Supplemental Feeding of Bluegill as a Small Impoundment Enhancement for Largemouth Bass

by

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Abstract

Several pond enhancements are commonly used to increase fish production or enhance angling opportunities. I investigated whether providing supplemental feed to bluegill leads to higher reproductive rates, and if the indirect effects of bluegill feeding improve largemouth bass growth. During 2009 and 2010, adult bluegill and largemouth bass were stocked into nine 0.1-ha ponds; ponds were provided with no pelleted food (control), a low ration (1.52-kg·ha⁻¹·d⁻¹), or a high ration (2.68-kg·ha⁻¹·d⁻¹). Supplemental feeding increased growth of initially-stocked bluegill, female bluegill gonad weight, larval bluegill density, and age-0 largemouth bass growth increased compared to the control. Adult largemouth bass size and fall age-0 bluegill density and biomass did not increase with feeding. Supplemental pellet feeding is clearly beneficial when the pond management goal is to increase bluegill size and reproductive output, and this improved condition of the bluegill population resulted in enhanced growth of age-0 largemouth bass.

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Introduction

Small impoundments or ponds are generally reservoirs less than 40-ha surface area (Dauwalter and Jackson 2005). These man-made water features are abundant across the United States with an estimated 2.6 million located on private land (Smith et al. 2002). Although used for a variety of purposes, such as irrigation, swimming, or livestock water, small impoundments are most often used for recreational fishing (Dauwalter and Jackson 2005; Haley 2009). Fishing in these ponds initially requires fish stocking, but the number and species of fishes to stock in small impoundments continues to be questioned (Modde 1980; Dauwalter and Jackson 2005). While other species are sometimes stocked, largemouth bass, *Micropterus salmoides*, and bluegill, *Lepomis macrochirus*, are most commonly stocked (Swingle and Smith 1941; Swingle 1946; Modde 1980; Dauwalter and Jackson 2005).

Swingle (1946) concluded that largemouth bass and bluegill could generate a balanced predator-prey interaction. Swingle and Smith (1941) found bluegill to be a sustainable prey choice for largemouth bass, because they have a diverse diet, tolerate a wide range of temperatures, and they reproduce multiple times in a season (Gross 1982). Bluegill are protracted spawners (Garvey et al. 2002; Lovshin and Matthews 2003), and spawning occurs in distinct synchronous bouts with several colonies forming and spawning at one period, which is followed by a period of inactivity before the next major spawning event (Cargnelli and Gross 1996). The number of these spawning bouts per year varies depending on a variety of interacting factors including latitude, temperature, weather, food availability, and other abiotic and biotic factors (Jolley et al. 2009).

Some of the goals of small impoundment owners are to produce harvestable size bluegill and largemouth bass, maximize fish catch, and maintain sustainable long-term fish harvest in their ponds. Maintaining a balanced predator-prey system that accomplishes these goals can be a challenge, leading to the development of a wide variety of enhancement techniques that can be used to elevate fish production in the pond (Haley 2009). These enhancements include stocking supplemental forage species such as threadfin shad *Dorosoma petenense* (Noble 1981), installing fish attractors, and using supplemental pellet feed (Schmittou 1969; Lewis and Heidinger 1971; Berger 1982; Porath et al. 2003). While these enhancements are commonly used in practice, they have not always been scientifically evaluated.

Supplemental feeding with prepared pelleted feeds is used by pond owners to increase fish productivity, because fish growth often is limited by food availability (Schmittou 1969; Lewis and Heidinger 1971; Murnyak et al. 1984; Porath et al. 2003). Fish feeders are installed around the pond to provide supplemental food for fish and to improve the condition of stunted fish populations limited by food resources (Berger 1982; Murnyak et al. 1984). Another added benefit to supplemental feeding is that it attracts prey fish from other parts of the pond to the feeding areas (Berger 1982). The addition of pellet feed is targeted towards prey fish, bluegill, to improve growth and body condition. The prey fish are also sometimes pellet fed with the goal of improving largemouth bass growth and condition. In theory prey species that are supplementally fed should grow to larger sizes and have greater energy reserves and therefore should produce more young (i.e. prey for largemouth bass). However, this link between supplemental feed and greater prey resources for largemouth bass has not been evaluated.

The quantity of supplemental feed to be distributed on a daily basis required to produce the best growth in bluegill is unknown and likely varies across ponds. It would be beneficial to identify such a rate to reduce loss via excess feed while maximizing feeding effects. Feeding at high rates can also result in algal blooms. Current recommendations suggest feeding bluegill no more than what they will eat in 10 to 15 minutes, or not more than 11 kg/ha per day (Wright and Masser 2004). In other studies bluegill were fed based on their estimated body weight: Schmittou (1969) fed bluegill at a rate of 3% of total fish weight per day and stated that more than 11 kg/ha of feed was not used. Twibell et al. (2003) fed bluegill at a food allotment equivalent to 4% of the fish body weight each day. Yet, feeding bluegill based on body weight is impractical in small impoundments because fish are continuously growing, and modification of the amount of pellet feed would need to be adjusted frequently in proportion to the biomass of bluegill in the pond. Supplemental feeding can be expensive for pond owners and it is important to know if it is biologically beneficial to bluegill reproduction and largemouth bass condition and growth.

Several studies have examined the effects of pellet feeding of bluegill with feeds of differing protein levels, measuring the resulting fish growth in aquaria (Tidwell et al. 1992; Hoagland et al. 2003; Twibell et al. 2003). Higher protein pellet feeds containing 37 to 44% crude protein are more beneficial to bluegill weight gain than lower protein feeds (Tidwell et al. 1992; Hoagland et al. 2003). However, the cost of feed can be prohibitive, because protein in the pellet feed represents a major cost in the formation of a feed (Hoagland et al. 2003). Determining the protein percentage in pellet feed that is most cost effective depends on the purpose of feeding. Aquaculture facilities raising

bluegill at high densities (>10,000/ha) may be able to afford a higher protein feed (38-44% crude protein), which is often formulated as feed for salmonids or other gamefish species. Yet, private pond owners who want only to provide supplemental feed for bluegill stocked at average densities (2,500/ha) can use lower protein diets (28-36% crude protein) that are less expensive but still provide sufficient calories and protein to enhance fish growth. It is also suggested by nutritionist's that bluegill get sufficient protein from natural foods and the pellets largely give them calories which spares the natural protein (R. A. Wright, personal communication).

Although feeding bluegill can increase their size and condition (Schmittou 1969; Berger 1982; Hoagland et al. 2003; Twibell et al. 2003), it is unknown what effects supplemental feeding has on their reproductive rates. Aday et al. (2006) compared bluegill somatic and gonad tissue growth in unfertilized and fertilized ponds. Mature female bluegill in unfertilized ponds had lower absolute gonad weights than mature females in fertilized ponds, suggesting preferential allocation of energy to somatic tissue when food is scarce (Aday et al. 2006). Therefore, the amount of resources available may influence bluegill total reproductive output, which may directly increase largemouth bass food supply. Supplemental fed bluegill may produce more eggs, or they may spawn more often in a season than unfed bluegill, but to date there is no evidence for this.

Here I examine whether supplemental feeding of bluegill in small impoundments enhances largemouth bass growth and condition. More specifically, I am asking the following questions:

1) Does feeding bluegill lead to higher bluegill reproductive rates, as measured by larval fish density during the spawning season, fall age-0 density, and gonad weight?

2) Do largemouth bass size and relative weight improve in ponds where bluegills are provided supplemental feed?

Methods

Pond Setup

I conducted two separate whole-pond experiments at the E.W. Shell Fisheries Center, South Auburn Unit, Auburn University, Auburn, Alabama, one in 2009 and one in 2010. Nine 0.1-ha ponds (2-m deep at one end, and <0.5-m deep in the opposite end) were drained and treated with lime $CaCO_3$ (12,000 kg/ha) in March 2009 to increase alkalinity, which increases the effectiveness of fertilizer (Wright and Masser 2004). New filters (300-µm mesh size) were added to the experimental pond inflow pipes to prevent fish larvae from entering the ponds as they were filled from an adjacent reservoir pond. After filling, all ponds were fertilized with 9.4 L/ha of 10-34-0 (N-P-K) liquid fertilizer to stimulate a phytoplankton bloom (Wright and Masser 2004). Because it is standard pond management practice for maintaining a phytoplankton bloom, additional fertilizer was added periodically during the experiment (Table 1) to attempt to maintain a uniform secchi depth of 80-cm in all ponds and prevent excessive pond weed growth. When pond weeds (Potomogeton spp.) started to grow in the ponds in May of 2010, a herbicide (Reward[®] active ingredient: diquat dibromide) was applied once to all ponds with a sinker (Pro-Mate[®] Sinker) at a rate of 9.4 L/ha. Dissolved oxygen levels were monitored closely for the next 72 hours, and when the dissolved oxygen dropped to less than 4.0 mg/L, water was flowed through all ponds to circulate and aerate the water. All dead weeds were raked out of the ponds after the herbicide treatment.

All ponds were stocked with bluegill and largemouth bass, the typical community stocked across the United States. Bluegill fingerlings (40 -70 mm TL) are normally stocked into ponds at a density of 2,500/ha (Modde 1980; Wright and Masser 2004;

Dauwalter and Jackson 2005). Because there are no recommendations for stocking intermediate size reproductively mature bluegills (75-120 mm TL) we stocked them at half the recommended fingerling rate (1,250/ha) in 2009. In 2010, adult bluegill (75-120 mm TL) were stocked at the recommended fingerling rate (2,500/ha). Due to unanticipated problems in finding 210-260 mm TL adult largemouth bass in 2009, age-0 largemouth bass (120-170 mm TL) were stocked instead of adults in early August at a rate of 150/ha. Adult largemouth bass were stocked at a rate of 250/ha (210-260 mm TL) in April 2010 immediately following bluegill spawn.

Supplemental Feeding

Pellet feeding occurred from June to September in 2009 and April to August in 2010. There were three experimental treatments, each replicated in three separate ponds: two feeding treatments and a control. Ponds were provided with no pelleted food (control), a low ration (1.52 kg·ha⁻¹·d⁻¹), or a high ration (2.68 kg·ha⁻¹·d⁻¹). The three treatments were randomly assigned to the nine ponds, with three ponds per treatment. Automatic fish feeders (Moultrie Directional Fish Feeder; 23 L capacity) were installed beside each treatment pond, and timers were calibrated to disperse a defined amount of food once daily at 0800 hours, when feeding activity is typically high. I used commercial floating catfish food (F-R-M Catfish Fingerling Grower/ 36% crude protein; distributed by Flint River Mills in Bainbridge, GA).

Abiotic Measures and Plankton Sampling

Temperatures were measured at a depth of 1-m in the deep section of each pond at two-hour intervals with waterproof Hobo[®] temperature pendant data loggers (Model UA-002-64). Dissolved oxygen (mg/L) was measured at 1-m depth from the deep end of

each pond at 0900 hours every 72 hours (Yellow Springs Instrument Model 51 B). Water samples were collected once every 14 days for chlorophyll *a* and turbidity in 500-ml dark polyethylene bottles that were placed directly on ice. Turbidity was measured with a nephelometer (NTU; HF Scientific, Inc. Microw TPW) and chlorophyll *a* concentrations were determined using a fluorometer (μ g/L; Turner Designs Aquafluor). Water samples (500-ml) were filtered onto 47-mm diameter glass fiber disc (Millipore[®]) and chlorophyll *a* was extracted in cold 95% ethanol for 24h, followed by fluorometric analysis (Welschmeyer 1994). A summary of all these measures and their sampling frequency is given in Table 2.

Zooplankton were collected from each pond once every 14 days with a vertical tow of a zooplankton net (30-cm diameter; 50-µm mesh) from 1-m to the surface at 0800-1000 hours. Samples were preserved in 90% ethanol for later identification in the laboratory under a dissecting microscope. In the laboratory, samples were enumerated until at least 200 individuals of the most abundant taxa were counted or until the entire sample was counted (Dettmers and Stein 1992; Welker et al. 1994). Cladocerans were identified to genus, and copepods were identified as cyclopoids, calanoids, harpacticoids, or nauplii.

Fish Sampling

Limnetic larval fish were sampled once per week during the bluegill spawning season from April to September with an ichthyoplankton net (0.5-m diameter; 500-µm mesh) fitted with a flow meter to allow determination of towing speed and water volume sampled for estimation of larval fish density. The ichthyoplankton net was pulled the length of each pond, with two replicate samples collected from each pond on each

sampling date. Once every 30 days we conducted a 15-minute transect in each pond using boat-mounted pulsed-DC electrofishing (Smith-Root Inc. DC electrofisher, 5.0 GPP, 1000 W) to collect random samples of adult largemouth bass and bluegill. Collected fish were measured (TL; nearest mm) and weighed (wet weight; nearest g) and returned to the pond.

Ponds were drained and all fish were harvested in September of 2009 and August of 2010. Adult fish were collected, weighed (g), sexed, measured (mm TL), and frozen for later analysis. Age-0 bluegill were collected, all individuals in a random subsample were counted (n= approximately 500), and the entire sample was weighed (nearest g). The number of fish and weight of the subsample was then extrapolated to estimate the number of age-0 bluegill in the pond.

To determine if there were differences in growth rates of age-0 bluegill between experimental feeding treatments, saggital otoliths were removed from age-0 bluegill in 2009 and otolith daily rings were counted to estimate age in days (Taubert and Coble 1977). A random subsample of age-0 bluegill was measured (nearest 0.01 mm TL) and individuals were put into size classes (n=5 per 10-mm size class; typical size range 15-85 mm TL). Then the otoliths of those fish were removed and mounted on microscope slides using thermoplastic cement. Otoliths were ground on the saggital plane (1,000-grit sandpaper) and polished. We counted daily rings under oil immersion with a compound microscope (400X magnification). We were interested in the first 15 days of life for the age-0 bluegill, and we took measurements from the core of the otoliths to the 15th daily ring. Age-0 otoliths were not removed in 2010, instead (n=5) larval fish otoliths were removed from each pond every week. These otoliths were mounted and read using the

same process above. Each otolith was aged independently by two different readers, and if estimates were within 10% they were averaged. If they were not within 10%, then they were recounted until 10% was reached.

Calorimetry

Bomb calorimetry was used to determine if there were differences in mean energy density of adult and age-0 bluegill among feeding treatments. Adult bluegill (n=10, >130 mm TL) from each pond were dried at 70°C until a constant mass was achieved for two consecutive days (<0.01 g between days), and the final dry mass recorded. Individual age-0 bluegill were combined within 10-mm size classes (typical size range =15-85 mm TL) and dried. Dried adult bluegill samples were blended to a homogenous mixture using a coffee grinder, and dried age-0 bluegill were blended with mortar and pestle; samples were dried again to a constant weight (<0.01 g between days) to remove any moisture accumulated during the mixing process (Glover et. al 2010). Two 0.1 to 0.2-g pellets were then formed and ignited in a semimicro bomb calorimeter (Parr Instrument Co., Model 1425 and Model 6725) to measure bluegill caloric energy content (Glover et. al 2010). Multiple age-0 bluegill in the small size class (15-25 mm TL) were required to create large enough pellets (0.1-0.2 g). Adult largemouth bass caloric densities were determined using the techniques outlined by Glover et. al (2010). Mean caloric densities of the age-0 bluegill size classes, adult bluegill, and adult largemouth bass were compared among feeding treatments.

Analyses

All data were analyzed using the Statistical Analysis System (SAS Institute Inc., Cary, North Carolina, USA). I used a mixed-model analysis of variance (ANOVA),

where means of the ponds (random factor) were nested within the fixed feeding treatments (low, high, and control; PROC MIXED; SAS Institute 2008). Normality and homogeneity of variance were assessed to ensure that the assumptions of ANOVA were met. When significant treatment effects were detected, least-squares means was used to examine where differences existed. Using a mixed-model ANOVA, we tested for differences in the length of age-0 bluegill at 15 days and adult bluegill gonad weight (g). Mixed-model ANOVA was also used to test for treatment differences in caloric density of adult largemouth bass, adult bluegill, and age-0 bluegill. An analysis of covariance (ANCOVA) was used to determine if significant correlations existed for age-0 bluegill body mass among treatment type for caloric density after determining that interactions were insignificant.

Density and biomass of age-0 bluegill and age-0 largemouth bass at harvest were compared among treatments with a mixed-model ANOVA. Mean weight (g) and mean total length (mm) of age-0 largemouth bass were compared among treatments with a mixed-model ANOVA. Using mixed-model repeated-measures analysis of variance (RMANOVA), we tested for differences in mean larval fish density, larval fish growth (mm/day), adult bluegill and adult largemouth bass weight (g) and total length (mm) among treatments. Temperature, secchi depth, dissolved oxygen, turbidity, chlorophyll *a*, and zooplankton density were log-transformed to meet assumptions of variance and then separate RMANOVAs were run for each variable. A first-order autoregressive covariance structure was used in all of the RMANOVAs to account for correlations among observations within the fixed feeding treatments. Percent survival was calculated as n_f/n_i , where n_i was the initial number of fish stocked into the pond, and n_f was the number of fish recovered from the ponds (Sager and Winkelman 2006). Relative weight (W_r) was calculated to estimate condition for each bluegill and largemouth bass (Wege and Anderson 1978). RMANOVA was used to test for differences in largemouth bass and adult bluegill relative weight (W_r) among treatments. The gonadosomatic index (GSI) was calculated to indicate the reproductive allocation in male and female bluegill (Wootton 1990). GSIs were compared among treatments and sex with a mixed-model ANOVA.

Results

Abiotic Measures and Plankton

Temperature (Figure 1), dissolved oxygen (Figure 2), secchi depth (Figure 3), turbidity (Figure 4), and chlorophyll *a* (Figure 5) were not statistically different among treatments during either the 2009 or 2010 experiments (Table 3). Zooplankton density also did not differ among treatments during either 2009 or 2010 (Table 3; Figure 6), nor were there any differences in density of zooplankton taxa among treatments in 2009 (mixed-model RMANOVA: $F_{24,234} = 0.47$; P = 0.98) or 2010 ($F_{30,520} = 0.45$; P = 0.99). The most abundant taxonomic groups were calanoid copepods, copepod nauplii, *Diaphanosoma*, and *Bosmina* for both 2009 and 2010.

Adult Bluegill

In 2009, adult bluegill average weight (mixed-model RMANOVA: $F_{2,6} = 16.22$; P = 0.0038); Figure 7a) and length ($F_{2,6} = 4.08$; P = 0.076; Figure 8a) in the high and low feeding treatments was significantly higher than the control at the end of the experiment. There was no difference between the high and low feeding treatments. Mean weight in the high and low feeding treatments was significantly higher than the control in August and September 2009, but not in June and July ($F_{6,1516} = 48.55$; P < 0.0001; Figure 7a). Length in the high and low feeding treatments was significantly higher than the control in September 2009, but not during June through August ($F_{6,1516} = 14.46$; P < 0.0001; Figure 8a). In 2010, adult bluegill weight ($F_{2,6} = 13.84$; P = 0.0057; Figure 7b) and length ($F_{2,6} = 9.04$; P = 0.016; Figure 8b) were significantly higher in the high treatment than the low treatment, which in turn was significantly greater than the control, at the end of the experiment. The high treatment, low treatment, and control ponds all differed from one

another as above during May through August, but during June the high treatment was greater than the low and control, and in March and April there were no differences between treatments in adult bluegill weight ($F_{12,3359} = 27.85$; P < 0.0001; Figure 7b) or length ($F_{12,3359} = 15.56$; P < 0.0001; Figure 8b).

Adult bluegill relative weight in the high and low feeding treatments was significantly higher than the control at the end of the experiment in 2009 (mixed-model RMANOVA: $F_{2.6} = 10.52$; P = 0.011; Figure 9a), but the high and low feeding treatments did not differ. The high and low feeding treatments were significantly higher than the control in August and September, but not in June and July ($F_{6.1516} = 16.18$; P < 0.0001; Figure 9a). In 2010, adult bluegill relative weight in the low feeding treatment did not differ from that in the high feeding treatment or control ponds ($F_{2.6} = 3.72$; P = 0.089; Figure 9b), but was significantly higher in the high feeding treatment versus the control. Relative weight was significantly higher in the high treatment than the low treatment, and the low treatment was greater than the control at the end of the experiment during July and September ($F_{12,3359} = 14.65$; P < 0.0001; Figure 9b). The high treatment differed from the control but not the low feeding treatment in June and August.

Adult bluegill whole-body caloric density in the high and low feeding treatments at the end of the experiment was significantly higher than in the control in 2009 (mixedmodel ANOVA: $F_{2,6} = 11.96$; P = 0.0081; Figure 10a), with no difference between the high and low feeding treatments. In 2010, adult bluegill whole-body caloric density in the high treatment at the end of the experiment was significantly higher compared to the control ($F_{2,6} = 4.41$; P = 0.066; Figure 10b), and there was no significant difference between the high and low feeding treatments. There were no significant differences in caloric density between male and female bluegill in either 2009 ($F_{1,34} = 0.03$; P = 0.87) or 2010 ($F_{1,80} = 0.89$; P = 0.35).

In 2010, the mean adult bluegill gonad weight in the high treatment, low treatment, and control ponds all differed significantly at the end of the experiment (mixed-model ANOVA: $F_{2,6} = 10.69$; P = 0.011). Female bluegill gonad weight was significantly higher in the high treatment compared to the low treatment and the control ($F_{2,436} = 21.44$; P < 0.0001; Figure 11a). The gonadosomatic index (GSI) of adult bluegill did not differ among treatments in 2010 ($F_{2,6} = 2.38$; P = 0.17). However, when sex was specifically examined the female bluegill GSI was significantly higher in the high treatment compared to the low treatment and the control ($F_{2,436} = 7.74$; P = 0.0005; Figure 11b). There were no differences in adult male gonad weight and GSI among treatments.

Larval and Age-0 Bluegill

There were no significant differences in larval bluegill density among treatments at the end of the experiment in 2009 (mixed-model RMANOVA: $F_{2,6} = 0.01$; P = 0.99; Figure 12), but the low treatment differed from the high treatment and control ponds the first two weeks in August ($F_{16,128} = 2.22$; P = 0.0073; Figure 12). In 2010, larval bluegill density was greater at the end of the experiment in the high feeding treatment compared to the low feeding treatment and control ($F_{2,6} = 4.80$; P = 0.057; Figure 13), and the low feeding treatment and the control did not differ. Larval bluegill density was significantly higher in the high treatment than the low treatment and control ponds throughout July, and the low treatment was greater than the control ponds throughout August, but the low and high treatment did not differ in August ($F_{34,247} = 2.15$; P = 0.0005; Figure 13). There were no significant differences for larval bluegill growth among treatments based on otolith daily rings in 2010 (mixed-model RMANOVA: $F_{2,6} = 0.22$; P = 0.81; Figure 14), although growth rates did vary across sampling dates ($F_{14,519} = 5.73$; P < 0.0001; Figure 14). Fish in the low feeding treatment grew faster than in the high feeding treatment and control throughout June ($F_{28,519} = 2.09$; P = 0.001; Figure 14). There were also no significant differences for age-0 bluegill backcalculated length at the 15th daily ring among treatments in 2009 (mixed-model ANOVA: $F_{2,6} = 2.38$; P = 0.17; Figure 15), but trends suggest that age-0 bluegill in the high and low feeding treatments grew faster than in the control.

The mean number of fall age-0 bluegill did not differ among treatments in 2009 (mixed-model ANOVA: $F_{2,6} = 0.67$; P = 0.55; Figure 16a) or 2010 ($F_{2,6} = 0.52$; P = 0.62; Figure 17a), and age-0 bluegill biomass similarly did not differ among treatments in 2009 ($F_{2,6} = 0.12$; P = 0.88; Figure 16b) or 2010 ($F_{2,6} = 0.43$; P = 0.67; Figure 17b). An analysis of covariance for fall age-0 bluegill whole-body caloric density revealed that slopes did not differ among treatments in 2009. After dropping the interaction term between length and treatment from the model because they were not significant, wholebody caloric density did not differ among treatments (mixed-model ANCOVA: $F_{2,6} =$ 0.98; P = 0.43; Figure 18). Similarly in 2010 age-0 bluegill whole-body caloric density did not differ among treatments (mixed-model ANCOVA: $F_{2,6} =$ 19). The slopes of the feeding treatments and the control were significantly different from one another due to the high and low feeding treatments having a higher caloric density than the control in the 100-120 mm size class ($F_{2,102} = 8.80$; P = 0.0003; Figure 19), but the high and low treatments did not differ from each other.

Adult and Age-0 Largemouth Bass

The weight of the initially-stocked adult largemouth bass did not differ among treatments throughout the experiment in 2010 (mixed-model RMANOVA: $F_{2,6} = 13.84$; P = 0.56; Figure 20a), nor did adult largemouth bass length ($F_{2,6} = 0.34$; P = 0.72; Figure 20b). Relative weight of adult largemouth bass in the two feeding treatments did not differ significantly from the control at the end of the experiment in 2010 ($F_{2,6} = 0.20$; P = 0.83; Figure 21), nor did relative weight differ among treatments throughout the experiment ($F_{10,238} = 1.54$; P = 0.13; Figure 21). Largemouth bass survival was low, but was not affected by treatment (mixed-model ANOVA: $F_{2,6} = 1.07$; P = 0.40; Table 4). In 2010, there were no differences among treatments in adult largemouth bass whole-body caloric density (mixed-model ANOVA: $F_{2,6} = 0.41$; P = 0.68; Figure 22).

In 2009, stocked age-0 largemouth bass weight in the high feeding treatment was significantly larger than the low treatment and control at the end of the experiment ($F_{2,6} = 6.75$; P = 0.029; Figure 23a), and there was no difference between the low treatment and the control. Initially-stocked age-0 largemouth bass length was also greater in the high treatment compared to the low treatment and control at the end of the experiment in 2009 ($F_{2,6} = 5.92$; P = 0.038; Figure 23b). In 2010, age-0 largemouth bass were the offspring of the adult largemouth bass. Mean age-0 largemouth bass weight at the end of the experiment did not differ among treatments in 2010 (mixed-model ANOVA: $F_{2,6} = 1.75$; P = 0.25; Figure 24a), nor did mean age-0 largemouth bass length ($F_{2,6} = 1.34$; P = 0.33; Figure 24b) although the trend of fish being heavier and longer in the high feeding treatment was similar to the 2009 results. However, a length-frequency histogram of 2010 age-0 largemouth bass did show a significant difference in the length-frequency

distributions among treatments at the end of the experiment (Kruskal-Wallis Test: χ^2 = 89.59; *P* < 0.0001; Figure 25), because the high treatment length-frequency distribution was significantly greater than the low treatment and the control (Tukey's: *t*₄₆₉= 3.33; *P* < 0.05). Age-0 largemouth bass number at harvest did not differ among treatments in 2010 (*F*_{2,6} = 0.10; *P* = 0.91; Figure 26a). There was also no difference among treatments in 2010 in age-0 largemouth bass total biomass (*F*_{2,6} = 1.52; *P* = 0.29; Figure 26b).

Discussion

Increased resource supply likely increases the total reproductive output of prey species (Wootton 1973), which in turn may lead to increased prey availability to predators at higher trophic levels. In many warmwater systems in North America, bluegill is a common prey of the largemouth bass. Because fish growth is frequently limited by food availability (Hewett and Kraft 1993) and fish fecundity is often directly related to body size (Wootton 1979; Roff 1984), supplemental feeding is commonly used as a pond enhancement technique to fuel this predator-prey relationship in controlled recreational fishing ponds (Schmittou 1969; Lewis and Heidinger 1971; Berger 1982; Porath et al. 2003), with the added benefit of attracting prey fish from other parts of the pond to the feeding areas (Berger 1982). That is, bluegill with an augmented diet may produce more young either through producing more eggs at each spawn or by spawning more often in a season than unfed bluegill thereby providing more food for largemouth bass. The indirect effects of bluegill feeding mediated through increased production as prey, might improve largemouth bass growth and condition, but to date these effects have not been evaluated. In my whole-pond experiments conducted in two years I found increased bluegill gonad weight and larval bluegill density in feeding treatments compared to the control, and that this improved condition of the bluegill population resulted in enhanced growth of age-0 largemouth bass.

Bluegill

As there is often a direct correlation between fish size and fecundity (Wootton 1979; Fletcher and Wootton 1995), I expected increased reproductive output in larger, fed bluegill. Absolute gonad weights were significantly higher for mature adult female

bluegill in the high feeding treatment compared to the low feeding treatment and control, presumably because bluegill were able to allocate more energy into reproduction. It is likely that mature bluegill females in the low feeding and control ponds compensated for reduced caloric intake by investing a greater proportion of calories into somatic versus gonadal tissue growth (Lambert and Dutil 2000; Aday et al. 2006), or maintained their investment in somatic growth despite decreasing energy intake. Different allocation strategies in fish can be indicated through the use of the gonadosomatic index (GSI; Crim and Glebe 1990), particularly for approximating reproductive allocation in females for fish with one restricted spawning period. However, for a protracted spawning species, such as pumpkinseed and bluegill, reproductive allocation may not be effectively estimated with GSIs over the course of an entire spawning season (Fox and Crivelli 1998). Nevertheless, GSIs were significantly higher for mature adult female bluegill in the high feeding treatment compared to the low feeding treatment and control.

Increased adult bluegill gonad weight should correspond with an increase in the number of eggs spawned (Wootton 1979; Roff 1984; Fletcher and Wootton 1995), but a complex set of interacting environmental factors contributes to egg and larval fish mortality (Dahlberg 1979). In the 2009 experiment, I did not see any differences in the number of larval fish produced among feeding treatments. However, during that experiment bluegill were stocked later in the spawning season, and it is possible that bluegill did not have adequate time to develop sufficient gonad tissue from the pellet food to increase reproductive output among feeding treatments. This has been observed in crappie, where limited prey resources during the months preceding spawning can affect gonad investment and limit ovary production (Bunnell et al. 2007). However, crappie

spawn only once a year and they rely on energy stores that have been acquired over a long period of time to allocate to gonad growth (i.e. 'capital' spawners); bluegill are protracted spawners and must rely on recently acquired energy stores to donate to gonad growth (i.e. 'income' spawners; Bonnet et. al 1998, Bunnell et al. 2007). Interestingly, bluegill stocked earlier in the 2010 field season yielded greater densities of larval fish in the feeding treatment ponds compared to the control. The longer study duration and earlier feeding date in 2010 likely allowed bluegill to allocate more energy to gonad growth. Supplemental feeding also may have had less of an effect in 2009, because there was more food per fish in the feeding treatments due to the lower bluegill stocking density in 2009 compared to 2010. However, by the fall of each year there were no differences in age-0 bluegill numbers and biomass among treatments suggesting densitydependence was operating in my experimental ponds.

In my experiments, growth of initially-stocked bluegill increased in response to supplemental feeding, consistent with several other studies (Schmittou 1969; Lewis and Heidinger 1971; Berger 1982; Porath et al. 2003). Fish growth and biomass can be higher in systems with high levels of productivity. Fertilization of ponds with phosphorous and nitrogen is a common practice to stimulate planktonic algae blooms and thereby increase the productivity of the entire foodweb (Swingle and Smith 1938). Supplemental feeding can lead to plankton blooms similar to those stimulated by fertilization (Wright and Masser 2004). In order to isolate the effect of feeding from planktonic algae, all the experimental ponds were fertilized periodically to maintain a constant secchi depth. No abiotic parameters or plankton densities differed significantly among treatments in either year, indicating that fertilization helped control abiotic factors

and plankton, resulting in fish within all ponds, regardless of feeding treatment, experiencing similar environments throughout the sampling year. Zooplankton density and zooplankton taxon-specific densities were also similar among all ponds, and bluegill used them as a food resource in addition to the supplemental feed. Thus, increased growth of fed bluegill can be attributed to the supplemental feeding and not variation in abiotic parameters or plankton densities. Because fertilization enhanced condition of bluegill in the control ponds relative to what would be seen in field situations without fertilization, the effects of supplemental feeding through all the trophic levels might have been even more pronounced had feeding treatments been compared to a control bluegill population without fertilization.

Largemouth Bass

There were no differences in end-of-experiment adult largemouth bass weight, length, and condition among feeding treatments in 2010, despite an increase in adult bluegill reproductive output. There were trends in adult largemouth bass weight, but they were not significant perhaps due to a lack of power. Additional replication or increased study duration may have enhanced differences in weight for adult largemouth bass among feeding treatments. In a longer study more pronounced effects of bluegill reproduction could result from stored-lipid carryover from previous years (McCormick and Gagliano 2008), which could result in detectable differences in largemouth bass growth and condition among feeding treatments that consumes these bluegill.

The age-0 largemouth bass stocked in July in 2009 in the high feeding treatment did receive a benefit from feeding. In 2010, age-0 largemouth bass were not stocked, but the stocked adult largemouth bass were able to spawn, and the resulting age-0 largemouth

bass population attained larger lengths and weights in the high feeding treatment compared to the low feeding treatment and the control. There was no evidence of pellet food in the diets of randomly-selected age-0 largemouth bass from each pond in either 2009 or 2010. Therefore, the age-0 largemouth bass were not likely receiving a direct benefit from the pelleted food, but rather an indirect resource enhancement from the increased reproductive output of adult bluegill.

Management Implications

Supplemental feeding is often employed as a pond enhancement, but the link between supplemental feed for bluegill and increased prey resources for largemouth bass has not been explicitly evaluated. Feeding has positive effects on bluegill growth and condition (Schmittou 1969; Lewis and Heidinger 1971; Tidwell et al. 1992; Hoagland et al. 2003; Aday et al. 2006; Sager and Winkelman 2006). Additionally, the gonad weight of adult female bluegill and larval bluegill density increased in feeding treatment ponds compared to control ponds. Adult largemouth bass growth and condition were not enhanced, but age-0 largemouth bass in feeding treatments achieved larger sizes compared to those in the control. I expected to see increased adult largemouth bass growth and condition with a corresponding increase in prey items that were available to them, but this did not occur. Thus, there did not appear to be any indirect effects of supplemental feeding on adult largemouth bass, but it did enhance growth of age-0 largemouth bass. The response of predator populations at high trophic levels often lags behind changes in prey populations at lower trophic levels. For example, the lynx preys specifically on snowshoe hares and the population growth and decline of the lynx lags slightly behind the rise and fall of the snowshoe hare population (Elton and Nicholson

1942). Similarly, the adult largemouth bass may show a lagged growth response behind the increase in bluegill reproductive output due to supplemental feeding. Thus, longerterm experiments must be used to determine whether supplemental feed provided to bluegill yields long-term indirect benefits for adult largemouth bass growth. Supplemental pellet feeding is clearly beneficial when the pond management goal is to directly increase bluegill size and reproductive output, thereby enhancing the growth of age-0 largemouth bass.

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2009 Fertilization Dates							
Feeding Treatment	Pond#	May 27	Jun 15	Jun 24	Jul 20	Aug 17	Aug 24
Low	201	Yes	Yes	Yes	Yes	Yes	Yes
Control	202	Yes	Yes	Yes	Yes	Yes	Yes
High	203	Yes	Yes	Yes	Yes	No	No
Low	204	Yes	Yes	Yes	Yes	Yes	Yes
High	205	Yes	Yes	Yes	Yes	No	No
Control	206	Yes	Yes	Yes	Yes	Yes	Yes
Control	207	Yes	Yes	Yes	No	Yes	No
High	208	Yes	Yes	Yes	No	No	No
Low	209	Yes	Yes	No	No	Yes	No
	2010 Fertilization Dates						
Feeding Treatment	Pond#	Feb 12	Mar 8	Mar 22	Apr 5	Jun 1	Jun 15
Control	201	Yes	Yes	Yes	Yes	Yes	Yes
High	202	Yes	Yes	Yes	Yes	Yes*	Yes
Low	203	Yes	Yes	Yes	Yes	Yes	Yes
Low	204	Yes	Yes	Yes	Yes	No	No
Control	205	Yes	Yes	Yes	Yes	Yes	No
High	206	Yes	Yes	Yes	Yes	Yes	Yes
Low	207	Yes	Yes	Yes	No	Yes*	Yes*
High	208	Yes	Yes	Yes	No	Yes	Yes
Control	209	Yes	Yes	Yes	Yes	Yes*	Yes*

Table 1. Fertilization schedule for 2009 and 2010 Field Seasons

Yes = 0.95 L of liquid fertilizer 10-34-0 (N-P-K) was added to pond

 $Yes^* = 0.47 L$ of liquid fertilizer was added to pond

No = no liquid fertilizer was added to pond

2009 Field Season				
Measure	Frequency	Timeline		
Temperature °C	Every 2 hours	June-September		
Secchi Depth (cm)	Every Week	June-September		
Dissolved Oxygen (mg/L)	Twice a week	June-September		
Larval Fish (No./m ³)	Every Week	June-September		
Zooplankton (No./m ³)	Every 2 Weeks	June-September		
Chlorophyll <i>a</i> (µg/L)	Every 2 Weeks	June-September		
Turbidity (NTU)	Every 2 Weeks	June-September		
Electrofishing	Every 30 Days	June-September		
2010 Field Season				
Measure	Frequency	Timeline		
Temperature °C	Every 2 hours	February-August		
Secchi Depth (cm)	Twice a week	May-August		
Dissolved Oxygen (mg/L)	Twice a week	May-August		
Larval Fish (No./m ³)	Every Week	May-August		
Zooplankton (No./m ³)	Every 2 Weeks	February-August		
Chlorophyll <i>a</i> (µg/L)	Every 2 Weeks	February-August		
Turbidity (NTU)	Every 2 Weeks	February-August		
Electrofishing	Every 30 Days	February-August		

Table 2. Summary of measures for the 2009 and 2010 field seasons

	2009 Yes	ar	2010 Year		
Treatment Effects					
Measure	F-statistic	P-value	F-statistic	P-value	
Temperature (°C)	$F_{[2,6]} = 0.23$	p= 0.80	$F_{[2,6]} = 0.52$	p= 0.62	
Secchi Depth (cm)	$F_{[2,6]} = 0.35$	p=0.72	$F_{[2,6]} = 0.48$	p= 0.64	
Dissolved Oxygen (mg/L)	$F_{[2,6]} = 1.12$	p= 0.39	$F_{[2,6]} = 2.50$	p= 0.16	
Turbidity (ntu)	$F_{[2,6]} = 0.29$	p=0.76	$F_{[2,6]} = 0.35$	p= 0.72	
Chlorophyll-a (µg/L)	$F_{[2,6]} = 0.69$	p= 0.53	$F_{[2,6]} = 1.19$	p= 0.37	
Zooplankton (No./m ³)	$F_{[2,6]} = 1.08$	p= 0.40	$F_{[2,6]} = 0.20$	p= 0.83	
	Time Eff	ects			
Temperature (°C)	$F_{[89,534]} = 267.95$	p< 0.01	$F_{[181,1448]} = 1665$	p< 0.01	
Secchi Depth (cm)	$F_{[7,56]} = 1.80$	p= 0.10	$F_{[48,384]} = 4.57$	p< 0.01	
Dissolved Oxygen (mg/L)	$F_{[13,104]} = 5.74$	p< 0.01	$F_{[33,264]} = 3.12$	p< 0.01	
Turbidity (ntu)	$F_{[7,56]} = 9.74$	p< 0.01	$F_{[13,104]} = 5.98$	p< 0.01	
Chlorophyll-a (µg/L)	$F_{[7,56]} = 10.74$	p< 0.01	$F_{[13,104]} = 9.88$	p< 0.01	
Zooplankton (No./m ³)	$F_{[7,432]} = 40.43$	p< 0.01	$F_{[13,911]} = 20.73$	p< 0.01	
Interaction Effects (Time * Treatment)					
Temperature (°C)	$F_{[178,534]} = 1.24$	p= 0.04	$F_{[362, 1086]} = 0.40$	p= 1.00	
Secchi Depth (cm)	$F_{[14,42]} = 0.77$	p= 0.69	$F_{[96,288]} = 0.81$	p= 0.89	
Dissolved Oxygen (mg/L)	$F_{[26,78]} = 0.61$	p= 0.92	$F_{[66,198]} = 0.69$	p= 0.96	
Turbidity (ntu)	$F_{[14,42]} = 1.07$	p=0.41	$F_{[26,78]} = 0.70$	p= 0.85	
Chlorophyll-a (µg/L)	$F_{[14,42]} = 0.69$	p=0.53	$F_{[26,78]} = 0.84$	p= 0.69	
Zooplankton (No./m ³)	$F_{[14,418]} = 2.59$	p< 0.01	$F_{[26,885]} = 0.66$	p= 0.92	

Table 3. Abiotic and plankton model results among feeding treatments for separate mixed-model RMANOVAs.

	Blu	legill	Largemouth Bass		
Feeding Treatment	2009	2010	2009	2010	
Control	0.40 (±0.047)	0.75 (±0.049)	0.27 (±0.11)	0.20 (±0.082)	
Low	0.43 (±0.013)	0.71 (±0.053)	0.23 (±0.15)	0.38 (±0.14)	
High	0.41 (±0.042)	0.74 (±0.039)	0.23 (±0.041)	0.27 (±0.082)	

Table 4. Adult fish percent survival (± 1 SE) for the 2009 and 2010 field seasons

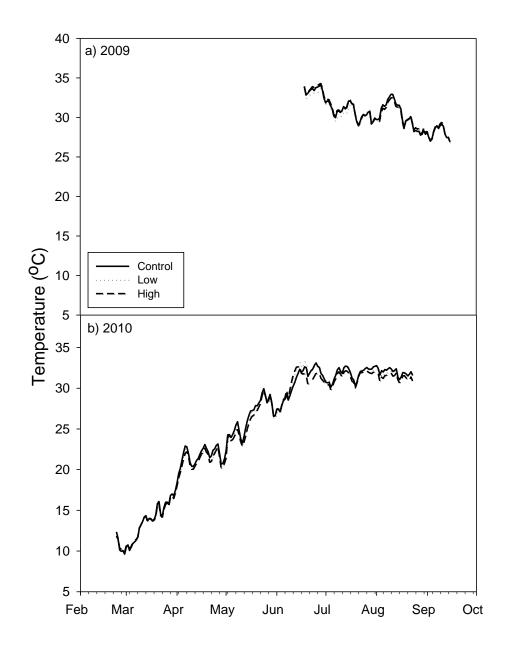


Figure 1.

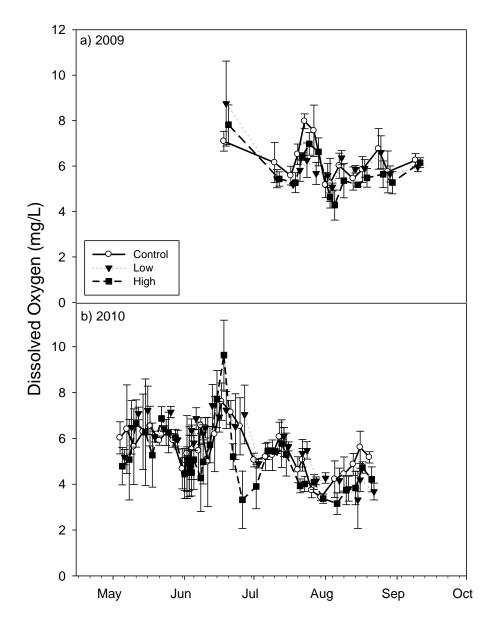


Figure 2.

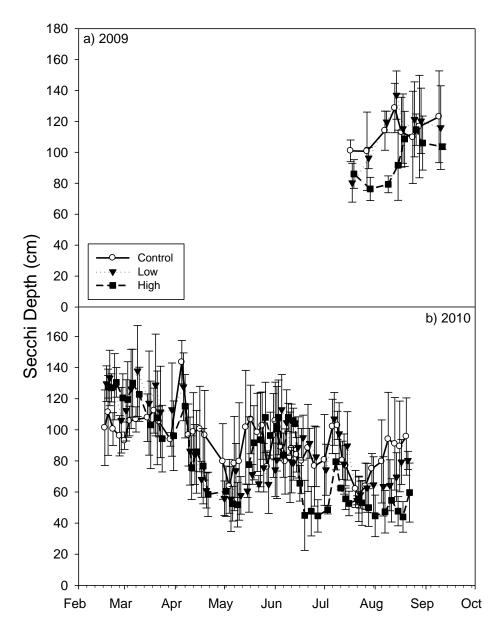


Figure 3.

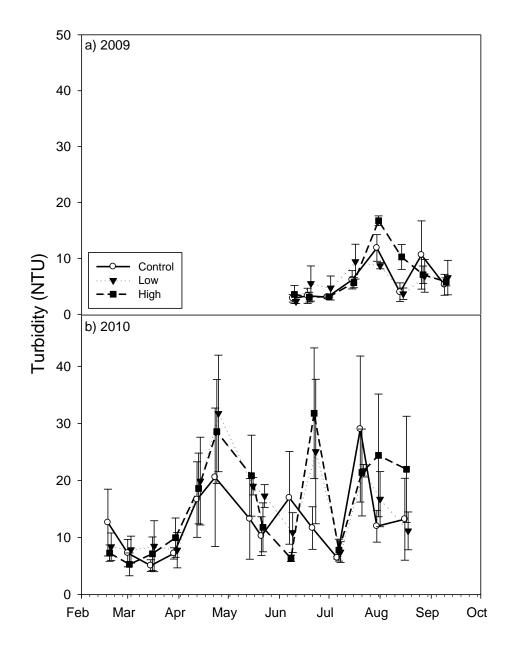


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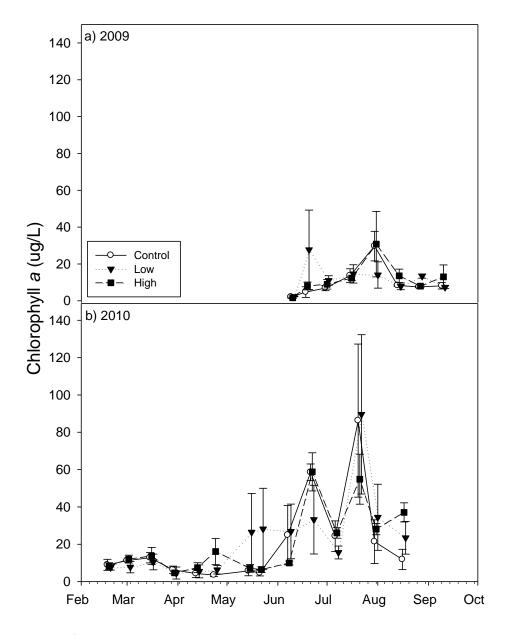


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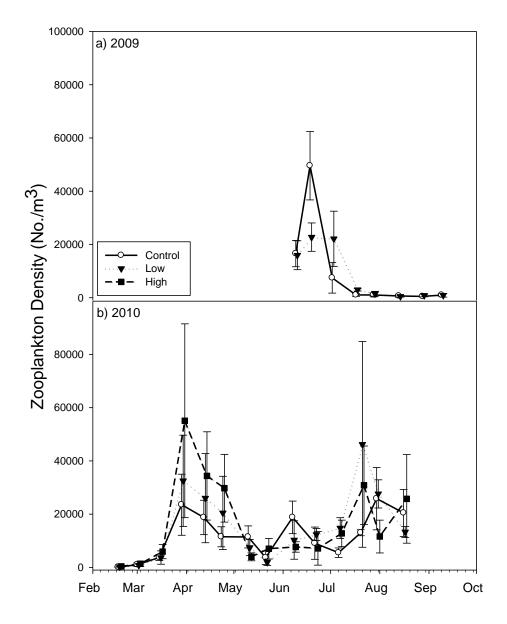


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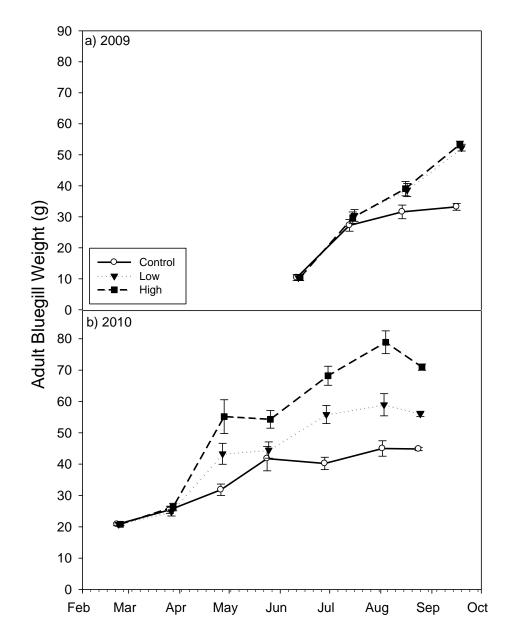


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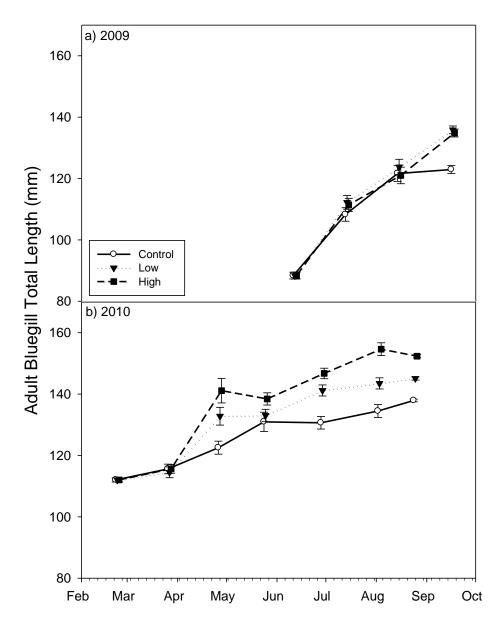


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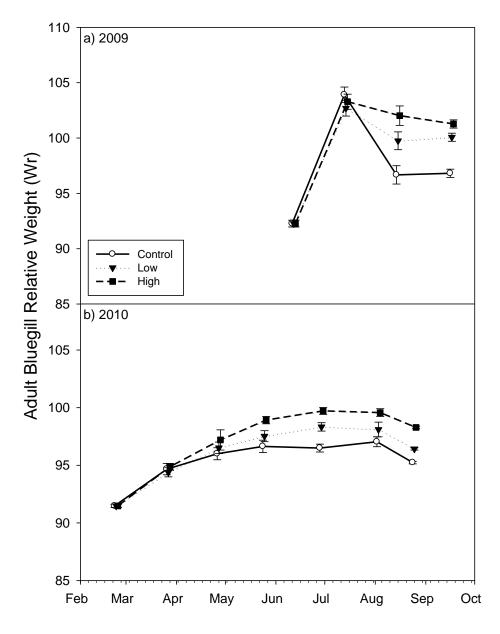


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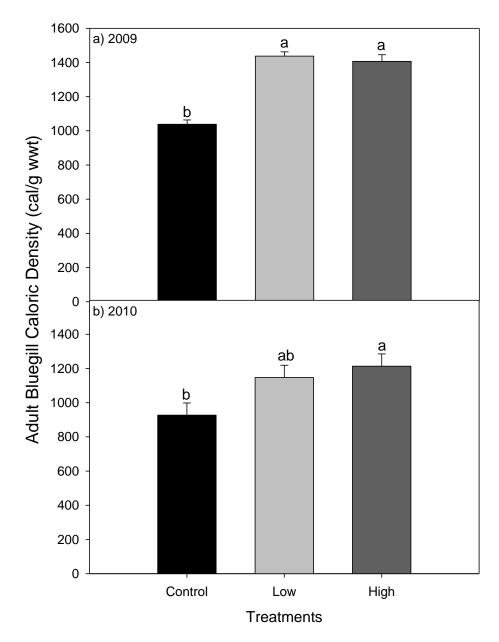


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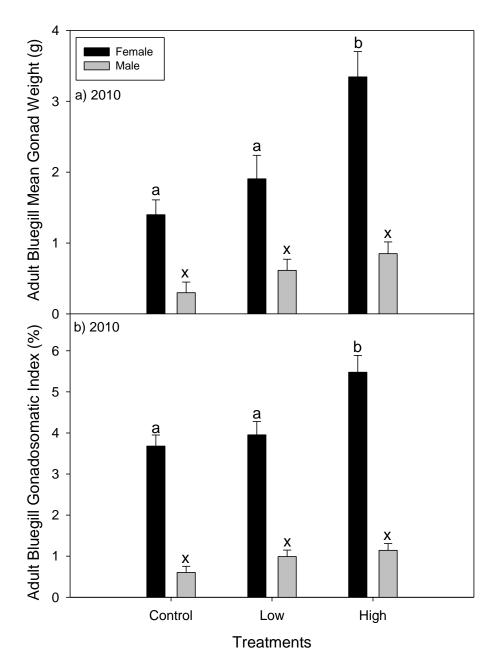


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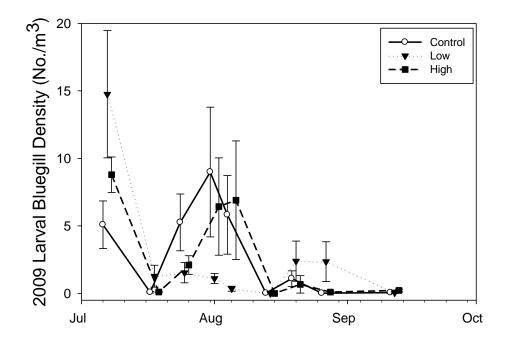


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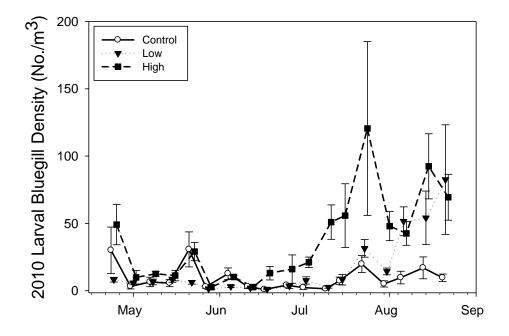


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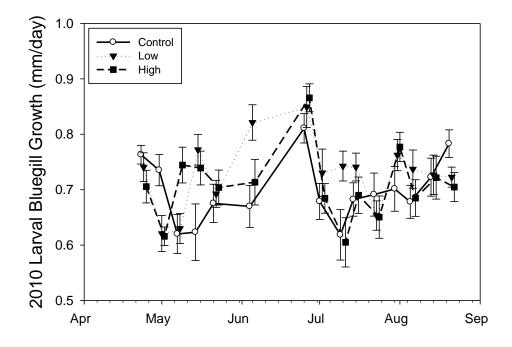


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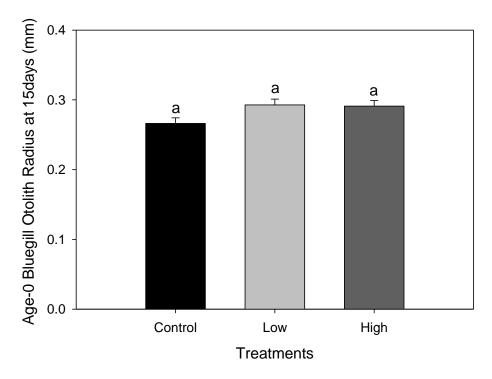


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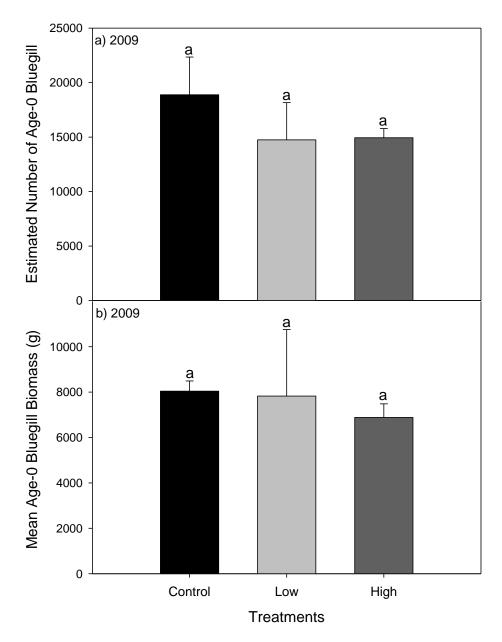


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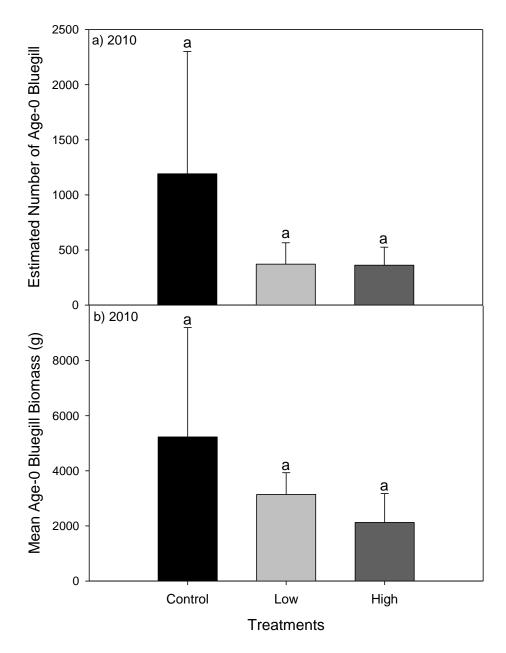


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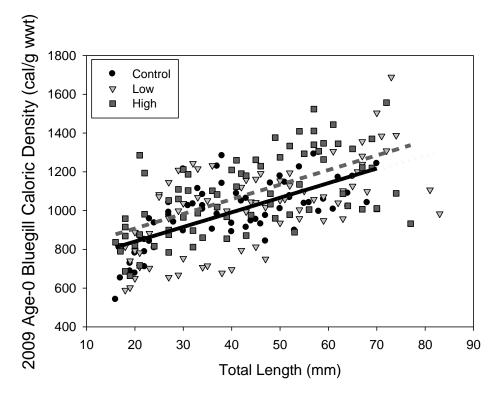


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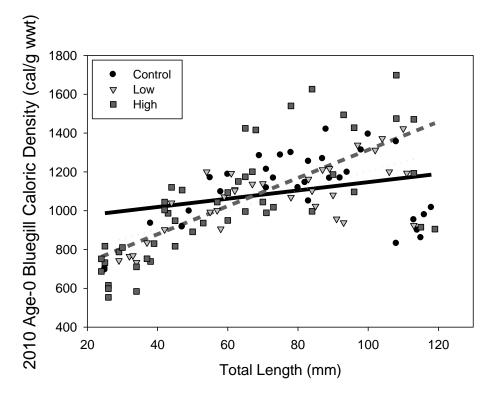


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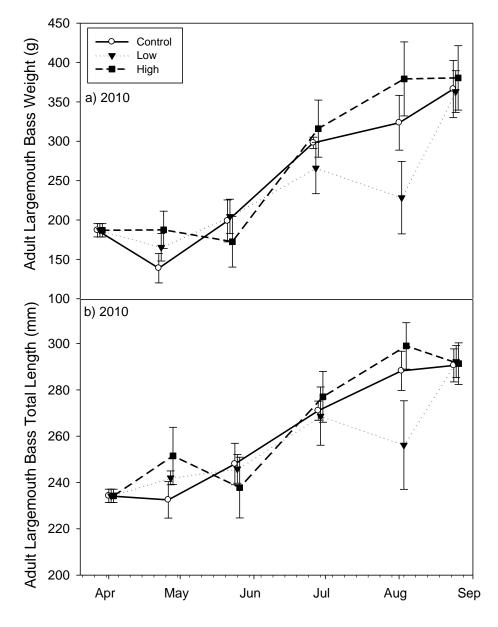


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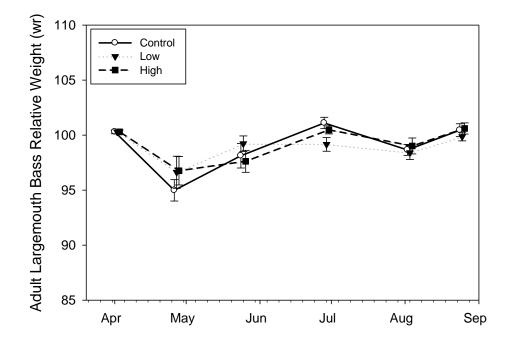


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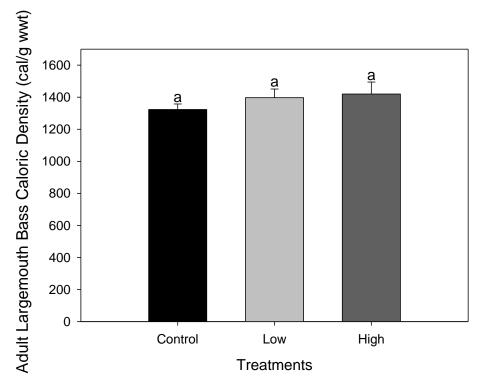


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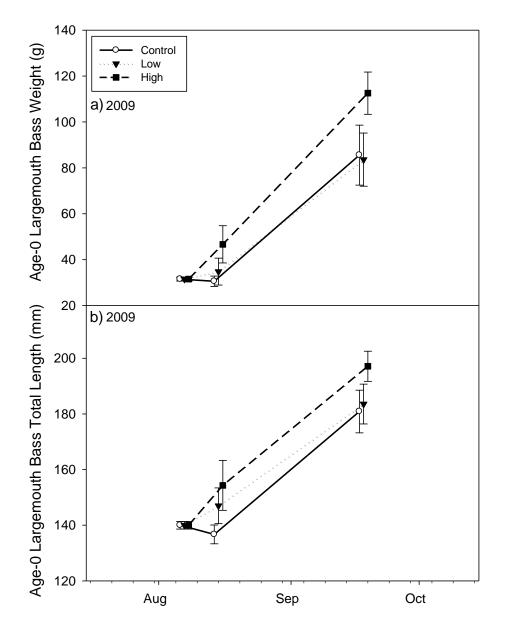


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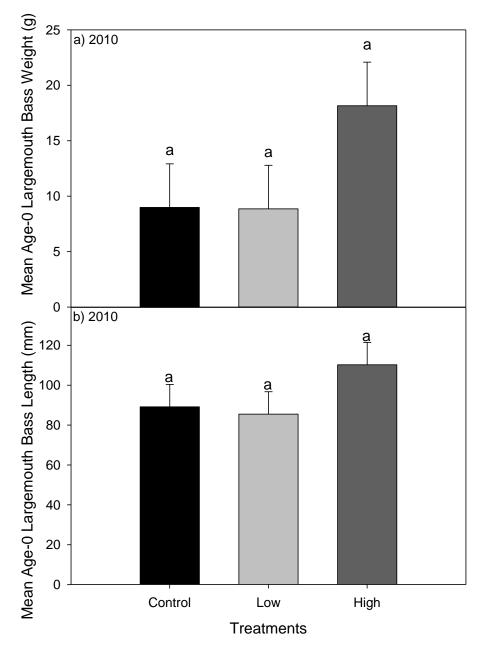


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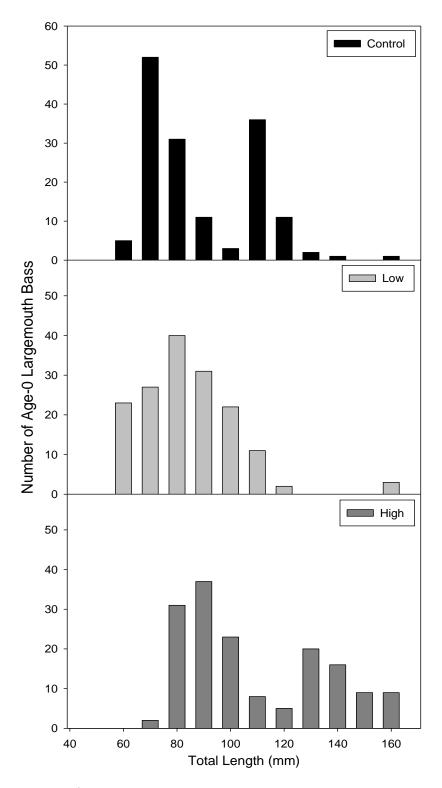


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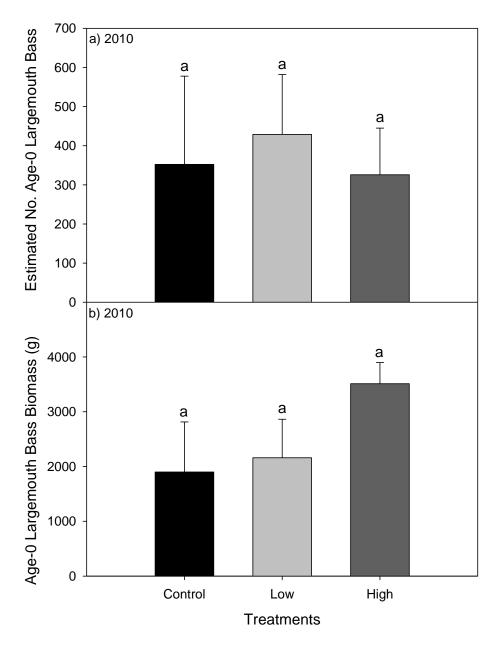


Figure 26.