvenile male bluegill in a common-garden experiment. Juvenile male bluegill collected from two different wild source populations, one with parental males that are large (>190mm total length) and one with parental males that are stunted (<155mm total length), were placed in a common environment and the social structure was varied by controlling the presence or absence of large, mature male bluegill collected from a third population. Juvenile male bluegill from both populations allocated significantly more energy to reproduction in the absence of large males than in their presence. Within ponds, differences in growth and maturation rates between juvenile males from the two source populations were small but significant. These results indicate both genetic and environmental components to growth and maturation in bluegill, but emphasize the importance of social interactions in shaping individual life-history strategies.

A second set of pond experiments was designed to examine the relative influence of prey resources as well as social structure to maturation rates of bluegill. We assessed how resource availability and timing of maturation interact to influence individual body size of bluegill. Resource availability (high and low food) and the social structure of the population (presence or absence of large, mature males) were varied in experimental ponds. Results showed food rationing affected growth (larger fish in the high food treatments) and the social structure of the population affected timing of maturation (early maturation of males in the absence of large males). Treatment effects, however, were sex-specific; males responded to the social structure of the population and females were more responsive to resource availability. We also found that individuals that became sexually mature were smaller than those that remained immature, although results were sex-specific and resource dependent. For males, individuals that matured were smaller when resources were limited; mature and immature females showed no difference in body size regardless of food ration. We also showed both resource availability and the processes that control timing of maturation interact in sex-specific ways to influence body size of bluegill. These results suggest that a more robust explanation for variable body size requires consideration of sex-specific interactions between ecological (food and growth) and evolutionary (timing of maturation) mechanisms.

Four hypotheses have been proposed to explain what causes and/or maintains stunting in bluegill populations: adult overharvest, cuckolder overproduction, density-dependent growth limitation, and socially influenced early maturation. To test the relative importance of each of the four hypotheses in determining size structure of bluegill populations in Illinois, we assessed key life history characteristics of 50 populations throughout the state. In each lake, we sampled bluegill during the spawning season using boat electrofishing techniques, and for each population we determined sex specific size-at-age, age-at-first-maturity, gonosomatic index (GSI), and relative abundance of cuckolders. None of the populations sampled provided evidence supporting a role for either the adult overharvest hypothesis or the cuckolder overproduction hypothesis. Although population density and resource availability likely influence growth rates in all bluegill populations, there was no evidence among the 50 Illinois bluegill populations studied that density-dependent growth limitation causes or maintains stunting. Size structure, however, was highly correlated with age-at-first-maturity; individuals in stunted populations matured significantly earlier than those in quality populations. To manage bluegill populations effectively, therefore, strategies should be focused on increasing the age-at-first-maturation, not on simply manipulating growth rates. These strategies include increasing abundance of larger bluegill (e.g. limiting harvest) in order to influence social structure of bluegill and delaying maturation.

In Job 101.3, a management experiment was implemented to attempt to manage for quality bluegill populations. Thirty-two lakes were designated stunted or quality based on the size structure of bluegill populations present. These lakes were divided into four treatments (8 per treatment) with 4 quality and 4 stunted lakes in each. Treatments were an experimental regulation of 8-inch minimum size with a 10 fish bag limit, largemouth bass stocking to increase predator density, regulation and stocking in combination, and a control with no manipulations. In order to evaluate changes in bluegill populations, fish were collected using AC electrofishing in the spring and brought back to the laboratory where they were measured, weighed, dissected, scored for maturity and otoliths removed and aged. Sampling was conducted and samples were collected at the beginning of the experiment (1996-1997) and again at the conclusion (2004-2005). This data was used to calculate catch of various size classes, age of maturity (z-age), proportion of quality male bluegill over 170 mm (PQM 170), and mean length for each age class.

Few differences in growth and abundance were observed over the course of the experiment. Catch rates of bluegill from electrofishing samples did not change significantly with experimental treatment for CPUE of all bluegill, CPUE of bluegill larger than 200 mm, CPUE of bluegill larger than 170 mm, or bluegill from 100 mm to 170 mm in length. Length at age also remained relatively unchanged in each lake. Size specific growth rates were higher in quality lakes than stunted lakes for 50 mm bluegill suggesting that growth differed at early life stages. These differences were also observed in annual growth rates of bluegill in the 100 mm size class.

No significant changes were observed associated with the experimental treatments in PSD 200, PQM 170, or male and female z-age. PQM 170 remained significantly higher in quality lakes than stunted lakes. Changes in z-age were observed, but they were not related to experimental treatments. Lakes that had quality bluegill populations tended to decrease in z-age throughout the experiment, while lakes that were stunted tended to have increased z-age. When age of maturity did change, it was similar in male and female bluegill. The changes in z- age during the experiment resulted in no significant correlation with z-age and size structure in 2004. Z-age in 2004 was not significantly correlated to PQM 170 and no significant difference existed between z-age of quality and stunted lakes. Results suggest that implementation of an 8-inch minimum size limit and 10 fish bag limit will not have negative affects on bluegill populations and may help maintain the quality status of some populations.

We examined biotic and abiotic characteristics of the lakes to examine if they changed during the study and could have influenced the outcome of the experiment. Prey resources, predation pressure, and lake-habitat characteristics were examined. We found some variation in zooplankton and benthos densities across years, however the fluctuation was small and overall densities remained unchanged. In addition, we found no overall differences in prey resources between lakes with different management treatments. These results suggest that macrozooplankton and benthic invertebrate abundance and utilization are not expected to cause any changes in bluegill growth rates that will mask any changes in size structure due to the management manipulations.

Compliance to the regulation was evaluated through creel data and conservation police officer checks. Creel data showed low levels of compliance in all lakes. Anglers were more compliant in quality lakes than stunted lakes, but there was no significant difference in harvest of fish under the 8-inch minimum limit in regulation and non-regulation lakes. Anglers continued to harvest small bluegill even when the regulation was in place. Conservation officer compliance checks showed high levels of compliance to the regulation indicating that anglers were more compliant in the presence of conservation officers and emphasizing the importance of officer presence in enforcing regulations.

We summarized data on the contribution of stocked largemouth bass to existing predator populations to assess potential effects on the success of the management experiment. We found that the contribution of stocked largemouth bass was variable across lakes. Stocked largemouth bass contributed to the natural bass population in most study lakes, but overall relative abundance has not increased in a majority of study lakes. In lakes where stocked bass have high survival, an increase in CPUE from electrofishing was observed. Higher densities of bass were not shown to decrease juvenile bluegill density. Bass stocking may not be a successful management strategy for bluegill populations due to variable stocking success and no evidence for largemouth bass reducing bluegill density.

Because of negative relationships between gizzard shad densities and bluegill growth (see Job 2) we examined potential effects on bluegill population size structure. Gizzard shad abundance was significantly higher in experimental lakes designated as stunted than quality. Gizzard shad density was also negatively related to PQM 170 and to abundance of juvenile bluegill. Our results suggest gizzard shad populations may have detrimental affects on bluegill abundance and size structure. Management efforts directed at controlling gizzard shad populations and increasing water clarity (sediment reduction, vegetation establishments) will have positive effects on bluegill populations.

In Job 101.4, all data were analyzed and recommendations presented in the individual jobs of this report. We examined changes in a large number of response variables associated with the management experiment. Overall, few changes in bluegill populations were observed that could be directly related to the experimental treatments. Lakes with bluegill populations that were designated quality at the beginning of the experiment, typically maintained a quality population throughout the experiment. These included lakes receiving both the regulation as well as the regulation and largemouth bass stockings. In addition, PQM 170 continued to be greater throughout the experiment in quality lakes than in stunted lakes. Combined these results suggest that implementation of an 8-

inch minimum size limit and 10 fish bag limit will not have negative affects on bluegill populations and may help maintain the quality status of some populations. In contrast, the regulation does not appear to improve either growth rates or size structure of bluegill in stunted populations in the short term. In general few changes in growth, catch rates, or maturity status were observed consistently across treatments.

The management experiment yielded few changes in bluegill size structure and no changes that were consistent across treatments. Lack of changes in the experimental lakes were likely due to difficulties with the treatments due to low levels of angler compliance to the regulation and variable stocking success of largemouth bass. Future management efforts using regulations should evaluate potential angler compliance as a factor influencing success. Largemouth bass stocking was not effective in reducing densities of small bluegill and was therefore not successful in increasing bluegill size structure. Largemouth bass stockings should also be assessed to determine factors influencing success and to evaluate in which lakes future stockings are warranted. Controlling gizzard shad populations may also be important when managing species such as bluegill due to their potential for competition for food resources. We currently have no evidence to suggest an 8-inch minimum size with a 10 fish bag limit will effectively increase the size of bluegill harvested by anglers. Continuing to follow population changes in a small number of lakes with the regulation and with increased enforcement efforts would be valuable to assess the long term potential (over multiple bluegill generations) of these management approaches to reducing stunting in bluegill populations.

Job 101.1 Categorization of bluegill populations in Illinois impoundments

OBJECTIVE

To use existing creel and standardized sampling databases to categorize bluegill populations based on adult size structure.

INTRODUCTION

Bluegill are a key component of Illinois sport fisheries, serving both as an important prey species and providing anglers with harvestable size fish. In Illinois lakes where creel surveys documenting harvest and total catch have been conducted, bluegill were consistently caught and harvested in great numbers. Bluegill are susceptible to high levels of exploitation, which can shift size structures toward populations dominated by small fish (Coble 1988). Size structures of bluegill populations have deteriorated in many lakes within the Midwest over the past 40 years (Drake 1997). Anglers harvest fewer large bluegill from many exploited lakes that now only support large populations of small bluegill and the number of trophy-sized bluegill have also declined across the region (Olson and Cunningham 1989).

If we are to manage bluegill populations effectively, we need to understand how exploitation and/or various management activities alter these life-history characteristics. Only by understanding these complex interactions can the success of bluegill regulations and other management strategies be predicted and realized effectively.

PROCEDURES

Job 101.1 was designed to use creel surveys, conducted under project F-69-R, to evaluate the implementation of various management actions under Job 101.3. Lakes were selected according to one of four experimental treatments (control, regulation, predator stocking, regulation & predator stocking; see Table 1-1). Creel surveys were conducted from 1988 to 2000 providing a baseline of information on bluegill population size structure as well as angler success. Although study treatments were initiated in 1999, five lakes (Apple Canyon, Sterling, Murphysboro, Woods and Red Hills) were surveyed for pre-treatment data in 2000 under the assumption that 1) the effects of regulations and/or predator stockings would not be observed in creel data for several seasons; and 2) control lakes did not require pre-treatment assessments prior to 1999. Post-treatment creel surveys were conducted from 2003 to 2005. Creel surveys are conducted from March through October of each year.

In 2004, Lake Mermet experienced a severe fish-kill on or about July 25, 2004, resulting in an estimated 90% kill of adult sport fish (Chris Bickers, personal communication). Analyses of creel data for Mermet Lake (2004) presented in this report only include data from March 15 – July 25, 2004.

Electrofishing data collected by the Illinois Department of Natural Resources (IDNR) biologists was compared to INHS samples to assess incorporating into the analysis. Electrofishing data was compiled through the FAS database, which includes annual sampling performed by IDNR biologists. Data from fall AC electrofishing transects was summarized and reported as mean CPUE of all bluegill, bluegill abundance greater than 150 mm, and bluegill abundance greater than 200 mm. The FAS data included 17 of the 32 experimental lakes. CPUE from FAS was then compared to INHS data to determine if any differences existed.

FINDINGS

Catch per unit effort (CPUE) and catch per unit area (CPUA), of bluegill caught by anglers were estimated from creel surveys before and after application of study treatments (Table 1-2). There were no changes in CPUE attributable to treatment effects across the management experiment, although there was an increasing trend in CPUE in quality lakes receiving the regulation treatment (Figure 1-1). There was also no change in CPUA attributable to treatment effects across the experiment (Figure 1-2). These findings indicate that angler efficiency was relatively constant over the course of the experiment, although the variance around these mean estimates within each treatment type was large.

Mean total length (mm) of angled bluegill was also estimated from creel surveys before and after the application of study treatments (Table 1-2). There was no change in mean TL due to treatment effects across the experiment. Although the manipulation treatment (predator stocking) did show a tendency to decrease mean total length in quality and stunted populations (Figure 1-3), this result is not statistically significant.

We also calculated differences in mean TL between pre-treatment and post-treatment surveys (Table 1-3). Control lakes averaged a 9.4 mm increase in bluegill total length (Table 1-4). Regulation lakes showed a similar average increase of 9.7 mm, while stocking lakes showed an average decrease of 13.4 mm. Lakes with combination regulation and stocking treatments averaged a 1.8 mm increase in total length of bluegill caught by anglers. Differences in average length of angled bluegill between pre-treatment and post-treatment surveys showed no effect of any treatment in the experiment (Figure 1-4).

Angler success rates (CPUE, CPUA) may affect mean TL of angled bluegill if angling success is size selective. Size selectivity in angler effectiveness could alter the interpretation of changes in mean TL relative to study treatments. For example, a substantial decrease in CPUE for smaller size classes of bluegill would result in an overall increase in mean TL across all treatments, potentially masking treatment effects of the experiment. Although creel data does not allow for calculations of size specific CPUE estimates, if a decrease in size-specific CPUE occurred, changes in CPUE should be correlated with changes in mean TL. Analysis revealed that no significant correlation exists between changes in CPUE and changes in mean TL from pre-treatment and post-treatment surveys ($R^2 = 0.01$, Figure 1-5). Similarly, CPUA changes and mean TL changes were not correlated ($R^2 = 0.11$, Figure 1-6). Both results indicate no changes in size-selective angler efficiency that may have affected interpretation of the effects of study treatments.

The proportion of bluegill caught by anglers larger than 170mm (PQBG.170) applied to creel survey data is an analogous metric to PQM.170 used in Job 101.3 (Table

1-5). There was no change in PQBG.170 due to treatment effects across the experiment. Although the manipulation treatment (predator stocking) did show a tendency to decrease mean total length in quality and stunted populations (Figure 1-7), this result is not statistically significant.

Electrofishing CPUE from FAS and INHS sampling differed considerably. Total CPUE was not significantly correlated between the two samples ($r = 0.034$, $P = 0.80$) with INHS CPUE significantly greater than FAS CPUE ($t = -2.13$, $P = 0.04$). CPUE of bluegill in the FAS and INHS sampling was significantly correlated for bluegill greater than 150 mm ($r = 0.53$, $P < 0.001$), however the FAS samples had significantly higher CPUE than INHS samples ($t = 4.10$, $P < 0.001$). However, the CPUE of fish greater than 200 mm was similar between the FAS and INHS sampling ($r = 0.401$, $P < 0.001$) and were not significantly different ($t = -0.73$, $P = 0.47$).

The catch rates of larger bluegill suggest that the sampling performed by both the INHS and DNR were similar in describing the abundance of these sizes of bluegill. The differences in the number of smaller fish caught were due to likely differences in the fish sizes targeted. The INHS sampling targeted only bluegill and more attention could be focused on netting smaller fish. The FAS sampling targeted all species and smaller bluegill were under-represented in the sampling due to netting other fish present. The targeted sampling is required to adequately measure the catch rates of a single species. As a result, we used INHS data only throughout this report in order to measure bluegill catch rates.

RECOMMENDATIONS

Creel survey data failed to show any significant changes in bluegill population size structure as a result of the treatments implemented in this study. Angler success, as measured by CPUE estimates, did not significantly change during the course of the experiment. Mean TL (mm) of bluegill caught by anglers and the proportion of bluegill larger than 170mm (PQBG.170) both failed to change as a result of the regulation treatment, predator stocking treatment, or the regulation/predator stocking combination treatment.

Changes in control lakes and regulation lakes from pre-treatment to post-treatment assessments were nearly identical (and positive). Although no statistical changes in bluegill population size structure were apparent, the predator stocking treatment did show a tendency to decrease bluegill size. That treatment had the largest effect on size structure, and the only negative effect of the treatment combinations. The combination regulation/predator stocking treatment had little effect on bluegill population size structure.

One of the drawbacks of this aspect of the study was the logistic limitation of implementing the creel surveys. Pre-treatment surveys were not scheduled or conducted with this study in mind; rather the creels were executed to meet priorities of DNR Fisheries. This resulted in inconsistent intervals between baseline surveys and post-treatment assessments that may hinder a clear assessment of the effects of the treatments.

As a result, data from the creel surveys will be combined with other metrics to assess the management experiment (see Job 3).

We found differences in catch rates of bluegill smaller than 200 mm between FAS and INHS sampling. Based on these results, we recommend targeted sampling be used if the goal is describing bluegill population size structure. For the remainder of this report, only INHS sampling will be used in describing bluegill catch rates. The INHS sampling targeted bluegill and was standardized with similar electrofishing settings (~9Amps) and sampling effort.

Job 101.2. Evaluation of bluegill life-history variation in Illinois impoundments.

OBJECTIVE

To determine the extent of variation in important bluegill life-history characteristics in selected impoundments throughout Illinois.

INTRODUCTION

One of the main goals of fisheries management is to provide anglers the opportunity to catch a sustainable number of quality size fish. Bluegill sunfish *Lepomis macrochirus* are one of the most popular sport fishes in North America and often within a lake or stream, their catch in terms of both numbers and weight exceeds that of all other species combined (Drake et al. 1997). Recently, anglers have become increasingly dissatisfied with the large number of small bluegill in their catch. Stunted growth (few fish longer than 150 mm) is a common management problem among bluegill populations and is prevalent in many midwestern states, including Illinois (Aday et al. 2002). The occurrence of stunted size in bluegill has been attributed to excessive angler exploitation (Coble 1988), ecosystem changes (Swingle 1950), and inadequate food resources (Gerking 1962). In order to improve the management of bluegill populations and to help alleviate small population size structure, it is desirable to determine how environmental conditions and fish community composition influence bluegill growth.

The overall adult size of bluegill (and most other fish) is regulated by the combination of four factors; growth rate before becoming sexually mature, growth rate after sexual maturation, age of sexual maturation, and life span. The age of sexual maturation is an especially important factor regulating the adult size of fish because growth rate generally decreases after maturing (Wootton 1985) as mature fish divert a significant portion of their energy into reproduction. There is considerable plasticity in the age of maturation of bluegill with some individuals maturing 1-3 years earlier than others (Diana et al. 2005). Stunted populations typically develop in systems where individuals mature at a young age. We examined these mechanisms for bluegill in a series of pond experiments and field evaluations.

Many studies have related lake morphology and environmental conditions to bluegill growth and adult body size. For instance, it has been shown in Minnesota that secchi depth and lake maximum depth are negatively correlated and total alkalinity, percent littoral area, and temperature are positively correlated with bluegill length at ages 1-6 (Tomcko and Pierce 2001). A study in Iowa found similar results (Mitzner 1998) but also suggest that age specific growth is positively correlated with a smaller largemouth bass size structure and high bluegill angling pressure. No studies have determined the factors that influence the age specific growth of bluegill in Illinois. Therefore, one objective of this job was to evaluate the biotic and abiotic factors that influence the age specific growth of bluegill in reservoirs across the state. Another goal was to relate various environmental and community variables to the size specific growth of bluegill. We believe that analyzing the size specific growth of bluegill will give us a better understanding of the factors that influence the growth of bluegill because in fish, growth is primarily a function of size rather than age (Putman et al. 1995).

PROCEDURES

Age and Size Spacific Growth

To examine the effects of biotic and abiotic variables on bluegill growth and population size structure, we sampled several Illinois reservoir bluegill populations. All of the study sites were shallow impoundments located throughout Illinois with surface areas ranging from 5 to 250 ha (Figure 1). Study lakes were generally located in state parks with predominantly forested watersheds. Fish communities were similar and dominated by bluegill and largemouth bass M*icropterus salmoides*. For the age specific growth analysis, we collected bluegill from 23 impoundments during the spring and early summer months of 1996 and 1997. For the size specific growth analysis, we collected bluegill from 16 impoundments during the spring and early summer months of 2004 and 2005. The fish for both analyses were frozen in the field and were returned to the laboratory where they were thawed and dissected. We measured length (TL), and weight of each fish and determined its sex. We also weighed the gonads and scored them using an established scoring system (Aday et al. 2002). Saggital otoliths were removed from each fish, and these otoliths were independently aged by two experienced readers. The radius of each otolith was measured to each annulus using a computer digitizing tablet and microscope. If the two readers could not agree on the age of a fish (occurred in <1% of fish), the fish was removed from analysis.

For the age specific growth analysis, length-at-age-4 for male bluegill was used to estimate growth. To assess size structure we calculated relative stock densities (RSD) at 180mm. Relative stock density was determined by dividing the number of 180-mm bluegill by the number of 80-mm bluegill (Anderson and Gutreuter 1983). Although 200mm is the preferred size for bluegill as classified by Gabelhouse (1984), we chose 180mm because many of our lakes did not contain 200-mm individuals.

For the size specific growth analysis, ten fish from each age class (1-5) were selected from each lake and the Fraser-Lee method (DeVries and Frie 1996) was used to estimate the growth (mm) of each fish during every year of life. These growth increments were then plotted against the initial length of each fish at the beginning of each growing season and the best-fit least-squares regression function (linear, quadratic, or log-linear) was determined for each reservoir (Figure 2-1). The best-fit regression equation was then used to estimate the average size specific growth rate of fish in each lake at 50, 100, and 150 mm.

For both the age specific and size specific growth analysis, we collected information on several environmental variables and community parameters within each lake. These variables include air temperature, secchi depth, total zooplankton density, total benthic invertebrate density, and bluegill, largemouth bass, and gizzard shad *Dorosoma cepedianum* AC electrofishing catch per unit effort (fish metrics only used in size specific growth analysis, based on the average of spring and fall samples). The data used for the age specific growth analysis are the means of all samples collected in 1996. The data used for the size specific growth analysis are the means of samples collected from 1999-2003. This represents the life span of the fish included in the size specific growth analysis. We included creel survey estimates of the number of fish harvested per acre per year from each lake and the average age of maturation of male bluegill from each population. For the age specific growth analysis, the creel data and average age of maturation estimates were based on samples collected in 1996. For the size specific growth analysis, these estimates were based on samples collected in 2004.

The zooplankton samples used in both analyses were collected monthly from May through September at four offshore sites by vertical tows of a 0.5-m diameter, 64-µm mesh zooplankton net. Samples were collected from the thermocline (or from the lake bottom when the lake was not stratified) to the surface, preserved in a 4% Lugols solution, and returned to the laboratory for processing. During processing, subsamples were counted until reaching either 200 organisms from the major taxonomic groups or until 10% of the total sample was counted (Dettmers and Stein 1992; Welker et al. 1994).

Benthic macroinvertebrates were collected in June and August at six sites in each lake using a modified stovepipe sampler (20 cm diameter). Samples were washed through a 250-µm sieve bucket and preserved in ETOH and rose bengal. In the laboratory, invertebrates were sorted and identified to order or family. Total macroinvertebrate densities and those of the most abundant invertebrate taxa (from all reservoirs combined) were analyzed to determine any taxon-specific differences among reservoirs.

Water quality was measured monthly from May through September at a fixed site in each lake. Transparency was measured with a secchi disk, and temperature and dissolved oxygen were taken at 1-m intervals from the surface to the bottom with a YSI Model-55 meter. Because we did not have daily water temperature data for all lakes, daily air temperature data from the Illinois State Water Survey were analyzed for a better metric of lake temperature conditions. For the age specific growth analysis, cooling degree days were averaged across years for each lake from the nearest weather station. For the size specific growth analysis, the cumulative heating degree days from the nearest weather station were calculated from May 1- September 31 for each year.

The relationship between the age specific and size specific growth rates and the environmental and community variables were assessed using Akaike's information criterion (AIC; Burnham and Anderson 2002). The use of the AIC approach allowed us to select multiple GLM models that have substantial support. We used AIC because multiple regression tends to lead to the development of over-fit, spurious models (Anderson et al. 2000). We calculated AIC using the residual sum of squares from pre-selected least squares regression models using the formula:

$$\text{AIC} = n \log(\sigma^2) + 2K$$

Where σ^2 = residual sum of squares/n and K = number model parameters. Candidate models were developed based on likely factors influencing bluegill growth and not an "all possible models" approach. We used corrected AIC (AIC_c) values since our n/K ratio was less than 40. Models with Δ_i values of less than 2.0 have substantial support while those over 10.0 have little or no support (Burnham and Anderson 2002). We also calculated Akaike weights (w_i) to assess the relative likelihood of each model. Model-averaged parameter estimates (β) were derived from the 95% confidence set of models based on Akaike weights. We examined the relative importance of explanatory variables in our models by taking the sum of w_i across all models in the 95% confidence set where that variable occurred.

Pond Experiments

We conducted pond experiments to assess how age of maturity is related to bluegill population size structure. We examined the relative strength of genetic (population source) and environmental (population social structure) factors on variation in growth and timing of maturation for juvenile male bluegill in a common-garden experiment. Juvenile male bluegill collected from two different wild source populations, one with parental males that are large (>190mm total length) and one with parental males that are stunted (<155mm total length), were placed in a common environment and the social structure was varied by controlling the presence or absence of large, mature male bluegill collected from a third population. Detailed procedures for this experiment can be found in Appendix A, Aday, D. Derek, David H. Wahl, and David P. Philipp. 2003. Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. Ecology 84:3370-3375.

A second pond experiment was designed to examine the relative influence of prey resources as well as social structure to maturation rates of bluegill. We assessed how resource availability and timing of maturation interact to influence individual body size of bluegill (*Lepomis macrochirus*). Resource availability (high and low food) and the social structure of the population (presence or absence of large, mature males) was varied in experimental ponds. Detailed procedures for this experiment can be found in appendix B, Aday, D. Derek, David P. Philipp, and David H. Wahl. 2006. Sex-specific life history patterns in bluegill (*Lepomis macrochirus*): interacting mechanisms influence individual body size. Oecologia 147: 31-38.

Field Studies

Four hypotheses have been proposed to explain what causes and/or maintains stunting in bluegill populations: adult overharvest, cuckolder overproduction, density-dependent growth limitation, and socially influenced early maturation. To test the relative importance of each of the four hypotheses in determining size structure of bluegill populations in Illinois, we assessed key life history characteristics of 50 populations throughout the state. In each lake, we sampled bluegill during the spawning season using boat electrofishing techniques, and for each population we determined sex specific size-at-age, age-at-first-maturity, gonosomatic index (GSI), and relative abundance of cuckolders. Detailed procedures for this assessment are found in appendix C, Claussen, Julie. E., John Hoxmeier, D. Derek Aday, David H. Wahl, and David P. Philipp. (In review) What Controls the Size Structure of Bluegill Populations? Transactions of the American Fisheries Society.

FINDINGS

Age Specific Growth

Temperature, secchi, prey, and age at maturity were all included in the top ranked model for size at age 4. However, this model had little weight of evidence, suggesting other competing models. Temperature and secchi were included in most of the top models, whereas prey and age at maturity had some support in the top models (Tables 2-1 and 2-2). Temperature, secchi, and prey were all positively associated with size at age 4, whereas age at maturity was negatively associated.

Size at age 5 was included in all of the top ranked models for RSD180. This result suggests that growth during the first five years is the most important factor influencing size structure. Harvest pressure and size at age 2 were also included in the top ranked models; however, both of these variables had low parameter likelihoods.

Size Spacific Growth

We found that the size specific growth rate of bluegill varied from reservoir to reservoir (Table 2-3). Except for Apple Canyon, we found that our regressions do a good job of describing the relationship between fish length at the start of a year and growth in the next year ($r^2 = 0.27$-0.92). The size specific growth rate at 50 mm TL ranged from 35.0 (Sterling) to 67.7 mm/yr (Walnut Point). At 100 mm, the size specific growth rate ranged between 19.9 (Sterling) and 62.5 mm/yr (Kakusha). The size specific growth rate at 150 mm ranged between 0.9 (Wood) to 62.4 mm/yr (Kakusha). As expected, size specific growth rates generally decrease as the length of a fish at the start of the growing season increases (Figure 2-1).

Our AIC analysis showed that several factors influence the size specific growth of bluegill. In addition, the variables that influence bluegill growth change as a function of fish size (Table 2-4). The most parsimonious models that predict size specific growth at 50 mm TL were most heavily influenced by the age of maturation of male bluegill in the population ($r^2 = 0.39$, $P < 0.01$) and the combined effect of gizzard shad density and secchi depth ($r^2 = 0.71$, $P < 0.01$). For bluegill at 50 mm TL, the combined effect of gizzard shad density and secchi depth had a stronger influence on bluegill growth than either variable alone (Table 2-4). As bluegill size increases, the importance of the average age of maturation of males in the population decreases. Gizzard shad density had a strongest effect on size specific growth at 100 and 150 mm TL (100 mm: $r^2 = 0.60$, $P < 0.01$, 150 mm: $r^2 = 0.65$, $P < 0.01$). At 100 mm TL, we found that gizzard shad density ($r^2 = 0.60$, $P < 0.01$), the combined effect of gizzard shad density and secchi depth (adjusted $r^2 = 0.77$, $P < 0.01$) and the combined effect of gizzard shad and zooplankton densities (adjusted $r^2 = 0.65$, $P < 0.01$) all had a strong influence on bluegill size specific growth.

Across all sizes, we found that the presence of gizzard shad had a stronger influence on the size specific growth of bluegill than any other factor (Table 2-4). At all sizes, there was a negative correlation between gizzard shad density and bluegill size specific growth (Figure 1-2). At 50 and 100 mm TL, gizzard shad appear to influence bluegill growth indirectly by increasing water turbidity. Our data shows that there is an inverse correlation between gizzard shad density and secchi depth ($N = 16$, $r = -0.55$, $P = 0.03$). At 100 and 150 mm TL, gizzard shad appear to influence bluegill growth through competition for food resources.

Pond Experiments

The first set of pond experiments showed juvenile male bluegill from both populations allocated significantly more energy to reproduction in the absence of large males than in their presence. Within ponds, differences in growth and maturation rates between juvenile males from the two source populations were small but significant. These results indicate both genetic and environmental components to growth and maturation in bluegill, but emphasize the importance of social interactions in shaping individual life-history strategies. Findings for this experiment can be found in Appendix A, Aday et al. 2003.

Results of the second set of pond experiments showed how food ration affected growth (larger fish in the high food treatments) and how the social structure of the population affected timing of maturation (early maturation of males in the absence of large males). Treatment effects, however, were sex-specific; males responded to the social structure of the population and females were more responsive to resource availability. We also found that individuals that became sexually mature were smaller than those that remained immature, although results were sex-specific and resource dependent. For males, individuals that matured were smaller when resources were limited. Despite being more responsive to resource availability as a whole, there were no differences in body size between mature and immature females in the different ration treatments. Findings of this experiment can be found in Appendix B, Aday et al. 2006.

Field Studies

Field analysis of size structure showed none of the populations sampled provided evidence supporting a role for either the adult overharvest hypothesis or the cuckolder overproduction hypothesis. Although population density and resource availability likely influence growth rates in all bluegill populations, there was no evidence among the 50 Illinois bluegill populations studied that density-dependent growth limitation causes or maintains stunting. There was also low relative abundance of cuckholders in the study lakes suggesting they have little influence on size structure. Size structure, however, was highly correlated with age-at-first-maturity; male bluegill in stunted populations matured significantly earlier than those in quality populations. The findings for this analysis is found in Apendix C, Claussen et al. (In review).

RECOMMENDATIONS

The results from the growth analyses show that multiple factors influence the growth of bluegill. Age specific growth analyses suggest that temperature and secchi depth have the greatest influence on the growth of bluegill. Meanwhile, the results from the size specific growth analysis suggest that gizzard shad have the greatest influence on the growth of bluegill. Gizzard shad seem to influence the growth of smaller bluegill by increasing turbidity, which decreases the forage success and growth of bluegill. Meanwhile, gizzard shad seem to influence the growth of larger bluegill through direct competition for forage. The size specific growth analysis also revealed that the average age of maturation of male bluegill in the population has a strong influence on the growth of smaller fish.

The results of the age specific growth analyses indicate that temperature and secchi depth have the greatest influence on the growth of bluegill. Given that temperature and prey consumption are the basic tenants of any growth model, it was not unexpected to have these two variables rank as the most important in our models. Similar results for temperature have been found with largemouth bass (McCauley and Kilgour 1990), and bluegill in Minnesota lakes (Tomcko and Pierce 2001). Higher prey densities have been shown to increase growth of walleye *Sander vitreus* (Hoxmeier et al. 2006) and largemouth bass (Olson 1996). The positive relationship between growth and transparency suggests that bluegill were able to feed more effectively in clearer water. In mesocosm studies, consumption of zooplankton by larval bluegill decreased in turbid conditions (Miner and Stein 1993). Conversely, secchi depth was negatively correlated with bluegill growth in Minnesota lakes (Tomcko and Pierce 2001).

Effects of angling were more pronounced in determining size structure; however, it had a low parameter likelihood. Model averaged parameter estimates were positive for harvest in both age 4 and RSD 180 models, which is counterintuitive. We expected lakes with higher angler pressure and bluegill harvest to have a truncated size structure due to harvest of larger individuals. What we included as a explanatory variable may have actually been a response variable. It is possible that anglers were targeting lakes with larger bluegill size structure.

Results from size specific growth analysis show that there is considerable variation in size specific growth rates of bluegill across Illinois. These growth rates vary both between and within populations. It appears that differences in size specific growth rates between populations can be explained by presence or absence of gizzard shad and differences in gizzard shad density and age of maturation of the male bluegill among reservoirs. Environmental conditions thus have a strong influence on the growth of bluegill. Within a population, size specific growth rates generally decreases with increasing total length at the beginning of the growing season. Larger fish divert a larger portion of their energy from growth into reproduction. Bluegill from higher quality populations delay when they become sexually mature and generally mature at a larger total length. As a result, fish from these higher quality populations are expected to have greater size specific growth rates across all sizes because they wait until a larger total length and age before they begin diverting energy from growth into reproduction.

We found that gizzard shad have a stronger influence on the size specific growth of bluegill than any other factor. At 50 and 100 mm TL, the synergistic effect of gizzard shad density and secchi depth influences bluegill growth. Gizzard shad are known to increase water turbidity and this probably decreases the forage success of younger bluegill, reducing their growth. Juvenile gizzard shad are primarily pelagic planktivores feeding on zooplankton therefore increasing algal populations and turbidity. Adult gizzard shad feed primarily on benthic detritus (Stein et al. 1995) and likely disturb the sediment as they feed, also increasing turbidity. It has been speculated in other studies that increased turbidity due to gizzard shad foraging reduces bluegill adult size (Aday et al. 2003) In the laboratory, high turbidity reduces bluegill forage rates and success (Gardner 1981). It appears that the effect of gizzard shad on water clarity has less of an influence on the growth rates of larger bluegill. Instead, gizzard shad seem to influence the size specific growth of larger bluegill through direct competition or behavioral interactions. Our results suggest that competition for zooplankton and benthic invertebrate prey between bluegill and gizzard shad has a stronger influence on the growth of larger bluegill.

The results of our AIC analysis show that gizzard shad either directly or indirectly influence the size specific growth of all size classes of bluegill. However, it is apparent that the average age of maturity of the males in a population also has a strong influence on the size specific growth of smaller bluegill. Other jobs of this project have shown that male bluegill from non-stunted populations mature 1-2 years later than individuals from stunted populations. Therefore, bluegill from these non-stunted populations delay when they begin diverting energy into reproduction and consequently, they obtain a larger adult size. The results from this analysis add to a growing body of literature that suggests that the social structure (size and age of maturation of males) of a bluegill population influences the growth rate of individuals in the population (Aday et al. 2003a, Aday et al. 2003b). We found that the age of maturity of the males in the population have a stronger effect on the growth of 50 mm bluegill but not larger fish. Because some individuals may begin to mature by 100 mm, the social structure of the population would be expected to have less of an influence on the size specific growth of fish after some individuals begin to mature.

Previous research has shown that many biotic and abiotic factors influence the growth of bluegill. Similar to the findings of our AIC analysis, other studies have shown that there is a negative correlation between secchi depth and bluegill growth (Tomcko and Pierce 2001, Snow and Staggs 1994). While these studies link secchi depth to various abiotic factors such as water depth or shoreline development, they did not make the connection between increased turbidity and gizzard shad density. Our results suggest that the synergistic effect of shad density and secchi depth has a very strong influence on the size specific growth of 50 and 100 mm bluegill. In contrast, Theiling (1990) found that macrophyte density, zooplankton size, and benthic invertebrate biomass are the biotic factors that have the strongest influence on the growth of bluegill in Michigan. The fish communities (particularly the absence of gizzard shad), temperature regime, and lake morphology of the lakes used in these previous studies at northern latitudes are different than the reservoirs examined in our study. In addition, these studies considered age specific and not the size specific growth rates of bluegill and it would be valuable to use these approaches in future studies.

The results of our age specific growth analysis suggest that temperature and secchi depth have a significant influence on the adult size structure of a bluegill population. Obviously, managers can do little to control water temperature. However, turbidity can in some cases be managed by limiting sedimentation or by planting macrophytes. Meanwhile, the results of our size specific growth analysis suggest that gizzard shad have a significant influence on the growth of bluegill. It appears that gizzard shad compete with larger bluegill for forage reducing bluegill growth. Meanwhile, gizzard shad seem to influence the growth of smaller bluegill by increasing turbidity which decreases the forage success and growth of bluegill. When considered together, the results of both analyses suggest that managers can improve the growth of bluegill by controlling gizzard shad density and turbidity.

Pond experiments highlighted the link of both social structure (presence of large males) and genetics in determining growth and maturity in bluegill populations. The presence of large males as well as whether the bluegill was from a stunted or quality population both influenced growth and maturity. This suggests that management to protect larger bluegill may increase age of maturity for bluegill and ultimately growth rates if numbers of larger bluegill are successfully increased. However, these changes have potential to be slow due to the past genetics of the bluegill population and may take several generations.

The second pond experiment also showed available prey resources are important in growth of bluegill. In systems where resources are limiting, bluegill will experience lower growth rates. Limiting competition for resources may be achieved through reducing abundances of bluegill. Management for reducing the abundance of smaller bluegill may increase growth rates. We also showed both resource availability and the processes that control timing of maturation interact in sex-specific ways to influence body size of bluegill. These results suggest that a more robust explanation for variable body size requires consideration of sex-specific interactions between ecological (food and growth) and evolutionary (timing of maturation) mechanisms. Food resources however were not related to bluegill population size structure in the field. Field data did show a relationship between age of maturation and size structure. To manage bluegill populations effectively, therefore, strategies should be focused on increasing the age-at-first-maturation through increasing abundance of larger mature male bluegill (e.g. reducing harvest), not on simply manipulating growth rates.

Job 101.3 Pre- and post-regulation characterization of experimental study lakes.

OBJECTIVE

To gather detailed baseline data on bluegill life-history characteristics as well as the biotic and abiotic variables that may affect bluegill recruitment, growth, and maturation in the chosen experimental study lakes.

INTRODUCTION

An important goal of this study was to examine the impact of various management actions (i.e., harvest regulations and predator stocking) on bluegill growth rates and size- and age-at-maturation, and determine how each acts to affect size structure among stunted bluegill populations in Illinois. Four aspects of a species' life-history trajectory determine the ultimate size structure of the adult population in a given water body: pre-maturation (larval/juvenile) growth rate, age at maturation, post-maturation (adult) growth rate, and longevity. These four aspects can be affected by a variety of variables within a water body. Age-at-maturation and longevity are directly affected by the social relationships among surviving adults and, therefore, can be greatly impacted by harvest. Both pre- and post-maturation growth rates are directly affected by density-dependent processes (i.e., slower growth rates due to intraspecific competition when there is an overabundance of bluegill and/or underabundance of prey) at all bluegill life stages. Additionally, biotic (e.g., inter and intra-specific competition, predation) and abiotic (e.g., temperature, dissolved oxygen saturation) factors can also influence all four aspects of a life-history trajectory. This job is designed to elucidate how these processes may act and interact to alter bluegill population size structure under different management options.

Results from Job 101.2 indicate that factors controlling the age-at-maturation may have the greatest influence in determining size structure of bluegill populations throughout the state. Quality populations were characterized by a later age- and larger size-at-maturity than stunted populations. Manipulative experiments associated with this project also showed that the social structure of the population, specifically the presence or absence and densities of large, mature males, has a direct impact on age-at-maturation of juvenile male bluegill in the population and, therefore, a direct impact on population size structure. Management actions designed to increase the size structure of wild bluegill populations (i.e., convert stunted populations to quality populations) need to increase PQM170. From an evolutionary standpoint, that requires reaching a new life history state, in which age-at-maturation is increased; i.e., males delay to older ages and larger sizes prior to maturing and entering the slower post-maturation growth phase. Moving a population from a stunted to a quality life history state, however, might be accomplished by increasing pre-maturation growth rates, increasing post-maturation growth rates, extending longevity, or increasing age-at-maturation directly. Which route successful management actions will use is unclear. As a result, we collected juvenile and mature bluegill from study lakes to monitor size, age, and maturity status.

Both pre- and post-maturation growth rates may be increased by an underabundance of bluegill or an increase of prey. This density-dependent alteration in growth rate can occur at any or all life stages of the bluegill. Bluegill feed on both zooplankton and benthic invertebrates throughout their life. Competition for food resources (intra- and interspecific) can occur at each life stage (i.e., larval, juvenile, adult) that could affect growth. Identifying the importance of altering competition for limited resources relative to other potential mechanisms designed to increase growth rates will be important for evaluating the success of any management strategy designed to alleviate stunting. Monitoring prey resources and bluegill densities in the study lakes is necessary to assess the role that density-dependent mechanisms may play in altering size structure of our test bluegill populations and influencing the results of the management experiment.

Predator abundance may also influence bluegill size structure and may be important at each life stage. Largemouth bass are the primary predator in these centrarchid-dominated experimental lakes and can consume large numbers of larval and juvenile bluegill. In addition, bass may compete with bluegill for available resources at the larval and juvenile stages.

PROCEDURE

In this job, we developed a management experiment to evaluate the success of different lake manipulations on improving bluegill size structure. We evaluated data collected from experimental bluegill populations to determine the influence of the management manipulations on population size and age structure. Thirty-two lakes across the state of Illinois were divided into four treatments (8 lakes per treatment): harvest regulations (8-inch minimum size limit, 10 fish daily creel limit); predator stockings (largemouth bass added to increase predation on juvenile bluegill), harvest regulations and predator stockings in combination; and control (Table 1-1). Regulations were implemented in 1998 and remained on until 2005. Predator stockings took place annually starting in 1998. Four-inch largemouth bass fingerlings were stocked in July at a target density of 60 per hectare. All stocked bass were given pelvic fin clips that alternated left to right with stocking year.

Analysis of the management experiment focused on three factors: 1) bluegill population parameters (adult abundance, size structure, age-at-maturation, and juvenile growth and abundance); 2) biotic variables (e.g., prey availability, predation); and 3) abiotic variables (e.g., temperature, lake productivity, lake-habitat characteristics).

Bluegill Population Parameters

Bluegill populations were monitored throughout the experiment in order to monitor changes in size structure and abundance. Bluegill were collected using electrofishing, seining and larval fish pushes. Electrofishing samples were performed on each study lake using an three phase AC powered, boat mounted electrofishing unit in the fall and spring. Three shoreline transects on each lake were electrofished for 0.5 hours each on each sampling date. All fish were collected, identified to species, and measured for total length. Inshore bluegill density (primarily juveniles) was assessed by shoreline seining (9.2 x 1.2 m bag seine, 3.2 mm mesh) at four fixed sites within each lake. Effort was calculated as the length of the haul (nearest m). All fish were counted and a minimum of 50 individuals of each species collected were measured (total length in mm). Density (#/m of seine haul) was calculated for bluegill throughout the study period. Larval fish were collected in 8 of the 32 lakes at 6 offshore sites. Larval fish were collected from each offshore site by pushing an icthyoplankton net (0.5m diameter, 500 mm mesh) for 5 minutes. Volume of water filtered was calculated with a calibrated flow meter mounted inside the mouth of the net. Larval fish were picked from the sample, identified to species and counted.

In order to evaluate the management experiment, intense bluegill collection were performed in 1996-1997 (beginning of the experiment) and 2004-2005 (end of the experiment). Bluegill were collected in all lakes using targeted electrofishing during the spring (May and June). All bluegill sampled were frozen and brought to the lab for dissection. To analyze the bluegill collected in each lake sampled, individuals were thawed and total length, weight, and sex determined. In addition, gonads were identified as to stage of development and weighed. Individuals were given a gonad score of 1 - 5 (immature - mature) based on the degree of maturation of the testes or ovaries (Aday et al. 2002). Individuals with scores of 1 - 3 were considered immature, having no or very little gonad development, whereas individuals with scores of four and five exhibited mature gonads; yolked eggs were present (females; Justus and Fox 1994) or testes were fully developed and running sperm (males). This data was used to determine the age of maturity for the bluegill population in each study lake. Otoliths were also removed from each bluegill for age and growth analysis. This data was used to determine age-specific growth curves, age at maturation, and abundance of cuckolders, males that mature early and steal fertilizations. All otoliths were read in whole view. When reader ages disagreed, a third reader was used to verify the correct age. The final age was then used to evaluate changes in growth using length-at-age for male and female bluegill separately.

Age of maturity and the percent of quality males larger than 170 (PQM170) were the response variables used in evaluating the management experiment. Age of maturity was determined by calculating Z-age for each lake. Z-age is a statistic that is calculated for each sex using the proportion of individuals that are mature in the age class where there is a transition from immature to mature. In the case that this transition is occurring over two age classes, z-age is calculated for each age and the mean is taken to yield the z-age for the lake. PQM 170 was also calculated for each lake using the bluegill collections. PQM170 is calculated as the proportion of mature male bluegill that were over 170 mm in total length. The treatments were examined for changes in z-age and PQM170 using repeated measures ANOVA using proc mixed in SAS. Significant differences were examined using Least Squared Difference with Tukey correction.

Prey Availability

Prey availability may influence the relative abundance of bluegill and affect growth at all life stages. Macroinvertebrates and zooplankton are important food items to larval, juvenile, and adult bluegill. We determined the abundance of these food resources in 16 (7 stunted and 9 quality) of the experimental lakes. To quantify zooplankton abundance, collections were taken using vertical tows with a 0.5 m diameter, 64 um mesh zooplankton net at four inshore and four offshore sites (one tow per site). Zooplankton samples were preserved in a Lugols solution (4%) for later processing. Samples were filtered and condensed into a 20 mL vial. A subsample of 1 mL was removed using a Henson's stemple and counted and identified to family and a total length was measured on 10 individuals of each family.

Inshore macroinvertebrates were collected using a stovepipe sampler (20 cm diameter) at 6 sites (one sample per site) within each lake. Depth of each sample collection was measured. Samples were cleaned in a 250 mm mesh benthos bucket and preserved in an ethanol/rose bengal solution (70%) for processing. Macroinvertebrates were separated from the sample, counted, identified to order and total length was measured for fifteen individuals of each order. We examined changes in total zooplankton, macrozooplankton, and total benthos densities throughout the management experiment. Monitoring the densities of bluegill prey will allow us to determine if changes in bluegill size structure are related to changes in prey availability rather than the management manipulations.

Predator Abundance

Predator abundance may also influence bluegill size structure and may be important at each life stage. Largemouth bass are the primary predator in these centrarchid-dominated experimental lakes and can consume large numbers of larval and juvenile bluegill. In addition, bass may compete with bluegill for available resources at the larval and juvenile stages.

As part of the management experiment, 16 lakes were stocked with advanced fingerling largemouth bass to increase predator densities. We assessed the contribution of adult stocked bass that were initially stocked as fingerlings to the bass population and any changes in total abundance of largemouth bass. We monitored growth and survival of stocked bass through the first fall after they were stocked and in subsequent years. To quantify largemouth bass abundance, fall and spring electrofishing surveys were conducted on five all of the study lakes. Largemouth bass were collected on three 30 minute shoreline transects by day AC electrofishing targeting largemouth bass only. All largemouth bass were examined for marks and measured for total length. We summarized the contribution the stocked bass are making to the standing stock of largemouth bass in the experimental lakes. We examined CPUE for all bass in the system as well as determining the proportional contribution of natural and stocked bass.

Other Biotic and Abiotic Factors

Abiotic variables may also influence bluegill population parameters. We measured water transparency, dissolved oxygen, temperature, total dissolved phosphorous, and chlorophyll *a* on 16 lakes. Water transparency was measured with a secchi disc. Temperature and dissolved oxygen profiles were measured at one-meter intervals. Water samples were collected monthly with an integrated water sampler for analysis of total phosphorous and chlorophyll *a*. These were examined to determine their influence on bluegill growth and the success of the regulations.

Angler Compliance

To assess compliance of anglers to the experimental regulations, compliance cards were given to conservation officers at all lakes with experimental regulations. Conservation officers were asked to record the number of anglers fishing for bluegill along with the number of legal and sub-legal length bluegill harvested by each group of anglers. Conservation officers completed these cards each time they performed a bluegill regulation check on an experimental lake. The compliance data was used to evaluate the success of the regulation. Creel data was also used to assess angler compliance. All experimental lakes had creels performed on them at during the initial phase of the experiment and at the end (see Job 1). Creel data was used to calculate noncompliance by dividing the number of fish smaller than 8 inches by the total number of fish caught for each lake with the experimental regulation. The level of harvest of fish smaller than 8 inches was also compared between regulation and non-regulation lakes.

FINDINGS

The management experiment was evaluated by examining at a number of different bluegill population parameters and how they changed from the beginning of the experiment in 1996 to the conclusion in 2005. Bluegill population parameters that were examined for changes included CPUE of bluegill of differing sizes, RSD of bluegill over eight inches, length at age, age of maturity, and PQM 170. Examining changes in these parameters for each of the treatment groups will allow us to evaluate the success of the experimental techniques and make management recommendations.

We first examined CPUE for a number of different size groups to examine changes in abundance of bluegill during the experiment. Total CPUE of bluegill increased from 1996 to 2005 (Figure 3-1), however there were no significant differences among experimental treatments (F = 0.41, P = 0.75) or between quality and stunted lakes (F = 0.87, P = 0.36). CPUE of bluegill over 200 mm (8 inches) was examined for changes in abundance of large bluegill greater than the regulation limit in the study lakes (Figure 3-2). We observed some increases in CPUE in quality lakes with the experimental regulation alone, as well as in combination with bass stocking. However, there were no significant differences in CPUE of 200 mm bluegill among treatment (F = 0.03, P = 0.99) or between quality and stunted lakes (F = 1.45, p = 0.24). We also examined CPUE of bluegill larger and smaller than 170 mm because this was the size used to determine a bluegill population of quality size for other metrics (PQM 170) (Figure 3-3). CPUE of bluegill larger than 170 mm and those from 100 to 170 mm did not change during the course of the experiment. Finally, we examined RSD 200 for changes in ratio of small to large bluegill throughout the experiment. RSD 200 was calculated as the CPUE of bluegill larger than 200 mm divided by the CPUE of bluegill larger than 100 mm (stock size). We used a minimum cut off of 100 mm because bluegill at this size were fully susceptible to the electrofishing gear and sampled efficiently. Control lakes with quality populations had a higher RSD 200 than the other treatments at the end of the experiment (Figure 3-4), however no other significant differences were observed among treatments (F = 0.74, p = 0.54) or between quality and stunted lakes (F = 2.84, p = 0.11) both before and after the experiment. Overall, few differences were observed in CPUE for different size classes of bluegill during the course of the experiment.

Mean length was calculated for each age for male and female bluegill for each population in the study (Figures 3-5 to 3-20). Very few changes in mean size-at-age were observed for both male and female bluegill between initial samples in 1996 and those in 2004. Some lakes showed an increase in the maximum age we observed (Le Aqua Na, Pierce), and as a result there was some increase in overall size structure. These changes were small and the increase in the number of older fish was low. Some lakes showed decreases in length at age (Jacksonville, Murphysboro) that resulted in reduced maximum length in these lakes. We compared mean length at age 2 and 5 for males and females across treatments (Figures 3-21 and 3-22). We did not observe any changes in size at age

2 and 5 that were consistent across treatments. In general, growth rates of bluegill in the management experiments appear to remain relatively unchanged in all treatments.

Annual growth rate increments were also examined for differences among treatments. Annual growth rates were calculated for each lake for bluegill of 50 and 100 mm in total length as described in Job 2. Annual growth rate of 50 mm bluegill was significantly higher in quality lakes than stunted lakes (F = 9.95, P = 0.004), but there was no difference among experimental treatments (F = 2.97, P = 0.052). Annual growth rate of 100 mm bluegill were also significantly higher in quality than stunted lakes (F = 24.82, P < 0.001). However, for this size class there was a significant difference among experimental treatments (F = 4.97, P = 0.008; Figure 3-23). The regulation treatment had significantly higher annual growth rates for 100 mm fish than both the stocking treatment (t = 3.66, adj. P = 0.006) and the stocking and regulation treatment (t = 2.89, adj. P = 0.04).

The proportion of mature males in the population greater than 170 mm (PQM 170) was used in designating bluegill populations as quality or stunted and was calculated for each lake in 1996 (pre treatment) and 2004 (post treatment) (Table 3-1). Lakes that were initially designated as quality populations had significantly higher PQM 170 scores than stunted lakes (F = 54.7, P < 0.001). There were no significant differences between 1996 (pre experiment) and 2004 (post experiment) PQM scores between quality and stunted lakes (F = 0.43, P = 0.52; Figure 3-24). Mean PQM 170 was also calculated for each treatment to evaluate changes in relation to the management experiment (Figure 3-25). Changes in PQM 170 were examined to determine if experimental treatments were successful in increasing the proportion of mature males larger than 170 mm. Change in PQM score was calculated as the difference of the scores between 2004 and 1996. No significant differences were observed in change in PQM 170 by treatment (F = 1.19, P = 0.34) or between stunted and quality populations (F=2.85, P = 0.10) (Figure 3-26). There was some variation in PQM 170 scores, however it was not associated with the experimental treatments.

Age of maturity can affect bluegill growth and could be affected by the experimental treatments. We calculated Z-age for each experimental lake (Table 3-2) in order to evaluate changes in age of maturity in response to the experimental treatments. Mean z-age scores were compiled for each treatment for both quality and stunted populations (Figure 3-27). Change in z-age was calculated as the difference between 2004 and 1996 for both males and females. Change in z-age for males showed no significant differences by treatment (F = 0.41, P = 0.75). However, change in male z-age was significantly different between stunted and quality populations across all treatments from the beginning to the end of the experiment (F = 5.43, P = 0.03; Figure 3-28). Male z-age increased in stunted lakes and decreased in quality lakes. Similar changes were observed in female z-age score. Female z-age did not change significantly in response to the treatments (F = 2.01, P = 0.14). However, change in female z-age was significantly different between stunted and quality populations across all treatments from the beginning to the end of the experiment (F = 4.61, P = 0.04; Figure 3-24). Female z-age also increased in stunted lakes and decreased in quality lakes. Male z-age score was related to female z-age score in both 1996 (r = 0.75, P < 0.001) and 2004 (r = 0.63, P < 0.001). Change in male z-age score was also significantly correlated with change in female z-age score (r = 0.63, p < 0.001; Figure 3-29). These relationships suggest that male and female z-age score are affected by similar factors and a change in one will result in a change in the other. Z-age score however did not vary by treatment for male or female bluegill populations suggesting little affect of the experimental manipulations on age at maturation.

Environmental changes in the lakes unrelated to the management experiment could affect the expected response of the bluegill populations. To assess these potential effects, multiple years of data (1998-2005) were included to examine differences from each population in prey resources throughout the management experiment. Incorporating multiple years of data helped control for high variation among study lakes. There was some fluctuation in zooplankton and benthic invertebrate densities from 1998–2005 (Figure 3-30). These fluctuations were generally small and no change in bluegill growth would be expected from this natural variation. The lack of changes in prey resources would imply that any changes in the bluegill size structure are due to the management manipulations.

We also evaluated whether or not the experimental treatments were successfully implemented. This was done through assessing angler compliance to the regulation and the contribution of stocked largemouth bass to natural populations. The treatments must be implemented successfully for predicted change to be observed in the bluegill population size structure. The contribution of largemouth bass in stocked lakes varied greatly by lake (Figures 3-31 to 3-34). Most experimental lakes sampled throughout the experiment showed some contribution of stocked largemouth bass to the total bass population. In lakes where CPUE of stocked bass was greater than one bass per hour of electrofishing, we did observe an increase in mean CPUE of all largemouth bass (Figure 3-35). When stocked largemouth bass experience greater survival, there is potential to increase the predator density. However, the relative abundance of bass in the stocking lakes has been variable throughout the management experiment and has not shown an overall increase. The CPUE of largemouth bass greater than 250 mm at the end of the experiment (2001-2005) from fall electrofishing were similar across all treatments (Figure 3-36). There was no increase in mean CPUE observed in the bass stocking treatment lakes. The varied success with increasing the number of predators in the study lakes likely caused varied success with the stocking treatments.

We examined relationships between largemouth bass populations and bluegill densities in the experimental lakes to evaluate the affects that bass predators have on bluegill densities. The total number of bass in a lake greater than 250 mm was positively correlated to the density of bluegill found in seine hauls (r = 0.35; P = 0.047). This relationship was not expected since we were attempting to reduce juvenile bluegill numbers by increasing bass abundance. CPUE of stocked bass larger than 250 mm in fall electrofishing at the end of the experiment (2001-2005) was also positively correlated with CPUE of bluegill during the same time period from fall seine samples (r = 0.37, p = 0.036). These results suggest that stocked bass were not successfully reducing the densities of juvenile bluegill in the stocking treatment lakes. Mean bluegill density from seine samples were similar in the early experiment (1996-2000) and late experiment (2001-2005) samples. There was no decrease in bluegill density in either the stocking or stocking and regulation treatments (Figure 3-37). As a result, there is no evidence that increasing the number of largemouth bass predators had any affect on bluegill densities.

Angler compliance was assessed through checks completed by conservation police officers and creel clerks. Compliance to the regulation based on officer checks was high in most lakes (Table 3-2) except for two lakes that had low compliance (Busse 0%; Jacksonville 54%). Compliance was not significantly correlated with the number of checks on a lake ($r = 0.194$; $P = 0.47$). Compliance was also assessed through creel surveys conducted at all study lakes at the end of the experiment (see Job 1). The percent compliance was calculated for each study lake as the total number of bluegill harvested larger than 8 inches divided by the total number of bluegill harvested. Compliance was then compared for the experimental regulation lakes between the creel and conservation officer data (Figure 3-38). The percent of anglers compliant was not correlated between the two assessment methods ($r = 0.19$, $P = 0.48$) and compliance levels observed in the creel were significantly lower than compliance in conservation officer checks ($t = 5.98$, $P < 0.001$). This suggests that anglers are more likely to comply with a regulation when conservation officers are present, however checks performed by creel clerks may more accurately represent angler level of compliance to regulations. Compliance to the experimental regulation from creel data was significantly higher in lakes with quality bluegill populations than in lakes with stunted populations ($F = 14.58$, $P = 0.002$). Lakes with more bluegill available over the size limit were more likely to have anglers who comply with the regulation.

Creel data was also used to determine compliance levels on lakes without the experimental regulation. Similar to compliance in experimental regulation lakes, anglers harvested a significantly higher proportion of fish larger than 8 inches for lakes with quality bluegill populations than lakes with stunted populations ($F = 9.93$, $P = 0.004$). Anglers harvested similar proportions of bluegill larger than 8 inches in lakes with the experimental regulation as in lakes with no regulation ($F = 3.66$, $P = 0.07$). The percent compliance was low in stunted lakes receiving the regulation and the number of fish harvested less than 8 inches was high (Figure 3-39). Anglers exhibit greater compliance to regulations in lakes where larger bluegill are available. However, regulations do not necessarily deter anglers from harvesting small bluegill when conservation officers are not present. Overall low levels of compliance suggest that the experimental regulation was not successfully implemented in many lakes and may have affected the success of the management technique.

The importance of gizzard shad on bluegill populations was highlighted in Job 2. As a result, we examined the effects of gizzard shad on the experimental treatments. Gizzard shad population abundance was evaluated using the mean CPUE from electrofishing samples throughout the experiment and were natural log transformed. Gizzard shad CPUE was significantly greater in lakes that were initially designated stunted than in quality lakes ($F = 4.73$, $P = 0.04$; Figure 3-40). PQM 170 in 2004 was also significantly correlated to gizzard shad CPUE ($r = -0.67$, $P < 0.001$; Figure 3-41). The abundance of gizzard shad may reduce bluegill growth through competition for prey resources. Gizzard shad CPUE was also significantly correlated with female z-age score in 2004 ($r = -0.54$, $P = 0.002$) however it was not correlated to male z-age in 1996 or 2004 or female z-age in 1996. Gizzard shad CPUE was also negatively correlated with bluegill densities from fall seine samples throughout the experiment ($r = -0.37$, $P = 0.04$). Competition for resources between gizzard shad and bluegill may limit bluegill survival. These relationships suggest that the presence and abundance of gizzard shad play an important role in bluegill growth and abundance.

RECOMMENDATIONS

We examined changes in a large number of response variables associated with the management experiment. Overall, few changes in bluegill populations were observed that could be directly related to the experimental treatments. Lakes with bluegill populations that were designated quality at the beginning of the experiment, typically maintained a quality population throughout the experiment. These included lakes receiving both the regulation as well as the combined regulation and largemouth bass stockings. In addition, PQM 170 continued to be greater throughout the experiment in quality lakes than in stunted lakes. Combined these results suggest that implementation of an 8-inch minimum size limit and 10 fish bag limit will not have negative affects on bluegill populations and may help maintain the quality status of some populations. In contrast, the regulation does not appear to improve either growth rates or size structure of bluegill in stunted populations in the short term. In general, few changes in growth, catch rates, or maturity status were observed consistently across treatments.

Few changes in CPUE from electrofishing were observed for all experimental lakes. CPUE remained unchanged in each treatment for CPUE of all bluegill, bluegill larger than 200 mm, bluegill, larger than 170 mm, and bluegill from 100 – 200 mm in length. Few changes in mean length at age were observed for all experimental lakes as well. We examined length at age for each lake as well as by treatment and observed very few changes in growth. Annual size specific growth did show some interesting differences between bluegill in stunted and quality experimental lakes. We found greater annual size specific growth rates in bluegill in the quality lakes than the stunted at sizes as small as 50 mm. These results suggest that differences in size structure are reflected in growth rates very early in the life history of bluegill. Size specific growth rates at 100 mm showed some differences in growth related to the experimental treatment. Bluegill in lakes with the experimental regulation experienced greater annual growth rates than those in lakes that were stocked with largemouth bass. The slower incremental growth in stocked lakes was also observed in lakes with the combined stocking and regulation treatment. The stocking of largemouth bass predators may have adverse affects on the growth of bluegill. Largemouth bass can cause bluegill to seek out refuge habitat forcing them to feed suboptimally in order to avoid predation. Increased competition for resources can result due to crowding of bluegill into refuge habitats. We have not observed long term increases in largemouth bass populations due to stocking efforts. However, immediately following stocking events, the abundance of largemouth bass predators is at least initially increased and may influence bluegill behavior in this way. Further research is warranted to evaluate these potential affects of stocked largemouth bass on bluegill growth.

The experimental regulation was implemented because we suspected that social interactions and the presence of large bluegill influenced the age of maturity of males in bluegill populations. It was hoped that protecting the larger fish in the population would increase the abundance of larger males causing smaller fish to delay reproduction and continue to grow. However we have no evidence that the regulation will induce these changes in the current experiment. Changing the life history of bluegill populations may take several generations in order to have an observed affect. Although the 8-year duration of this management experiment is a significant amount of time, it may not be long enough to change the maturation schedules of bluegill populations. Future work should include examining the effects of these regulations over a longer period of time. With successful implementation of the regulation, changes in life history and later ages of maturation may be observed.

Age of maturity of bluegill did change during the course of the experiment, however, these changes were not related to the management treatments nor were they reflected in the size structure of bluegill populations. When they occurred, changes in male and female z-age were highly correlated with each other. Changes in z-age were variable across treatments, but tended to increase in stunted lakes and decrease in quality lakes across treatments and did not change in relation to any size structure parameters. Z-age was positively related to PQM 170 in 1996 when the experiment was initiated, but was not significant in 2004 after the experimental treatments. Z-age was also not related to other measures of growth. One possible explanation is that the changes in age of maturity have not yet been reflected in the size structure of the bluegill population. Another is that age of maturity is not as important a driving factor in determining the growth of bluegill as initially hypothesized. At this time, we have only limited evidence to indicate that age of maturation is related to many common measures of size structure.

The size regulation needs a number of assumptions to be met in order to increase population size structure. First, bluegill harvest must be high enough to influence bluegill size structure. Results in Job 1 show high harvest rates for bluegill in all study lakes and reducing or controlling this harvest should influence bluegill populations. Second, bluegill anglers must be compliant with the regulation. Compliance in the study lakes to the regulation was low and angler catch of bluegill less than 8 inches was not influenced by the presence of the regulation. Creel data showed a similar ratio and catch rate of fish harvested that were less than the 8-inch minimum size in both lakes with and without the regulation. Anglers appear to harvest smaller bluegill whether it is illegal or not. Compliance was somewhat higher in quality than stunted lakes, but fish below the minimum size limit were being harvested in all lakes with the regulation. Compliance to the regulation was high in checks performed by conservation officers, but not in creel surveys. Anglers may not harvest illegally sized fish when conservation officers are present. We feel that the data collected by the creel surveys is more reliable in assessing angler compliance. The creel data was based on harvested fish from a larger sample of anglers than the conservation officer spot checks. The higher level of angler compliance suggests that conservation officer presence is important in enforcing regulations. Adequate posting of regulation signs and other forms of angler education are also likely important to increase awareness and understanding of the regulation.

The other treatment examined in the management experiment was the stocking of largemouth bass. Results from the largemouth bass stocking had variable success and we did not observe consistent increases in largemouth bass densities in the stocking treatments. When survival of stocked bass was high (measured as over 1 fish per hour in electrofishing samples) we did observe an increase in total largemouth bass abundance in the lake. The increase in largemouth bass abundance however was not related to a decrease in juvenile bluegill abundance as expected. The goal of the largemouth bass stocking was to reduce juvenile bluegill densities in order to reduce competition for food resources. Lakes with higher largemouth bass abundance also had higher bluegill abundance. Lake productivity or available food resources in a lake may simultaneously allow for greater largemouth bass and bluegill densities. In these situations, largemouth bass predation may not control bluegill densities. These results are contrary to popular management strategies for reducing small bluegill abundance. Regardless, our data suggests that stocking largemouth bass may not be a successful management strategy for reducing bluegill densities due to variable stocking success.

Results in Job 2 indicate that the presence of gizzard shad have an important influence on bluegill growth. We found evidence for competition for resources between bluegill and gizzard shad. Gizzard shad abundance was correlated with a number of measurements of bluegill size structure. Lower abundance of juvenile and large bluegill was found in lakes with high gizzard shad densities. Gizzard shad abundance was also higher in stunted bluegill lakes than quality lakes. Bluegill can compete for similar resources as gizzard shad, reducing growth or increasing mortality in bluegill. Gizzard shad can also affect feeding rates of bluegill by decreasing water clarity. Management efforts directed at controlling gizzard shad populations and increasing water clarity (sediment reduction, vegetation establishments) will have positive effects on bluegill populations.

Overall, the management experiment yielded few changes in bluegill size structure and no changes that were consistent across treatments. The regulation treatment with a minimum size of 8 inches and a 10 fish bag limit did maintain quality populations of bluegill. However, These effects were not significantly different than control lakes where no regulation was implemented. Largemouth bass stocking was not effective in reducing densities of small bluegill and was therefore not successful in increasing bluegill size structure. Lack of changes in the experimental lakes were likely due to difficulties with the treatments due to low levels of angler compliance to the regulation and variable stocking success of largemouth bass. Future management efforts using regulations should evaluate potential angler compliance as a factor influencing success. Future largemouth bass stockings should also be assessed to determine factors influencing success and to evaluate in which lakes future stockings are warranted. Controlling gizzard shad populations may also be important when managing species such as bluegill due to their potential for competition for food resources. We currently have no evidence to suggest an 8-inch minimum size with a 10 fish bag limit will effectively increase the size of bluegill harvested by anglers. Continuing to follow population changes in a small number of lakes with the regulation with increased enforcement efforts would be valuable to assess the long term potential (over multiple bluegill generations) of these approaches to reduce stunting in bluegill populations.

Job 101.4. Analysis and reporting.

OBJECTIVE

To prepare annual and final reports that provide guidelines for bluegill management in Illinois impoundments.

FINDINGS

All data were analyzed and recommendations presented in the individual jobs of this report (see Job 101.1-101.3). In addition, study results and recommendations are presented in the following appendices:

Appendix A:

Aday, D. Derek, David H. Wahl, and David P. Philipp. 2003. Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. Ecology 84:3370-3375.
Derek 2006

Appendix B:

Aday, D. Derek, David P. Philipp, and David H. Wahl. 2006. Sex-specific life history patterns in bluegill (*Lepomis macrochirus*): interacting mechanisms influence individual body size. Oecologia 147: 31-38.

Appendix C:

Claussen, Julie. E., John Hoxmeier, D. Derek Aday, David H. Wahl, and David P. Philipp. (In review) What Controls the Size Structure of Bluegill Populations? Transactions of the American Fisheries Society.

REFERENCES

Aday, D.D., J.E. Claussen, J.H. Hoxmeier, T.E. Edison, D.H. Wahl, D.P. Philipp. 1999. Quality managment of bluegill: factors influencing population size structure. Illinois Natural History Survey Technical Report.

Aday, D.D., C.M. Kush, D.H. Wahl, and D.P. Philipp. 2002. The influence of stunted body size on the reproductive ecology of bluegill, *Lepomis macrochirus*. Ecology of Freshwater Fish 11:190-195.

Aday, D.D., D.H. Wahl, D.P. Philipp 2001a. Genetic and environmental contributions to variation in life history strategies of bluegill. Oecologia. In review.

Aday, D.D., J.H. Hoxmeier, D.H. Wahl. 2001b. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society. In review.

Aday, D. D., R. J. H. Hoxmeier, and D. H. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society 132: 47-56.

Aday, D.D., D.H. Wahl, and D.D. Philipp. 2003a. Assessing population-specific and environmental influences on bluegill life histories: a common-garden approach. Ecology 84:3370-3375.

Aday, D. D., D. H. Wahl, and D, P. Philipp. 2003b. A mechanism for social inhibition of sexual maturation in bluegill. Journal of Fish Biology 62: 486-490.

Aday, D. Derek, David P. Philipp, and David H. Wahl. 2006. Sex-specific life history patterns in bluegill (*Lepomis macrochirus*): interacting mechanisms influence individual body size. Oecologia 147: 31-38.

Anderson, D. R., K. P. Burnham, and W. L. Thompson 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Anderson, R.O. and S.J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283-300 *in* L.A. Neilsen and D.L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Bayley P.B., S.T. Sobaski, D.J. Austen 1993. The fisheries analysis system (FAS): creel survey and lake analysis. Aquatic Ecology Technical Report 93/7, Illinois Natural History Survey, Champaign, IL.

Bayley, P.B., S.T. Sobaski, M. Halter, D.J. Austen 1992. Comparison of creel surveys and the precision of their estimates. American Fisheries Symposium 12:206-211.

Beard, T.D. and T.E. Essington 2000. Effects of angling and life history processes on bluegill size structure: insights from an individual based model. Transactions of the American Fisheries Society 129: 561-568.

Belk, M.C. and L.S. Hales, Jr. 1993. Predation-induced differences in growth and reproduction of bluegills (Lepomis macrochirus). Copeia 1993: 1034-1044.

Benjamin, D. M., R. A. Illyes, T. Kassler, and D. P. Philipp. 2000. Database management and analysis of fisheries in Illinois. Annual Progress Report, Illinois Natural History Survey, Champaign, IL.

Borowsky, R.L. 1978. Social inhibition of maturation in natural populations of Xiphophoris variatus (Pisces: Poeciliidae). Science 201:933-935.

Burnham, K.P. and D.R. Anderson. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer Verlag, New York, NY.

Callahan, S.P., D.H. Wahl, and C.L. Pierce. 1996. Growth of bluegill, largemouth bass, and channel catfish in relation to fish abundances, food availability, and other limnological variables. Trans. Am. Fish. Soc. (in review).

Chapman, L.J., D.L. Kramer, and C.A. Chapman. 1991. Population dynamics of the fish Poecilia gillii (Poeciliidae) in pools of an intermittent tropical stream. J. of An. Ecol. 60:441-453.

Claussen, J.C. 1991. Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. M.S. Thesis, U. Toronto.

Claussen, J.E., D.D. Aday, J.H. Hoxmeier, J.L. Kline, D.H. Wahl, and D.P. Philipp. 1999. Quality management of bluegill: factors affecting population size structure. Aquatic Ecology Technical Report 99/1, Illinois Department of Natural Resources, Champaign, IL.

Claussen, Julie. E., John Hoxmeier, D. Derek Aday, David H. Wahl, and David P. Philipp. (In review) What Controls the Size Structure of Bluegill Populations? Transactions of the American Fisheries Society.

Coble, D.W. 1988. Effects of angling on bluegill populations: management implications. North American Journal of Fisheries Management 8:277-283.

Dettmers, J. M., and R. A. Stein. 1992. Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. Transactions of the American Fisheries Society 121:494-507.

DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic Sciences 49:1216-1227.

DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483-512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Diana, M.J., J. Stein, J.W. Hoxmeier, R.W. Oplinger, J.E. Clausen, D.H. Wahl, D.P. Phillip. 2005. Quality Management of Bluegill: Factors affecting Population Size Structure. Division of Fisheries, Illinois Department of Natural Resources, Federal Aid in Fish Restoration, F-128-R, Annual Report.

Drake, M.T., J.E. Claussen, D.P. Philipp, and D.L. Pereira. 1997. A comparison of bluegill reproductive strategies and growth among lakes with different fishing intensities. North American Journal of Fisheries Management 17: 496-507.

Fox, M.G. and A. Keast. 1991. Effect of overwinter mortality on reproductive life history characteristics of pumpkinseed (Lepomis gibbosus) populations. Can. J. Fish. Aqu. Sci. 48:1792-1799.

Gabelhouse, D.W., Jr. 1984. A length categorization system to assess fish stocks. North American Journal of Fisheries Management 4:273-283.

Gardner, M. B. 1981. Effects of turbidity on feeding rates and selectivity of bluegills. Transactions of the American Fisheries Society 110:446-450.

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

Gross, M.R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Z. Tierpsychol 60: 1-26.

Gross, M.R. and E.L. Charnov 1980. Alternative male life histories in bluegill sunfish. Proc. Natl. Acad. Sci. 77: 6937-6940.

Hoxmeier, R.J.H., D.D. Aday, and D.H.Wahl. 2001. Factors influencing precision of age estimation from scales and otoliths of bluegills in Illinois reservoirs. North American Journal of Fisheries Management 21:374-380.

Jennings, M.J. 1991. Sexual selection, reproductive strategies and genetic variation in the longear sunfish (Lepomis megalotis). Ph.D. dissertation, University of Illinois, Urbana.

Jennings, M.J. and D.P. Philipp. 1992. Reproductive investment and somatic growth in longear sunfish. Envir. Biol. of Fish 35:257-271.

Jennings, M.J., J.E. Claussen and D.P. Philipp. 1997. Effect of population size structure on reproductive investment among male bluegill. North American Journal of Fisheries Management 17: 516-524.

Justus, J.A., and M.G. Fox. 1994. The cost of early maturation on growth, body condition, and somatic lipid content in a lake pumpkinseed (*Lepomis gibbosus*) population. Ecology of Freshwater Fish **3**:9-17.

McCauley, R. W., and D. M. Kilgour. 1990. Effect of air temperature on growth of largemouth bass in North America. Transactions of the American Fisheries Society 119:276-281.

Miner, J.G. and R.A. Stein. 1993. Interactive influence of turbidity and light on larval bluegill (*Lepomis macrochirus*) foraging. Canadian Journal of Fisheries and Aquatic Sciences 50:781-788.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

Mittelbach, G.G. 1986. Predator-mediated habitat use: some consequences for species interactions. Env. Bio. Fish. 16:159-169.

Mitzner, L. 1998. Assessment of the impact of physical, chemical, and biological factors and angling upon bluegill and crappie populations. Federal Aid to Fish Restoration Annual Report Mississippi River Investigations Project No. F-160-R.

Nibblink, N.P. and S.R. Carpenter. 1998. Interlake variation in growth and size structure of bluegill (Lepomis macrochirus): inverse analysis of an individual-based model. Canadian Journal of Fisheries and Aquatic Sciences 55:387-396.

Olson, D.E., and P.K. Cunningham. 1989. Sport-fisheries trends shown by an annual Minnesota fishing contest over a 58-year period. North American Journal of Fisheries Management 9: 287-297.

Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179-190.

Philipp, D.P. and M.R. Gross. 1994. Genetic evidence for cuckoldry in bluegill Lepomis macrochirus. Molecular Ecology 3:563-569.

Putman, J. H., C. L. Pierce, and D. M. Day. 1995. Relationships between environmental variables and size-specific growth rates of Illinois stream fishes. Transactions of the American Fisheries Society 124: 252-261.

Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64:862-873.

Salant, P. and D. A. Dillman. 1994. How to conduct your own survey. John Wiley & Sons, Inc. United States of America pp. 54-8.

Silverman, H.I. 1978. The effects of visual stimulation upon age at first spawning in the mouth-brooding cichlid fish Sarotherodon (Tilapia) mossambicus (Peters). An. Beh. 26:1120-1125.

Snow, H. E. and M. D. Staggs. 1994. Factors related to fish growth in northwestern Wisconsin lakes. Wisconsin Department of Natural Resources Research Report 162.

Sobaski, S.T., P.J. Perea, P.B. Bayley, and D.P. Philipp. 1995. Data Base Management and Analysis of Fisheries in Illinois Lakes: Optimizing Fisheries Management (F-69-R-8). Aquatic Ecology Technical Report 95/14, Illinois Natural History Survey, Champaign, IL.

Stearns, S.C. and J. A. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893-913.

Stein, R.A., D.R. DeVries, and J. M. Dettmers. 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. 1950. Relationships and dynamics of balanced and unbalanced fish populations. Alabama Polytechnic Institute, Agricultural Experiment Station Bulletin 274, Auburn.

Theiling, C. H. 1990. The relationships between several limnological factors and bluegill growth in Michigan lakes. Michigan Department of Natural Resources, Fisheries Research Report 1970, Ann Arbor.

Tomcko, C.M. and R.B. Pierce. 2001. The relationship between bluegill growth, lake morphometry, and water quality in Minnesota. Transactions of the American Fisheries Society 130:317-321.

Welker, M.T., C.L. Pierce, and D.H. Wahl. 1994. Growth and survival of larval fishes: roles of competition and zooplankton abundance. Transactions of the American Fisheries Society 123:703-717.

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

Wootton, R.J. 1985. Energetics of reproduction. pp. 231-254 in P.Tyler and P. Callow (eds) Fish Energetics: New Perspectives. Johns Hopkins University Press, Baltimore, M

Table 1-1: Experimental management lakes, controlling for region (north, south), lake size (large, small), and population size structure (quality, stunted). Treatments include control, restrictive regulation (8 inch minimum size limit, 10 fish creel limit), predator stocking, and combination of restrictive regulation and predator stocking.

Type	Region	Lake Size	Control	Regulation	Predator Stocking	Regulation/Predator Stocking
Quality	North	Large	Apple Canyon	Busse South	Spring Lake South	Bloomington
	North	Small	Siloam Springs	Walnut Point	Woods	Kakusha
	South	Large	Lincoln Trail	Mermet	Murphysboro	Forbes
	South	Small	Glendale	Red Hills	Sam Parr	Homer
Stunted	North	Large	Round	Tampier	Spring Lake North	Pierce
	North	Small	Sterling	Lake of the Woods	Le-Aqua-Na	Bullfrog
	South	Large	Paris	Pana	Mingo	Jacksonville
	South	Small	Hillsboro	Dolan	Mcleansboro	Walton Park

Table 1-2. Angler CPUE, CPUA, and mean TL(mm) from creel surveys conducted before and after experimental treatments.

Lake	Treatment	Quality/Stunted	Pre-Treatment				Post Treatment			
			Year	CPUE	CPUA	TL(mm)	Year	CPUE	CPUA	TL(mm)
Apple Canyon	Control	Q	2000	0.806	171.98	173	2005	1.185	180.86	190
Glendale	Control	Q	1999	0.828	103.82	138	2003	0.313	52.52	147
Lincoln Trail	Control	Q	1996	0.089	13.93	175	2004	0.629	158.14	173
Siloam Springs	Control	Q	1997	0.279	129.29	145	2005	0.342	92.08	178
Hillsboro	Control	S	1999	0.158	19.40	135	2003	0.261	28.69	149
Paris East	Control	S	1999	0.438	68.03	143	2004	0.473	66.69	145
Round	Control	S	1999	0.227	13.86	151	2004	0.419	25.38	151
Sterling	Control	S	2000	0.212	77.58	127	2003	0.154	66.14	129
Murphysboro	Stocking	Q	2000	0.642	83.36	156	2004	0.535	73.77	139
Sam Parr	Stocking	Q	1997	1.671	481.15	154	2005	0.341	84.92	184
Spring Lake South	Stocking	Q	1996	0.319	40.42	158	2005	1.369	106.95	153
Woods	Stocking	Q	2000	0.473	89.28	201	2003	0.142	66.29	121
Le-Aqua-Na	Stocking	S	1994	0.147	110.85	165	2004	0.467	332.47	147
McLeansboro	Stocking	S	1999	0.094	10.53	166	2003	0.305	58.30	158
Mingo	Stocking	S	1999	0.393	93.14	143	2003	0.457	126.84	142
Spring Lake North	Stocking	S	1999	1.948	135.45	137	2004	0.659	24.36	129
Busse	Regulation	Q	1989	0.100	52.88	141	2004	0.380	104.94	153
Mermet	Regulation	Q	1997	0.050	4.12	172	2004	0.725	34.76	180
Red Hills	Regulation	Q	2000	0.284	101.62	179	2003	0.479	197.46	163
Walnut Point	Regulation	Q	1997	0.308	112.59	151	2003	0.996	394.81	166
Dolan	Regulation	S	1998	0.388	128.21	138	2003	0.123	50.31	151
Lake of the Woods	Regulation	S	1998	0.817	819.72	121	2005	0.312	374.95	143
Pana	Regulation	S	1999	0.226	12.05	138	2005	0.569	27.19	146
Tampier	Regulation	S	1998	0.117	167.35	112	2004	0.172	99.55	128
Bloomington	Reg + Stock	Q	1996	0.286	24.72	167	2003	0.240	26.48	177
Forbes	Reg + Stock	Q	1999	0.470	44.98	153	2005	0.182	12.38	147
Homer	Reg + Stock	Q	1999	0.300	139.29	152	2003	0.522	192.68	145
Kakusha	Reg + Stock	Q	1998	0.137	39.67	172	2004	0.528	150.04	149
Bullfrog	Reg + Stock	S	1998	0.362	951.55	123	2005	0.752	573.16	138
Jacksonville	Reg + Stock	S	1999	0.304	11.62	130	2004	0.065	1.06	162
Pierce	Reg + Stock	S	1999	0.207	115.90	126	2003	0.382	170.49	140
Walton Park	Reg + Stock	S	1999	0.108	35.48	130	2004	0.186	122.60	109

Table 1-3. Changes in TL(mm), CPUE and CPUA between pre-treatment and post-treatment creel surveys on each experimental lake.

Lake	Treatment	Quality/Stunted	TL(mm)	CPUE	CPUA
Glendale	Control	Q	9	-0.515	-51.30
Siloam Springs	Control	Q	33	0.063	-37.21
Apple Canyon	Control	Q	17	0.379	8.88
Lincoln Trail	Control	Q	-2	0.540	144.21
Sterling	Control	S	2	-0.058	-11.44
Paris East	Control	S	2	0.035	-1.34
Hillsboro	Control	S	14	0.103	9.29
Round	Control	S	0	0.192	11.52
Sam Parr	Stocking	Q	30	-1.330	-396.23
Woods	Stocking	Q	-80	-0.331	-22.99
Murphysboro	Stocking	Q	-17	-0.107	-9.59
Spring Lake South	Stocking	Q	-5	1.050	66.53
Spring Lake North	Stocking	S	-8	-1.289	-111.09
Mingo	Stocking	S	-1	0.064	33.70
McLeansboro	Stocking	S	-8	0.211	47.77
Le-Aqua-Na	Stocking	S	-18	0.320	221.62
Red Hills	Regulation	Q	-16	0.195	95.84
Busse	Regulation	Q	12	0.280	52.06
Mermet	Regulation	Q	8	0.675	30.64
Walnut Point	Regulation	Q	15	0.688	282.22
Lake of the Woods	Regulation	S	22	-0.505	-444.77
Dolan	Regulation	S	13	-0.265	-77.90
Tampier	Regulation	S	16	0.055	-67.80
Pana	Regulation	S	8	0.343	15.14
Forbes	Reg + Stock	Q	-6	-0.288	-32.60
Bloomington	Reg + Stock	Q	10	-0.046	1.76
Homer	Reg + Stock	Q	-7	0.222	53.39
Kakusha	Reg + Stock	Q	-23	0.391	110.37
Jacksonville	Reg + Stock	S	32	-0.239	-10.56
Walton Park	Reg + Stock	S	-21	0.078	87.12
Pierce	Reg + Stock	S	14	0.175	54.59
Bullfrog	Reg + Stock	S	15	0.390	-378.39

Table 1-4. Changes in TL(mm), CPUE, and CPUA between pre-treatment and post-treatment creel surveys for each experimental treatment.

Treatment	Change Between Pre/Post Treatment		
	TL(mm)	CPUE	CPUA
Control	9.4	0.092	9.08
Regulation	9.8	0.183	-14.32
Stocking	-13.4	-0.177	-21.29
Regulation & Stocking	1.8	0.085	-14.29

Table 1-5. PQBG.170 values from creel surveys conducted before and after experimental treatments.

Lake	Treatment	Quality/ Stunted	Pre Treatment		Post Treatment	
			Year	PQBG.170	Year	PQBG.170
Apple Canyon	Control	Q	2000	36.4	2005	59.3
Glendale	Control	Q	1999	24.8	2003	17.2
Lincoln Trail	Control	Q	1996	6.8	2004	12.4
Siloam Springs	Control	Q	1997	28.9	2005	34.8
Hillsboro	Control	S	1999	6.7	2003	28.2
Paris East	Control	S	1999	16.8	2004	12.0
Round	Control	S	1999	23.5	2004	21.0
Sterling	Control	S	2000	2.3	2003	3.3
Murphysboro	Stocking	Q	2000	26.2	2004	13.0
Sam Parr	Stocking	Q	1997	29.8	2005	53.2
Spring Lake South	Stocking	Q	1996	30.3	2005	18.0
Woods	Stocking	Q	2000	67.5	2003	0.5
Le-Aqua-Na	Stocking	S	1994	50.0	2004	45.5
McLeansboro	Stocking	S	1999	44.2	2003	33.6
Mingo	Stocking	S	1999	6.1	2003	8.1
Spring Lake North	Stocking	S	1999	18.0	2004	5.8
Busse	Regulation	Q	1989	3.9	2004	26.0
Mermet	Regulation	Q	1997	50.3	2004	42.4
Red Hills	Regulation	Q	2000	51.8	2003	39.1
Walnut Point	Regulation	Q	1997	30.4	2003	43.3
Dolan	Regulation	S	1998	10.2	2003	12.4
Lake of the Woods	Regulation	S	1998	45.9	2005	21.5
Pana	Regulation	S	1999	6.6	2005	12.1
Tampier	Regulation	S	1998	2.4	2004	4.8
Bloomington	Reg + Stock	Q	1996	74.7	2003	57.9
Forbes	Reg + Stock	Q	1999	19.6	2005	10.4
Homer	Reg + Stock	Q	1999	23.8	2003	11.0
Kakusha	Reg + Stock	Q	1998	61.4	2004	18.0
Bullfrog	Reg + Stock	S	1998	3.6	2005	5.1
Jacksonville	Reg + Stock	S	1999	3.5	2004	30.4
Pierce	Reg + Stock	S	1999	6.0	2003	8.7
Walton Park	Reg + Stock	S	1999	1.9	2004	0.9

Table 2-1: Ranking of regression models predicting growth of bluegill to age 4 and bluegill size structure index RSD 180. Explanatory variables in the regression models include prey abundance (prey), average summer air temperature (temp), age at maturity (mat), number of bluegill per hour of electrofishing (cpue), number of bluegill harvested per acre (harv), and secchi depth (secc). Corrected Akaike's Information Criterion (AIC_c), difference in AIC_c between the *i*th and the top-ranked model (Δ_i), Akaike weights (w_i), and adjusted model R^2 values for the 95% confidence set of models based on Akaike weights.

Model	AIC_c	Δ_i	w_i	R^2
Age 4				
temp, secc, prey, mat	122.62	0.00	0.19	0.57
temp, secc, prey	122.73	0.10	0.18	0.51
temp, secc	123.79	1.17	0.10	0.41
temp, secc, mat	124.41	1.79	0.08	0.47
temp, prey	124.49	1.87	0.07	0.39
temp, secc, harv	125.35	2.73	0.05	0.45
temp, secc, prey, harv	125.65	3.03	0.04	0.51
temp, secc, prey, cpue	125.95	3.33	0.04	0.51
temp, prey, mat	125.96	3.33	0.03	0.43
temp, secc, prey, mat, harv	126.26	3.64	0.03	0.58
temp	126.33	3.71	0.03	0.26
temp, secc, prey, cpue, mat	126.33	3.71	0.03	0.57
temp, secc, mat, harv	126.73	4.11	0.02	0.49
temp, secc, cpue	126.75	4.13	0.02	0.41
temp, prey, harv	126.96	4.34	0.02	0.41
temp, prey, cpue	127.17	4.54	0.02	0.40
temp, secc, cpue,mat	127.67	5.04	0.01	0.47
temp, secc,cpue, harv	128.66	6.04	0.01	0.45
temp, prey, mat, harv	129.01	6.39	0.01	0.44
temp, prey, cpue, mat,	129.07	6.45	0.01	0.44
temp, secc, prey, cpue, harv	129.29	6.66	0.01	0.52
temp, secc, cpue, mat, harv	130.42	7.80	0.00	0.49
temp, secc, prey, cpue, mat, harv	130.46	7.84	0.00	0.58
RSD 180				
age5	96.82	0.00	0.35	0.37
age2, age5	98.12	1.30	0.18	0.41
age5, harv	98.56	1.74	0.15	0.40
age5, mat	99.32	2.49	0.10	0.38
age2, age5, harv	100.21	3.39	0.06	0.43
age2, age5, mat,	101.06	4.24	0.04	0.41
age5, mat, harv	101.40	4.58	0.04	0.40
harv	101.49	4.67	0.03	0.23

Table 2-2: Parameter likelihoods and model-averaged parameter estimates (β) for explanatory variables included in the 95% confidence set of candidate models.

Variable	N w_i	β
	Age 4	
Temperature	1.00	4.64
Secchi	0.81	35.07
Prey	0.67	10.11
Maturity	0.42	-33.70
CPUE	0.15	-0.22
Harvest	0.19	0.53
	RSD 180	
Age 5	0.96	0.31
Age 2	0.30	-0.04
Harvest	0.29	6.22
Maturity	0.19	1.80

Table 2-3: Best-fit size specific growth function, function type (linear, quadratic cubic, or log-linear), and r^2 of the best-fit function for the 16 lakes from which size-specific growth rates were calculated. The size-specific growth increment at 50, 75, 100, 125, and 150 mm TL are also shown. These size-specific growth increments were related to lake environmental parameters using AIC. In the equations shown in the table, Y is the estimated growth (mm) for a fish in the next year that begins the year at a specified total length (x).

Lake	Formula	50 mm	100 mm	150 mm	Type	r^2
Apple Canyon	$Y = -0.000037x^3 + 0.0099x^2 - 0.609x + 45.072$	34.75	46.17	51.60	Cubic	0.27
Dolan	$Y = -0.41278x + 81.595$	60.96	40.32	19.68	Linear	0.87
Forbes	$Y = -0.386x + 68.401$	49.10	29.80	10.50	Linear	0.78
Homer	$Y = -0.251x + 59.816$	47.27	34.72	22.17	Linear	0.75
Kakusha	$Y = 63.3209x^{-0.002796}$	62.63	62.51	62.44	Log-Linear	0.67
Lake of the Woods	$Y = 0.0019x^2 - 0.519x + 56.950$	43.67	29.19	19.47	Quadratic	0.75
LeAquaNa	$Y = 0.00095x^2 - 0.432x + 62.894$	35.75	24.05	21.85	Quadratic	0.78
Lincoln Trail	$Y = -0.186x + 61.043$	51.74	42.44	33.14	Linear	0.43
Mingo	$Y = -0.32584x + 58.168$	41.88	25.58	9.29	Linear	0.77
Murphysboro	$Y = 0.00152x^2 - 0.61055x + 68.987$	42.26	23.13	11.60	Quadratic	0.90
Paris	$Y= 0.0015x^2 - 0.671x + 76.617$	46.82	24.52	9.72	Quadratic	0.92
Pierce	$Y = 0.0007x^2 - 0.381x + 59.326$	42.03	28.23	17.93	Quadratic	0.77
Red Hills	$Y = -0.00079x^2 - 0.140x + 62.530$	53.56	40.63	23.76	Quadratic	0.58
Sterling	$Y = 0.003177x^2 - 0.7804x + 66.159$	35.08	19.89	20.58	Quadratic	0.85
Walnut Point	$Y = -0.00323x^2 + 0.331x + 59.198$	67.67	60.00	36.17	Quadratic	0.48
Wood	$Y = -0.4674x + 71.051$	47.68	24.31	0.94	Linear	0.87

Table 2-4: The AIC$_c$ value, ΔAIC$_c$, and Akaike Weight of each model tested to predict size specific growth for bluegill at 50, 100, and 150 mm TL. Shaded models (ΔAIC$_c$ < 2.0) have the strongest influence on the size specific growth of bluegill at each size. Z-age refers to the average age of maturation of male bluegill, zp = zooplankton density, temp = temperature, and benthos = benthic invertebrate density.

50 mm

Model Name	AICc	ΔAIC	weight	r^2	p
Z-Age	32.69	0.00	0.49	0.39	<0.01
Shad + Secchi	34.21	1.52	0.23	0.71	<0.01
ZP	36.79	4.10	0.06	0.30	0.03
Secchi	37.75	5.06	0.04	0.19	0.09
Shad	38.28	5.59	0.03	0.13	0.17
Temp	38.55	5.85	0.03	0.09	0.25
LMB	38.90	6.21	0.02	0.05	0.42
# harvested/acre	39.19	6.49	0.02	0.01	0.76
BGL	39.21	6.52	0.02	0.00	0.83
Benthos	39.22	6.53	0.02	0.00	0.90
Secchi + ZP	40.00	7.31	0.01	0.35	0.06
Shad + ZP	40.00	7.31	0.01	0.33	0.07
Temp + Secchi	41.21	8.52	0.01	0.21	0.21
Shad + Benthos	41.90	9.21	0.00	0.13	0.40
Global	104.25	71.56	0.00	0.88	0.03

100 mm

Model Name	AICc	ΔAIC	weight	r^2	p
Shad + Secchi	36.63	0.00	0.34	0.77	<0.01
Shad	36.80	0.16	0.32	0.60	<0.01
Shad + ZP	38.63	2.00	0.13	0.69	<0.01
Shad + Benthos	40.29	3.66	0.06	0.61	<0.01
ZP	40.98	4.35	0.04	0.27	0.04
# harvested/acre	42.37	5.73	0.02	0.11	0.21
Benthos	42.72	6.09	0.02	0.06	0.34
LMB	42.80	6.17	0.02	0.05	0.39
Z-Age	43.07	6.43	0.01	0.01	0.06
BGL	43.10	6.47	0.01	0.01	0.69
Temp	43.11	6.48	0.01	0.01	0.71
Secchi	43.13	6.49	0.01	0.01	0.75
Secchi + ZP	43.55	6.92	0.01	0.38	0.05
Temp + Secchi	46.73	10.10	0.00	0.01	0.91
Global	110.75	74.11	0.00	0.83	0.08

150 mm

Model Name	AICc	ΔAIC	weight	r^2	p
Shad	38.86	0.00	0.48	0.65	<0.01
Shad + Benthos	41.14	2.28	0.15	0.71	<0.01
Shad + ZP	42.22	3.36	0.09	0.66	<0.01
Shad + Secchi	42.45	3.59	0.08	0.65	<0.01
Temp	44.66	5.80	0.03	0.19	0.10
Benthos	44.76	5.91	0.03	0.17	0.11
Secchi	44.84	5.98	0.02	0.16	0.12
LMB	45.07	6.21	0.02	0.14	0.16
ZP	45.16	6.30	0.02	0.13	0.18
Secchi + ZP	45.17	6.31	0.02	0.48	0.01
# harvested/acre	45.23	6.37	0.02	0.12	0.20
Z-Age	45.38	6.52	0.02	0.10	0.24
BGL	45.99	7.13	0.01	0.01	0.66
Temp + Secchi	47.72	8.87	0.01	0.25	0.15
Global	114.08	75.23	0.00	0.82	0.09

Table 3-1: Pre and Post treatment values for male and female z-age and PQM 170 for each lake in the management experiment. Fish were collected through spring AC electrofishing and dissected for maturity status. Type refers to the pre experiment designation of quality (Q) or stunted (S) bluegill populations. Treatment is the experimental manipulation of the 8” 10 fish bag limit (Reg), largemouth bass stocking (Stock), a combination of stocking and regulation (RegStock), or control (Control).

Lake	Type	Treatment	Pre Treatment 1996			Post Treatment 2004		
			F Z-Age	M Z-Age	PQM 170	F Z-Age	M Z-Age	PQM170
Apple Canyon	Q	Control	2.91	3.76	0.57	3.46	3.91	0.61
Bloomington	Q	RegStock	2.63	3.48	0.35	2.12	3.20	0.17
Bullfrog	S	RegStock	2.21	3.38	0.00	2.79	3.43	0.00
Busse	Q	Reg	2.17	2.71	0.18	2.08	3.02	0.16
Dolan	S	Reg	2.04	3.23	0.21	2.19	2.83	0.02
Forbes	Q	RegStock	3.21	4.60	0.39	2.44	3.33	0.41
Glendale	Q	Control	2.73	4.18	0.94	2.86	3.5	0.67
Hillsboro	S	Control	2.15	3.19	0.24	2.43	3.19	0.21
Homer	Q	RegStock	2.57	3.29	0.12	2.33	3.59	0.16
Jacksonville	S	RegStock	2.42	3.54	0.08	2.87	4.34	0.00
Kakusha	Q	RegStock	2.31	3.21	0.41	3.07	3.43	0.67
Lake ot Woods	S	Reg	2.54	3.40	0.13	3.00	3.88	0.04
LeAquaNa	S	Stock	2.43	3.36	0.02	2.56	3.57	0.17
Lincoln Trail	Q	Control	2.66	3.67	0.94	2.85	3.65	0.95
McLeansboro	S	Stock	2.15	3.5	0.14	2.03	3.36	0.33
Mermet	Q	Reg	2.13	3.20	0.57	2.02	3.04	0.57
Mingo	S	Stock	2.93	3.85	0.17	2.60	3.42	0.19
Murphysboro	Q	Stock	2.41	3.04	0.71	2.23	3.76	0.00
Pana	S	Reg	2.38	3.56	0.00	2.29	4.23	0.00
Paris	S	Control	2.20	3.17	0.11	2.53	2.82	0.01
Pierce	S	RegStock	2.25	2.75	0.02	2.63	3.42	0.31
Red Hills	Q	Reg	2.31	3.80	0.90	2.42	3.54	0.71
Round	S	Control	2.40	3.2	0.04	3.28	3.88	0.04
Sam Parr	Q	Stock	2.27	2.96	0.56	2.68	3.26	0.62
Siloam Springs	Q	Control	3.50	4.21	0.98	3.13	3.86	0.96
Spring North	S	Stock	3.30	3.95	0.14	3.32	4.36	0.09
Spring South	Q	Stock	2.47	4.10	0.33	2.39	3.18	0.07
Sterling	S	Control	2.42	3.19	0.00	3.03	3.82	0.00
Tampier	S	Reg	2.46	2.85	0.00	2.05	2.62	0.03
Walnut Point	Q	Reg	2.24	3.26	0.62	2.43	3.04	0.88
Walton Park	S	RegStock	2.05	3.14	0.00	2.46	3.94	0.00
Woods	Q	Stock	2.85	4.29	0.39	1.97	2.97	0.00

Table 3-2: Total number of compliance checks and the percent of anglers checked that were compliant over the course of the study for all lakes in either the regulation or the stocking and regulation treatment.

Lake	Total # of Checks	Percent Compliant
Bloomington	41	88
Bullfrog	17	100
Busse	8	0
Dolan	39	85
Forbes	65	94
Homer	41	100
Jacksonville	19	53
Kakusha	13	100
Lake of the Woods	65	95
Mermet	15	93
Pana	6	100
Pierce	285	93
Red Hills	128	95
Tampier	14	100
Walnut Point	93	98
Walton Park	68	100

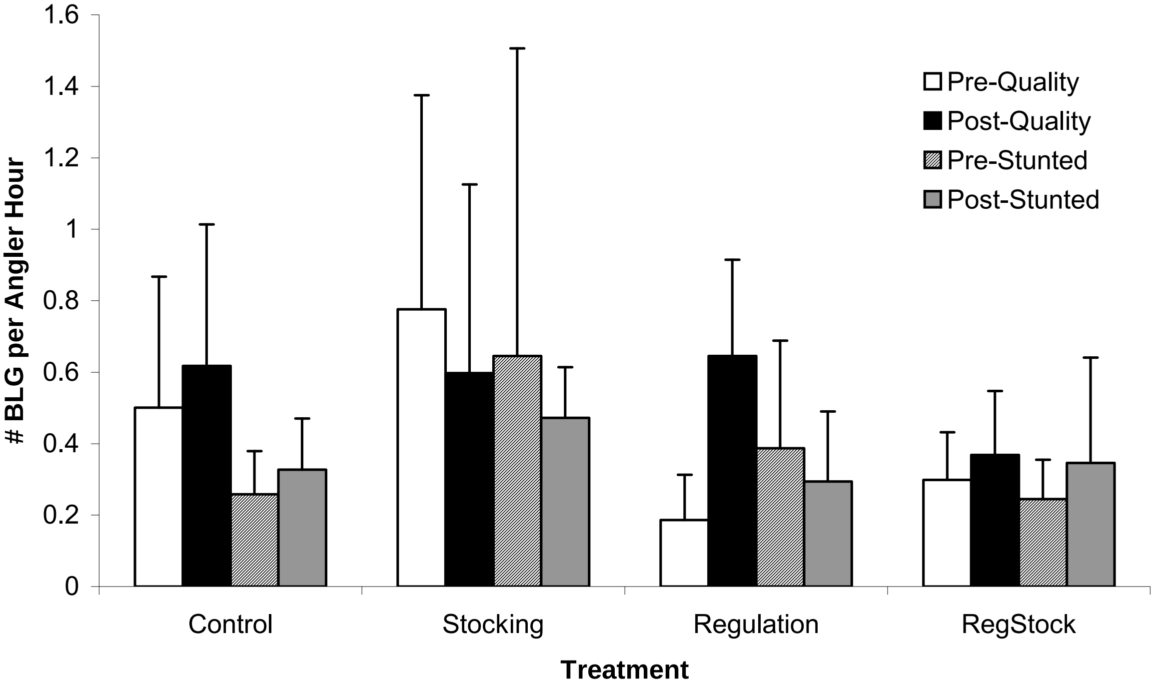


Figure 1-1. Comparison of treatment specific CPUE estimates from pre-treatment and post-treatment creel surveys. Error bars are 95% confidence limits (alpha = 0.05).

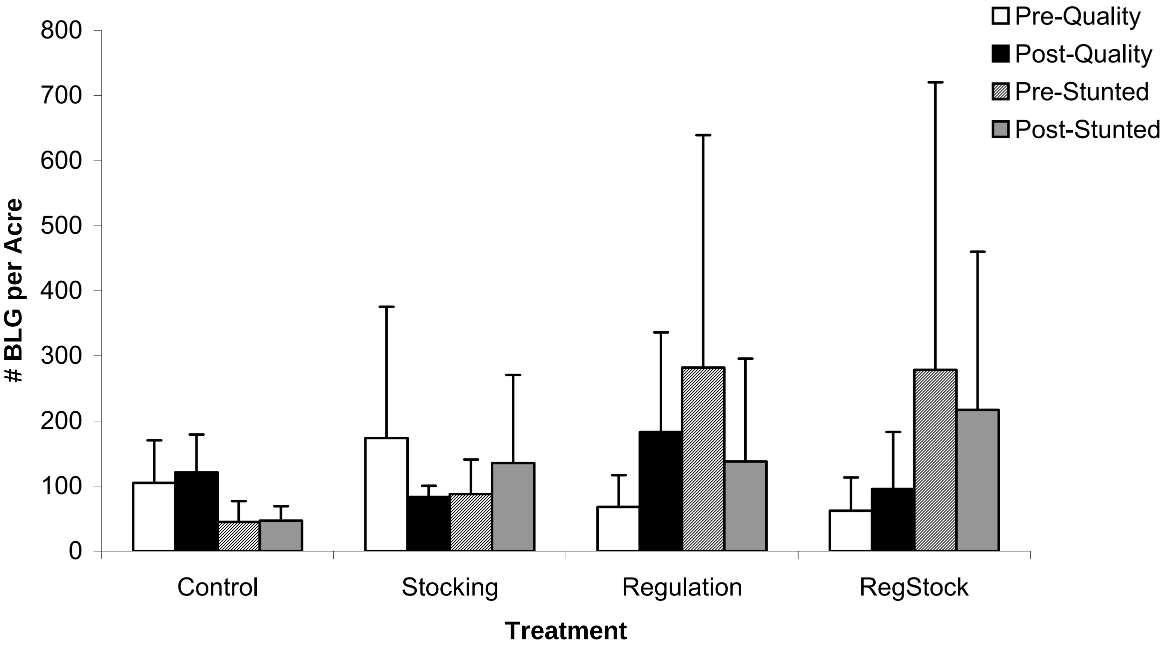


Figure 1-2. Comparison of treatment specific CPUA estimates from pre-treatment and post-treatment creel surveys. Error bars are 95% confidence limits (alpha = 0.05).

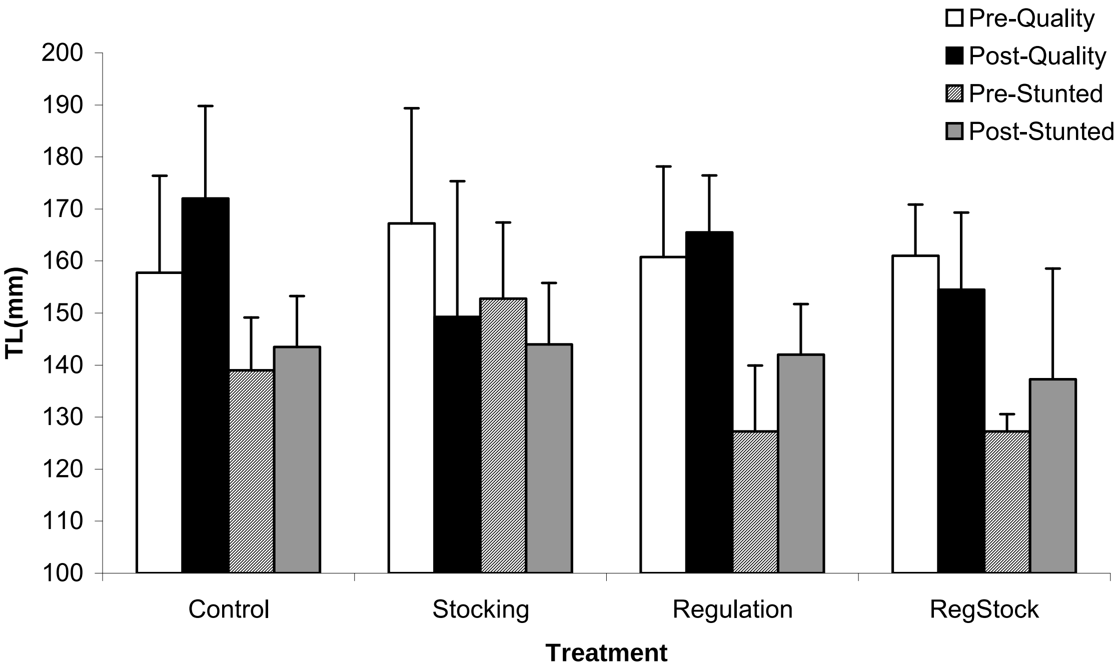


Figure 1-3. Comparison of treatment specific mean TL(mm) estimates from pre-treatment and post-treatment creel surveys. Error bars are 95% confidence limits (alpha = 0.05).

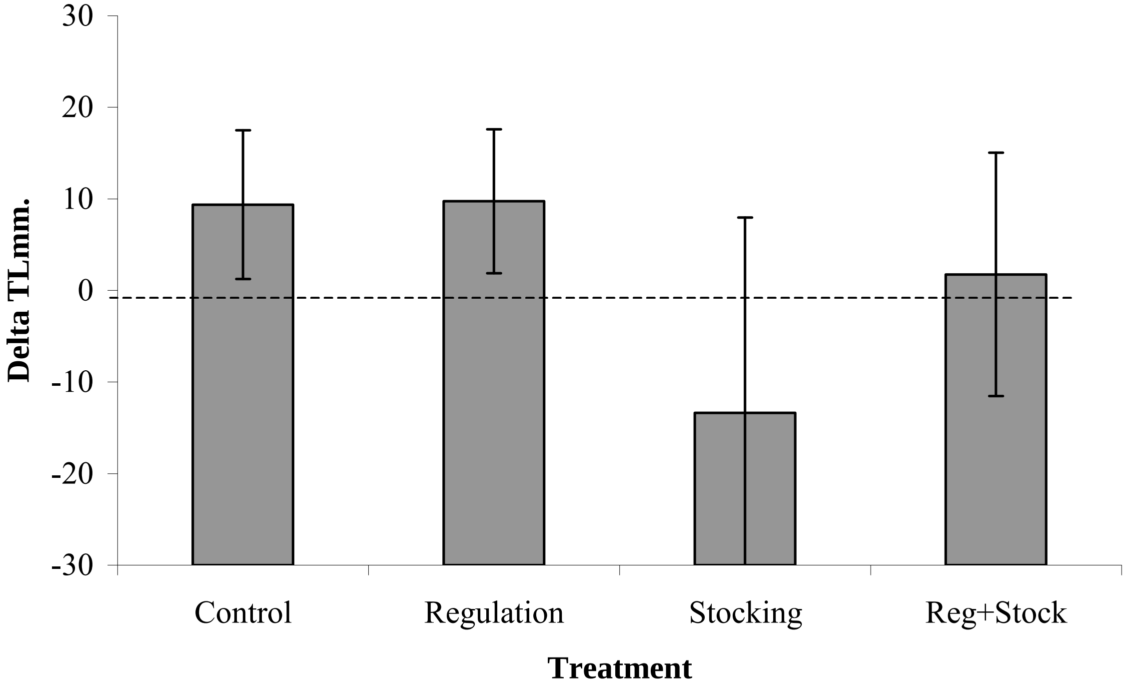


Figure 1-4. Differences in mean total length (TL) between pre-treatment and post-treatment creel surveys. Error bars are 95% confidence limits (alpha = 0.05).

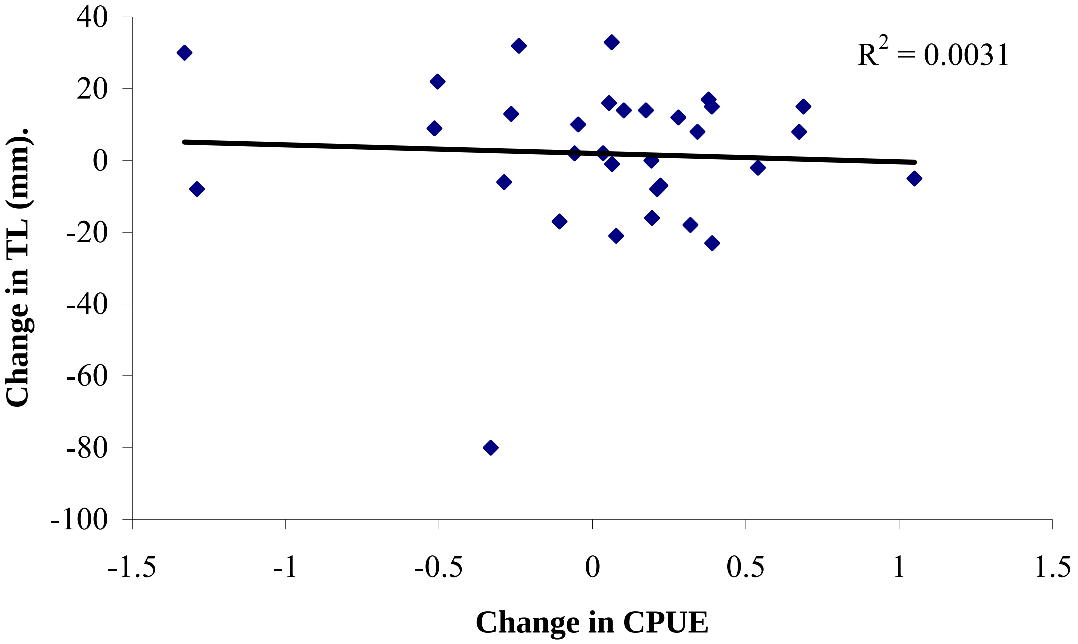


Figure 1-5. Correlation between changes in mean TL (mm) and CPUE from pre-treatment and post-treatment creel surveys.

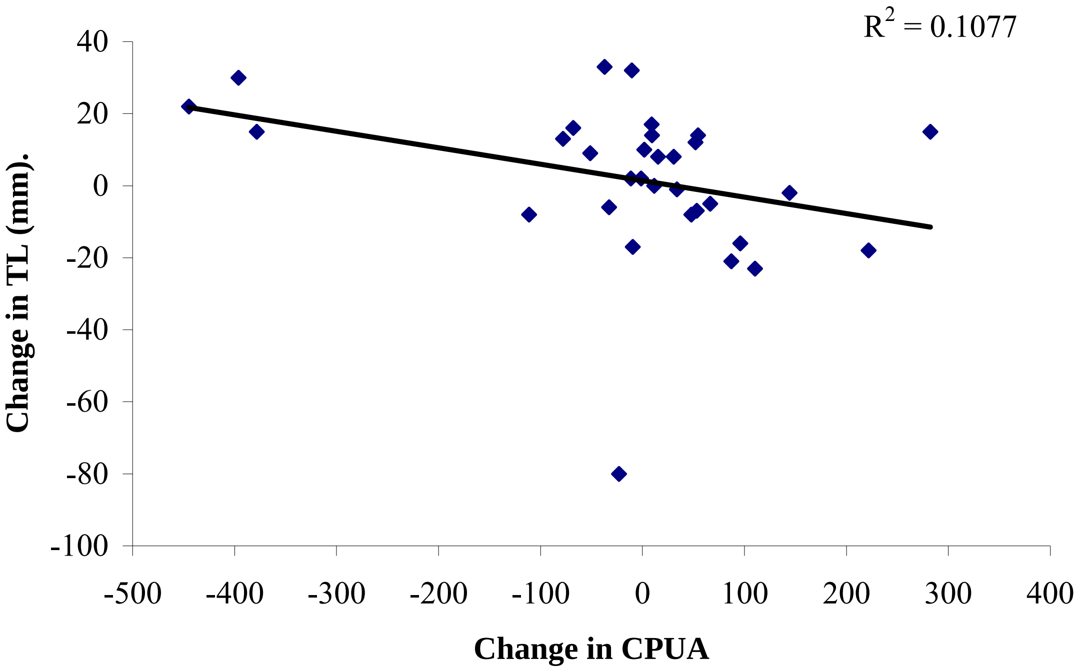


Figure 1-6. Correlation between changes in mean total length (mm) and CPUA from pre-treatment and post-treatment creel surveys.

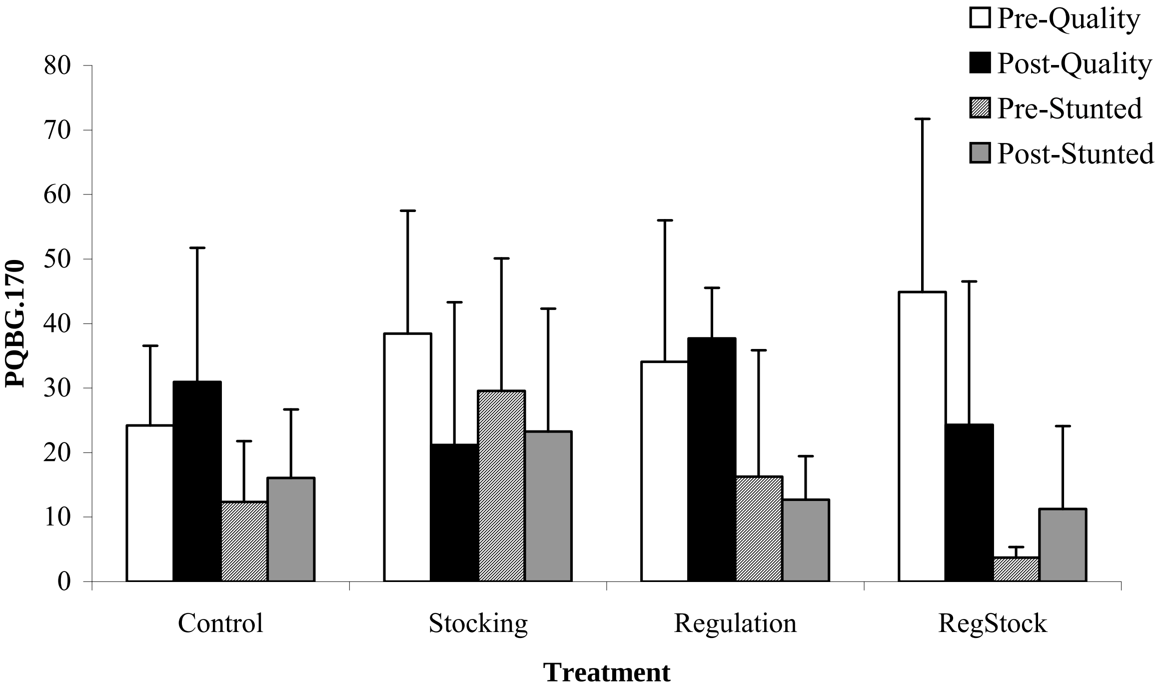


Figure 1-7. Comparison of treatment specific PQBG.170 estimates from pre-treatment and post-treatment creel surveys. Error bars are 95% confidence limits (alpha = 0.05).

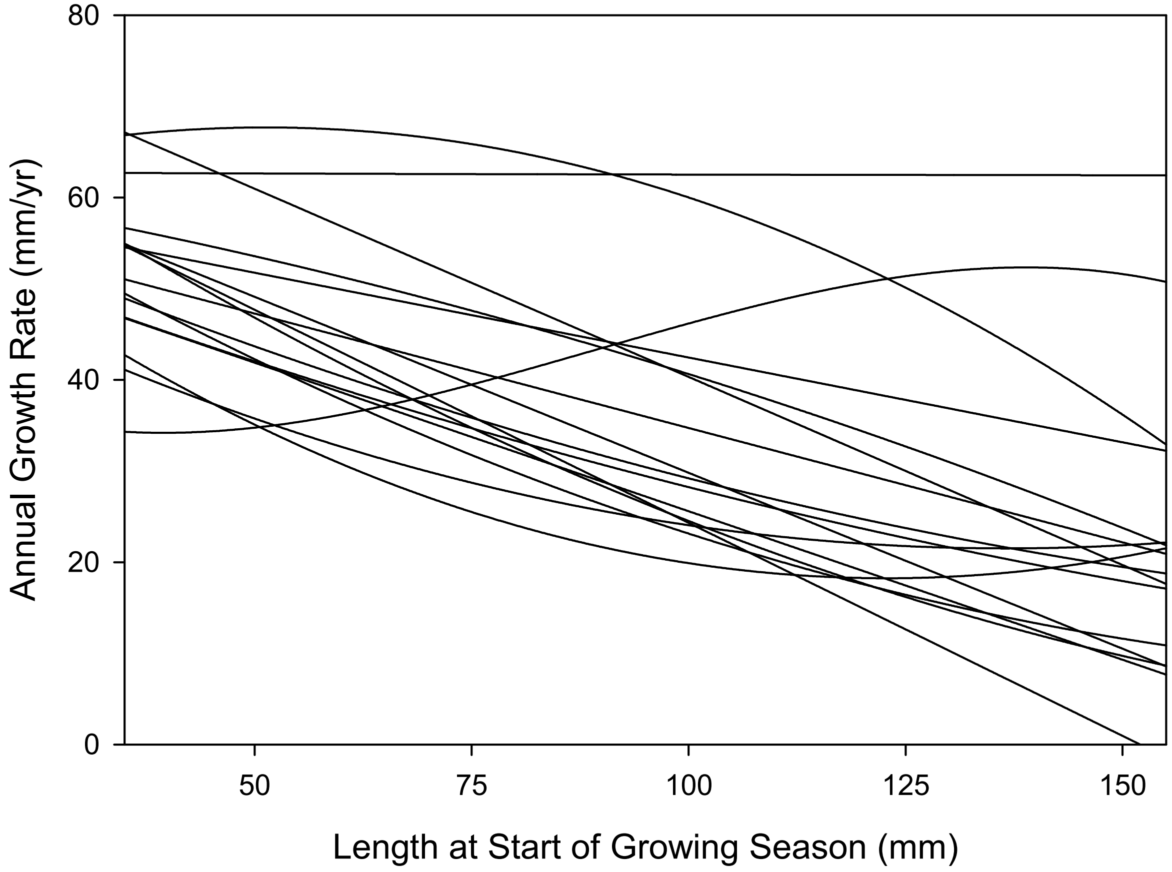


Figure 2-1: A plot showing the relationship between the length of a bluegill at the start of the growing season (mm) and the average amount of growth in the next year from 16 Illinois reservoirs. A sample of 50 fish was used from each reservoir. The figure shows that this relationship varies from reservoir to reservoir. The age of each fish was determined using otoliths and the radius to each annulus was measured using a computer digitizing tablet. The Fraser-Lee Method was used to backcalculate the growth of each fish to each annulus and regression was used to develop a formula that described the growth profile for each reservoir.

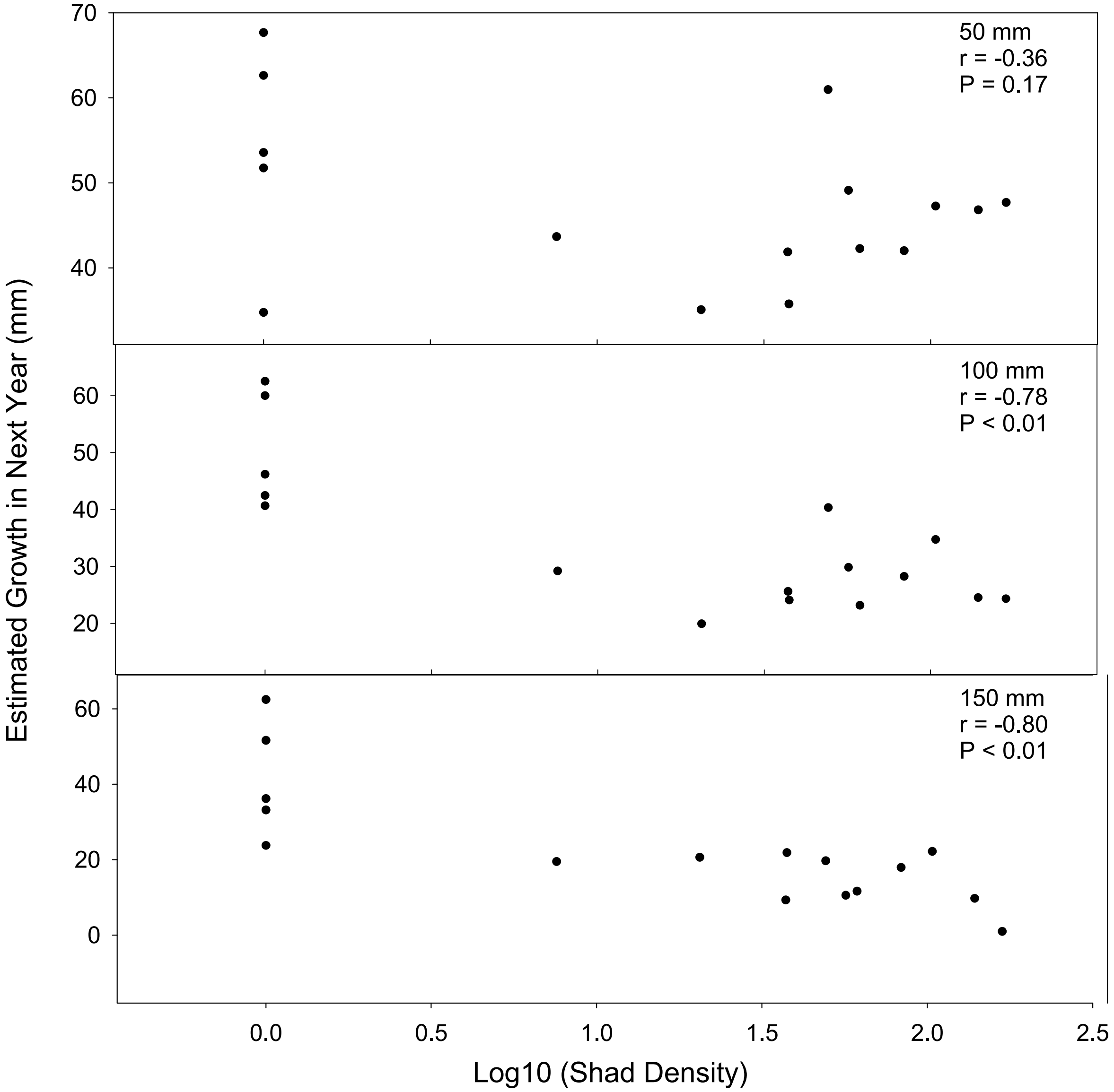


Figure 2-2: Relationship between the size specific growth of bluegill that start a year at either 50, 100, or 150 mm TL and gizzard shad density (Log transformed).

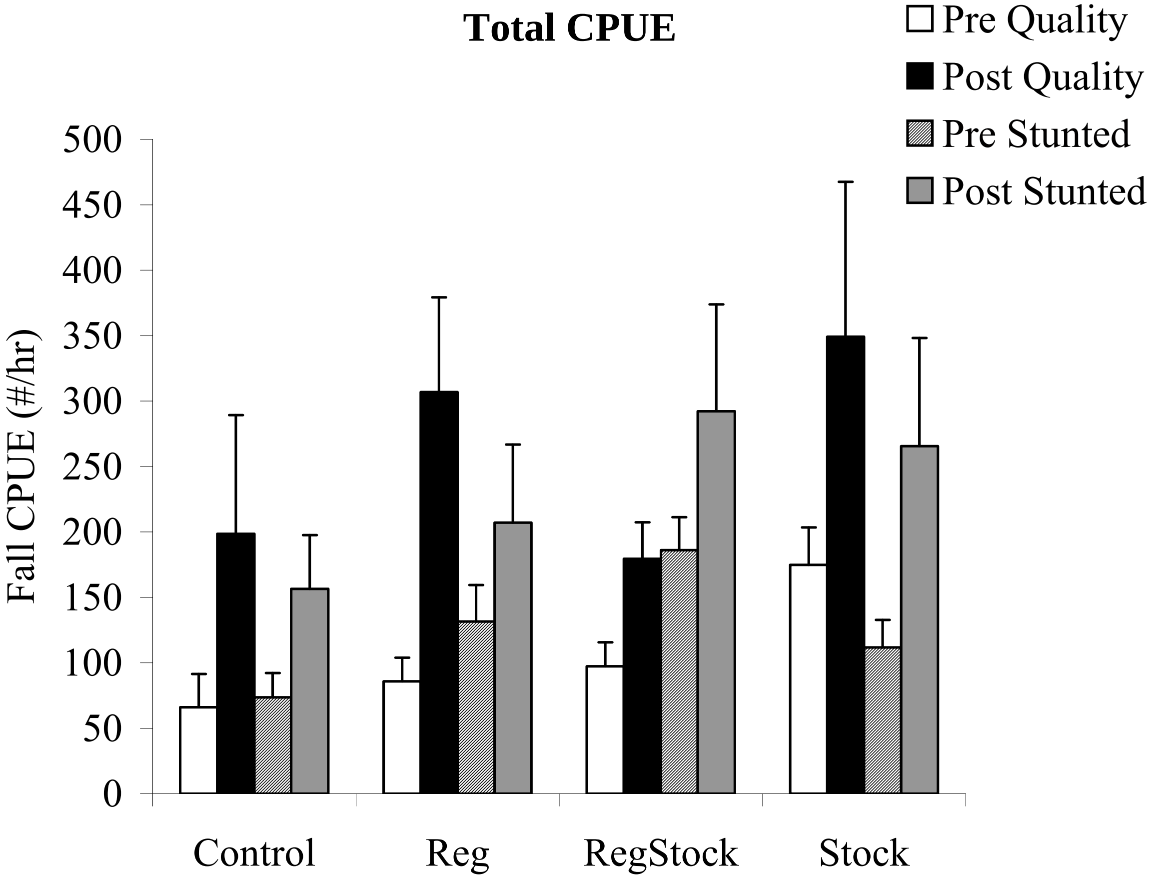


Figure 3-1: CPUE of all bluegill collected in fall electrofishing samples for each of the experimental treatments. Bars labeled pre are the means of electrofishing samples from 1997-2000 and the bars labeled post are the mean of 2003-2004. Quality refers to lakes designated as having quality bluegill populations at the beginning of the experiment and stunted were lakes with stunted bluegill populations. Error bars represent the standard error.

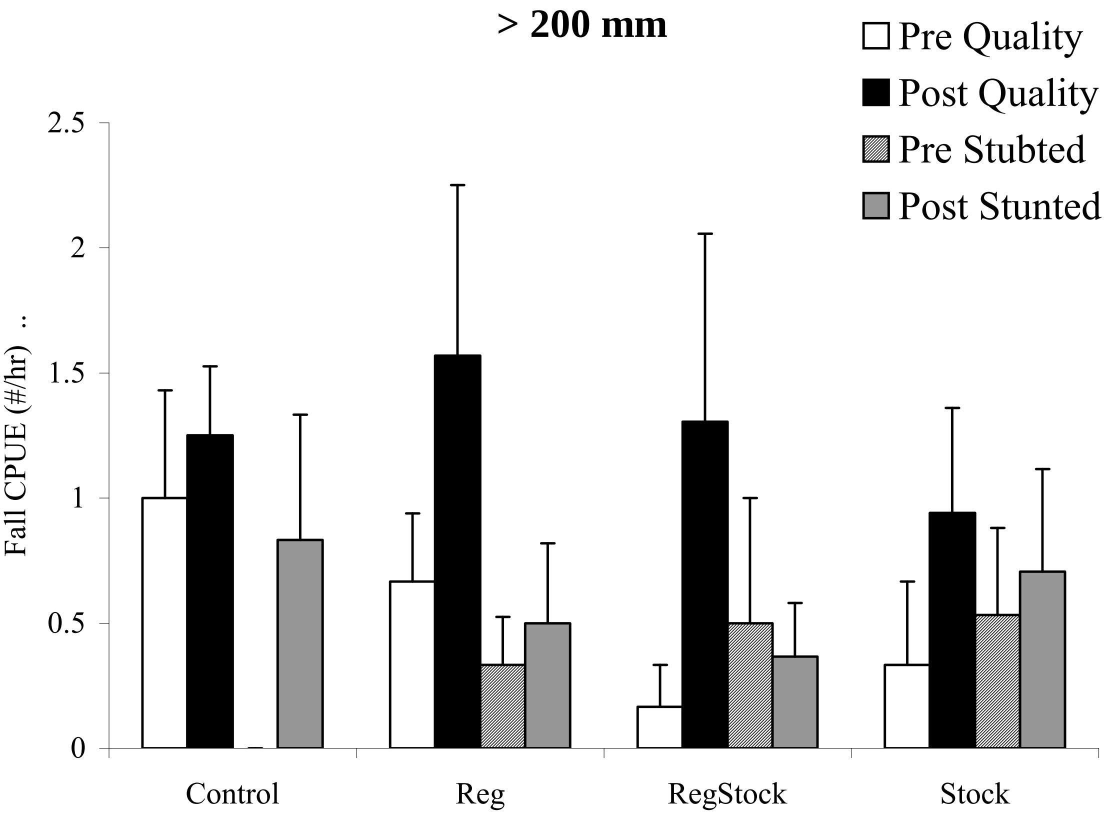


Figure 3-2: CPUE of bluegill larger than 200 mm collected in fall electrofishing samples for each of the experimental treatments. Bars labeled pre are the means of electrofishing samples from 1997-2000 and the bars labeled post are the mean of 2003-2004. Quality refers to lakes designated as having quality bluegill populations at the beginning of the experiment and stunted were lakes with stunted bluegill populations. Error bars represent the standard error.

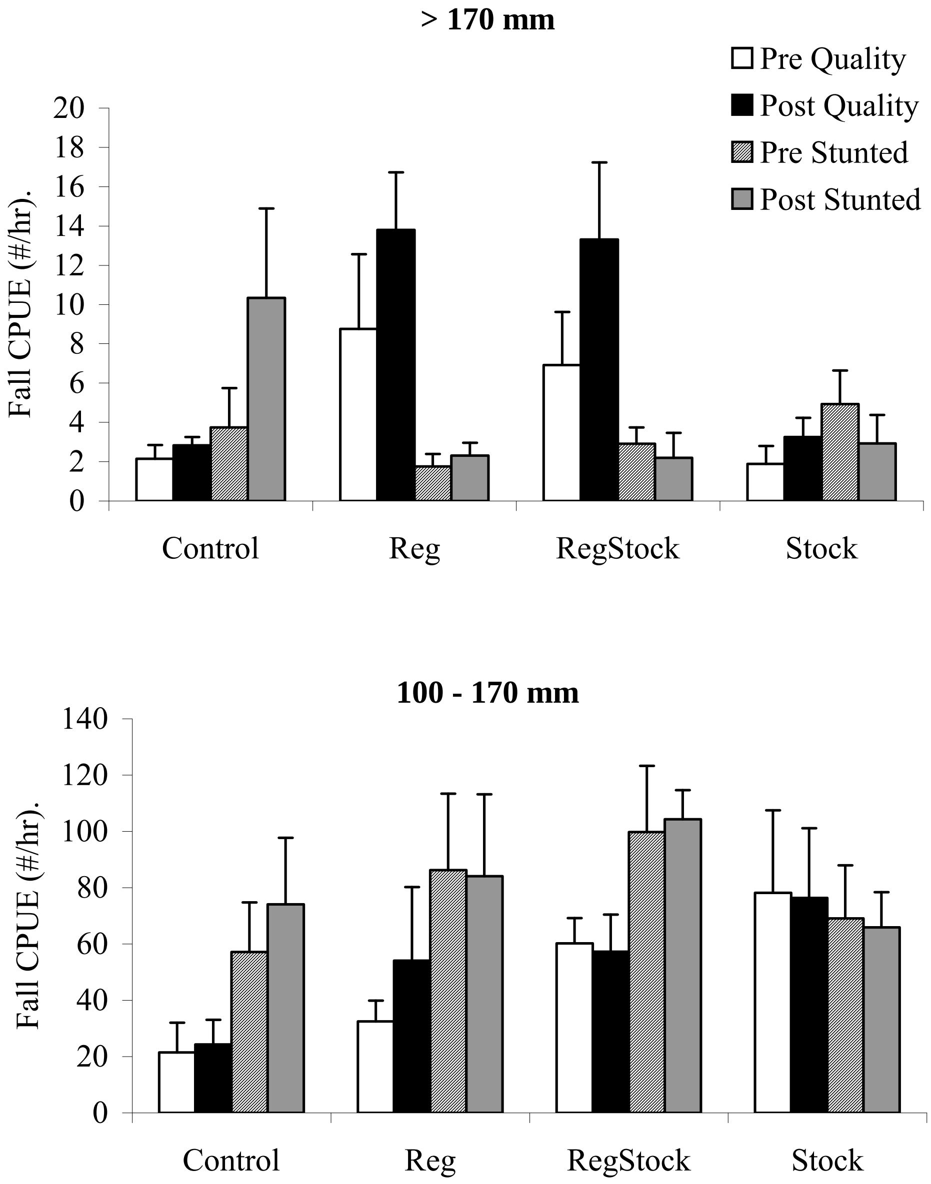


Figure 3-3: CPUE of bluegill larger than 170 mm and from 100 to 170 mm collected in fall electrofishing samples for each of the experimental treatments. Bars labeled pre are the means of electrofishing samples from 1997-2000 and the bars labeled post are the mean of 2003-2004. Quality refers to lakes designated as having quality bluegill populations at the beginning of the experiment and stunted were lakes with stunted bluegill populations. Error bars represent the standard error.

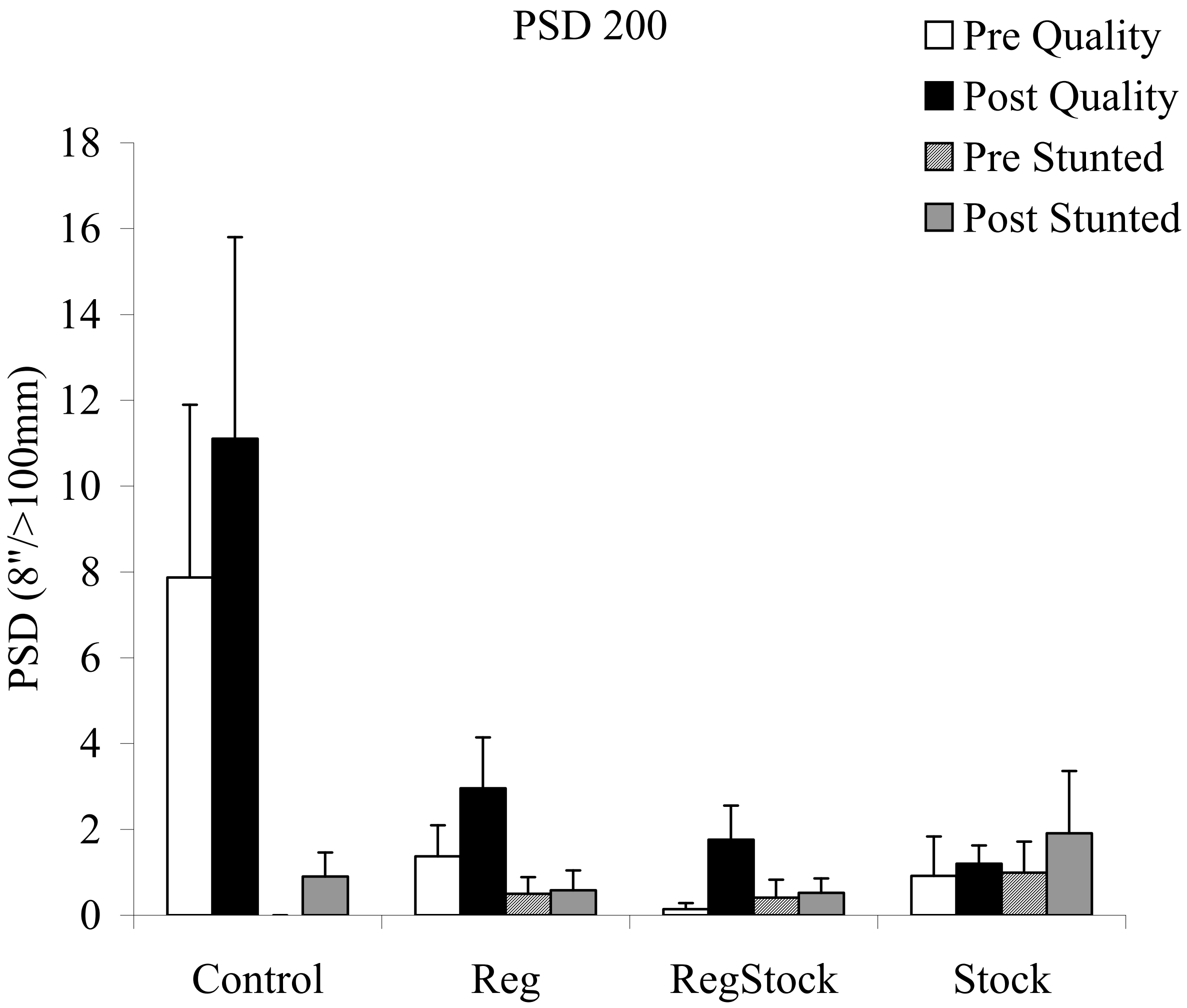


Figure 3-4: PSD 200 for collected in fall electrofishing samples for each of the by experimental treatments. PSD 200 is the ratio of CPUE for bluegill larger than 200 mm to bluegill larger than 100 mm. Bars labeled pre are the means of electrofishing samples from 1997-2000 and the bars labeled post are the mean of 2003-2004. Quality refers to lakes designated as having quality bluegill populations at the beginning of the experiment and stunted were lakes with stunted bluegill populations. Error bars represent the standard error.

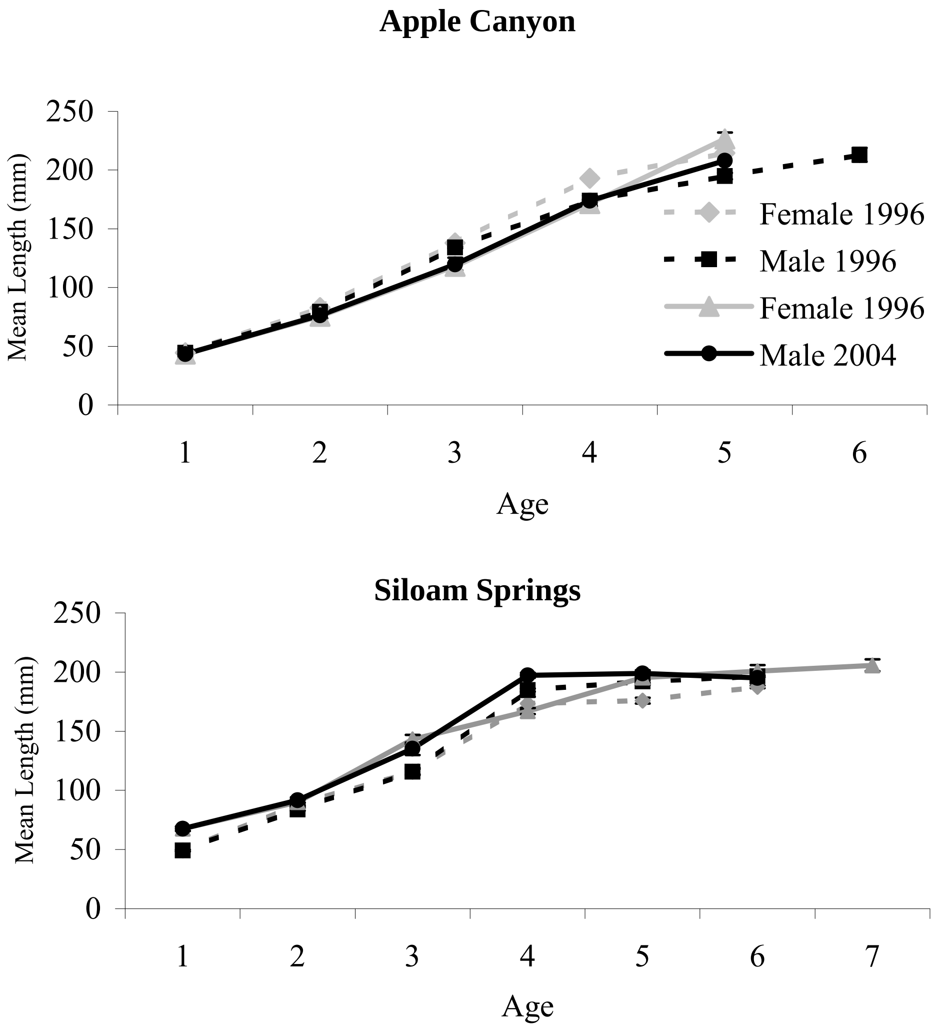
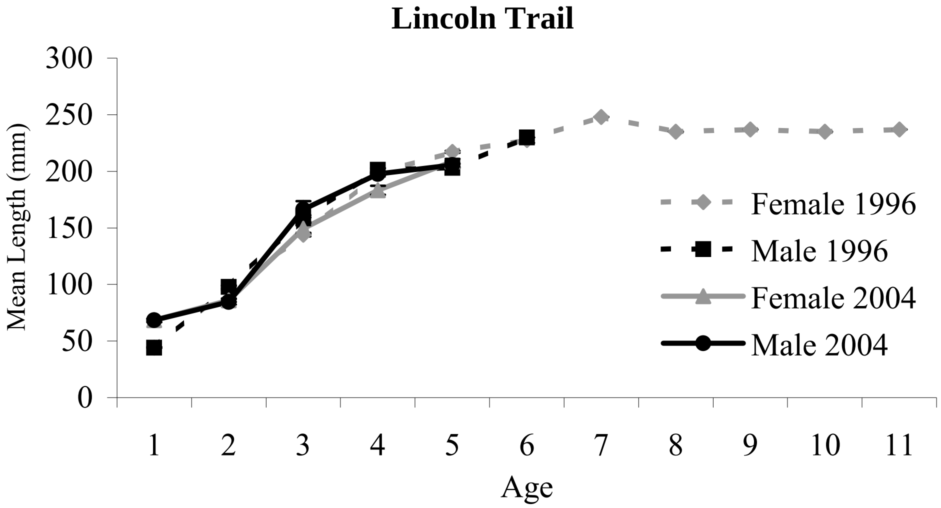


Figure 3-5: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated quality in the control treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



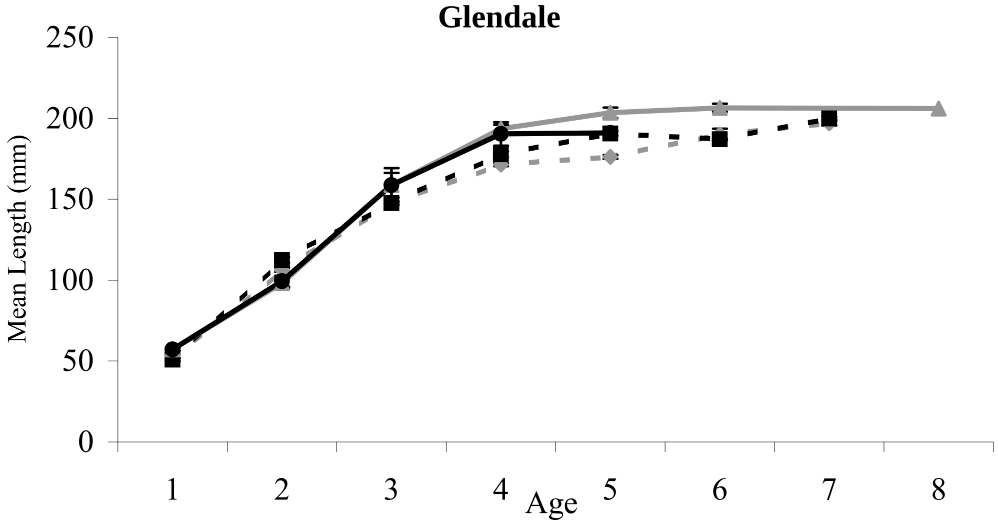
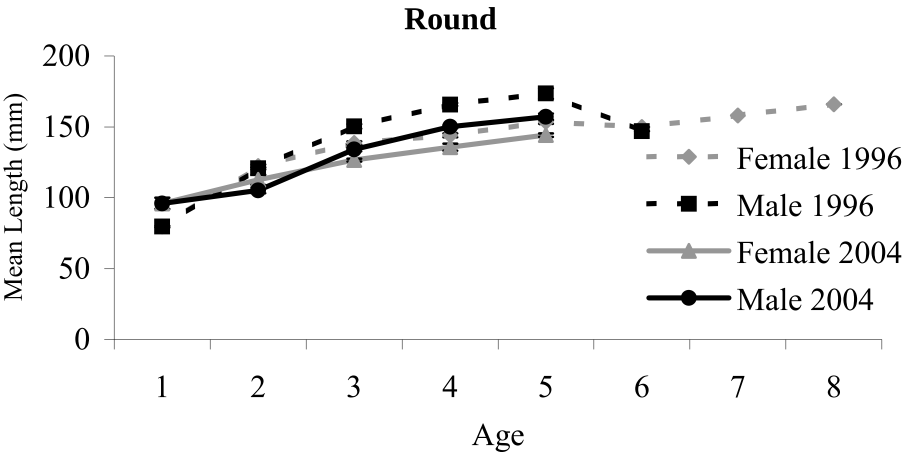


Figure 3-6: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated quality in the control treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



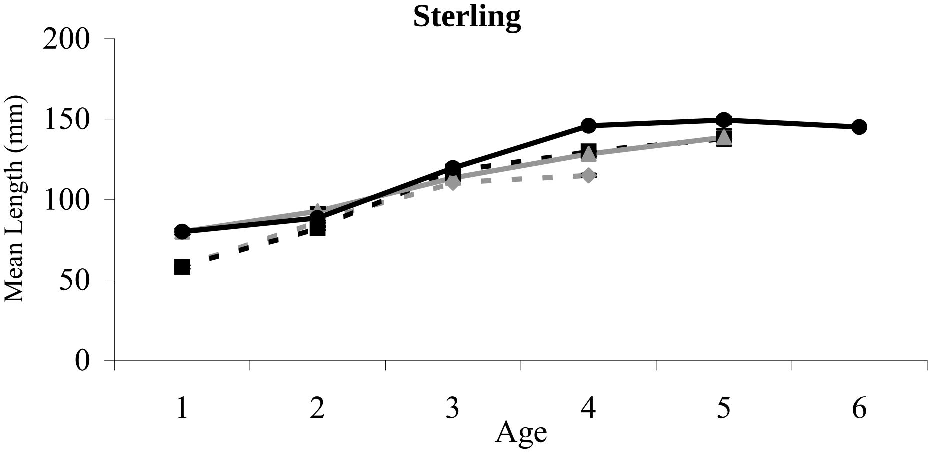
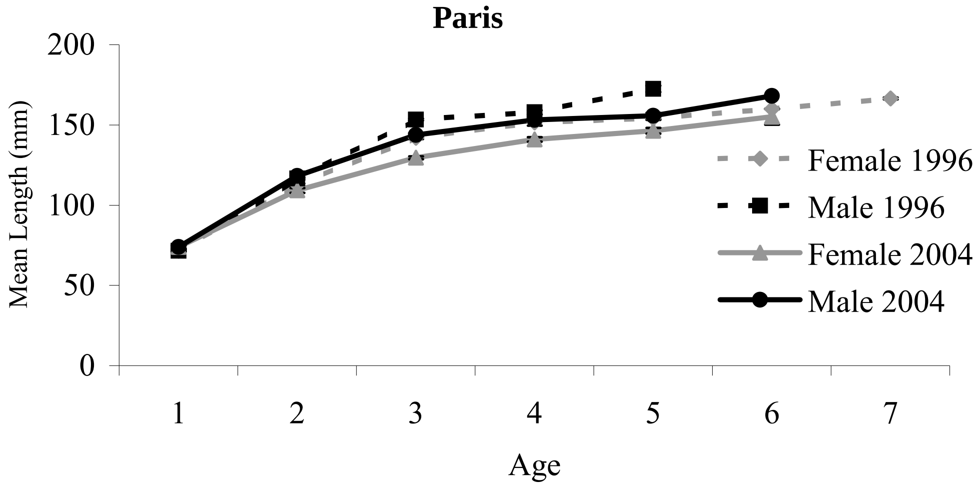


Figure 3-7: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated stunted in the control treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



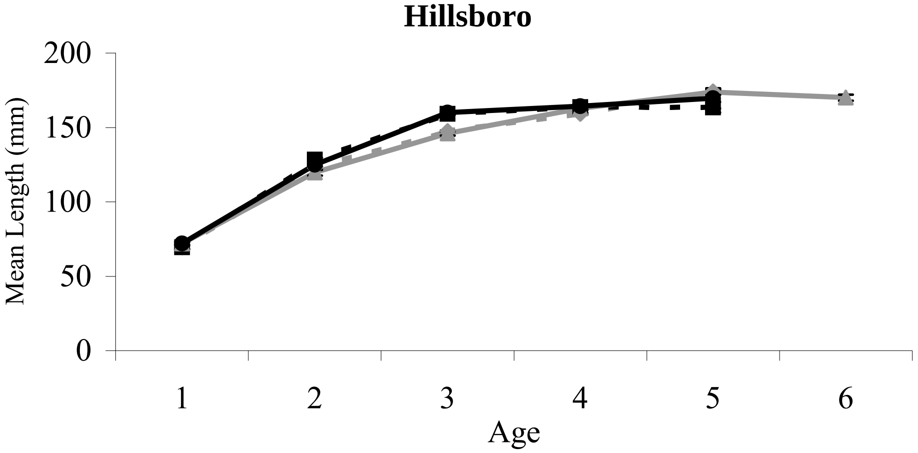


Figure 3-8: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated stunted in the control treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

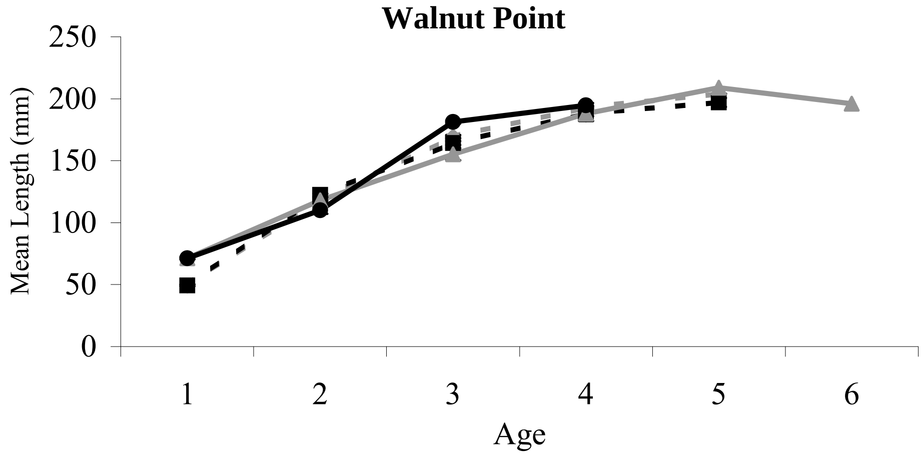


Figure 3-9: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated quality in the regulation treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

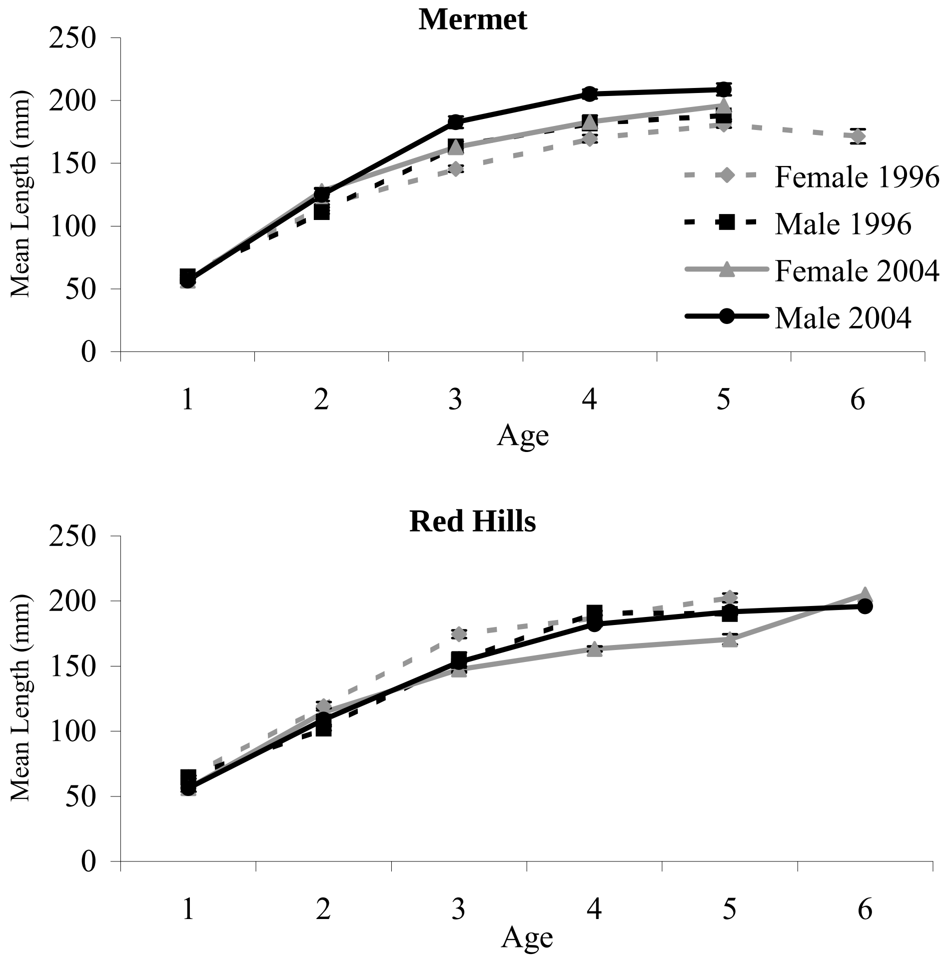
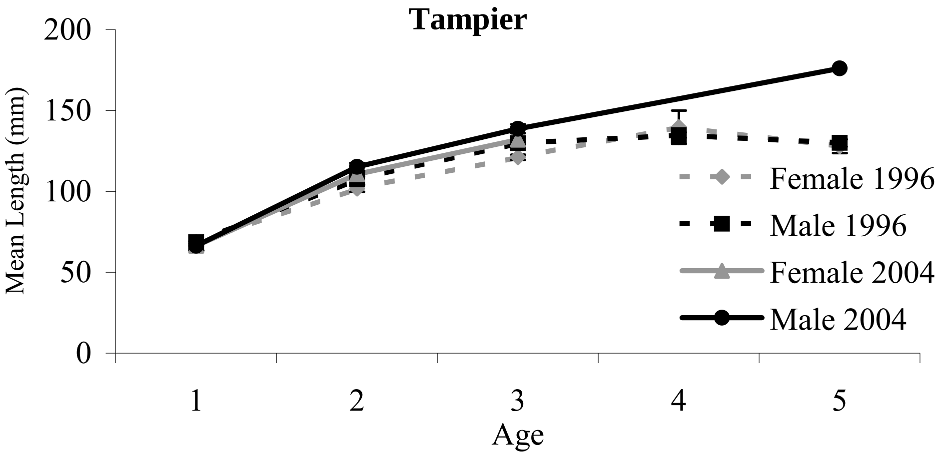


Figure 3-10: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated quality in the regulation treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



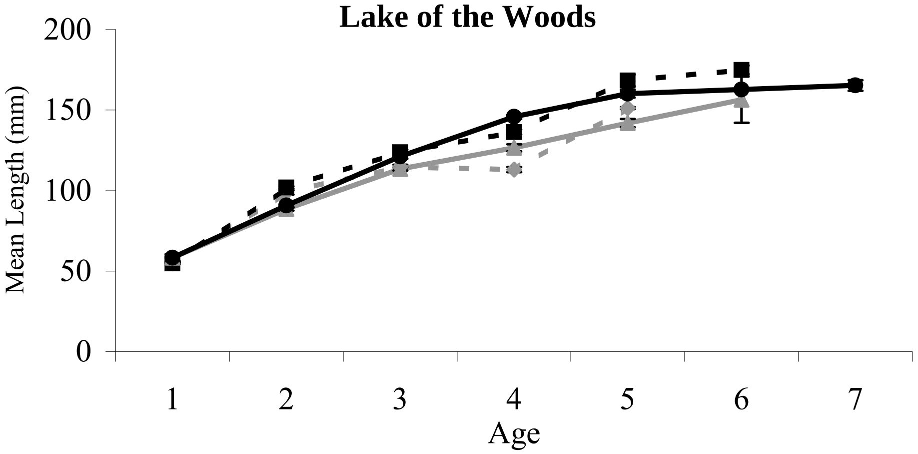
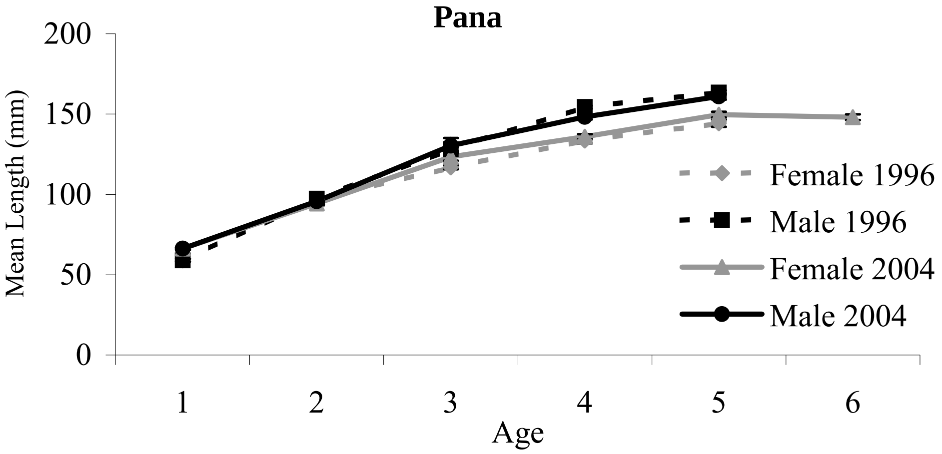


Figure 3-11: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated stunted in the regulation treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



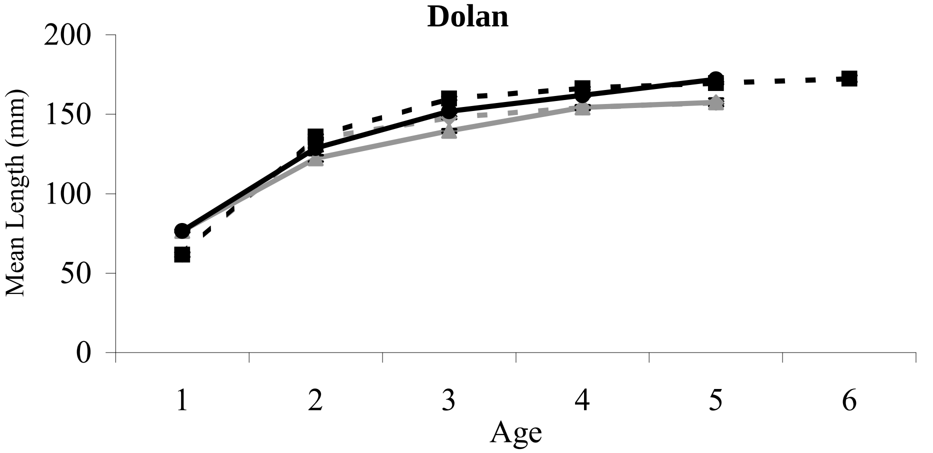


Figure 3-12: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated stunted in the regulation treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

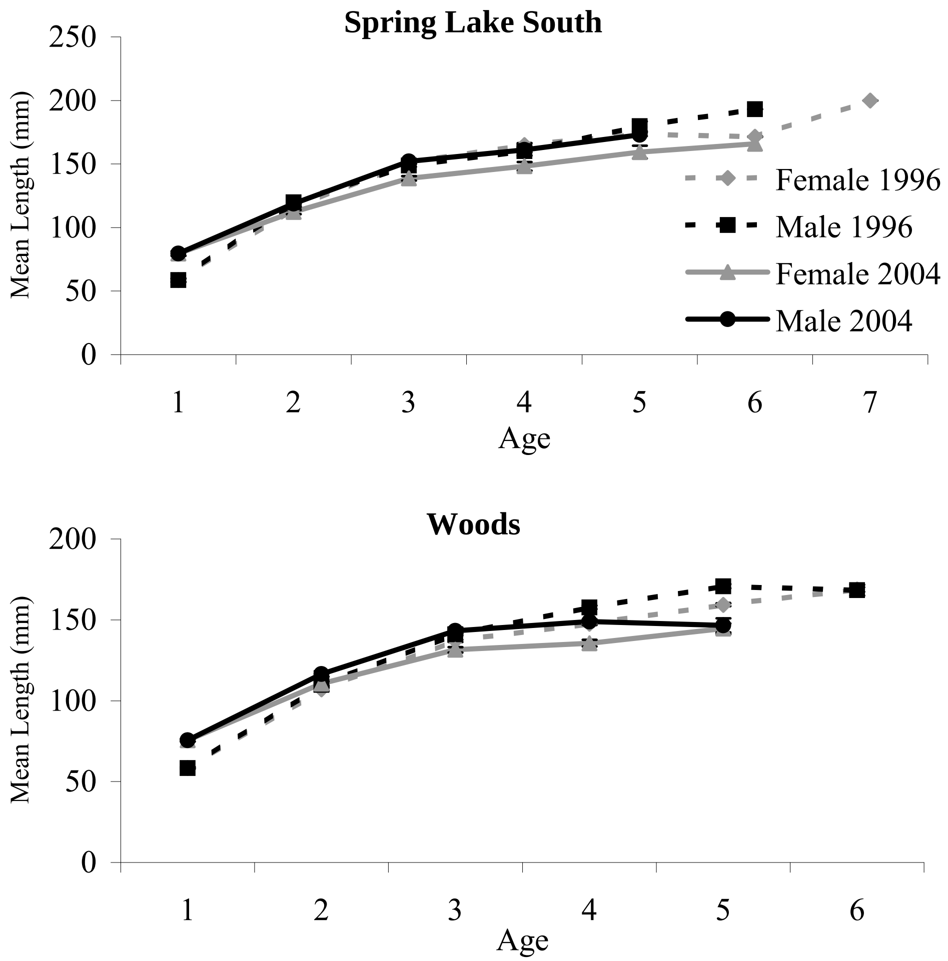
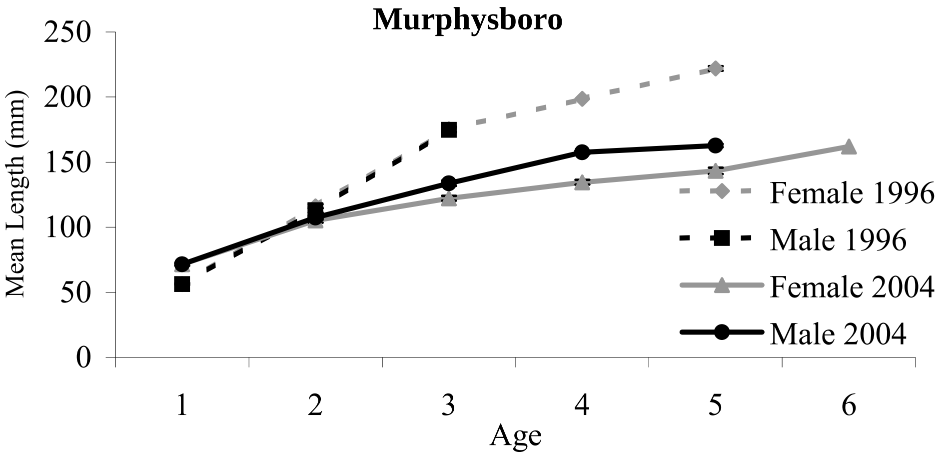


Figure 3-13: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated quality in the stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



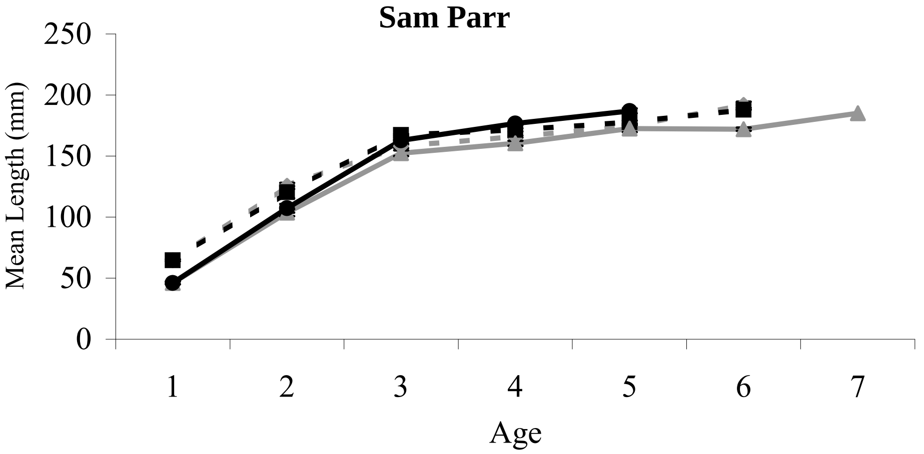


Figure 3-14: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated quality in the stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

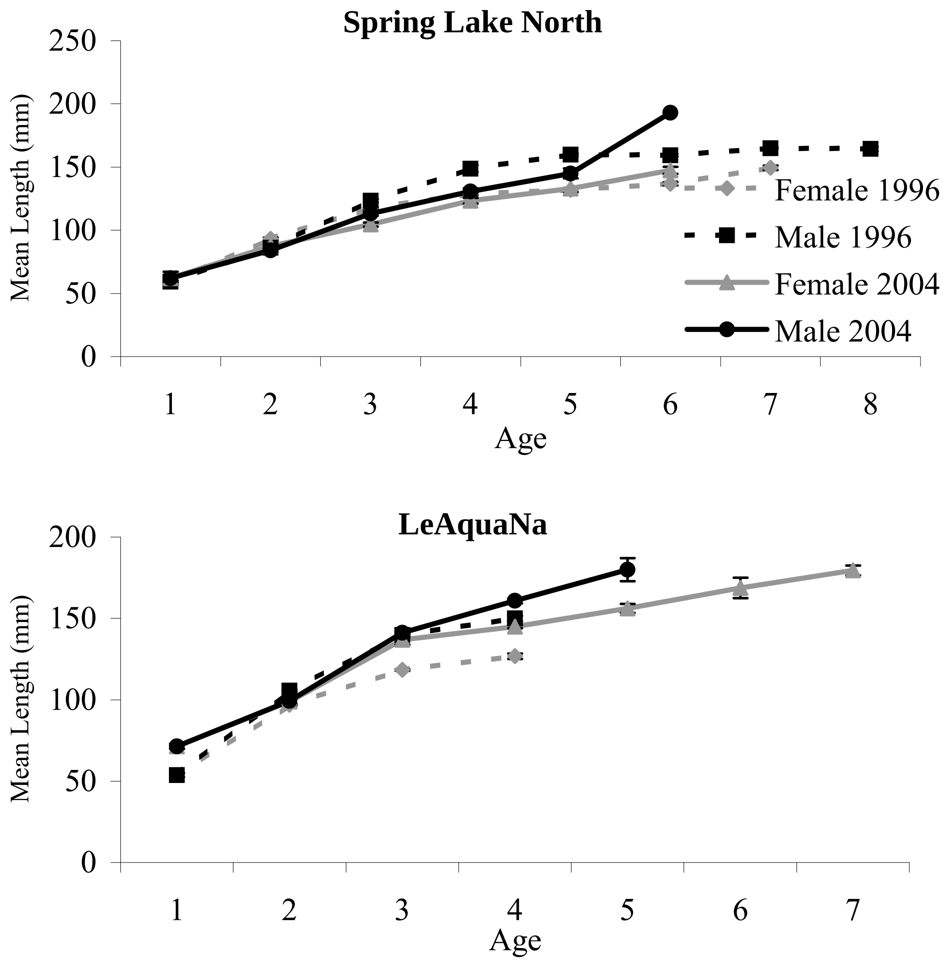
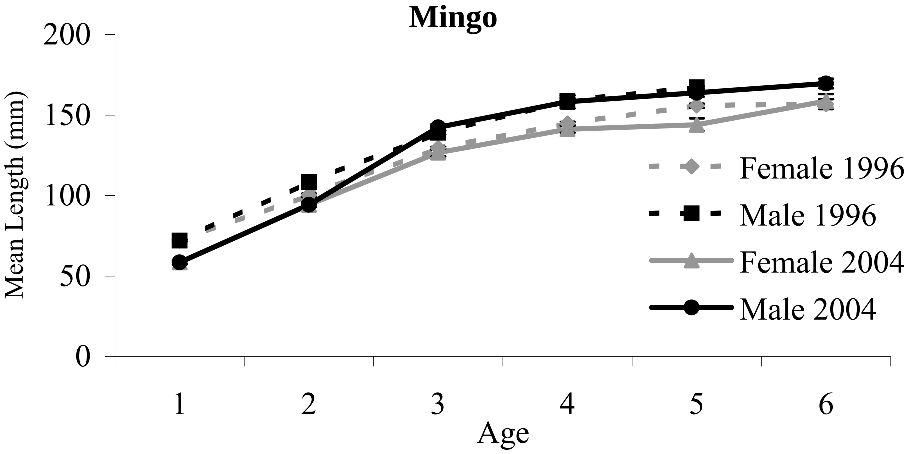


Figure 3-15: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated stunted in the stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



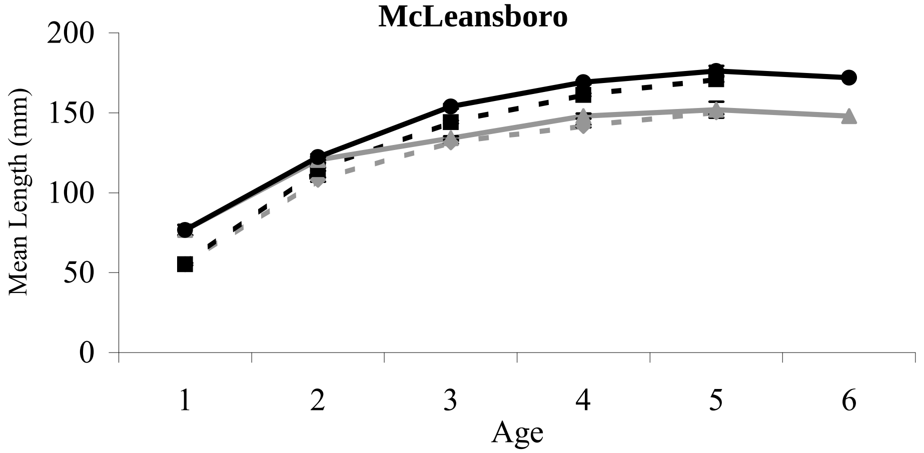
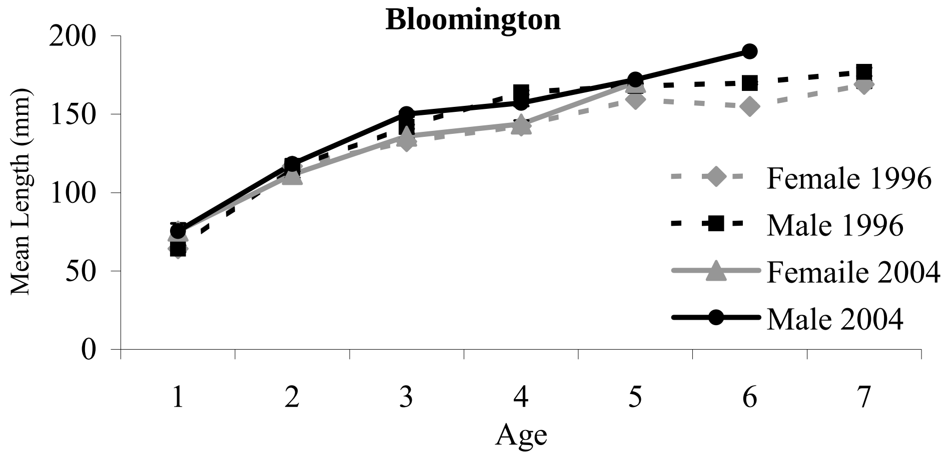


Figure 3-16: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated stunted in the stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



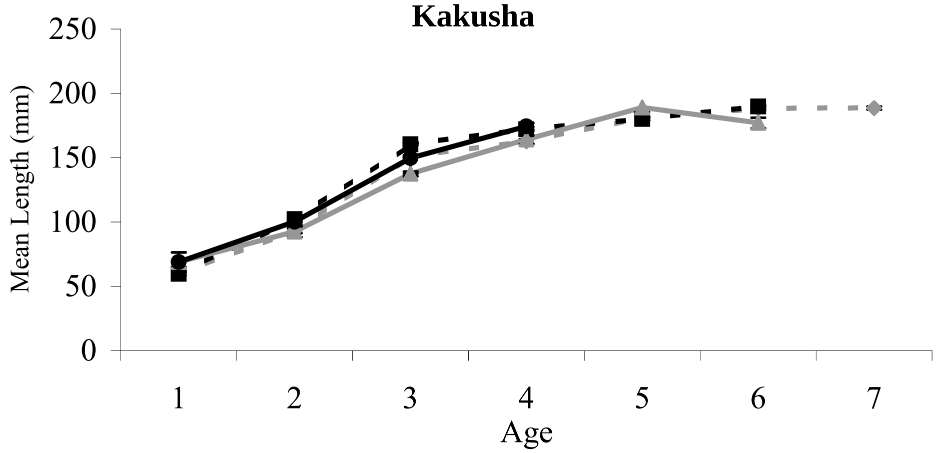
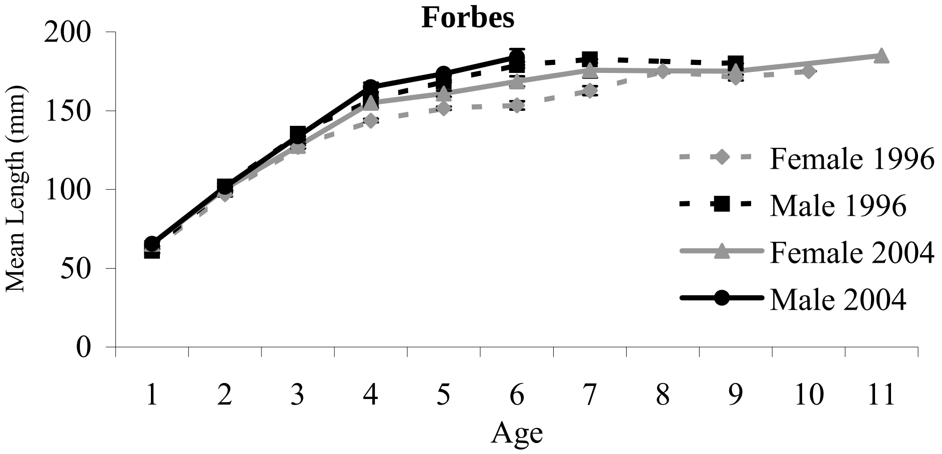


Figure 3-17: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated quality in the regulation and stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.



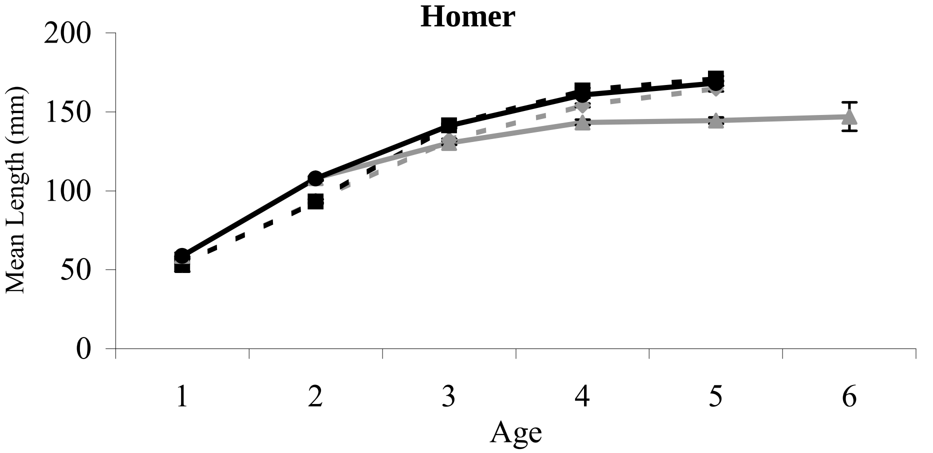


Figure 3-18: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated quality in the regulation and stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

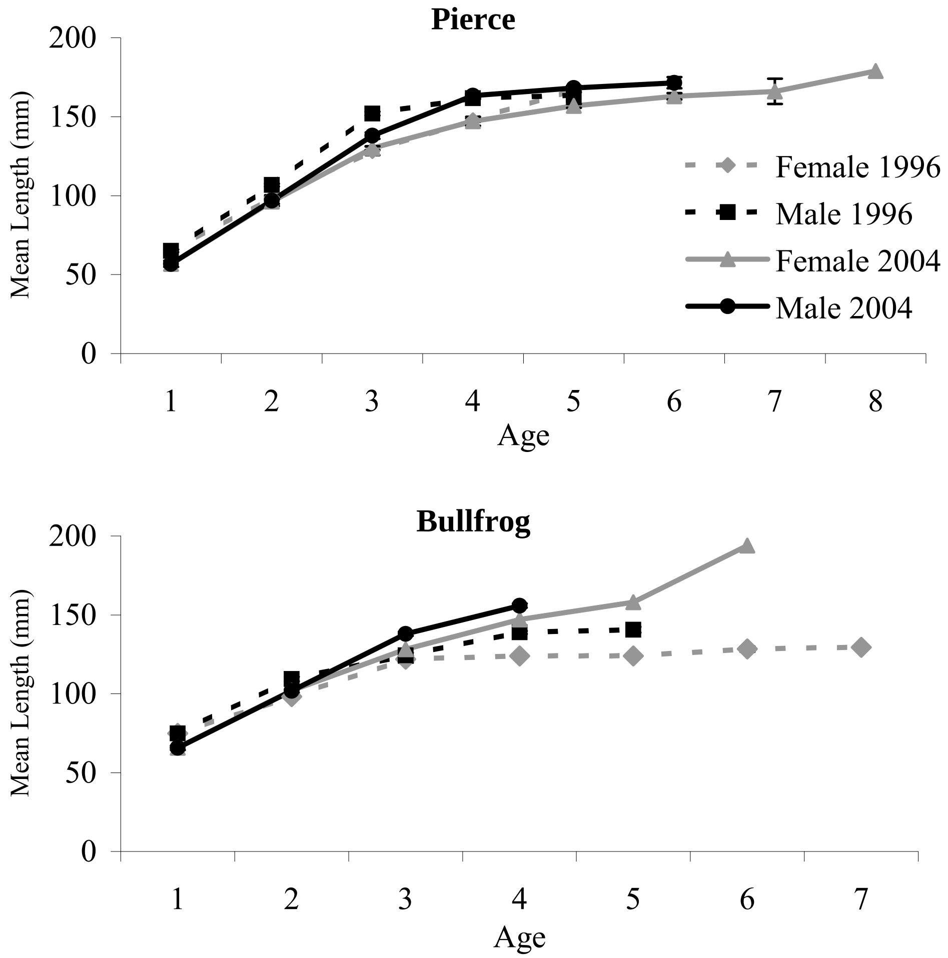


Figure 3-19: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the northern zone designated stunted in the regulation and stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

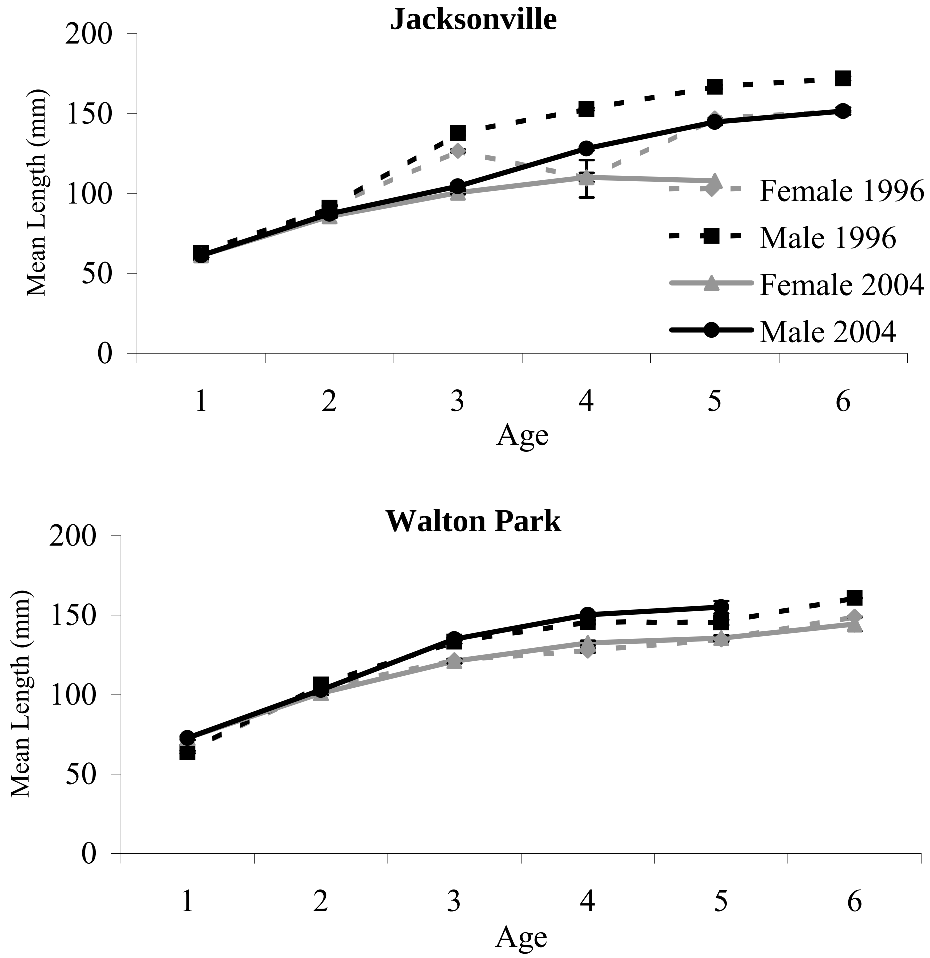


Figure 3-20: Mean length for each age of bluegill sampled in 1996 (dotted lines) prior to the experiment and 2004 (solid lines) at the conclusion of the experiment for lakes in the southern zone designated stunted in the regulation and stocking treatment group. Female bluegill are shown in grey and males are shown in black. Error bars represent standard error.

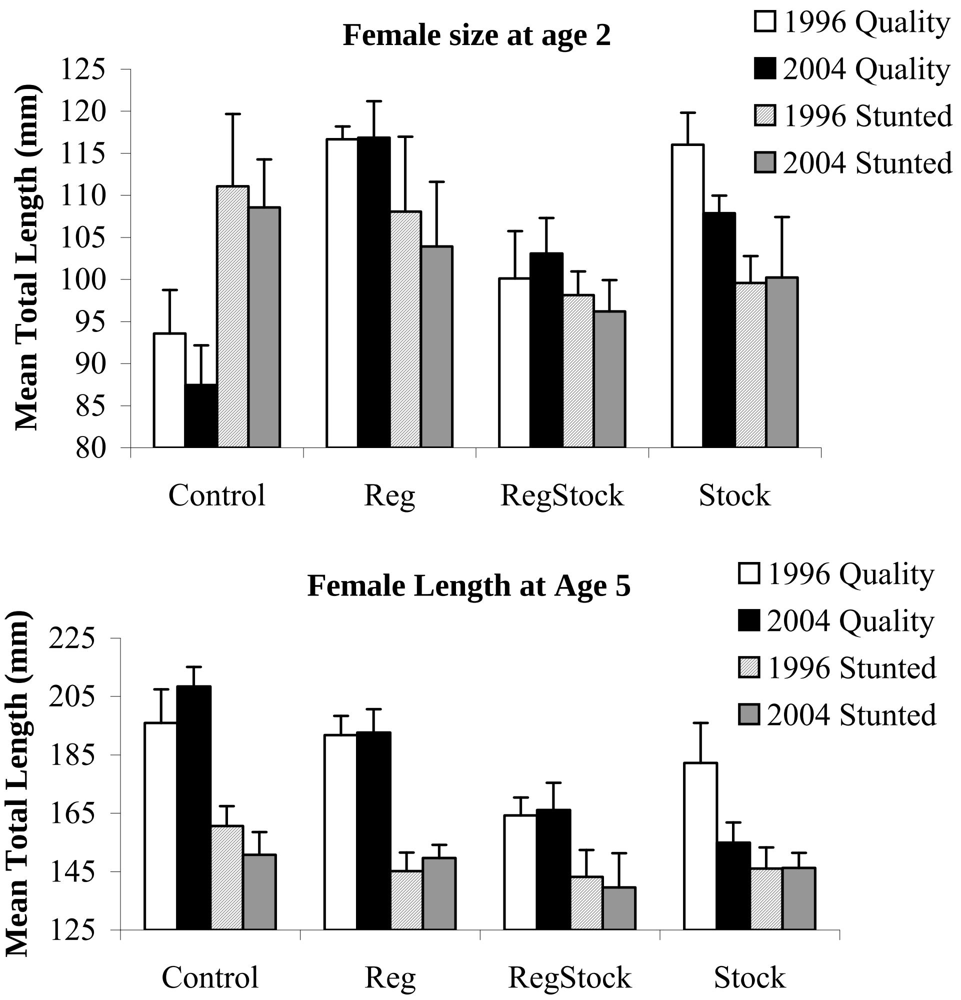
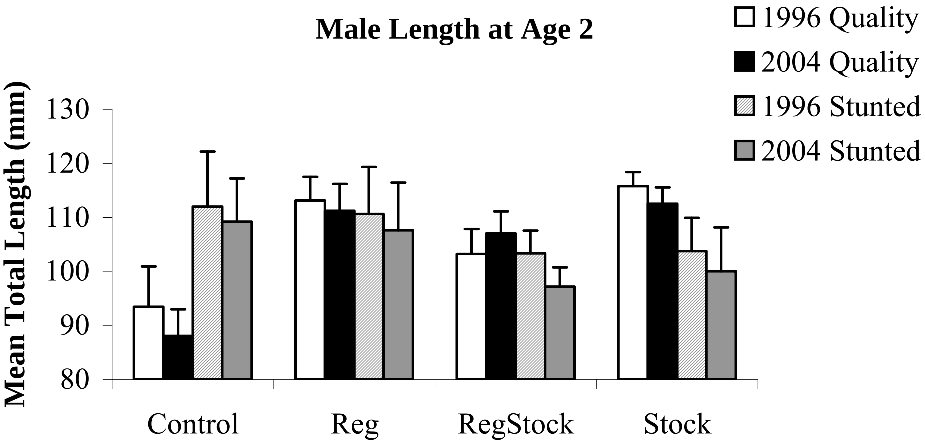


Figure 3-21: Mean total length for female bluegill at age 2 and 5 from spring electrofishing samples performed in 1996 and 2004. Error bars represent standard error.



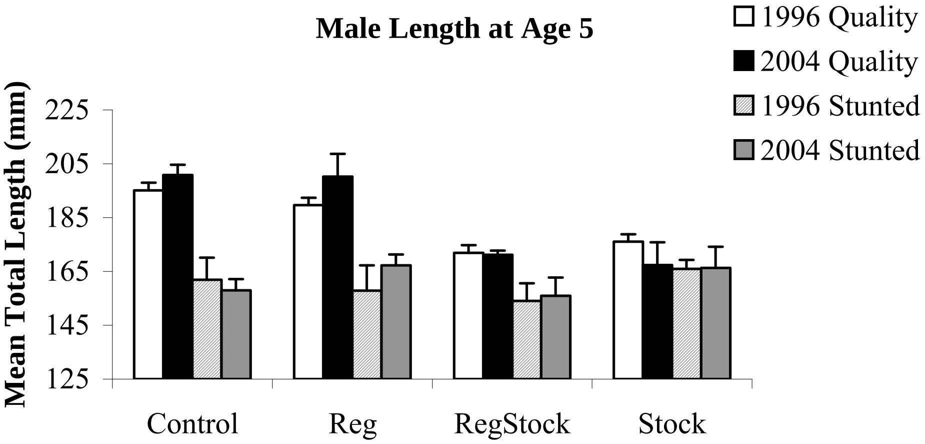


Figure 3-22: Mean total length for males bluegill at age 2 and 5 from spring electrofishing samples performed in 1996 and 2004. Error bars represent standard error.

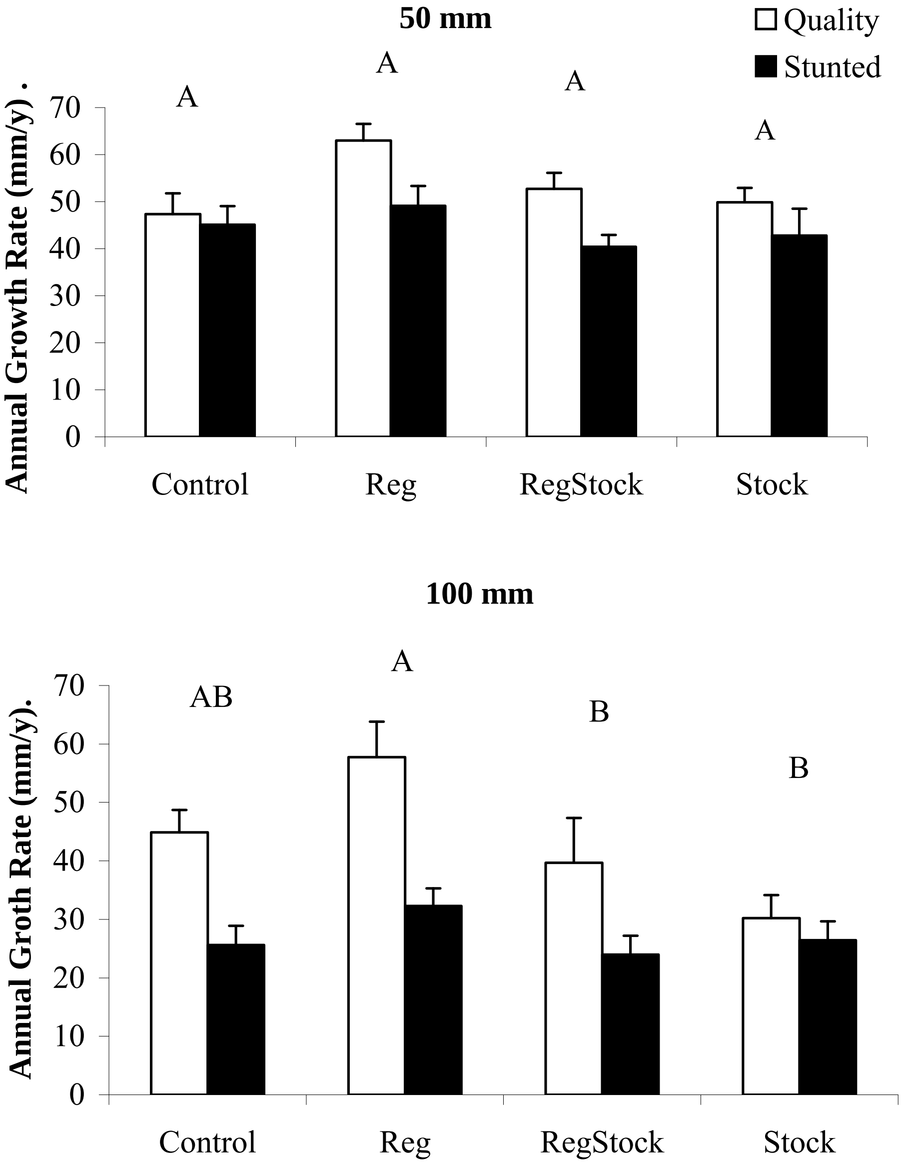


Figure 3-23: Annual growth rates for bluegill starting at 50 and 100 mm separated by treatment (control, regulation, regulation and stocking, and stocking) and between populations initially designated as stunted and quality. Similar letters indicate bars that are not significantly different and error bars represent the standard error.

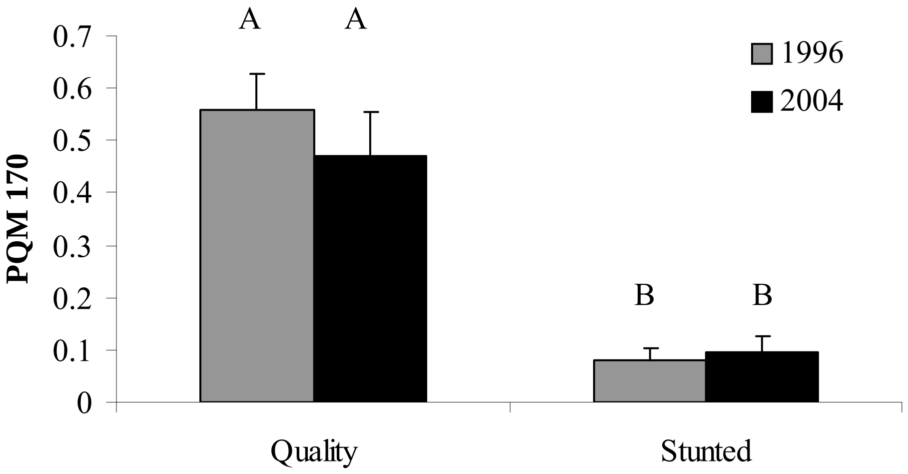


Figure 3-24: Mean PQM170 for lakes designated as quality and stunted before the management experiment (1996) and again after the management experiment (2004). Bluegill were collected by AC electrofishing in spring and dissected for maturity status. Letters indicate bars that are not significantly different (p >0.05), and error bars represent standard error.

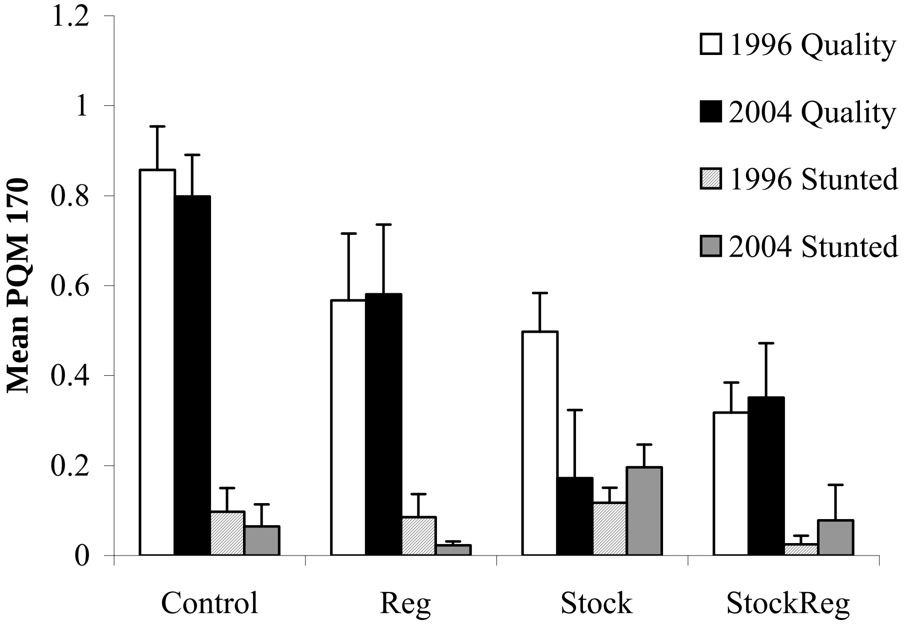


Figure 3-25: PQM 170 for pre (1996) and post (2004) experiment in each of the four treatments (control, regulation, stocking, and both regulation and stocking) separated by the pre experiment designation of quality or stunted. Error bars represent the standard error.

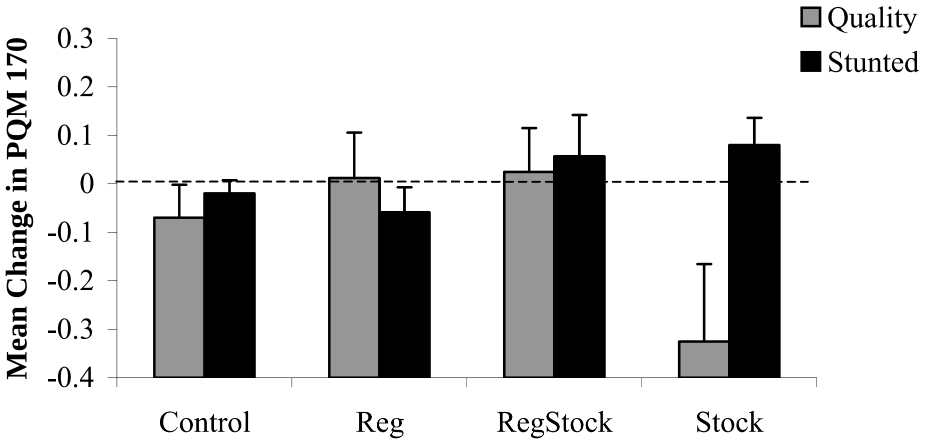


Figure 3-26: Mean change in PQM170 for lakes designated as quality and stunted before the management experiment for each lake of the four treatments. Bluegill were collected by AC electrofishing in spring and dissected for maturity status. Treatment is the experimental manipulation of the 8” 10 fish bag limit (Reg), largemouth bass stocking (Stock), a combination of stocking and regulation (RegStock), or control (Control). No significant differences were observed among treatments (P >0.05), and error bars represent standard error.

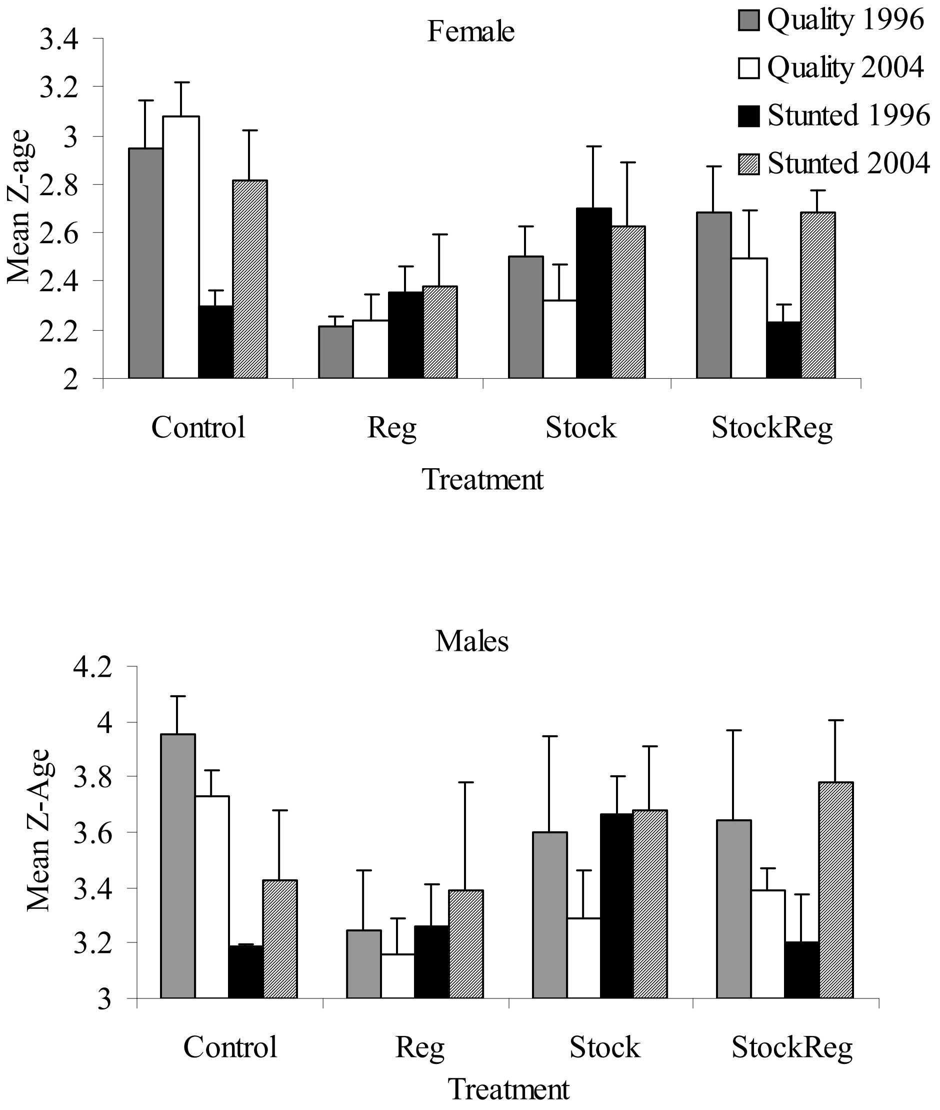


Figure 3-27: Mean Z-age scores for pre and post experimental treatments based on the pre experiment designation of quality or stunted. Error bars represent the standard error.

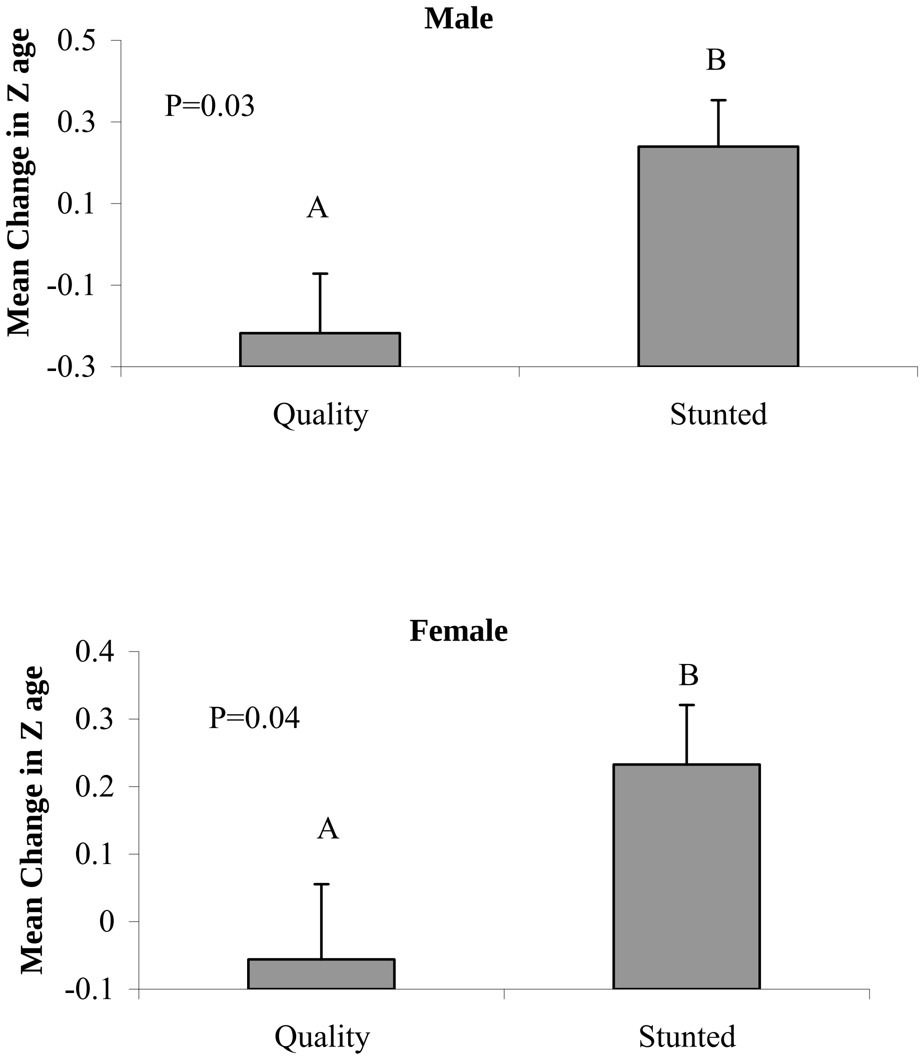


Figure 3-28: Mean change in z-age score for lakes designated as quality and stunted before the management experiment. Bluegill were collected by AC electrofishing in spring and dissected for maturity status. Different letters indicate bars that are significantly different and error bars represent standard error.

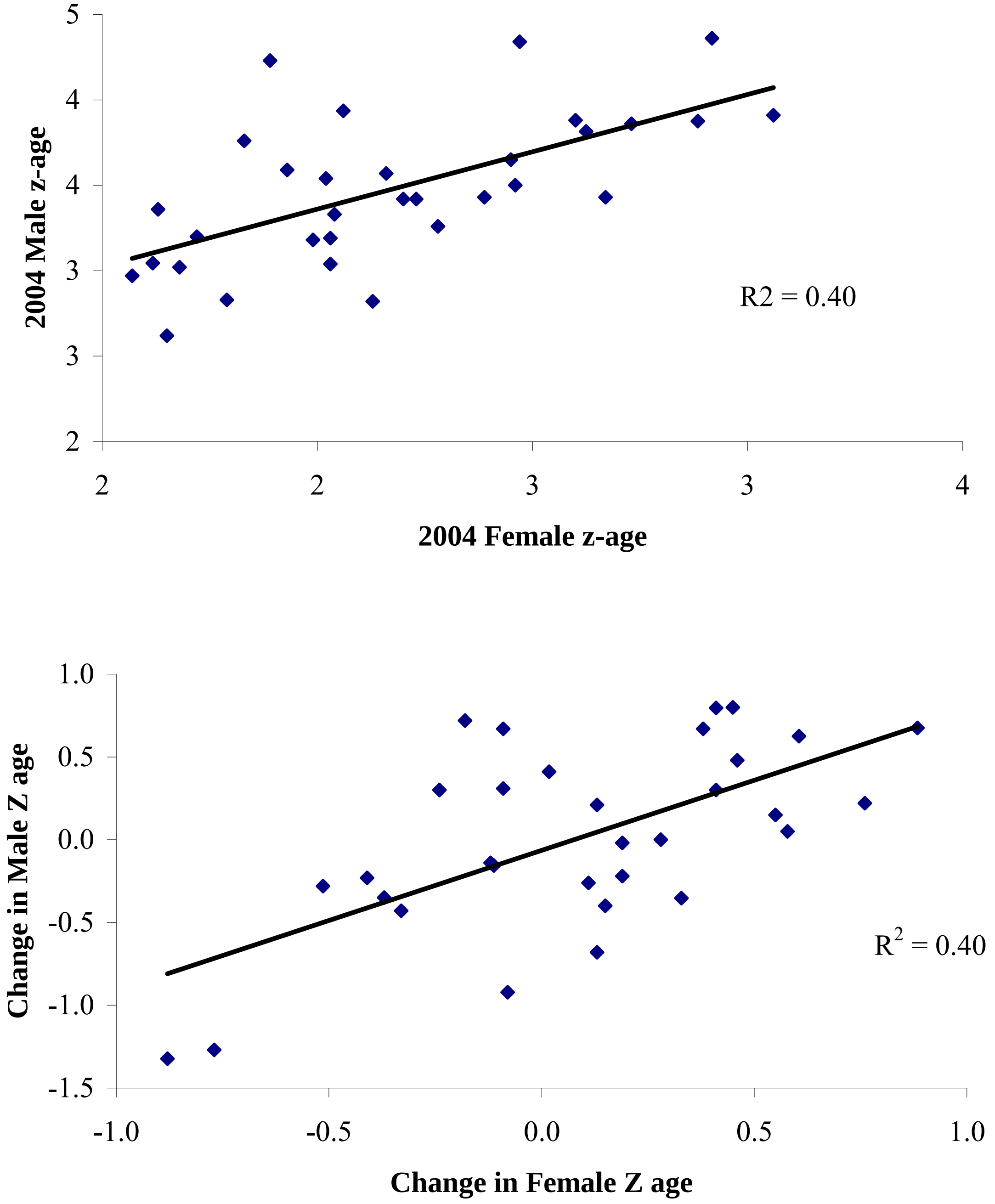


Figure 3-29: Relationship between z-age score for male and female bluegill populations in 2004 (top) and change in z-age score from 1996 to 2004 (bottom).

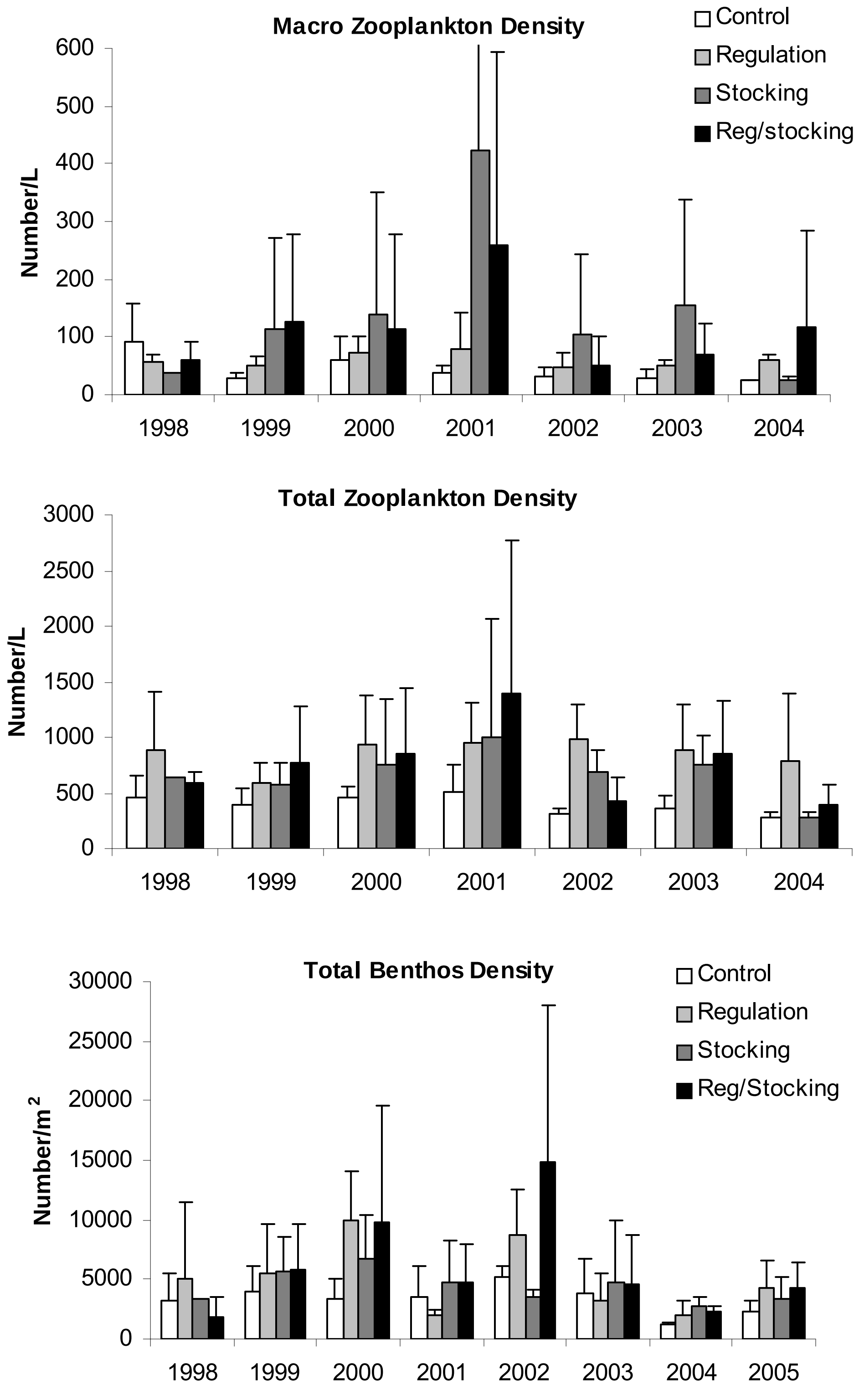


Figure 3-30: Mean macrozooplankton, zooplankton, and benthos density by year for each treatment of the bluegill management experiment. Bars indicate standard deviation.

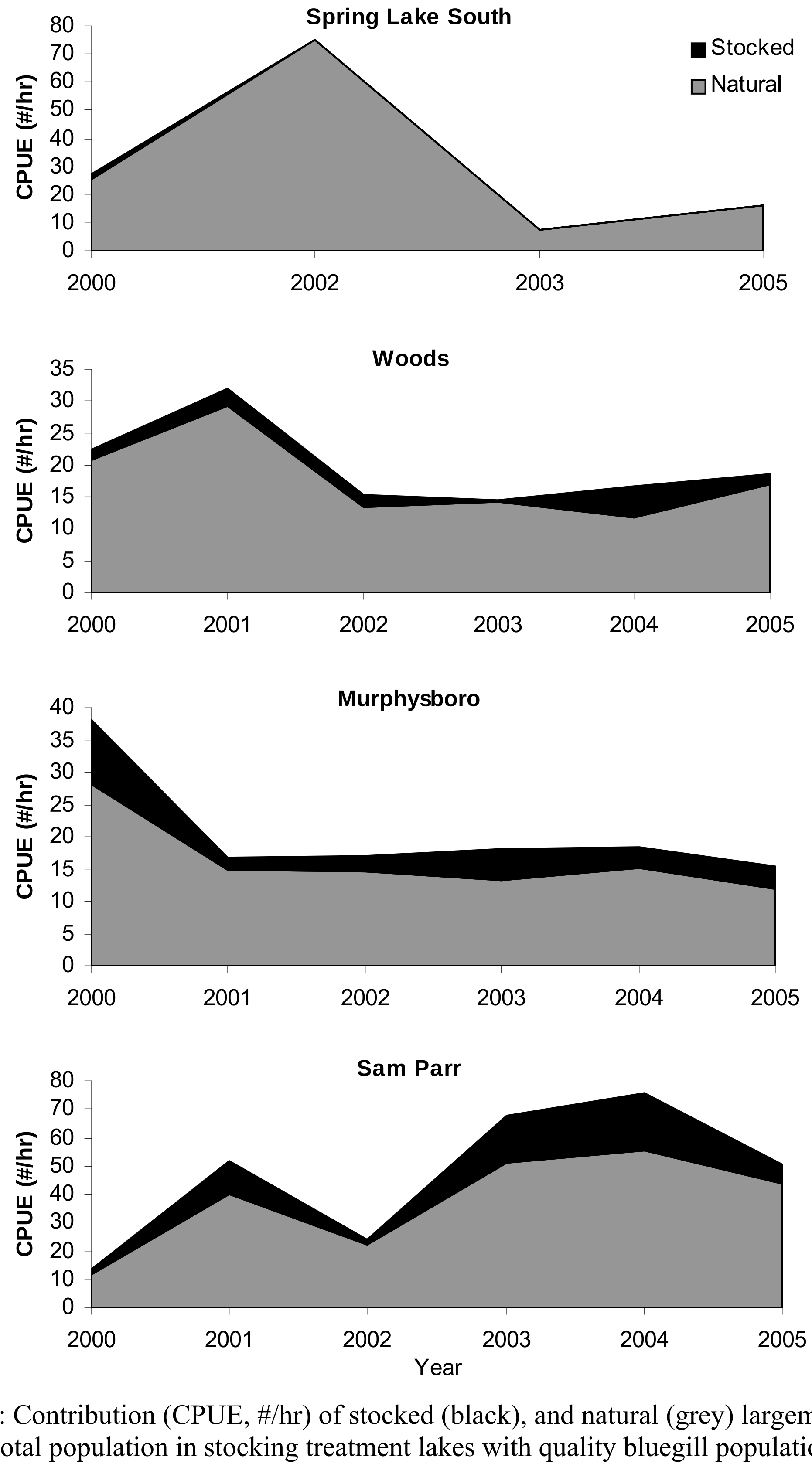


Figure 3-31: Contribution (CPUE, #/hr) of stocked (black), and natural (grey) largemouth bass to the total population in stocking treatment lakes with quality bluegill populations during 2000-2005. Electrofishing samples were performed in the spring during May and June.

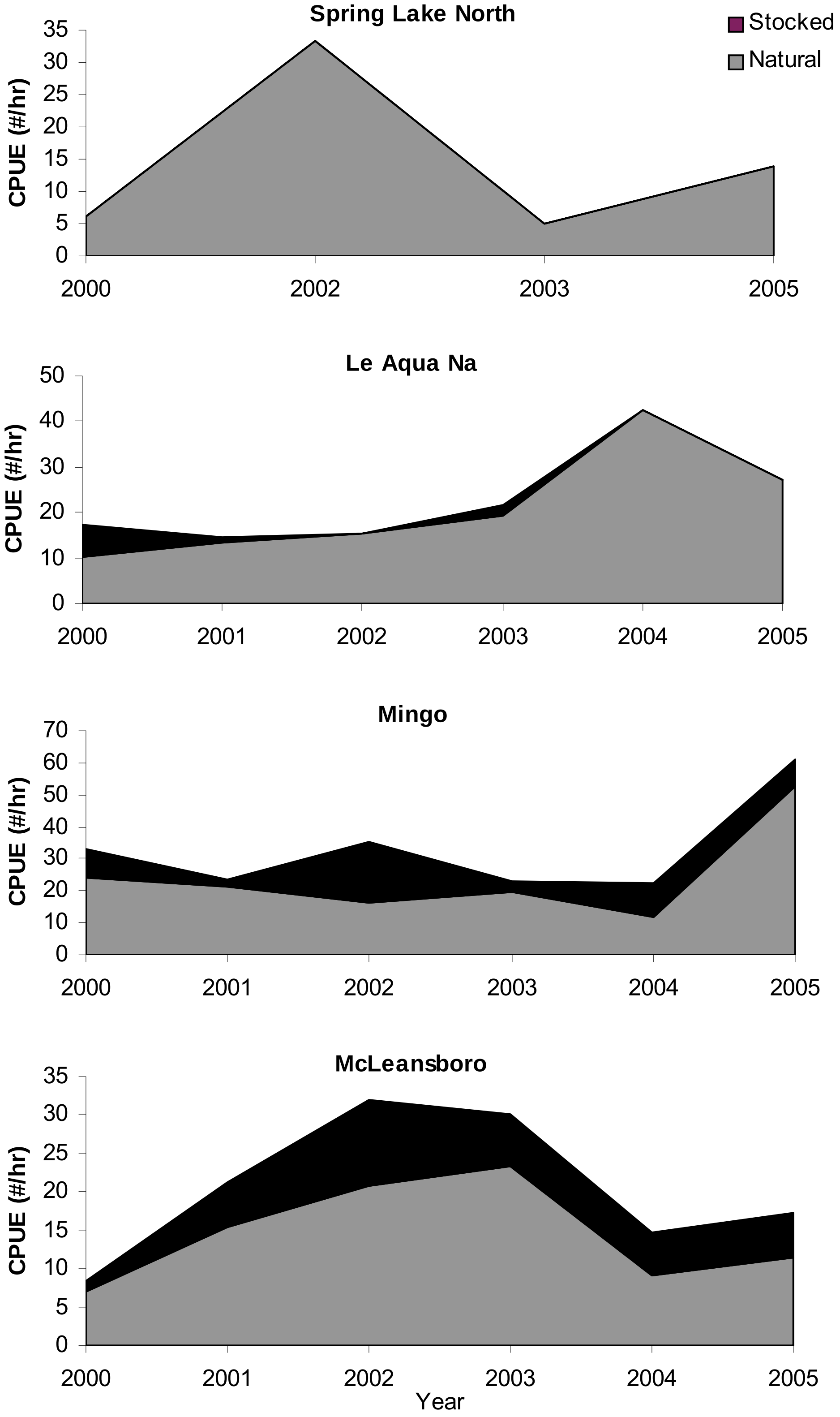


Figure 3-32: Contribution (CPUE, #/hr) of stocked (black), and natural (grey) largemouth bass to the total population in stocking treatment lakes with stunted bluegill populations during 2000-2005. Electrofishing samples were performed in the spring during May and June.

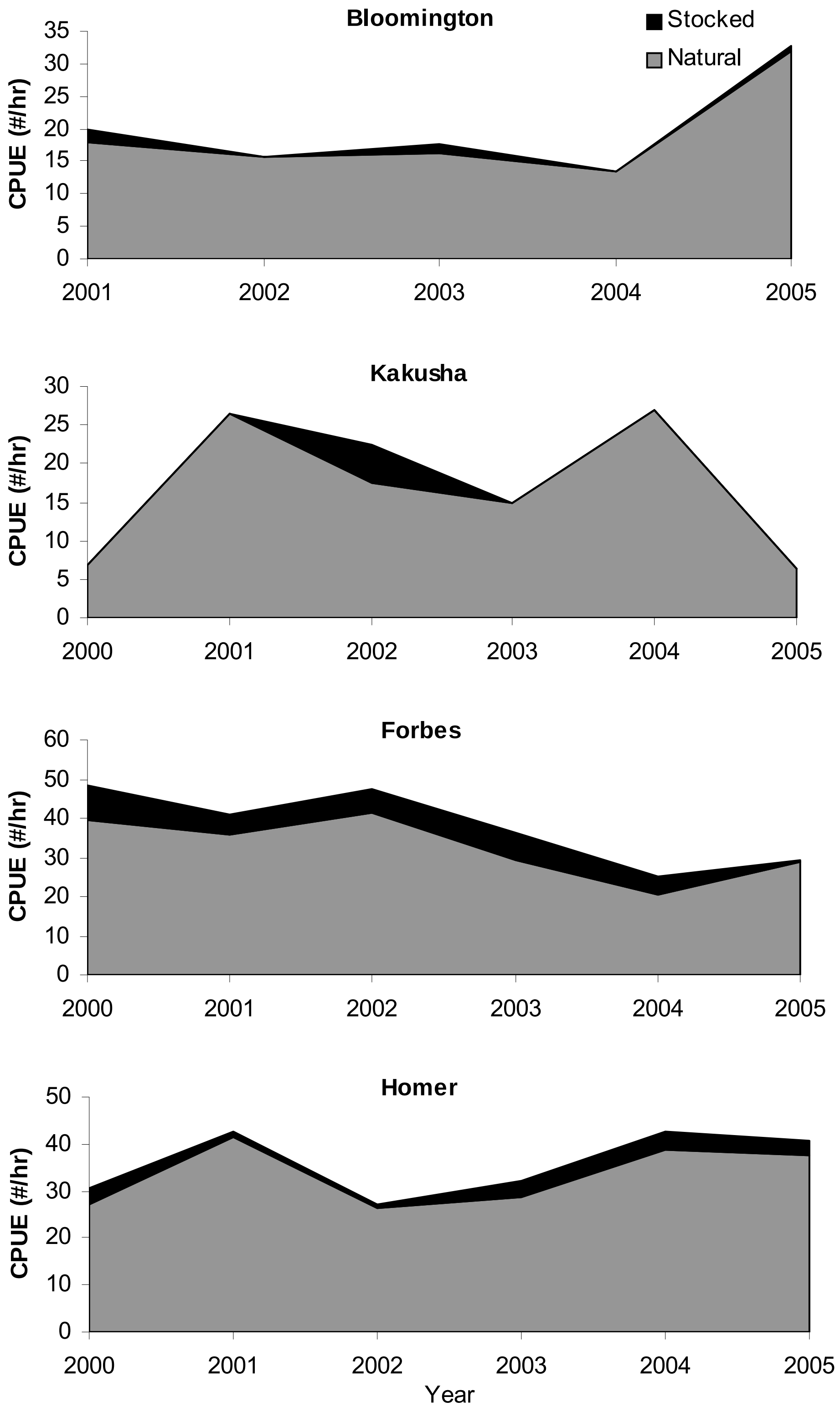


Figure 3-33: Contribution (CPUE, #/hr) of stocked (black), and natural (grey) largemouth bass to the total population in stocking and regulation treatment lakes with quality bluegill populations in 2000-2005. Electrofishing samples were performed in the spring during May and June.

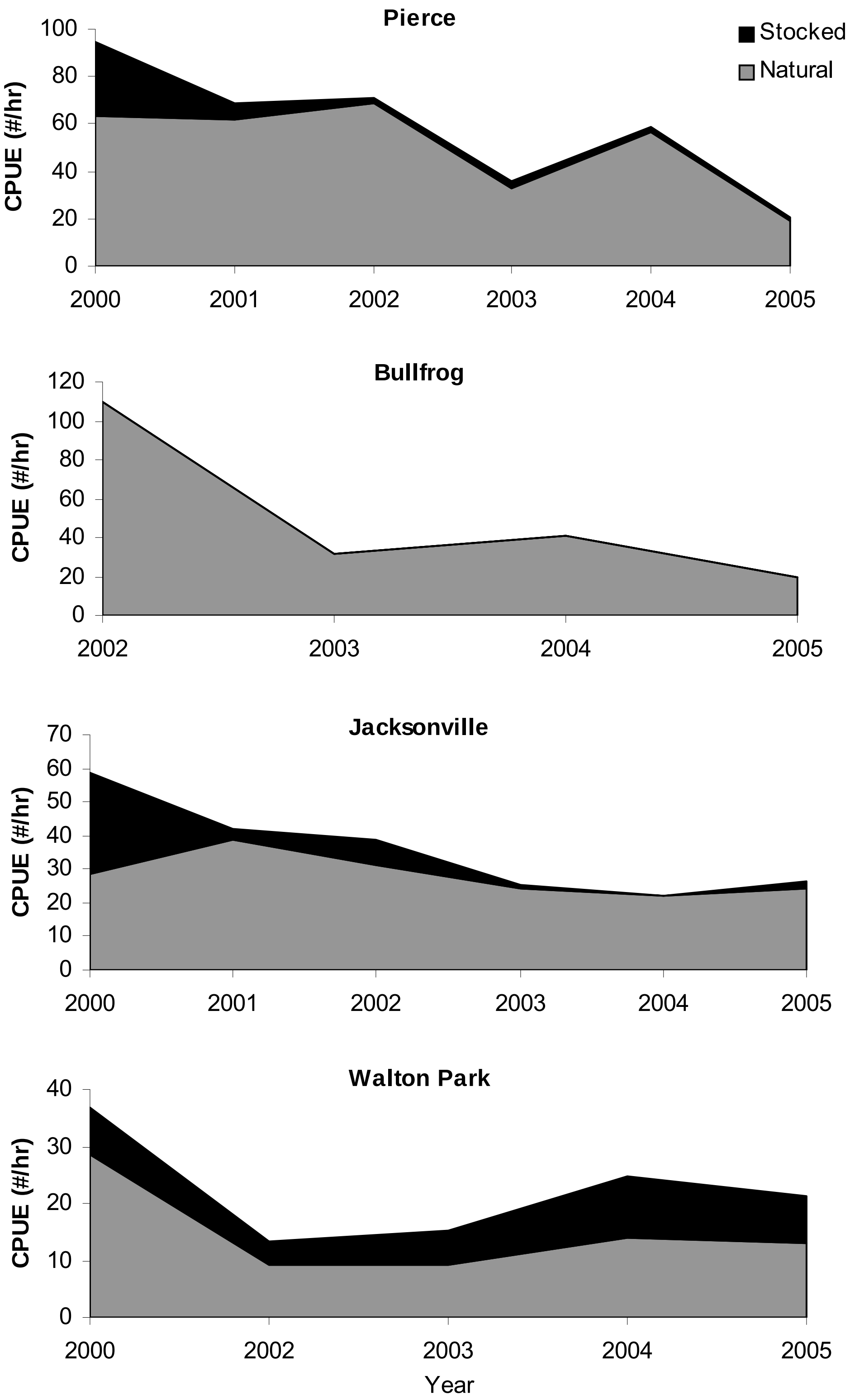


Figure 3-34: Contribution (CPUE, #/hr) of stocked (black), and natural (grey) largemouth bass to the total population in stocking and regulation treatment lakes with stunted bluegill populations in 2000-2005. Electrofishing samples were performed in the spring during May and June.

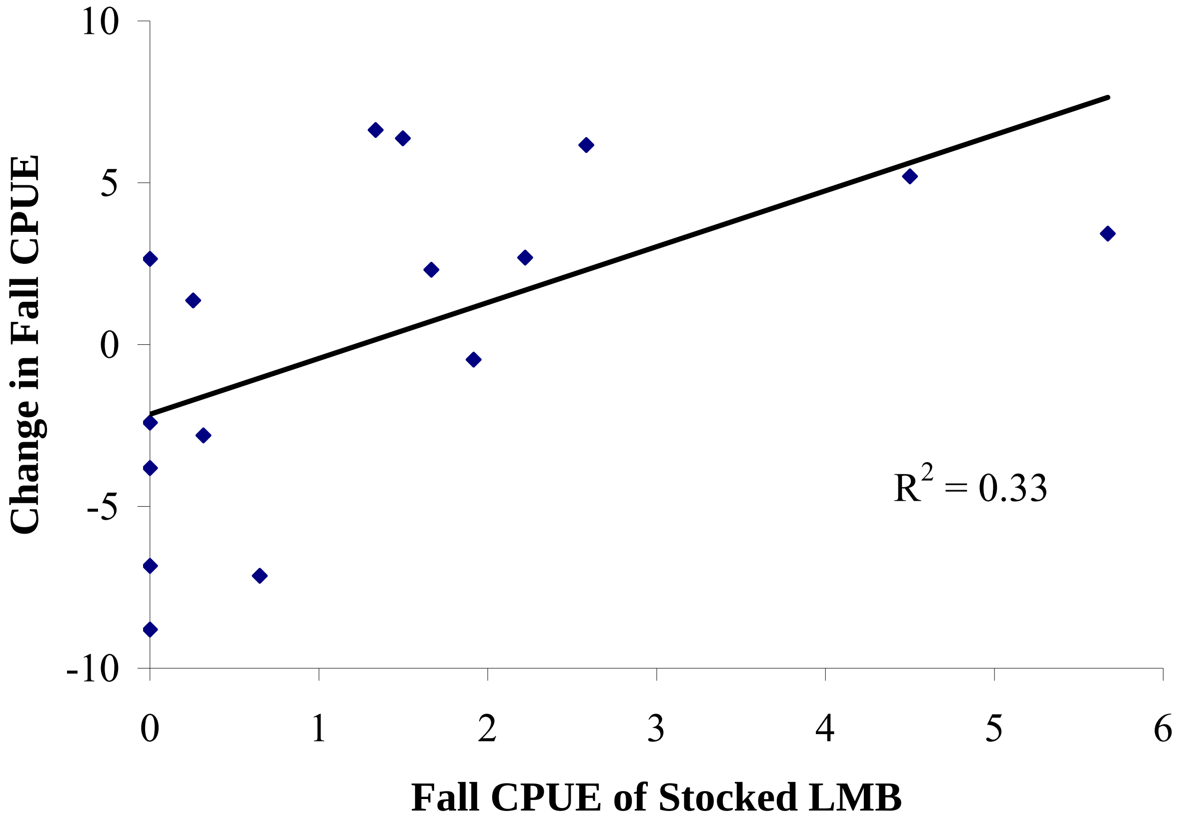


Figure 3-35: Relationship between mean fall CPUE for stocked largemouth bass and change in CPUE of largemouth bass larger than 250 mm in lakes with either the stocking or regulation and stocking treatment.

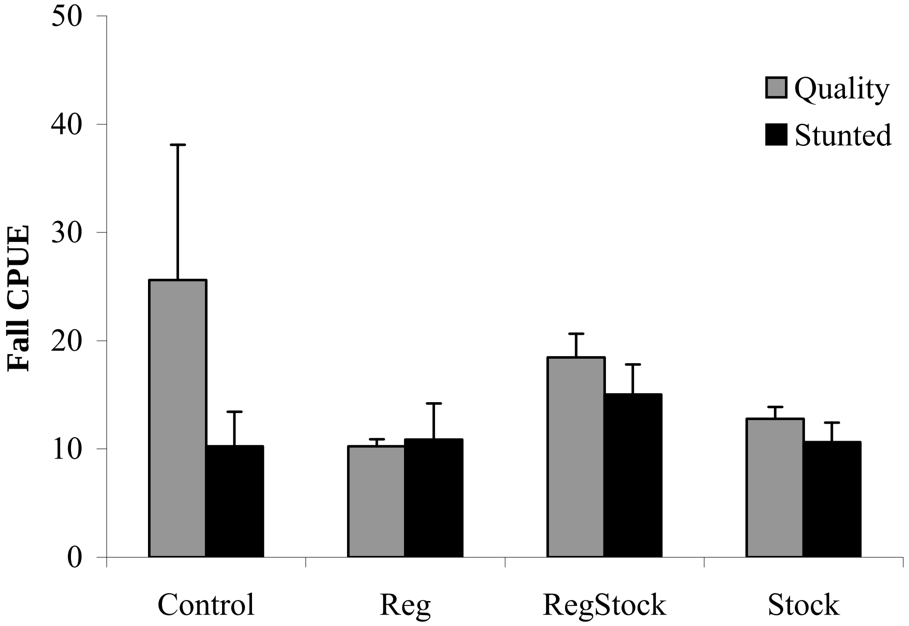


Figure 3-36: Mean fall CPUE (catch per unit effort) for largemouth bass greater than 250 mm during the experiment (2001-2005) for each treatment and population size structure of bluegill. Error bars represent the standard error.

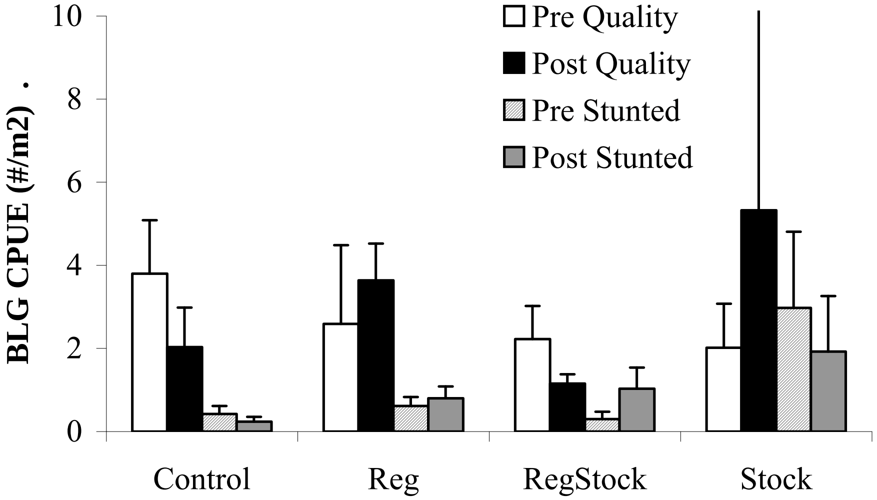


Figure 3-37: Mean bluegill abundance from seine samples for pre experiment (1996-2000) and post experiment (2001-2005) for each of the four experimental treatments. Error bars represent the standard error.

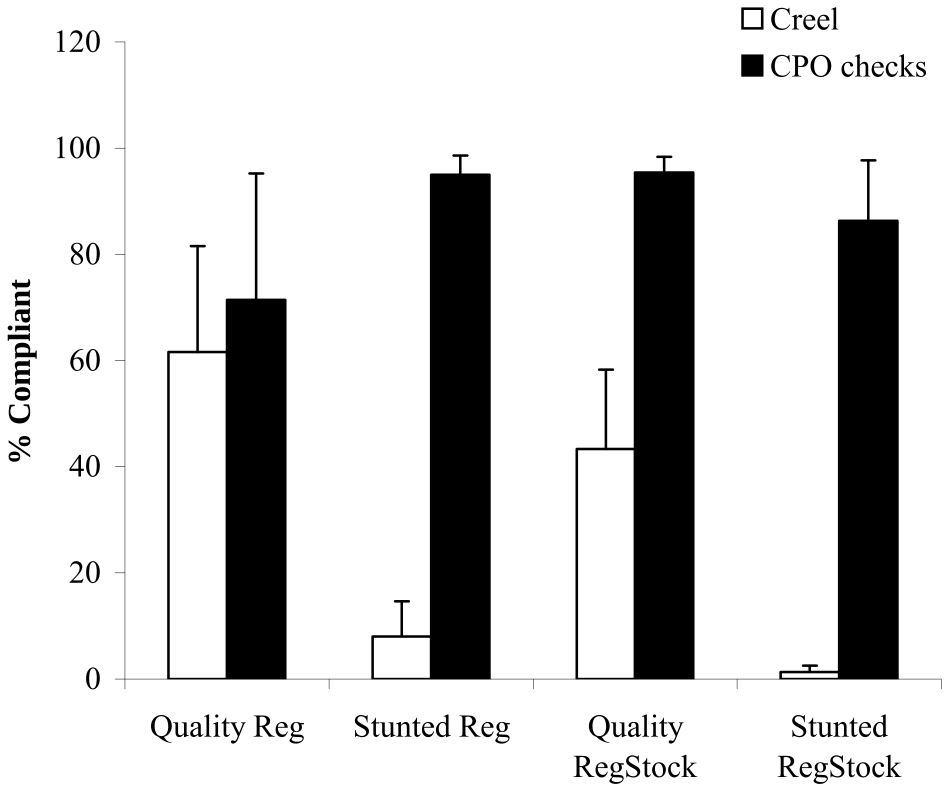


Figure 3-38: Angler compliance in all lakes with an experimental regulation of 8 inch minimum size and 10 fish bag limit for lakes designated as having quality or stunted bluegill populations for the two experimental treatments (regulation and both regulation and stocking). Percent compliance was estimated from creel surveys and conservation police officer (CPO) checks performed in 2001-2005. Error bars represent standard error.

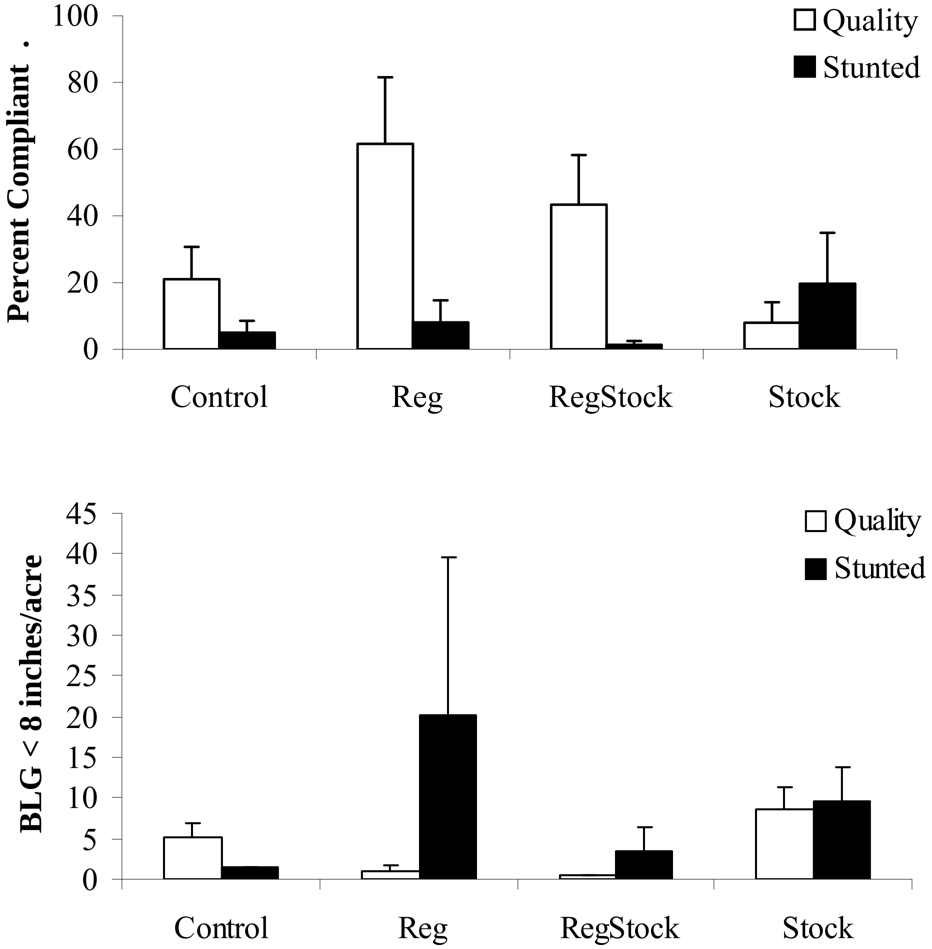


Figure 3-39: Angler harvest data from creel surveys conducted in 2002-2005. Percent compliance is the number of bluegill harvested larger than 8 inches divided by the total number of bluegill harvested on each experimental lake (top). Compliance was also assessed for each lake (bottom) as the total number of bluegill less than 8 inches harvested by anglers per surface area (acre) for each lake measured in the creel. Error bars represent standard error.

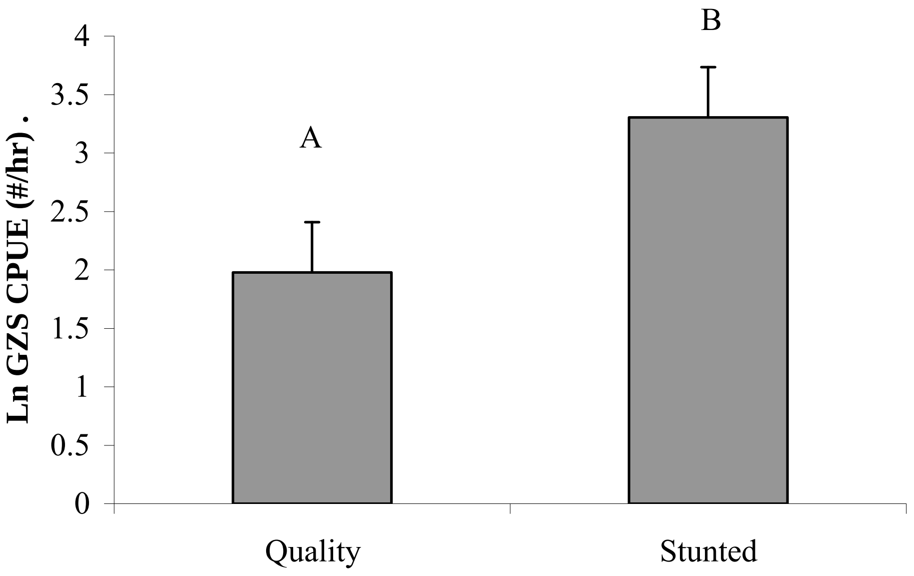


Figure 3-40: Mean gizzard shad CPUE from electrofishing samples throughout the management experiment (1996-2005) for lakes with stunted and quality bluegill populations. Error bars represent standard error and different letters represent means that are significantly different ($P < 0.05$).

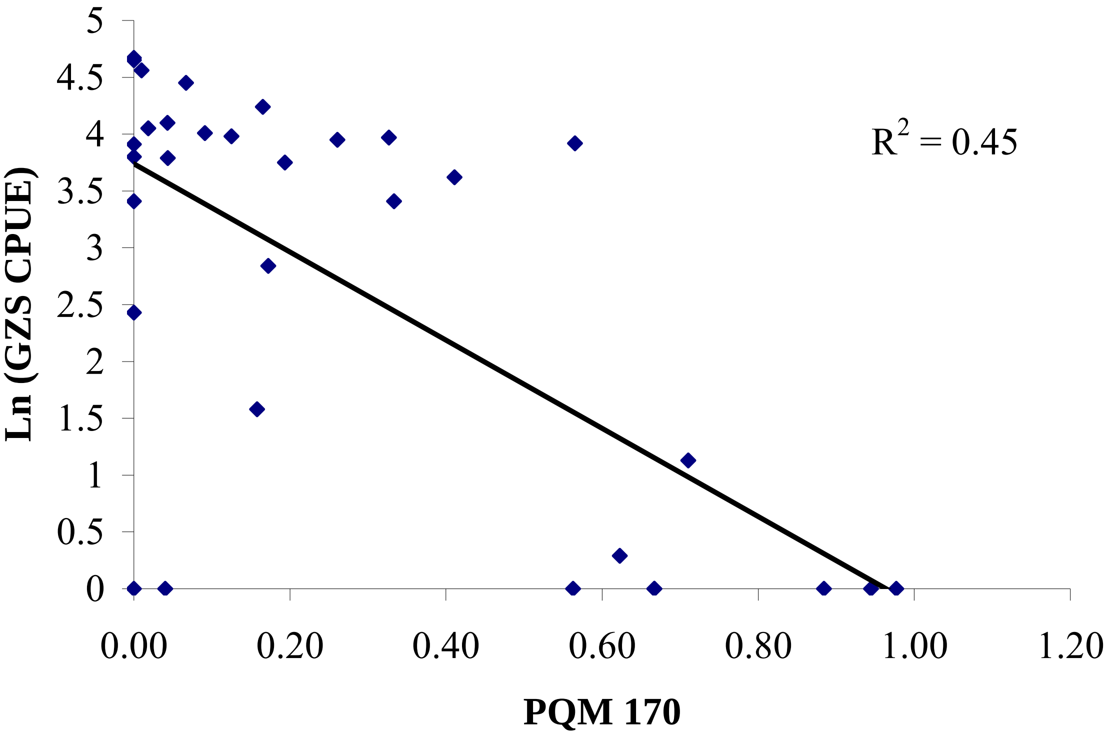


Figure 3-41: Mean gizzard shad CPUE from electrofishing samples and PQM 170 from bluegill collected in spring electrofishing samples in 2004. Gizzard shad CPUE was natural log transformed.

Appendix A

ASSESSING POPULATION-SPECIFIC AND ENVIRONMENTAL INFLUENCES ON BLUEGILL LIFE HISTORIES: A COMMON GARDEN APPROACH

Running head: genetic and social control of bluegill maturation

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Abstract. Investigations into vertebrate life histories have demonstrated trade-offs between growth and reproduction that can result in individual and population-specific variation in life-history strategies. Mechanisms to explain variation among populations, however, often remain unidentified. We examined the relative strength of genetic (population source) and environmental (population social structure) factors on variation in growth and timing of maturation for juvenile male bluegill in a common-garden experiment. We placed juvenile male bluegill collected from two different wild source populations, one with parental males that are large (>190mm total length) and one with parental males that are stunted (<155mm total length), in a common environment and varied the social structure by controlling the presence or absence of large, mature male bluegill collected from a third population. Juvenile male bluegill from both populations allocated significantly more energy to reproduction in the absence of large males than in their presence. Within ponds, differences in growth and maturation rates between juvenile males from the two source populations were small but significant. These results indicate both genetic and environmental components to growth and maturation in bluegill, but emphasize the importance of social interactions in shaping individual life-history strategies.

Key Words: social influence, maturation, population, stunted, trade-offsIntroduction

A fundamental tenant of life-history theory is that organisms must make trade-offs between somatic growth and reproductive activities (Williams 1966, Gadgil and Bossert 1970, Bell 1980, Partridge and Harvey 1988). For organisms with indeterminate growth, such as fish, this trade-off is particularly significant because fecundity is often directly related to body size (Roff 1984, Fox 1994). Life-history theory predicts that size- and age-at-maturation should evolve to maximize the lifetime reproductive success of the individual (Gadgil and Bossert 1970, Fox 1994). As a consequence, variation in timing of maturation within and among populations is common, and individuals do not always mature at the earliest opportunity (Roff 1984, Bertschy and Fox 1999). Although evidence for variable life-history strategies and documentation of the costs and consequences associated with that variation appears in the literature (see Reznick 1985 for review), underlying mechanisms driving population-specific variation often remain unexamined.

Both genetic and environmental effects can control the expression of early life-history traits (Haugen 2000). Genetic differences associated with population-specific variation in growth and maturation rates have been documented for various species of fish, particularly those in the family Salmonidae (e.g., Ricker 1981). Genetic control of timing of maturation is seen in the Montezuma swordtail (Xiphophorus montezumae), a species in which the timing of maturation is based on the presence of an ‘early’ or ‘late’ allele for a gene located on the sex chromosome (Kallman 1983). A number of environmental variables can also influence life-history strategies, and one that has been shown to have considerable influence on growth and maturation rates is the social structure of a population, e.g., large, mature males inhibiting maturation of smaller males (Borowsky 1978, Bushman and Burns 1994, Jennings et al. 1997, Danylchuk and Tonn 2001). For example, the presence of either large, mature males or large juvenile males inhibits maturation of small, juvenile male platyfish (Xiphophorus variatus Meek;

Borowsky 1978, 1987). Similarly, small fathead minnows (Pimephales promelas R.) modulate their seasonal reproductive activity based on the social structure of the population, becoming mature and spawning only in the absence of large, socially dominant males (Danylchuk and Tonn 2001). Combined, these studies elucidate the myriad mechanisms that can influence individual life histories. However, the relative importance of these variables has not been assessed, and the variable outcomes of these studies suggest the need to simultaneously consider the relative influence of genetic and environmental factors in a single experiment.

Bluegill (Lepomis macrochirus) populations exhibit complex social structures, and the life histories of individuals can be shaped by social interactions within the population (e.g., Gross 1982, Jennings et al. 1997). Jennings et al (1997) showed that the presence of large, mature males delayed the maturation of immature males. As has been the case with other species, however, the potential for genetic contribution to variation in the observed growth and maturation schedules was not assessed. It is possible that historical selection differences among populations could cause evolutionary divergence among those populations, resulting in genetic differences in life-history strategies. On the other hand, plasticity in the timing of maturation might be universal across bluegill populations; all individuals may be able to respond facultatively to environmental cues and mature at a time that optimizes their fitness. The underlying question is, what is the relative contribution of genetic and environmental factors to population-specific variation in life histories?

In this experiment, we assess the importance of genetics (population source) and environment (social interactions based on varying population size structure) in determining maturation schedules by rearing bluegill in a common environment. Juvenile individuals from two populations with different size structures and maturation schedules were used to establish experimental populations with varying social structures (presence or absence of large, mature male bluegill). We centered our analyses on males because males of many species, including bluegill, often experience strong sexual selection (e.g., Gross 1982, Jennings and Philipp 1992, Morris et al. 1992) that results in large variation in male growth rates and size-at-maturation within and among populations.

Materials and Methods

Two lakes in southeastern Illinois with established bluegill populations were chosen as sources for the juvenile males, Paris Lake, which contains a historically stunted bluegill population (mean total length of mature parental male bluegill ± 1 S.E.; 151 ± 3.9 mm, n = 200) and Lincoln Trail Lake, which contains a historically non-stunted bluegill population (198 ± 4.2 mm, n = 450). Parental males in the stunted population, in addition to being smaller, generally mature at a younger age than parental males in the non-stunted population (D. D. Aday, unpublished data). Both populations were sampled extensively via seining and electrofishing in 1996-1997 to determine the abundance, size, and age structure of the resident bluegill population. These populations were re-sampled annually (1997-2000) to ensure temporal stability in population parameters. Large, mature parental males and mature females used in the experiment were collected from a third population, Forbes Lake (also in southeastern Illinois), to avoid any relatedness with either group of juveniles.

Immature bluegill collected from each of the two source populations were added to six 0.04-ha experimental ponds at a density of 150 fish (75 from each source) per pond. Densities were within the range of natural systems (Wahl and Stein 1988), and allowed us to 1) account for initial mortality and 2) obtain a reasonable sample size of males (because only immature fish were stocked it was not possible to separate males from females). After stocking, ponds were monitored daily to remove dead or moribund fish; mortality was consistent among ponds and no mortality was observed after 6 days. Prior to establishing these experimental populations, all juveniles were measured (total length, TL; mm), given a distinctive fin clip to identify population source, and a sub-sample ($\underline{n}$ = 100; 50 from each source population) of the juveniles was removed from the initial collection. Each individual removed from the sub-sample was weighed (g), dissected to determine maturity status by visual inspection of the gonads, and aged using annual rings on scales (Regier 1962). After addition of juveniles from both source populations and five mature females from the third population to each pond, five mature males (also from the third population) were added to half of the ponds, creating a split-plot design. Mature individuals of both sexes ranged from 175-190mm in TL.

Experimental populations were established on May 15. After three months the experiment was terminated, ponds were drained, and all immature bluegill were collected, euthanized in MS-222, sorted by source population of origin (all fin clips were retained and unequivocally identified), and frozen. For analysis, all juvenile bluegill were thawed, measured (TL, mm), weighed (g), and dissected to determine sex. For males, two metrics were used to assess maturity status. The primary indication of maturation was the gonadosomatic index (GSI) for individuals, which was calculated as the ratio of wet gonad weight to total wet fish weight. Second, we assigned a gonad score (1-5) to each male to indicate maturity status based on sperm production capability; a gonad score of 1 indicated total lack of gonad development (gonads invisible or just strings weighing less than 0.01g), whereas scores of 2-5 indicated some relative degree of further gonad development (5 representing a fish in spawning condition with white testes that emitted sperm when palpated at the time of collection; Aday et al. 2002).

Also at the conclusion of the experiment, to compare the maturation status of fish in the experimental ponds with their cohorts remaining in their wild source populations, we again sampled the two source populations, collecting individuals ($\underline{n}$ = 100; 50 per population) of the same size and age cohort of the juvenile bluegill used in the experiment. These individuals were returned to the laboratory and processed identically to that of the experimental fish

Results

The size and maturity status of immature fish placed into the experimental ponds was similar at the beginning of the experiment; i.e., there was no difference (t-test, $F_{1,898} = 0.94$, $P = 0.33$) in initial total length of fish from the stunted (mean ± 1 SE; 82.0 ± 0.75mm TL, $n=450$) and non-stunted (83.1 ± 1.07mm TL, $n = 450$) source populations. There was also no difference (t-test, $F_{1,98} = 1.00$, $P = 0.32$) in weight of individuals removed from the initial sub-sample (non-stunted, 8.8 ± 0.51g, $n = 50$; stunted, 7.9 ± 0.81g, $n = 50$). In addition, all sub-sampled fish were aged 1-2 years and exhibited no gonad development or secondary sexual characteristics (i.e., all were sexually immature).

Maturation Schedules

We found both an effect of source population (split-plot, two factor ANOVA; $F_{1,4} = 13.0$, $P = 0.02$) and social structure ($F_{1,4} = 108.5$; $P = 0.0005$) on maturation schedules of juvenile males. The mean GSI of males was higher in individuals from the non-stunted population (0.10 ± 0.01, $n = 165$, versus 0.07 ± 0.01, $n = 134$ in the stunted population) and when large males were absent (Fig. 1, open bars, separated for stunted and non-stunted individuals). There was no significant interaction ($F_{1,4} = 0.06$, $P = 0.82$) between these factors in the model. Because both main factors had a significant influence on GSI, we examined the relative strengths of each factor by partitioning the variance in the model with type III sums-of-squares. These results indicated that the environmental effects (presence or absence of large males), which explained 53% of the total variation in the model, were much stronger than effects due to source population differences, which explained only 6% of the variation. The second measure of maturation, gonad score, showed similar results; gonad scores of experimental males were higher ($F_{1,4} = 10.07$; $P = 0.03$) when large males were absent (2.0 ± 0.08) than when they were present (1.1 ± 0.03). There was also no significant interaction ($F_{1,4} = 3.48$, $P = 0.14$) between the main factors (genetics and environment) on the gonad score of juveniles. The influence of mature males on gonad score is, biologically, quite meaningful. In the treatment with large males present, the average gonad score of 1.1 indicates essentially no gonad development whatsoever. In the treatment with large males absent, however, the average gonad score of 2.0 indicates that most males experienced at least some degree of maturation of the testes. Combining males with gonad scores of 2-5 from treatments with and without large males revealed that over 60% of experimental males in the treatment without large males initiated maturation during the experiment, compared to only 13% in the treatment with large males, reiterating the strong influence of large, mature males on timing of maturation of juvenile males. There was no concomitant source-population influence on gonad score; experimental males from the stunted (1.4 ± 0.06) and non-stunted (1.6 ± 0.07) populations had similar ($F_{1,4} = 1.27$; $P = 0.32$) scores.

Growth rates

At the end of the pond experiment, slight differences in growth rates were apparent between the experimental males originating from the two source populations. Although there was no difference in final total length of fish, males from the non-stunted population were heavier at the end of the experiment than males from the stunted source population (Table 1). There was no significant influence of social structure on length or weight of males (Table 1), nor was there a significant interaction between the genetic and environmental factors in the model for either length or weight ($F_{1,4} > 1.26$, $P > 0.32$). Additionally, no difference in growth of female bluegill collected in the initial sampling of the two source populations was apparent at the end of the experiment (Table 1).

Experiment versus source population comparison

We compared the maturity status of experimental males to those of the same size cohort collected from each source population at the end of the experiment. Males from each source population showed similar maturation rates (GSIs) to their cohorts in the experiment when the social structure of the experimental treatment matched the social structure of the source population (Figure 1). For example, juvenile males (0 = 107.9 ± 2.01 mm TL, n=22) collected at the end of the experiment from Lake Paris (stunted; no large, mature males present) exhibited high GSIs, similar to their experimental cohorts in treatments without large males present (Figure 1A). Likewise, juvenile males (0 = 106.9 ± 4.7 mm TL, n=22) collected from Lincoln Trail Lake (non-stunted; large, mature males present) exhibited low GSIs, similar to their cohorts in experimental treatments with large, mature males present (Figure 1B). The results from this final comparison confirm that juveniles have different maturation trajectories in the stunted and non-stunted source populations, suggesting that the maturation trajectories of juveniles in the experimental populations were a result of the treatments experienced.

Discussion

Life-history variation is common and trade-offs between growth and maturation are well documented for a variety of organisms. Understanding the mechanisms associated with population-specific variation, however, can be complicated by the potential role of genetic differences among populations. Our study is unique in that it examines genetic and environmental influences in a common environment, allowing assessment of the relative strength of each factor in shaping individual life histories. This approach is necessary to understand how genetic differences among populations might influence their responses to selective pressures in the environment. We document that there is indeed a genetic component to growth rates and maturation schedules of bluegill, but that their life histories are quite plastic and exhibit a strong response to the social structure of the population. The practical implication of this finding is that stunting may not always be an ecological condition, but rather the result of a strategic life-history decision to mature early when social conditions permit (also see Jansen 1996).

Regardless of their origin, experimental male bluegill responded facultatively to environmental cues in making decisions regarding timing of maturation; in general, juveniles delayed maturation in the presence of large, mature males and initiated gonad development in their absence. Social interactions can have a marked influence on the life histories of individuals, and social inhibition of maturation is seen in diverse taxa (see Huntingford and Turner 1987 for review). Among fish, many poeciliids exhibit male-dominated social control of maturation (e.g., Borowsky 1978, 1987, Bushman and Burns

1994). In certain wrasse species, social interactions influence the ability of females to reverse sex (Sale 1980, Warner 1984), which ultimately has a tremendous influence on an individual's reproductive success (Warner 1984). Comparisons of individuals used in the present experiment with their cohorts from each original source population confirm the importance of this mechanism in bluegill, and suggest that similar social-influence mechanisms are likely regulating maturation rates of bluegill in non-experimental populations. As with other species (e.g., Borowsky 1978, Bushman and Burns 1994), size of mature males appears to be an important determinant in these social interactions, as juveniles were not inhibited by the small parental males in the stunted source population.

In our experimental ponds, differences in population-specific growth rates and GSI were small but statistically significant; males from the non-stunted population gained more weight and exhibited higher GSIs than males from the stunted population. Because no difference in growth was apparent between females from the two sources, the difference in weight of males was either an artifact of the experiment or a sex-specific phenomenon. The variation in weight gain and GSI of males from the different source populations may reflect genetic differences between the populations. In previous studies investigating population- or stock-specific life-history parameters in species such as rainbow trout (Oncorhynchus mykiss Walbaum; Reinitz et al. 1979, Wangila and Dick 1988), chinook salmon (Oncorhynchus tshawytscha W.; Ricker 1981, Heath et al. 1993), and channel catfish (Ichtalurus punctatus R.; Silverstein et al. 1999), variable growth and maturation schedules have been attributed to genetic differences. These studies demonstrate the potential role genetic differences can play in explaining variation in life-history traits. These variable growth and maturation rates could also reflect maternal effects or prior conditioning of bluegill before addition to the experimental ponds. In any case, differences in weight gain and GSI of males from the two source populations were minor, and individuals from both source populations had sufficient plasticity to respond to environmental cues. As such, the strength of the source-population effect on timing of maturation was small relative to the influence of the social environment.

To maximize lifetime reproductive success, fish have likely evolved the ability to manipulate maturation schedules in response to environmental cues (e.g., Jennings and Philipp 1992). Our data provide evidence of the relative importance of social interactions and genetic influences on maturation schedules in male bluegill, demonstrating that individuals from isolated populations respond similarly to social cues when placed in a common environment. As such, we suggest that plasticity in maturation rates of juvenile male bluegill is not an isolated phenomenon, but rather a common one. Plastic maturation schedules would benefit fish by providing some insurance of reproductive success in a variable environment (Garvey et al. 2002). For example, in environments in which adult mortality is high, early maturity might be favored (e.g., Fox 1994). Because of trade-offs between growth and maturation, however, early maturation will likely also result in a smaller, stunted body size that might reduce competitive ability in other environments. Because of the direct relationship between body size and reproductive success in bluegill (Gross 1982), the ability of a juvenile male to assess future reproductive success before making energetically expensive maturation decisions is likely critical for optimization of fitness (Borowsky 1973). This pattern of plastic maturation schedules influenced by environmental cues may be common; similar studies will be necessary with other species to fully understand the relative contributions of genetic and environmental variation to individual life-history strategies, and how that variation influences populations.

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Literature Cited

Aday, D.D., C.M. Kush, D.H. Wahl, and D.P. Philipp. 2002. The influence of stunted body size on reproductive ecology of bluegill Lepomis macrochirus. Ecology of Freshwater Fish. **11**:190-195.

Bell, G. 1980. The costs of reproduction and their consequences. American Naturalist **116**:45-76.

Bertschy, K.A., and M.G. Fox. 1999. The influence of age-specific survivorship on pumpkinseed sunfish life histories. Ecology **80**:2299-2313.

Borowsky, R.L. 1973. Social control of adult size in males of Xiphophorous variatus. Nature **245**: 332-335.

Borowsky, R.L. 1978. Social inhibition of maturation in natural populations of Xiphophorus variatus (Pisces: Poeciliidae). Science **201**:933-935.

Borowsky, R.L. 1987. Agonistic behavior and social inhibition of maturation in fishes of the genus Xiphophorus (Poeciliidae). Copeia **1987**:792-796.

Bushman, P.J., and J.R. Burns 1994. Social control of male sexual maturation in the swordtail characin, Corynopoma riisei. Journal of Fish Biology **44**:263-272.

Danylchuk, A.J., and W.M. Tonn. 2001. Effects of social structure on reproductive activity in male fathead minnows (Pimephales promelas). Behavioral Ecology **12**:482-489.

Fox, M.G. 1994. Growth, density, and interspecific influences on pumpkinseed sunfish life histories. Ecology **75**:1157-1171.

Gadgil, M., and W.H. Bossert. 1970. Life historical consequences of natural selection. American Naturalist **104**:1-24.

Garvey, J.E., T.P. Herra, and W.C. Leggett. 2002. Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. Ecological Applications **12**:194-205.

Gross, M.R. 1982. Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. Zeitschrift. Tierpsychologie **60**:1-26.

Haugen, T.O. 2000. Early survival and growth in populations of graylings with recent common ancestors-field experiments. Journal of Fish Biology **56**:1173-1191.

Heath, D.D., N.J. Bernier, J.W. Heath, and G.K. Iwama. 1993. Genetic, environmental, and interaction effects on growth and stress response of Chinook salmon (Oncorhynchus tshawytscha) fry. Canadian Journal of Fisheries and Aquatic Sciences **50**:435-442.

Huntingford, F.H. and A. Turner. 1987. Animal conflict. Chapman and Hall, London, UK.

Jansen, W.A. 1996. Plasticity in maturity and fecundity in yellow perch *Perca flavescens* (Mitchill): comparisons of stunted and normal-growing populations. Annales Zoologici Fennici **33**:403-415.

Jennings, M.J. and D.P. Philipp. 1992. Reproductive investment and somatic growth in longear sunfish. Environmental Biology of fishes **35**: 257-271.

Jennings, M.J., J.E. Claussen, and D.P. Philipp. 1997. Effect of population size structure on reproductive investment of male bluegill. North American Journal of Fisheries Management **17**:516-524.

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Kallman, K.D. 1983. The sex determining mechanism of the poecilid fish Xiphophorus montazumae and the genetic control of the maturation process and adult size. Copeia **1983**:755-768.

Morris, M.R., P. Batra, and M.J. Ryan. 1992. Male-male competition and access to females in the swordtail Xiphophorus nigrensis. Copeia **1992**:980-986.

Partridge, L., and P.H. Harvey. 1988. The ecological context of life history evolution. Science **241**:1449-1454.

Regier, H.A. 1962. Validation of the scale method for estimating age and growth of bluegills. Transactions of the American Fisheries Society **91**:362-374.

Reinitz, G.L., L.E. Orme, and F.N. Hitzel. 1979. Variations of body composition and growth among strains of rainbow trout. Transactions of the American Fisheries Society **108**:204-207.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257-267.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences **38**:1636-1656.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences **41**:989-1000.

Silverstein, J.T., W.R. Wolters, and M. Holland. 1999. Evidence of differences in growth and food intake regulations in different genetic strains of channel catfish. Journal of Fish Biology **54**:607-615.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanography and Marine Biology Annual Review **18**:367-421.

Wahl, D.H., and R.A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society **117**: 142-151.

Wangila, B.C.C., and T.A. Dick. 1988. Influence of genotype and temperature on the relationship between specific growth rate and size of rainbow trout. Transactions of the American Fisheries Society **117**:560-564.

Warner, R.R. 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: A test of the life historical consequences. Evolution **38**:148-162.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist **100**:687-690.

Table 1. Final sizes of juvenile bluegill from the two source (non-stunted and stunted) populations in the experimental ponds (half with large mature males, half without).

	Males		Females	
	TL [†] (mm)	TW [‡] (g)	TL (mm)	TW (g)
Source populations:				
Stunted	104 (0.8)	19.3 (0.6)	103 (0.7)	19.4 (0.3)
Non-stunted	106 (0.6)	21.1 (0.5)	105 (0.7)	19.6 (0.5)
P-value	0.12	0.04	0.14	0.92
Social structure:				
Large males present	102 (0.6)	18.0 (0.4)	102 (0.72)	18.0 (0.3)
Large males absent	108 (0.7)	23.0 (0.5)	106 (0.6) (0.4)	21.6
P-value	0.13	0.08	0.25	0.14

[†] TL is total length

[‡] TW is total weight Notes: Data are means ± 1 SE. P-values generated with split-plot ANOVA procedure. Data were log transformed to meet assumptions of ANOVA.

Figure legends

Fig. 1. Mean gonadosomatic indices of experimental males in the treatment ponds with and without large, mature males (open bars) and from their cohorts collected during the re-sampling of the source populations at the end of the experiment (shaded bars). The top panel shows results for males collected from the stunted population and the bottom panel for males collected from the non-stunted population. Error bars are ± 1 standard error. Different letters over error bars represent significant differences between groups (ANOVA; ∀ = 0.05).

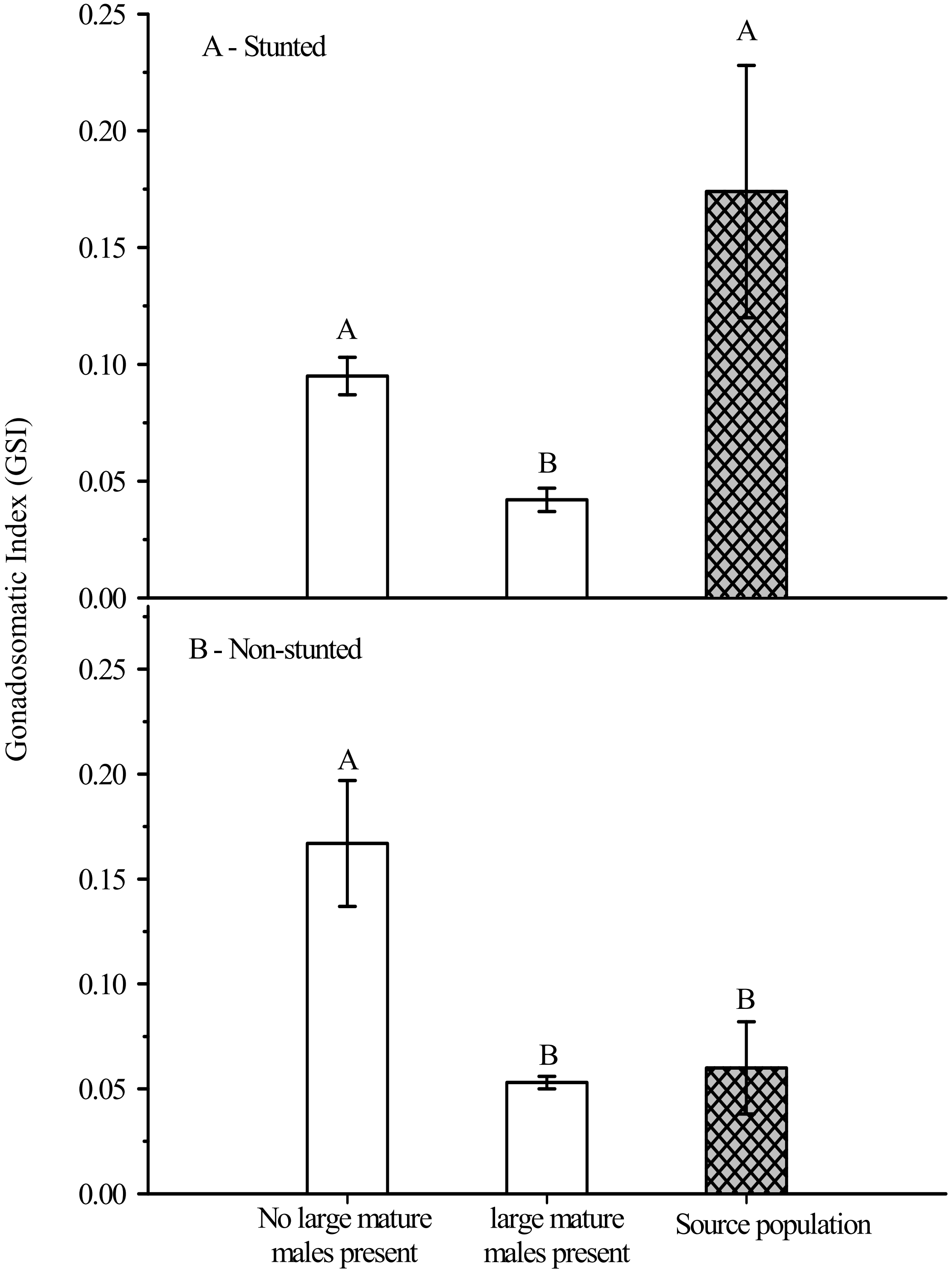
A - Stunted
B - Non-stunted
Gonadosomatic Index (GSI)
0.00
0.05
0.10
0.15
0.20
0.25
A
B
A
A
B
B
No large mature males present
large mature males present
Source population

Figure 1.

Appendix B

Sex-specific life history patterns in bluegill (*Lepomis macrochirus*): interacting mechanisms influence individual body size

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Abstract The ultimate body size that individual fish achieve can be a function both of direct effects of growth or indirect effects associated with the timing of sexual maturation (and associated energetic tradeoffs). These alternatives are often invoked to explain variation in body size within and among fish populations, but have rarely been considered simultaneously. We assessed how resource availability and timing of maturation interact to influence individual body size of bluegill (*Lepomis macrochirus*). Resource availability (high and low food) and the social structure of the population (presence or absence of large, mature males) was varied in experimental ponds. Food ration affected growth (larger fish in the high food treatments) and the social structure of the population affected timing of maturation (early maturation of males in the absence of large males). Treatment effects, however, were sex-specific; males responded to the social structure of the population and females were more responsive to resource availability. We also found that individuals that became sexually mature were smaller than those that remained immature, although results were sex-specific and resource dependent. For males, individuals that matured were smaller when resources were limited; mature and immature females showed no difference in body size regardless of food ration. We show that both resource availability and the processes that control timing of maturation interact in sex-specific ways to influence body size of bluegill. These results suggest that a more robust explanation for variable body size requires consideration of sex-specific interactions between ecological (food and growth) and evolutionary (timing of maturation) mechanisms.

Key words: variation, resource availability, social influence, body size

Introduction

The variable nature of individual life histories has been well documented in a wide variety of fish species (e.g.,Schaffer and Elson 1975; Ricker 1981; Roff 1984). Understanding the consequences of that variation requires consideration of tradeoffs that individuals face when allocating energy to major life processes (e.g., growth, reproduction, and survival; e.g., Williams 1966; Gadgil and Bossert 1970; Stearns 1976). Because of these tradeoffs in energetic expenditures, individual variation in life-history strategies should result in population-level variation in age and, in particular, size structure. Fish make particularly good models for examining life-history variation and energetic tradeoffs because they exhibit indeterminate growth and, as such, there is often a direct relationship between fecundity and body size (Roff 1983, 1984). Additionally, inter-population variation in size structure is common. Despite considerable interest in this particular aspect of population structure (e.g., Mann and McCart 1981; Diana 1987; Jansen 1996; Ylikarjula et al. 1999), we lack a clear understanding of the underlying mechanism(s), particularly in relation to the ways in which the ecology and life history of organisms might interact to influence body size.

One question is whether interpopulation variation in adult body size is primarily a reflection of ecological (e.g., food resources influence growth rates) or evolutionary (e.g., timing of sexual maturation) processes. To date, much attention to mechanisms associated with intraspecific variation in population size structure has focused on resource levels and growth rates (e.g., Persson 1983; Belk 1993; Mittelbach and Osenburg 1993). A variety of proximate factors can lead to slow growth, including competition for limited resources (e.g., Diana 1987), lack of appropriate size and taxa of prey (Konkle and Sprules 1986; Donald and Alger 1986; Amundsen and Klemetsen 1988), and absence of top predators (e.g., Damsgard and Langeland 1994; Ridgway and Chapleau 1994), and this slow growth should conceivably diminish individual body size of adults. An alternative explanation considers variable body size within the context of life-history theory, and focuses on the energetic tradeoff between growth and maturation. Numerous investigations have considered this energetic tradeoff and the influence it has on adult body size (e.g., Danylchuk and Fox 1994; Jennings et al. 1997; Ylikarula et al. 1999; Morita and Morita 2002).

Although the ‘ecology vs. evolution’ dichotomy can serve as a framework for understanding variable size structure, the underlying mechanisms may be complex. That is, food availability (presumably an ‘ecological’ mechanism) might indeed influence body size directly via growth rate. Conversely, expectation of future food availability could indirectly influence body size by affecting individual decisions regarding timing of sexual maturation (a more ‘evolutionary’ response, e.g., Roff 1983, 1984). The latter response can be further complicated in species that also exhibit social control over maturation processes, particularly when the social interactions are size-based. This creates an interaction between body size and timing of maturation that might be influenced by current or future food availability.

In this investigation, we quantify sex-specific growth and maturation patterns for bluegill (*Lepomis macrochirus*), a species that exhibits size-based social interactions and highly variable population size structures. Specifically, we were interested in the ways in which resource availability and social conditions might influence tradeoffs between growth and timing of maturation, and how this might translate into effects on individual body size. The variable nature of aquatic environments (e.g., Winemiller and Rose 1992) provide an appropriate system in which to test these hypotheses; variation in environmental conditions place ecological constraints on organisms that must be responded to via evolutionary pathways. Further, because of their variable life histories and virtually ubiquitous distribution in freshwater ecosystems, bluegill represent an excellent model system for understanding interactions between growth and maturation in different environments. From previous investigations, it appears that both growth rate (e.g., Swingle and Smith 1941; Otis et al. 1998) and the timing of maturation (Jennings et al. 1997; Aday et al. 2003) influence population size structure. We know that the bluegill is a particularly social species (Gross 1982), and that interactions with large, adult males can cause juvenile males to delay maturation (Jennings et al. 1997; Aday et al. 2003). As such, we would predict that body size of both males and females would be influenced directly by resource availability, and that males would also be influenced by social interactions. We currently lack empirical quantification, however, of interactions between these resource-based energy allocation decisions and socially-mediated maturation schedules. That is, it is not clear how social interactions might be influenced by variable food resources, e.g., can additional food resources negate the influence of large males by allowing juvenile males to both mature and continue to grow despite the presence of large males? Are females similarly influenced by the male social environment? There are also uncertainties regarding how the outcome of these interactions might be manifested differently in males, which provide parental care to eggs and fry (Gross 1982), and females, which provide no parental care and, therefore, have different energetic requirements associated with reproduction.

Herein, we assess the interaction between growth and timing of maturation for bluegill raised in ponds with different levels of food resources and ask two questions. First, how does resource availability and the social structure of the population influence growth and maturation schedules of immature male and female bluegill? Second, how does growth interact with timing of maturation to influence individual size in different environments? To examine these two questions, we manipulated both the food resources (high or low) and the social structure (presence or absence of large, mature males) of bluegill populations established in experimental ponds. Because bluegill, like many fish species, exhibit sex-specific differences in life-history strategies (e.g., Gross 1982), we evaluated growth and maturation for each sex independently.

Materials and methods

Experiments were conducted in eight 0.04-ha ponds located at the Illinois Natural History Survey's Sam Parr Biological Station in south-central Illinois. The ponds were clay lined and supported naturally colonized zooplankton, macroinvertebrates, and aquatic vegetation. Before the experiment, all ponds were drained and allowed to remain dry for several weeks. To discourage macrophyte growth we applied Sonar® herbicide to each pond at a rate of 1.8 l ha^{-1} in early spring. This treatment reduced macrophyte density but did not eliminate plant growth in the ponds. To create differences in resource availability, ponds were either fertilized to encourage zooplankton growth and production (high food treatment ponds; n = 4) or treated with copper sulfate ($CuSO_4$) to decrease algal production (low food treatment ponds, n = 4). To the high food treatment ponds, organic fertilizer was applied on two separate occasions in spring, prior to the addition of experimental fish, by adding a 10:1 ratio of pelleted alfalfa and ground soybean (227 kg ha^{-1}) to dry yeast (22.7 kg ha^{-1}). On the same dates, CuSO4 (an algacide commonly used in aquatic systems due to its low residual toxicity; Boyd and Lichtkoppler 1979) was applied at a rate of 5.7 kg ha^{-1} to the low food treatment ponds.

To determine baseline food availability for each pond, at the beginning of the experiment zooplankton were collected with a clear acrylic tube sampler (2.0 m long X 0.03-m diameter, 2 samples per pond), filtered through a 64-:m mesh net, and preserved in Lugols solution. In the laboratory, zooplankton samples were standardized to a constant volume (100ml) and 1-ml subsamples were drawn for identification and enumeration. Zooplankton were identified to the lowest possible taxa with a dissecting microscope, counted until reaching either 200 individuals from each taxon or until 10% of the sample was processed, and the subsamples were used to determine total numbers of zooplankton in the original samples (Dettmers and Stein 1992, Welker et al. 1994). After addition of fish, bluegill in the high food treatment ponds received supplemental feeding of 3-mm pelleted food (40% protein, 10% fat, 6% fiber, 10% moisture, 10% fish) throughout the experiment at a rate of 1.2 kg ha^{-1} day^{-1}. Because supplemental food was provided to the high-food treatments, zooplankton samples were not collected after initiation of the experiment. Ponds in the low food treatment group received no supplemental feeding.

Bluegill used in the experiment were collected from two lakes; mature males and females were collected from Forbes Lake (Marion Co., IL; Latitude: 384250, Longitude: 884455) and immature bluegill were collected from Sam Parr Lake (Jasper Co., IL; Latitude: 390052, Longitude: 88078). Sam Parr Lake has a non-stunted bluegill population and individuals generally become sexually mature at ages 2-4. Although this lake contains males of normal size, we chose to collect the mature individuals from Forbes Lake due to its high abundance of large individuals. Sex determination of mature fish was done by visual inspection; bluegill exhibit sexual dimorphism and males are easily distinguished from females when mature. Because immature fish exhibit no secondary sexual characteristics, no attempt was made to determine sex of these individuals prior to experimentation. All mature males and females were measured (total length, TL; all individuals > 200mm) and weighed (g; all individuals > 150g). A sub-sample (n=160) of juveniles was measured (TL, mm) and weighed (g) before addition to experimental ponds. Ten mature female bluegill and 50 immature bluegill were added to all experimental ponds. Ten mature male bluegill were added randomly to half of the ponds, thus creating a factorial design (two ponds each: high food plus large, mature males; low food plus large, mature males; high food without large, mature males; low food without large, mature males). Ponds were completely stocked on 2 June and were individually drained from 16-17 August (approximately eight weeks after introduction of fish), well within the natural spawning period of bluegill in south-central Illinois

(Santucci and Wahl 2003). All fish were collected, weighed (g), measured (TL, mm) and frozen for later analysis. In the laboratory, fish were thawed and their gonads were dissected and weighed (g). We used gonad weight and maturity status (see below) as an indication of the degree of sexual maturation for each bluegill.

Our response variable for sexual maturation included both a quantitative and a qualitative component. First, we weighed the gonad mass of each individual. Next, we determined the maturity status of all individuals collected by visually assessing their gonads. Males were considered sexually mature when they had gonad:body weight ratios of at least 0.5% and testes were fully developed and running sperm. Females were considered sexually mature when they had gonad:body weight ratios of at least 1.0% and yolked eggs were present (e.g., Justus and Fox 1994). A higher threshold value was assigned to females because ovaries are generally larger than testes in similarly-sized fish. We chose this combined qualitative and quantitative assessment of maturity status because it provided a more robust indication of maturity than either metric individually (e.g., although many individuals had large, ripe gonads, others had gonads that were large but undeveloped or small and ripe). This classification of individuals allowed us to compare growth of mature and immature individuals (across ponds, and within high and low resource ponds) and to determine the ways in which food resources interact with maturation schedules to influence individual body size.

Statistical Analyses

The experiment was designed as a 2 X 2 nested factorial, with individual fish nested within ponds. This design accounts for pond-to-pond variation when interpreting the influence of the main effects on response variables. Data were analyzed with two-factor analysis of variance (ANOVA), with food level and presence/absence of males as the main effects. We tested for differences in body size and maturation rates of previously immature male and female bluegill. Two-factor ANOVA was also used to analyze larval fish numbers and biomass in experimental ponds. Single-factor ANOVA was used to determine the difference in body size and gonad weight between mature and immature fish in high and low resource ponds. Significant ANOVAs were followed by pairwise tests using least-squares mean separation. Chi-square analysis and contingency tables were used to determine differences in the percent of individuals that became mature or remained immature in ponds with or without large males and with high or low food resources.

Results

Initial Conditions

Zooplankton densities at the beginning of the experiment were higher in the high food treatment ponds than in the low food ponds, indicating that the fertilization and herbicide treatments had the predicted effect on zooplankton production. We focused on crustacean zooplankton (excluding copepod nauplii and rotifers) because these taxa are important prey for bluegill, and because they dominated our zooplankton samples. Crustacean zooplankton density was significantly higher (ANOVA; $\underline{F}_{1,7} = 117$, $\underline{P} < 0.0001$) in the fertilized (high food) ponds (mean ± 1 SE; 300 ± 20 L^{-1}) than in the unfertilized (low food) ponds (61 ± 20 L^{-1}). Despite this difference in resource level, ponds in the low food treatment still contained substantial zooplankton populations. At the beginning of the experiment there was no difference among treatments (two factor ANOVA; $\underline{F}_{1,4} < 2.53$, $\underline{P} > 0.19$; interaction term; $\underline{F}_{1,4} < 0.47$, $\underline{P} > 0.53$) for initial length or weight of bluegill (Table 1).

Growth

At the end of the experiment, the interaction between food resources and presence of large males did not significantly affect length or weight of either sex ($\underline{F}_{1,4} < 1.3$, $\underline{P} > 0.32$). Individually, however, food resources influenced body size of both sexes; juveniles were significantly longer (ANOVA; males: $\underline{F}_{1,4} = 15$, $\underline{P} = 0.01$; females: $\underline{F}_{1,4} = 8.0$, $\underline{P} = 0.05$) and heavier (males: $\underline{F}_{1,4} = 13$, $\underline{P} = 0.02$, Fig. 1; females: $\underline{F}_{1,4} = 6.0$, $\underline{P} = 0.07$, Fig. 2) in the high food treatment ponds than in the low food ponds. The presence of large males, conversely, had no influence on length or weight of juvenile males ($\underline{F}_{1,4} = 0.14$, $\underline{P} = 0.71$, Fig. 1) or females ($\underline{F}_{1,4} = 1.5$, $\underline{P} = 0.23$, Fig. 2) in the experiment.

Maturation

Across all ponds and both sexes, about one-third of the previously-immature bluegill became sexually mature. Spawning occurred in all experimental ponds (even those without mature males added), providing evidence that juveniles indeed became sexually mature. Further, larvae were collected in each of the ponds. There were, however, sex-specific differences in the proportion of individuals that became mature; across all ponds, almost half of the females matured, whereas only about 13% of males matured (Fig. 3). In addition, social structure had a strong influence ($X^2 = 7.7$, $\underline{P} = 0.005$, df = 1) on the proportion of males that matured; the rate of maturation for juvenile males in the absence of large males was four times higher than in their presence (Fig. 3). In contrast, food ration had no effect ($X^2 = 0.20$, $\underline{P} = 0.66$, df = 1) on the proportion of juvenile males that matured. For females, the presence of large males had no influence ($X^2 = 0.007$, $\underline{P} = 0.9$, df = 1) on the proportion of individuals that matured, whereas food ration had a large influence ($X^2 = 20$, $\underline{P} = 0.0001$, df = 1); over twice as many females matured in the high food treatment ponds as in the unsupplemented ponds (Fig. 3).

We also compared length and weight of fish that remained immature to those that became mature and found that, across both sexes and all ponds, individuals remaining immature were significantly longer (ANOVA; $\underline{F}_{1,321} = 3.6$, $\underline{P} = 0.05$) and heavier ($\underline{F}_{1,321} = 8.7$, $\underline{P} = .003$) than those that matured. The size difference between mature and immature individuals, however, was both sex-specific and dependent on food resources. For juvenile males, individuals that became mature in the low food ponds were significantly smaller ($\underline{F}_{1,84} = 7.15$, $\underline{P} = 0.009$) than those that remained immature (Table 2). In the high food treatment, however, there was no difference in length ($\underline{F}_{1,82} = 1.55$, $\underline{P} = 0.22$) or weight ($\underline{F}_{1,82} = 0.84$, $\underline{P} = 0.36$) of mature and immature individuals (Table 2). For females, there was no difference ($\underline{F} < 1.98$, $\underline{P} > 0.16$) in length or weight of individuals that became mature and those that remained immature in either food treatment (Table 2).

Discussion

Life history theory assumes that individuals face energetic tradeoffs between growth and maturation, and previous studies have established predictions for the ways in which various energy – allocation strategies might influence body size (e.g., Roff 1984; Stearns and Koella 1986). Our investigation builds on that literature by specifically examining the factors affecting individual, sex-specific patterns of energy allocation. We demonstrate that male and female bluegill respond to different environmental cues when determining when to mature and how much energy to invest in reproduction; males respond to social interactions and females respond to resource availability. These patterns have implications for understanding variation in adult body size, and are consistent with theoretical predictions regarding sex – specific energetic constraints and fitness.

For females, theory suggests that fitness is often resource limited, due in part to relative high (compared to males) energetic demand of gamete production (e.g., Bateman 1948; Trivers 1972; Whiteman 1997). As with other organisms, in most teleost fishes this results in a direct relationship between body size and female fecundity (Bell 1980; Roff 1983). A number of investigations have quantified the influence of resource availability on female reproductive strategies (e.g., Abrahams and Dill 1989; Whiteman 1997; Fox and Crivelli 1998), and we find similar patterns with bluegill. Despite most females in our experiment exhibiting some gonad development, there was a substantial difference between the treatments in the proportion of females that actually became reproductively mature; a much higher proportion of females in the high food ponds had mature eggs ready for spawning than in the low food ponds (which had a much higher proportion of individuals with underdeveloped egg masses). This indicates that resource availability influences not just gonad maturation, but also reproductive output of female bluegill. A similar relationship between resource availability and reproductive output of females has been suggested for other fish (Hirshfield 1980; Fletcher and Wootton 1995), including the congeneric pumpkinseed sunfish (*Lepomis gibbosus;* Fox 1994; Fox and Crivelli 1998).

Bateman's principle suggests that because sperm is not costly to produce, male fitness should be driven instead by access to females (Bateman 1948), and our results are consistent with that hypothesis. Maturation of juvenile males in our experiment was strongly influenced by social interactions with large males regardless of resource level. Male bluegill compete for access to the best positions in colonies, and reproductive success is often directly related to body size (e.g., Gross 1982; Aday et al. 2002). Access to females appears to drive this pattern, as females have been shown to spawn preferentially with large males that can better defend their offspring or that can compete for positions in colonies that reduce predation on eggs and fry (Gross and MacMillan 1981; Claussen 1991). The inhibition of juvenile males forces them to invest in growth to achieve a larger body size before becoming mature, presumably increasing their reproductive success by being better able to compete for access to females. Although social inhibition of male maturation has been documented in a variety of fish (e.g., Borowsky 1978, 1987; Sohn 1978; in bluegill: Jennings et al. 1997; Aday et al. 2003), this is the first investigation we are aware of that quantifies the interaction between socially – mediated maturation schedules and resource availability. Our results demonstrate that juvenile males are inhibited by larger males regardless of resource level, and also point to the potential for interesting growth – maturation tradeoffs that are dependent on resource availability (see below).

Body Size

Body size is a fundamental determinant of an organism's ecology (Werner and Gilliam 1984), and our results indicate sex – specific patterns associated with body size and maturity. Males that became reproductively mature were smaller than those that remained immature in the low resource treatments, yet mature and immature females were of similar size regardless of resource level. One interpretation of the result with males is that the difference in body size is reflective of a somatic cost to sexual maturation. Because we do not have data on individual growth rates of juveniles after initiation of maturation, we cannot specifically quantify a growth cost associated with sexual maturity. However, measuring the difference in body size between these groups may provide some insight into growth - maturation tradeoffs that individuals would be expected to face under natural circumstances. For example, individual males that matured early in the low food treatment were significantly smaller at the conclusion of the experiment than those that remained immature, whereas there was no decrease in size of early-maturing fish in the high food treatment. These results could reflect the interaction between socially - mediated early maturation schedules and resource availability. When resources are limited, individuals likely face an energetic tradeoff between growth and maturation in which gonad maturity occurs at the expense of growth. An alternative to this explanation is that maturation in our experiment was simply a function of initial body size (i.e., only initially very large or small individuals became mature). If the difference in body size does reflect an energetic tradeoff, however, this observation has implications for understanding the potential influence of size - selective angling practices that often disproportionately remove large males from populations (Coble 1988). In resource-limited environments, the removal of large males and disruption of social interactions could result in a reduction in the size of adult males due to their early investment in maturation (as in Beard and Essington 2000).

In the case of females, food resources were apparently abundant enough to allow continued somatic tissue growth during and immediately after gonad maturation. In the high food ponds, juvenile females presumably had adequate resources to allow for growth and maturation, similar to juvenile males in the high food treatments. In the low food ponds, where a tradeoff would be expected, however, mature females were not significantly smaller than immature females. Anecdotally, females in the low resource ponds exhibited lower gonad weights than those in the high resource ponds. Lower gonad weights of mature females in the low-resource ponds than in the high-resource ponds may indicate a compensatory response in which females favored somatic growth when food was scarce, thus maintaining body size at the expense of further gonadal growth. This resource - allocation pattern may have contributed to the lack of difference in body size between mature and immature fish. Another explanation is that our experiment was too short to observe differences between mature and immature females that are often found only after the reproductive season ends. Justus and Fox (1994) found that mature and immature female pumpkinseeds showed no difference in size during the reproductive season, but that differences in growth became apparent after spawning ceased. Additional studies beyond the reproductive season will be necessary to determine whether bluegill females ultimately face a quantifyable cost of maturation.

Previous investigations have demonstrated that growth rates and maturation schedules can each influence body size (e.g., growth: Persson 1983; Belk 1993; Mittelbach and Osenburg 1993; maturation: Stearns 1992). Our study is unique, however, in that we specifically examine the interaction between factors that directly influence growth and timing of maturation and the consequences these interactions have for juveniles of both sexes in a system characterized by complex social interactions. From a theoretical standpoint, our study has implications for understanding the ways in which different fitness consequences and energetic constraints for males and females result in sex-specific life history strategies. Our results also have application in the context of resource management. For example, we demonstrate that traditional, single-dimension paradigms regarding interpopulation variation in size structure do not accurately reflect the complex nature of ecological and evolutionary mechanisms that can ultimately cause high variability in adult body size. Using ‘stunting’ (a condition in which all individuals in certain populations remain small relative to conspecifics in other populations) as an example, we believe that resource conservationists will often be faced with multiple mechanisms that contribute to the creation and maintenance of stunted populations, and that the proximate and ultimate solutions to remedying the problem may be different. In the case of bluegill, management manipulations that focus only on resource availability (as has often been the case in the past) would fail to address what is one underlying problem, early maturation of small males. A more robust approach would both foster conditions in which individuals can obtain adequate food resources and simultaneously protect large, vulnerable individuals from harvest, thereby conserving the size - structured interactions within the population.

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References

Abrahams MV, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. Ecology 70:999-1007

Aday DD, Kush CM, Wahl DH, Philipp DP (2002) The influence of stunted body size on the reproductive ecology of bluegill *Lepomis macrochirus.* Ecol Freshwat Fish 11:190-195

Aday DD, Wahl DH, Philipp DP (2003) Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. Ecology 84: 3370-3375

Amundsen, P.A., and Amundsen PM, Klemetsen A (1988) Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr, *Salvelinus alpinus* L., in Takvatn, northern Norway. J Fish Biol 33:697-709

Bateman AJ (1948) Intrasexual selection in Drosophila. Heredity 2:349-368

Beard TD, Essington TE (2000) Effects of angling and life history processes on bluegill size structure: Insights from an individual-based model. Trans Am Fish Soc 129:561-568

Belk MC (1993) Growth and mortality of juvenile sunfishes (*Lepomis sp.*) under heavy predation. Ecol Freshwat Fish 2:91-98

Bell G (1980) The costs of reproduction and their consequences. Am Nat 116:45-76

Borowsky RL (1978) Social inhibition in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). Science 201:933-935

Borowsky RL (1987) Agonistic behavior and social inhibition of maturation in fishes of the genus Xiphophorus (Poeciliidae). Copeia 1987:792-796

Boyd CE, Lichtkoppler F (1979) Water quality management in pond fish culture. Research and Development Series 22. Auburn University, Auburn, Alabama.

Claussen JC (1991) Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. Master's Thesis, University of Toronto, Toronto

Coble DW (1988) Effects of angling on bluegill populations: management implications. N Am J Fish Man 8:277-283

Damsgard B, Langeland A (1994) Effects of stocking piscivorous brown trout, *Salmo trutta*, L. on stunted Arctic charr, *Salvelinus alpinus*, L. Ecol Freshwat Fish 3:59-66

Danylchuk AJ, Fox MG (1994) Seasonal reproductive patterns of pumpkinseed (*Lepomis gibbosus*) with varying body size characteristics. Can J Fish Aquat Sci 51:490-500

Dettmers JM, Stein RA (1992) Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. Trans Am Fish Soc 121:494-507

Diana JS (1987) Simulation of mechanisms causing stunting in Northern pike populations. Trans Am Fish Soc 116:612-617

Donald DB, Alger DJ (1986) Stunted lake trout (*Salvelinus namaycush*) from the Rocky mountains. Can J Fish Aquat Sci 43:608-612

Fletcher DA, Wootton RJ (1995) A hierarchical response to differences in ration size in the reproductive performance of female three-spined sticklebacks. J Fish Biol 46:657-668

Fox MG (1994) Growth, density and interspecific influences on pumpkinseed life histories. Ecology 75:1157-1171

Fox MG, Crivelli AJ (1998) Body size and reproductive allocation in a multiple spawning centrarchid. Can J Fish Aquat Sci 55:737-748

Gadgil M, Bossert WJ (1970) Life historical consequences of natural selection. Am Nat 104:1-24

Gross MR (1982) Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. Z Tierpsychol 60:1-26

Gross MR, MacMillan AM (1981) Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). Behav Ecol Sociobiol 8:163-174

Hirshfield MF (1980) An experimental analysis of reproductive effort and cost in the Japanese Medaka *Oryzias latipes.* Ecology 61:282-292

Jansen WA (1996) Plasticity in maturity and fecundity of yellow perch, *Perca flavescens* (Mitchill): comparisons of stunted and normal-growing populations. Ann Zool Fennici 33:403-415

Jennings MJ, Claussen JE, Philipp DP (1997) Effect of population size structure on reproductive investment of male bluegill. N Am J Fish Man 17:516-524

Justus JA, Fox MG (1994) The cost of early maturation on growth, body condition, and somatic lipid content in a lake pumpkinseed (*Lepomis gibbosus*) population. Ecol Freshwat Fish 3:9-17

Konkle BR, Sprules WG (1986) Planktivory by stunted lake trout in an Ontario lake. Trans Am Fish Soc 115:515-521

Mann GJ, McCart PJ (1981) Comparison of sympatric normal and dwarf populations of least cisco (*Coregonus sardinella*) inhabiting Trout Lake, Yukon Territory. Can J Fish Aquat Sci 38:240-244

Mittelbach GG, and Osenburg CW (1993) Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology 74:2381-2394

Morita K, and Morita SH (2002) Rule of age and size at maturity: individual variation in the maturation history of resident white-spot charr. J Fish Biol 61:1230-1238

Otis KJ, Piette RR, Keppler JE, Rasmussen PW (1998). A largemouth bass fishery to control an overabundant bluegill population in a Wisconsin lake. J Freshwat Ecol 13:391-403

Persson L (1983) Food consumption and competition between age classes in a perch Perca fluviatilis population in a shallow eutrophic lake. Oikos 40:197-207

Ricker WE (1981) Changes in the average size and average age of Pacific salmon. Can J Fish Aquat Sci 38:1636-1656

Ridgway LL, Chapleau F (1994) Study of a stunted population of yellow perch (*Perca flavescens*) in a monospecific lake in Gatineau Park, Quebec. Can J Zool 72:1576-1582

Roff DA (1983) An allocation model of growth and reproduction in fish. Can J Fish Aquat Sci. 40:1395-1404

Roff DA (1984) The evolution of life history parameters in teleosts. Can J Fish Aquat Sci 41:989-1000

Santucci VJ Jr, Wahl DH (2003) The effects of growth, predation, and first-winter mortality on recruitment of bluegill cohorts. Trans Am Fish Soc 132:346-360

Schaffer WF, Elson PF (1975) The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577-590

Sohn JJ (1977) Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. Science 195:199-201

Stearns SC (1976) Life history tactics: a review of the ideas. Q Rev Biol 51:3-47
Stearns SC (1992) The evolution of life histories. Oxford University Press.

Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893-913

Swingle HS, Smith EV (1941) The management of ponds with stunted fish populations. Trans Am Fish Soc 71:102-105

Trivers RL (1972) Parental investment and sexual selection. P 136-179 in B. Campbell, ed. Sexual selection and the descent of man. Aldine, Chicago.

Welker MT, Pierce CL, Wahl DH (1994) Growth and survival of larval fishes: roles of competition and zooplankton abundance. Trans Am Fish Soc 124:703-717

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Ann Rev Ecol Syst 15:393-425

Whiteman HH (1997) Maintenance of polymorphism promoted by sex-specific fitness payoffs. Evolution 51: 2039-2044

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack’s principle. Am Nat 100:687-690

Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. Can J Fish Aquat Sci 49:2196-2218

Ylikarjula J, Heino M, Dieckmann U (1999) Ecology and adaptation of stunted growth in fish. Evol Ecol 13:433-453

Table 1. Initial mean (and minimum and maximum) total length (mm) and total weight (g) of juvenile bluegill used in the experiment in the food treatment (high food or no supplemental food) and the social treatment (large males present or absent).

Treatment	Mean Length	Min.	Max	Mean Weight	Min.	Max
High Food	123 ± 0.91	104	140	34.2 ± 0.87	20	53
No Supplement	124 ± 1.17	103	142	35.8 ± 1.12	19	58
P-value	0.75			0.27		
+Large Males	123 ± 1.14	103	142	34.0 ± 1.06	18	52
No Large Males	124 ± 0.93	104	141	36.0 ± 0.94	20	54
P-value	0.25			0.19		

Data are means ± 1 S.E. P-values generated with two-way ANOVA.

Table 2: Final sizes for juvenile males and females that remained immature and that matured in the treatment ponds with high food and no supplemental food.

	High Food			No Supplement	
	Immature	Mature	P-value	Immature	Mature P-value
Males:					
Total length (mm)	156 ± 1.0	161 ± 9.6	0.22	146 ± 1.2	136 ± 4.7 0.009
Total weight (g)	75.6 ± 1.6	81.8 ± 15	0.36	60.1 ± 1.6	48.7 ± 6.2 0.02
Females:					
Total length (mm)	138 ± 1.0	138 ± 1.8	0.78	143 ± 1.2	147 ± 1.6 0.16
Total weight (g)	47 ± 1.3	46 ± 2.0 0.28	0.70	54 ± 1.6	57 ± 2.4

Notes: See text for details on determination of sexual maturity. Data are means ± 1 SE. P-values generated with one-way ANOVA.

Figure Captions

Figure 1. A) Total length (mm) and B) mass (g) of juvenile male bluegill (*Lepomis macrochirus*) in four experimental ponds with high food and four ponds with no food supplement (means ± SE). Asterisks (*) indicate significant differences between treatment means (two way ANOVA; $P \leq 0.02$). Ponds with large adult males (shaded bars) indicate no influence of their presence on growth of juvenile males

Figure 2. A) Total length (mm) and B) mass (g) of juvenile female bluegill (*Lepomis macrochirus*) in four experimental ponds with high food and four ponds with no food supplement (means ± SE). Asterisks (*) indicate significant differences between treatment means (two way ANOVA; $P \leq 0.07$). Ponds with large adult males (shaded bars) indicate no influence of their presence on growth of juvenile females

Figure 3. Percent mature bluegill for originally juvenile A) males and B) females in eight experimental ponds with high food (shaded bars) or no food supplement (open bars) and with presence or absence of large adult males. See text for explanation of maturity. Note difference in scale for panels A and B. For males, the presence of large adult males (but not food ration) had a strong inhibitory effect on maturation (chi-square analysis, $P = 0.005$). For females, food ration (but not the presence of large adult males) had a strong influence on percent maturity (chi-square analysis, $P = 0.0001$)

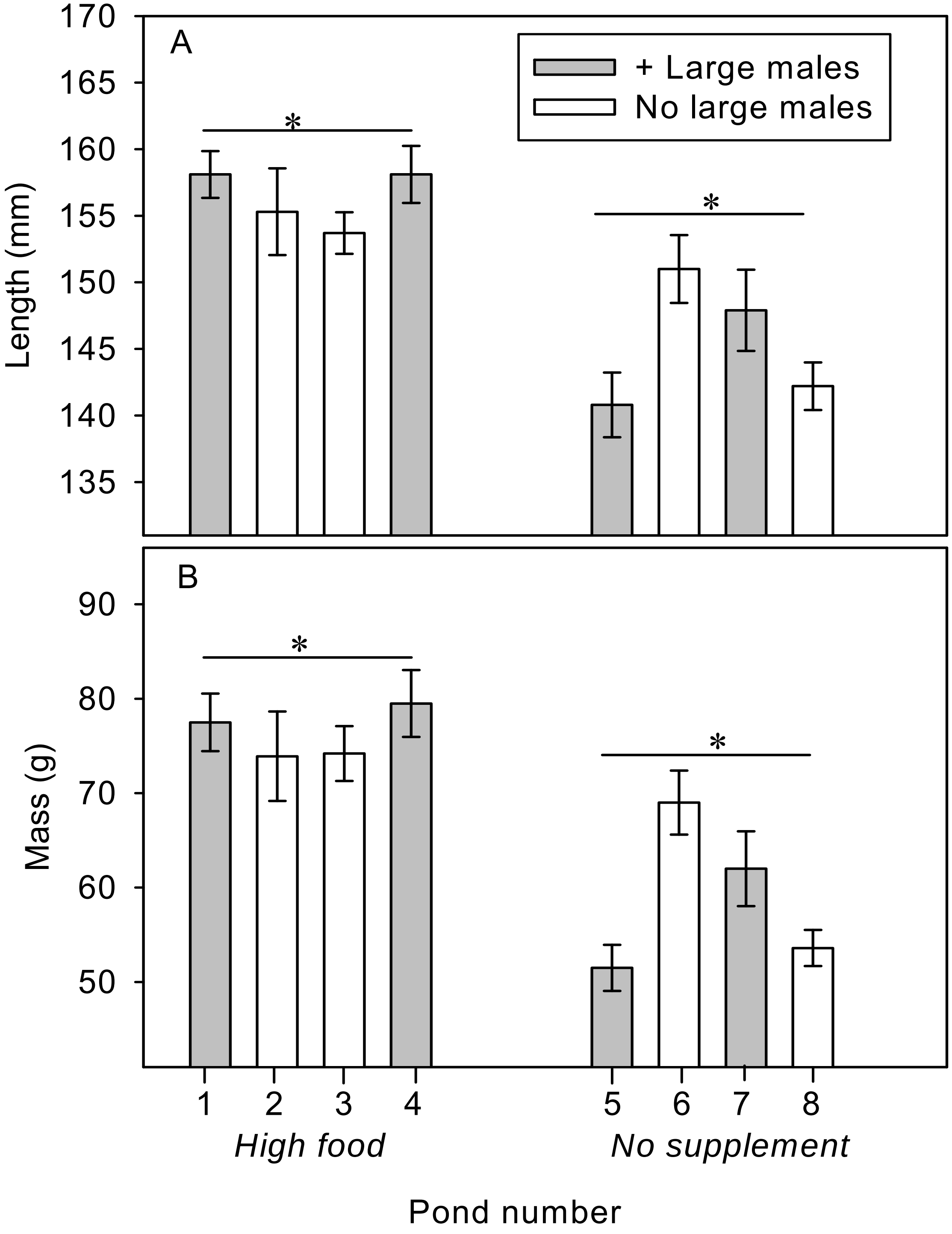
A
B
Length (mm)
Mass (g)
170
165
160
155
150
145
140
135
90
80
70
60
50
+ Large males
No large males
*
*
*
*
1
2
3
4
5
6
7
8
High food
No supplement
Pond number

Figure 1.

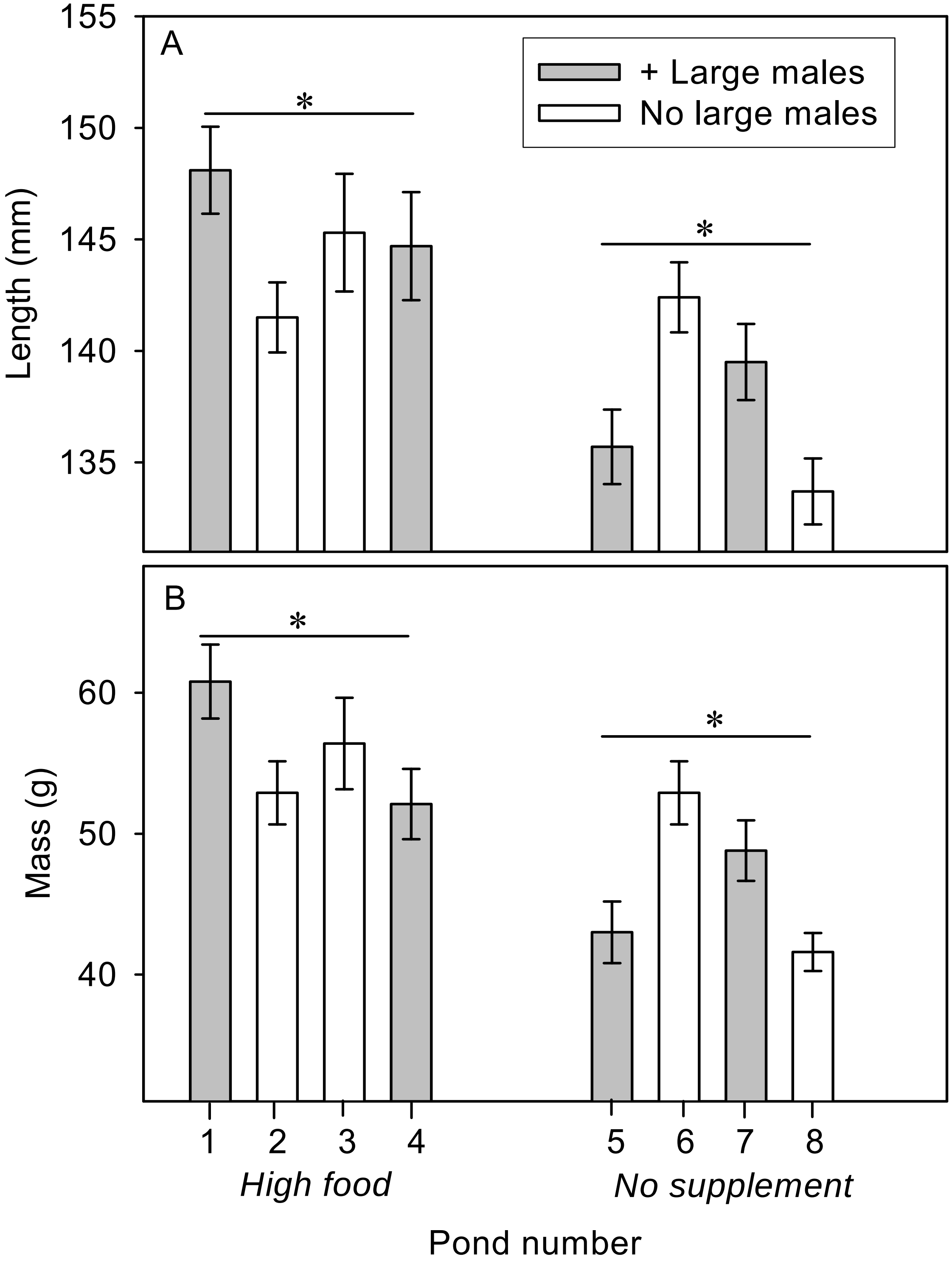
155
150
145
140
135
Length (mm)
A
+ Large males
No large males
*
*
60
50
40
Mass (g)
B
*
*
1
2
3
4
5
6
7
8
High food
No supplement
Pond number

Figure 2.

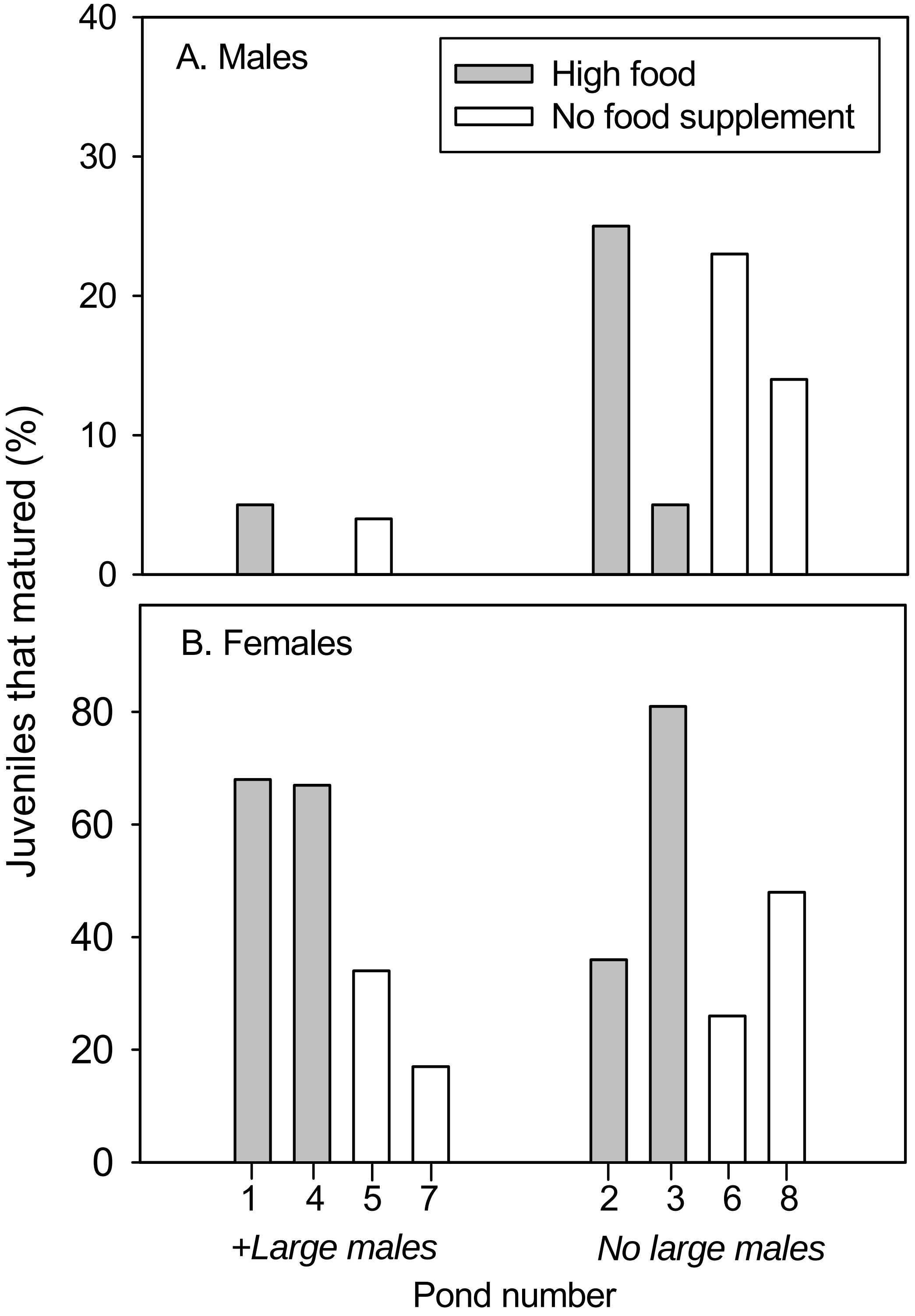
A. Males
High food
No food supplement
B. Females
Juveniles that matured (%)
0
10
20
30
40
0
20
40
60
80
1
4
5
7
2
3
6
8
+Large males
No large males
Pond number

Figure 3.

Appendix C

What Controls the Size Structure of Bluegill Populations?

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ABSTRACT

The prevention or improvement of poor size structure, often referred to as stunting, in bluegill populations is a major management focus for many agencies. Four hypotheses have been proposed to explain what causes and/or maintains stunting in bluegill populations: adult overharvest, cuckolder overproduction, density-dependent growth limitation, and socially influenced early maturation. To test the relative importance of each of the four hypotheses in determining size structure of bluegill populations in Illinois, we assessed key life history characteristics of 50 populations throughout the state. In each lake, we sampled bluegill during the spawning season using boat electrofishing techniques, and for each population we determined sex specific size-at-age, age-at-first-maturity, gonosomatic index (GSI), and relative abundance of cuckolders. None of the populations sampled provided evidence supporting a role for either the adult overharvest hypothesis or the cuckolder overproduction hypothesis. Although population density and resource availability likely influence growth rates in all bluegill populations, there was no evidence among the 50 Illinois bluegill populations studied that density-dependent growth limitation causes or maintains stunting. Size structure , however, was highly correlated with age-at-first-maturity; individuals in stunted populations matured significantly earlier than those in quality populations. To manage bluegill populations effectively, therefore, strategies should be focused on increasing the age-at-first-maturation, not on simply manipulating growth rates.

INTRODUCTION

Bluegill, *Lepomis macrochirus*, constitute one of the most popular recreational fisheries in the Midwest, with total harvest exceeding that of most other sportfish (Bayley et al 1993). The size structure of bluegill populations, however, varies greatly among different lakes, and anglers are often dissatisfied with populations that have high numbers of predominantly small bluegill. As a result, "stunting" among bluegill populations is considered a substantial and recurring management problem. The most commonly cited causes for stunting are excessive exploitation (Goedde and Coble 1981; Coble 1988), alteration of predator populations (Swingle 1950; Anderson and Schupp 1986; Colby et al 1987; Guy and Willis 1990) and inadequate food supply (Gerking 1962). By focusing on the above factors, however, no consistently effective management strategies have been developed to improve the size structure of bluegill populations in the wild. That failure likely results from the fact that past approaches to the problem have come from an agricultural perspective, rather than from an evolutionary one (Williams 1966).

Bluegill exhibit complex reproductive behaviors (e.g., colonial nest construction, territorial defense, courtship of females, and male parental care) that include alternative male reproductive strategies (Gross 1982). Some males delay maturation to reach a large size and reproduce as parental males; others mature precociously at a much smaller size and younger age and reproduce as cuckolders (Gross and Charnov 1980). Beyond that variation, however, the age at which parental males (and females) in a population first mature varies widely among lakes, not only latitudinally as a result of variation in the length of the growing season, but also as a result of the social structure of the population

(Jennings and Philipp 1992; Aday et al 2002). Because reproductive activities require high energetic investment, including the diversion of energy from somatic growth to the production of gametes, spawning, and parental care activities the process of maturation has significant impacts on the growth trajectory for all males and females; (Reznick 1985, Coleman and Fisher 1991; Claussen 1991; Fox and Keast 1991; Jennings 1991; Jennings and Philipp 1992).

Growth trajectories for parental male bluegill (and most other fish as well) follow a pattern in which growth slows significantly following sexual maturation (Wootton 1985). Four components of this "typical pattern of growth" (Figure 1) determine a population's size structure: pre-maturation growth rate, age-at-first-maturity, post-maturation growth rate, and longevity. As a result, alterations that affect any one of these four components can impact population size structure. Jennings et al (1997) proposed four alternative hypotheses to explain the cause and/or maintenance of stunting in a bluegill population.

In the first of these, the Adult Overharvest Hypothesis (Figure 2a), growth rates and sexual maturation schedules remain typical of "normal" populations. Large bluegill (typically, mature parental males) are not found in the population because they are removed rapidly by anglers before they reach an acceptable size threshold. In support of this hypothesis Coble (1988) reported that size-selective harvest can quickly reshape the size distribution of bluegill within a fished population. How widespread this situation is in the wild, as well as how long the impacts of such harvest last within a population, remain unclear. Drake et al (1997), however, did show that there was an inverse relationship between angling pressure and the size and age at first maturity of parental male bluegill among several Minnesota lakes.

In the second, the Cuckolder Overproduction Hypothesis (Figure 2b), growth rates and sexual maturation schedules are also typical of "normal" populations. Some perturbation (e.g., acute overharvest or winterkill) causes many fewer males than normal to delay maturation to become parental males, with most males maturing early as cuckolders instead. Evidence supporting this hypothesis was reported from spawning colonies sampled in some southern Wisconsin lakes (Ehlinger 1997); an inverse relationship was observed between the percentage of cuckolders and the prematuration growth rate of parental males. Although quantitative measures of the percentage of males entering the two life histories has only been determined for the bluegill population in Lake Opinicon, Ontario (Gross 1982; Philipp and Gross 1994), both life histories clearly exist among populations throughout the Midwest (Drake et al 1997; Ehlinger 1997)

In the third, the Density-Dependent Growth Limitation Hypothesis (Figure 2c), although sexual maturation schedules are typical of "normal" populations, large individuals are not produced in the population because early growth rates are diminished in response to overly high bluegill densities (caused by any one of a number of factors, such as, reduction in predation, changes in habitat, poor water quality, etc.). Competition for resources certainly occurs among sunfishes; when densities of small fish are high, growth rates are low (Mittelbach 1984, 1986). In a comparative study of reservoir bluegill populations, Belk and Hales (1993) proposed that differences in the availability of resources among habitats, including both food resources and refuges from predators such as largemouth bass, influenced growth rate. What remains unclear, however, is whether or not differences in first year growth rates actually affect the eventual maximum size of individuals.

In the fourth, the Socially Influenced Early Maturation Hypothesis (Figure 2d), early growth rates are typical of "normal" populations, but in response to some perturbation in the population that has removed large males (e.g., acute overharvest or winterkill), parental males (and likely females) mature and reproduce at younger ages and smaller sizes. This "earlier than normal" maturation occurs because younger, smaller, and normally immature males can now compete effectively for nest sites in colonies and access to females for spawning. Because sexual maturation occurs at an earlier age (and size), the associated post-maturation decrease in growth rate also occurs earlier, and as a result, the size of mature individuals in the population is reduced. Although this relationship between male size/age structure and the onset of sexual maturation has been predicted from a theoretical standpoint (Reznick 1983; Stearns and Koella 1986), it has been tested in bluegill only recently (Jennings et al 1997; Aday et al 2003). Both studies showed that the presence of large parental male bluegill inhibited the maturation of smaller, immature parental males, a phenomenon seen in other species as well (Browsky 1973, 1978; Warner 1984; Reznick 1985; Bushman and Burns 1994; Fox 1994; Danylchuk and Tonn 2001).

Successful management of bluegill populations has often eluded us because we have not determined what really controls size structure of this important species. The goal of the current study was to test the relative importance of these four alternative hypotheses in determining bluegill population size structure by comparing bluegill life histories (growth trajectories, maturation schedules, and longevities) with bluegill size structure for populations across Illinois.

METHODS

Study sites:

Discussions with Illinois District Biologists (Division of Fisheries, Illinois Department of Natural Resources) identified a list of over 75 moderately sized lakes in the state with substantive bluegill populations. A final list of 50 target populations (Table 1) was selected to maximize geographic coverage within the state; 16 of the populations were located in the northern third of the state, 20 in the central third, and 14 in the southern third. Of the 50 final study lakes, 27 were greater than 100 acres in surface area.

Sample Collection:

Sampling of the 50 study populations was conducted by boat electrofishing after bluegill spawning activity had been initiated in each lake and before it ceased in mid-summer (i.e., a period from early-May to mid-July). Electrofishing began with an initial run (30 - 60 min in duration), in which all individuals of all sizes were collected. These bluegill were sorted to determine the number of individuals in each of eight specified size classes (<50mm, 50-99mm, 100-149mm, 150-159mm, 160-169mm, 170-179mm, 180-189mm, >189mm). The goal was to obtain at least 50 individuals from each size class.

Additional runs were then conducted in an attempt to supplement those size classes for which sample sizes were below 50. All lakes were sampled in 1996, with additional collections being made in 1997 for those few lakes where some size class collections remained low even following the additional runs. All samples were frozen whole and stored at –20C until further analysis.

Life History Determination:
Sampled fish were thawed slowly in a refrigerator. Total length (mm), weight (g), and sex was determined for each individual in all samples. In addition, the stage of gonadal development was scored for each individual using a scale from 1 to 5, with a score of 1 representing an immature fish (gonads were barely distinguishable) and a score of 5 representing a fish with fully ripe gonads that either were running milt or contained fully matured eggs. When size allowed (i.e., fish with gonads having scores of 2 or more), gonads were weighed.

Scales and otoliths were removed for subsequent age determination. All otoliths were read in whole view by at least two independent readers, and the results compared. If there was a disagreement between the readers, or if crowding of annuli occurred, the otolith was then sectioned using one of two methods, by cracking the otolith in half and reading the transverse section with fiber optic light or by mounting the mid-section on a slide and reading it with transmitted light.

For each population sampled, the proportion of mature individuals of each sex was determined for each age class. For example, for age-3 males:

$$\text{P (Mature)} = {}^{\text{(\# Mature age-3 males)}} / {}_{\text{(\# Immature and Mature age-3 males)}}$$

Only those age classes in which >10% and/or <90% of the individuals of a given sex were mature, were used to calculate Z-age, the average age-at-first-maturity for that population.. For most populations, only a single age class met that criterion. In those cases, Z-age was calculated by the following formula:

$$\text{Z-age} = \text{Age Class} + 1 - \text{P(Mature)}$$

For those populations where two or more age classes met that criterion, values for each year class were averaged. In those cases, Z-age was calculated by the following formula:

$$\text{Z-age (population)} = \underline{\text{[Age Class +1 – P (Mature)] Age Class A + [Age Class +1 –P (Mature)] Age Class B}} /_{2}$$

Size Structure Classification:
To calculate a descriptor of the size structure for each population that could be used to classify it as quality, stunted, or intermediate, we designed an index based on the sizes of only the mature parental bluegill in the population. Proportion of Quality Males (PQM.170) for a given bluegill population is calculated by dividing the number of mature parental males having a total length >170mm by the total number of mature parental males collected. A PQM.170 of 0.00-0.05 was considered indicative of stunted status; a PQM.170 of > 0.50 – 1.00 was considered indicative of quality status; and a PQM.170 of 0.06 - 0.49 was indicative of intermediate status.

RESULTS

Summary data for all 50 study lakes and bluegill populations are shown in Table 1. The PQM.170 values ranged from 0.00 (i.e., none of the mature parental males being over 170mm TL) to a high of 0.98 (i.e., 98% of the mature parental males being over 170mm TL). Of the 50 study populations, 13 were classified as stunted, 23 as intermediate, and 14 as quality. The size (TL in mm) of age-2 males (all of where were immature in all populations, excluding cuckolders) ranged from 79-138, and the size of age-5 males (all of which were mature in all populations) ranged from 130 - 203. The Z-age for males ranged from 2.5-4.6, whereas the Z-age for females ranged from 1.8-3.6. Cuckolders were identified in the samples from all but four of the populations, with the highest ratio of cuckolders to mature parental males observed in the samples being 0.52. These summary data were used to test the predictive outcomes of each of the four hypotheses independently, as described below.

Adult Overharvest Hypothesis:

In this hypothesis, there is no change in life history; growth rates (both pre and post-maturation), age at maturation, and cuckolder production rates remain the same (Figure 2a). Low PQM.170 values are caused by the largest bluegill in the population being removed at a high rate through excessive angling harvest. In this scenario, the relative abundance of mature males should be lower in stunted populations than in quality populations (i.e., bluegill populations with low PQM.170 values to those with high PQM.170 values),. This hypothesis predicts that across the 50 study populations there should be a positive relationship between the PQM.170 values and the ratio of the number of large mature males to the number of immature males (Figure 3A). A regression analysis (Figure 3B) using the data from our 50 study populations (see Table 1) shows that there is no positive relationship between PQM.170 and the ratio of immature:mature males ($P = 0.778$, $r_2 = 0.002$). Our data, therefore, do not support this hypothesis; stunted bluegill populations are not simply a short-term result of excessive overharvest of the larger individuals.

Cuckolder Overproduction Hypothesis:

In this hypothesis stunted size structures are caused by an overabundance of cuckolders; i.e., there is a great increase in the number of immature males that enter the cuckolder life history pathway compared to those that enter the parental male pathway (Figure 2B). In this scenario an increase in the abundance of cuckolders relative to mature parental males causes a decrease in PQM.170 (Figure 4A). A regression analysis of PQM.170 versus the relative abundance of cuckolders versus mature parental males in each of the 50 study populations (Figure 4B) revealed no significant relationship ($P = 0.338$, $r_2 = 0.019$). Our data, therefore do not support this hypothesis either; stunted bluegill populations are not a result of changes in the proportion of males maturing early as cuckolders.

Density-Dependent Growth Limitation Hypothesis:

In this hypothesis the causal factor in stunting is density-dependent slow growth, resulting from increased competition among overly abundant young bluegill. In this scenario age-at-first-maturity remains unchanged, but pre and/or post-maturation growth rates decrease (Figure 2C). Initial growth rates should be slower in stunted populations than in quality ones; that is, among the 50 study populations there should be a positive relationship between size at age-2 and PQM.170 (Figure 5A). The regression analysis depicted in Figure 5B, however, shows that this relationship does not exist ($P = 0.916$, $r_2 = 0.001$); initial growth rates have little impact on the ultimate size structure of a bluegill population. In fact, some of the highest quality bluegill populations in Illinois have some of the lowest sizes at age 2. So although density dependence is important for determining growth rates, a slow growth rate does not determine whether or not a population becomes stunted.

Social Influence/Early Maturation Hypothesis:
In this hypothesis pre- and post-maturation growth rates remain unchanged for both quality and stunted populations. Instead stunting is caused by a reduction in the age-at-first-maturity. In this scenario parental males begin maturing at a younger age (and smaller size), and as a result, their post-maturation decrease in growth rate starts much earlier in life (Figure 2d). This hypothesis predicts that parental males in stunted populations would have a lower Z-age than parental males in quality populations (Figure 6a). Regression analysis (Figure 6B) shows a strongly positive and highly significant relationship between male Z-age and PQM.170 ($P = 0.001$, $r_2 = 0.272$). Stunted populations do, in fact, have males with a lower age-at-first-maturation.

DISCUSSION

In many Illinois lakes bluegill are consistently caught and harvested in great numbers. In fact, many bluegill populations, are likely experiencing levels of exploitation that are high enough to shift size structures toward ones that are dominated by small fish (Coble 1988; Drake et al 1997). Across the Midwest the size structure of bluegill populations has deteriorated and the number of trophy-sized bluegill angled each year has declined (Olsen and Cunningham 1989) in response to high exploitation rates over the past 40 years. Developing effective management strategies to correct this problem of "stunting" has become a priority for many management agencies (Jennings 1991). Before effective management strategies can be developed, however, we need to understand how the factors controlling growth and maturation of bluegill ultimately affect the sizes attained by individuals.

The size structure of a bluegill population is determined by the combination of four factors: growth rate before maturation (when all energy investment is directed toward somatic growth), age-at-first-maturation (which is highly plastic in Lepomis spp.), growth rate after maturation (when energy investment is directed toward reproduction as well as growth), and longevity (which is impacted by angling). Although competition for resources certainly occurs among sunfishes when densities of small fish are high (Mittelbach 1984, 1986), it remains unclear as to what extent density-dependent limitations to growth rate affect the ultimate size structure of bluegill populations. In addition, because sexual maturation and the expression of reproductive behaviors are energetically expensive, many fish species, including the sunfishes, have evolved to respond facultatively to social cues in a way that maximizes lifetime reproductive success

(Stearns and Koella 1986, Jennings and Philipp 1992). Even though social control of reproductive behaviors has been demonstrated across a wide range of fish taxa (Robertson 1972, Borowsky 1978, Silverman 1978, Chapman et al. 1991, Fox and Keast 1991, Jennings 1991), we still do not know how these socially mediated shifts in life history impact the ultimate size structure of a population.

Four main hypotheses have been proposed to explain the cause(s) of stunting in bluegill, (1) Adult Overharvest, (2) Overproduction of Cuckolders, (3) Density-dependent Growth Limitation, and (4) Socially Influenced Early Maturation. Our results, using life history data from 50 bluegill populations across Illinois, clearly indicate that Hypothesis 4, Socially Influenced Early Maturation, is the dominant causative factor explaining small size structure. Stunted bluegill populations are caused by fish maturing at an early age, thereby beginning the period of slowed post-maturation growth rates at an earlier age. This early maturation is in response to a lack of large parental males in the population, the presence of which normally delays the maturation of younger males to a larger size before they attempt to spawn (Jennings et al 1997, Aday et al 2003).

If we are to manage bluegill populations effectively, we need to understand the evolutionary forces that shape bluegill life histories and how exploitation and/or various management activities alter key life-history characteristics. To increase the size structure of a bluegill population, the focus for management needs to be on delaying the onset of the post-maturation decrease in growth rate, i.e., increasing size and age-at-first-maturity. That strategy recognizes the important role that sexual selection plays in determining when parental males mature. Males delay maturation until they reach a size (and age) at which they can compete with their peers for acquiring good nest sites within a colony and access to females for reproduction. If large males are removed from the population (for whatever reason), smaller and younger males become competitive, and they mature (Jennings et al 1997, Aday et al 2003). That strategy, which takes an evolutionary approach to management, is in stark contrast to strategies that employ an agricultural approach in which we simply try to increase growth rates by providing more resources, either by adding resources directly or by decreasing bluegill population densities. Bluegill are not domesticated organisms like chickens or corn and they do not exist in environments almost totally controlled by man like chicken coops or agricultural fields. If we are to manage wild fish populations effectively, we need to recognize that fact and stop treating them like an agricultural crop. Bluegill populations look and act like they do because they have been shaped by natural selection, not by humans.

REFERENCES

Aday, D.A., D. H. Wahl, and D.P. Philipp. 2003. Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. Ecology 84:3370-3375.

Aday, D.A., C.M. Kush, D. H. Wahl, and D.P. Philipp. 2002. The influence of stunted body size on reproductive ecology of bluegill *Lepomis macrochirus*. Ecology of Freshwater Fishes 11:190-195.

Anderson, D.W. and D.H. Schupp. 1986. Fish community response to northern pike stocking in Horseshoe Lake, Minnesota. Minnesota Dept. of Natural Resources, Section of Fisheries Investigational Report 387.

Bayley P.B., S.T. Sobaski, D.J. Austen. 1993. The fisheries analysis system (FAS): creel survey and lake analysis. Aquatic Ecology Technical Report 93/7, Illinois Natural History Survey, Champaign, IL.

Belk, M.C. and L.S. Hales, Jr. 1993. Predation-induced differences in growth and reproduction of bluegills (Lepomis macrochirus). Copeia 1993: 1034-1044.

Borowsky, R.L. 1973. Social control of adult size in males of *Xiphophoris variatus* (Pisces: Poeciliidae). Nature 245:332-335.

Borowsky, R.L. 1978. Social inhibition of maturation in natural populations of *Xiphophoris variatus* (Pisces: Poeciliidae). Science 201:933-935.

Bushman, P.J. and J.R. Burns. 1994. Social control of male sexual maturation in the swordtail characin, *Corynopoma riisei*. Journal of Fish Biology 44:263-272.

Chapman, L.J., D.L. Kramer, and C.A. Chapman. 1991. Population dynamics of the fish *Poecilia gillii* (Poeciliidae) in pools of an intermittent tropical stream. Journal of Animal Ecology 60:441-453.

Claussen, J.C. 1991. Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. M.S. Thesis, U. Toronto.

Coble, D.W. 1988. Effects of angling on bluegill populations: management implications. North American Journal of Fisheries Management 8:277-283.

Coleman, R. M. and R. U. Fisher. 1991. Brood size, male fanning effort, and the energetics of a nonshareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae). Erthology 87: 177-188.

Colby, P.J., P.A. Ryan, D. H. Schupp, and S.L. Serns. 1987. Interactions in north-temperate lake fish communities. Canadian Journal of Fisheries and Aquatic Sciences 44 (supplement 2):104-128.

Danylchuk, A.J. and W.M. Tonn. 2001. Effects of social structure on reproductive activity in male fathead minnows (*Pimephales promelas*). Behavioral Ecology 12:482-489.

Fox, M.G. and A. Keast. 1991. Effect of overwinter mortality on reproductive life history characteristics of pumpkinseed (*Lepomis gibbosus*) populations. Canadian Journal of Fisheries and Aquatic Scences 48:1792-1799.

Fox, M.G. 1994. Growth, density, and interspecific influences on pumpkinseed sunfish life histories. Ecology 75:1157-1171.

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

Goedde, L.E. and D.W. Coble. 1981. Effects of angling on a previously fished and unfished warmwater community in two Wisconsin lakes. Transactions of the American Fisheries Society 110:594-605.

Gross, M.R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Z. Tierpsychol 60: 1-26.

Gross, M.R. and E.L. Charnov. 1980. Alternative male life histories in bluegill sunfish. Proc. Natl. Acad. Sci. 77: 6937-6940.

Guy, C.S., and D.W. Willis. 1990. Structural relationships of largemouth bass and bluegill populations in South Dakota ponds. North American Journal of Fisheries Management 10:338-343.

Jennings, M.J. 1991. Sexual selection, reproductive strategies and genetic variation in the longear sunfish (*Lepomis megalotis*). Ph.D. dissertation, University of Illinois, Urbana.

Jennings, M.J. and D.P. Philipp. 1992. Reproductive investment and somatic growth in longear sunfish. Environmental Biology of Fish 35:257-271.

Jennings, M.J., J.E. Claussen and D.P. Philipp. 1997. Effect of population size structure on reproductive investment among male bluegill. North American Journal of Fisheries Management 17: 516-524.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

Mittelbach, G.G. 1986. Predator-mediated habitat use: some consequences for species interactions. Environmental Biology of Fish 16:159-169.

Olsen, D.E. and P.K. Cunningham. 1989. Sport fisheries trends shown by an annual Minnesota fishing contest over a 58-year period. North American Journal of Fisheries Management 9:287-297.

Philipp, D.P. and M.R. Gross. 1994. Genetic evidence for cuckoldry in bluegill Lepomis macrochirus. Molecular Ecology 3:563-569.

Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64:862-873.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257-267. Robertson, D.R. 1972. Social control of sex reversal in a coral-reef fish. Science 177:1007-1009.

Silverman, H.I. 1978. The effects of visual stimulation upon age at first spawning in the mouth-brooding cichlid fish *Sarotherodaon* (Tilapia) *mossambicus* (Peters). Animal Behavior 26:1120-1125.

Stearns, S.C. and J.A. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size of maturity. Evolution 40:893-913.

Swingle, H.S. 1950. Relationships and dynamics of balanced and unbalanced fish populations. Alabama Polytechnic Institute, Agricultural Experimental Station Bulletin 274, Auburn.

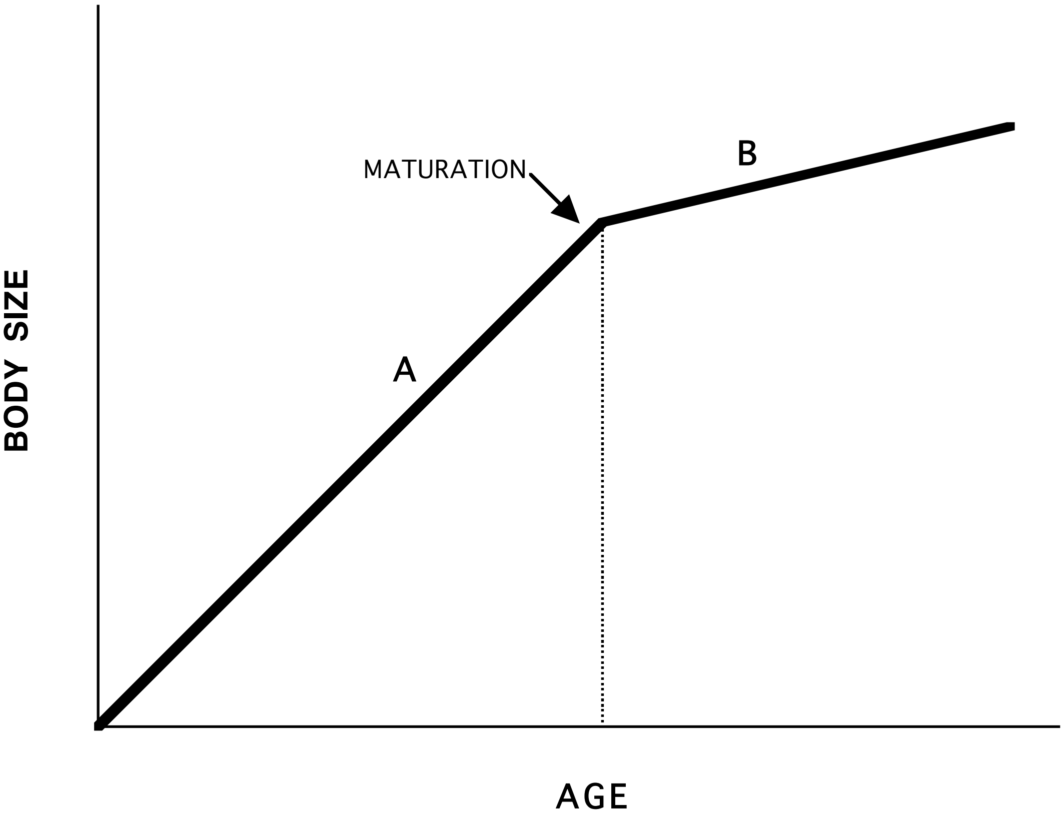
Warner, R.R. 1984. Deferred reproduction as a response to sexual selection in a coral reed fish: a test of the life history consequences. Evolution 38:148-162.

Williams, G.C. 1966. Natural Selection, the cost of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.

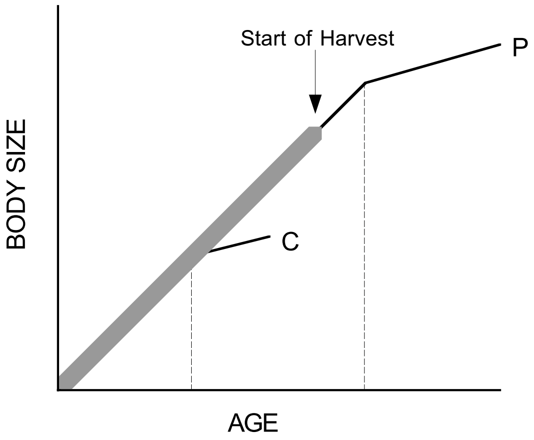
Wootton, R.J. 1985. Energetics of reproduction. pp. 231-254 in P. Tyler and P. Callow (eds) Fish Energetics: New Perspectives. Johns Hopkins University Press, Baltimore, MD.

Table 1. Summary data from the 50 study populations. Lakes are arranged alphabetically within their type groups. Under the Type heading S = stunted, I = intermediate Q= quality. In the table headings F = Female and M = Male.

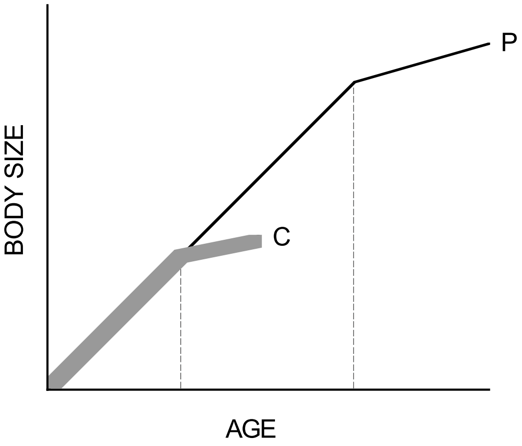
LAKE NAME	Type	Region	Lake Size	Z-age F	Z-age M	PQM. 170	PQM. 180	Mean Male Size at 2	Mean Male Size at 5	# Immature Males at 2	Total # Males at 2	Total # 2's (M+F)	# Parental Males	# Cuckolders	Total# Sampled
Bullfrog	S	N	S	2.2	3.4	0.00	0.00	109	138	11	11	45	27	13	323
Busse Main	S	N	L	1.8	2.5	0.00	0.00	121	148	7	13	22	19	5	178
George	S	N	L	2.2	3.1	0.01	0.00	101	147	38	38	108	69	17	393
Johnson Sauk	S	N	S	2.6	3.2	0.02	0.00	94	158	90	90	198	192	2	525
Le Aqua Na	S	N	S	2.4	3.3	0.02	0.00	106	150	153	153	264	46	24	467
Long	S	N	L	2.2	2.5	0.00	0.00	112	152	38	73	131	45	12	182
Pana	S	C	L	2.4	3.5	0.00	0.00	97	152	14	14	27	34	1	152
Paradise	S	C	L	2.1	2.8	0.02	0.00	130	174	36	38	69	46	1	238
Pierce	S	N	L	2.3	2.7	0.02	0.00	107	164	53	71	143	43	2	306
Round	S	N	L	2.4	3.2	0.04	0.04	120	165	38	42	87	24	3	223
Sterling	S	N	S	2.4	3.2	0.00	0.00	83	134	22	22	37	24	4	120
Tampier	S	N	L	2.5	2.8	0.00	0.00	108	130	12	26	65	96	15	429
Walton Prk	S	C	S	2.0	3.1	0.00	0.00	108	150	50	54	113	71	7	312
Baumann	I	N	S	2.8	3.2	0.09	0.04	82	175	107	107	181	46	9	368
Beaver Dam	I	C	S	2.8	3.3	0.25	0.00	120	170	5	5	10	8	1	61
Bloomington	I	C	L	2.6	3.5	0.35	0.04	116	167	14	14	34	68	4	210
Busse South	I	N	L	2.2	2.7	0.18	0.09	116	184	31	42	134	19	0	167
Carleton	I	N	S	2.7	3.4	0.13	0.03	92	176	19	19	38	120	8	301
Charleston	I	C	L	2.0	3.2	0.40	0.08	128	172	5	10	49	60	1	238
Dolan	I	S	S	2.0	3.2	0.21	0.00	138	170	23	26	54	34	0	198
Forbes	I	S	L	3.2	4.6	0.39	0.16	101	166	15	15	34	44	6	205
Hillsboro	I	C	S	2.1	3.2	0.24	0.01	128	164	15	15	35	109	3	283
Homer	I	C	S	2.6	3.3	0.12	0.01	93	171	25	25	62	75	1	251
Jacksonville	I	S	L	2.4	3.5	0.08	0.00	91	167	17	17	48	39	9	328
Kakusha	I	N	S	2.3	3.2	0.41	0.27	102	180	18	18	34	44	6	189
LOTW	I	C	S	2.5	3.4	0.13	0.00	102	164	34	37	61	16	3	353
Mcleansboro	I	S	S	2.1	3.5	0.14	0.03	115	171	39	39	61	35	8	313
Mingo	I	C	L	2.9	3.9	0.17	0.00	108	167	17	17	46	23	9	354
Nellie	I	S	S	2.3	3.6	0.22	0.01	115	165	11	11	26	87	0	242
Oakland	I	C	S	2.0	3.1	0.20	0.02	124	180	22	23	68	59	5	195
Paris	I	C	L	2.2	3.2	0.11	0.02	117	172	49	56	112	50	2	432
Shabbona	I	N	L	2.4	3.3	0.38	0.19	112	183	66	66	160	32	9	327
Spring North	I	C	L	3.3	4.0	0.14	0.00	82	160	5	5	10	44	13	253
Spring South	I	C	L	2.5	4.1	0.33	0.14	119	183	61	61	108	21	1	308
Weldon Springs	I	C	S	2.6	4.0	0.17	0.02	104	158	8	9	14	56	25	291
Woods	I	C	S	2.9	4.6	0.39	0.13	110	170	33	33	75	23	3	458
Apple Canyon	Q	N	L	2.9	3.8	0.57	0.36	79	195	75	75	169	76	10	428
Dutchman	Q	S	L	2.8	4.3	0.61	0.04	96	173	34	34	73	56	0	247
East Fork	Q	S	L	3.4	4.1	0.59	0.14	109	171	31	32	70	63	4	280
Glendale	Q	S	S	2.7	4.2	0.94	0.76	113	191	40	40	80	34	1	258
Lincoln Trl	Q	C	L	2.7	3.7	0.94	0.81	98	203	56	56	97	16	3	393
Mermet	Q	S	L	2.1	3.2	0.57	0.24	109	188	41	42	112	30	2	243
Mill Creek	Q	C	L	3.0	4.1	0.71	0.34	104	174	83	83	164	79	6	299
Murphysboro	Q	S	L	2.4	3.1	0.71	0.29	113	196	46	46	87	22	5	315
Red Hills	Q	S	S	2.3	3.8	0.90	0.80	102	198	20	20	40	21	4	187
Sam Dale	Q	S	L	2.6	4.0	0.71	0.07	117	175	12	12	29	14	3	106
Sam Parr	Q	S	L	2.3	3.0	0.56	0.16	120	179	4	5	27	85	8	310
Siloam Springs	Q	C	S	3.6	4.2	0.98	0.91	84	192	71	71	126	54	14	333
St. Elmo	Q	S	S	2.9	3.5	0.90	0.64	126	186	26	27	66	72	4	234
Walnut Point	Q	C	S	2.2	3.3	0.62	0.88	122	197	27	27	64	26	5	333


BODY SIZE
MATURATION
A
B
AGE

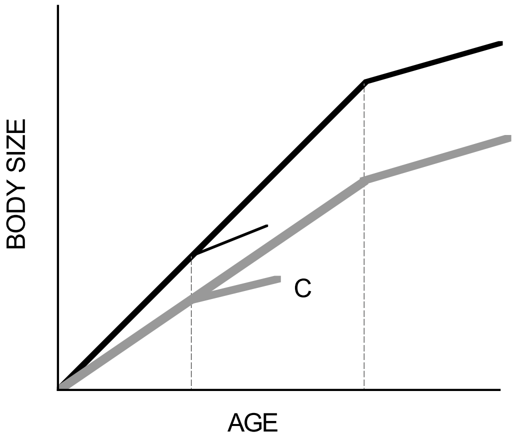
2A. THE ADULT OVERHARVEST HYPOTHESIS



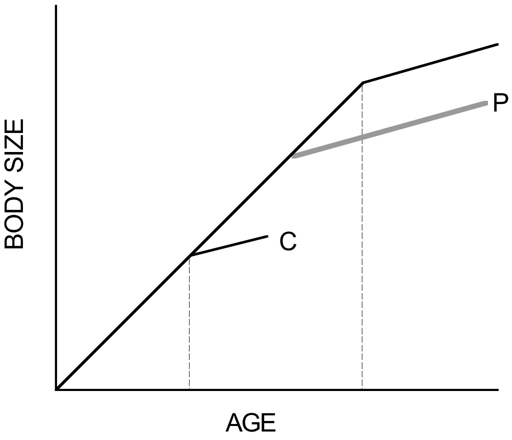
2B. THE CUCKOLDER OVERPRODUCTION HYPOTHESIS



2C. THE DENSITY-DEPENDENT GROWTH LIMITATION HYPOTHESIS



2D. THE SOCIAL INFLUENCE/EARLY MATURATION HYPOTHESIS



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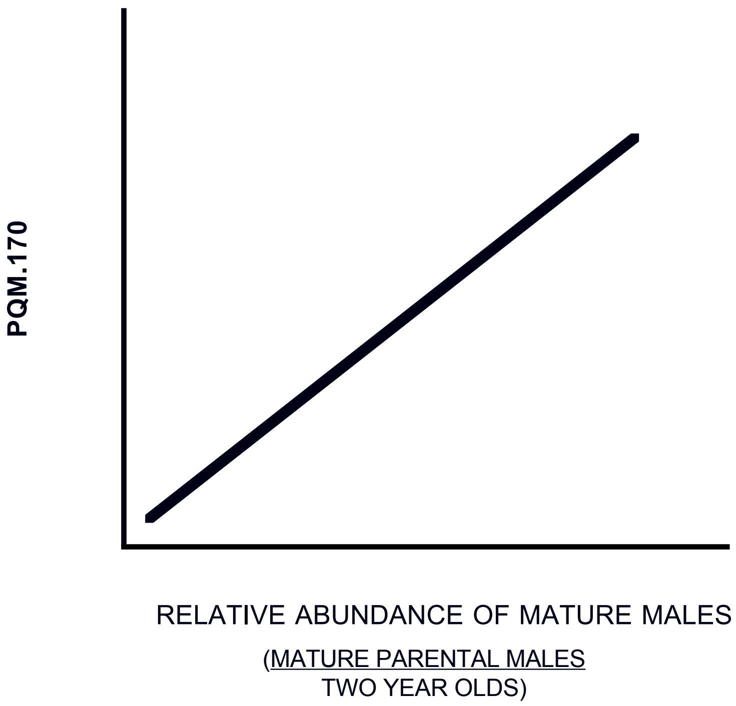
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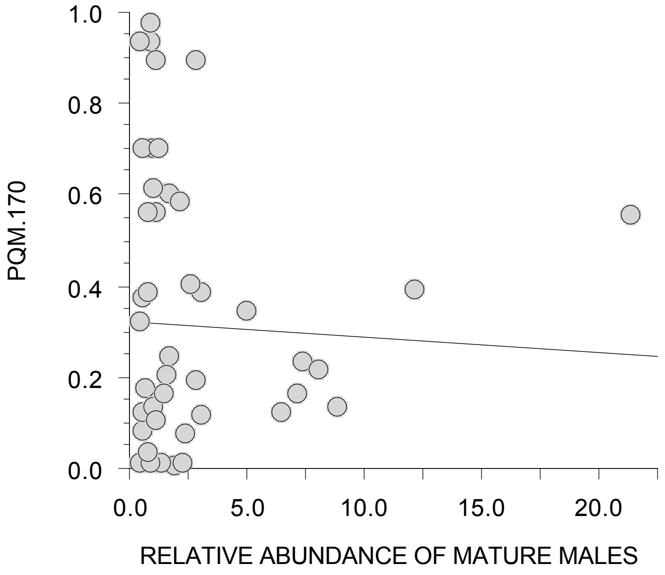
RELATIVE ABUNDANCE OF MATURE MALES
(MATURE PARENTAL MALES
TWO YEAR OLDS)

3B.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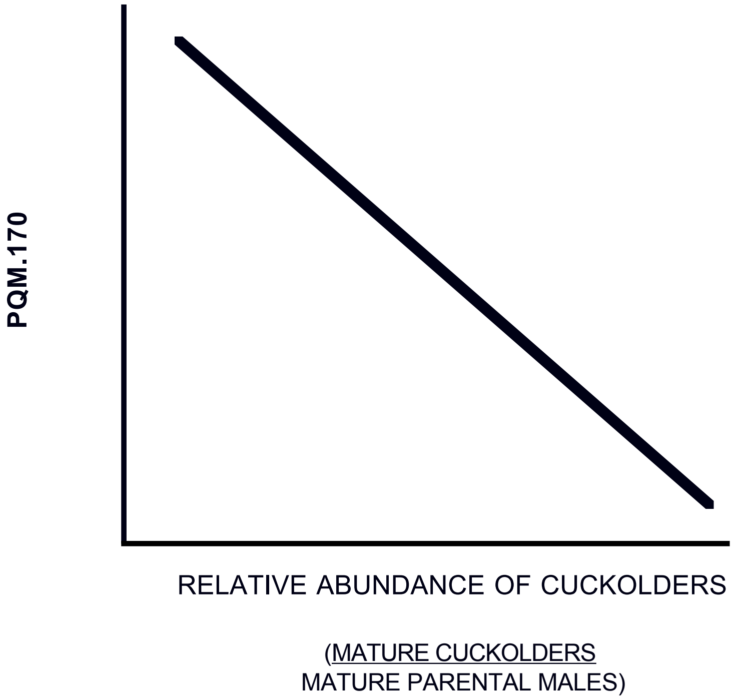
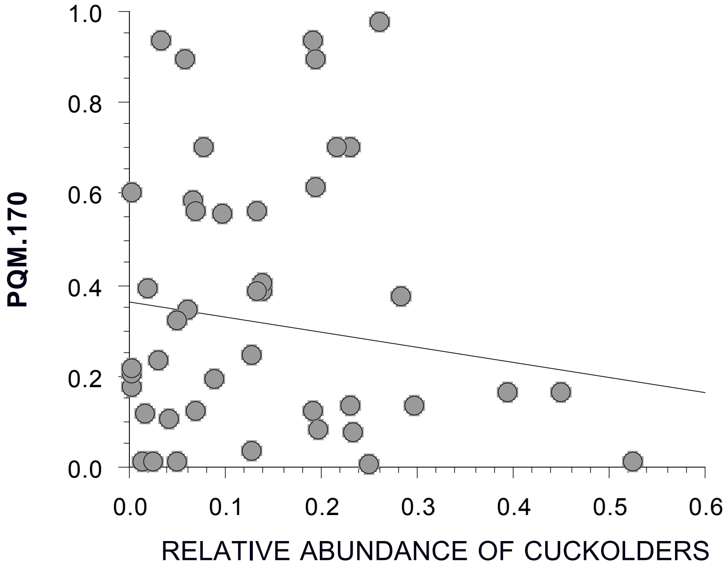
20.0
RELATIVE ABUNDANCE OF MATURE MALES

4A.


PQM.170
RELATIVE ABUNDANCE OF CUCKOLDERS
(MATURE CUCKOLDERS
MATURE PARENTAL MALES)

4B.


PQM.170
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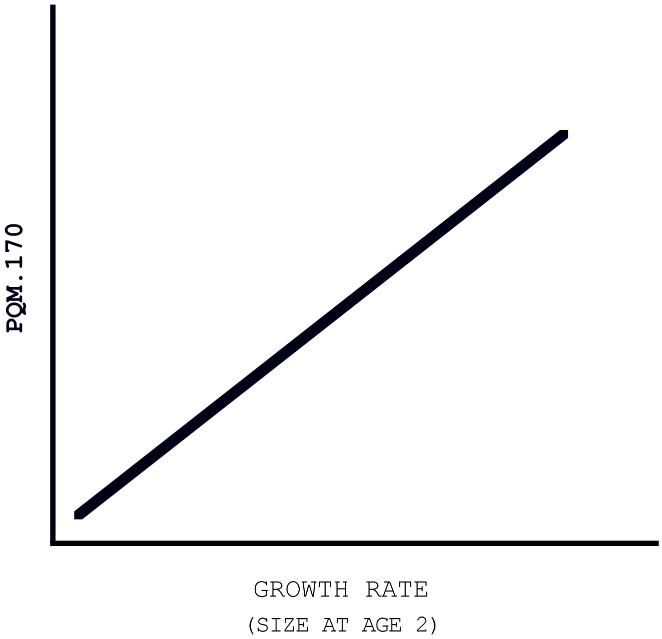
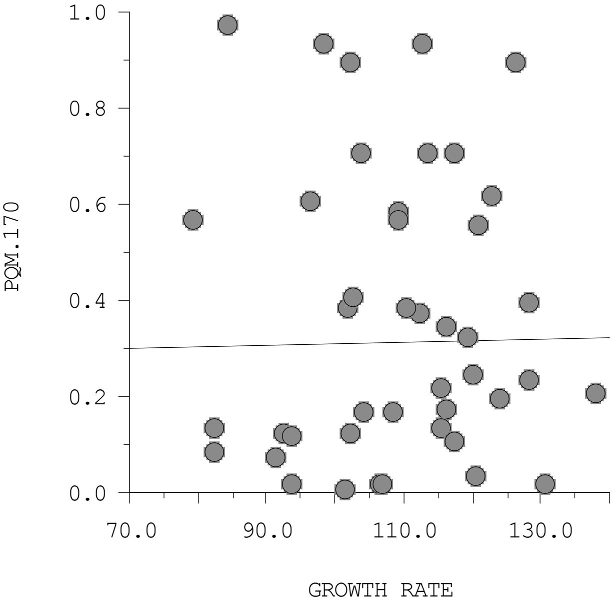
0.6
RELATIVE ABUNDANCE OF CUCKOLDERS

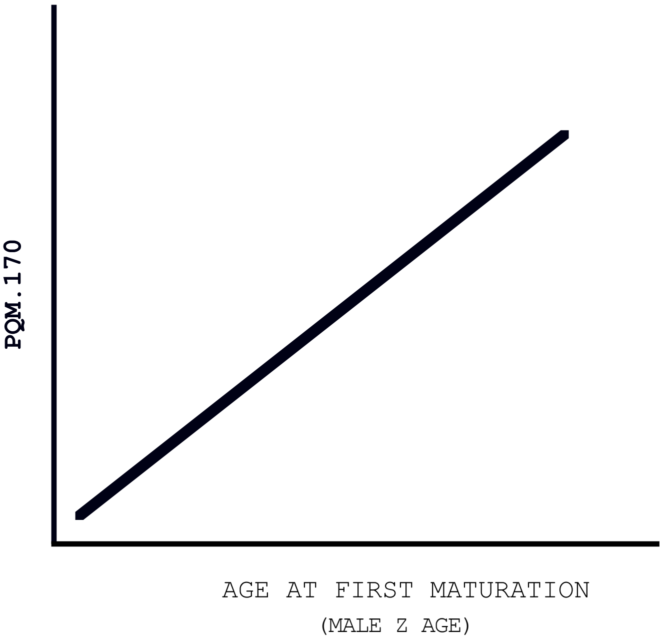
5A. Prediction of the Density-Dependent Growth Limitation Hypothesis



5B. Test of the Density-Dependent Growth Limitation Hypothesis
(r= .015, P = .916)



6A. Prediction of the Social Influence/Early Maturation Hypothesis



6B. Test of the Social Influence/Early Maturation Hypothesis
(r= .522, P = .001)