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[Article]

The Effect of Largemouth Bass Predation on Overwinter Survival of Two Size-Classes of Age-0 Bluegills

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Abstract.—Overwinter mortality is an important force structuring year-class strength of many fishes. Conventional wisdom is that overwinter mortality is primarily caused by starvation; however, recent research has demonstrated that piscivores continue to feed during winter and may also contribute to overwinter mortality of their prey populations. We conducted experiments in ten 0.04-ha earthen ponds in central Illinois to assess the effect of predation by largemouth bass *Micropterus salmoides* on survival of two size-classes (20–30 and 40–65 mm total length [TL]) of age-0 bluegills *Lepomis macrochirus*. Bluegills (400 fish/size-class) were stocked into each pond at the end of November. Half of the ponds also received five small (90–124 mm TL) and four large (166–192 mm TL) largemouth bass. Survival to the end of the 113-d experiment was higher for large bluegills than for small bluegills in all ponds. For both bluegill size-classes, the predator-present treatment had higher mortality than the predator-free treatment. Relative to the predator-free treatment, mortality of bluegills in the predator-present treatment increased by 16% for the large size-class and 49% for the small size-class. Mean length and relative condition (K_n) of both bluegill size-classes increased by the end of the experiment in both treatments, suggesting that the observed mortality was not caused by starvation. Further exploration is needed to elucidate why bluegills in the predator-free treatment suffered overwinter mortality despite the increase in K_n during the experiment. Length and K_n of largemouth bass increased (large size-class) or stayed the same (small size-class), suggesting that at least some of the predators foraged during winter. Our results indicate that size-specific overwinter mortality of bluegills occurs at the middle latitudes of the species' range. Further, winter predation can be an important component influencing size-specific overwinter survival and size-structured interactions between fishes.

For many fishes, first-year overwinter mortality structures year-class strength (Post and Evans 1989; McCollum et al. 2003). Reduced survival during winter has been attributed to low food availability or consumption (Post and Evans 1989; Kirjasniemi and Valtonen 1997), metabolic–digestive inefficiencies (Schultz and Conover 1999), reduced swimming ability (Larimore and Duever 1968; Jonas and Wahl 1998), osmotic stress (Morris and Bull 1968; Lankford and Targett 2001), and increased vulnerability to disease or toxicants (Lemly 1993). Overwinter mortality of age-0 fish is often size specific, affecting smaller individuals to a greater extent than larger individuals (Post and Evans 1989; Miranda and Hubbard 1994a; Cargnelli and Gross 1996; Bernard and Fox 1997; but see Toneys and Coble 1979; McCollum et al. 2003; Santucci and Wahl 2003), presumably because large individuals have greater energy reserves and lower mass-specific metabolic rates (Miranda and Hubbard 1994a; Schultz and Conover 1999). Overwinter mortality is usually more dramatic in years with harsh (longer or colder) winter conditions (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).

Predation may also cause size-specific overwinter mortality. Predation has traditionally been considered unimportant during winter, as piscivores were believed to be inactive and to cease feeding during that period (Johnson and Charlton 1960; Coutant 1975; Crawshaw 1984). However, recent studies suggest that piscivorous largemouth bass *Micropterus salmoides* do eat during winter (Miranda and Hubbard 1994b; Fullerton et al. 2000; Micucci et al. 2003; Ostrand et al. 2005) and that predation reduces overwinter survival of age-0 fish (Garvey et al. 2004). Reductions in prey species' survival could be caused by direct consumption, increased energy expenditures by fish as they evade predation (Post and Prankevicius 1987; Miranda and Hubbard 1994b; Garvey et al. 1998), or both. These mechanisms could also cause size-specific overwinter mortality, as larger prey fish (1) may occupy a size refuge from smaller predators (Lawrence 1958) and (2)

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typically have larger energy reserves and more-efficient metabolism (Schultz and Conover 1999) to better withstand the increased energy demands of predator evasion. Anecdotal evidence suggests that size-structured overwinter survival occurs for age-0 largemouth bass (Garvey et al. 1998); however, this has not been experimentally tested.

Several studies have found an overwinter shift toward larger lengths in the length distribution of age-0 bluegills *Lepomis macrochirus* (Toneys and Coble 1979; Cargnelli and Gross 1996; Garvey et al. 2002). Only one of these studies (Cargnelli and Gross 1996), from the northernmost portion of the species' range, was able to determine that this shift was caused by size-specific overwinter mortality rather than growth. However, other research suggests that overwinter mortality is not an important size-structuring force for age-0 bluegills (Santucci and Wahl 2003). Therefore, the extent to which overwinter mortality is size specific in this species is unclear. Where size-specific overwinter mortality of bluegills does occur, no information exists about the mechanisms underlying the process. Because bluegills often inhabit lakes that contain largemouth bass, predation is a possible source of overwinter mortality. Given the protracted spawning behavior of bluegills, there is a large amount of variation in size among age-0 fish that could lead to disparate survival if length-specific overwinter mortality exists. The purpose of this study was to (1) determine whether size-specific overwinter mortality occurs for bluegills in the middle latitudes of the species' range and (2) determine the effect of largemouth bass predation on overwinter survival of two length-classes of age-0 bluegills.

Methods

Experiments were conducted in 0.04-ha earthen ponds at the Sam Parr Biological Station, Kinmundy, Illinois (38.7°N) during the winter of 2003–2004. Ponds were clay lined and had a depth of 1.0–1.5 m (gradually sloping towards a drainage valve). Ponds had been full during the summer and fall but were drained and refilled with water from Forbes Lake (filtered to exclude fish) approximately 3 weeks before the start of the experiment. Therefore, zooplankton and benthic invertebrates were available to fish at the beginning of the experiment. Previous winter studies in these ponds indicated that the refilling of the ponds with lake water provided an ample supply of prey for juvenile fish (Garvey et al. 2004; Ostrand et al. 2005). All ponds were generally devoid of vegetation except for sparse emergent species (predominantly American water willow *Justicia americana* and senescing coontail *Ceratophyllum demersum*).

Small (20–30 mm total length [TL], 0.17 ± 0.01 g [mean wet weight ± SE]) and large (40–65 mm TL, 1.31 ± 0.05 g) age-0 bluegills (400 fish/size-class) were introduced into each of 10 ponds during the last week of November through the first week of December (equal numbers of fish were added to all ponds at the time of each introduction). This produced a total bluegill density of 14.6 kg/ha, which is within the range of natural densities for these length-classes in lakes with balanced largemouth bass–bluegill populations (Hackney 1979). Fish were obtained from area lakes and ponds and from the Jake Wolf Memorial Fish Hatchery, Topeka (Illinois Department of Natural Resources). Approximately equal numbers of fish from both length-classes were introduced from each source into each pond using a stratified random design. A random sample of 210 bluegills was measured (mm) and weighed (nearest 0.01 g). Twenty fish of each length-class were retained in floating cylindrical cages (1-m diameter; 2-m depth; 0.32-cm delta mesh) in three randomly selected ponds for 5 d to assess initial postintroduction mortality.

Five small (90–124 mm TL, 14.26 ± 0.64 g [mean wet weight ± SE]) and four large (166–192 mm TL, 67.43 ± 2.59 g) largemouth bass were added to each of five randomly selected ponds during the last week of November. The remaining five ponds were predator free. Largemouth bass lengths were matched to the two bluegill length-classes such that all predators had prey of a size that optimized (minimized) the handling time per unit weight consumed (Hoyle and Keast 1987). Total largemouth bass biomass (8.42 kg/ha) was within a range of natural densities for these length-classes in lakes with balanced largemouth bass–bluegill populations (Hackney 1979). Temperature was recorded by OnSet temperature data loggers at 0.3 m below the surface and on the bottom in a pond every 4 h during the experiment.

Ponds were drained during the second week in March, and all surviving bluegills and largemouth bass were measured and weighed. Vegetation that could interfere with fish recovery was heavily senesced, and ponds were searched in a systematic pattern to visually confirm that all fish had been recovered after draining. Relative condition (K_n) was calculated for each species as:

$$K_n = W/W',$$

where W is the actual weight (g) of the individual and W' is the length-specific mean weight for fish of the same length within the population. Values of W' were derived from the least-squares, best-fit length–weight regression equation determined for each species at the

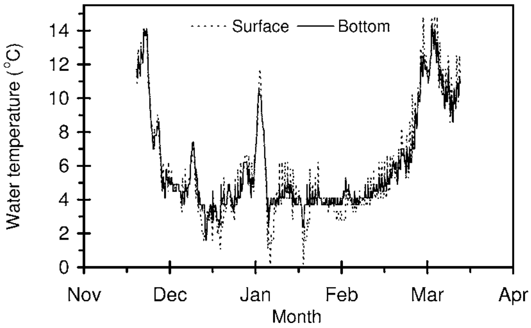

FIGURE 1.—Temperatures (surface: 0.3-m depth; bottom: 1.5-m depth) measured during winter 2003–2004 in ponds at the Sam Parr Biological Station, Kinmundy, Illinois, where largemouth bass predation effects on size-specific overwinter survival of age-0 bluegills were examined.

beginning of the experiment (Anderson and Neumann 1996):

Bluegill:

$$\log_{10}(W') = [3.267 \times \log_{10}(\mathrm{TL})] - 5.353 \quad \text{and}$$

Largemouth bass:

$$\log_{10}(W') = [3.168 \times \log_{10}(\mathrm{TL})] - 5.304.$$

Changes in mean TL and K_n of largemouth bass were tested using separate two-factor (length-class and time), repeated-measures analyses of variance (ANOVAs; ponds were treated as subjects). Changes in mean TL and K_n of bluegills were tested using separate three-factor (predation risk, bluegill length, and time), repeated-measures ANOVAs (ponds were treated as subjects or plots; bluegill length was treated as the split-plot factor). Mean number of bluegills surviving was analyzed as a two-factor (predation risk and length-class), split-plot design with ponds as plots and bluegill length as the split-plot factor. All analyses were conduced using the MIXED procedure of the Statistical Analysis System (SAS Institute 2004). In all instances, the data did not deviate from a normal distribution (Shapiro–Wilk test: all $P > 0.05$). Significant effects ($P < 0.05$) identified by ANOVA were subsequently examined with Tukey's tests.

We used Fish Bioenergetics version 3.0 (i.e., Wisconsin bioenergetics model; Hanson et al. 1997) to estimate consumption of bluegills by each length-class of largemouth bass based on predator weight gain during the experiment. These estimates were then compared with the increased bluegill mortality that occurred in the predator-present treatment relative to the predator-free treatment. For purposes of model simulations, three largemouth bass that died during the experiment were assumed to survive to the midpoint of the study. For the simulations, largemouth bass diets were assumed to include primarily bluegill prey. Mean daily temperature was determined from temperature loggers in the ponds, and the energy density of bluegills was set at 4,186 J/g (Hanson et al. 1997).

TABLE 1.—Mean (SE in parentheses) total length (TL, mm), relative condition (K_n), and survival (%) of two largemouth bass length-classes (small: 90–124 mm; large: 166–192 mm; 5 small fish and 4 large fish in each of 5 ponds) at the start (November 2003) and end (March 2004) of a 113-d experiment examining the effects of largemouth bass presence on bluegill overwinter survival in 0.04-ha earthen ponds at the Sam Parr Biological Station, Kinmundy, Illinois.

	Nov		Mar	
Metric	Small	Large	Small	Large
TL (mm)	108.7 (1.65)	177.7 (1.61)	107.6 (1.73)	179.4 (1.80)
K_n	1.00 (0.01)	1.00 (0.01)	1.00 (0.02)	1.09 (0.02)
Survival (%)	100 (0.00)	100 (0.00)	100 (0.00)	85 (0.06)

Results

Pond temperature during the experiment ranged from 0°C to 14.8°C at the 0.3-m depth and from 1.6°C to 14.4°C at the bottom (Figure 1). During winter (early December–February), temperature was between 1.6°C and 7.4°C at the pond bottom except during a 4-d period in the first week of January, when temperature reached 10°C. Mean average air temperature during the experiment followed a similar pattern and was typical for winter in southern Illinois (i.e., temperature was within 1 SD of the 1936–2006 winter mean; NOAA 2006).

No mortality due to handling was detected in the mortality cages, indicating that initial mortality in the experiment was very low and similar between bluegill length-classes. All but three largemouth bass survived to the end of the experiment (Table 1), and no pond had more than one largemouth bass mortality. The small size-class of largemouth bass showed no change in TL (Tukey's test: $P = 0.42$) or K_n (Tukey's test: $P = 0.99$) during the experiment. The large size-class of largemouth bass was significantly longer (Tukey's test: $P = 0.03$) and had a greater K_n (Tukey's test: $P = 0.02$) than the small size-class at the end of the experiment (largemouth bass length × time interaction for TL: $F_{1,8} = 13.61$, $P = 0.01$; for K_n: $F_{1,8} = 7.17$, $P < 0.03$).

The predation risk × bluegill length interaction was nonsignificant, indicating that the effects of predation treatment on survival were similar for both length-classes ($F_{1,16} = 0.29$, $P = 0.60$). Mean survival of bluegills differed between treatments (Figure 2). Survival was significantly higher for large bluegills than for small bluegills ($F_{1,16} = 5.02$, $P = 0.04$). Fish in

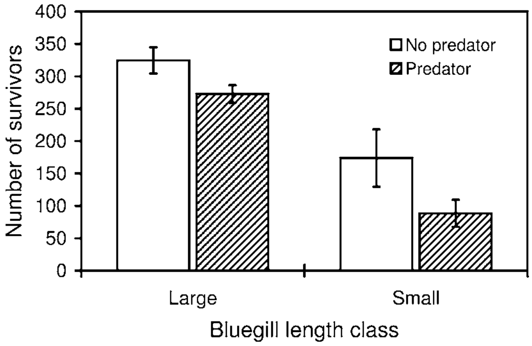

FIGURE 2.—Mean (±SE) numbers of large (40–65 mm total length [TL]) and small (20–30 mm TL) age-0 bluegills that survived to the end of a 113-d experiment (initial number = 400 fish/size-class in each pond) testing the effects of largemouth bass (predator) presence on bluegill overwinter survival in 0.04-ha earthen ponds at the Sam Parr Biological Station, Kinmundy, Illinois, 2003–2004.

the predator-present treatment had lower survival than those in the predator-free treatment ($F_{1,16} = 29.88$, $P < 0.01$). Survival was higher for large bluegills in the absence of predators (81%) than in the presence of predators (68%). Similarly, survival of small bluegills was higher in the predator-free treatment (43%) than in the predator-present treatment (22%). Therefore, 16% of large bluegills and 49% of small bluegills that died in the predator-present treatment could be attributed to largemouth bass presence (i.e., a 13% increase in mortality for large bluegills and a 21% increase for small bluegills).

The bioenergetics model predicted that in each pond containing predators, the small size-class of largemouth bass would consume 13.0 g of bluegill prey and the large size-class would consume 50.3 g (total consumption = 63.3 g). The mean bluegill biomass losses (small bluegills: 14.6 g; large bluegills: 81.0 g; combined: 95.6 g) in the predator-present treatment exceeded those in the predator-free treatment. The total bluegill biomass loss was considerably higher than could be explained by the largemouth bass consumption estimates from the bioenergetics model.

The initial TL of bluegills from either length-class did not differ between treatments (Tukey's test: $P > 0.99$). Both length-classes of bluegills were significantly longer (5–8% increase) by the end of the experiment (Tukey's test: $P < 0.01$; bluegill length × time interaction: $F_{1,32} = 21.97$, $P < 0.01$; Figure 3). Bluegill TL was greater in the predator-free treatment than in the predator-present treatment at the end of the experiment (Tukey's test: $P = 0.03$; predation risk × time interaction: $F_{1,32} = 4.43$, $P = 0.04$). The lack of either a significant predation risk × bluegill length interaction ($F_{1,32} = 2.34$, $P = 0.14$) or a significant three-way interaction (predation risk × bluegill length × time: $F_{1,32} = 2.34$, $P = 0.14$) indicated that the effects of predation on TL structure were similar for both length-classes of bluegills.

Initial bluegill weight did not differ for either length-class between predation treatments (Tukey's test: $P > 0.99$). Both length-classes of bluegills had significantly greater mass at the end of the experiment (Tukey's test, large bluegills: $P < 0.01$; small bluegills: $P = 0.05$; bluegill length × time interaction: $F_{1,24} = 137.65$, $P < 0.01$; Figure 3). The effects of predation on size (weight) structure were similar for both length-classes, as indicated by the nonsignificant predation × bluegill length interaction ($F_{1,24} = 2.79$, $P = 0.11$) and the nonsignificant three-way interaction (predation risk × bluegill length × time: $F_{1,24} = 2.79$, $P = 0.11$).

Initial values of K_n did not significantly differ between treatments for either bluegill length-class (Tukey's test: $P = 0.97$). Both bluegill length-classes exhibited significant increases in K_n during the experiment (bluegill length × time interaction: $F_{1,32} = 5.58$, $P = 0.02$; Tukey's test: $P < 0.01$ for both length-classes; Figure 3). Small fish had a greater increase in K_n than large fish (Tukey's test: $P < 0.01$). The presence of predators did not significantly affect the K_n of bluegills (predation risk × bluegill length × time interaction: $F_{1,32} = 1.95$, $P = 0.17$; predation risk × time interaction: $F_{1,32} = 3.07$, $P = 0.09$; predation risk × bluegill length interaction: $F_{1,32} = 1.95$, $P = 0.17$; predation risk main effect: $F_{1,32} = 3.07$, $P = 0.09$).

Discussion

Our study is the first quantification of predation effects on overwinter survival of bluegills. Predation accounted for a 16–49% increase in mortality above that occurring in predator-free ponds, confirming that piscivores can cause significant overwinter mortality of bluegill populations. These effects could be the result of indirect behavioral changes (Werner and Hall 1988; Shoup et al. 2003) or direct consumption. The increase in growth and K_n for the large size-class of largemouth bass and the lack of decline in K_n for the small size-class suggest that at least some of the bluegill mortality was due to direct consumption. Overwinter mortality in treatments with and without predators was size specific (higher for small bluegills), as has been previously reported for bluegills at the northernmost portion of the species' range (Cargnelli and Gross 1996). However, the effect of predation on survival was not size specific. We produced similar predatory pressure on both length-classes of bluegills by using two length-classes of predators. In natural systems, size-specific predation effects on bluegill mortality may differ depending on

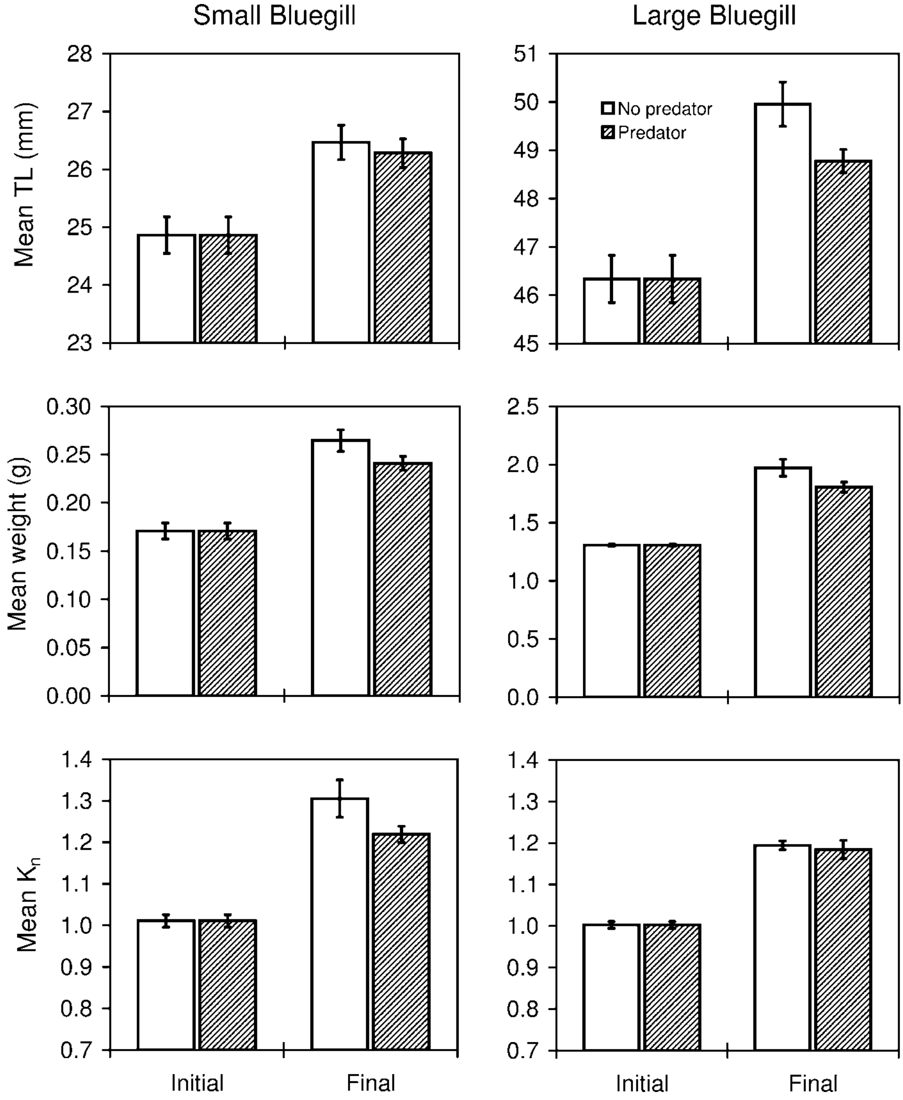

FIGURE 3.—Mean (±SE) total length (TL), weight, and relative condition (K_n) of two age-0 bluegill size-classes (small: initial TL = 20–30 mm; large: initial TL = 40–65 mm) at the start and end of a 113-d experiment examining the effects of largemouth bass (predator) presence on bluegill overwinter survival in 0.04-ha earthen ponds at the Sam Parr Biological Station, Kinmundy, Illinois, 2003–2004. Note the change in scale (TL or weight) between left and right panels.

the size structure of the predator and prey populations (Santucci and Wahl 2003). Furthermore, the type and abundance of protective cover may alter the extent of predation in natural systems.

The bioenergetics model prediction of bluegill consumption by largemouth bass was insufficient to account for the difference in bluegill survival between predator-free and predator-present treatments. The presence of predators could cause indirect mortality by altering bluegill behavior, thereby resulting in increased energy expenditure or decreased food consumption (Werner et al. 1983; Savino and Stein 1989; Shoup et al. 2003) that ultimately leads to mortality from starvation. However, both bluegill length-classes showed increased length, weight, and K_n in the presence of largemouth bass, which implies that bluegills were able to consume enough to meet energy demands. A more likely explanation is that the bioenergetics model did not function well for largemouth bass at the winter temperatures examined. While their deviations were different from ours, Wright et al. (1999) also found that two models derived from the

Wisconsin bioenergetics model did not perform well in predicting consumption at winter temperatures during a laboratory study of largemouth bass.

Our results indicate that size-specific overwinter mortality of age-0 bluegills can occur in the middle latitudes of the species' range, even in the absence of predation. Size-specific overwinter mortality in bluegills has also been documented at the northern extent of the range (Cargnelli and Gross 1996), but we are not aware of any overwinter mortality studies from southern latitudes. For many species, the extent of overwinter mortality is positively correlated with latitudinal clines in winter severity (Fullerton et al. 2000; McCollum et al. 2003; Hurst 2007), although mortality may also become less size specific with increased latitude (Garvey et al. 1998). For other species, overwinter mortality is more severe under moderate or mild winter temperatures (Schultz et al. 1998), presumably because metabolic rates increase while food abundance is still low. Given our results, predation pressure could, at least in part, modify the extent of overwinter mortality that would be expected based on latitude (Hurst 2007; this study). Further research is needed to determine the role of predation in overwinter survival across latitudinal gradients.

Several mechanisms have been proposed to explain overwinter mortality of age-0 fishes (see Hurst [2007] for a review). These mechanisms can be grouped into two categories: energetics–food limitation and physiological mechanisms. Most previous work has focused on size-specific energy limitation, assuming either that food is unavailable (Mookerji et al. 1998; Baldwin et al. 2000) or that fish choose not to feed (Crawshaw 1984; Metcalfe and Thorpe 1992; McCollum et al. 2003). This leads to mortality by direct starvation or by increased vulnerability to predation (Jonas and Wahl 1998). These mechanisms also explain how overwinter mortality could be size specific, as larger individuals have greater energy reserves and lower biomass-specific metabolic rates (Schultz and Conover 1999). In our experiment, we observed significant TL growth and an increase in K_n, indicating that the surviving bluegills successfully found, ingested, and assimilated food. Therefore, these starvation-related hypotheses seem unlikely as the source of the bluegill mortality we observed. This is similar to results found in other recent studies (Brown et al. 1989; Gotceitas et al. 1999; McCollum et al. 2003). Physiological stress associated with low temperatures can cause overwinter mortality through osmotic imbalance (Johnson and Evans 1996; Lankford and Targett 2001) or greater (sometimes size-specific) vulnerability to diseases or toxic substances (Lemly 1993). These mechanisms seem to provide the most likely explanations for the mortality of bluegills in ponds without predators. For other species that appear to be affected by similar mechanisms, exposure to temperatures below a minimum threshold of around 3°C, even for just a few days, dramatically increases the probability of mortality (Malloy and Targett 1991; Johnson and Evans 1996; Hales and Able 2001; Lankford and Targett 2001). In our ponds, temperatures were below 4°C for 44 d and were below 3°C for 9 d (6 d were consecutive; Figure 1). Additional work is needed to determine whether a similar temperature threshold exists for bluegills.

In addition to affecting survival, predator presence also decreased growth rates of age-0 bluegills. Increased body size is often positively related to bluegill survival (Dewey et al. 1997; Schneider 1999), and overwinter effects may extend to other seasons if reduced growth results in higher mortality at other times of the year. This may be particularly important in the northern portions of the species' range, where colder temperatures cause slower growth that extends the period of juvenile bluegill vulnerability to gape-limited predators (Modde and Scalet 1985). Further research is needed to determine the full extent of mortality related to overwinter predation risk.

Size-structured interactions between predators and prey can be important ecological and evolutionary forces that structure communities of fishes and other organisms (Werner and Gilliam 1984). Size-specific information is often needed to accurately predict mortality, as predator abundance alone is usually inadequate (Rice et al. 1993). Size-specific predation risk therefore regulates a host of other interactions, including ontogenetic changes in habitat and diet and ultimately interspecific competition among different size-classes (Werner and Gilliam 1984). The effects of these interactions have been well studied but only during the growing season. Our results for bluegills and results from studies of other fishes (Pratt and Fox 2002) suggest that size-specific interactions could be equally important during winter. Winter food availability is often low (Mookerji et al. 1998; Baldwin et al. 2000), making the accumulation of energy reserves before winter an important selection pressure. However, energy accumulation often comes at the cost of reduced growth and an increased period of vulnerability to size-specific predation (Post and Parkinson 2001) and may even cause a direct reduction in survival through physiological mechanisms (Munch and Conover 2003). Early spawning is an alternative mechanism that would allow age-0 fish to attain a large size while still accumulating sufficient energy reserves for winter. However, this may produce trade-offs related to spring prey availability and competition (Stein et al. 1988) and could even cause increased summer predation pressure (Santucci and Wahl 2003).

Size-structured interactions are very complex, involving a suite of trade-offs that are optimized differently in different environments. Our results suggest that winter not only selects for maximization of energy reserves but also enhances the importance of prey body size relative to predator size structure. Additional research examining these evolutionary trade-offs, including winter predation risk, will add to our understanding of the complex set of interactions that influence size-structured survival of age-0 fishes.

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