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Comparative Temperature-Dependent Growth Rates of Largemouth and Smallmouth Bass Fry[1,2]

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Abstract

First-month growth was temperature-dependent for fry of largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieui* that were raised simultaneously under identical conditions. Similar temperatures (25–27 C) produced the fastest growth rates in both species, although largemouth bass grew most rapidly at the higher end of this range. Largemouth bass generally grew faster than smallmouth bass, particularly in the 25 to 30 C range (average 1.4 times). Variance about the mean standard length increased at higher temperatures. Differing temperature-dependent growth rates and size distributions for the two species may influence their relative abilities to survive predation and to form strong year classes in temperature regimes that differ due to latitude or weather.

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Production and survival of juvenile fishes determine densities of adult populations. Kramer and Smith (1960) concluded that year-class strength of largemouth bass is established within the first 2 weeks of life. Differences in early growth rates between two closely related species, particularly as these rates vary with environmental factors such as temperature, may influence their relative year-class strengths and may determine which species ultimately dominates within a particular water body.

In this study, we tested the hypothesis that there are inherent differences in growth rates of fry of largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieui,* and that these differences are influenced by environmental temperature. These closely related species show a latitudinal gradient of numerical abundance (smallmouth bass dominate in northern latitudes) and they show annual variations in relative year-class strengths in midlatitudes. Power-station thermal effluents also appear to favor largemouth bass (Stroud and Clepper 1975). Although data exist on temperature-dependent growth rates for juvenile largemouth and smallmouth bass (see reviews by Coutant 1975; Shuter et al. 1980), the studies involved different sizes of fish and experimental procedures or timing. Growth rates in the laboratory for young-of-the-year and yearlings of largemouth bass and smallmouth bass appear optimal between 25 and 29 C.

We experimentally obtained growth rates and size dispersions of newly emerged largemouth and smallmouth bass fry under nearly identical holding and feeding conditions over a range of constant temperatures. Some results for smallmouth bass that led to a model for growth and size dispersion were reported previously (DeAngelis and Coutant 1979). The model provided an initial theoretical framework for evaluating differences in experimental results for the two species.

Young-of-the-year fish are highly susceptible to predation and cannibalism by larger fish. Size variations within or among cohabiting predator species result in the smaller fish becoming prey and the larger fish surviving (Cooper 1937; Murphy 1949; Tarrant 1960; Wright 1970; Snow 1971). Cooper (1937) found that cannibalism among age-0 largemouth bass in ponds occurred when the larger fish exceeded the length of the smaller by a factor of 1.6. Factors that encourage size differences thus stimulate both intraspecific and interspecific predation and accentuate differences in survival proba-

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bilities for faster and slower growing individuals.

Methods

Largemouth bass fry were obtained from 0.1-hectare rearing ponds at our laboratory. The ponds were stocked in early April with adults collected from Fort Loudoun Reservoir (Tennessee River). Swim-up fry were collected in the last week of April and moved to laboratory holding tanks at the pond's ambient temperature, 17 C. Smallmouth bass fry were obtained from the Cohutta (Georgia) National Fish Hatchery shortly after swim-up and similarly held in the laboratory. Both stocks were divided into groups of 20 each and their temperatures were gradually changed (about 2 C/day) to the test temperatures, nominally 15, 20, 23, and 25–32 C (at one-degree intervals) (Table 1). Largemouth bass also were tested at 33 and 34 C. The test of smallmouth bass at 25 C was aborted because of excessive early mortality.

Rearing was conducted in polyethylene cages, 16 cm in diameter and 13.5 cm deep, floated in 1.22-m-diameter fiberglass tanks. The cages were constructed from commercial wash tubs in which four 5-cm-square windows were cut and covered with nylon screening. Water depth in each floating cage was about 10 cm. The tanks, each of which held one cage for largemouth bass and one for smallmouth bass, received about 0.25 liter/second of temperature-controlled well water. Cage temperatures varied slightly from tank temperatures; average temperatures of cages (±SD) over the study period were used for reporting results (Table 1). Largemouth and smallmouth bass cages were always within 0.15 C of each other.

Fish were fed ad libitum on mixed zooplankton obtained from the laboratory's secondary sewage oxidation pond. *Daphnia* species predominated, but other small invertebrates were available as well. This food is typical of that normally utilized by bass fry in nature. Fresh zooplankton was added to each cage twice daily in sufficient quantity to assure the presence of live plankters at all times.

Fish lengths were determined photographically at twice-weekly intervals, generally at least four times (exceptions were the largemouth bass at the two highest temperatures, which were photographed only three times). All fish from each cage were transferred to a 14.5-cm-diameter glass dish underlain by a centimeter rule and containing just enough water to cover the fish; after being photographed they were returned to the experimental cages. Standard lengths later were obtained from the photographs by use of dividers and the included centimeter scale. Because some fish moved during exposure, length samples usually represented fewer than the 20 fish initially stocked (but generally 15 or more). Length data were summarized by mean, standard deviation, and variance for each photographic session. These data were used to parameterize and evaluate the equation that was used to describe growth of a cohort of young fish (equation 8 of DeAngelis and Coutant 1979):

$$f_s(L,t) = (2N_{0,s}/b_s t\pi^{\frac{1}{2}}) \cdot \exp[-(L - V_s t - L_{0,s})^2/b_s{}^2 t^2], \qquad (1)$$

where $f_s(L,t)$ is the distribution of lengths (L) as a function of time (t), $N_{0,s}$ is the total number of fish in the group, V_s is the average growth rate as mm/day, $L_{0,s}$ is the initial length of the cohort, and b_s is the slope of the regression of variance over time.

The chi-square statistical test was used on experimental data to evaluate whether or not temperature treatments influenced growth rates within a species. A paired t-test evaluated the difference between species in their growth responses to temperature.

Results

Average growth of all groups of both largemouth and smallmouth bass fry was linear over the approximately 3-week experimental period (Table 1). Rates of growth, that is, slopes of linear regressions for each group in Table 1, differed significantly across the range of temperatures tested for each species ($P < 0.001$). These average growth rates were generally low at 15.2 and 20.1 C, high in the mid-temperature range, and low again at high temperatures (Fig. 1). Smallmouth bass growth data for 29.3 C were unreliable due to heavy mortality after May 20.

Largemouth bass exhibited significantly higher ($P < 0.01$) average rates of growth than smallmouth bass over the range of temperatures studied (Fig. 1). Exceptions to the general trend were at 15.2 C (where it was less) and at 25.6 C and 32.5 C (where it was the same). The largemouth bass fry at 25.6 C and 32.5 C, and

TABLE 1.—*Average standard lengths/standard deviation (mm) of largemouth and smallmouth bass groups held at constant temperatures/standard deviation (C) and measured on dates in May 1976. Group sizes were 20–22 fry at the start and average lengths are based on 7–22 fish. Growth rate of each group is indicated by slope (b) of the linear regression, for which an r^2 value is given; σ^2 is the final variance in length. Fry gradually were raised to test temperatures beginning on April 30 (largemouth bass) or May 5 (smallmouth bass).*

May dates	Constant temperature (C)/SD						
	15.2/0.0	20.1/0.1	23.2/0.2	24.9/0.2	25.6/0.1	26.3/0.1	27.3/0.1
			Largemouth bass				
4		12.6/1.1	12.4/1.1	11.9/1.2	12.9/1.7	12.3/1.6	12.4/1.4
6	10.4/1.2						
7		14.6/1.2	15.1/1.8	14.8/1.6	16.4/1.7	15.3/1.4	16.6/1.1
11	11.8/1.1	17.0/1.5	18.3/1.6	18.4/1.4	18.9/1.4	18.2/1.6	21.4/1.5
14	12.1/1.2	18.7/1.3	21.6/1.5	22.5/1.4	21.9/1.6	20.3/1.6	24.1/2.0
17							
18	12.8/1.6	20.6/1.5	25.7/2.0	25.4/1.2	24.4/1.9	22.7/2.0	27.9/2.2
21							
25							
b	0.19	0.57	0.94	0.99	0.81	0.73	1.10
r^2	0.30	0.81	0.90	0.92	0.85	0.83	0.91
σ^2	2.69	2.40	3.82	1.54	3.67	3.84	4.94
			Smallmouth bass				
5	10.1/1.1						
6		11.6/1.1	11.3/1.0				
7					11.2/0.9		
10						13.5/1.0	13.2/1.5
11	11.6/1.0	13.4/1.3	14.7/1.3		15.4/1.0		
12							
13							
14	12.2/0.7	15.3/1.5	17.7/1.4		17.5/1.3	17.1/1.7	16.8/2.2
17							
18	13.5/1.1	16.5/1.7	20.1/1.7		20.4/2.3	19.6/1.4	19.2/2.5
21	13.7/0.7	18.0/1.9	22.6/1.9		24.2/2.5	20.9/2.4	22.3/2.8
25	14.4/1.4	19.1/2.1	24.6/2.3		25.7/3.1	22.7/2.4	23.0/3.0
b	0.22	0.41	0.72		0.82	0.59	0.67
r^2	0.66	0.73	0.88		0.85	0.72	0.68
σ^2	1.93	4.40	5.31		9.76	5.83	9.13

both largemouth and smallmouth bass fry at 26.3 C, showed growth rates that were depressed from the trend exhibited by other groups. The temperature of maximal growth rate was slightly higher for largemouth (about 27 C) than for smallmouth (about 25–26 C), based on a visual interpretation of data trends made with knowledge of the general unimodal shape of temperature-growth curves for fish, which, in turn, is based on bioenergetic physiological information (for example, Brett et al. 1969; Cox and Coutant 1981). Statistical curve-fitting (polynomial regressions), which has no physiological basis, did not improve resolution over merely drawing the curves among the highest points. Parabolic fits indicated apexes at 24.8 C (smallmouth bass) and 25.3 C (largemouth bass). When apparent peak average growth rates for each species are compared, largemouth bass grew 1.3 times as fast as smallmouth bass. At the temperature of peak growth rate for largemouth bass, this species grew 1.5

TABLE 1.—*Extended.*

May dates	Constant temperature (C)/SD						
	28.5/0.1	29.3/0.1	31.1/0.1	31.9/0.1	32.5/0.2	34.7/0.1	35.5/0.2
			Largemouth bass				
4	12.5/1.8						
6							
7	16.6/1.3	15.0/2.3	12.7/1.1				
11	20.0/1.8	17.7/2.3	13.3/2.0				
14	22.8/2.0	20.4/2.4	15.8/1.2	12.3/1.0			
17					23.7/1.3		
18	25.2/1.4	24.1/2.7	18.6/1.5	14.3/0.9	24.0/1.4	25.0/2.7	28.1/2.1
21				16.0/1.3	25.5/0.8	26.9/2.6	28.9/1.8
25				18.8/1.1	26.4/1.8	27.0/2.6	29.4/2.2
b	0.90	0.83	0.57	0.59	0.35	0.28	0.18
r^2	0.87	0.66	0.68	0.82	0.40	0.09	0.06
σ^2	2.03	7.18	2.16	1.30	3.26	6.75	4.89
			Smallmouth bass				
5							
6							
7							
10							
11	13.6/1.2						
12		13.6/1.6					
13			17.5/2.3				
14	17.6/1.2	16.1/1.1		19.4/1.6			
17					18.9/1.2		
18	19.1/1.8	19.6/2.9	19.7/2.7	20.4/2.5	19.3/1.5		
21	21.2/1.9	22.3/3.1	21.5/3.1	21.9/2.6	20.6/2.1		
25	23.2/2.2	24.8/3.7	22.9/2.6	23.2/2.6	21.7/2.3		
b	0.64	0.88	0.46	0.35	0.35		
r^2	0.76	0.71	0.29	0.29	0.27		
σ^2	4.74	13.61	14.89	6.89	5.51		

times as fast as smallmouth bass, for smallmouth bass growth at that temperature had fallen below maximum. Over the temperature range of fastest growth for both species, about 23–30 C, largemouth bass grew an average of 1.3 times as fast as smallmouth bass. The temperature range yielding the largest growth rate differential was about 25–30 C (average 1.4 times).

Variance about the mean standard length increased through time as each group grew, as was previously summarized for the smallmouth bass groups (DeAngelis and Coutant 1979). This increase in variance was temperature-dependent for smallmouth bass and less so for largemouth bass, based on simple linear regression of final variances (Fig. 2). The r^2 values were low (0.32 and 0.20, respectively), however, indicating a highly variable response. There is a weak suggestion that variance for smallmouth bass was greatest at temperatures near 30 C, which was above optimum temperature but was

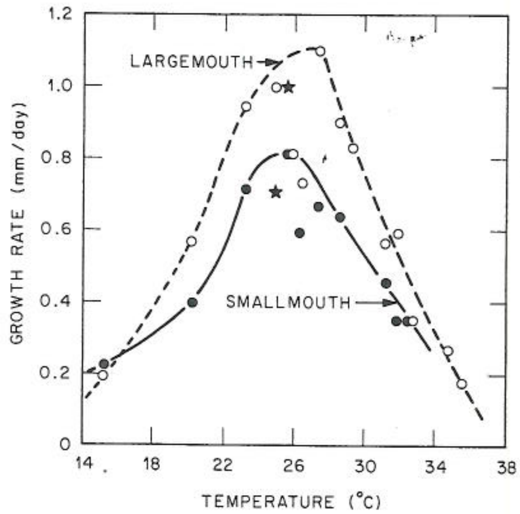

FIGURE 1.—*Average growth rates of largemouth and smallmouth bass fry smaller than 30 mm standard length over a range of constant temperatures in the laboratory. Curves are visual interpretations of the major trends which account for depressed growth in some groups. Stars indicate apexes of parabolic-curve fits (not shown) of all data for each species.*

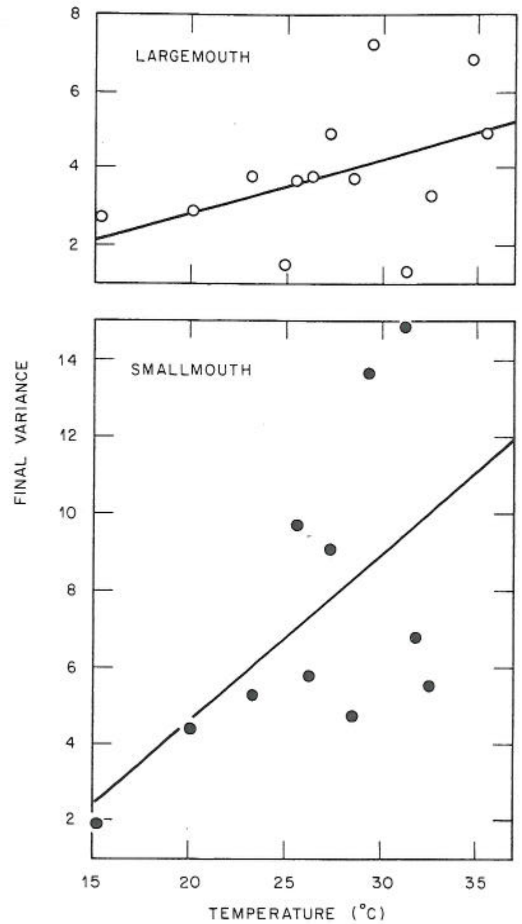

FIGURE 2.—*Temperature (T) effect on variance (σ^2) about the average size of largemouth and smallmouth bass at the end of a 3 week growth period. Lines are simple linear regressions. Largemouth bass: $\sigma^2 = -0.089 + 0.138T$; $r^2 = 0.20$. Smallmouth bass: $\sigma^2 = -3.900 + 0.429T$; $r^2 = 0.32$.*

not the highest tested. When the two highest temperatures were deleted from the smallmouth regression, the r^2 rose to 0.62. Despite the wide variance within some test groups, we observed no cannibalism.

Discussion

Our data support the hypotheses of inherent differences in average growth rates between smallmouth and largemouth bass and of a temperature dependence of some of those differences. The physiological and feeding responses of these young fish to temperature are more complex than simple statistical curve-fitting can elucidate. We have, therefore, used judgement in interpreting the data trends, based on physiological knowledge and our own atempts to develop general growth models. Although young fish in nature do not live under constant-temperature conditions, these results indicate the incremental growth rates that might be experienced under normally fluctuating temperatures (Cox 1978).

Some of the differences in growth rate seem clearly unrelated to temperature. Largemouth bass grew faster than smallmouth bass through most of the temperature range studied. This observation agrees with abundant field data that show the average largemouth bass to grow faster and to be larger at any given age than the average smallmouth bass (however, field data include the effects of size-selective mortality on average size). We feel that our data help quantify this inherently greater growth potential of largemouth bass and show that the difference is manifested within the first month.

Although less definitive, we believe our data also show somewhat different responses by the two species to temperature. Growth rate in both species generally follows the unimodal pattern that is typical of growth rate versus temperature in fish that have been studied (Brett 1970). By drawing the curves smoothly through the highest points for each species we estimate the maximum potential growth rate at each temperature, unencumbered by experimental vagaries or artifacts of statistical curve-fitting when data are necessarily limited in number. We interpret the resulting curves to show (1) a difference in temperature of maximal growth rate of slightly more than one degree (C), (2) little difference or a slight growth rate advantage for smallmouth bass at temperatures close to spawning temperatures (about 15 C), and (3) maximum difference in the "inherently greater growth potential" of largemouth bass in the 25–30 C range.

If these differences between the species in growth rate versus temperature are real, then latitudinal and weather-related year-to-year temperature differences during the first month may contribute to determining a species' numerical dominance. There is a rapid coupling of air temperature with water temperature in shallow habitats inhabited by bass fry. Shuter et al. (1980) found much better correlations between air temperatures and smallmouth bass growth in Baie du Dore, Ontario than they did between growth and water temperatures recorded in the main water body. Littoral-zone temperatures greater than 25 C are not uncommon on sunny days in Tennessee in the first month after bass spawning. By applying the average growth rates at various temperatures (Fig. 1) to contrasting scenarios of fluctuating spring temperatures, one can visualize a varying disparity in growth for the two species. In cool years, growth rates would remain similar, whereas in warm years, the average largemouth bass would have a distinct growth-rate advantage. As noted in the introduction, a growth advantage may be translated to a survival advantage through decreased susceptibility to predation.

The growth-rate differences discussed so far are differences in the average growth rates of fish in the smallmouth and largemouth bass cohorts. Growth rate actually varies from individual to individual within cohorts, with the result that there are size distributions within cohorts. Moreover, these size distributions can change through time. As DeAngelis and Coutant (1979) indicate, the variance of the size distribution about the mean generally increases as the square of time. We show here that the size distributions also differ with increasing temperature. The relationship is probably more complex than the linear plots we present in Fig. 2.

We have attempted to use the model of DeAngelis and Coutant (1979) to explicitly characterize the changes of variance with both time and temperature. In DeAngelis and Coutant (1979) we made tentative inferences about b as a function of temperature. We did so, not by comparing final variances, but by fitting individual curves of variances versus time (see Fig. 3 of that paper). In the present paper, final variance as a whole, $\sigma_L^2 = b_s^2 t^2$, is plotted versus temperature, showing a clear positive correlation. Trends in b for all data from both species were less distinct. One value of using the present model as a conceptual guide was the realization that our assumptions about change in growth-rate variance with the magnitude of growth rate needed additional testing, both theoretical and empirical. We have examined several relationships, some based on existing physiological models, but they will not be presented here.

The effects of an increase in variance coincident with increased disparity of average size can be dramatic. Wide differences in theoretical susceptibility to predation are generated between the smallest of the slower-growing species and the largest of the faster-growing one. Some early attempts to use these data to simulate the predatory responses between largemouth and smallmouth bass under different temperature–growth regimes were presented by Coutant et al. (1979). A more realistic scenario would involve the relative vulnerability of each of these species to other predators.

The growth-rate differences shown in this experiment fall in a pattern that relates well to known distribution patterns for largemouth and smallmouth bass (Stroud and Clepper 1975). The northern latitudes where smallmouth bass predominate rarely have midsummer water temperatures that exceed 26 C. Spring temperatures during early juvenile growth are less than 25 C, as shown by Shuter et al. (1980) for Lake Opeongo and Baie du Dore, Ontario, even in the shallows. In midlatitudes of North America, smallmouth bass predominate in cooler waters, although this species survives and grows well as far south as the Tennessee River valley (Hubert and Lackey 1980; Wrenn 1980). No rigorous analysis of relative year-class strengths of largemouth or smallmouth bass versus water temperature has been conducted in midlatitude zones, even though temperature has been shown to be a strong determinant of year-class strength where smallmouth bass occur alone in Canada (Shuter et al. 1980). In that study, warmer-than-normal temperatures for Ontario favor enhanced growth and survival.

If largemouth bass are superior to smallmouth bass at reducing vulnerability to predation by growing faster at warmer temperatures in midsouthern North America, why do smallmouth bass populations continue there? Whereas we believe that temperature has an important and definable influence on relative abundances (we have not considered here other aspects such as low winter temperatures), other factors such as food supply, space limitations, and substrate or light preferences often may have a greater influence on growth and survival. The relative wealth of information on largemouth and smallmouth bass, particularly that contained in Stroud and Clepper (1975), suggests that temperature may not usually be a primary factor in determining the relative abundance of these species under sympatric conditions. Because of distinctly different habitat selection (Jenkins 1975; Miller 1975), there is probably little direct interspecific interaction between the two species at a young age and it is unlikely that largemouth bass would prey directly on smallmouth bass to any significant extent regardless of size–growth differences. Both species are actively preyed upon by other fishes, however, and those interactions may convert the different physiological responses to temperature into differential mortality. Predation often is one of the most important factors that determine year-class abundances, and a thorough understanding of all factors that influence it is desirable. Smallmouth bass also are known to reduce predation on fry by having males guard schools (containing fry up to 26 mm) for up to 4 weeks (Vogele 1981).

Another mechanism for increasing population survival of smallmouth bass may lie in the greater growth-rate variance generated within cohorts grown at higher temperatures. Temperatures above optimum for average growth of smallmouth bass, and within the range of superior average growth performance by largemouth bass, appear to induce an acceleration of growth by a few smallmouth bass individuals. Our largemouth bass fry showed less increase in variance at high temperature. The result could be a few rapidly growing smallmouth bass that may escape the general predation upon their cohort. Further studies of size-related dynamics of interacting populations clearly are needed.

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