Relationships Between Diet and Growth of Age-0 Largemouth Bass in a Kentucky Lake Embayment

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Abstract: Diet and growth of the 1993 year-class of age-0 largemouth bass were determined in Ledbetter Embayment of Kentucky Lake. Diet was analyzed to determine the relationship between diet quality and the resulting size structure of the cohort. Length-weight and head capsule-weight regressions were used to estimate the dry weight of prey items in the diet. Largemouth bass were divided into 2 size classes (large and small) based on the mean length for each sampling date. Growth rates were calculated for both classes and compared with piecewise linear regression of total length on day of the year with the use of an additional dummy variable. There was a pivotal period in mid-July when there was a divergence in growth rates. The growth rate of small age-0 fish slowed dramatically, while the growth of large age-0 largemouth bass increased. During this period the large age-0 largemouth bass were consuming more prey fishes and fewer insects and zooplankton by weight than were small age-0 largemouth bass. After July, small age-0 largemouth bass consumed 2.5 times more prey items and prey of much smaller size than large fish. Early in life, the condition of small age-0 largemouth bass was significantly higher, resulting in the conclusion that small age-0 largemouth bass were possibly allocating more assimilated energy towards growth in weight, while large fish were assimilating more energy towards growth in length. The variation in growth observed within the cohort resulted in a multi-modal length-frequency distribution by the end of the summer.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 55:175–193

Black bass species, which include largemouth bass *(Micropterus salmoides)*, are the most popular sport fish in Kentucky (U.S. Dep. Int. 1997*a*) and throughout the United States (U.S. Dep. Int. 1997*b*). Information on the ecology and population dynamics of largemouth bass is essential to the successful management of the species. For example, the number of largemouth bass surviving at the end of the first growing season has been generally assumed to be the best indicator of year-class strength (Kramer and Smith 1960). First-year growth rates of individual fish also play a role in determining the survivorship of the year-class. Several authors have

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noted size selective winter mortality of smaller members of age-0 largemouth bass cohorts (Aggus and Elliott 1975, Shelton et al. 1979, Toneys and Coble 1979, Miranda and Hubbard 1994). Assuming the cessation of growth during winter with continuing mortality, Gutreuter and Anderson (1985) modeled subsequent recruitment of age-0 largemouth bass. A bimodal distribution with 25% of the fish over 130 mm yielded almost 5 times more recruits than a unimodal distribution with all fish less than 80 mm. Thus the length distribution at the end of the initial growing season, rather than simply the mean total length, determined year-class strength.

Differential growth of age-0 largemouth bass has been well documented. Factors causing differential growth include disrupted (Summerfelt 1975) or extended spawning seasons (Goodgame and Miranda 1993), differences in diet related to prey availability (Aggus and Elliott 1975, Shelton et al. 1979, Timmons et al. 1980, Keast and Eadie 1985), and combinations of factors (Pasch 1975, Miller and Storck 1984, Maceina and Isely 1986). A lengthy spawning season, interrupted or not, results in a length advantage for earlier hatched members of a cohort. The length advantage allows those individuals to make the ontogenetic diet shift to piscivory earlier and maintain a size advantage over their prey (Olson 1996, Ludsin and DeVries 1997). The size advantage enables the larger individuals to consume fishes throughout the growing season resulting in faster growth rates because fish prey are of a higher caloric value than invertebrates as prey (Cummins and Wuycheck 1971, Keast and Eadie 1985). There is a time threshold where, if smaller age-0 largemouth bass cannot begin a piscivorous diet, they are often outgrown by prey fishes and must use other, lower quality food resources much or all of their first growing season, which may result in slower growth. So, the initial length advantage of earlier hatched age-0 largemouth bass in a cohort is amplified to produce a bimodal, multimodal, or skewed length distribution by the completion of first year growth.

Timmons et al. (1980) observed the occurrence of a bimodal length distribution arising from an initially unimodal distribution of age-0 largemouth bass in West Point Lake (Ala.-Ga.). They attributed the phenomenon to a shortage of prey for small, slow-growing members of the cohort. Spawning was continuous over a 2-month period, although the lengthy spawning season allowed first-hatched fish a length advantage over later-hatched fish.

Through the use of a mathematical model and the data of Timmons et al. (1980), DeAngelis and Coutant (1982) corroborated the hypothesis that size-dependent prey availability was responsible for variable growth within age-0 largemouth bass cohorts. They took into consideration the data on prey availability to adjust growth rates for smaller largemouth bass as the growing season progressed. Using the unimodal initial size distribution of Timmons et al. (1980), the model predicted a bimodal size distribution 4 months later, which was very similar to the actual data reported by the authors.

Keast and Eadie (1985) also observed growth depensation in an age-0 largemouth bass population that initially had a unimodal distribution. The spawning season lasted less than a month and resulted in only an 11-mm length differential of age-0 largemouth bass immediately after the spawning season. Even with this narrow size disparity early in the growing season, some members of the cohort were able to grow fast enough to continue to feed on fishes while prey fishes outgrew others.

First year growth and resulting length frequency distributions are important factors influencing year class strength in largemouth bass populations. The size structure of an age-0 cohort is regulated by largemouth bass diet. Defining these interactions might allow fishery managers more flexibility to modulate weak year classes such as with remedial stockings of largemouth bass or prey fish species.

The objectives of the current research were to 1.) examine the growth of the age-0 largemouth bass cohort spawned in Ledbetter Embayment of Kentucky Lake in 1993, 2.) determine the diet of age-0 largemouth bass, and 3.) determine how diet affected the resulting size structure of the cohort.

We wish to thank the students and staff at the Hancock Biological Station for assistance in the field and in the lab. K. Fairbanks provided advice on statistical analyses. C. Woods assisted with the production of graphs and high quality slides for the presentation of this manuscript. We are grateful to T. Forsythe and D. White for reviewing earlier drafts and to 3 anonymous reviewers for their suggestions for improving this manuscript. This represents contribution number 70 from the Center for Reservoir Research at Murray State University.

Methods

Study Area

Kentucky Lake, located in western Kentucky and Tennessee, is the lowermost reservoir on the Tennessee River. The reservoir was formed with the completion of Kentucky Dam at Tennessee River mile (TRM) 22 in 1944. Surface area is approximately 64,800 ha, with 21,000 ha within Kentucky and 43,800 ha within Tennessee. Kentucky Lake is a eutrophic, moderately turbid reservoir with Secchi depths normally ranging from 0.5 to 1.2 m.

Sampling for age-0 largemouth bass was confined to the littoral areas in the back of Ledbetter Embayment. This embayment is located in the Kentucky portion of the reservoir just south of the U.S. Highway 68-80 bridge at approximately TRM 42.5. The littoral zone at summer pool contained scattered areas of both emergent and submergent vegetation. The sampling area was characterized by 2 emergent plants, water willow *(Justicia americana)* and button bush *(Cephalanthus occidentalis)*, and the submerged Eurasian water milfoil *(Myriophyllum spicatum).*

Fish Collection and Diet Analysis

Age-0 largemouth bass were collected weekly beginning on 19 May 1993 and ending on 9 September 1993. Fish were initially collected using a 15.2-m bag seine with 3.2-mm mesh. Later in the summer, to minimize the chance of larger fish avoiding the gear, a 15.2-m bag seine with 6.4-mm mesh was used to collect fish. The larger mesh collected less debris, thereby reducing drag and allowing the seine to be pulled at a more rapid pace. Seining was conducted during mid-afternoon in and around patches of aquatic vegetation.

Table 1. List of taxa found in the diet of age-0 largemouth bass. Asterisks denote lowest taxa to which organisms were identified. Major headings are the 5 major prey categories used for diet analysis.

Fish

- Clupeidae
    - *Dorosoma**
- Hiodontidae*
- Cyprinidae*
- Poeciliidae
    - *Gambusia affinis**
- Atherinidae
    - *Labidesthes sicculus**
- Centrarchidae
    - *Lepomis**
    - *Micropterus**
- Percidae
    - *Perca flavescens**
- Unidentified fish*

Insect

- Collembola*
- Ephemeroptera
    - Baetidae naiad*
    - Caenidae naiad*
    - Ephemeridae
        - *Hexagenia* naiad*
- Odonata
    - Anisoptera adult*
    - Anisoptera naiad*
    - Zygoptera adult*
    - Zygoptera naiad*
- Hemiptera
    - Corixidae*
    - Gerridae*
    - Naucoridae*
- Trichoptera
    - Hydroptilidae larvae*
- Coleoptera larvae*
- Diptera adult*
    - Ceratopogonidae larvae*
    - Chironomidae larvae*
    - Chironomidae pupae*

Malacostraca

- Amphipoda*
- Isopoda*
- Mysidacea
    - *Taphromysis louisianae**

Zooplankton

- Rotifera
    - Brachionidae
        - *Brachionus**
        - *Keratella**
    - Lecanidae
        - *Lecane**
    - Synchaetidae
        - *Ploesoma**
    - Trichocercidae
        - *Trichocerca**
- Cladocera
    - Sididae
        - *Diaphanosoma**
        - *Latona**
        - *Sida**
    - Chydoridae
        - *Alona**
        - *Camptocercus**
        - *Chydorus**
        - *Eurycercus**
        - *Leydigia**
        - *Pleuroxus**
    - Daphniidae
        - *Ceriodaphnia**
        - *Daphnia**
        - *Daphnia lumholtzi**
        - *Simocephalus**
    - Bosminidae
        - *Bosmina**
    - Leptodoridae
        - *Leptodora kindti**
- Copepoda
    - Calanoid*
    - Cyclopoid*
    - Harpacticoid*
    - Nauplii*

Miscellaneous

- Acari*
- *Argulus** (fish lice)
- Terrestrial oligochaete* (earthworm)
- Hylidae* (tree frog)
- Oligochaeta*
- Ostracoda*
- Araneae* (spider)

Largemouth bass were immediately preserved in 10% formalin and later washed with several changes of water and stored in 45% isopropyl alcohol. The fish were measured to the nearest millimeter in total length (TL), blotted dry, and weighed. Specimens under 1 g were weighed to the nearest mg; larger fish were weighed to the nearest 0.01 g. Larger bass of questionable age were confirmed as age-0 fish by examination of scales.

The esophagus and stomach were removed from age-0 largemouth bass for diet analysis. Stomach contents were viewed under a dissecting scope, enumerated, identified, and measured using an ocular micrometer. The stomach contents were grouped into 5 higher taxonomic categories for diet comparisons (Table 1). Prey fishes were identified to genus except for the cyprinids and a single specimen in the family Hiodontidae. Fishes unidentifiable because of digestion were assigned as unidentified fish. Insects were generally identified to family. Rotifers and cladocerans were identified to genus. Copepods were identified as calanoid, cyclopoid, harpacticoid, or nauplii. Organisms in the Malacostraca and miscellaneous categories were identified to various levels. Measurements were fitted to weight-length or weight-head capsule regressions to estimate dry weight of each item. Prey dry weight regressions (available from the authors) were obtained either from the literature (Dumont et al. 1975; Rogers et al. 1976, 1977; Rosen 1981; Smock 1980) or calculated in the laboratory using specimens from stomachs or specimens taken directly from Kentucky Lake. The organisms were measured, dried at a temperature of 80 C to a constant weight, desiccated, and then weighed. Dry weight was then regressed on length or head capsule width to determine the slope and intercept values. The dry weight of some stomach items was determined directly. Dry weights of some prey categories were estimated using regressions from taxonomically related species and species with similar body shape. Each prey category was reported as percent composition by number, percent composition by weight, and percent frequency of occurrence in the diet.

Size Class Differences in Growth and Diet

To investigate differences in diet that may affect growth, each largemouth bass sample collected after May was separated into 2 size classes as suggested by Keast and Eadie (1985). Age-0 largemouth bass greater than the mean length for a sample were assigned to the "large" size class and those smaller than the mean length were assigned to the "small" size class. Two early samples (19 and 25 May) were excluded from this analysis because of the narrow length range of age-0 largemouth bass present in those early samples.

Growth rates of the 2 size classes were calculated during 2 periods of the growing season with piecewise linear regression (Mendenhall and Sincich 1996). The regression fits 2 lines to the data of possibly different slopes joined at the point of interest. The model, with an additional dummy variable, allows the comparison of growth rates between periods and within each period between the 2 size classes of age-0 largemouth bass. The piecewise linear regression of total length on day of the year was for the periods of 19 May to 26 July and 26 July to 9 September. The dummy variable, Q, was equal to 1 for large fish and 0 for small fish. The dummy variable, Z, was equal to 0 if day of the year $< t^*$ and 1 if day of the year $\geq t^*$, where $t^* = 73$ = 26 July (day of the year was corrected for graphing purposes, setting 14 May equal to day of the year of 0). The piecewise linear regression model has the following form

$$L = \beta_0 + \beta_1 D + \beta_2 D^* + \beta_3 Q + \beta_4 QD + \beta_5 QD^*$$

where L = total length (mm), D = day of the year, $D^* = Z(D - 73)$, Q = dummy variable for size, QD = crossproduct of Q and D, and QD* = crossproduct of Q and D*.

Size class differences in diet were determined by comparing percent composition by number, percent composition by weight, and percent frequency of occurrence between small and large fish for each sample. Initially, differences in the percent composition by number between the 2 size classes for all prey categories together were determined using the Fisher exact test (Mehta and Patel 1983). If the test was significant, prey categories were tested individually for significant differences between size classes with the Fisher exact test. A multivariate analysis of variance (MANOVA) was used to test differences in diet described by percent composition by weight for all prey categories together. The test used was Wilk's Lambda *F*-test, which is equivalent to Hotteling's T^2 test (Johnson and Wichern 1982). If the test was significant, size classes were compared for individual prey categories with a univariate analysis of variance (ANOVA). Size class differences in the frequency of occurrence of each prey category were tested individually using the Fisher exact test.

The slope of a $\log_{10}$ transformed length-weight regression equation can give an index of body condition or plumpness. The condition of small and large size classes of age-0 largemouth bass over all sampling dates was compared using a length-weight regression incorporating size class as a dummy variable. The equation is expressed as follows:

$$\log_{10}W = \beta_0 + \beta_1 \log_{10}L + \beta_2 Q + \beta_3 QL$$

where W = weight (g), L =total length (mm), Q = dummy variable for size, QL = crossproduct of Q and L. All statistical tests were designated significant at ($\alpha = 0.05$ unless otherwise noted. Statistical analyses were performed using SAS software (SAS Inst. 1985).

Results

Growth

There was a single cohort of largemouth bass spawned in Ledbetter Embayment in late April/early May 1993. Water temperature steadily increased with no extended periods of cold weather that would disrupt spawning activities. Early samples showed both the mean total length and the minimum total length continued to increase at a steady rate (Fig. 1) and the length-frequency was normally distributed (Fig. 2), indicating there was no recruitment from a later spawning event. The narrow range of lengths found in the 19 and 25 May samples supported the conclusion of a single spawning period of short duration.

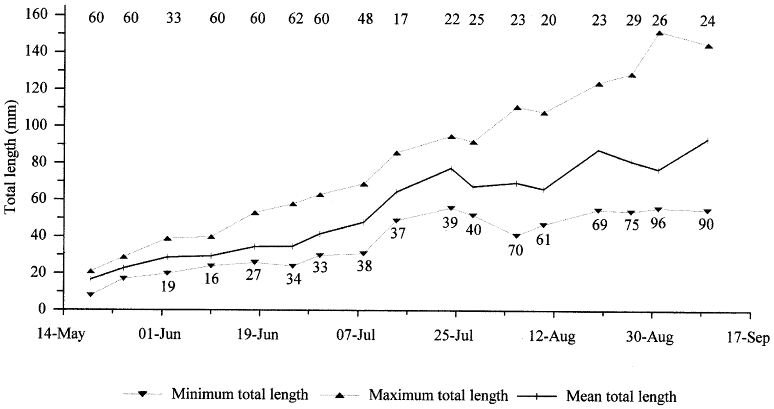

Figure 1. Length of age-0 largemouth bass collected in 1993. Sample size is indicated above each point. The difference between the maximum and minimum total length is given below each point beginning with the 2-June sample.

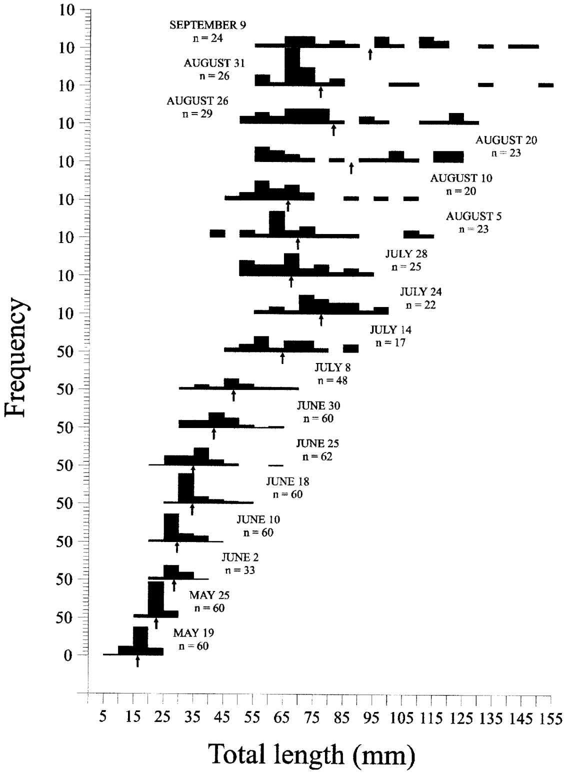

Figure 2. Length frequency distribution of age-0 largemouth bass collected in 1993. Arrows indicate the mean lengths. Note scale change on the y-axis.

There appeared to be 2 distinct periods of growth for age-0 largemouth bass in 1993, with late July being the pivotal period. The range in lengths showed a rapid increase in late July through the conclusion of sampling. At the same time, the minimum length remained relatively constant, resulting in a decrease in the mean length of the cohort (Fig. 1). The length-frequency histogram was consistently multi-modal after late July and some smaller members of the cohort were exhibiting little or no growth (Fig. 2). Also, the majority of the differences in diet, discussed later, occurred after the 24 July sampling date.

The estimated piecewise linear regression model was

$$L = 10.68 + 0.61\ D - 0.25\ D^* + 1.56\ Q + 0.23\ QD + 0.45\ QD^*$$

The single multiple regression model contains 4 simple linear regression models based on the values of Q and Z. The models were

large fish:

$D < t^*$ $$L = 12.24 + 0.84\ D \quad (1)$$

$D \geq t^*$ $$L = -2.36 + 1.04\ D \quad (2)$$

small fish:

$D < t^*$ $$L = 10.68 + 0.61\ D \quad (3)$$

$D \geq t^*$ $$L = 28.93 + 0.36\ D \quad (4)$$

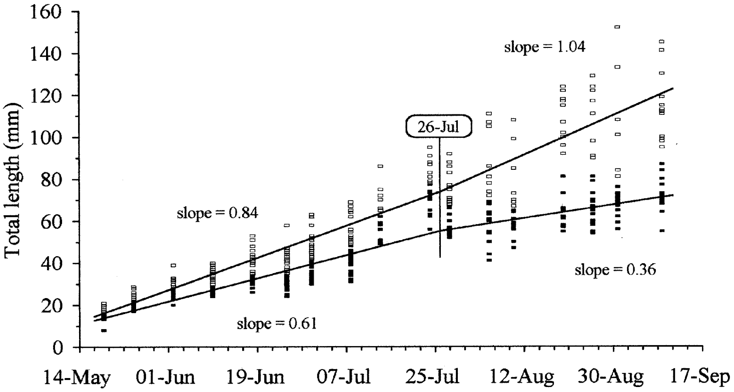

Figure 3. Growth rates (mm/day) of small and large age-0 largemouth bass before and after 26 July 1993. Slopes of the lines were determined with piecewise linear regression. Slopes are significantly different between sizes of fish both early and late and within both sizes between seasons ($P < 0.01$).

The slope in each of the models corresponds with the growth rate in mm/day (Fig. 3). The growth rate of large fish increased significantly (from 0.84 mm/day before 26 July to 1.04 mm/day afterwards (equations 1 and 2; $F_{1,646} = 18.12$; $P < 0.001$). Small age-0 largemouth bass growth significantly decreased (0.61 mm/day to 0.36 mm/day) after this date (equations 3 and 4; $F_{1,646} = 9.73$; $P = 0.002$). The growth rate of large fish was significantly greater than small age-0 largemouth bass both before (equations 1 and 3; $F_{1,646} = 50.31$; $P < 0.001$) and after 26 July (equations 2 and 4; $F_{1,646} = 119.31$; $P < 0.001$).

Diet

The diet of age-0 largemouth bass was highly variable. There were 54 different taxa identified, with the majority being zooplankton (Table 1). There were at least 8 fish species, 13 insect species, 23 zooplankton species, 3 Malacostraca species, and 7 species classified as miscellaneous. Very few age-0 largemouth bass stomachs were empty (25 of 443, or 5.6%). Large fish had a higher percentage of empty stomachs, ranging from 0% to 42% per sampling date. Small age-0 largemouth bass stomachs were rarely empty (0% to 10%).

Diets of both size classes of largemouth bass were compared from 15 approximately weekly samples collected between 2 June and 9 September. Dry weights were obtained for 52 different taxa or life stages found in the diet of age-0 largemouth bass. Thirty were from published weight-length regression equations, 13 were from regression equations derived in the laboratory, 6 taxa were dried and weighed directly, and 3 were mean dry weights of a subsample.

Percent by Number

The overall test of significant difference in percent by number between the 2 size classes was significant ($P < 0.01$) in all samples except on 24 July (Table 2). All other samples were then tested for differences between size classes for each prey category. Large age-0 largemouth bass had a higher percentage of fishes in the diet than small age-0 largemouth bass in 14 out of 15 samples, with 8 of the differences significantly higher. On 10 August, small age-0 largemouth bass had a significantly higher percent by number of fishes in the diet. However, 2 small age-0 largemouth bass contained 63 *Lepomis* larvae (5–6 mm) out of a total of 78 prey fishes (81%) in the stomachs of both size classes combined. In 9 of 15 samples, the diet of small age-0 largemouth bass was less than 3% prey fishes. Large age-0 largemouth bass also consumed more insects than small age-0 largemouth bass (Table 2). Large fish had a higher percentage of insects in the diet in 12 of 15 samples, with 6 of these differences significant. On only 1 date (5 Aug) was there a significantly higher percentage of insects in the stomachs of small age-0 largemouth bass compared with large members of the cohort.

Small age-0 largemouth bass consumed a higher percent by number of zooplankton than large age-0 largemouth bass in 14 of 15 samples, with 10 of the differences significantly higher (Table 2). Large fish consumed a higher percentage of zooplankton than small fish on 5 August, although the difference was not significant.

Table 2. Comparison of the percent by number of major prey categories in the diet of large and small age-0 largemouth bass by the Fisher exact test. Overall significant differences are indicated beside each date. The sample size, *N*, is the pooled number of items in the diet of each size class for each sampling date.

Date	Size	*N*	Fish	Insect	Mala-costraca	Zoo-plankton	Miscellaneous
2 Jun[b]	Large	730	0.68	60.14[b]	0.14	38.90	0.14
	Small	319	0.00	36.36	0.00	63.64[b]	0.00
10 Jun[b]	Large	392	2.04[b]	2.04	0.00	95.15	0.77
	Small	2424	0.00	1.44	0.00	98.18[b]	0.37
18 Jun[b]	Large	121	11.57[b]	19.01[a]	0.83	66.94	1.65
	Small	428	2.57	10.28	0.47	86.21[b]	0.47
25 Jun[b]	Large	138	2.17	44.93[b]	11.59[a]	40.58	0.72
	Small	217	0.46	16.59	4.15	78.80[b]	0.00
30 Jun[b]	Large	104	34.62	40.38	16.35	7.69	0.96
	Small	198	25.76	29.29	18.18	25.25[b]	1.52
8 Jul[b]	Large	88	4.55	92.05[b]	0.00	3.41	0.00
	Small	136	4.41	69.12	0.00	22.06[b]	4.41
14 Jul[b]	Large	22	40.91[b]	59.09	0.00	0.00	0.00
	Small	42	9.52	83.33	0.00	7.14	0.00
24 Jul	Large	27	40.74	33.33	0.00	0.00	25.93
	Small	25	36.00	36.00	0.00	16.00	12.00
28 Jul[b]	Large	23	56.52[b]	26.09	0.00	0.00	17.39[b]
	Small	104	0.96	24.04	4.81	68.27[b]	1.92
5 Aug[b]	Large	75	12.00	12.00	0.00	74.67	1.33
	Small	399	9.27	26.82[b]	0.00	63.91	0.00
10 Aug[b]	Large	51	9.80	70.59[b]	3.92	13.73	1.96
	Small	231	31.60[b]	42.86	6.93	18.61	0.00
20 Aug[b]	Large	30	46.67[b]	50.00[b]	0.00	3.33	0.00
	Small	420	0.48	13.57	9.29	75.71[b]	0.95
26 Aug[b]	Large	21	14.29[a]	61.90	0.00	19.05	4.76
	Small	313	1.92	39.94	7.99	49.84[b]	0.32
31 Aug[b]	Large	8	37.50[b]	62.50	0.00	0.00	0.00
	Small	205	0.00	41.46	17.07	39.51[a]	1.95
9 Sep[b]	Large	14	21.43[b]	64.29	0.00	14.29	0.00
	Small	253	1.19	62.85	2.37	32.81	0.79

a. indicates significant at $P < 0.05$.

b. indicates significant at $P < 0.01$.

This sampling date was the only instance after 18 June in which a category other than fishes or insects was the dominant prey of large age-0 largemouth bass. The occurrence coincided with the peak abundance of *Daphnia lumholtzi* in 1993. One large fish measuring 74 mm consumed 39 *D. lumholtzi*. This fish's consumption represented approximately 70% of the zooplankton eaten by all large age-0 largemouth bass combined on 5 August The percent by number of zooplankton in the diet of small fish decreased from 10 June (98%) through 14 July (7%). Zooplankton consumption by small fish increased over the last 8 sampling dates (ranging from 16% to 76%) and was the highest percentage of any prey category in 4 of these samples.

There were few significant differences between size classes in percent by number of the Malacostraca and miscellaneous prey categories. One interesting observation was the mysid, *Taphromysis louisianae*, in the diet of small age-0 largemouth bass (*T. louisianae* has only recently been found outside of the extreme southern United States). *T. louisianae* first appeared in the diet on 10 August and was present through the conclusion of sampling on 9 September. None were found in the stomachs of large members of the cohort. Further, except for 2 dates in late Jun, few malacostracans were consumed by large age-0 largemouth bass.

Percent by Weight

There were few significant differences in the diet of large and small age-0 largemouth bass size classes when comparing the percent by weight of all prey categories combined. The MANOVA test used did not pool the diet, but compared the mean percent by weight of the prey categories from individual largemouth bass between size classes. This method resulted in low sample sizes and had a greater effect on discerning differences between sizes in percent by weight in comparison to percent by number.

Large age-0 largemouth bass consumed a greater percent by weight of fishes than small age-0 largemouth bass on all 15 sampling dates, although there was a statistical difference on only 4 dates (Table 3). Small age-0 largemouth bass did not begin consuming fishes until 18 June and never had more than 26% of fishes in their diet after 24 July. By contrast, large age-0 largemouth bass consumed fishes on all 15 dates, had at least 37% fishes in all but 3 samples, and contained greater than 63% fishes on 7 of the sampling dates.

Small age-0 largemouth bass contained a greater percent by weight of insects than large fish on all dates except 1, although only 3 of the differences were significant (Table 3). Large age-0 largemouth bass contained a range of 15% to 88% insects, while small age-0 largemouth bass had a range of 25% to 89%. There were no significant differences between the 2 size classes in percent by weight of zooplankton, Malacostraca, or miscellaneous prey categories.

Percent Frequency of Occurrence

Large age-0 largemouth bass consumed a higher percent frequency of fishes than small age-0 largemouth bass in all but the 30 June sample (Table 4). Five of the differences were significant. In all the samples after 25 June no less than 42% of large age-0 largemouth bass contained fishes, whereas after 24 July the number of small age-0 largemouth bass stomachs containing fishes ranged from 0% to 33%.

There were generally no significant differences between the size classes in the percent frequency of insects occurring in the diet (Table 4). Only 1 sample was significant, where a higher percentage of small age-0 largemouth bass stomachs con-

Table 3. Comparison of the percent by weight of major prey categories in the diet of large and small age-0 largemouth bass. Overall test of significance by MANOVA (indicated beside each date) and individual tests by ANOVA. The sample size, *N*, is the number of non-empty stomachs of each size class for each sampling date.

Date	Size	*N*	Fish	Insect	Mala-costraca	Zoo-plankton	Miscellaneous
2 Jun	Large	19	8.09	87.71	0.39	3.82	0.00
	Small	11	0.00	88.80	0.00	11.20	0.00
10 Jun[a]	Large	8	37.17[b]	18.91	0.00	43.78	0.14
	Small	22	0.00	31.95	0.00	67.85	0.20
18 Jun	Large	10	47.01	40.96	8.63	3.40	0.00
	Small	19	24.75	48.08	0.90	26.26	0.01
25 Jun	Large	17	9.50	85.73	4.16	0.61	0.00
	Small	13	6.05	73.96	5.21	14.77	0.00
30 Jun	Large	10	63.63	35.28	1.04	0.05	0.00
	Small	20	47.35	43.73	8.45	0.47	0.01
8 Jul	Large	9	37.49	62.45	0.00	0.06	0.00
	Small	14	33.34	66.55	0.00	0.10	0.01
14 Jul	Large	7	68.40	31.60	0.00	0.00	0.00
	Small	8	45.01	54.85	0.00	0.14	0.00
24 Jul	Large	9	73.11	15.87	0.00	0.00	11.03
	Small	10	65.12	24.79	0.00	0.00	10.08
28 Jul[a]	Large	10	75.70[b]	20.68	0.00	0.00	3.62
	Small	12	8.33	66.37[a]	8.76	10.55	5.99
5 Aug	Large	7	79.16	6.50	0.00	14.32	0.02
	Small	14	25.40	61.63	0.00	12.97	0.00
10 Aug	Large	8	37.44	49.18	0.83	0.06	12.50
	Small	12	20.62	73.94	5.19	0.25	0.00
20 Aug[a]	Large	11	80.56[b]	19.44	0.00	0.00	0.00
	Small	11	9.39	62.76[a]	17.92	9.88	0.06
26 Aug	Large	7	32.93	52.72	0.00	14.34	0.00
	Small	19	14.80	78.53	5.62	1.05	0.00
31 Aug[b]	Large	4	74.75[b]	25.25	0.00	0.00	0.00
	Small	18	0.00	86.90[b]	12.49	0.60	0.00
9 Sep	Large	7	42.86	57.12	0.00	0.02	0.00
	Small	12	22.15	63.06	10.98	3.78	0.02

a. indicates significant at $P < 0.05$.

b. indicates significant at $P < 0.01$.

tained insects. There was an overall trend of insects being more common in the diet of small fish.

There was a strong trend of large age-0 largemouth bass having a lower percent frequency of occurrence of zooplankton in the diet when compared with small fish of the cohort (Table 4). On 4 sampling dates, the differences were statistically significant. Of 10 samples collected after June, no more than one third of large fish's stomachs contained zooplankton; on 4 of the 10 dates large age-0 largemouth bass consumed no zooplankton. In comparison, no less than 55% of small age-0 largemouth bass stomachs contained zooplankton in any of the samples after 24 July.

Table 4. Comparison of the percent frequency of occurrence of 5 major prey categories in the diet of large and small age-0 largemouth bass by the Fisher exact test. The sample size, *N*, is the number of non-empty stomachs of each size class for each sampling date.

Date	Size	*N*	Fish	Insect	Mala-costraca	Zoo-plankton	Miscellaneous
2 Jun	Large	19	26.32	100.00	5.26	94.74	5.26
	Small	11	0.00	100.00	0.00	100.00	0.00
10 Jun	Large	8	37.50^a	50.00	0.00	100.00	37.50
	Small	22	0.00	68.18	0.00	100.00	40.91
18 Jun	Large	10	60.00	70.00	10.00	70.00	20.00
	Small	19	36.84	73.68	5.26	100.00^a	10.53
25 Jun	Large	17	11.76	94.12	41.18	94.12	5.88
	Small	13	7.69	92.31	38.46	100.00	0.00
30 Jun	Large	10	70.00	40.00	30.00	50.00	10.00
	Small	20	75.00	65.00	35.00	70.00	10.00
8 Jul	Large	9	44.44	88.89	0.00	33.33	0.00
	Small	14	42.86	92.86	0.00	57.14	35.71
14 Jul	Large	7	71.43	71.43	0.00	0.00	0.00
	Small	8	50.00	75.00	0.00	37.50	0.00
24 Jul	Large	9	77.78	66.67	0.00	0.00	22.22
	Small	10	70.00	60.00	0.00	20.00	20.00
28 Jul	Large	10	80.00^b	50.00	100.00	0.00	10.00
	Small	12	8.33	75.00	75.00	75.00^b	16.67
5 Aug	Large	7	85.71^a	42.86	0.00	42.86	14.29
	Small	14	28.57	78.57	0.00	85.71	0.00
10 Aug	Large	8	50.00	75.00	12.50	25.00	12.50
	Small	12	33.33	91.67	41.67	66.67	0.00
20 Aug	Large	11	81.82^b	27.27	100.00^b	9.09	0.00
	Small	11	18.18	90.91^b	36.36	81.82^b	9.09
26 Aug	Large	7	42.86	71.43	0.00	28.57	14.29
	Small	19	31.58	94.74	31.58	78.95^a	5.26
31 Aug	Large	4	75.00^b	50.00	0.00	0.00	0.00
	Small	18	0.00	94.44	55.56	55.56	11.11
9 Sep	Large	7	42.86	57.14	0.00	14.29	0.00
	Small	12	25.00	91.67	16.67	58.33	16.67

a. indicates significant at $P < 0.05$.

b. indicates significant at $P < 0.01$.

There was a distinct trend in the percent frequency of occurrence of Malacostraca (Table 4). On early sampling dates, large age-0 largemouth bass showed a greater preference for malacostracans than small fish. The malacostracans were amphipods in samples 2 June through 30 June. No malacostracans were present again in the diet of either size class until 28 July. From the end of July until 9 September malacostracans were consumed primarily by small age-0 largemouth bass; only 1 individual was found in large fish during this period. All of the malacostracans found in small age-0 largemouth bass were identified as *Taphromysis louisianae*. There were no statistically significant differences in the percent frequency of occurrence of the miscellaneous prey category.

Condition of Age-0 Largemouth Bass

There was no significant difference in the overall condition (slopes) of small and large size classes of age-0 largemouth bass ($F_{1,528} = 0.2$; $P = 0.656$). The 2 equations were:

$$\frac{\text{Large } (n = 229;\ r^2 = 0.996)}{\log_{10}W = -5.21 + 3.13 \log_{10}L}$$

and

$$\frac{\text{Small } (n = 303;\ r^2 = 0.994)}{\log_{10}W = -5.18 + 3.12 \log_{10}L}$$

The length-weight equations from samples collected between 2 June and 25 June were compared to investigate any differences in condition between the size classes early in life. The 2 equations were:

$$\frac{\text{Large } (n = 93;\ r^2 = 0.976)}{\log_{10}W = -5.21 + 3.12 \log_{10}L}$$

and

$$\frac{\text{Small } (n = 122;\ r^2 = 0.939)}{\log_{10}W = -5.53 + 3.35 \log_{10}L}$$

The small age-0 largemouth bass equation had a significantly higher slope ($F_{1,211} = 6.28$; $P = 0.013$), indicating small fish were in better condition than large fish early in life.

Mean Number and Weight of Stomach Contents

The mean number and prey item mean dry weight in non-empty stomachs was compared between the 2 size classes for each sample. Small age-0 largemouth bass generally contained a higher number of prey items of a lower prey dry weight than large fish (Fig. 4). Large age-0 largemouth bass stomachs contained means of 2 to 49 items with a mean prey dry weight ranging from 0.1 to 84 mg. Small age-0 largemouth bass stomachs averaged 3 to 110 items with a mean prey dry weight of 0.01 to 16.6 mg. However, large fish had a higher mean number of prey on 2 June, and there was a period between 30 June and 24 July when the mean number of prey items was similar. In all of the samples from 28 July to the conclusion of sampling, small age-0 largemouth bass averaged no less than 2.5 times as many prey items as large fish. Large age-0 largemouth bass always had a higher mean prey dry weight than small fish. The difference was especially noticeable after 28 July, with large age-0 largemouth bass mean prey weight being 4 to 110 times greater than small age-0 largemouth bass prey weight. Thus, large age-0 largemouth bass were consuming fewer prey items of a larger size than small fish, which were feeding on relatively more prey items of a smaller size.

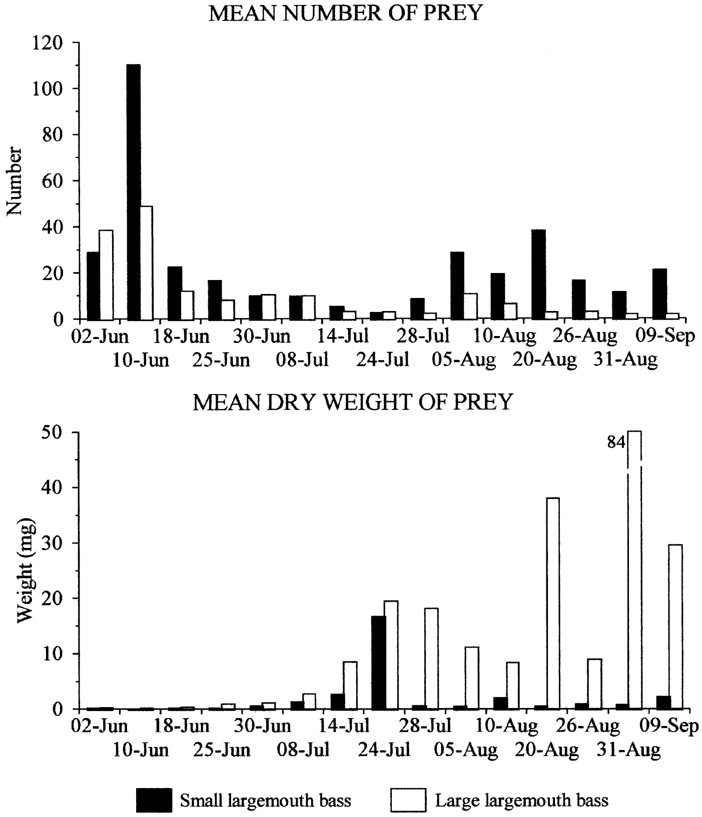

Figure 4. Mean number and prey item mean dry weight (mg) in stomachs of small and large age-0 largemouth bass.

Discussion

There were 2 distinct periods of growth of age-0 largemouth bass in Ledbetter Embayment in 1993. The growth rate of large age-0 largemouth bass showed an increase after 26 July while the growth rate of small age-0 largemouth bass was slowing, resulting in the doubling of the length range of largemouth bass collected during the latter part of the growing season of 1993. The length-frequency distribution indicated that the smallest members of the cohort may have ceased all growth after Jul, whereas growth of fish in the large size class continued. Miranda and Hubbard (1994) found similar late season growth patterns of age-0 largemouth bass in a Mississippi reservoir.

Jackson and Noble (1995) questioned the effectiveness of using either a seine for the collection of largemouth bass greater than 60 mm or a traditional boom-mounted electrofishing unit for largemouth bass less than 150 mm. When compared with a hand-held electrofishing unit, they found collections with a seine substantially underestimated the mean length of the age-0 largemouth bass population in an embayment of Jordan Lake, North Carolina. There were several notable differences between their sampling and the current sampling. First, their comparisons were based on the use of a 9-m bag seine and the current sampling was conducted with a 15.2-m bag seine. Second, Jordan Lake was devoid of any substantive aquatic vegetation, whereas all seining in the current study was conducted in scattered beds of Eurasian water milfoil and water willow except at the lowest of water levels. A longer seine and fish concentrated in patches of vegetation should have minimized the probability of age-0 largemouth bass avoiding capture. Also, in early October boom-mounted electrofishing samples, the Kentucky Department of Fish and Wildlife Resources found a mean length of 96.5 mm for the age-0 largemouth bass cohort in 1993 (Buynak 1994). In the current study, the mean length of the last sample a month earlier (9 Sep) was 93.6 mm. This means that if Buynak was correct we overestimated the true mean length in September using the seine, or alternatively, our mean length was correct and Buynak underestimated the true mean in October using electrofishing, both of which would be counterintuitive given the gear. The true mean length is likely somewhere in between. We contend that the sampling methodology used in the current study did not underestimate the mean length of the age-0 largemouth bass cohort, and the seine effectively sampled all sizes in the age-0 largemouth bass population of Ledbetter Embayment.

The differential growth occurring in this age-0 largemouth bass cohort was not the result of an extended or disrupted spawning season as found by several authors (Pasch 1975, Summerfelt 1975, Miller and Storck 1984, Maceina and Isely 1986, Goodgame and Miranda 1993). There was a very narrow initial length range, and the length-frequency distributions in early collections were normally distributed. Timmons et al. (1980) ruled out the possibility of sexual differences in growth rates of age-0 largemouth bass because both sexes were equally distributed in their bimodal length-frequency distribution.

Differences in growth appear to be related to the diet quality of the 2 size groups. There were significant differences throughout the study period when comparing the percent by number of the 5 prey categories between the 2 size classes of age-0 largemouth bass. Large age-0 largemouth bass generally were more piscivorous, whereas insects, zooplankton, and malacostracans dominated the diet of small individuals. The majority of the observed significant differences in percent by weight and frequency of occurrence of prey in the diet were during the period in late summer when the growth of small age-0 largemouth bass was slowing. After July, large individuals were consuming fewer prey items but of a much larger size than small age-0 largemouth bass. The high variability in length attained by late summer in this age-0 largemouth bass cohort resulted from slower growth in length of small age-0 largemouth bass initially, which in turn appears to have resulted from the invertebrate diet. Large fish became piscivorous earlier, enabling them to maintain a higher degree of piscivory throughout the summer, which resulted in faster growth. Prey availability for each of the size classes of age-0 largemouth bass was not quantified, but it can be assumed that if prey fishes were available to small age-0 largemouth bass they would have utilized this higher quality resource to a greater extent. The lack of suitable size prey fishes for smaller age-0 largemouth bass is the primary factor found responsible for differential growth in several studies (Aggus and Elliott 1975, Shelton et al. 1979, Timmons et al. 1980, Keast and Eadie 1985). Size-related differences in prey fish availability have also been observed to play a role in the occurrence of differential growth when there is a lengthy spawning period (Pasch 1975, Miller and Storck 1984, Maceina and Isely 1986). Differential growth can occur even when the initial size disparity is very small (Keast and Eadie 1985), as seen in the present study.

Another factor that may lead to variation in growth that has not been considered for age-0 largemouth bass is size-class segregation because of predation risk. Werner et al. (1983) were able to demonstrate that small bluegill sunfish *(Lepomis macrochirus)*, in the presence of a predator (largemouth bass), had slower growth rates than small bluegills in the absence of predators. In avoiding predation, the small bluegills were limited to vegetated areas where foraging return rates were lower than more open habitats. Because the reduced utilization of the open habitats by small bluegills left more resources for larger bluegills that were less vulnerable to the predators, growth rates of larger bluegills were increased relative to the control. The results demonstrate that predation risk can force the smaller fish of a cohort to less desirable foraging areas, possibly contributing to variation in growth of age-0 largemouth bass.

The theory of differences in diet and prey availability may explain the occurrence of differential growth in age-0 largemouth bass, but can the initial size disparity arise in the absence of a disrupted or prolonged spawn? Goodgame and Miranda (1993) found no relationship between the size of largemouth bass larvae at swim-up and parental length. Aggus and Elliott (1975) stated that some age-0 largemouth bass began feeding on fish while others were continuing to feed on plankton and insects even though there was not a significant difference in size of the largemouth bass.

Keast and Eadie (1985) speculated on a possible mechanism for initial size divergence. They found that larger age-0 largemouth bass had a condition factor significantly lower than smaller fish, suggesting that larger individuals may allocate more of the assimilated energy into increases in length at the expense of weight. These individuals could obtain a greater length more rapidly but would have a lower condition factor. Mouth size, and thus the size of prey that can be ingested, is determined by body length rather than body weight. Therefore, larger fish would be able to maintain a size advantage over age-0 prey fishes and hence consume a higher quality diet than smaller largemouth bass. However, Keast and Eadie (1985) hypothesized that the disadvantage of the "length growth strategy" might be that in years with early autumns large fish would be unable to increase their condition rapidly enough before the onset of winter.

Findings in the current study tend to support Keast and Eadie's (1985) hypothesis of a mechanism for initial size divergence. While there were no differences in condition between the size classes of age-0 largemouth bass over all dates, there was a significant difference in condition during early growth. The higher condition of small fish resulted in the conclusion that, early in life, small age-0 largemouth bass were possibly allocating more assimilated energy towards growth in weight, while large fish were assimilating more energy towards growth in length. This observation is curious considering that the conventional ecological theory of fishes is that the fishes growing fastest in length should have the best chances of survival, because predation by other piscivorous fishes is a function of size. Slower growth rate increases the amount of time smaller fishes are most vulnerable to predation, in addition to starvation and physicochemical factors, thus increasing mortality. DeAngelis and Coutant (1982) note that the fastest growing individuals may be the most important members of an age-0 year class. Faster growing fish may be the primary contributors to year-class strength if they are more likely to survive to maturity. Werner and Gilliam (1984) state that growth and mortality rates were intricately related so those factors affecting growth may indirectly regulate recruitment and population size. Further, fitness would be higher for a fish that has a higher growth rate (in length) in the summer, if followed by a winter in which growth ceases and mortality rate is a declining function of size.

Literature Cited

Aggus, L. R. and G. V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317–322 *in* R.H. Stroud and H.E. Clepper, eds. Black bass biology and management. Sport Fishing Inst., Washington, D.C.

Buynak, G. L. 1994. Statewide fisheries investigation project. Black bass investigation. Ky. Dep. Fish and Wildl. Resour., Fish. Div., D-J Project F-40 Segment 16, Annual Perf. Rep. 117pp.

Cummins, K. W. and J. C. Wuycheck. 1971. Calorific equivalents for investigations in ecological energetics. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 18:1–158

DeAngelis, D. L. and C. C. Coutant. 1982. Genesis of bimodal size distributions in species cohorts. Trans. Am. Fish. Soc. 111:384–388.

Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia (Berl.) 19:75–97.

Goodgame, L. L. and L. E. Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. Trans. Am. Fish. Soc. 122:131–138.

Gutreuter, S. J. and R. O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. Trans. Am. Fish. Soc. 114:317–327.

Jackson, J. R. and R. L. Noble. 1995. Selectivity of sampling methods for juvenile largemouth bass in assessments of recruitment processes. North Am. J. Fish. Manage. 15:408–415.

Johnson, R. A. and D. W. Wichern. 1982. Applied multivariate statistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 594pp.

Keast, A. and J. M. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Trans. Am. Fish. Soc. 114:204–213.

Kramer, R. H. and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, *Micropterus salmoides* (Lacépède) and some related ecological factors. Trans. Am. Fish. Soc. 89:222–233.

Ludsin, S. A. and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. Ecol. Applications 7:1024–1038.

Maceina, M. J. and J. J. Isely. 1986. Factors affecting growth of an initial largemouth bass year class in a new Texas reservoir. J. Freshwater Ecol. 3:485–492.

Mehta, C. R. and N. R. Patel. 1983. A network algorithm for performing Fisher's exact test in R x C contingency table. J. Am. Stat. Assoc. 78:427–434.

Mendenhall, W. and T. Sincich. 1996. A second course in statistics: regression analysis. 5th ed. Prentice-Hall, Inc., Upper Saddle River, N.J. 899pp.

Miller, S. J. and T. Storck. 1984. Daily growth rings in otoliths of young-of-the-year largemouth bass. Trans. Am. Fish. Soc. 111:527–530.

Miranda, L. E. and W. D. Hubbard. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Trans. Am. Fish. Soc. 123:80–87.

Olson, M. H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179–190.

Pasch, R. W. 1975. Some relationships between food habits and growth of largemouth bass in Lake Blackshear, Georgia. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 28:307–321.

Rogers, L. E., R. L. Buschbom, and C. R. Watson. 1977. Length-weight relationships of shrub-steppe invertebrates. Annals Entomol. Soc. Am. 70:51–53.

______, W. T. Hinds, and R. L. Buschbom. 1976. A general weight versus length relationship for insects. Annals Entomol. Soc. Am. 69:387–389.

Rosen, R. A. 1981. Length-dry weight relationships of some freshwater zooplankton. J. Freshwater Ecol. 1:225–229.

SAS Institute, Inc. 1985. SAS User's guide: statistics, version 5 ed. SAS Inst., Inc., Cary, N.C. 956pp.

Shelton, W. L., W. D. Davies, T. A. King, and T. J. Timmons. 1979. Variation in the growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. Trans. Am. Fish. Soc. 108:142–149.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. 10:375–383.

Summerfelt, R. C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 166–174 *in* R. H. Stroud and H. E. Clepper, eds. Black bass biology and management. Sport Fishing Inst., Washington, D.C.

Timmons, T. J., W. L. Shelton, and W. D. Davies. 1980 Differential growth of largemouth bass in West Point Reservoir, Alabama and Georgia. Trans. Am. Fish. Soc. 109:176–186.

Toneys, M. L. and D. W. Coble. 1979. Size-related first winter mortality of freshwater fishes. Trans. Am. Fish. Soc. 108:415–419.

U.S. Department of Interior. 1997*a*. 1996 National survey of fishing, hunting, and wildlife-associated recreation. U.S. Dep. Int., Fish and Wildl. Serv., Washington, D.C. 115pp.

U.S. Department of Interior. 1997*b*. 1996 National survey of fishing, hunting, and wildlife-associated recreation: Kentucky. U.S. Dep. Int., Fish and Wildl. Serv., Washington, D.C. 47pp.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. and Systematics 15:393–425.

______, ______, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.