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ENERGETICS, PREDATION, AND RATION AFFECT SIZE-DEPENDENT GROWTH AND MORTALITY OF FISH DURING WINTER

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Abstract. Winter temperatures may reduce energy costs for ectotherms. However, variable mid-temperate and low-latitude winters may interact with scaling of size, metabolism, and energy reserves to cause energy deficits and require trade-offs between foraging and predation. A dynamic optimization model explored how ration, fall fat, and both non- and size-selective predation influenced foraging (i.e., fast or forage) and energy allocation (i.e., length or fat) decisions that maximize winter survival of age-0 largemouth bass (*Micropterus salmoides*). During a mid-latitude (38° N) winter, a pond experiment in which age-0 fish occurred with or without adult conspecific predators tested a subset of the model.

In the model without predators, winter foraging occurred, with small size only reducing survival when low ration and low fall fat caused small fish to exhaust reserves. With predation, all sizes foraged to maintain mass and fat reserves when ration was sufficiently high, with small fish also growing in length. When modeled predation was nonselective, size-dependent mortality varied in complex ways. In contrast, size-selective predators consistently reduced survival of small fish. Generally consistent with the model, fish in ponds without predators gained mass and energy content, while those with predators only maintained these parameters. All small individuals grew more than large counterparts in length. Mortality in ponds never depended on size but was ~20% higher with predators. Energy deficits often demand active foraging during mid-temperate winters, with predation rather than energy depletion influencing size-dependent survival.

Key words: ectotherm; fat; growth; largemouth bass; length; Micropterus salmoides; *predation; survival; winter.*

INTRODUCTION

During periods of scarcity and environmental stress, biotic interactions often intensify, mandating important physiological and behavioral trade-offs. Winter is challenging for many organisms because temperature and food decline, while predation may increase (Houston and McNamara 1993, Garvey et al. 1998). For many endotherms, maintaining body temperature against a large temperature gradient during winter is problematic, particularly during the night or when predators impede foraging (Houston and McNamara 1993, Bednekoff and Houston 1994, Pravosudov and Lucas 2000). For ectotherms, in contrast, declining body temperature and metabolism during winter reduce energy costs (Niimi and Beamish 1974, Love 1980, Beamish 1990). Thus, ectotherms are widely assumed to become dormant, avoid biotic interactions, and rely solely on reserves to survive winter and other times of environmental stress (Pough 1980, Crawshaw 1984).

Growth of many ectotherms is indeterminate and varies tremendously among years (Heino and Kaitala 1999), potentially affecting winter energetics. In temperate fishes, cohort strength is typically determined during the first winter of life when body size varies widely (Hubbs and Trautman 1935, Sogard 1997, Garvey et al. 2003*b*, Parkos and Wahl 2003). Allometries of size, metabolic rates, and energy reserves cause conflicts between maintaining energy stores and foraging (Post and Parkinson 2001, Hurst and Conover 2003). In short, energy use increases exponentially with body mass with an exponent less than one, whereas fat reserves scale linearly with mass. As such, small individuals catabolize reserves much faster (Downhower 1976). Slow first-year growth, small size, and low fall reserves may reduce survival, ultimately affecting populations.

Because many fishes do become dormant and starve during winter, size-dependent differences in physiological scaling have been invoked as the major mechanism causing high mortality of small individuals (Oliver et al. 1979, Post and Evans 1989, Cargnelli and Gross 1997, Hurst and Conover 2003). This may be particularly relevant during north-temperate winters in

freshwater, because stable temperatures (4°C) occur under ice, ensuring predictable metabolic costs. Conversely, winter temperatures at mid-temperate latitudes may only temporarily decline to stable levels because ice cover is rare. During the remainder, temperatures vary, albeit at levels far below growth optima (Magnuson et al. 1979). Energy costs rise and may require foraging to prevent depletion of reserves.

For age-0 largemouth bass (*Micropterus salmoides*) at mid-temperate latitudes, foraging does occur during winter, although mortality often remains higher for small fish in the field (Fullerton et al. 2000). Predation appears to influence patterns of size-dependent mortality during winter in this species (Miranda and Hubbard 1994*a*, Garvey et al. 1998). As with many organisms, small largemouth bass must weigh the risk of becoming conspicuous to predators by actively foraging against the benefit of consuming food to maintain energy reserves or increase body size (Lima and Dill 1990). The extent by which foraging interacts with predation to influence patterns of growth and survival during winter is not well understood, particularly given the prevailing assumption that overwintering costs are low relative to endotherms.

We developed a dynamic state-variable model to explore differences in optimal energy allocation and foraging decisions of age-0 largemouth bass with temperature-dependent consumption and growth potential during a mid-temperate latitude winter (Garvey and Marschall 2003). These models consider state- and condition-dependent limitations to find evolutionarily optimal responses that maximize expected survival (Mangel and Clark 1988). Backward iteration finds these optimal strategies through a sequence of decisions (Bellman 1957, Mangel and Clark 1988). To determine how foraging decisions vary with predation, we varied risk of foraging-induced, predatory mortality in the model (Schindler 1999). A winter pond experiment explored how adult largemouth bass, a common predator, affected size-dependent survival, growth in length, and energy condition of age-0 largemouth bass. We expected that the model would predict and the experiment would confirm that predators reduce foraging, potentially causing higher mass-specific energy depletion and mortality of small individuals (see Pratt and Fox 2002 for a similar prediction).

METHODS

Model

The bioenergetics of largemouth bass is generally well understood and underlying relationships have been incorporated into a mass-balance model that has produced robust, field-verified results (Rice and Cochran 1984). Modeled temperature and size dependencies in metabolism and consumption (Rice et al. 1983, Trebitz 1991, Wright et al. 1999) may interact with predation to influence energy allocation and foraging decisions.
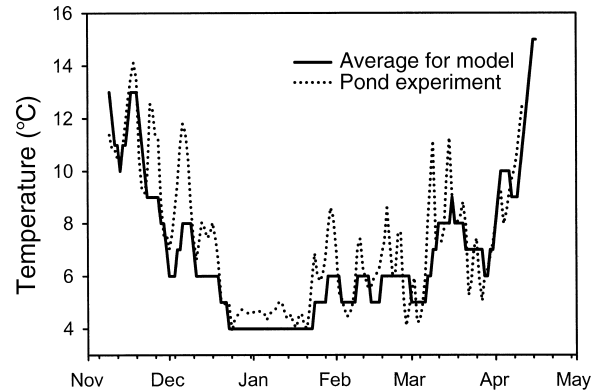

FIG. 1. Temperatures used in the dynamic model and temperatures in experimental ponds. Daily temperatures used in the dynamic model are averages between two years in ponds at Sam Parr Biological Station, Illinois, USA. These temperatures better reflect temperatures affecting selection for dynamic decisions than estimates from a single winter at this latitude. Experimental temperatures are daily means for two of the experimental ponds at the same location during fall 2001 through spring 2002.

We embedded the bioenergetics algorithm in the dynamic optimization model.

Winter duration and temperatures in the dynamic model derive from an average across two years for the ponds used in the winter experiment described below (Fig. 1). Rather than using specific experimental daily temperatures (Fig. 1), an average across years better reflects the mean winter conditions that select for energy allocation and behavioral strategies. For each day t ($t = 0, 1, \ldots, 159$) of winter in the dynamic state-variable model, we calculated the maximum expected future winter survival, $F(L, w, t)$, of an age-0 largemouth bass of length L (millimeters of total length), having fat reserves at w proportion of their maximum. Maximum fat reserves are assumed to be increasing functions of body length L. For any given week, a modeled fish compares expected future fitness (i.e., probability of survival) from each possible allocation strategy φ ($\varphi = (\varphi_L)$) and foraging strategy λ. If a fish forages ($\lambda = 1$), it allocates a proportion φ_L of that week's net energy intake to growth in length and a proportion $1 - \varphi_L$ to growth in fat reserves. Otherwise, no energy is consumed ($\lambda = 0$). Foraging ($\lambda = 1$) incurs daily mortality ($1 - \kappa$) due to predation, where κ is daily survival.

An allocation φ and foraging λ strategy during a given winter day t ($t = 0, 1, \ldots 159$) by a fish having state values L and w results in state values the following day of $L'(\varphi, \lambda)$ and $w'(\varphi, \lambda)$. The fish chooses the allocation strategy that maximizes expected winter fitness beginning at the present, such that

$$F(L, w, t) = \max_{\varphi, \lambda} F\{\kappa(\lambda)[L'(\varphi, \lambda), w'(\varphi, \lambda)], t + 1\}.$$

$$(1)$$

The actual amount of energy allocated to length and fat is limited by the amount of food ingested on a given day. We represent energy ingested as a proportion ρ of the maximum possible (C_{max}; joules per day) for a largemouth bass of that size:

$$C_{max} = 0.33M^{0.675}z \times 4187 \qquad (2)$$

where M is wet mass (grams) excluding fat and is calculated as $M = 1.35 \times 10^{-5}L^{2.98}$ (Trebitz 1991) and z is a temperature-dependent multiplier (Rice et al. 1983). We assumed a prey energy density of 4187 J/g (Wright et al. 1999). Fat could make up no more than 3% of total wet mass (Miranda and Hubbard 1994b, Oster 2002). We used W to represent grams of body mass in fat, $W = w(0.03M)$. Daily metabolic costs α (joules) were estimated as a function of temperature τ (°C) and total wet mass N (grams), including mass of the current fat, $N = M + W$. These were included in a metabolic cost function (Trebitz 1991):

$$\alpha = (0.0868N^{-0.355}e^{0.0811\tau+0.0196}K_{act}0.078)$$
$$\times N \times 4187 \qquad (3)$$

where we assume that largemouth bass energetic density is 4187 J/g (Garvey et al. 1998). K_{act} is an activity multiplier that causes small largemouth bass ($<$60 mm) to grow at realistic rates (Trebitz 1991):

$$K_{act} = \begin{cases} 1 & \text{for } \tau < 10°C \\ 1.1N^{-0.1} & \text{for } \tau \geq 10°C \text{ and } N \leq 2.594 \text{ g.} \\ 1.0198 & \text{for } \tau \geq 10°C \text{ and } N > 2.594 \text{ g.} \end{cases}$$
$$(4)$$

Daily costs I (joules per day) due to egestion and excretion were estimated as fixed proportions of ration according to the model by Trebitz (1991):

$$I = SDA(C_{max}) + B(C_{max}) + S(C_{max}) \qquad (5)$$

where SDA is specific dynamic action, B is feces, and S is excretion. Costs of converting consumed energy into each type of body mass were assumed to be included in I.

We assumed that metabolic costs are paid from energy ingested each day. Costs in excess of energy are paid from fat reserves. Thus, length and proportion of maximum fat reserves change with each day as a function of net energy intake (which is a function of gross energy intake, temperature, and body size) and energy allocation according to the following equations:

$$L'(\varphi, \lambda) = \begin{cases} L + \{17.67[\varphi_L(\rho\lambda C_{max} - \alpha - I)]^{0.3357}\} \\ \quad \text{for } \rho\lambda C_{max} > \alpha + I \\ L \quad \text{for } \rho\lambda C_{max} \leq \alpha + I \end{cases}$$
$$(6)$$

where 17.67 and 0.3357 convert joules to total length (Garvey et al. 1998), and

$$w'(\varphi, \lambda) = \begin{cases} \dfrac{W + (1 - \varphi_L)(\rho\lambda C_{max} - \alpha - I)}{0.03M'} \\ \quad \text{for } \rho\lambda C_{max} > \alpha + I \\ \dfrac{W + (\rho\lambda C_{max} - \alpha - I)}{0.03M'} \\ \quad \text{for } \rho\lambda C_{max} \leq \alpha + I \end{cases}$$
$$(7)$$

where M' is the somatic wet mass of a fish of length $L'(\varphi, \lambda)$. When new state values were intermediate between discrete values used in the model, we calculated expected fitness using trilinear interpolation (Press et al. 1992).

Fitness is determined by winter survival, which depends on fat reserves:

$$F(w) = \begin{cases} 1 & \text{for } w > 0 \\ 0 & \text{for } w = 0. \end{cases} \qquad (8)$$

Largemouth bass with $w = 0$ die.

We ran three dynamic models, in which daily predation mortality was $(1 - \kappa(1)) = 0$ (i.e., no predation), $(1 - \kappa(1)) = 0.0022$ (i.e., total potential mortality during winter = 30%), and $(1 - \kappa(1)) = 0.014$ (i.e., total potential mortality = 90%) if foraging occurred ($\lambda = 1$). A fourth dynamic model explored how size-dependent predation affected decisions and expected survival by linearly increasing foraging-induced predation from the highest level (0.014) at 50 mm to zero at 220 mm. We combined these modeling scenarios with four constant-ration treatments, in which fish consumed $\rho = 0.3, 0.4. 0.5,$ and 0.6 of their C_{max} for the entire winter. We calculated the optimal allocation for each combination of state values: $w = 0.2, 0.4, \ldots, 1.0$ and $L = 50$–220 mm by 10-mm increments.

We used optimal energy allocation and foraging decisions generated by the dynamic state-variable model to simulate daily growth through winter of age-0 largemouth bass across all lengths, with $w = 0.2$, $w = 0.6$, and $w = 0.8$ at $t = 0$. Growth was simulated using the same bioenergetic routines and rations used in the dynamic state-variable experimental design (Garvey and Marschall 2003). Proportional allocation decisions for length and fat states intermediate between values generated by the dynamic state-variable model were estimated with trilinear interpolation. Because both the dynamic model and growth simulations generated large data arrays, we only present subsets of results spanning the range of fall condition, body size, and ration.

Experiment

To determine how predation affects winter growth and survival of age-0 largemouth bass, we conducted an experiment in 10, 540-m² ponds (1.5 m deep) at the Sam Parr Biological Station, Illinois Natural History Survey, Kinmundy, Illinois, USA (latitude 38°42′50.0″ N, longitude 88°44′55.0″ W) during 1 November 2001 through 15 April 2002. At the experiment's start, each

PLATE 1. Wide range of sizes of age-0 largemouth bass produced in an annual cohort, representative of those in the pond experiment at Sam Parr Biological Station, Illinois, during November 2001 through April 2002. The middle fish has a caudal fin clip. Photo credit: Russell A. Wright, Auburn University.
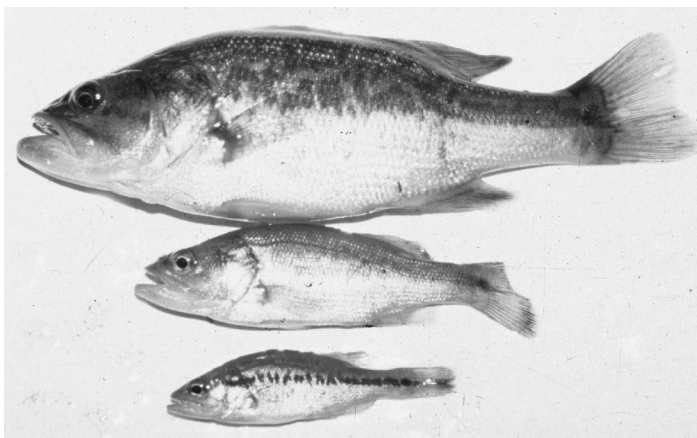
pond received 75 small (mean total length $\pm$ 1 SD = 66 $\pm$ 5 mm) and 50 large (94 $\pm$ 8 mm) age-0 largemouth bass reared in ponds at Sam Parr (see Plate 1). All small and large fish received unique size-specific fin clips and were measured (millimeters total length). All ponds contained vegetation. In addition, 150 pieces of 12 cm long, 8 cm diameter PVC pipe were placed in each pond to provide cover for age-0 largemouth bass. Two adult largemouth bass, each with a unique fin clip, were then added to each of five randomly selected ponds (overall mean length = 330 $\pm$ 31 mm; mean combined mass per pond = 1.0 $\pm$ 0.06 kg). Prey for largemouth bass in ponds included naturally occurring zooplankton, insect larvae, and crayfish. Semicontinuous temperature loggers were placed in two of the ponds. At the end of the experiment, each pond was drained into a catch basin in which both remaining age-0 largemouth bass and adults were collected and measured.

At the start of the experiment, a size-stratified sample of ~50 largemouth bass stocked into ponds were frozen for wet mass, dry mass, and total energy content; in spring, ~50 age-0 bass from each pond also were frozen. These individuals were weighed and ~30 bass across all sizes from the fall subsample and from each pond during spring were dried at 60°C to a constant mass. Dried tissue was ground, pelletized, and the energy content was quantified in a semimicro, oxygen bomb calorimeter (Rand et al. 1994). Whether predation affected proportional change in length in the small and large size classes was determined with a one-way multivariate analysis of variance (MANOVA), in which the two size classes were the dependent variables. All proportions were arcsine transformed to meet assumptions of normality. An analysis of covariance (ANCOVA) of log-transformed length (the covariate) vs. either dry mass or total energy content was used to determine how these dependent variables changed between fall and spring in both the no-predator and predation treatments. Size-dependent mortality in both treatments was determined by comparing the propor-

tion of marked individuals within the small and large size classes before and after winter with a G test (Garvey et al. 1998). The overall percentage of mortality of small and large individuals was compared between treatments with a MANOVA. Combining the mass change of each adult largemouth bass with known winter temperatures (Fig. 1), we determined the total consumptive demand using the bioenergetics model (Hanson et al. 1997).

RESULTS

Model

By using foraging and energy allocation predictions generated by the dynamic model and then simulating growth, we found that growth in length and fat should vary with initial fat reserves, size, predation, and daily ration (Fig. 2). With low available ration (40% maximum consumption, C_{max}) and low fall fat, no sizes of largemouth bass (with or without foraging-induced predatory mortality) allocated energy to length (Fig. 2A). Large individuals lost less fat, with those without predators losing slightly less fat than counterparts with predation (Fig. 2B). As available ration increased to 60% of C_{max}, lengths of small largemouth bass with predation increased, while those without predation did not (Fig. 2C). Fat reserves increased without predation and were maintained with predation (Fig. 2D). With high fall fat, growth in length was generally similar to that with low fall fat (Fig. 2E, G). Conversely, individuals with high fall fat lost ~50% fat reserves (Fig. 2F, H). We also modeled responses at 30% and 50% of C_{max}. Patterns for 30% of C_{max} were identical to those for 40% of C_{max} except that all size classes lost 100% of fat when fall fat was 20%. Patterns for 50% of C_{max} were intermediate between 40 and 60% of C_{max} for both low and high fall fat.

Expected winter survival in the dynamic model depended on fall energy reserves, ration, and foraging-induced predation. With low fall energy reserves, low ration, and no or low (30%) predation, small large-
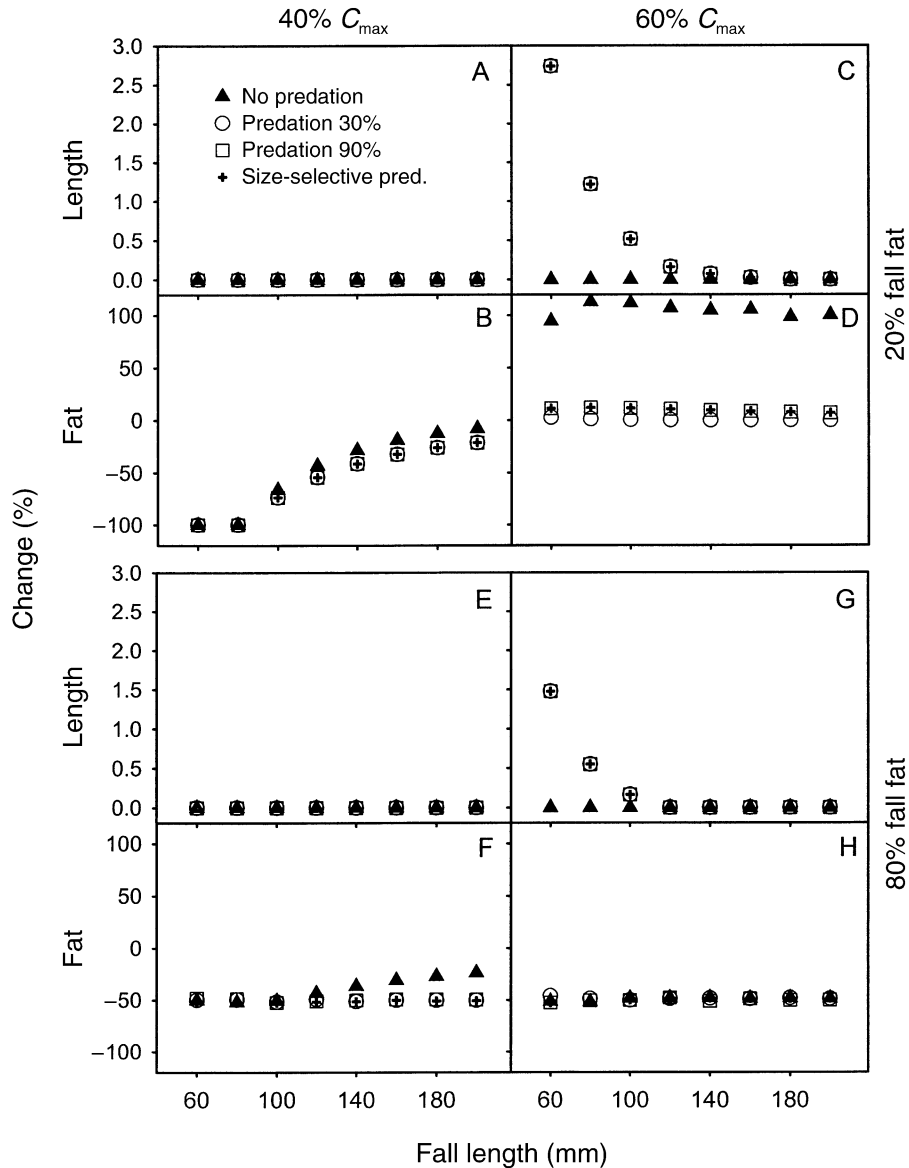
FIG. 2. Predicted percentage change of length (mm) and fat (g) of age-0 largemouth bass as a function of fall length, predation, and ration (percentage maximum daily consumption, C_{max}) during a simulated mid-latitude winter (38° N, Illinois, USA). Predictions were generated from a dynamic optimization model that generated foraging and energy allocation decisions maximizing winter survival. A bioenergetics simulation then used these optimal decisions to generate patterns of growth. Initial fall fat in this simulation was either 20% (panels A–D) or 80% (panels E–H) of maximum. Foraging with predation incurred a low (30%), high (90%), or length-dependent cumulative mortality rate. For each fall length, all four symbols are present, although they may overlap.

mouth bass had low expected survival, whereas large counterparts did not (Fig. 3A, B). At higher rations, expected survival reached 100% for all sizes of large-mouth bass with no predation, and ~80% with 30% predation (Fig. 3C, D). At 90% winter predation, expected survival was low for all sizes with low fat reserves, increasing from near 0% at 30% of maximum consumption to ~20% at 60% of C_{max} (Fig. 3A–D). When predation was size dependent, survival increased with length at all rations (Fig. 3A–D). High, nonse-

lective predation may mask size-dependent patterns of survival induced by winter energy depletion if all sizes of fish are in poor condition in fall. Conversely, selec-tive predators will create a size-dependent survival pat-tern regardless of food availability.

Fundamentally different patterns of expected winter survival arose with high fat reserves in fall. Although expected survival was again size dependent with a low ration and no or low predation, overall survival of large fish was much higher when fall energy reserves were
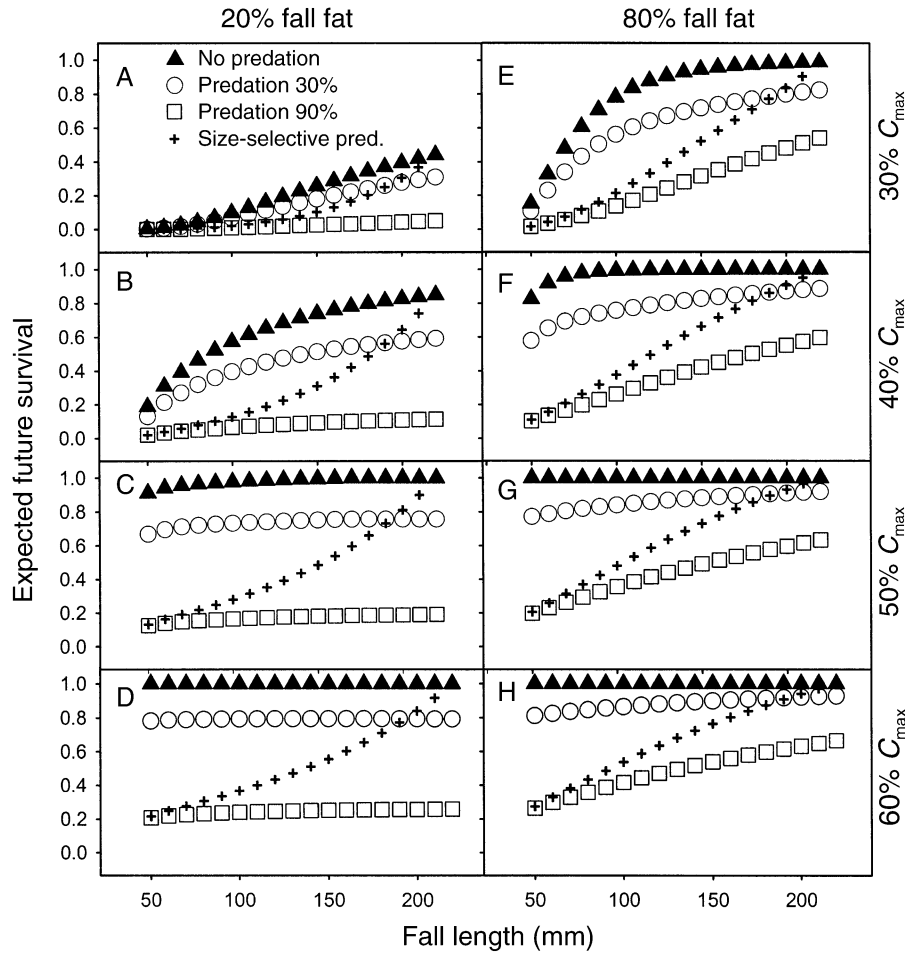
FIG. 3. Expected winter survival probability of individual age-0 largemouth bass as a function of fall length, fall fat reserves (percentage of maximum), ration (percentage of maximum daily consumption, C_{max}), and foraging-induced predation during a simulated mid-latitude winter (Illinois). Predictions were generated from a dynamic optimization model in which age-0 largemouth bass could either forage or fast. If foraging occurred, energy was allocated either to length or fat reserves. All survival values are >0. Predation is the same as in Fig. 2.

high (Fig. 3E, F). With high ration and low predation, patterns were very similar to those with low fall fat reserves, although expected winter survival was higher for all sizes (Fig. 3G, H). When predation risk was high (90%) or size selective, expected survival was size dependent regardless of ration (Fig. 3E–H).

Predicted foraging activity depended on fall fat, available ration, body size, and predation (Fig. 4). With low fall energy reserves and low ration, foraging activity of small individuals was low (Fig. 4A, B). For the remaining individuals and rations with low fall fat, foraging activity was generally high (Fig. 4A–D), with the exception of large individuals with a low ration plus high predation (Fig. 4A), and all individuals at high ration without predators (Fig. 4D). With high fall fat at low rations, foraging declined with increasing size with predation and remained high without predation (Fig. 4E, F). At higher rations with high fat,

foraging declined with increasing length under all scenarios (Fig. 4G, H).

Experiment

Growth in length, total energy content, and energy content depended on largemouth bass size class and predation treatment. Proportional change in length for either small or large size classes was unrelated to predation (MANOVA Predation effect: Wilks' lambda = 0.81, $F_{2,7} = 0.82$, $P = 0.48$). Change in length averaged 11% and 8% for small individuals in the no-predator and predator treatments, respectively; for large individuals, mean percentage length change was 4.1% and 6.2% without and with predators. Pooling percentage length change across treatments for small and large size classes ($N = 10$ ponds for each size class) revealed that length changed more for small than for large largemouth bass (one-way ANOVA, $F_{1,19} = 10.64$, $P =$
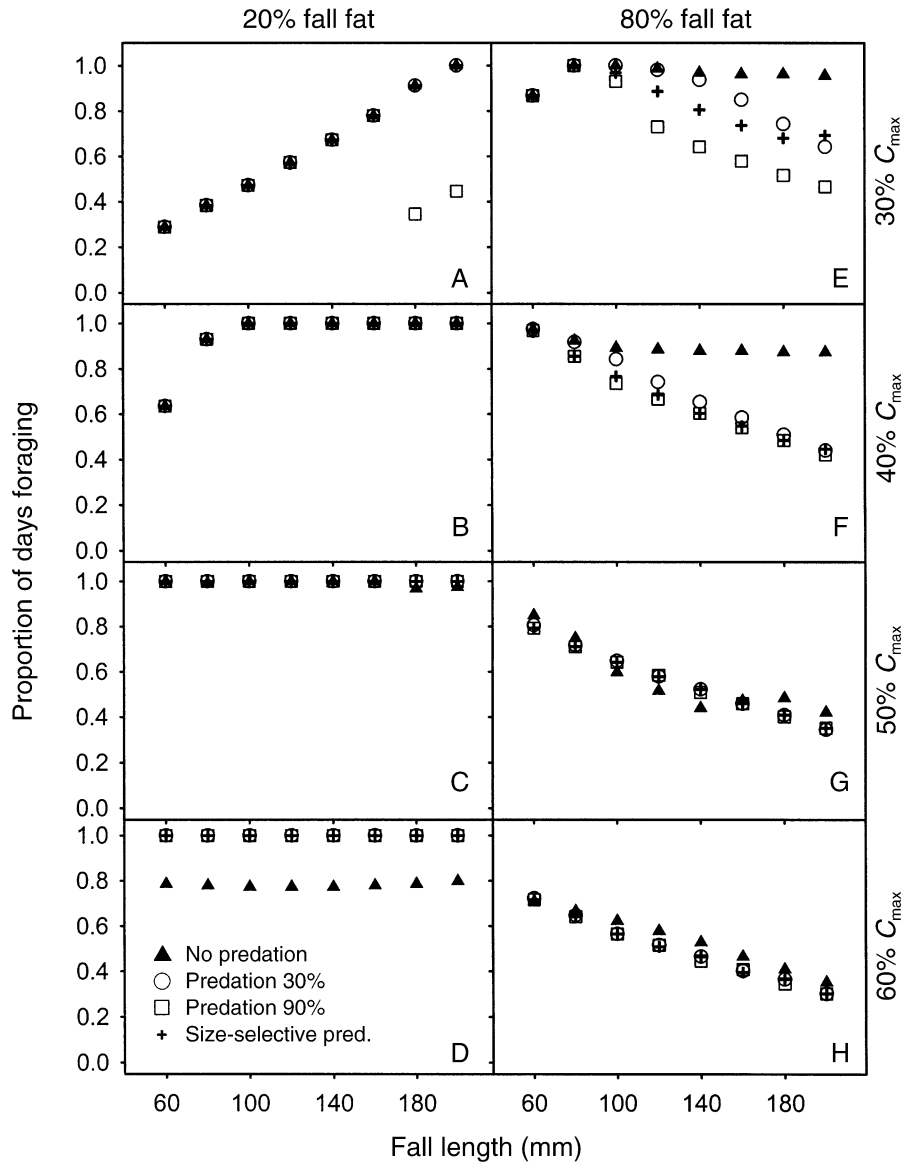
FIG. 4. Expected proportion of days spent foraging by individual age-0 largemouth bass as a function of fall length, ration (percentage of maximum daily consumption, C_{max}), and foraging-induced predation during a simulated mid-latitude winter (Illinois). Predictions were generated from a dynamic optimization model that generated foraging and energy allocation decisions maximizing winter survival. A bioenergetics simulation then used these optimal decisions to generate patterns of growth. Initial fall fat reserves were either 20% or 80% of maximum. Predation is the same as in Fig. 2. For each fall length, all four symbols are present, although they may overlap.

0.004). In spring, total length (mean $\pm$ 1 SD) pooled between treatments was 73 $\pm$ 6 and 98 $\pm$ 8 mm for small and large individuals, respectively.

Both dry mass and total energy content varied positively with length in largemouth bass in the fall and in both treatments in the spring (all regression models: $P = 0.0001$; $R^2 > 0.95$; Fig. 5, Table 1). For all ANCOVA models, no significant interaction between the covariate (length) and treatment occurred, suggesting that all slopes were equivalent (Table 1). The only significant ANCOVA models occurred when comparing

spring dry mass or total energy content in the no-predator treatment with fall levels (Table 1, Fig. 5). Hence, both dry mass and total energy increased for all sizes of largemouth bass during winter when predators were absent, but did not change when predators were present.

The proportion of largemouth bass in the small and large size classes in spring did not differ from those in the fall in either the no-predator or predator treatments (G test pooled across ponds: no-predator, $G = 0.014$, $P = 0.9$; predator, $G = 0.60$, $P = 0.6$). Of the 60% small and 40% large individuals stocked into
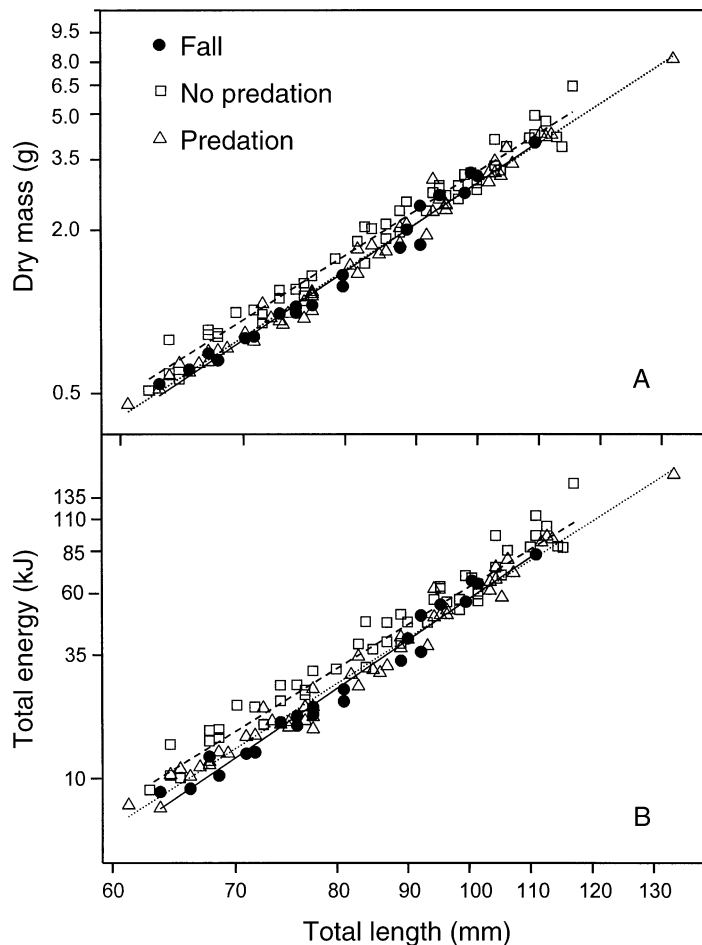
Fig. 5. Change in (A) dry mass and (B) total energy of age-0 largemouth bass as a log–log regression on fish length during the period from 1 November 2001 (fall; solid regression line) through 15 April 2002 in experimental ponds in which two adult largemouth bass predators were absent (No predation; 5 ponds; dashed line) or present (Predation; 5 ponds; dotted line). Regression and ANCOVA statistics are in Table 1.

ponds in fall, the same proportion was present in the spring in ponds with no predators; with predators, the percentage of small and large individuals was 59% and 41%, respectively. Although the relative percentage of sizes recovered did not change, mortality differed substantially between treatments, with abundances of small and large individuals declining by 9 and 8% without predators, but by 28 and 23% with predators (MAN-OVA treatment effect: Wilks' lambda = 0.27, $F_{2,7}$ = 9.28, P = 0.01).

Of the five predation treatment ponds, we retrieved both adult largemouth bass from all but one pond, in which only one adult was found. Across all ponds, wet mass change of adults was 5.7 ± 17% (N = 8 largemouth bass). A weighing error likely occurred for one individual, which was recorded to have lost 43% of its mass and thus was excluded from the mean. For the three ponds in which we retrieved both adults and were confident of the mass estimates, we estimated consumption with the bioenergetics model based on observed growth. Estimated combined consumption by the two adults in each pond during winter was 447 ± 9 g wet mass (N = 3 ponds). This consumption estimate was much higher than the estimated 192 ± 69 g (N =

3 ponds) of age-0 largemouth bass lost to mortality in each of the three ponds during winter.

DISCUSSION

At mid-temperate latitudes, ectotherms face energetic and behavioral challenges during winter that are similar to those of many endotherms (Bednekoff and Houston 1994, McNamara et al. 1994, Creswell 1998, Brodin 2000). Reaching fall sizes that ensure first-winter survival has often been the rationale for why rapid first-year growth is strongly selected in populations (Conover and Schultz 1995, Schultz et al. 1998). Although potentially valid at north-temperate latitudes, our research confirms that the influence of fall size on first-winter survival is highly conditional at lower latitudes. Because the energy demands of predators likely increase with warmer, more variable winters, winter interactions between predation and body size should intensify with declining latitude (Garvey et al. 2003a). At higher latitudes, biotic interactions may also be important when cold-active predators such as walleye or trout are abundant (Pratt and Fox 2002). Although size-dependent interactions certainly are not confined to winter (Olson 1996), seasonally declining production

TABLE 1. Results of linear regressions and ANCOVA for largemouth bass, including either $\log_e$-transformed dry mass (measured as grams) or total energy content (measured as joules) during fall 2001 and spring 2002 in ponds at Sam Parr Research Station, Illinois, USA.

Dependent variable and treatment	No. age-0 bass	Regression parameters		ANCOVA treatment effect		
		a	b	F	df	P
Dry mass						
No predator	50	1.07×10^{-6}	3.23	26.5	1, 69	0.0001
Predator	50	5.30×10^{-7}	3.36	0.46	1, 69	0.4
Start	22	4.00×10^{-7}	3.42			
Total energy						
No predator	50	1.74×10^{-2}	3.28	25.5	1, 69	0.0001
Predator	50	9.85×10^{-3}	3.38	2.75	1, 69	0.10
Start	22	3.93×10^{-3}	3.58			

Notes: Log$_e$-transformed length is the independent variable or covariate in each model. The form of each linear regression model is: dependent variable = $a \times$ length^b. All ANCOVA models compare either the no-predator or predator results to the fall (start) values. Fish in the fall (start) derive from a common subsample of largemouth bass released into ponds.

and relatively cool, suboptimal temperatures render winter particularly important to the early life history stages of fishes and likely other organisms with similar ontogenies (e.g., anurans, insects; Hurst and Conover 2003).

Some unexpected predictions about the interaction between body size and predation during winter emerged from the dynamic model and were supported experimentally. Small age-0 largemouth bass exposed to predation grew in length at the expense of risky foraging. Mortality was high but not size selective in ponds with predators. Although untested experimentally, the model predicted that size-selective patterns of mortality should only occur under specific combinations of predatory risk and system productivity, and that predation will create these patterns even when the predators are not directly gape limited or size selective. Below, we explore the modeling results relative to energy allocation and survival patterns, and then assess how they lend insight into mechanisms underlying patterns in ponds and in other systems.

Allocation and foraging decisions

General energy allocation and associated foraging strategies generated by the model depended on predation. Without predators, the model predicted that fat reserves should be maintained at some set point rather than maximized as predicted by other investigators (Post and Parkinson 2001). Foraging and energy accumulation only occurred in the model to offset expected deficits, maintain a positive energy balance, and ensure survival. In the experiment with predators absent, energy reserves increased during winter, which was more consistent with an energy maximization strategy. Thus, the model apparently failed to incorporate factors that elicit an energy maximization strategy in young fish without predators.

Regardless of the intensity or selectivity of predation in the model, with predators present, foraging by young

largemouth bass only occurred to offset energy costs; for small individuals, foraging also occurred to increase length, in order to avoid predation mortality. This expectation was supported experimentally. Because body length of small individuals increased with nonselective predation, it apparently does not have to be related to growing large to evade size-dependent (e.g., gape-limited) predators (Brönmark and Miner 1992). Rather, it may reduce mass-specific metabolic costs and increase fat reserve capacity (Downhower 1976), which should ultimately reduce the total time spent foraging and thus being consumed by predators. With size-selective predators, an increase in length should further reduce costs of foraging-induced predation (Christensen 1996).

Declining environmental predictability should increase the importance of adopting optimal energy allocation strategies for largemouth bass with or without predators. If the predictability of future ration, temperature, and predation declined in the model, a fat maximization strategy might best offset unanticipated future energy deficits and foraging-induced mortality (Post and Parkinson 2001, Bunnell and Marschall 2003), which is more congruent with experimental patterns. Individuals with uncertain futures should forage whenever net energy can be invested in fat to ensure the availability of adequate reserves during times of scarce energy returns and potentially high foraging costs.

Size-dependent survival

Our results indicate that the effect of first-year growth on winter survival and thus population dynamics should vary with winter conditions and biotic interactions at mid-temperate latitudes. Without predation in the model, mortality was higher for small fish when winter ration was limited, because small individuals exhausted reserves more rapidly (Post and Evans 1989, Sogard 1997, Schultz et al. 1998). Increasing ration during the modeled winter in the ab-

sence of predation reduced this size dependency, because all sizes of fish could forage and maintain their reserves, as has been demonstrated experimentally for this species (Garvey et al. 1998, Fullerton et al. 2000). Initial fall fat reserves were important, with fish with high reserves persisting with reduced rations.

The model revealed that predation may either create or mask size-dependent patterns of winter mortality. With nonselective predation, survival of fish in poor fall condition consuming a low ration was weakly related to size because all fish were forced to participate in risky foraging to offset energy deficits. Conversely, when fall condition was high, nonselective predators created size-dependent patterns of survival; small individuals with limited fat capacity still needed to forage and risk predation, while large counterparts did not. As ration increased, this size dependency declined because small individuals could reduce the frequency of foraging. Thus, size-selective winter mortality may occur under very different conditions than the low food or body condition typically expected if energy depletion was responsible (Ludsin and DeVries 1997). In contrast, if predators select small individuals preferentially, then size-dependent patterns of winter mortality should occur regardless of fall condition and ration. Clearly, it is very important that investigators understand the proximate and ultimate causes (i.e., predation or reserve depletion) of mortality during winter to understand population dynamics (Garvey et al. 1998).

How experimental survival results meshed with conditions and predictions of the dynamic model depended on the level of ration, condition, and predation in ponds. Bioenergetics modeling of age-0 largemouth in ponds without predators suggested that they were consuming food at ~60% of their maximum daily possible intake to achieve observed growth (J. E. Garvey, *unpublished data*). Energy content was high in fall across all sizes, implying that individuals started winter in good condition. Bioenergetics modeling of adults revealed that adults needed to consume twice the biomass of age-0 largemouth bass that died in ponds during winter to achieve their observed growth; hence, these predators likely consumed alternative prey (e.g., crayfish) in addition to age-0 largemouth bass. Vegetation and artificial shelters in ponds likely further reduced predatory risk and mortality (Miranda and Hubbard 1994*a*, Miranda and Pugh 1997). Densities of adult predators in ponds were realistic and perhaps low relative to natural systems.

Given that experimental ponds were productive with high invertebrate prey (Ostrand et al., *in press*), and that predatory mortality and perhaps risk was low to moderate, a similar scenario without size-selective predators within the dynamic model would generate no size-dependent mortality. If adult largemouth bass were size selective in ponds, mortality would have been higher for small individuals, which did not occur. With-

out directly quantifying overall foraging risk (e.g., varying predator density, alternative prey, or shelters), we can only speculate about specific mechanistic linkages between the model and experiment. Because surviving age-0 largemouth bass did not have a negative energy balance in spring, mortality was likely due to predation and not exhaustion of reserves, revealing that intercohort cannibalism during winter is an important factor affecting first-winter survival of age-0 fish (Johnson and Post 1996, Wahlstrom et al. 2000). This is congruent with the model demonstrating that energy needs demand active foraging; mortality with predators is a consequence of foraging-induced predation and not starvation.

Other adaptations

Although the dynamic model appears to have captured some of the important decisions maximizing winter survival, other unexplored trade-offs likely exist. The model did not incorporate a future reproductive benefit to growing in somatic growth, although enhanced growth rates should facilitate early maturation (Garvey and Marschall 2003). Additionally, individuals may have the flexibility to reduce winter metabolism (Wright et al. 1999, Slaughter et al. 2004), although reduced activity and diminished growth capacity under variable environmental conditions may offset the benefit of reducing metabolism (Evans 1990, Schmidt-Nielsen 1997). Although the model explored how winter foraging influenced energy intake and predation risk, it failed to incorporate the energy costs of remaining active and foraging (Micucci et al. 2003). Further, the physical process of consuming food and shunting energy to digestion may impair predator avoidance behavior (Billerbeck et al. 2001, Lankford et al. 2001). These unexplored potential trade-offs should further resolve our understanding of behavioral and growth dynamics during winter.

Significance

Experimental results confirmed predictions by the dynamic model that age-0 largemouth bass, like many organisms, possess a broad foraging reaction norm that responds to predation risk (Lima and Dill 1990). This phenotypic plasticity in behavior and perhaps other physiological pathways offset costs incurred during times of environmental stress with predators. Although winter is assumed to be a period of inactivity, winters at low latitudes may pose particular challenges to young ectotherms. Conditions that tax energy reserves but lead to poor net growth mandate critical energetic and behavioral decisions. These dynamic decisions should be particularly important when winter is a critical ontogenetic period, ultimately affecting the contribution of cohorts of fish and other organisms to populations.

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