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ARTICLE

Body Size, Food, and Temperature Affect Overwinter Survival of Age-0 Bluegills

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Abstract

For many species of fish, size-specific overwinter mortality is an important factor structuring year-class strength. Protracted spawning by bluegill *Lepomis macrochirus* leads to extreme variation in individual size going into winter that could result in strong, size-specific overwinter mortality, particularly in locations with limited food resources or long, cold winters. We performed laboratory trials to test the effects of winter temperature (4°C or 9°C) and food availability (food present or no food) on the survival of two size-classes (20–30 or 50–60 mm total length) of young-of-year bluegills. Mortality was strongly size selective and appeared to be related to relative condition, suggesting that energy limitation was the primary mechanism of mortality. Fish of both sizes were less active at colder temperatures, leading to increased survival (presumably via reduced energy expenditure). Bluegills fed heavily in food treatments (wet weight/d consumed was typically 2–4% for both large and small fish in the warm treatment, 1–2.5% for small fish in the cold treatment, and 0.4–0.8% for large fish in the cold treatment) and experienced increased survival. However, small fish in all treatments had more than 55% mortality after 150 d, indicating that some of the mortality was not due to starvation. It appears that late-spawned, small fish are unlikely to survive lengthy periods of winter conditions and will therefore be selected against at northern latitudes. Mechanisms other than overwinter mortality that lead to increased lifetime reproductive success may explain the persistence of late-summer or fall spawning at these latitudes.

For many fishes, first-year overwinter mortality structures year-class strength (Post and Evans 1989; McCollum et al. 2003). Mortality is often size specific, affecting smaller individuals more often than larger individuals (Oliver et al. 1979; Post and Evans 1989; Cargnelli and Gross 1996; Bernard and Fox 1997). Size-specific mortality has been suggested to be caused by larger fish having greater energy reserves and lower mass-specific metabolic rates (Schultz and Conover 1999), making them better suited to long periods of low food availability associated with winter (Post and Evans 1989; Kirjasniemi and Valtonen 1997). However, reduced swimming ability (Larimore and Duever 1968), osmotic stress (Morris and Bull 1968; Lankford and Targett 2001), and increased vulnerability to disease or toxicants (Oliver et al. 1979; Lemly 1993) have also been suggested as potential mechanisms of size-specific overwinter mortality. Overwinter mortality is usually more dramatic in years with longer periods of cold temperatures or lower average temperatures (Fullerton et al. 2000; McCollum et al. 2003). However, warm winters can lead to higher mortality than cold winters when food availability is low (Sogard and Olla 2000), and winter severity may not affect all length-classes of age-0 fish in the same way (Connolly and Petersen 2003). These differences could be related to activity associated with warmer temperatures as activity has been associated with decreased overwinter mortality (Bernard and Fox 1997; Micucci et al. 2003).

Little is known about overwinter mortality in protracted-spawning fishes such as bluegill *Lepomis macrochirus*. Bluegills begin spawning as early as May, continuing as late as the

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beginning of September at the middle latitudes of the species range (Santucci and Wahl 2003). As a result, large variation in individual lengths of the age-0 cohort exists at the beginning of winter. Size variation may cause decreased survival in years when overwinter mortality is strongly biased against small (younger) fish, as occurs in the northern extent of the species range (Cargnelli and Gross 1996), suggesting late-season spawning may not be adaptive. However, little is known about overwinter mortality of bluegills at the middle or southern latitudes of the range of this species. Late-spawned fish may survive the warmer and shorter winters typical of these latitudes. Further, little is known about the mechanisms responsible for size-specific overwinter mortality at the latitudes where it has been observed. In this study, we investigated the effect of food availability and winter severity (average temperature and duration of winter) on the overwinter survival of two size-classes of age-0 bluegills to determine the relative importance of these variables in producing size-specific overwinter mortality and provide information about the likelihood of size-specific mortality outside the previously studied northern extent of the species' range.

METHODS

Laboratory trials.—Two hundred eighty small (20–30-mm total length [TL]) and 280 large (50–60-mm TL) age-0 bluegills were collected from Ridge Lake, Illinois, during the second week of November 2001. Surface water temperature during this time ranged from 7°C to 10°C. Fish were held in outdoor tanks for at least 1 week at the Kaskaskia Biological Station, Sullivan, Illinois (temperature ranged from 5°C to 9°C). Fish were then measured (mm; TL) and weighed (wet weight; ±0.01 g) and randomly assigned to aquaria (10 fish/aquarium). Small fish were held in 38-L aquaria, larger fish in 76-L aquaria (both had approximately 0.02 g fish/L). Aquaria were assigned to treatments with one of two food levels (starved or fed) and one of two temperatures (4 or 9 ± 1°C, simulating a harsh or mild winter, respectively) to create a full factorial design (fish size × food level × temperature). After fish were transferred to the aquaria, they were acclimated to experimental temperatures for 1 week before trials began. During this time, fish that died were replaced with similar-sized fish (2.5% mortality occurred during this period), after which no additional fish died for the next month. Temperatures were maintained by housing the tanks in two environmental chambers. Both environmental chambers had a 10 h light : 14 h dark photoperiod typical of winter at mid-latitudes of the USA. Each treatment combination (fish size × food level × temperature) was replicated in seven aquaria (10 fish per aquarium). All tanks had a 25% water exchange every 2 weeks to maintain water quality. Replacement water was tempered and aerated 24 h prior to adding to experimental tanks.

Fish in the fed treatment were fed to satiation or until they had consumed a maximum of 4% of their body weight per day using a combination of live mixed zooplankton from local ponds, freeze-dried zooplankton, live rinsed brine shrimp *Artemia* spp. (first instar), and frozen chironomids. The maximum 4% ration is the upper end of the reported range of summer daily rations for this species (Gerking 1954 [3%]; Seaburg and Moyle 1964 [1.5–2.3%]; Windell 1966 [2.0–2.8%]; Keast and Welsh 1968 [2.5%]; Whitledge and Hayward 2000 [1–4%]). All replicates were offered the same type(s) of food each day. Measured quantities of food were added throughout the day to each fed tank until fish no longer ate. Uneaten food was left in tanks so that food was always available to fish that ate less than the maximum ration. The amount of uneaten food was visually estimated at the time of feeding and again prior to the next day's feeding to provide a rough measure of the amount consumed. All uneaten food was removed prior to feeding the next day.

Dead fish were removed, measured (mm; TL) and weighed (±0.01 g) each day. Every 2 weeks, activity levels were measured to determine if activity was related to mortality rates. Activity was quantified by placing an acetate grid over the front of the tank and determining the number of centimeters moved in 30 s by three randomly selected individuals in each tank (or all surviving fish in treatments where less than three surviving fish remained). Observations were always made 1 h or more after a feeding event and 15 min or more after entering the environmental chamber. At the end of the 150-d experiment (at the longer end of typical winter duration within the bluegill's geographic range), surviving fish were again measured and weighed.

Cumulative mortality probabilities over time were modeled using SAS PROC LIFEREG with type I censuring (experiment with fixed end time, fish surviving at end of experiment were right censured; SAS Institute 2004). Differences in mortality curves between treatments were tested using a Wilcoxon chi-square test in PROC LIFETEST (SAS Institute 2004). If significant differences were found, pairwise comparisons among all treatments were made using the rank scores and the covariance matrix from the Wilcoxon statistics to calculate *Z*-scores, with an overall significance level of 0.05 (Fox 2001). Mean fish length, weight, relative condition (K_n), and activity level were compared among treatments using separate three-factor analysis of variances (fish size × temperature × food level) with repeated measures (aquaria treated as subjects). Relative weight could not be calculated because no standard weight equation exists for bluegills as small as those used in this experiment. Therefore, K_n was calculated using the length–weight relationship from the beginning of the experiment to produce reference weights (W'; Anderson and Neumann 1996).

Field samples.—Bluegill diets were collected from Ridge Lake, Charleston, Illinois (a 5.6-ha impoundment located at 39°27′N, 80°09′W; mean depth = 2.8 m; maximum depth = 6.5 m), during the same winter as the overwinter laboratory trials such that the fish in the lake and those used in the experiment (which came from this lake) were in the same physiological condition at the beginning of winter. Stomach contents of

36 juvenile bluegills (eight to nine individuals from each 10-mm length-class ≤ 60-mm TL) were collected the day after ice-out (March 13, 2002) to determine if fish were eating during winter. Prey items were identified and measured (nearest 0.01 mm) for conversion to predigestion dry mass using regression equations (Dumont et al. 1975; Smock 1980; Sample et al. 1993). Diets were quantified as percent by weight (a measure of relative energetic value) and percent by number (a measure of foraging effort), and the percent of empty stomachs was analyzed by logistic regression (PROC GLIMMIX in SAS 2004) to test for differences related to fish size.

RESULTS

Laboratory Trials

Both sizes of bluegills in both temperature regimes ate food in the fed treatments. Consumption was highest in the warm treatments, where both large and small bluegills typically consumed 2–4% their body weight/d (fish in the majority of tanks consuming most of the food that was offered). In the cold treatment, small fish typically consumed 1–2.5% of their body weight/d and large fish consumed 0.4–0.8% of their body weight/d.

Mortality probabilities varied by treatment (Wilcoxon $\chi^2 = 713.36$, df $= 7$, $P < 0.01$) and were always best described using a Weibull distribution model (SAS Institute 2004). There was no mortality in any treatment until day 42; after that time, mortality probability was strongly affected by fish size, and temperature and food availability were important in some treatment combinations (Figure 1). Mortality probabilities were higher for all small fish than large fish treatments, except small fish in the cold, fed treatment were not significantly different from that of large fish in the warm, unfed treatment ($Z < 0.26$, $P > 0.40$; all other Z-tests, $P < 0.01$; Figure 1). Within the small bluegill treatments, mortality was highest in the warm, no food treatment; intermediate in the cold, no food and warm, fed treatments (comparing these treatments: $Z = 1.63$, $P = 0.06$); and lowest in the cold, fed treatment (all other Z-tests, $P < 0.01$). However, even in the cold, fed treatment, mortality of small bluegills was greater than 55% by the end of the experiment. All large fish treatments exhibited low mortality (<10%) throughout the 150-d experiment except the warm, no-food treatment, which exhibited increased mortality starting around day 90 that resulted in significantly higher mortality by the end of the experiment (all Z-tests, $P < 0.01$; Figure 1).

No small fish survived to the end of the experiment in the unfed treatments; therefore, these treatments were excluded from the total length and K_n analyses. No difference in mean total length was detected among any treatment combinations within size-classes (size × food: $F_{1,40} = 2.48$, $P = 0.12$; size × temperature: $F_{1,40} = 2.24$, $P = 0.14$; size × food × temperature: $F_{1,40} = 0.01$, $P = 0.94$). There were no differences among K_n of any treatments at the beginning of the experiment (all Tukey; $P > 0.77$). At the end of the experiment, the condition of all fish had declined ($K_n = 1$ indicates condition was the same as the beginning of the experiment). Larger fish had higher K_n than smaller fish in treatments where individuals of both size-classes survived to the end of the experiment ($F_{13,47} = 16.90$, $P < 0.01$; all Tukey $P < 0.01$; Figure 2). For large fish, K_n was highest for fed fish, but cold temperatures also appeared to help fish maintain their K_n (Figure 2). Condition of large fish in fed treatments did not significantly differ from the beginning of the experiment (all Tukey, $P > 0.37$). In all other treatments, K_n of both size-classes was significantly lower by the end of the experiment (all Tukey, $P < 0.01$). Because no changes in length were observed during the experiment, changes in K_n were caused by changes in fish weight.

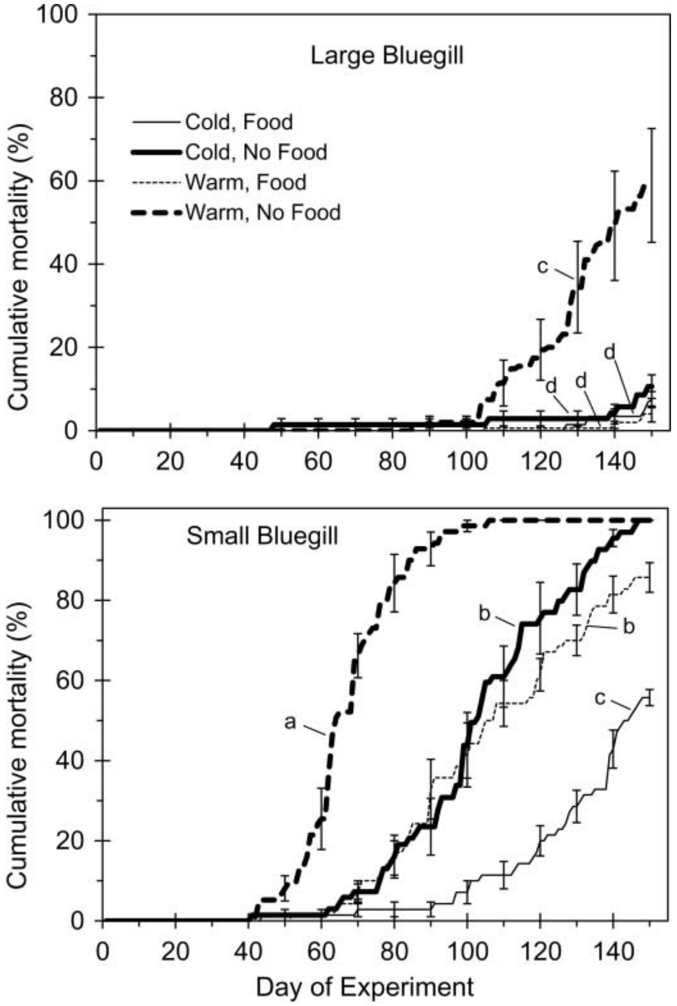

FIGURE 1. Cumulative mortality curves for small (20–30-mm) and large (50–60-mm) age-0 bluegills held in aquaria at cold (4°C) and warm (9°C) temperatures with and without food for 150 d. Different letters indicate treatments with significantly different mortality curves; error bars are SEs.

There was significant size × food × temperature interaction for fish activity level ($F_{1,40} = 15.85$, $P < 0.01$; Figure 3). For both size-classes, activity was highest in the warm, fed treatment, and small fish had significantly higher activity than large fish (Tukey, $P < 0.05$). Activity did not differ between

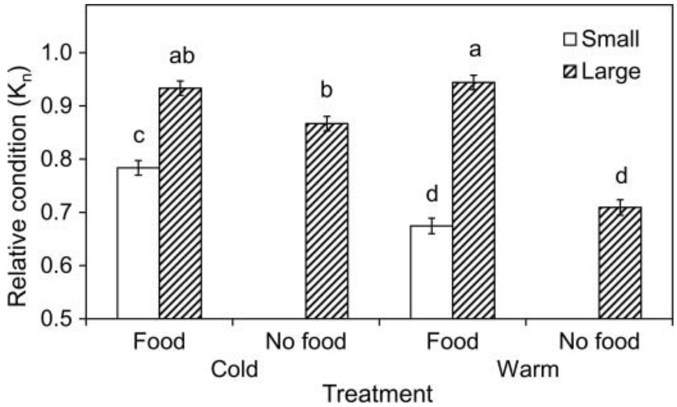

FIGURE 2. Relative condition of small (20–30-mm) and large (50–60-mm) age-0 bluegills surviving after 150 d in aquaria at cold (4°C) and warm (9°C) temperatures with and without food. Different letters indicate significant differences; error bars are SEs.

size-classes in any other treatment combination. Both temperature and food level were significantly related to activity level (Figure 3). Activity was intermediate for all fish in the warm, unfed and cold, fed treatments, and lowest for both sizes of fish in the cold, unfed treatment (although no significant difference was found between small fish in the warm, no-food treatment and either size-class in the cold, unfed treatment).

Field Samples

Temperatures were nearly uniform (5.3–5.8°C) at all depths and locations sampled on the day ice first melted (March 13). Smaller length-classes of bluegills collected on that date ate more food and had fewer instances of empty stomachs than large length-classes (Figure 4). Logistic regression indicated a significant relationship between fish size and the frequency of empty stomachs ($F_{1,\,33} = 8.85$, $P < 0.01$). The odds ratio of 1.13 indicates 59-mm fish were 44 times more likely to have empty stomachs than 20-mm fish. Smaller bluegills (20–39 mm TL) ate primarily zooplankton (cyclopoid copepods and chydorids, with lesser amounts of *Bosmina* spp.), whereas larger bluegills (50–59 mm TL) ate primarily benthic invertebrates (chironomids and coleopteran; Table 1). Intermediate-size

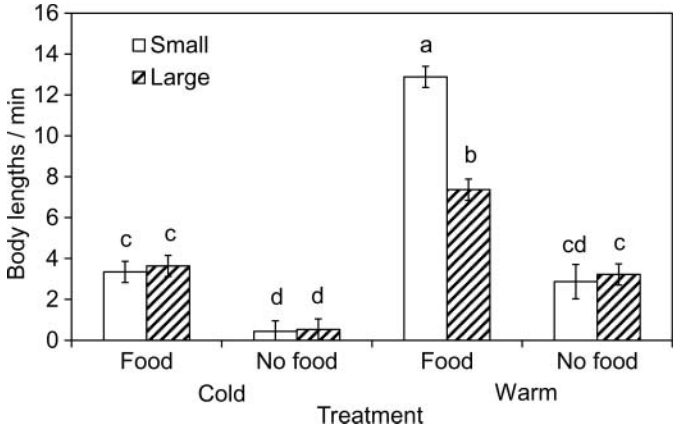

FIGURE 3. Mean activity (number of body lengths moved/min) of small (20–30-mm) and large (50–60-mm) age-0 bluegills held in aquaria at cold (4°C) and warm (9°C) temperatures with and without food during a 150-d experiment. Different letters indicate significant differences; error bars are SEs.

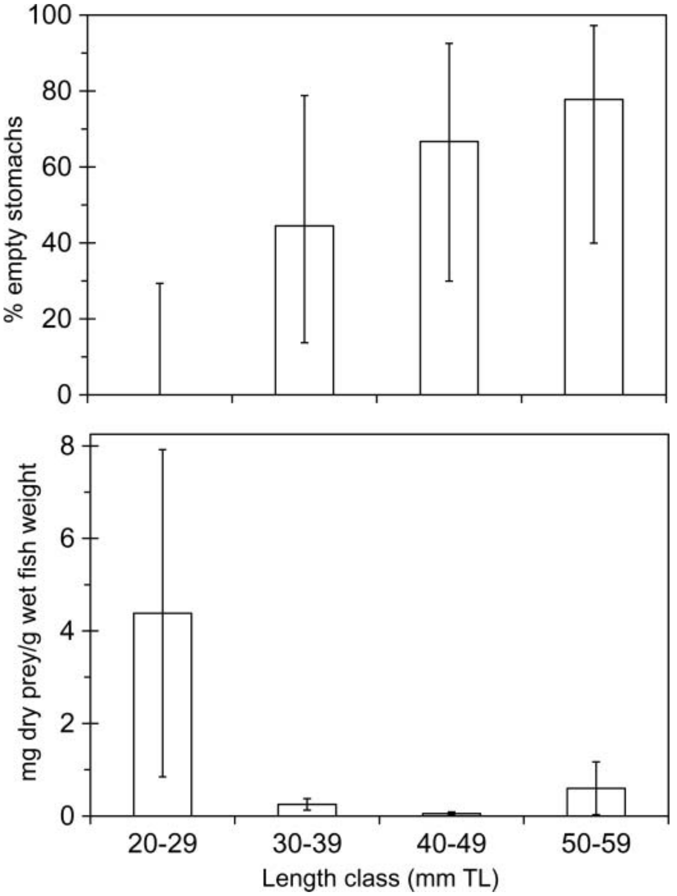

FIGURE 4. Percent empty stomachs (upper panel; error bars are 95% binary confidence intervals using the exact method) and mean predigested weight (lower panel) of food (error bars are SEs) from four length-classes of age-0 bluegills 1 d after ice-out (March 13) in Ridge Lake, Illinois, 2002.

TABLE 1. Diets of juvenile bluegills (percent by number and weight) 1 d after ice-out (March 13) in Ridge Lake, Illinois, 2002.

Length-class (mm TL)	Taxon	
	Zooplankton	Benthic invertebrates
	Percent by number	
20–29	99.5	0.5
30–39	100.0	0.0
40–49	50.0	50.0
50–59	0.0	100.0
	Percent by weight	
20–29	99.4	0.6
30–39	100.0	0.0
40–49	50.0	50.0
50–59	0.0	100.0

bluegills (40–49-mm TL) had diets intermediate to those of smaller and larger length-classes, eating approximately equal amounts of water column zooplankton and benthos (cyclopoid copepods and benthic ostracods; Table 1).

DISCUSSION

Because of their protracted spawning behavior, bluegills have a much greater size range at the beginning of winter than fish species with more discrete spawning seasons. The largest age-0 bluegills can be three to four times longer than the smallest (Santucci and Wahl 2003), as opposed to species for which the largest age-0 fish are only 1.3–2.0 times longer than the smallest fish (Post and Evans 1989; McCollum et al. 2003). Consistent with this wide range of sizes, we found a high degree of size-specific overwinter mortality in our laboratory study. The importance of mortality was a function of both winter severity and food availability. Size-specific overwinter mortality tends to select against smaller individuals both at the northern extent (Cargnelli and Gross 1996) and middle latitudes (Shoup and Wahl 2008) of the species range. Our laboratory results suggest size-specific overwinter mortality could also occur at warmer temperatures such as those experienced at the southern extent of the range, at least when cold temperature ($\leq$9°C) lasts more than about 65 d without food or 110 d with more abundant food resources. However, mortality could be moderated at southern latitudes if colder temperatures (i.e., closer to 4°C) were experienced during the short winter typical of these latitudes.

Large body size can enhance the survival of age-0 fish in several ways. Larger fish have greater energy reserves and lower biomass-specific metabolic rates that allow them to better-withstand periods of low food availability (Schultz and Conover 1999). Larger fish may also better tolerate osmotic stress (Morris and Bull 1968; Lankford and Targett 2001), disease or toxicants (Oliver et al. 1979; Lemly 1993), and wintertime predation (Jonas and Wahl 1998; Pratt and Fox 2002; Garvey et al. 2004; Shoup and Wahl 2008). However, larger individuals require more food and may survive better when inactive than when attempting to feed if prey abundance is low or search costs are high (Micucci et al. 2003). Food availability clearly was an important factor affecting mortality, as survival and K_n were always higher in fed treatments. When food was not available, cool temperatures appeared to mediate mortality by lowering fish activity and presumably basal metabolic rate.

Small fish experienced significant mortality at warm temperatures even when fed, suggesting other mechanisms cause mortality for this size-class. Despite consuming all of the food offered (a summer daily ration), these fish had poor condition at the end of the experiment. Small fish are either unable to effectively assimilate their food or have metabolic inefficiencies that created a very high energy demand. High overwinter mortality of age-0 fish has also been found in other species when food was available (Thompson et al. 1991; Gotceitas et al. 1999; Ostrand et al. 2005) or somatic energy reserves existed (Schultz and Conover 1999; McCollum et al. 2003; Shoup and Wahl 2008), indicating mechanisms not related to energetic needs (e.g., osmotic stress, reduced swimming ability, increased disease vulnerability, etc.) can be important in causing overwinter mortality of age-0 fish. It is also possible that the availability of food stimulates activity, increases metabolic rates of fish, or both during winter (Micucci et al. 2003). However, at the ration sizes used in our experiment, fed fish always survived better than starved fish, so this hypothesis alone cannot explain the high mortality observed for small, fed fish.

It is often suggested that fish are inactive during winter and do not eat much (Coutant 1975; Crawshaw 1984; Metcalfe and Thorpe 1992; McCollum et al. 2003). However, our results suggest that bluegills will eat large quantities of food when it is available and that this increases survival. This was also supported by the high frequency of food in bluegill stomachs in Ridge Lake on the day after ice melt. Other studies have documented feeding of fish during winter (Brown et al. 1989; Fullerton et al. 2000; Shoup and Wahl 2008), suggesting wintertime feeding may be more important than previously thought. Our field diet data came from samples collected on a single date, and further research is needed to better describe winter feeding habits of this species. However, our results clearly demonstrate some feeding occurs during winter for age-0 bluegills. Food is likely more important at warmer winter temperatures (Sogard and Olla 2000) when fish may not have the option of surviving solely on energy reserves (assuming metabolism increases at warmer temperatures). In our laboratory trials, cool temperatures allowed large fish to have low mortality (10%) even in the absence of food, but at warm temperatures, mortality was more extreme (60%). The benefits of cold temperatures were also observed for small fish but were not strong enough to allow high survival for the entire experiment, even when food was available.

Larger fish always had greater survival than smaller fish, suggesting that natural selection should favor early spawning by bluegills. However, protracted spawning may be maintained by other selective forces (Garvey et al. 2002). For example, early-spawned bluegills may have higher mortality if early spring temperatures are cold (Garvey et al. 2002). Similarly, bluegills spawned in early spring may have higher summer mortality from predation, either due to the prolonged exposure to predation or because they are selectively targeted because they are larger than their later-spawned cohorts (Santucci and Wahl 2003). It is also possible that fish that are too small to reproduce in spring could mature and produce their first clutch later that summer (Danylchuk and Fox 1994; Belk 1995). If at least some of these later clutches survive, it may increase fitness over a strategy of not reproducing until the following spring, especially in environments with a high risk of adult mortality (Fox and Keast 1991; Hutchings 1993). Similarly, large fish that spawn early in the year may be able to produce a second clutch later in the season (Garvey et al. 2002), which could increase fitness even if this clutch has lower survival than earlier-spawned fish. Factors influencing survival of early versus late-spawned bluegills are complex and reflect tradeoffs, where the most successful strategy may be to bet-hedge and produce multiple clutches (Slatkin 1974), especially in cases with highly unpredictable environmental conditions (Winemiller and Rose 1992). With short winters (i.e., <60–110 d, depending upon prey abundance), late-spawned, small fish may not experience heavy mortality and will have avoided much of the summer predation mortality. However, with long winters (i.e., >110–150 d), substantial overwinter mortality of small, age-0 bluegills is likely, especially when food resources are not abundant. In these conditions, the late-spawned fish will be eliminated, favoring allocation of resources to early spawning.

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