Relationships between Environmental Variables and Size-Specific Growth Rates of Illinois Stream Fishes

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Abstract.—We quantified size-specific growth of small and large rock bass *Ambloplites rupestris,* bluegill *Lepomis macrochirus,* largemouth bass *Micropterus salmoides,* smallmouth bass *M. dolomieu,* and channel catfish *Ictalurus punctatus* from Illinois streams. Growth rates for each species fell within ranges previously reported for lakes and rivers in Illinois and adjacent states, although growth rates in our study averaged slightly lower. Intraspecific growth rate comparisons of small and large individuals were not significantly correlated for bluegill and rock bass. This suggests ontogenetic shifts occurred in diet or habitat use of these two species, similar to those reported for lentic populations. Using 12 biological, 22 physical, and 8 chemical variables collected concurrently with the fish, we developed simple- and multiple-regression models of growth for each species and size. Our best multiple-regression models accounted for 67–99% of the growth variation in seven species–size combinations, with substrate variables contributing to models for all species except rock bass. Although these models require testing against independent data for general applicability, they demonstrate the potential for predicting the growth of stream fish from commonly collected, and often readily available, habitat data. These empirical relationships with environmental variables may also enhance the efficiency of stream fisheries management by providing an inexpensive, a priori basis for directing management efforts.

Growth is an important component in the ecology and management of freshwater fisheries (Summerfelt and Hall 1987). Growth rates directly influence production, potential yield, angler satisfaction, the ecological role played by individuals of various sizes, and interactions between predators and prey. Growth reflects the overall well-being of an individual, integrating the effects of ingestion, metabolism, maintenance, excretion, and reproduction. Growth may also reflect habitat quality or "integrity" (Karr 1991). Unfortunately, growth data are labor intensive and expensive to collect, costing about 10 times more than length and weight data (Johnson and Nielsen 1983). High cost may make examination of stream fish growth impractical because of the large number and unique characteristics of individual streams. This

probably contributes to the relative scarcity of growth data for warmwater stream fishes.

Empirical models allow predictions to be made about phenomena such as growth, which may be difficult or expensive to measure directly. This modeling approach can use more easily collected and often readily available data from routine monitoring surveys to reduce costs, increase the efficiency of management surveys, and search for unknown patterns in nature (Rigler 1982; Hoenig et al. 1987). A trade-off exists between the limited amount of precise data that can be measured directly and the nearly unlimited potential for somewhat less precise data generated by means of existing databases and predictive models. The reality of limited budgets suggests that consideration should be given to predictive modeling techniques.

Numerous studies have successfully developed predictive models for fish biomass and yield in lakes and reservoirs (Carline 1986). Similarly in warmwater streams, fish production (Pajak and Neves 1987), biomass (Paragamian 1981; Layher and Maughan 1985; McClendon and Rabeni 1987), and abundance (Lyons 1991) have been predicted from habitat variables. Given the success of these studies in relating population variables to habitat features, we might expect similar success in predicting growth. Growth rates of numerous species

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have been examined in many reservoirs and lakes (Carlander 1969, 1977), but few of these studies have developed predictive growth models (e.g., Adams and McLean 1985; Gutreuter and Childress 1990). In contrast, relatively few studies have examined the growth of warmwater stream fish. These typically rely on time series data from one or a few locations (e.g., Paragamian and Wiley 1987), and thus are limited in their applicability and inferences.

Most published growth studies have used age-specific comparisons. However, fish growth and ecology are primarily functions of size, rather than age (Gerking and Raush 1979, Werner and Gilliam 1984). Because fish of a given age are not necessarily the same size, they should not be expected to grow at similar rates. Therefore, age-specific growth studies cannot assume that fish of the same age will exhibit similar growth responses under similar conditions, a key assumption of most population comparisons. An initial call for size-specific treatment of growth data by Larkin et al. (1957) has gone largely unnoticed. Gerking and Raush (1979) experimentally demonstrated that size controlled growth of Amargosa pupfish *Cyprinodon nevadensis* at least through the juvenile stage. Because young age-classes are typically most abundant, most fish in a population should exhibit size-specific growth responses to their environment. In Texas reservoirs, size accounted for a significantly greater proportion of annual growth variation than age (40 versus 32%) for largemouth bass *Micropterus salmoides* (Gutreuter 1987). These studies provide both empirical and experimental evidence suggesting that a size-specific rather than age-specific approach is preferable in many instances.

We examined size-specific growth of five species of warmwater stream fish: rock bass *Ambloplites rupestris*, bluegill *Lepomis macrochirus*, largemouth bass, smallmouth bass *Micropterus dolomieu*, and channel catfish *Ictalurus punctatus*. Evidence suggests that many of these species exhibit ontogenetic diet and habitat shifts (Larkin et al. 1957; Werner and Gilliam 1984; Osenberg et al. 1988), that growth of these species may be related to environmental variables (Paragamian and Wiley 1987; but see Tyus and Nikirk 1990), and that these variables can provide useful predictors of growth. Thus, our objectives were to: (1) quantify and compare growth responses within species, across a range of environmental conditions; (2) examine the relationships of growth with physical habitat, water chemistry, and fish com-
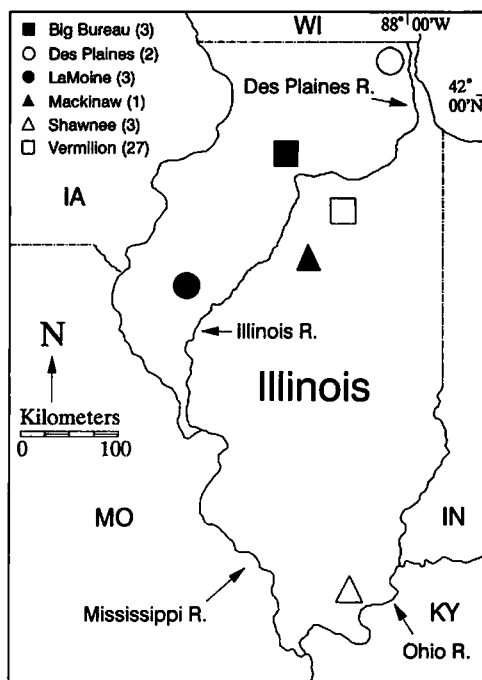

FIGURE 1.—Locations of the six Illinois drainage basins sampled. Numbers in parentheses indicate the number of sampling sites in each basin.

munity variables; and (3) generate simple- and multiple-regression models for describing growth, based on environmental data commonly collected and readily available from many natural resource agencies.

Methods

We made single collections of fish and of physical habitat and water chemistry data from 39 sites in six drainage basins in Illinois (Figure 1). Fish from all 39 sites and environmental data from 30 sites were collected between 1 August and 27 September 1990. Environmental data were collected from two sites in 1986, two sites in 1987, and three sites in 1988. Use of these earlier collections was justified because they fell within the life span of the species in our study, and any relationship with recent growth provides a conservative test for our second objective. No habitat or water quality data were used from the two Des Plaines River sites because the most recent data available were from 1984 and considerable stream habitat restoration had taken place since then. A diversity of land use patterns, including open agricultural areas, urban areas, and forested sandstone hills, is found in the watersheds of the streams sampled in this study.

TABLE 1.—Means and ranges for single samples of 42 fish community, physical habitat, and water chemistry variables measured at 39 Illinois stream sites in 1986, 1987, 1988, or 1990.[a]

Variable	Mean	Range
Fish community[b]		
Index of biotic integrity	42	31–54
Species richness	21	11–31
Number of sucker species (catostomids)	5	1–10
Number of sunfish species (centrarchids)	4	1–6
Number of darter species (percids)	1	0–6
Number of intolerant species	4	1–9
Individuals as green sunfish *Lepomis cyanellus* (%)	14	0–54
Individuals as hybrids (%)	0	0–2
Individuals as omnivores (%)	15	0–46
Individuals as insectivorous cyprinids (%)	32	0–82
Individuals as piscivores (%)	5	0–19
Individuals diseased (%)	1	0–3
Physical habitat		
Stream order	5	3–6
Mean width (m)	20	6–62
Mean depth (m)	0.4	0.1–0.7
Mean velocity (cm/s)	11	0–34
Discharge (m^3/s)	0.7	0–2.6
Instream cover (%)	7	1–32
Length of reach as pool (%)	32	0–100
Length of reach as riffle (%)	11	0–60
Area of reach shaded between 1000 and 1600 hours (%)	24	0–88
Silt (<0.06 mm) substrate (%)	11	0–91
Sand (0.06–2 mm) substrate (%)	17	0–60
Fine gravel (3–8 mm) substrate (%)	14	0–34
Medium gravel (9–16 mm) substrate (%)	12	0–37
Coarse gravel (17–64 mm) substrate (%)	12	0–35
Small cobble (65–128 mm) substrate (%)	9	0–33
Large cobble (129–256 mm) substrate (%)	6	0–19
Boulder (>256 mm) substrate (%)	5	0–22
Bedrock substrate (%)	5	0–54
Claypan substrate (%)	5	0–23
Detritus substrate (%)	2	0–27
Area instream vegetation (%)	3	0–21
Area submerged logs (%)	1	0–7
Water chemistry		
Dissolved oxygen (mg/L)	9.0	0.3–19.7
pH	7.9	6.7–8.8
Conductivity (μS/cm)	706	140–858
Total suspended solids (mg/L)	32	2–168
Ammonia nitrogen (mg/L)	0.05	0.00–0.23
Nitrate + nitrite nitrogen (mg/L)	5	0–17
Total phosphorus (mg/L)	0.19	0.00–0.83
Hardness (mg/L as $CaCO_3$)	339	58–409

[a] No recent habitat or water quality data were available for two Des Plaines River sites.

[b] See Karr et al. (1986).

Site selection was based on the availability of historical data (fish samples and water quality), seasonal persistence of flow, and accessibility.

At each site 42 variables were quantified: physical habitat (22); water chemistry (8); fish community metrics (11); and the index of biotic integrity (IBI; Karr et al. 1986) (Table 1). Total number of individuals sampled (an IBI metric) and catch per effort were not used in model development because of the difficulty in comparing the different collecting gear used across sites.

Habitat data for each site were collected from 11 transects at 10-m intervals. Habitat and water chemistry data were collected with standard methods by personnel of the Illinois Environmental Protection Agency (IEPA 1987). Fish were collected by electric seine (Bayley et al. 1989) or boat electrofishing (Reynolds 1983). Wadeable sites were shocked in a single pass over 200–500 m with a 10-m electric seine powered by a 1,600-W, 120-V, three-phase generator. Sites deeper than 1 m were boat electrofished for 1 h with a 3,000-W, 210-V generator, followed by several seine hauls from shallow areas to compensate for the electrofishing sampling bias towards larger fish. About 10 scales were removed from each bluegill, largemouth bass, rock bass, and smallmouth bass (Jearld 1983), and left pectoral spines were removed from each channel catfish for aging and growth back-calculation. Fish larger than 10 g were identified to species, weighed (± 5 g), measured for total length (TL, ± 1 mm), and released. Fish smaller than 10 g were preserved in 10% formalin and returned to the laboratory for similar processing (weighed ± 1 g).

Scales were impressed on acetate slides, and spines were sectioned according to Sneed (1951). Hard parts were viewed at 25× magnification with a dissecting microscope equipped with a camera lucida. Radii and interannular distances were recorded with a digitizing tablet connected to a microcomputer, after Frie (1982). From 1 to 10 scales were measured from each fish, and replicate measurements were averaged. A subsample of scales was aged by a second person to verify age estimates. Lengths at each previous year were back-calculated from the averaged scale measurements with Fisheries Analysis Tools software (MDOC 1989) by the Fraser–Lee method. Standard values for a, the intercept of the linear body–scale regression, were obtained from Carlander (1982). We used a value of $a = 0$ for channel catfish, based on the intercept from a regression of total length against spine radius from data pooled for all individuals collected.

We plotted annual growth increments against initial length at the beginning of the growing season from pooled data for all individuals in each population (i.e., species–site combination) from which we collected three or more individuals (e.g., Figure 2A). Negative quadratic, log-linear, and lin-

TABLE 2.—Total lengths used to define small and large sizes, ranges of annual growth for each size, and ranges of length at age 3 for five species of Illinois stream fish. Annual growth was calculated from site-specific regressions for each species. Lengths at age 3 from this study were obtained directly by back-calculation; lengths at age 3 from other studies represent means reported from Illinois and adjacent states (Carlander 1969, 1977). Weighted means of annual growth and length at age 3 are in parentheses.[a]

Species	Total length, mm		Annual growth, mm		Mean total length at age 3, mm	
	Small	Large	Small	Large	This study	Other studies
Bluegill	50	125	26–57 (38)	3–34 (20)	61–142 (112)	144–171 (153)
Rock bass	50	150	36–50 (41)	9–26 (20)	102–180 (131)	159–161 (160)
Largemouth bass	100	a	34–116 (82)	a	202–313 (259)	259–361 (284)
Smallmouth bass	100	200	60–88 (71)	16–60 (40)	146–287 (226)	183–291 (258)
Channel catfish	100	300	42–89 (74)	29–71 (54)	157–317 (237)	193–315 (287)

[a] No growth data for large largemouth bass due to insufficient sample size.

ear regressions were then fit to the data (e.g., Figure 2B) in an attempt to most precisely describe the growth pattern of each population. A negative quadratic regression was necessary because growth of age-0 fish was often less than growth of age-1 fish (e.g., Figure 2). After age 1, growth declined as expected with increasing size. When regressions were not significant, we used the overall mean growth increment from that site. Regressions and mean growth increments were applied only over the range of sizes collected at that site (e.g., Figure 2B) and never extrapolated. Because we sampled late in the growing season, growth data from each population in 1990 were compared to growth from previous years by analysis of covariance (ANCOVA, $\alpha = 0.05$) and dropped from further analysis when significantly lower. We tested for heterogeneity of slopes among individual fish within each population using ANCOVA (type I sums of squares, SS) with an interaction term to justify further comparison of individual effects of ANCOVA (type III SS). The same procedure was then used to test within each population for differences in growth among years and to test for differences in growth of each species among sites.

Within each species, we estimated annual growth of two discrete sizes: small, approximating growth of age-1 fish, and large, approximating growth at the onset of maturity (Table 2). The two sizes for each species were selected to encompass the range in which most known ontogenetic diet and habitat shifts occur. Estimates of growth for each size were obtained by solving size-specific regression equations at the discrete sizes listed in Table 2. Next, growth estimates for small and large sizes from each site were compared within species by means of Spearman's rank correlation. We used a nonparametric rank test because our research concerned only the relative relationship between faster and slower growth sites, not deviations from

a linear association. Lack of correlation or a negative correlation between large and small individuals may indicate a change in growth pattern, suggesting an ontogenetic shift in diet, physiology, habitat, or other resource use.

Simple- and multiple-regression models describing the growth of each species and size were then developed from combinations of fish com-
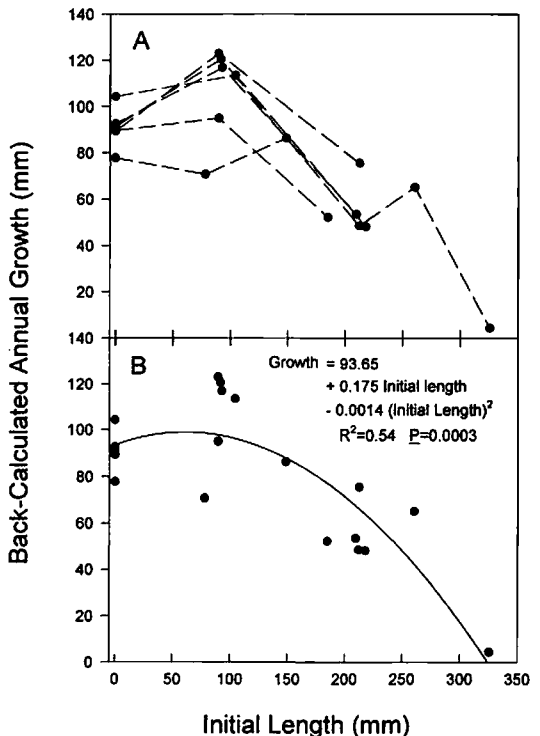

FIGURE 2.—An example showing development of a size-specific regression with data for six largemouth bass from one site in the Vermilion drainage basin. (A) Back-calculated growth trajectories for individual fish. (B) The same data as in (A) with a negative quadratic regression summarizing growth at this site.
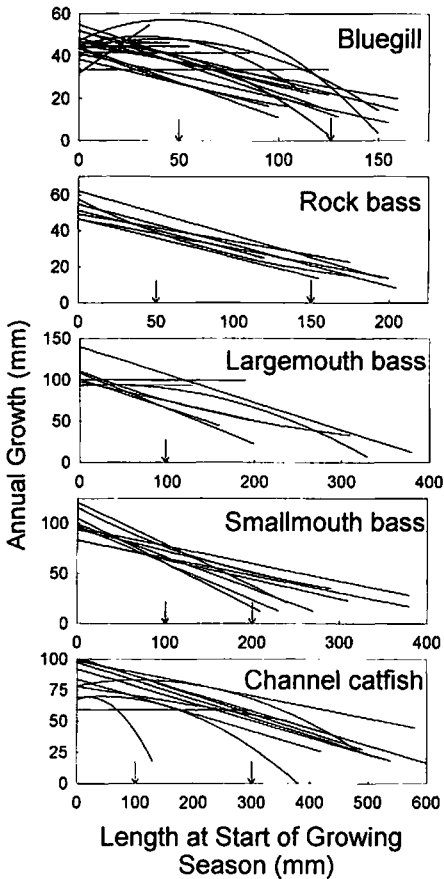
FIGURE 3.—Regression lines describing size-specific growth at individual sites for five species of Illinois stream fish. Lines encompass the range of back-calculated lengths used to establish regressions at each site and were used to generate size-specific growth estimates. Arrows indicate small and large sizes for each species. No growth estimates were made for large largemouth bass.

munity, habitat, and water chemistry variables. We developed simple regressions for each variable correlated with growth (Table 3). We created one best (highest R^2) multiple-regression model for each species and size with a forward stepwise technique, beginning with the single variable most highly correlated with growth. Additional variables were added, based on the highest significant correlation with residual model variance. Only variables not significantly correlated with those already included in the model were added to avoid autocorrelation. Variables were added as long as model coefficients remained significant (t-test). However, models were restricted to three or fewer variables to avoid artificially increasing R^2 values.

Habitat, water chemistry, and fish community variables were transformed as needed to approximate normal distributions. Percentage data were arcsine, square-root-transformed, and all other data were $\log_{10}(x + 1)$-transformed. Regression and ANCOVA analyses were performed with the REG and GLM procedures of the SAS Institute (1988). All statistical tests were conducted at $\alpha = 0.05$, except regression analysis was performed at $\alpha = 0.01$.

Results

We found that growth of fish populations could be summarized precisely with regression techniques. Ages assigned by two scale readers agreed to within 1 year for 70 (89%) of 79 randomly selected individuals. Slopes of growth trajectories for individual fish within a population were not significantly different (ANCOVA interaction term) for 30 (86%) of 35 populations described by linear regression. Growth differences among individual fish were not significant (ANCOVA main effect) for 26 (87%) of the 30 populations with interpretable main effects. Slopes of annual growth increments versus initial length among years (ANCOVA interaction term) were not significantly different for 27 (77%) of 35 populations, and year effects within a population (ANCOVA main effect) were not significant for 21 (78%) of the 27 populations with interpretable main effects. We believed that the homogeneity of individual and year effects within each population justified the use of these regressions to summarize size-specific growth of each population (e.g., Figure 2B).

Quadratic, log-linear, and linear regressions included data from 3 to 35 individuals per site and were significant for 47 (87%) of 54 of the populations. The remaining 7 populations were represented by the mean annual growth of all individuals for each back-calculated year, implying no relationship with initial length. Differences in slopes of linear growth regressions among sites were significant (ANCOVA interaction term) for all species except channel catfish, rendering adjusted mean growth differences among sites uninterpretable. However, the differences in growth trajectories that caused this interaction indicated variable differences in size-specific growth among sites (Figure 3). For channel catfish, site effects were interpretable, showing significant growth rate differences among sites (ANCOVA main effect).

Annual growth of all species and size-classes was highly variable across the 39 sites (Table 2) and generally decreased with increasing fish size

(Figure 3). Our means and ranges of length at age 3 were lower than those reported for streams and lakes in Illinois and adjacent states (Table 2), although the ranges usually overlapped. Within each species, growth of large and small sizes was correlated for smallmouth bass ($r = +0.68$, $N = 9$) and channel catfish ($r = +0.90$, $N = 9$). Intraspecific comparisons of small and large size-classes were uncorrelated for bluegill and rock bass.

We developed significant multiple-regression models for six of nine species–size combinations, with physical habitat variables contributing to most models (Table 3). Multiple regressions with three or fewer variables accounted for 67–99% of growth rate variation. No significant relationships were found for small channel catfish or small smallmouth bass. Fourteen variables contributed 11 simple and 9 multiple regressions (Table 3). Substrate composition contributed to regression models describing growth of all species, except rock bass. Growth of rock bass was best described with percentages of diseased fish, piscivores, and instream cover (Table 3).

Discussion

Previous size-specific growth studies have grouped fish into 5–25-mm size-groups and plotted growth as a histogram by size (Larkin et al. 1957; Gutreuter 1987; Osenberg et al. 1988). In our study we have fit a continuous regression to each population. The histogram approach would have required us to use broad size-groups or make interpolations for missing size-classes. Regressions were significant for 87% of our populations. Year effects were not significant in 77% of the populations, which was similar to results found for bluegill in Michigan lakes (Osenberg et al. 1988). Because of high coefficients of determination for our regressions (range, 0.56–0.98) and largely nonsignificant individual and year effects, we believe our approach represented growth of each population with reasonable accuracy. Previous research has shown that the size-specific approach summarizes growth within a fish population more precisely than traditional age-specific methods (Gutreuter 1987) and allows more meaningful comparisons among populations (Osenberg et al. 1988), especially when growth responses are related to environmental factors. We urge other researchers to consider this approach when quantifying and comparing growth rates.

During development from juvenile to adult, many species undergo at least one shift in diet or habitat use (Werner and Gilliam 1984). For example, bluegill in lakes are known to switch prey and migrate from littoral to limnetic habitat when they reach 50–83 mm standard length (SL: Werner and Hall 1988). Largemouth bass, smallmouth bass, and rock bass show a general diet shift from insects to fish and crustaceans between 40 and 100 mm TL (Carlander 1977). Channel catfish, which are believed to consume primarily invertebrates as juveniles, switch toward omnivory as adults (Carlander 1969).

Depending on these patterns of habitat and resource use, growth of different size-classes within a species will vary directly, inversely, or independently of one another. For instance, the ontogenetic niche shifts in bluegill are reflected by a change in growth pattern at 55 mm SL (Osenberg et al. 1988). Similarly, a diet shift affected growth trajectories of rainbow trout *Oncorhynchus mykiss* (Larkin et al. 1957); small individuals exhibited slow growth due to competition with other fish species for invertebrates, but growth increased when they grew large enough to switch to piscivory. Although we did not quantify diet or habitat use, similar ontogenetic shifts in resource use were suggested by the lack of correlation between growth of small and large sizes of bluegill and rock bass. Intraspecific comparisons of growth between small and large size-classes were positively correlated for channel catfish and smallmouth bass. This suggests that these two species may not undergo a pronounced niche shift within these size-ranges or that growth was limited by factors independent of body size.

In the Green River, Colorado, channel catfish ages 1–9 displayed similar growth responses across seven sites that varied widely in habitat conditions (Tyus and Nikirk 1990). Growth at these sites was evidently limited by regionally short growing seasons, low summer temperature, limited food resources, or high summer discharge rather than site-specific habitat characteristics. Temperature, as described in a habitat suitability index, also contributed to a successful predictive model of channel catfish biomass in Oklahoma streams (Layher and Maughan 1985). Layher and Maughan (1985) reported an optimum water temperature range of 35–40°C, using a habitat suitability index. It is possible that channel catfish growth was limited by temperature at our sites because water temperature, measured at the time of collections (August and September), never exceeded 32°C. We were unable to assess the effect of temperature because we measured our environmental variables at a single point in time. The

TABLE 3.—All significant ($P \leq 0.01$) simple regressions and the one multiple-regression model that accounted for the most variation in predicted annual growth (G_p, mm) for each species and size. No significant models were found for small channel catfish or large smallmouth bass. Insufficient data were available for large largemouth bass; MSE = mean square error and N = number of sites.

| Model | Significance (P) | | R^2 | MSE | N |
	Coefficient	Model			
Small bluegills					
$G_p = 45.13$	<0.001	0.008	0.45	27.17	14
$\quad - 12.14 \cdot \sin^{-1}(\% \text{ area shaded})^{0.5}$	0.008				
$G_p = 40.20$	<0.001	0.002	0.67	17.72	14
$\quad - 11.89 \cdot \sin^{-1}(\% \text{ area shaded})^{0.5}$	0.003				
$\quad - 22.25 \cdot \sin^{-1}(\% \text{ large cobble})^{0.5}$	0.020				
Large bluegills					
$G_p = 34.13$	0.001	0.010	0.73	34.22	7
$\quad - 45.76 \cdot \sin^{-1}(\% \text{ coarse gravel})^{0.5}$	0.010				
$G_p = 24.04$	0.001	0.002	0.96	6.28	7
$\quad - 51.17 \cdot \sin^{-1}(\% \text{ coarse gravel})^{0.5}$	0.001				
$\quad + 19.41 \cdot \sin^{-1}(\% \text{ piscivores})^{0.5}$	0.009				
Small rock bass					
$G_p = 46.88$	<0.001	0.008	0.78	5.06	7
$\quad - 66.54 \cdot \sin^{-1}(\% \text{ diseased})^{0.5}$	0.008				
$G_p = 43.10$	<0.001	0.002	0.93	2.07	7
$\quad - 70.86 \cdot \sin^{-1}(\% \text{ diseased})^{0.5}$	0.002				
$\quad + 17.69 \cdot \sin^{-1}(\% \text{ instream cover})^{0.5}$	0.046				
$G_p = 38.70$	<0.001	0.001	0.99	0.16	7
$\quad - 67.95 \cdot \sin^{-1}(\% \text{ diseased})^{0.5}$	0.002				
$\quad + 21.77 \cdot \sin^{-1}(\% \text{ instream cover})^{0.5}$	0.001				
$\quad + 13.67 \cdot \sin^{-1}(\% \text{ piscivores})^{0.5}$	0.006				
Large rock bass					
$G_p = 10.10$	0.029	0.020	0.78	5.26	6
$\quad + 17.65 \cdot \sin^{-1}(\% \text{ piscivores})^{0.5}$	0.020				
Small largemouth bass					
$G_p = 61.38$	<0.001	0.012	0.57	281.04	10
$\quad + 412.64 \cdot \log_{10}(\text{phosphorous} + 1)$	0.012				
$G_p = 40.62$	0.016	0.009	0.60	261.39	10
$\quad + 129.67 \cdot \sin^{-1}(\% \text{ coarse gravel})^{0.5}$	0.009				
$G_p = 119.96$	<0.001	0.005	0.66	222.66	10
$\quad - 99.82 \cdot \sin^{-1}(\% \text{ sand})^{0.5}$	0.005				
$G_p = 68.59$	0.006	0.001	0.86	102.77	10
$\quad - 102.38 \cdot \sin^{-1}(\% \text{ sand})^{0.5}$	0.001				
$\quad + 0.07(\text{conductivity})$	0.015				
Large smallmouth bass					
$G_p = 57.30$	<0.001	0.002	0.76	53.18	9
$\quad - 71.78 \cdot \sin^{-1}(\% \text{ green sunfish})^{0.5}$	0.002				
$G_p = 63.99$	<0.001	0.014	0.61	88.77	9
$\quad - 88.68 \cdot \sin^{-1}(\% \text{ large cobble})^{0.5}$	0.014				
$G_p = 73.65$	<0.001	0.007	0.81	49.10	9
$\quad - 104.72 \cdot \sin^{-1}(\% \text{ large cobble})^{0.5}$	0.003				
$\quad - 111.32 \cdot \sin^{-1}(\% \text{ detritus})^{0.5}$	0.042				
$G_p = 79.22$	<0.001	<0.001	0.98	7.84	9
$\quad - 135.54 \cdot \sin^{-1}(\% \text{ large cobble})^{0.5}$	<0.001				
$\quad - 147.06 \cdot \sin^{-1}(\% \text{ detritus})^{0.5}$	0.001				
$\quad + 161.19 \cdot \sin^{-1}(\% \text{ diseased})^{0.5}$	0.002				

TABLE 3.—Continued.

Model	Significance (P)		R^2	MSE	N
	Coefficient	Model			
Large channel catfish					
$G_p = 35.70$	<0.001	0.005	0.70	53.98	9
$+ 1.10$(water velocity)	0.005				
$G_p = 15.84$	0.068	0.001	0.80	35.59	9
$+ 220.09 \cdot \sin^{-1}(\%$ instream cover$)^{0.5}$	0.001				
$G_p = 22.70$	0.003	<0.001	0.94	13.09	9
$+ 211.42 \cdot \sin^{-1}(\%$ instream cover$)^{0.5}$	<0.001				
$- 8.55 \cdot \sin^{-1}(\%$ pools$)^{0.5}$	0.011				
$G_p = 25.99$	<0.001	<0.001	0.99	3.11	9
$+ 235.34 \cdot \sin^{-1}(\%$ instream cover$)^{0.5}$	<0.001				
$- 9.43 \cdot \sin^{-1}(\%$ pools$)^{0.5}$	0.001				
$- 22.76 \cdot \sin^{-1}(\%$ medium gravel$)^{0.5}$	0.006				

effect of temperature on annual growth rates is probably cumulative throughout the growing season. These effects may also be responsible for a lack of correlation between growth of small channel catfish and any of the 42 environmental variables.

Smallmouth bass are known to undergo a size-specific diet shift. Our small size-class (100 mm) may have been too large to detect this change of diet. A shift toward piscivory occurs in smallmouth bass as small as 40 mm TL, although invertebrates remain an important diet component throughout life (Carlander 1977). The consistent nature of the invertebrate component in the diet may have also blurred any effect on growth caused by the shift to piscivory.

We also observed no correlation between growth of small smallmouth bass and our selected environmental variables. Biomass and density of smallmouth bass have been positively correlated with coarse substrates (Paragamian 1981) and instream cover (McClendon and Rabeni 1987). The percent of large cobble substrate exerted a negative influence on large smallmouth bass growth in our multiple-regression model. If density increases with percent large cobble substrate, competition could contribute to our findings of slower growth at sites with large cobble. There was also no relationship between growth of small or large smallmouth bass and discharge in our models. A unimodal relationship exists between discharge and age-1 smallmouth bass growth in Iowa streams, with maximum growth occurring at a discharge of 10 m³/s (Paragamian and Wiley 1987). We found no correlation between discharge and growth of small smallmouth bass, although discharges at our sites were on the increasing side of this function

(Table 1). Our finding for large smallmouth bass concur with a lack of relationship reported between discharge and growth of age-2–4 smallmouth bass (Paragamian and Wiley 1987).

Growth of the remaining species–size combinations were correlated with several variables. McClendon and Rabeni (1987) found that rock bass abundance and density were both positively related to instream vegetation, woody structure, and coarse substrates. Instream cover made a positive contribution in our multiple-regression model for small rock bass, but growth of large rock bass was unrelated to cover and substrate (Table 3). Growth of small bluegills was negatively related to percent area shaded. Shading and turbidity may limit primary productivity in Illinois prairie streams (Wiley et al. 1990). If small bluegill feed on herbivores or grazers, as they do in lakes and reservoirs, shading may contribute to lower growth rates via reduced primary production and grazer abundance.

Several previous attempts to model largemouth bass growth in reservoirs have been successful. Adams and McLean (1985) were able to explain 88–90% of age-1, and 70–90% of age-2 growth variation in largemouth bass by using the liver somatic index, metabolic rates, and temperature. Gutreuter and Childress (1990) accounted for 63–76% of largemouth bass growth by using condition indices and length at the beginning of the growing season. Models derived in these studies were unsuitable for indirect assessment of growth because they required prior knowledge of individual ages or back-calculated lengths. Gutreuter and Childress (1990) developed models independent of previous growth data by using length at capture and condition indices. Partial correlation ratios in-

dicated that relative weight (W_r) accounted for up to 54% of largemouth bass growth variation and complete models, including length at capture, could account for up to 68% of growth variation. Yurk and Ney (1989) reported a positive relationship between total phosphorous and largemouth bass and smallmouth bass biomass in a Virginia reservoir. Similarly, growth of small largemouth bass in our study was positively correlated with total phosphorous (Table 3). However, streams are generally less reliant on autochthonous production than reservoirs, so the functional relationship between chlorophyll and largemouth bass production may differ between the two systems.

The precision of many of our models is similar to that attained in previous attempts at predicting growth (Adams and McLean 1985; Gutreuter and Childress 1990) and population characteristics (reviewed in Carline 1986). We developed four models that could account for 95% or more of growth variation (Table 3); improved precision is unlikely due to natural environmental variation and sampling bias (Carline 1986). In contrast, significant models could not be developed for small channel catfish or small smallmouth bass. The inability to define significant growth models does not necessarily imply that growth of these species or size-classes is outside of environmental control or obscured by behavioral patterns. In these cases, growth could simply be limited by other abiotic factors or density-dependent factors such as competition. Alternatively, our single samples of temporally fluctuating variables may have been insufficient to detect patterns. However, the high precision obtained with the remaining models and simple regressions suggests that future attempts to model growth of stream fish by means of similar variables, or additional variables, can be successful.

In addition to defining some ecological relationships with fish growth, we propose that these multiple-regression models are useful in two other ways. First, because little growth information currently exists for stream populations of many of these species, predictions from these models can identify areas with potentially fast fish growth and provide a relatively quick a priori basis for stream fisheries management. With the use of models similar to ours, the environmental databases maintained by natural resource agencies represent potentially important predictive tools. Second, these models represent testable hypotheses for further research. Testing and further refinement with independent data sets is the next step in this empir-

ical approach and may enhance the utility of these models.

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