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## 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 an individual fish achieves 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) were 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 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.

**Keywords** 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 (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.

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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 et al. 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 versus 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 the 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 particularly a 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.

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## 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<sup>-1</sup> 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 ( $\text{CuSO}_4$ ) 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 ( $227 \text{ kg ha}^{-1}$ ) to dry yeast ( $22.7 \text{ kg ha}^{-1}$ ). On the same dates,  $\text{CuSO}_4$  (an algicide commonly used in aquatic systems due to its low residual toxicity; Boyd and Lichtkoppler 1979) was applied at a rate of  $5.7 \text{ kg ha}^{-1}$  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  $\times$  0.03-m diameter, 2 samples per pond), filtered through a 64- $\mu\text{m}$  mesh net, and preserved in Lugols solution. In the laboratory, zooplankton samples were standardized to a constant volume (100 ml) 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  $1.2 \text{ kg ha}^{-1} \text{ day}^{-1}$ . 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  $> 200 \text{ mm}$ ) and weighed (g; all individuals  $> 150 \text{ g}$ ). 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 8 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 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  $2 \times 2$  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

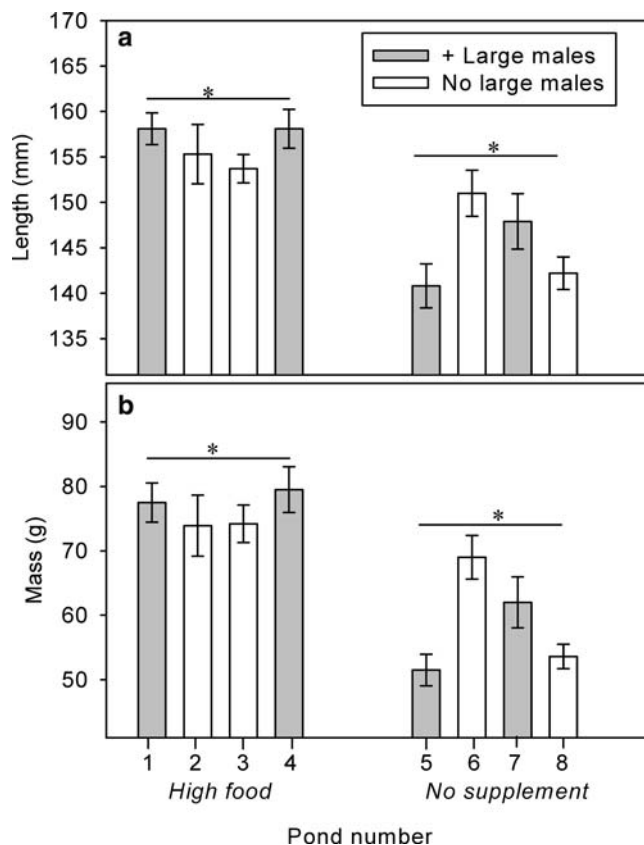
Zooplankton densities at the beginning of the experiment were higher in the high food treatment ponds than in the low food ponds, indicating that the fertilization and herbicide treatments had the predicted effect on zooplankton production. We focused on crustacean zooplankton (excluding copepod nauplii and rotifers) because these taxa are important prey for bluegill, and because they dominated our zooplankton samples. Crustacean zooplankton density was significantly higher (ANOVA;  $F_{1,7}=117$ ,  $P<0.0001$ ) in the fertilized (high food) ponds (mean  $\pm$  1 SE;  $300 \pm 20$  L<sup>-1</sup>) than in the unfertilized (low food) ponds ( $61 \pm 20$  L<sup>-1</sup>). 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;  $F_{1,4}<2.53$ ,  $P>0.19$ ; interaction term;  $F_{1,4}<0.47$ ,  $P>0.53$ ) 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 ( $F_{1,4}<1.3$ ,  $P>0.32$ ). Individually, however, food resources influenced body size of both sexes; juveniles were significantly longer (ANOVA; males:  $F_{1,4}=15$ ,  $P=0.01$ ; females:  $F_{1,4}=8.0$ ,  $P=0.05$ ) and heavier (males:  $F_{1,4}=13$ ,  $P=0.02$ , Fig. 1; females:  $F_{1,4}=6.0$ ,  $P=0.07$ , 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 ( $F_{1,4}=0.14$ ,  $P=0.71$ , Fig. 1) or females ( $F_{1,4}=1.5$ ,  $P=0.23$ , 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



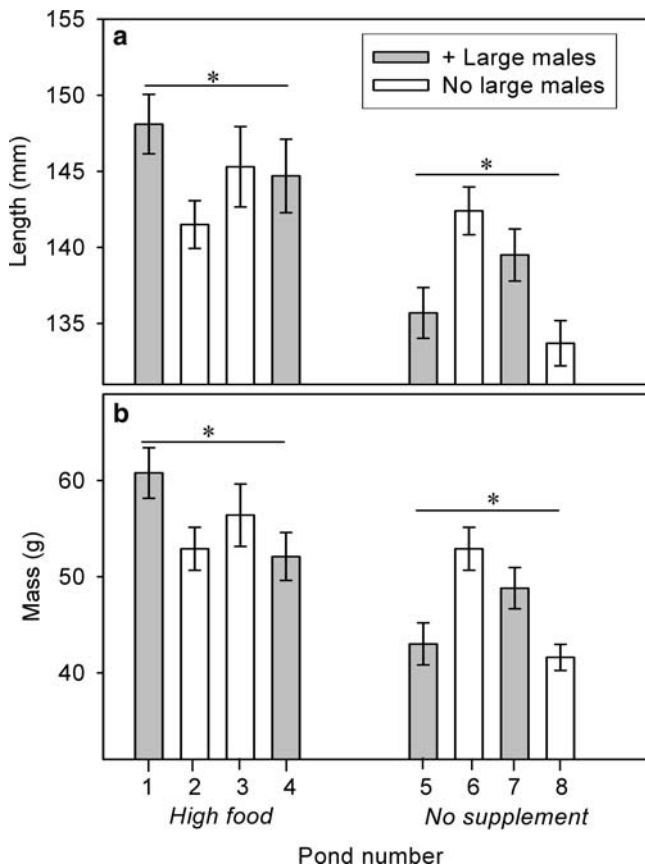
**Fig. 1** a Total length (mm) and b mass (g) of juvenile male bluegill (*Lepomis macrochirus*) in four experimental ponds with high food and four ponds with no food supplement (means  $\pm$  SE). Asterisks (\*) indicate significant differences between treatment means (two way ANOVA;  $P \leq 0.02$ ).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

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 ( $X^2=7.7$ ,  $P=0.005$ ,  $df=1$ ) 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 ( $X^2=0.20$ ,  $P=0.66$ ,

**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	Minimum	Maximum	Mean weight	Minimum	Maximum
High food	$123 \pm 0.91$	104	140	$34.2 \pm 0.87$	20	53
No supplement	$124 \pm 1.17$	103	142	$35.8 \pm 1.12$	19	58
<i>P</i> value	0.75			0.27		
+ Large males	$123 \pm 1.14$	103	142	$34.0 \pm 1.06$	18	52
No large males	$124 \pm 0.93$	104	141	$36.0 \pm 0.94$	20	54
<i>P</i> value	0.25			0.19		

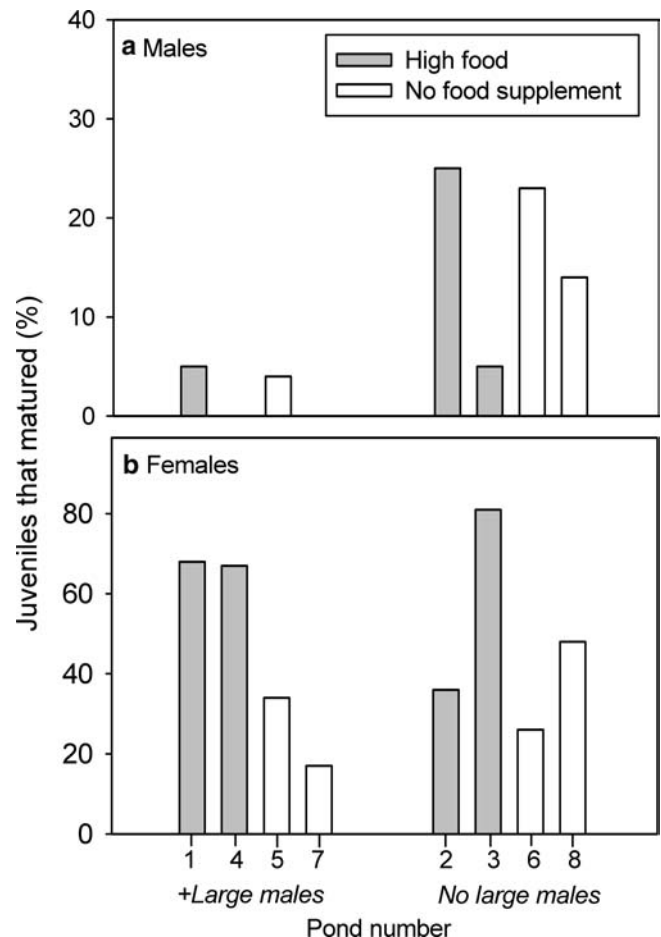
Data are means  $\pm$  1 SE. *P* values generated with two-way ANOVA



**Fig. 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  $\pm$  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

df=1) on the proportion of juvenile males that matured. For females, the presence of large males had no influence ( $X^2=0.007$ ,  $P=0.9$ , df=1) on the proportion of individuals that matured, whereas food ration had a large influence ( $X^2=20$ ,  $P=0.0001$ , 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;  $F_{1,321}=3.6$ ,  $P=0.05$ ) and heavier ( $F_{1,321}=8.7$ ,  $P=.003$ ) 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 ( $F_{1,84}=7.15$ ,  $P=0.009$ ) than those that remained immature (Table 2). In the high food treatment, however, there was no difference in length ( $F_{1,82}=1.55$ ,  $P=0.22$ ) or weight ( $F_{1,82}=0.84$ ,  $P=0.36$ ) of mature and immature individuals (Table 2). For females, there was no difference ( $F < 1.98$ ,  $P > 0.16$ ) in length or weight of individuals



**Fig. 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,  $P=0.0001$ )

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

**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	<i>P</i> value	Immature	Mature	<i>P</i> value
<b>Males</b>						
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
<b>Females</b>						
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	0.70	54 ± 1.6	57 ± 2.4	0.28

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

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 relatively 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 improving their ability 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 1977; 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.

### 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 quantifiable 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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