

## Size-specific growth of bluegill, largemouth bass and channel catfish in relation to prey availability and limnological variables

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Growth of sympatric populations of three important sport fish species: bluegill *Lepomis macrochirus*, largemouth bass *Micropterus salmoides* and channel catfish *Ictalurus punctatus*, in 14 Illinois reservoirs was assessed in an attempt to relate size-specific growth to environmental conditions. Multiple regression relationships for most species and size classes explained a large percentage of the variation in growth. Growth of small bluegill (50 mm total length,  $L_T$ ) showed a strong negative relationship with bluegill catch per unit effort (cpue), per cent littoral area and pH. Large bluegill (150 mm  $L_T$ ) growth was negatively related to *Daphnia* spp. and benthic macroinvertebrate abundance and lake volume, and positively related to bluegill cpue. Growth of small (100 mm  $L_T$ ) and large (250 mm  $L_T$ ) largemouth bass was not well explained by any of the measured variables. Growth of both small (300 mm  $L_T$ ) and large (450 mm  $L_T$ ) channel catfish was strongly positively related to forage fishes and ichthyoplankton abundance, and per cent littoral area while negatively related to benthic macroinvertebrates. By identifying environmental conditions associated with increased growth rates, these models provide direction for managing fish populations and suggest testable hypotheses for future study of the complex interactions between environmental conditions and growth.

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### INTRODUCTION

Growth is an important component of fish ecology, especially during early life-history stages (Sogard, 1994; Claramunt & Wahl, 2000). Smaller individuals are more susceptible to a larger range of predators (Post & Evans, 1989) and have fewer options for diet items due to gape limitations (Zaret, 1980). Growth may

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also play a crucial role in intraspecific competitive interactions. Greater size increases fecundity (Bagenal, 1978), reduces age at first reproduction (Baylis *et al.*, 1993), improves offspring quality (Monteleone & Houde, 1990), affects mating opportunities (Sogard, 1994), and increases fishery quality and therefore angler satisfaction (Anderson, 1980). Size may also be important in the occurrence and severity of overwintering mortality (Post & Evans, 1989).

Numerous studies have been conducted on the age and growth of fishes. While most studies focus on one or two populations of a single species, a few have attempted to examine factors influencing growth across a number of populations (Boisclair & Leggett, 1989*a, b*; Putman *et al.*, 1995). These studies have identified a number of environmental variables playing a role in determining growth. Temperature is one of the most important because of its control of fish metabolic processes (Brett & Groves, 1979). Bioenergetics models based on laboratory experiments show temperature and activity are important in determining fish growth (Kitchell *et al.*, 1977; Boisclair & Leggett, 1989*b*). Density-dependent mechanisms may also strongly influence fish growth through food limitations and competition (Bowen *et al.*, 1991). Exploitative competition, however, may not always be the mechanism for reduced growth rates of fishes at high densities. Increased activity costs may provide a better explanation for the inverse relationship observed between growth and average density of fishes in some circumstances (Boisclair & Leggett, 1989*b*). Other factors including stress (Meador & Kelso, 1990) and prey availability (Kitchell *et al.*, 1977) may affect growth as well.

While a large number of studies have quantified growth rates for several species (Carlander, 1977), only a few studies have developed empirical predictive growth models (Boisclair & Leggett, 1989*a*; Putman *et al.*, 1995). Growth data are more labour-intensive and more costly to obtain than length and mass data (Johnson & Nielsen, 1983). Therefore, the prediction of growth in natural populations of fishes would be simplified and more cost-efficient with the use of empirical models. This modelling approach generally uses information from routine monitoring surveys that often is readily available or can be easily collected. Empirical models have been used to describe fish assemblages and aquatic communities (Pierce *et al.*, 1994), biomass and production (Mahon & Balon, 1977), and yield and standing crop (Matuszek, 1978).

Previous growth studies have typically used age-specific growth rates, which may not best represent ecological and life-history attributes of fishes (Werner & Gilliam, 1984; Sogard, 1994). Fish growth is primarily a function of size rather than age (Gutreuter, 1987). Fishes of a given age, however, are not necessarily of the same size and thus should not be expected to grow at the same rate (Larkin *et al.*, 1957). Size-specific growth rates (Larkin *et al.*, 1957; Gutreuter & Childress, 1990; Putman *et al.*, 1995) allow more meaningful comparisons between populations than do age-specific growth rates (Osenberg *et al.*, 1988).

The purpose of this study was to generate empirical growth models that relate biotic and abiotic variables with size-specific growth rates of fishes from several populations to identify potential determinants of fish growth. This information will be useful to fisheries managers by identifying environmental conditions that are expected to result in faster growth rates for these species. Specifically, the relationship between morphometric, limnological and prey

availability variables and size-specific growth of two size classes of three sport fish species representing different functional groups: largemouth bass *Micropterus salmoides* (Lacépède) (a piscivore), bluegill *Lepomis macrochirus* Rafinesque (an invertivore) and channel catfish *Ictalurus punctatus* (Rafinesque) (a benthic omnivore) (Lee *et al.*, 1980) were investigated in 14 Illinois reservoirs.

## MATERIALS AND METHODS

### STUDY RESERVOIRS AND FISH COLLECTION

Fourteen reservoirs were selected to include the extremes in latitude for Illinois, U.S.A. (northernmost and southernmost lakes were *c.* 550 km apart; Fig. 1) and to encompass a wide range of values for biotic and abiotic variables (Austin, 1992). Each of the 14 reservoirs were sampled from June to October 1993 and from March to

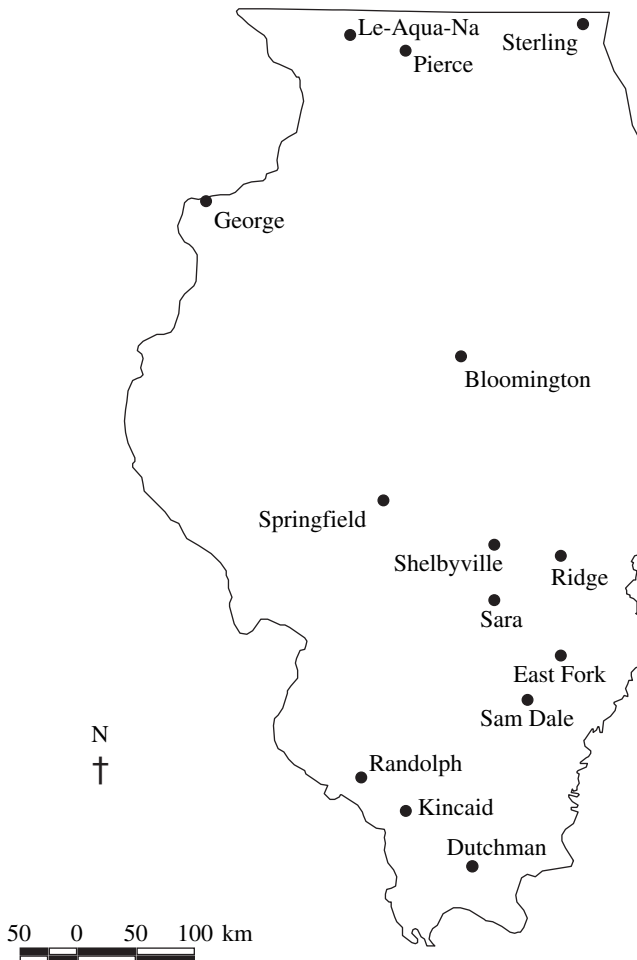


FIG. 1. Location of the 14 Illinois reservoirs sampled. Reservoirs encompassed a range of limnological and morphological characteristics (see Table II).

November 1994 to obtain up to 50 individuals of each fish species, representative of the observed size structure of the population, from each reservoir. Fishes were sampled by boat electrofishing, trap nets, gillnets and seining. Channel catfish were also obtained with the use of slat traps and trotlines.

## GROWTH DETERMINATION

Scales were used for ageing and backcalculating the total lengths ( $L_T$ ) at previous ages for largemouth bass and bluegill (Busacker *et al.*, 1990). Between three and 10 scales per fish were impressed into acetate slides. All scale impressions were viewed when age estimates were recorded. Channel catfish spines were decalcified (Ashley & Garling, 1980) and thin sections were cut at the distal end of the basal groove as described by Sneed (1951). The thin sections were placed in immersion oil to facilitate viewing of annuli. Increments were measured using a digitizing pad (Welker *et al.*, 1994). All ageing was done by two readers (90% agreement); when a discrepancy occurred, a third reader was used. If the third reader was not in agreement with one of the other two, then the fish was discarded (<3% of total fishes). The Fraser-Lee technique (Busacker *et al.*, 1990) was used for backcalculation of  $L_T$  at previous ages based on scale or spine growth increments. Fish >8 years for channel catfish and 5 years for the other species, were omitted from backcalculation to avoid potential errors from incorrect ageing of older fishes.

To determine size-specific growth rates, annual growth increments were regressed against initial  $L_T$  at the beginning of the growing season for all individuals in each species and reservoir combination (Putman *et al.*, 1995). This approach avoided the problems of the histogram approach (Larkin *et al.*, 1957), where broad size groups and the interpolation for missing size classes are inevitable (Putman *et al.*, 1995). Linear and quadratic equations were then fitted to the data in an attempt to most precisely describe the growth for the average fish in each population (Fig. 2). When regressions were not significant, the overall mean growth increment for that species and reservoir combination was used. When both linear and quadratic terms were significant, quadratic equations were used to improve fit. The regressions and mean growth increments were applied only to the sizes of fishes that were collected from the reservoirs and were not extrapolated.

Previous studies have demonstrated that changes in growth rates often occur with distinct ontogenetic shifts in diet or habitat (Larkin *et al.*, 1957; Mittelbach, 1981; Osenberg *et al.*, 1988). Bluegill in some systems switch, at a size between 55 and 80 mm  $L_T$ , from eating benthic and epiphytic invertebrates in littoral habitat to eating zooplankton in pelagic habitat (Osenberg *et al.*, 1988; Werner & Hall, 1988) although some do not undergo an ontogenetic shift but continue to eat invertebrates throughout their life (Schramm & Jirka, 1989). Largemouth bass undergo similar shifts in diet, switching from macroinvertebrates to fishes and crustaceans, between 100 and 150 mm  $L_T$  (Timmons *et al.*, 1980; Miller & Storck, 1984). Therefore, two discrete size classes were chosen from which to examine growth rates for bluegill and largemouth bass corresponding to these ontogenetic stages (Table I). Channel catfish stocking occurred in many of the study lakes and, because growth of these fish prior to stocking ( $\leq 250$  mm) would not be related to lake conditions, only adult sizes for this species were considered (Table I). Growth rate estimates for each species and size class from each lake were calculated using the size-specific regression equations (Fig. 2).

## ESTIMATING PREY RESOURCES AND LIMNOLOGICAL VARIABLES

Ten variables were chosen to describe prey resource availability and habitat conditions that were likely to effect growth. Potential prey populations were quantified as part of an intensive reservoir-monitoring programme (Clapp *et al.*, 1994). Unless specified otherwise, prey resources were sampled every other week at each of six fixed sites

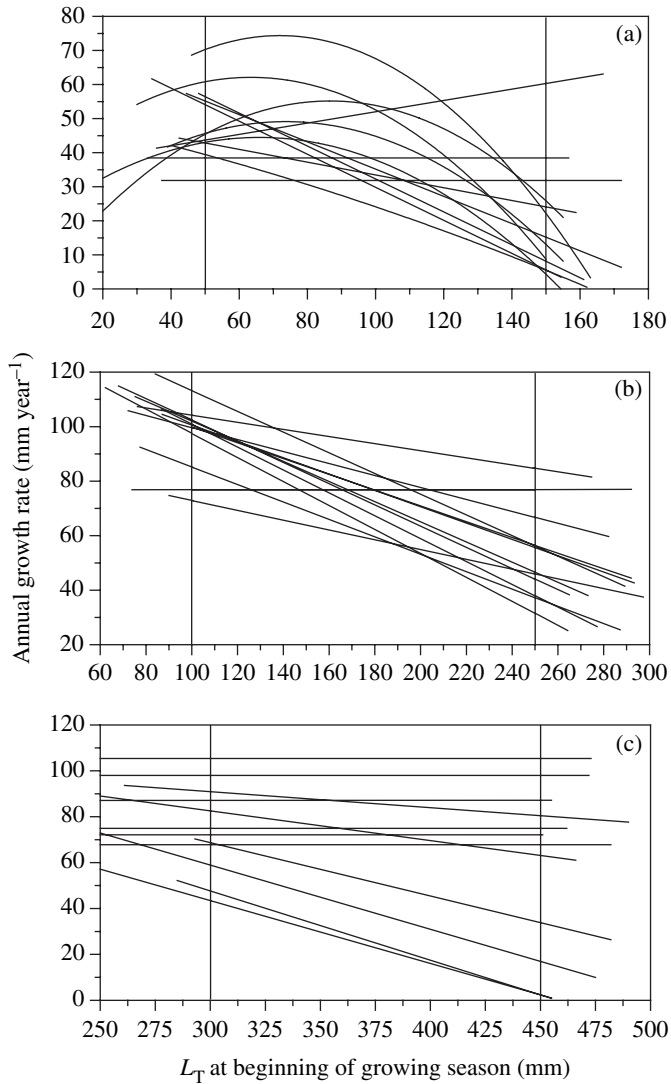


FIG. 2. Regression lines describing size-specific growth of (a) bluegill, (b) largemouth bass and (c) channel catfish in each of the 14 Illinois study reservoirs. Each curve encompasses the range of total lengths ( $L_T$ ) used to develop regressions for each lake and were used to estimate size-specific growth for small and large  $L_T$  classes (indicated by vertical lines) for each species.

on each reservoir from May to August in 1993 and 1994. Benthic macroinvertebrates were sampled using an Eckman or Ponar dredge and were preserved in a 70% ethanol and rose bengal solution. Samples were later sorted to the lowest possible taxonomic group and enumerated. Zooplankton were obtained by making vertical tows with a 0.5 m diameter, 64  $\mu$ m mesh net. Samples were preserved in sucrose-10% formalin solution. Later, samples were adjusted to a constant volume (100 ml) and sub-sampled by 1 ml (0.01) aliquot. Whole sub-samples were counted until at least 200 organisms of each of the most common taxa were enumerated (Welker *et al.*, 1994). Major zooplankton groups were identified, counted and measured (total length, not including spines or appendages). Published regression equations were used to convert total lengths to biomass

TABLE I. Total lengths selected to define 'small' and 'large' sizes of each species. Estimated growth rates are ranges calculated for each size using lake-specific regression equations from the 14 study lakes

Species	$L_T$ (mm)		Estimated growth rate (mm year <sup>-1</sup> )	
	Small	Large	Small	Large
Bluegill	50	150	33–69	0–64
Largemouth bass	100	250	67–114	32–85
Channel catfish	300	450	41–105	0–105

(Dumont *et al.*, 1975; Culver *et al.*, 1985). *Daphnia* spp. biomass was strongly correlated with total macrozooplankton biomass ( $r = 0.88$ ) and because large-bodied *Daphnia* spp. are a preferred prey type for many planktivorous fishes (Brooks, 1968), this metric was used to represent zooplankton prey resources. Potential prey fishes were sampled using surface ichthyoplankton tows (0.5 m long, 500  $\mu\text{m}$  mesh ichthyoplankton nets, 5 min duration) and shoreline seine hauls (9  $\times$  2 m seine, 3 mm mesh). Ichthyoplankton were preserved in 70% ethanol and later identified and enumerated. Seine-caught forage fishes were identified, counted, measured ( $L_T$ , mm) and then released. Only fishes that were small enough to be used as prey by largemouth bass and channel catfish were used in the analysis [ $L_T \leq 42$  mm for small predator size classes,  $L_T \leq 84$  mm for large predator size classes; based on Lawrence (1957) for largemouth bass and D. H. Wahl, unpubl. data for channel catfish]. Relative intraspecific competition was measured as seine catch per unit effort (cpue) for bluegill and small largemouth bass and as electro-fishing cpue for large largemouth bass. Channel catfish abundance data were not available for most lakes, so no measure of relative intraspecific competition was used for this species.

In addition to food availability, fish growth is often affected by lake morphology, amount of available habitat and temperature (Rutherford *et al.*, 1995; Tomcko & Pierce, 2001). Lake morphometry was quantified by lake volume; habitat was quantified as per cent littoral volume (littoral zone volume to reservoir volume ratio), average Secchi disc depth and average pH. Temperature was quantified as growing degree-days (sum of the positive differences between mean daily air temperature and 10° C for a given year; based on data from the U.S. National Weather Service, Asheville, NC, U.S.A.). Secchi disc depth was measured every other week from May to August in 1993 and 1994. All other measurements for each lake were obtained from the Illinois Environmental Protection Agency, Illinois Department of Natural Resources, and from Austin (1992).

## STATISTICAL ANALYSIS

Multiple-regression models were constructed to predict the growth of each size class for each species using the environmental variables. All combinations of the environmental variables were used in models for largemouth bass and channel catfish growth, and all variables except forage fish abundance in models for bluegill growth. Lake volume, forage fish abundance (seine cpue), benthic invertebrate abundance, *Daphnia* spp. biomass and bluegill cpue were ln transformed to normalize the data prior to analysis. Prior to analysis, univariate relationships were considered and regression lines were well supported by the data and not unduly influenced by outliers. The most parsimonious models were determined using second-order Akaike's information criteria (AIC<sub>c</sub>; because the ratio of parameters to observations was <40; Burnham & Anderson, 2002). For models found to have substantial support as the most parsimonious models (AIC<sub>c</sub> values within 2 units of the model with the lowest AIC<sub>c</sub>; Burnham & Anderson, 2002),  $r^2$  was calculated to determine the predictive power of the models.

## RESULTS

Mean resource levels and limnological conditions all varied to differing degrees among the 14 reservoirs (Table II). Estimated annual growth rates for all three species were also highly variable across reservoirs (Table I), and tended to decrease with increasing  $L_T$  (Fig. 2). Linear and quadratic regressions were significant for 34 of the 41 populations (83%). Coefficients of determination ( $r^2$ ) for these annual growth rate regressions were similar for bluegill (mean 0.68, range 0.58–0.79), largemouth bass (mean 0.73, range 0.65–0.88) and channel catfish (mean 0.58, range 0.49–0.81).

The most parsimonious multiple-regression models (models with  $AIC_c$  values within 2 units of the model with the lowest  $AIC_c$ ) explained a large amount of the variance in growth rates among lakes for several species-size combinations (Table III). Small bluegill (50 mm) growth was strongly related to bluegill cpue, pH and per cent littoral area (adjusted  $r^2 = 0.87$ ). Four parsimonious models were identified for large bluegill (150 mm), the best of these models explained 69% of the variance (adjusted  $r^2$ ) in bluegill growth using bluegill cpue, *Daphnia* spp. biomass, benthic invertebrate abundance and lake volume; however the slope for bluegill cpue was not significantly different from zero. Growth rates of both size classes of largemouth bass were not well described by the most parsimonious models (adjusted  $r^2 \leq 0.20$ ). The most parsimonious model for both size classes of channel catfish related growth rates with the abundance of forage fishes, benthic macroinvertebrates, ichthyoplankton and per cent littoral area. The models explained a large amount of the variance

TABLE II. Summary statistics for the nine environmental variables measured in 14 Illinois study reservoirs in 1993 and 1994. All data are untransformed

Character	Mean	Minimum	Maximum	S.E.
Lake volume ( $m^3 \times 10^6$ )	35.58	0.17	258.77	18.47
Growing degree-days ( $10^\circ$ C base)	3587	2748	4292	144
Littoral volume (%)	26	1	53	5
pH	8.12	6.40	9.47	0.20
Secchi disc depth (m)	0.97	0.48	1.73	0.08
<i>Daphnia</i> spp. biomass ( $mg\ l^{-3}$ )	28.72	0.20	190.15	14.30
Ichthyoplankton abundance (number $m^{-3}$ )	0.79	0.03	2.41	0.23
Small forage fish abundance (number seine $^{-1}$ ; <42 mm $L_T$ )	87.91	34.30	189.66	12.12
Small forage fish abundance (number seine $^{-1}$ ; <84 mm $L_T$ )	131.76	42.20	402.08	25.33
Benthic macroinvertebrate abundance (number $m^{-2}$ )	541.75	33.70	1276.94	591.83
Bluegill cpue (number seine $^{-1}$ )	65.67	12.89	282.89	19.8
Largemouth bass cpue (number seine $^{-1}$ )	14.52	3.50	35.25	2.77
Largemouth bass cpue (number $h^{-1}$ electrofishing)	29.71	6.42	57.67	4.44

$L_T$ , total length.

TABLE III. Models relating environment with fish growth in 14 Illinois lakes. Second-order Akaike's information criteria ( $AIC_c$ ) and the difference between each model and the model with the minimum  $AIC_c$  ( $\Delta_i$ ) were used to select the most parsimonious models. Lake volume, forage fish abundance, benthic invertebrate abundance, *Daphnia* spp. biomass and bluegill cpue were ln transformed

Model	Adjusted $r^2$	$AIC_c$	$\Delta_i$	Model parameter	Estimate	$P$
50 mm bluegill growth						
Model 1	0.87	80.7	0.00	Intercept	128.47	<0.01
				Bluegill cpue	-3.77	0.03
				Littoral area	-40.08	<0.01
				pH	-6.61	<0.01
150 mm bluegill growth						
Model 1	0.38	115.7	0.00	Intercept	13.35	0.73
				Bluegill cpue	8.92	0.23
				Benthic invertebrate abundance	-6.03	0.07
Model 2	0.21	115.8	0.03	Intercept	-42.15	0.18
				Bluegill cpue	14.56	0.07
Model 3	0.69	116.6	0.85	Intercept	23.33	0.45
				Bluegill cpue	10.53	0.06
				<i>Daphnia</i> spp. biomass	-10.70	<0.00
				Benthic invertebrate abundance	-11.73	<0.01
				Lake volume	-5.18	0.03
Model 4	0.50	117.2	1.48	Intercept	-1.23	0.97
				Bluegill cpue	9.56	0.16
				<i>Daphnia</i> spp. biomass	-5.27	0.10
				Benthic invertebrate abundance	-8.24	0.02
100 mm largemouth bass growth						
Model 1	0.08	111.8	0.00	Intercept	85.06	<0.01
				Largemouth bass cpue	0.57	0.18
Model 2	0.20	113.2	1.31	Intercept	84.42	<0.01
				Largemouth bass cpue	0.43	0.29
				Forage fish abundance	-1.62	0.14
250 mm largemouth bass growth						
Model 1	<0.01	116.3	0.00	Intercept	50.3395	<0.01
				Largemouth bass cpue	0.23815	0.441
Model 2	<0.01	116.9	0.58	Intercept	72.25	0.11
				Forage fish abundance	-3.14	0.73
300 mm channel catfish growth						
Model 1	0.90	99.2	0.00	Intercept	94.51	<0.01
				Littoral area	88.50	<0.01
				Forage fish abundance	7.95	0.02
				Benthic invertebrate abundance	-13.03	<0.01
				Ichthyoplankton abundance	9.93	<0.01
450 mm channel catfish growth						
Model 1	0.91	111.0	0.00	Intercept	42.91	0.12
				Littoral area	175.66	<0.01
				Forage fish abundance	16.21	0.01
				Benthic invertebrate abundance	-16.03	<0.01
				Ichthyoplankton abundance	17.45	<0.01



in the data for both size classes (300 mm fish, adjusted  $r^2 = 0.90$ , 450 mm fish, adjusted  $r^2 = 0.91$ ).

## DISCUSSION

Understanding the mechanisms that regulate growth is important to the field of fisheries management. The results of this study identify several environmental variables that are related to growth of three important game fish species. Life-history attributes in fishes are often more dependent on fish size than age. Therefore, a size-based analysis provides a more precise characterization of growth within fish populations (Gutreuter, 1987) and allows more meaningful ecological comparisons among populations (Osenberg *et al.*, 1988). The results are consistent with these observations as growth of different size classes was related to unique suites of environmental variables.

Some of the multiple-regression growth models based on the environmental variables explained a large amount of the variability in growth rates for some species and size classes (*i.e.* models for small bluegill and both small and large channel catfish). Variables used to measure intraspecific competition (*i.e.* cpue of the species being modelled) commonly occurred among the most parsimonious models predicting fish growth suggesting populations were probably resource limited. The other variables included in the models indicate what resources may have been most limiting.

For models that explained a large amount of variation, no single or group of variables was consistently most important in explaining variation in growth rates across species. This variation among species is probably a reflection of the different life histories and ontogenetic changes. For example, largemouth bass are piscivorous as adults but are insectivorous as juveniles (Olson, 1996). Adult bluegill often are planktivorous and use the pelagic habitat, whereas juvenile bluegill may be insectivorous in the littoral zone where they are less vulnerable to predation (Werner & Hall, 1988). Therefore, it may not be possible to alter growth rate of all ontogenetic stages of a species simultaneously, and may be even more difficult to affect growth of several species.

Some of the multiple-regression models only explained a small amount of the variance in fish growth (*i.e.* models for both size classes of largemouth bass). Low explanatory ability probably does not indicate a lack of environmental influence on growth of these species and size classes. Rather, it indicates that the combination of variables examined in this study do not reflect the conditions that affect growth rates for these populations. Lakes are highly variable habitats and empirically modelling growth may not be possible for some species due to frequent change in the factors influencing growth. It is also possible that growth was influenced by variables beyond those measured in this study.

An understanding of the potential mechanisms underlying the relationships described by the growth models developed for this study is important in their application. Growth rates for small bluegill were negatively correlated with three habitat variables (bluegill cpue, per cent littoral volume and pH). With the exception of a brief pelagic phase for larval fish (Werner & Hall, 1988; Welker *et al.*, 1994), smaller size classes of bluegill often move into macrophyte cover to avoid predators (Werner & Hall, 1988; Shoup *et al.*, 2003) even

though open water zooplankton provide the highest net energy gain for these sizes of bluegill (Mittelbach, 1981). Within the relatively complex littoral habitat, bluegill do not feed as efficiently (Mittelbach, 1984), resulting in slow growth. Larval bluegill inhabiting pelagic habitat have higher growth rates when zooplankton abundance is greater (Claramunt & Wahl, 2000). Therefore, bluegill in reservoirs with high per cent littoral volume may experience lower growth rates as a result of increased foraging in this habitat. This finding is consistent with Unmuth *et al.* (1999) who found increased bluegill growth rates after manual vegetation removal. Bluegill typically avoid habitats with pH  $\geq$  9.5 (Serafy & Harrell, 1993) but are tolerant of habitats with pH as low as 5.0 (Rahel, 1984). The lakes included in the present study had pH values ranging from 6.4 to 9.5, suggesting low growth rates for bluegill were caused by high pH. No previous laboratory study, however, has measured the effect of pH on growth of bluegill, suggesting further research is needed to quantify these relationships.

Unlike small bluegill, growth rates for large bluegill were negatively correlated with prey abundance (*Daphnia* spp. and benthic macroinvertebrates) and lake volume. The negative relationship with lake volume probably reflects adaptations to small or shallow habitats (Lee *et al.*, 1980). Bluegill typically eat *Daphnia* spp. and benthic macroinvertebrates (Sadzikowski & Wallace, 1976), however, and the negative relationships were unexpected. Colinearity between these variables and some other factor could also affect bluegill growth.

None of the variables significantly correlated with growth of either size class of largemouth bass. Perhaps there are other environmental characteristics not included in this study that would affect growth of largemouth bass. Other studies have found relationships between largemouth bass growth rates and total phosphorus in lakes (Yurk & Ney, 1989; Putman *et al.*, 1995) and substratum composition in streams (Putman *et al.*, 1995). Total phosphorus is a measure of lake productivity and this study's direct measure of prey availability should be more closely related to fish growth (Carpenter *et al.*, 1985). Zooplankton and benthic invertebrate prey measured in the present study are the primary prey of small largemouth bass (<100 mm; Timmons *et al.*, 1980; Miller & Storck, 1984). For adult largemouth bass, other prey species not well quantified by seine samples such as gizzard shad *Dorosoma cepedianum* (Lesueur) (Johnson *et al.*, 1988) or crayfishes may have more closely correlated with adult growth rates. Contrary to this study's results, other studies have found a relationship between largemouth bass growth rates and temperature (McCauley & Kilgour, 1990). It is possible that complex interactions among a number of factors that vary by lake may determine growth of largemouth bass.

Channel catfish was the only species in the study for which similar variables were the best predictors of growth for both size classes. This was not unexpected, as the size classes represented similar ontogenetic stages. Growth rates of both size classes of channel catfish were correlated with food availability (forage fish abundance, benthic macroinvertebrate abundance and ichthyoplankton abundance) and per cent littoral volume. Previous studies have demonstrated that channel catfish are primarily piscivorous or insectivorous (Hill *et al.*, 1995; Edds *et al.*, 2002), and typically inhabit littoral areas (Carlander, 1977; Edds *et al.*, 2002). The results of this study suggest that foraging in

littoral habitat is adaptive for this species and yields faster growth. The negative relationship between channel catfish growth and benthic macroinvertebrate abundance could indicate that macroinvertebrates are not as energetically valuable to channel catfish as are fish prey. This has not been empirically investigated, however, and further research is warranted.

These models include some variables that managers can attempt to manipulate to enhance growth. For example, managers can manipulate prey populations (Noble, 1981) or alter the per cent of littoral area (Unmuth *et al.*, 1999). Other variables, however, may not be easily manipulated (*e.g.* pH and temperature). In situations where competition was suggested, one possible management option is to reduce the population of the species of interest. These models are based on the combined effect of the variables included, and altering one of these variables alone may not enhance growth rates. Managers should consider the state of variables that may be beyond their control before considering management options, and manipulation efforts should be focused on lakes that already have conditions conducive to high growth.

Growth models can also be used to identify environments that should naturally have high or low growth rates for specific species and size classes of fishes. In this way, managers can identify which lakes have the best potential to create fisheries for specific species. For example, it will be most cost-effective to stock channel catfish in lakes where they are predicted to have the highest growth rates. Similarly, lakes to manage for trophy fishes can be chosen from those with variables indicating the potential for high growth.

The predictive models presented in this study identified factors that are related to growth for each species except largemouth bass. While correlations do not imply causality, managers desiring to improve growth rates of these species should give special consideration to these variables as potential determinants of growth. Several of these models also identified unexpected relationships between environmental factors and fish growth that represent testable hypotheses for further research. This also suggests that the complexity of lake environments may make it difficult to identify useable predictive growth models for some species (*i.e.* largemouth bass). The multivariate size-based analysis used in the present study takes into account potential interactions between variables that influence growth of fishes at different life-history stages. The results of this study demonstrate that different factors are related to growth of each species and to growth of different life-history stages of the same species. Successful management strategies will need to employ a multidimensional approach to produce high growth rates for multiple species or all size classes of a given species. In some cases, these differences among species may make it impossible to manage for high growth rates of multiple species in the same environment and is likely true of a number of aquatic systems with other species of fishes.

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