Rearing Male Bluegills Indoors May Be Advantageous for Producing Food-size Sunfish

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Abstract.—An indicated demand for sunfish (*Lepomis* spp.) as a food fish remains untested because of continuing inability to efficiently rear these fishes to required large sizes ($\geq$227 g; 0.5 lbs). A recent study involving parallel, indoor rearing of two sunfishes under favorable conditions showed that bluegills *Lepomis macrochirus* possessed markedly higher growth capacity than B × G hybrids (F$_1$: male bluegill × female green sunfish, *Lepomis cyanellus*). B × G hybrids had been thought to possess superior growth capacity and so have received more attention than bluegills as a food-fish candidate in many areas of the USA. Reanalysis of data from the recent study with emphasis on gender differences revealed that the male bluegills possessed much higher growth capacity than male B × G hybrids, at least from May to March as Age 1 and then early Age 2 fish. Male bluegills reached 67% of food-market weight within the 10-mo period from a starting weight of 7 g; male B × G hybrids reached only 24% of this weight. Male bluegills' more rapid growth versus male B × G hybrids' apparently involved less growth energy allocation to gonad development. Female bluegills grew slower than male bluegills but also outgrew male and female B × G hybrids whose growth trajectories declined in midsummer (June) and remained largely flat through March. The previous view that B × G hybrids possess higher growth capacity than bluegills was fostered by studies in ponds where bluegill growth can be impeded by high reproduction rates and, as this study reveals, by high densities and exposure to suboptimal temperatures when their growth potential is high. Indoor rearing of male bluegills should ameliorate most pond-related growth impediments and take fuller advantage of their rapid growth capacity.

Fish of the genus *Lepomis*, including some of their hybrids (collectively, sunfish), have long been reared mainly to small and intermediate sizes for recreational pond stocking throughout much of the USA (Flickinger et al. 1999; Heidinger 1999; Brunson and Morris 2000). More recently, demand has developed for large sunfish ($\geq$227 g; 0.5 lbs) as food fish (Chopak 1992; NCRAC 1999; Brunson and Morris 2000). Sunfish approaching food-market size are also desired by fee-fishing operations and by fisheries management agencies for warm-water stocking programs (Brunson and Morris 2000).

Although a handful of commercial producers have reared sunfish for food markets (Morris and Mischke 2000; R. Butz, Windridge Farm, Germantown, MD, USA, personal communication), techniques for the efficient rearing of large sunfish are not well established (NCRAC 1999; Loveshin and Matthews 2003). The consensus view of the North Central Regional Aquaculture Center's Sunfish Workgroup is that capacity to rear sunfish to $\geq$227 g within a 2-yr period of grow out must be achieved for their commercial production as food fish to become viable (R. Hayward, University of Missouri–Columbia, Columbia, MO, unpublished results). This time limit is consistent with maximum tolerable rearing times for a number of food-fish species (Loveshin and Matthews 2003).

Sunfish culture, whether aimed at stocking ponds or producing food fish, has remained almost exclusively pond based (Ricker 1948; Schmittou 1965; Lewis and Heidinger 1978; Tidwell et al. 1994; Loveshin and Matthews 2003). Among the sunfishes, bluegill *Lepomis macrochirus* and the B × G hybrid (F$_1$: male bluegill × female green sunfish, *Lepomis cyanellus*) have received the most attention as food-fish candidates (Hayward and Wang 2002). Besides possessing positive marketing qualities, which include good flesh texture and flavor and being well recognized (Webber and

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Riordan 1976; McLarney 1987), both fishes readily accept commercial diets (Lewis and Heidinger 1978; Ehlinger 1989) and exhibit fairly rapid growth over broad ranges of temperature (Heidinger 1975; Ellison and Heidinger 1978).

In some regions of the USA, the B × G hybrid has received more attention than the bluegill in efforts to rear large sunfish because pond studies have shown it to grow faster (Ellison and Heidinger 1978; Brunson and Robinette 1985, 1986). The B × G hybrid's faster growth in ponds has been ascribed to hybrid vigor (Brunson and Robinette 1985; Flickinger et al. 1999) arising, in part, because its populations comprise predominantly male fish (80–95%), which leads to fewer competing offspring in ponds than occurs with bluegill (Kurzawski and Heidinger 1982; Flickinger et al. 1999). Moreover, Lane and Morris (2002) found that B × G hybrids consume natural food items in production ponds, including their own progeny, to a much greater extent than do bluegills. This capacity, which may owe in part to the B × G hybrid's larger mouth, suggests that the hybrids profit both energetically and nutritionally by consuming their progeny, while simultaneously reducing numbers of trophic competitors. Together, these advantages may substantially underlie the more rapid growth observed for B × G hybrids versus bluegills in ponds, which has fostered the impression that the hybrid is an inherently faster grower than the bluegill. However, despite the B × G hybrid's faster growth in ponds, it has yet to be demonstrated that substantial numbers of these fish can be reared to food-market weights within 2-yr, grow-out periods.

A recent study (Hayward and Wang 2002) in which individually and group-held bluegills and B × G hybrids were grown in parallel in indoor tanks for 10 mo (May through March as Age 1 and ultimately Age 2 fish) found that bluegills possessed markedly higher inherent growth capacity than B × G hybrids. Inherent growth capacity was assessed by growing fish individually, without direct influences of social interaction, under continually favorable growth temperatures and feeding conditions. Unlike the B × G hybrids, whose inherent growth rates slowed beginning in July and remained low through March, the bluegills showed more rapid growth throughout the 10-mo study period and reached final weights that were twice those of the B × G hybrids (100 versus 50 g). The more rapid growth of bluegills that continued through fall and into winter in the laboratory, in contrast to the B × G hybrids, would not have occurred in ponds at most latitudes due to suboptimal fall/winter growth temperatures. Overall, a number of factors pointed to possible advantages associated with rearing bluegills in indoor tanks, including that reproduction would not occur, food availability may be increased, and fuller advantage would be taken of bluegill's higher growth capacity due to continually favorable rearing temperatures.

The present study derives from the data set of Hayward and Wang (2002) but, unlike the previous study, explores gender-related differences in growth capacity and social costs for bluegills and B × G hybrids reared in indoor tanks. Findings provide additional insights that are considered valuable relative to developing capacity to rear sunfish efficiently to large sizes.

Material and Methods

Feed-trained, Age 1 bluegills and B × G hybrids were obtained in April 2000 from the ponds of a major sunfish supplier in Missouri and transported to our laboratory. Bluegills and B × G hybrids were held separately in two 1000-L acclimation tanks at 19–21 C and provided liberal amounts of floating commercial pellet feed twice daily. Bluegills and B × G hybrids not used in Experiment 1 remained in the acclimation tanks under the conditions described while the experiment was run. Some of the fish that remained in the acclimation tank were used in Experiment 2, which immediately followed Experiment 1.

Experiment 1

Experiment 1 compared inherent growth capacity, food consumption, and feed conversion ratio (FCR) among male and female bluegills and B × G hybrids held individually under continually favorable growth conditions.
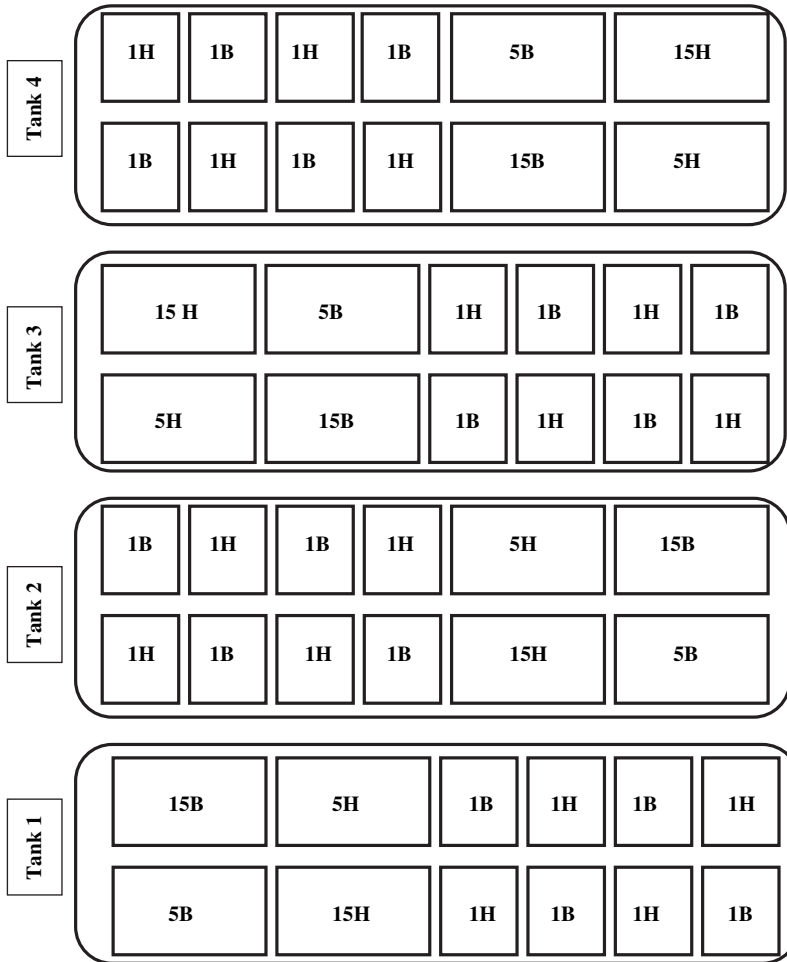
FIGURE 1. *Arrangement of small chambers holding either a single bluegill (1B) or a B × G hybrid (1H) and large chambers holding either 5 bluegills or B × G hybrids (5B or 5H, respectively) or 15 bluegills or B × G hybrids (15B or 15H, respectively) in each of the four 1000-L tanks during Experiment 1.*

A second objective was to quantify costs of social interaction according to fish type (bluegill or B × G hybrid) and gender, when each fish type was held in groups at two densities. Differences between mean growth rates of grouped fish and those held individually were taken to reflect costs of social interaction (Wang et al. 2000). Food amounts provided were unrestricted in all cases and so were believed not to limit fish growth.

Ninety-six fish of each type were selected from approximately the middle third of the respective fish size ranges in the acclimation tanks and randomly allocated to either individual or group holding. Individual fish were held in small perforated chambers (38 × 20 × 30 cm), while groups of 5 (lower density; 200 fish/m³) and 15 fish (higher density; 600 fish/m³) were held in larger perforated chambers (43 × 30 × 43 cm). The chambers were set in four 1000-L tanks, each equipped with biofiltration, aeration, and temperature control capacities. They were submerged to a depth of 24 cm such that their open tops were above the water surface, and water volumes within the small and large chambers were 10.6 and 25.7 L, respectively. There were 16 replicates each of individually held bluegills and

B × G hybrids, four bluegills and four hybrids being held individually in small chambers in each of the four 1000-L tanks. One lower and one higher density group of each fish type (total of four large chambers) were also set in each 1000-L tank, giving four replicates of each fish type and holding-density combination (Fig. 1).

Water temperature of 22 ± 0.5 C and a summer-like photoperiod (14 h light:10 h dark) were maintained throughout Experiment 1. Experimentation with individually held control fish ran for 100 d (Days 1–100, May–August 2000) and 75 d for the grouped treatment fish (Days 1–75). Throughout the experiment, fish were hand-fed three times daily to apparent satiation (i.e., until feeding activity ceased in a chamber) at 0800, 1300, and 1800 h to avoid feed restriction (Wang et al. 1998). Feed pellets (41% protein, 12% fat; Rangen Inc., Buhl, ID, USA) that remained floating in chambers 30 min after feed provisioning were removed and counted. After the last feeding of a day, any floating feed pellets or pellets on the bottoms of chambers were removed and counted. Mean weights of dry feed pellets were estimated so that unconsumed pellet counts could be converted to dry weights.

Dissolved oxygen concentrations were measured daily (YSI model 95 oxygen and temperature system, Yellow Springs Instrument Company, Yellow Springs, OH, USA) in each test chamber and in the water outside of the chambers. Measurements of pH, ammonia, nitrite, and nitrate were made weekly with water test kits (Wardley, Master Water Test Laboratory, Secaucus, NJ, USA) outside of the chambers and in one randomly selected lower density and higher density chamber in each tank. Partial water replacement was done every second day to ensure high water quality.

Combined daily food consumption (CDFC) by the fish in each chamber (1, 5, or 15 fish) was determined by subtracting the weight (g) of feed remaining in a feed cup after the last feeding of the day (plus the estimated dry weight of feed remaining in the chamber) from the feed weight in the cup prior to the first feeding of that day. Cumulative consumption (CC) was the estimated mean food weight (g) consumed by each of the N fish in a chamber (CDFC/N) on a given day, summed over a designated period of t days. CC for grouped fish could not be determined according to gender because fish's gender was determined only on completion of the experiment. Consequently, gender-related differences in CC were considered for individually held control fish only.

All fish in each chamber were weighed individually at the beginning of the experiment and on Days 25, 50, and 75. Individually held control fish, for which experimentation was continued an additional 25 d, were also weighed on Day 100. Prior to each weighing, fish were deprived of food for 16 ± 1 h; they were then blotted dry with a towel and added to a tared, water-filled container and weighed to the nearest 0.1 g. After final weighing, fish were euthanized by exposure to 500 mg/L of MS222 for 5 min followed immediately by cervical dislocation. Gender of each fish was determined by inspection of gonads, using a dissecting scope when needed; gonads were weighed to the nearest 0.1 g and gonadosomatic index (GSI) values computed as

$$GSI = 100 \times \text{gonad weight (g)}/ \text{whole-body weight (g)}.$$

For each individually held control fish, absolute growth rate (g/d) was determined over Days 1–75 (AGR75) for comparisons with grouped fish and also over Days 1–100 (absolute growth rate [AGR]) as $(W_f - W_i)/t$, where W_f and W_i are the final and initial weights over periods of t days (either 75 or 100 d). FCR was calculated for each control fish over the full 100 d as CC/$(W_f - W_i)$. Means (and SEMs) of CC, AGR, FCR, and GSI were determined for control fish over the 100-d experiment for male and female bluegills and B × G hybrids.

Costs of social interaction were determined separately for male and female bluegills and B × G hybrids that were reared in mixed-gender groups at the lower and higher densities. Social interaction costs were represented as the difference between AGR75 for fish held in groups and AGR75 for individually held control fish reared in parallel without direct social costs. For each of the 16 treatment-group chambers containing

TABLE 1. *Means (and SEMs) of initial and final weights, absolute growth rate (AGR), cumulative consumption (CC), feed conversion ratio (FCR), and gonadosomatic index (GSI) for individually held male and female bluegills and B × G hybrids in Experiment 1 (N = 16 for bluegills and for B × G hybrids) and in follow-on Experiment 2 in which two size groups of sunfish (larger and smaller) were separately evaluated (N = 8 for bluegills of each size group and likewise for B × G hybrids). Means of instantaneous growth rate (G) and final total length are given for each fish type/gender group in Experiment 2 in place of CC and FCR which could not be calculated due to data on CC not being collected. For each variable, means across the four (or three) fish type/gender groups that are followed by the same letter are not significantly different (P ≥ 0.05). In Experiment 2, one smaller size bluegill perished (N = 7), and no females occurred among the smaller size B × G hybrids.*

Fish type/gender	N	Initial weight (g)	Final weight (g)	AGR (g/d)	CC (g)	FCR	GSI
Experiment 1 (May 2000–August 2000 [100 d])							
BG-male	8	7.00 (0.37) a	47.67 (6.08) a	0.41 (0.06) a	38.97 (5.02) a	1.00 (0.05) b	0.94 (0.31) c
BG-female	8	6.32 (0.30) a	23.94 (1.27) b	0.18 (0.01) b	21.41 (1.38) b	1.23 (0.04) a	9.42 (0.95) a
HYB-male	13	7.60 (0.34) a	34.18 (3.03) ab	0.27 (0.03) b	28.53 (2.33) ab	1.13 (0.05) ab	1.92 (0.16) b
HYB-female	3	6.98 (0.41) a	24.62 (5.69) b	0.18 (0.05) b	19.47 (4.93) b	1.13 (0.05) ab	11.69 (1.65) a
					$G \times 100$	Final total length (cm)	
Experiment 2 (August 2000–March 2001 [200 d])							
Larger fish							
BG-male	3	34.80 (2.79) a	150.53 (15.84) a	0.58 (0.07) a	0.73 (0.04) a	18.23 (0.23) a	1.19 (0.18) b
BG-female	5	29.59 (1.70) a	76.86 (9.77) b	0.24 (0.04) b	0.46 (0.05) b	15.20 (0.44) b	5.93 (1.60) a
HYB-male	7	33.53 (1.49) a	54.47 (3.73) b	0.10 (0.02) c	0.24 (0.03) c	14.76 (0.24) b	1.47 (0.24) ab
HYB-female	1	23.87 —	36.10 —	0.06 —	0.21 —	12.80 —	10.83 —
Smaller fish							
BG-male	4	9.89 (0.84) a	89.48 (13.62) a	0.40 (0.07) a	1.09 (0.06) a	15.68 (0.48) a	1.19 (0.41) a
BG-female	3	8.05 (1.50) a	52.13 (10.05) ab	0.22 (0.06) ab	0.93 (0.19) ab	13.53 (0.47) b	2.82 (1.39) a
HYB-male	8	10.19 (0.62) a	36.55 (3.98) b	0.13 (0.02) b	0.63 (3.72) b	12.91 (0.37) b	0.81 (0.14) a

either 5 or 15 bluegills or B × G hybrids, each fish's AGR75 was estimated as $(W_\mathrm{f} - \overline{W}_\mathrm{i})/75$, where W_f is a fish's final weight on Day 75 and $\overline{W}_\mathrm{i}$ is the mean weight of all fish in the chamber at the beginning of Experiment 1. (Mean initial weights of the 5 or 15 fish in each chamber were used because the gender of each fish, determined only after completion of the experiment, could not be accurately ascribed to fish at the experiment's beginning.) Mean AGR75 values were then determined separately among male and female fish in each chamber and expressed as a percent difference from the mean AGR75 of individually held control fish of the same gender and fish type in each of the four tanks. Ultimately, there were four observations of percent difference in AGR75 for male and female bluegills at the lower and higher group-holding densities and likewise for B × G hybrids.

Experiment 2

A 200-d, follow-on study was conducted from August 2000 through March 2001 in our laboratory to compare growth capacities of bluegills and B × G hybrids beyond the 100-d period of Experiment 1. Eight bluegills and eight B × G hybrids (all Age 1) that had been held in the two acclimation tanks, and whose weights were similar to the final weights of control bluegills and hybrids from Experiment 1, were selected for Experiment 2. Hereafter, these selected fish will be called the "larger fish." In addition, eight bluegills and eight B × G hybrids (all Age 1) averaging 8–10 g (hereafter, "smaller fish") were also selected from the acclimation tanks to be grown in parallel with the larger fish. The 32 fish were held individually in test chambers set within two 1000-L tanks. Temperature, photoperiod, feed, and feeding regimen were identical to those in Experiment 1; partial water replacement was done less frequently (weekly versus every other day) due to the lower fish densities. Fish weights were determined every 15 d over the first 100 d of this study and every 50 d thereafter for growth comparisons. Food consumption by fish

was not determined. As in Experiment 1, gender of each fish and its GSI were determined on completion of the experiment.

Data Analyses

Differences in mean responses among three or more treatment groups were evaluated by one-way ANOVA ($P < 0.05$) followed by Tukey's HSD test for means separation when significant differences were indicated by ANOVAs (Neter and Wasserman 1974). Randomized block designs were used in ANOVAs relating to Experiments 1 and 2 (Table 1), wherein each of the four (Experiment 1) or two (Experiment 2) 1000-L tanks were considered as "blocks." In some cases ANOVAs were performed on ranked data when nonnormal distributions were indicated (Conover and Iman 1981). However, means and SEMs of untransformed data were always reported. Standard t-tests (Schulman 1992) were used whenever differences in mean responses between two groups were evaluated. All data analyses were run on SAS Version 9.1 software (SAS Institute, Inc., Cary, NC, USA).

Results

Experiment 1

Individually held, Age 1 male bluegills grew faster (AGR) than same-age male B × G hybrids, female bluegills, and female B × G hybrids over the 100-d experiment that ran from May to August 2000 (Table 1). No differences in growth rate were detected among the latter three fish types, although the estimated mean AGR of male B × G hybrids was substantially higher than those of female bluegills and female B × G hybrids. The estimated final mean weight of male bluegills was 40% greater than that of male hybrids and 96% greater than those of female bluegills and female hybrids. However, significant differences were indicated only between the final weight of male bluegills and those of the females of both fish types. There was some indication from estimated means that the high growth rate exhibited by male bluegills owed to both a higher consumption (CC) and lower FCR than for the other fish type/gender

combinations (Table 1); again, however, this indication was not fully supported by statistical outcomes. However, mean GSI for male bluegills was significantly lower than that of male B × G hybrids, while females of both fish types had significantly higher mean GSI values than either type of male at the end of the 100-d period in August.

Mean growth trajectories of male bluegills and male B × G hybrids tracked distinctly above those of female bluegills and female hybrids, reflecting sexually dimorphic growth for both fish types (Fig. 2A). However, whereas male bluegills' mean weight continued to increase along a persistent linear path throughout the summer period (May–August), a marked reduction in growth rate was evident for male B × G hybrids, and likewise, but to a lesser extent, for both female bluegills and female hybrids, throughout the latter half of the experiment (late June–August). The substantial decline in growth rate of male B × G hybrids during the latter half of Experiment 1 caused male bluegills to emerge as the fastest growers among all four fish type/gender combinations during the summer period.

Experiment 2

Male and female bluegills and B × G hybrids that were selected from the acclimation tanks for use in the follow-on study (Table 1, Experiment 2, larger fish) had mean weights that were within 2–27% of the final mean weights of each fish type/gender combination from Experiment 1. The greatest disparity was for male bluegills, whose final mean weight in Experiment 1 was 47.67 g and whose initial mean weight in Experiment 2 was 34.80 g (Table 1).

Among the larger fish evaluated in Experiment 2, mean growth rate (AGR) of male bluegills, again, was highest over the 200-d, follow-on experiment that ran from August 2000 through March 2001 (Table 1). Mean growth rate of male bluegills was 5.8 times higher than that of the male B × G hybrids. In contrast to Experiment 1, female bluegills showed the second highest growth rate followed by male B × G hybrids. Growth rates of female B × G hybrids could not be statistically compared because only one

such fish was present. Instantaneous growth rates (*G*), calculated because there was some disparity among the starting mean weights of the four fish types, confirmed that male bluegills grew the fastest, followed by female bluegills and then male B × G hybrids (Table 1).

The rapid growth trajectory of male bluegills and the moderate growth trajectory of female bluegills over the 200-d period contrasted markedly with those of the B × G hybrid males and females, which remained largely flat over the first 100 d and increased only slightly over the later 100 d (Fig. 2B). Early in Experiment 2, the growth trajectory of female bluegills crossed above that of the male hybrids and continued to increase above it. The sexually dimorphic growth patterns that were initially observed in Experiment 1 for bluegills and B × G hybrids persisted throughout Experiment 2 but became more pronounced for bluegills than for the B × G hybrids (Fig. 2B).

Among the larger fish, male bluegills reached a final mean weight of 151 g (67% of food-market weight of 227 g), which was 96, 176, and 317% greater than the mean final weights achieved by female bluegills, male B × G hybrids, and female B × G hybrids, respectively (Table 1). Final mean weight of male bluegills was significantly higher than those of female bluegills and male hybrids; however, no statistical difference was detected between final mean weights of the latter two fish types. Final mean length of male bluegills (18.23 cm) was also greater than those for female bluegills (15.20 cm) and male hybrids (14.76 cm), which did not differ statistically from each other. Mean GSI values for male bluegills and male B × G hybrids did not differ at the end of Experiment 2; means for male fish were substantially lower than those for females of both fish types.

Growth rate (AGR) trends, like those observed among the larger fish during August through March, were observed among the smaller fish as well (Table 1). Estimated mean growth rates of male and female bluegills were 208 and 82% greater than that of the male B × G hybrids, respectively. However, only male bluegills had a significantly higher growth rate than male B × G hybrids; no statistical distinc-

tion was found between growth rates of male and female bluegills or between female bluegills and male B × G hybrids. This same response (male bluegills significantly greater than male hybrids, with no differences detected between male and female bluegills, or female bluegills and male B × G hybrids) was observed for means of instantaneous growth rate and final weight (Table 1). Among the smaller fish, the estimated final mean weight of male bluegills was 72% greater than that of female bluegill and 145% greater than that of the male hybrids. No differences were detected among mean GSI values determined in March for the three fish types in the smaller group.

Rearing Density Effects on Growth

Distinct influences on growth rate were observed for male and female bluegills when they were grown together at the lower (200 fish/m³) and higher (600 fish/m³) density during Days 1–75 of Experiment 1. When in lower density groups, male bluegills grew at rates that were no less than those of male bluegills grown individually without social interaction effects ($P \geq 0.05$; Fig. 3), while female counterparts in the same tanks grew only half as fast as the individually reared female bluegill ($P < 0.05$). However, in higher density groups, the opposite occurred; on average, male bluegills grew 62% slower than individually reared male bluegills, whereas female bluegills grew at a rate not different from that of the individually reared female bluegills. Parallel patterns, although less pronounced, were observed for male and female B × G hybrids, with the exception that male hybrids reared at the higher density did not grow significantly slower than individually reared male hybrids; however, an estimated mean growth rate that was 9% below that of individually reared hybrid males was observed.

Discussion

In the related, previous study (Hayward and Wang 2002), individually held bluegills and B × G hybrids were reared in parallel under continually favorable indoor conditions from May through March as Age 1 and, ultimately, early
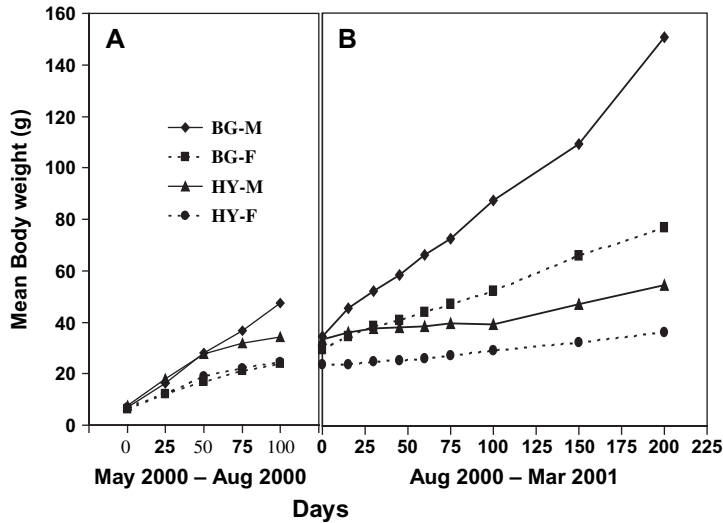
FIGURE 2. *Mean growth-in-weight trajectories of Age 1, male bluegills (BG-M), female bluegills (BG-F), male B × G hybrids (HY-M), and female B × G hybrids (HY-F) that were reared individually indoors and fed without restriction from May to August 2000 (100 d) in Experiment 1 (A) and likewise for Age 1 and subsequently Age 2 larger fish in Experiment 2 (B) throughout the 200-d (August 2000–March 2001) follow-on growth evaluation.*

Age 2 fish. Bluegills showed markedly higher growth than the B × G hybrids during the 10-mo study period, growing from an average of 7 to 100 g, whereas B × G hybrids of similar initial weight reached only 50 g. This observation was considered important because B × G hybrids were previously considered to be faster growers than bluegills based on comparative growth studies in ponds (Ellison and Heidinger 1978; Brunson and Robinette 1985, 1986). Because of this prevailing view, the B × G hybrid has received greater attention by researchers and fish producers than the bluegill as a sunfish candidate for the food-fish market in many areas of the USA (Tidwell et al. 1994; NCRAC 2004).

By focusing on differences according to gender, the present study reveals that the male bluegills vastly outgrew the B × G hybrid males, which constitute the majority of individuals (80–95%) in B × G hybrid populations (Brunson 1983; Tidwell et al. 1994). Even the female bluegills showed a higher growth capacity than the male B × G hybrids. Individually held male bluegills in Experiment 1 (May–August), whose growth was followed on (August–March) by the larger fish in Experiment 2, reached 67% of food-market weight in just 10 mo from a starting

weight of 7 g under favorable, indoor rearing conditions. In contrast, the male B × G hybrids reached only 24% of food-market weight from a similar starting weight. The far more rapid growth of the male bluegills involved a substantially more pronounced growth sexual dimorphism than was observed for the B × G hybrids, which exhibited surprisingly poor growth rates from June to March. Although sexually dimorphic growth in favor of males is well known for bluegills (Lane 1954; Sprugel 1954) and other nesting centrarchids (Hubbs and Cooper 1935; Noltie 1988), the more accentuated growth capacity of male bluegills versus male B × G hybrids has not been known and holds important implications for selecting an appropriate sunfish that will grow rapidly to required food-market sizes. The pronounced reduction in growth capacity that was observed for male B × G hybrids, and which is clearly not conducive to rapid rearing of food-market-size sunfish, has also not been elucidated previously. A substantially more rapid growth capacity of male bluegills versus male B × G hybrids was again demonstrated by the smaller fish in Experiment 2.

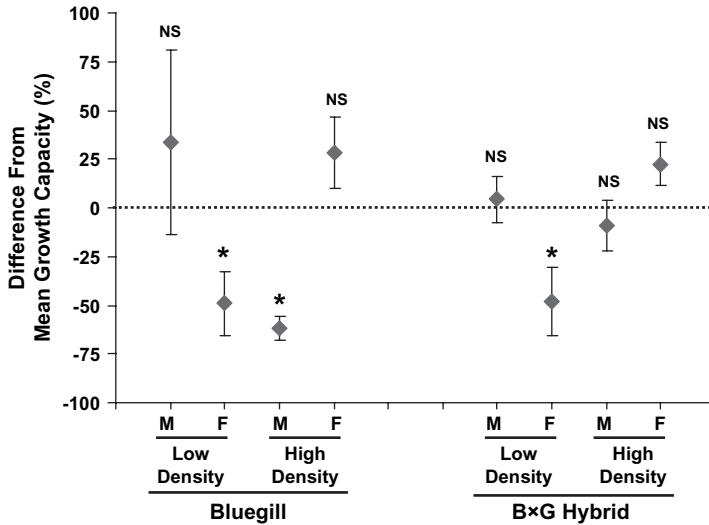Repeated observations of B × G hybrids outgrowing bluegills in ponds are in apparent

FIGURE 3. *Mean growth versus capacity of male (M) and female (F) bluegills and B × G hybrids reared in lower (200 fish/m³) and higher density (600 fish/m³) groups for 75 d during Experiment 1. Mean growth versus capacity of fish in groups is portrayed as percent difference relative to mean growth rates that each fish type/gender combination exhibited when reared individually. * and NS indicate that mean growth of reared groups was or was not significantly different (t-test; P = 0.05 level), respectively, from mean growth rates shown by individually held fish of the same type/ gender.*

contrast with the findings of Hayward and Wang (2002) and the present study, which show markedly higher growth capacity for bluegills. One explanation may be that bluegills reared in ponds under typical culture conditions grow substantially below their capacities while B × G hybrids grow at rates closer to their capacities in these settings. In support of this, we provide new evidence that male bluegills do, in fact, grow below capacity (<60%) when reared at higher densities, even when food is provided at unrestricted levels. Rearing densities for intensive pond culture of sunfish have ranged from 6000 fish/ha to in excess of 25,000 fish/ha (Loveshin and Matthews 2003). Such densities certainly exceed naturally occurring densities of sunfish in ponds and may approach the density at which we observed male bluegills to grow well below capacity, particularly if additions from in-pond reproduction are considered. As the gender with the higher growth capacity, reduced growth rates of male bluegills in ponds resulting from high rearing densities could markedly reduce average growth rates in bluegill populations. Also consistent with this expla-

nation is our laboratory observation that growth rates of B × G hybrids were much less reduced at the higher rearing density. Additionally, bluegill's tendency to have higher reproduction rates in ponds versus B × G hybrids is believed to reduce natural food supplies and, in turn, reduce adult growth rates as their abundant progeny act as trophic competitors for this important energy source (Loveshin and Matthews 2003). B × G hybrids, in contrast, appear to benefit both energetically and nutritionally by consuming their more limited numbers of progeny in ponds to greater extents than do adult bluegill (Lane and Morris 2002). Hence, there is evidence suggesting that, under culture conditions, bluegills grow well below capacity in ponds while B × G hybrids do not, which may account for our observing much higher growth rates of male bluegills versus male B × G hybrids in the laboratory while the opposite is observed in ponds.

Sexually dimorphic growth, wherein males achieve larger sizes at age than their female counterparts by "delaying" maturation, is a common reproductive strategy among nest-building centrarchid fishes (Hubbs and Cooper

1935; Noltie 1988). Such a pattern was evident for bluegills and B × G hybrids throughout Experiments 1 and 2, as females of both fishes grew slower than their male counterparts (Fig. 2) and showed higher GSI values in August and in March as well. The uninterrupted, rapid growth pattern of male bluegills throughout Experiments 1 and 2 indicated that little or no increase in growth energy allocation to gonads occurred, unlike for the male B × G hybrids whose growth rate initially paralleled the male bluegills' but abruptly declined midway through Experiment 1 in late June and remained low through March. The significantly higher mean GSI value of male B × G hybrids versus male bluegills at the end of Experiment 1 in August (Table 1) further indicated greater energy investment to enhance gonads by the male hybrids; the estimated mean GSI for male hybrids in March was 25% greater than that for male bluegills, however, a statistical difference was not indicated.

Our previous study (Hayward and Wang 2002) demonstrated that the pronounced growth rate decline observed for individually held B × G hybrids during Experiment 1 (both genders combined) involved a marked drop in their food consumption capacity accompanied by substantially declining feed efficiency (FE) beginning near Day 50. Both responses are characteristic of periods when energy allocation to gonadal tissues is increased in fishes (Frost 1954; Berglund et al. 1992). By focusing on intergender differences, the present study suggests that both male and female B × G hybrids underwent consumption capacity and FE declines during Experiment 1, as both genders exhibited markedly declining growth rates beginning on Day 50. The present study shows that only female bluegills underwent any decline in growth rate during Experiment 1, indicating that the modest decline in FE shown for bluegills in the previous study involved females only. A modest decline in FE without an accompanying decline in consumption capacity in the female bluegills is consistent with their having allocated more growth energy to gonads than the male bluegills but less so than by both genders of the B × G hybrids. Independent support for male bluegills being

least involved in building gonadal tissue is given by their mean GSI value in August, which was significantly lower than that of the male hybrids and the bluegill and B × G hybrid females. Brunson and Morris (2000) noted that green sunfish are prolific spawners at Age 1, whereas bluegills tend not to produce substantial numbers of progeny in ponds until reaching Age 2. This observation is consistent with the more rapid growth capacity that we observed for male and female bluegills versus male and female B × G hybrids as Age 1 and early Age 2 fish. B × G hybrids apparently acquire the green sunfish's earlier maturation schedule.

We believe that the comparatively rapid growth capacity of male bluegills versus B × G hybrids as Age 1 and early Age 2 fish is largely unknown. Most sunfish production occurs in ponds where fall and winter present suboptimal growth temperatures during substantial portions of the 8-mo period (July–March) over which we observed male bluegills to exhibit far superior growth capacity than B × G hybrids. Consequently, much of the high growth capacity of male bluegills that we observed is likely masked in pond settings due to suboptimal temperatures and, as previously described, from high stocking densities and high reproduction rates as well.

We suggest that more effective systems for producing large, food-market sunfish would involve rearing groups of predominantly male bluegills indoors under continually favorable growth conditions with respect to temperature, rearing density, food supply, and water quality. This might involve rearing male bluegills indoors for the entirety of grow out or an initial pond-rearing period followed by indoor rearing when suboptimal outdoor temperatures occur (fall–winter) to take full advantage of the male bluegills' rapid growth period. Clearly, advantages of growing male bluegills indoors, versus in ponds, should increase with latitude, where progressively shorter growing seasons would otherwise take less and less advantage of the male bluegill's rapid growth period. Although growth capacity of Age 2 male bluegills will likely diminish as the spawning period approaches, the substantial sizes that we observed

them to achieve by March (after 10 mo of rearing) should result in food-market weights being reached within the second year if favorable growth conditions persist. Moreover, because bluegills do not spawn in indoor rearing tanks in the absence of substrate, some growth energy savings may result and further enhance somatic growth.

Capacity has recently been developed to produce monosex male bluegill populations through the application of male androgens (Arslan and Phelps 2003). In addition, a practical grading procedure for size-selecting male bluegills from mixed-gender populations has been developed and shows good promise for forming predominantly ($\geq 70\%$) male groups (Doerhoff 2006).

Our findings concerning rearing-density effects on sunfish growth rates indicate that densities closer to our lower value (200 fish/m^3, 2.6 g/L) will promote the highest growth rates for predominantly male bluegill groups in indoor systems. We suspect that the 60% reduction of male bluegills' growth rate observed at the higher rearing density (600 fish/m^3, 7.9 g/L) was related to their inability to exercise typical territorial behavior. At lower rearing densities, we have observed larger, presumably male bluegill to defend peripheral water volumes through agonistic behavior. We suspect that male bluegills' capacity to defend these volumes diminishes with increasing fish density, much as was observed for young largemouth bass, *Micropterus salmoides* (Fleming and Johansen 1984), and that this leads to their reduced consumption and growth. Whereas reduction of agonistic behavior, as apparently occurred for male bluegills at the higher rearing density, often has beneficial consequences for overall growth rates in culture settings (Jobling 1994; de March 1997), the opposite appears true in the present case where male bluegills that possessed high capacity for growth grew much below capacity. The much less pronounced response to increased rearing density observed for B $\times$ G hybrid males is consistent with their less agonistic nature relative to bluegills (Hayward and Wang 2002).

Rearing predominantly male bluegills at lower densities in indoor systems is expected to increase capacity to produce large, food-size sunfish. However, it is expected that some negative effects of social interaction will persist. Approaches for further ameliorating social costs in indoor tanks, including those that may permit rearing of bluegills at higher densities, will likely warrant investigation. Development of more effective, complete diets for indoor-reared bluegills will also be important, as will bioeconomic evaluations that will identify indoor/outdoor rearing schedules that will yield the highest benefit-to-cost ratios.

Acknowledgments

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