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Growth of Bluegill, Largemouth Bass, and Channel Catfish in Relation to Fish Abundances, Food Availability, and Other Limnological Variables

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Abstract

Bluegill, largemouth bass, and channel catfish are widely distributed and popular sports species. We assessed growth of sympatric populations of these species in 14 reservoirs throughout Illinois, and attempted to relate growth to environmental factors. Principal components analysis (PCA) classified the lakes using 20 morphometric and limnological variables. We examined growth rate relationships with the principal components, via correlations, and also developed simple and multiple regression models using individual variables. Using size-specific growth for two size classes, percent littoral zone of a lake was correlated with growth of both channel catfish (300 and 450 mm) and small bluegill (50 mm). Lake latitude was correlated with growth of large bluegill (150 mm). There were no significant correlations for either size of largemouth bass (100 and 250 mm). Our empirical relationships provide working models of fish growth and suggest testable hypotheses for future study. The models, when tested against independent data sets, will provide managers with useful tools for making inexpensive, *a priori* assessments of a fishery resource.

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This thesis is dedicated to the memory of
Elizabeth Callahan.

Introduction

Growth is an important component of fish ecology (Brandt and Mason 1994; Sogard 1994; Summerfelt and Hall 1987), especially during early life history stages (Miller et al. 1988; Pepin 1991). Growth affects size-selective predation, with the smaller individuals in the population being more susceptible to a larger range of predators (Luecke et al. 1990; Post and Evans 1989), and may play a crucial role in intra-specific competitive interactions. Increased size has been shown to increase fecundity (Bagenal 1978), reduce age at first reproduction (Baylis et al. 1993), improve offspring quality (Buckley et al. 1991), affect mating opportunities (Sogard 1994), and increase angler satisfaction. Size may also be important in the occurrence and severity of overwinter mortality (Post and Evans 1989; Toneys and Coble 1979).

Numerous studies have been conducted on the age and growth of fish. Most of these studies documented growth of single species in single locations, reflecting narrow purposes such as determining the age of the fish caught in commercially exploited populations. As interest in growth rates of fish has increased, fisheries ecologists have begun to ask more sophisticated questions about the patterns and determinants of growth. Studies have shown that a number of environmental variables may play a role in determining

growth. Temperature is one of the most important due to its control of the metabolic requirements of a fish (Brett and Groves 1979). Bioenergetics models based on laboratory experiments show that temperature (Bevelhimer et al. 1985; Kitchell et al. 1977) and activity (Boisclair and Leggett 1989c) have an important role in determining fish growth. Density-dependent mechanisms may also strongly influence fish growth due to limits of prey availability and subsequent competitive interactions (Bowen et al. 1991; Walters and Post 1993). Others have suggested that it may not always be competitive exploitation that negatively affects growth, but rather an increase in activity costs, which provides a better explanation for the inverse relationship between growth and average fish density (Boisclair and Leggett 1989c). Other factors including stress (Meador and Kelso 1990), prey availability (Kitchell et al. 1977) and consumption rates (Condrey 1982; Soofiani and Hawkins 1985) may affect growth as well.

Carlander (1977) documented a large number of studies that examined the growth rates of several species, but only a few studies have developed predictive growth models (e.g. Adams and McLean 1985; Gutreuter and Childress 1990; Putman et al. 1995). Growth data are more labor intensive and more costly to obtain than length and weight data (Johnson and Nielsen 1983). The prediction of growth in natural populations of fish would be simplified and more

cost-efficient with the use of empirical models (e.g. Putman et al. 1995). This modelling approach generally uses more easily collected and often readily available information from routine monitoring surveys. Empirical models have been used to describe fish assemblages and communities (Matusek et al. 1990; Pierce et al 1994), biomass and production (Mahon and Balon 1977), and yield and standing crop (Matuszek 1978; Schneider 1978).

Most previous growth studies have used age-specific growth rates, which may not best represent ecological and life-history attributes (Miller et al. 1988; Pepin 1991; Sogard 1994; Werner and Gilliam 1984). Fish growth is primarily a function of size, rather than age (Gerking and Rausch 1979; Gutreuter 1987). Fish of a given age are not necessarily the same size and thus should not be expected to grow at the same rate (Larkin et al. 1957). Therefore, we examined size specific growth of three fish species representing three different functional groups: largemouth bass (Micropterus salmoides, a piscivore), bluegill (Lepomis macrochirus, an invertivore), and channel catfish (Ictalurus punctatus, a benthic omnivore). These species undergo ontogenetic niche shifts and associated changes in energetic requirements (Osenberg et al. 1988; Putman et al. 1995; Werner and Gilliam 1984), and growth of these species are probably related to a number of environmental parameters (Putman et al. 1995).

With these possible relationships in mind, our objectives were to: 1) quantify the range of variation in growth rates of these three species in Illinois, 2) compare patterns of growth rate variation among species and among size-classes within species, 3) explore relationships of growth with food resources, fish abundances, and limnological factors, and 4) generate general, empirical growth models that will provide useful management tools and help guide fisheries ecologists in understanding the determinants of fish growth.

Materials and Methods

Study lakes and fish collection

We chose several reservoirs that would encompass a wide range of abiotic and biotic parameters. We selected 14 reservoirs located throughout Illinois (Fig. 1) that encompassed the range of latitudes, and varied widely in their limnology and morphology as suggested by previous studies (Austin 1992).

We sampled each of the 14 lakes from June to October 1993 and from March to November 1994 to obtain up to 50 individuals, representative of the observed size structure of the population, of each species from each reservoir. Fish were sampled by boat electrofishing, trap nets, gill nets, and seining. Channel catfish were also obtained with the use of slat traps and trot lines.

Growth Determination

Scales were used for aging and backcalculating the lengths at previous ages for largemouth bass and bluegill (Busacker et al. 1990). Between 3 and 10 scales per fish were impressed into acetate slides. All scale impressions on the slides were viewed when age estimates were recorded. Channel catfish spines were decalcified (Ashley and 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. All aging was done by 2 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 fish).

We used the Fraser-Lee technique (Busacker et al. 1990) for back-calculation of lengths at previous ages based on scale or spine growth increments. Standard values for the intercept of the linear body-scale regression for largemouth bass and bluegill were obtained from Carlander (1982) and from Putman et al. (1995) for channel catfish. Fish older than 8 years, for channel catfish, and 5 years, for the other species, were omitted from backcalculation to avoid potential errors from incorrect aging of older fish.

Using the back-calculated lengths at previous ages and differences between successive lengths as estimates of annual growth increments, we regressed annual growth

increments against initial length (length at the start of the growing season) for each species in each lake. A detailed explanation and example of this procedure is given in Putman et al. (1995).

For each species, we chose two size-classes from which to examine growth rates (Table 1). These sizes represent different life-history stages with different diet and habitat requirements and thus each size-class may be under the influence of different environmental variables.

Estimating prey resources and limnological parameters

Benthic invertebrate, zooplankton, ichthyoplankton, and forage fish abundances in each lake were sampled monthly from March 1993 to October 1993 as part of an intensive reservoir monitoring program (Clapp et al. 1994). Prey resources were sampled at each of three fixed sites on each lake. Benthic invertebrates were obtained using an Eckman or Ponar dredge. Samples were filtered through a #30 sieve, preserved in a 70% ethanol and rose bengal solution and later sorted to the lowest possible taxonomic group, enumerated, and measured for conversion to biomass (Smock 1980). Zooplankton were obtained by making vertical tows with a 0.5 m diameter, 64 um mesh zooplankton net. Samples were preserved in a sucrose-10% formalin solution. Later, samples were adjusted to a constant volume (100 ml) and subsampled by 1 ml (1/100) aliquot. Major zooplankton

groups were identified, counted, and measured for biomass conversions (Culver et al. 1985; Dumont et al. 1975). Zooplankton were separated into two size groups for analysis (large > 1.0 mm, small < 1.0 mm). Potential prey fish were sampled using standardized surface ichthyoplankton tows (0.5 m, 5.0 min, 500 um larval fish nets) and shoreline seine hauls (9 x 2 m seine, 3 mm mesh). Larval fish were preserved in 70 % ethanol and later identified, counted, and measured to the nearest mm (TL). Seine-caught fish were identified, counted, measured to the nearest mm (TL), then released.

Macrophyte and epiphytic macroinvertebrate samples were collected in June and September 1993 from each of the study lakes. Macrophytes were sampled by taking 20 randomly chosen 0.19 m^2 quadrats. Samples were wet weighed (nearest gram), and mean biomass (g/m^2) determined. Epiphytic macroinvertebrates were sampled at 10 locations randomly chosen within macrophyte beds using a box sampler (Downing 1986). Organisms were washed and picked from the macrophytes, identified to the lowest possible taxonomic group, counted, and up to 30 individuals per group were measured for biomass conversions (Smock 1980). The box-sample macrophytes were weighed as described above. Macroinvertebrate density and biomass estimates were divided by the weight of the macrophytes from the box sample to obtain estimates per gram of macrophyte. All biotic

variables were analyzed as a yearly mean and as a spring mean if the peaks for densities occurred for all lakes within the same month.

Abiotic lake parameters were obtained from the Illinois Environmental Protection Agency, Illinois Department of Natural Resources, and the literature (Austen 1992). Parameters examined were latitude, surface area, mean and maximum depths, watershed, storage capacity, and total alkalinity.

Statistical Analysis

Box plots were used to determine normality for each variable examined. Where necessary, variables were transformed using either natural log (Ln (x+1); surface area, shore length, watershed, volume, benthic invertebrate and zooplankton densities) or arcsine transformations (Arcsine (x); littoral zone to lake volume and littoral zone to lake area).

Principal components analysis (PCA) was used to combine the individual variables into a new, smaller set of linear constructs that account for most of the variation observed among the lakes. Principal components were extracted from the correlation matrix. This technique is a powerful tool for detecting patterns in and reducing the dimensionality of complex multivariate data (Van Tongeren 1995). The examined variables were divided into an abiotic and biotic analysis

due to the limitations of PCA where the number of variables included should be less than the number of experimental units. Varimax rotation was used to better interpret the components. Relationships of PCA scores with growth rates were explored using Pearson correlation coefficients.

Simple and multiple regressions were developed to describe the growth of each size-class for each species. We created simple regression models for the variables found to be important, via significant correlations ($P<0.05$), in the PCA. We developed multiple regression models for each size and species with a forward stepwise technique, beginning with a single variable most highly correlated with growth. More variables were added to the model based on the highest significant correlation with residual model variance. Only independent variables that were not significantly correlated were used in this analysis to prevent autocorrelation. Variables were added as long as all model coefficients remained significant.

Results

Abiotic and biotic parameters were highly variable across the lakes (Tables 2 and 3). PCA ordination of the lakes based on the abiotic variables indicated little or no aggregation of lakes by their limnological and morphometric characteristics (Figure 2). Each component being a combination of the individual variables creating a new

independent, multivariate ,linear construct that accounts for a relatively high percent of the variation observed between the lakes. Principal component 1 (Abiotic 1) explained 41 % of the variation observed between the lakes. Abiotic 1 was defined by the characteristics that describe the size of a lake, including surface area, watershed area, storage capacity, and shore length (Table 4). Principal component 2 (Abiotic 2) best reflects the latitude and total alkalinity of the lake and explains an additional 27 % of the variation observed. Principal component 3 (Abiotic 3) explained 19 % of the variation and mainly reflected the percent littoral zone of the lake. Combined, the 3 components account for 87 % of the abiotic variation observed between the lakes.

PCA ordination of the lakes based on the biotic variables (Figure 3) also revealed no clustering or grouping. Principal component 1 (Biotic 1) explained 31 % of the variation and reflected benthic invertebrate densities (Table 5). Principal component 2 (Biotic 2) was defined by early in the year zooplankton densities and explained 31 % of the lakes variation. Principal component 3 (Biotic 3) explained an additional 17 % and was best defined by the forage fish densities of the lakes. The 3 biotic components account for 71 % of the variation observed between the lakes.

Annual growth rates were highly variable across the

lakes (Table 1). For all species and in most lakes, annual growth decreased as the fish became larger (Fig. 4). Among populations of channel catfish, growth of small and large size classes were strongly and positively correlated ($r = 0.92$, $P=0.001$, $N=13$). In contrast, growth rates between the two size classes of bluegill and largemouth bass were not significantly correlated. There were also no correlations between size classes of the different species.

Correlations between growth rates and the principal components revealed significant relationships for four of the six species-size combinations. Bluegill growth was related to different parameters. Growth of small bluegill (50 mm) was positively correlated with percent littoral zone of the lake (Abiotic 3, Fig. 5). As expected, small bluegill growth was regressed significantly against the littoral zone to lake area ratio (Table 6). The pH of the lakes was also significantly regressed with small bluegill growth. Large bluegill growth was positively correlated to the principal component that describes the latitude of the lakes (Abiotic 2, Fig. 6). Significant regressions were found between large bluegill growth and latitude and alkalinity (Table 6). Large bluegill growth was also significantly related to degree days (Table 6), a variable highly correlated with latitude ($r=0.91$, $P=0.001$, $N=14$). Storage capacity, mean depth and conductivity were also significantly regressed with large bluegill growth. The

correlation and regression analyses for bluegill growth indicate no significant relationships with the biotic PCA nor the individual biotic variables.

Unlike bluegill, largemouth bass growth was not significantly related to any of the components, abiotic or biotic. Growth of small largemouth bass was marginally, yet non-significantly, correlated with latitude of the reservoir (Abiotic 2, r=0.30, P=0.09, N=14). Growth of the large size-class was not significantly related to any of the principal components at the alpha=0.05 level, but there was a weak relationship between growth and the amount of littoral zone of the lake (Abiotic 3, r=-0.50, P=0.08, N=14).

Channel catfish growth at both sizes was significantly correlated to the multivariate descriptor littoral zone (Abiotic 3, Fig. 7). No relationships with the biotic components, nor the biotic variables, were evident. Several significant regressions were created for both size-classes including the variables percent littoral, mean depth and shore length (Table 6).

Discussion

To obtain size-specific growth rates, we fit a continuous regression to each of the populations; avoiding the problems of the histogram approach (e.g. Larkin et al. 1957), where broad size groups and the interpolation for

missing size classes is inevitable (Putman et al. 1995). Regressions were significant for 75 % of our populations. The high coefficients of determination (0.49 - 0.88) suggests that these growth trajectories accurately represent the growth of each population.

Use of size-specific growth rates (Gutrueter and Childress 1990; Larkin et al. 1957; Putman et al. 1995) allows more meaningful comparisons among populations (Osenberg et al. 1988). Many species undergo distinct ontogenetic habitat shifts as they attain larger sizes (Werner and Gilliam 1984). We chose the sizes for each species in an attempt to encompass these ontogenetic shifts. Previous studies have demonstrated that changes in growth trajectories occur with distinct shifts in diet or habitat (Larkin et al. 1957; Mittelbach et al. 1981; Osenberg et al. 1988;). Differences in growth rates of large and small size-classes of largemouth bass and bluegill indicate that we choose sizes that encompass such a shift. Bluegill, and other Lepomis spp., undergo a number of diet and habitat shifts with increasing size (Mittelbach et al. 1981; Osenberg et al. 1988; Werner and Hall 1988). Largemouth bass have a diet shift, from macroinvertebrates to fish and crustaceans, between 100 and 150 mm total length (Timmons et al. 1980). The lack of a difference in the channel catfish sizes indicates that we either chose sizes that do not encompass a diet shift or that growth was affected by

parameters other than size. Channel catfish are benthic omnivores as adults, but are primarily invertivores as juveniles (Carlander 1977). However, Putman et al. (1995) also failed to demonstrate differences between small (100 mm) and large (300 mm) channel catfish. If niche shifts occur for channel catfish, they likely do so at sizes less than 100 mm.

We used multivariate (PCA) and regression (simple and multiple) approaches to better understand a complex ecological system. Growth is likely not controlled by a single parameter, nor by a number of independent parameters. Instead, there are complex webs of interaction within and between abiotic and biotic factors operating in any natural system that may contribute to growth patterns. The PCA allow us to examine these interactions from a holistic ecological viewpoint. In contrast, the regression approach may be more useful as a management tool. These relatively simple models allow predictions with relatively low cost and reduced sampling effort.

Amount of littoral zone was related to growth rates more consistently than other variables for all species. Habitat complexity (i.e. macrophytes, woody debris) can dramatically alter trophic interactions in a lake. Macrophytes have been shown to negatively affect planktonic algal biomass, and to affect fish populations by altering the composition and abundance of zooplankton and

macroinvertebrate populations (Watkins et al. 1983; Wiley et al. 1984). Habitat complexity in the littoral zone alters predator - prey interactions (Savino and Stein 1982), and can increase competition by providing a common refuge for fish of the same size.

Lakes with higher percentages of littoral zone had relatively slower growth of small bluegill. Zooplankton provides the highest net energy gain for bluegill (Mittelbach et al. 1981), but smaller size-classes are forced into macrophyte cover to avoid predators (Mittelbach et al. 1988; Osenberg et al. 1988; Werner and Hall 1988). Therefore small bluegill are cut off from the high energy diet of the open water zooplankton. Within lakes with high percent littoral zones, bluegill are feeding on less profitable food items and are being preyed upon less due to increased habitat complexity. Within the macrophyte refuge, prey resources are often limiting due to high numbers of small centrarchids (Mittelbach 1984, 1986), resulting in slow growth. An alternative to this density-dependent exploitative interaction hypothesis is that the relationship between slower growth and predator induced fish density is a result of increases in fish activity levels as fish densities increase (Boisclair and Leggett 1989c). These hypotheses,(density-dependent competition and activity) should be examined further to determine which one plays a greater role in the relationship between bluegill growth and

percent littoral zone.

Large bluegill growth was not related to percent littoral zone, probably because 150 mm bluegill are free from the predation bottleneck and able to forage on open water zooplankton. However, growth of large bluegill was related to latitude, with southern populations having faster growing fish than lakes in the northern part of the state. Increased length of the growing season in lower latitudes probably drives these relationships. Significant regressions between large bluegill growth and total alkalinity are probably a reflection of the strong north to south gradient in alkalinity of the lakes and do not represent a direct effect on bluegill growth.

There have been a number of previous attempts to model largemouth bass growth. However, many of these are inadequate for reservoir management because they require intensive sampling for back-calculated lengths or individual ages (e.g. Gutrueter and Childress 1990) or have been derived in lotic systems (Putman et al. 1995). Models using condition indices (e.g. Adams and McLean 1985) and environmental qualities (e.g. Putman et al. 1995) have explained 60 to 90 % of the variation observed in largemouth bass growth. We found no significant relationships between largemouth bass growth and any of the components or variables. However, a few studies have developed significant models in the past for largemouth bass in

relation to environmental variables. Models developed in lotic systems have identified phosphorus, a number of sediment types, and a few community indices as being important for largemouth bass growth (Putman et al. 1995).

Both large and small sizes of channel catfish have faster growth in lakes with more littoral zone. Channel catfish are known to be benthic omnivores and prefer to forage in the littoral zone of lakes (Carlander 1977; Scott and Crossman 1973). We would expect faster growth in lakes with increased preferred foraging area. The exact mechanisms for these relationships should be examined in future studies.

Our growth models fell within the ranges of precision found in a number of other growth (Adams and McLean 1985; Gutreuter and Childress 1990; Larkin et al. 1957; Putman et al. 1995) and population (Carline 1986) studies. Both size-classes of bluegill and channel catfish had significant regressions; one of which explains at least 64 % of the growth variation. However, we cannot conclude that, due to a lack of significant regressions, growth of largemouth bass at either size is free from environmental or behavioral control. The presence of and precision of other models (Adams and McLean 1985; Gutreuter and Childress 1990; Putman et al. 1995) suggests otherwise. Perhaps there are other environmental characteristics yet unexamined, behavioral patterns or biotic-abiotic interactions not accounted for,

or density-dependent effects undetected in this study that would yield significant, useful models for largemouth bass.

Of the six species and size-class combinations, there were a number of significant relationships between the principal components and individual variables and growth. All of these, however, were derived from abiotic variables. The lack of significant relationships with biotic variables is contrary to a number of studies, particularly previous laboratory evaluations. Many laboratory studies have indicated a relationship between quantity of prey items consumed and growth (see Soofiani and Hawkins 1985). Other studies demonstrate a positive relationship between prey size and fish growth (e.g. Hart and Connellan 1984). Biotic variables, of which eight of nine are potential prey resources, did not appear to have any relationship to growth rates in this study. High variance in these variables require rigorous sampling regimes to quantify and could have obscured relationships. However, the sampling regime and methods we employed were as intensive as most previous studies in the literature (e.g. Welker et al. 1994). Complex ecological interactions between biotic variables, and also those between abiotic and biotic variables, could have prevented detection of their influences on fish growth in an empirical field study such as ours.

The multivariate analysis (PCA) yielded a number of ecologically significant relationships with fish growth.

The correlations allowed development of a number of regression models that created a number of testable hypothesis for future research on growth of these three species. This study did not examine all of the possible factors that might influence growth directly or that serve as indirect indicators of growth. However, we do believe the 20 variables examined encompass a large range of possible influential parameters. In order for these models to be proven useful they need to be tested for reliability with independent data sets. With large environmental data bases often available, these tested models will eventually enable managers to make a priori assessments of a reservoir to determine the relative growth rate of its resident fish.

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Table 1. Total lengths used to define small and large sizes and ranges of annual growth rates for three species of fish. Annual growth was calculated from lake-specific regressions for each species.

	Total length (mm)		Annual growth (mm)	
Species	small	large	small	large
Bluegill	50	150	33-69	2-64
Largemouth bass	100	250	67-99	32-84
Channel catfish	300	450	41-105	3-105

Table 2. Summary statistics for abiotic characteristics of the 14 reservoirs surveyed in this study. All data are untransformed.

Character	Mean	Min	Max	Standard error
Latitude	---	37^0 30'00"	42^0 28'26"	---
Surface area (ha)	634.7	5.6	4492.5	324.4
Mean depth (m)	4.36	2.3	7.56	0.41
Shore length (km)	48.2	0.9	276.8	20.51
Watershed area (ha)	30117	72	272986	19412
Storage capacity (1000 m^3)	25758	127	222051	15783
Total alkalinity (mg/l $CaCO_3$)	127.7	51.0	214.6	13.3
Growing degree days (50°F base)	181	152	206	4.2
% littoral volume	26.0	0.1	52.5	4.5
% littoral area	18.6	0.1	51.0	3.8
pH	8.12	6.40	9.47	0.198

Table 3. Summary statistics for biotic characteristics of the 14 reservoirs surveyed in this study. All data are untransformed; biomass data are wet mass.

Character	Mean	Min	Max	Standard error
Benthic invertebrate yearly mean density (number·m^{-2})	589.53	29.41	1894.41	185.05
Benthic invertebrate spring mean density (number·m^{-2})	786.39	20.22	3418.40	308.12
Forage fish density yearly mean (number per seine)	14.24	5.78	30.65	2.28
Forage fish density 40-100 mm yearly mean (number per seine)	6.83	2.50	14.17	1.03
Ichthyoplankton yearly mean (number·m^{-3})	1.79	0.06	6.72	0.68
Large zooplankton yearly mean (number·L^{-1})	11.50	1.21	42.81	3.45
Small zooplankton yearly mean (number·L^{-1})	5.06	0.64	12.15	1.18
Epiphytic invertebrate yearly mean (number·g of macrophyte^{-1})	0.79	0.05	2.86	0.22
Macrophyte yearly mean biomass (g·m^{-3})	751.87	24.20	1426.00	147.76

Table 4. Eigenvector coefficients from a PCA (varimax rotation) of abiotic variables for the 14 reservoirs. Underlining indicates variables strongly correlated (r>0.50) with individual components. Variables with an asterisk denote those that have been arcsin transformed.

	Principal Components		
	1	2	3
Log_e hectares	0.953	-0.001	0.248
Log_e watershed	0.933	-0.076	0.255
Log_e stor. cap.	0.956	-0.026	0.218
Log_e shore length	0.962	0.149	0.134
Pct. vol. as littoral*	-0.290	0.027	-0.922
Pct. area as littoral*	-0.222	0.264	-0.887
Growing degree days	0.110	0.937	-0.214
Latitude	-0.148	-0.949	-0.046
Total alkalinity	0.192	-0.904	0.150
Mean depth	0.525	0.022	0.045
pH	0.020	-0.211	-0.631
% variance explained	40.978	26.947	19.002

Table 5. Eigenvector coefficients from a PCA (varimax rotation) of biotic variables for the 12 of the 14 reservoirs. Underlining indicates variables strongly correlated (r>0.50) with individual components. Variables with an asterisk denote those that have been log transformed. Only reservoirs in which all variables were estimated were included in the analysis.

	Principal Compoments		
	1	2	3
Benthic invertebrates* (yearly mean)	0.909	0.317	0.033
Benthic invertebrates* (early mean)	0.958	0.193	-0.118
Small zooplankton (early mean)	0.035	0.936	-0.036
Large zooplankton* (early mean)	-0.008	0.910	-0.046
Epiphytic invertebrates* (yearly mean)	0.168	0.698	0.053
Ichthyoplankton* (yearly mean)	0.815	-0.352	0.110
Macrophyte (yearly mean)	-0.203	0.468	0.492
Forage fish* (yearly mean)	0.314	-0.342	0.806
Forage fish (40-100 mm yearly mean)	-0.424	0.144	0.774
% variance explained	30.649	30.213	16.958

Table 6. All significant ($P \leq 0.05$) simple and multiple regression models that accounted for variance in predicted annual growth (G_p, mm) for each of the species and sizes. There were no significant models for either size-class of largmouth bass. MSE = mean square error and N = number.

Model	Significance (P)		R^2	MSE	N
	Coefficient	Model			
	Small bluegill				
G_p=-22.84	0.050	0.009	0.43	7.20	13
+33.13 (arcsin pct. area litt.)	0.009				
G_p=40.65	0.050	<0.001	0.79	4.37	13
+33.35 (arcsin pct. area litt.)	<0.001				
-7.88 (pH)	0.001				
	Large bluegill				
G_p=179.72	0.015	0.022	0.34	9.86	13
-0.001 (latitude)	0.022				
G_p=-72.61	0.035	0.015	0.38	9.52	13
+0.48 (growing degree days)	0.015				
G_p=37.50	<0.001	0.005	0.49	8.63	13
-0.18 (total alkalinity)	0.005				
G_p=226.44	0.004	0.019	0.46	8.89	13
-0.001 (latitude)	0.008				
-2.41 (log storage capacity)	0.050				

Table 6. continued

Model	Significance (P)		R2	MSE	N
	Coefficient	Model			
		Large bluegill (continued)			
G_p=59.72	<0.001	0.001	0.72	6.52	12
-3.38 (mean depth)	0.029				
-0.08 (conductivity)	0.001				
		Small channel catfish			
G_p=212.37	0.003	0.030	0.33	17.17	12
-63.01 (arcsin pct. area litt.)	0.030				
G_p=217.09	0.001	0.012	0.55	14.11	12
+5.78 (log shore length)	0.039				
-74.66 (arcsin pct. area litt.)	0.006				
		Large channel catfish			
G_p=377.47	<0.001	0.003	0.74	19.68	12
-13.10 (mean depth)	0.026				
+26.49 (log shore length)	0.001				
-165.60 (arcsin pct. vol. litt.)	0.001				

Figure Captions

Figure 1. Location of Illinois lakes sampled in this study examining effects of biotic and abiotic variables on bluegill, largemouth bass, and channel catfish growth.

Figure 2. Principal component ordination of abiotic variables in Illinois lakes. Each axis represents a principal component. Abiotic 1 being defined by lake size variability, abiotic 2 by latitude, and abiotic 3 by the percent littoral zone of the lakes. Each data point represents a lake. Only lakes in which all variables could be obtained are included (N=13).

Figure 3. Principal component ordination of biotic variables in Illinois lakes. Each axis represents a principal component. Biotic 1 characterized by benthic invertebrate densities, biotic 2 by zooplankton densities, and biotic 3 by forage fish densities. Each data point represents a lake. Only lakes that had all variables measured are included (N=12).

Figure 4. Regression lines describing size-specific growth in each lake for each species. Each line encompasses the range of sizes used to develop regressions for each lake and were used to create size-specific growth estimates.

Vertical lines indicate small and large size-classes.

Figure 5. Relationship of small bluegill (50 mm) growth with scores from the third abiotic principal component (percent littoral zone).

Figure 6. Relationship of large bluegill (150 mm) growth with scores from the second abiotic principle component (latitude).

Figure 7. Relationship of small channel catfish (300 mm) growth with scores from the third abiotic principle component (percent littoral zone).

Figure 1

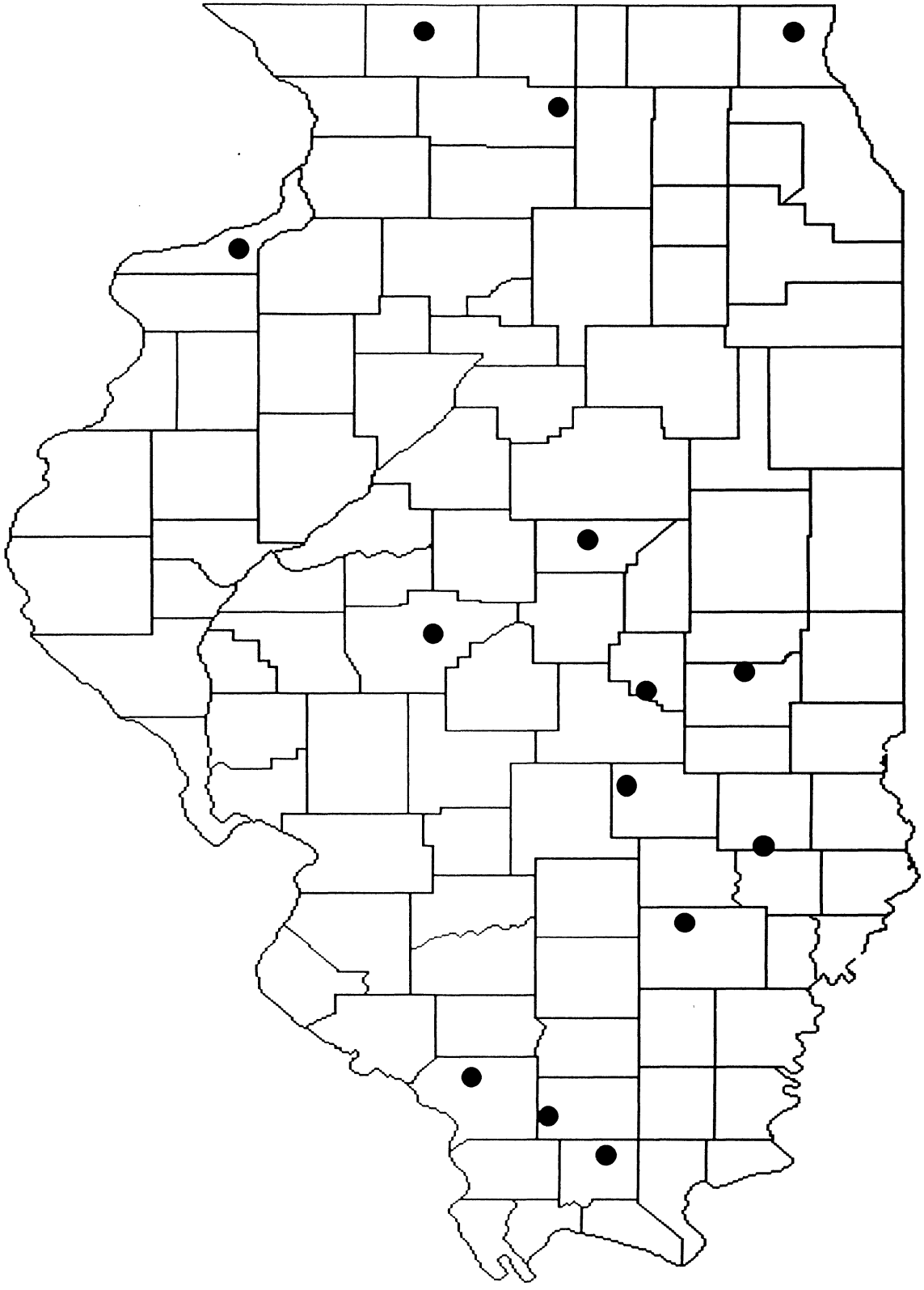


Figure 2

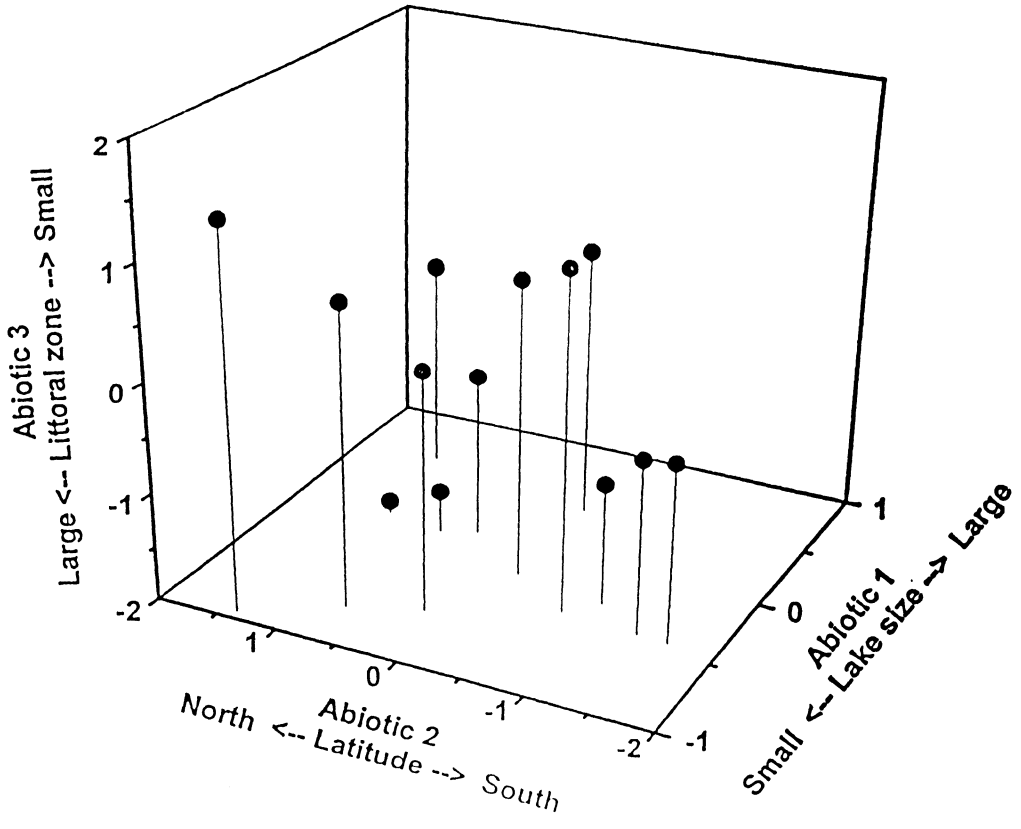

Abiotic 3
Large <-- Littoral zone --> Small
2
1
0
-1
-2
1
0
-1
-2
North <-- Latitude --> South
Abiotic 2
1
0
-1
Small <-- Lake size --> Large
Abiotic 1

Figure 3

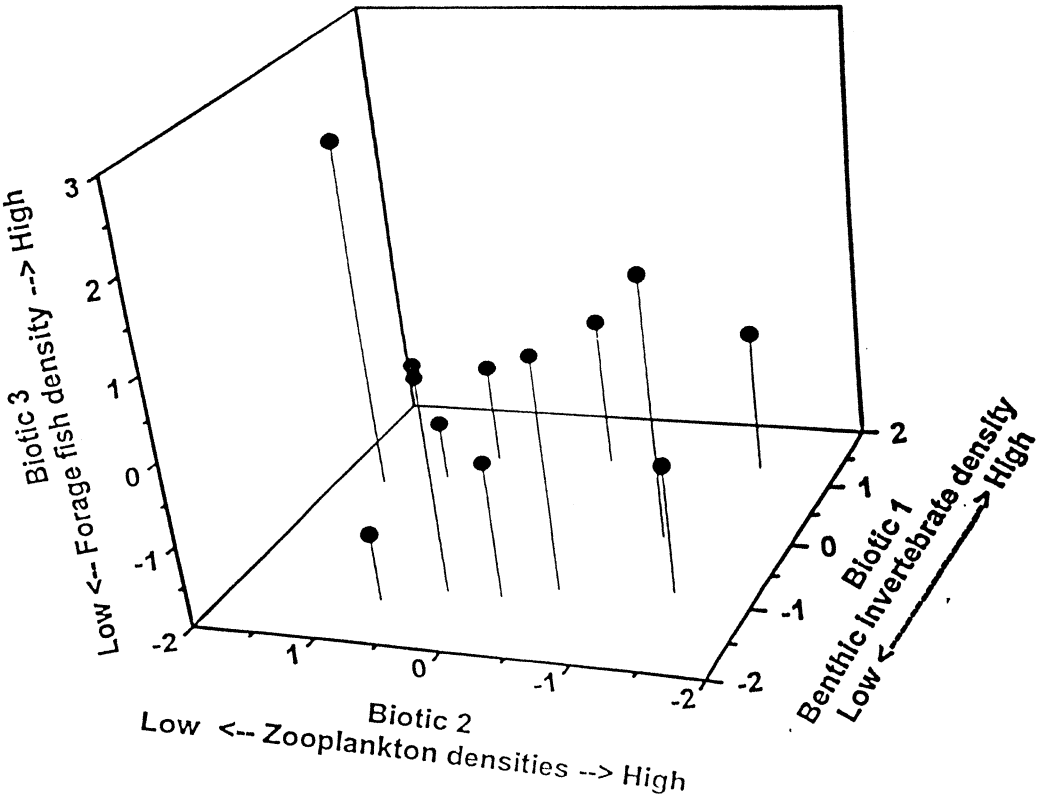

Biotic 3
Low <-- Forage fish density --> High
3
2
1
0
-1
-2
Biotic 2
Low <-- Zooplankton densities --> High
1
0
-1
-2
Biotic 1
Benthic Invertebrate density
Low <-- --> High
2
1
0
-1
-2

Figure 4

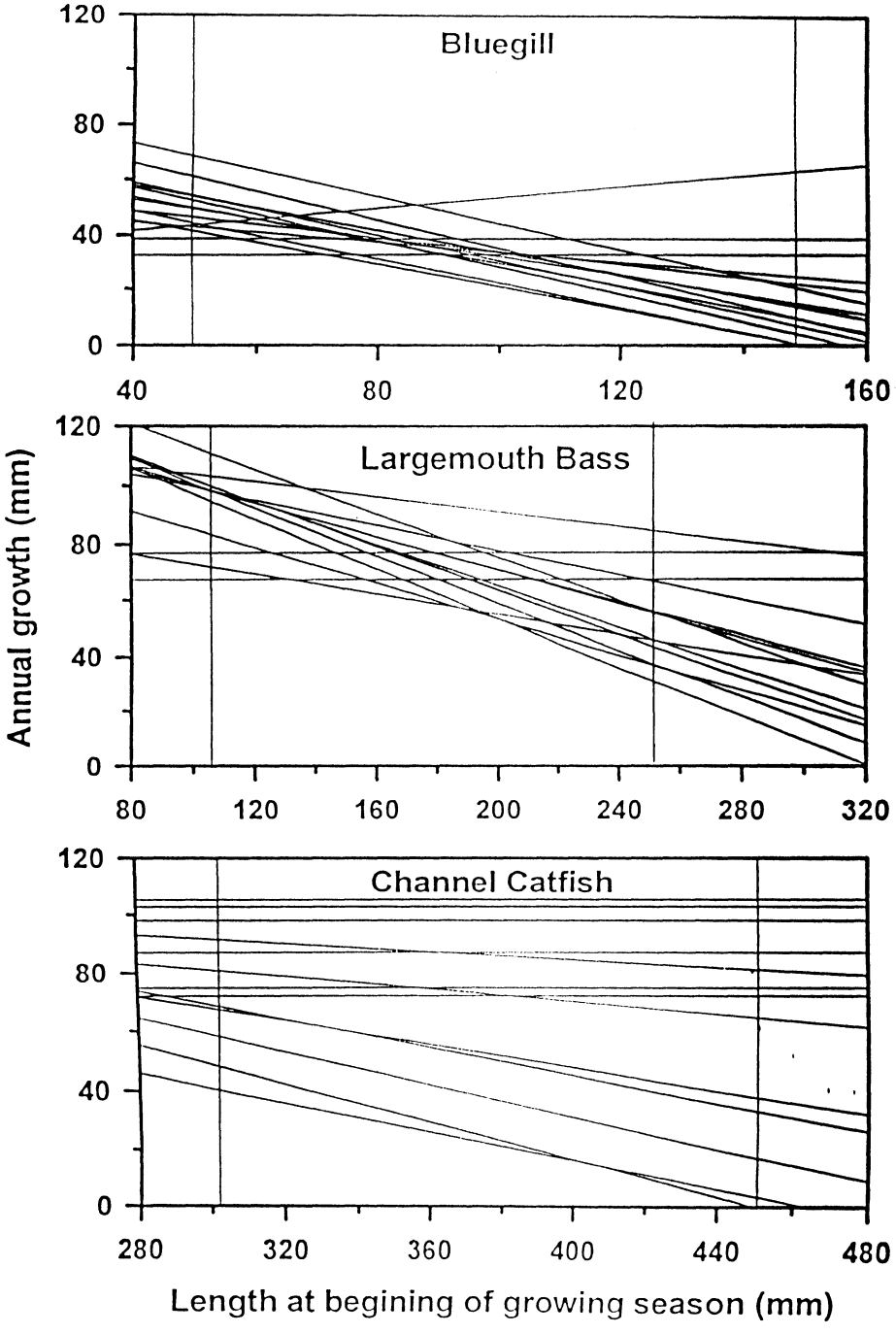

Bluegill
Largemouth Bass
Channel Catfish
Annual growth (mm)
Length at begining of growing season (mm)
120
80
40
0
40
80
120
160
80
120
160
200
240
280
320
280
320
360
400
440
480

Figure 5

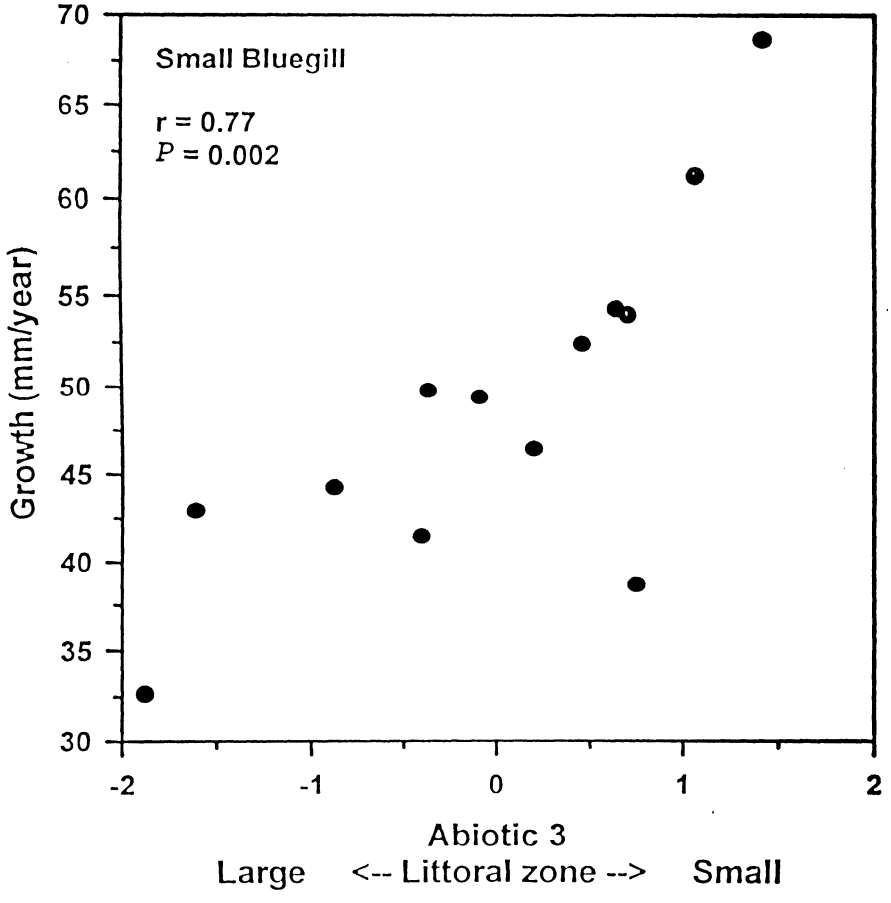

Small Bluegill
r = 0.77
P = 0.002
Growth (mm/year)
70
65
60
55
50
45
40
35
30
-2
-1
0
1
2
Abiotic 3
Large <-- Littoral zone --> Small

Figure 6

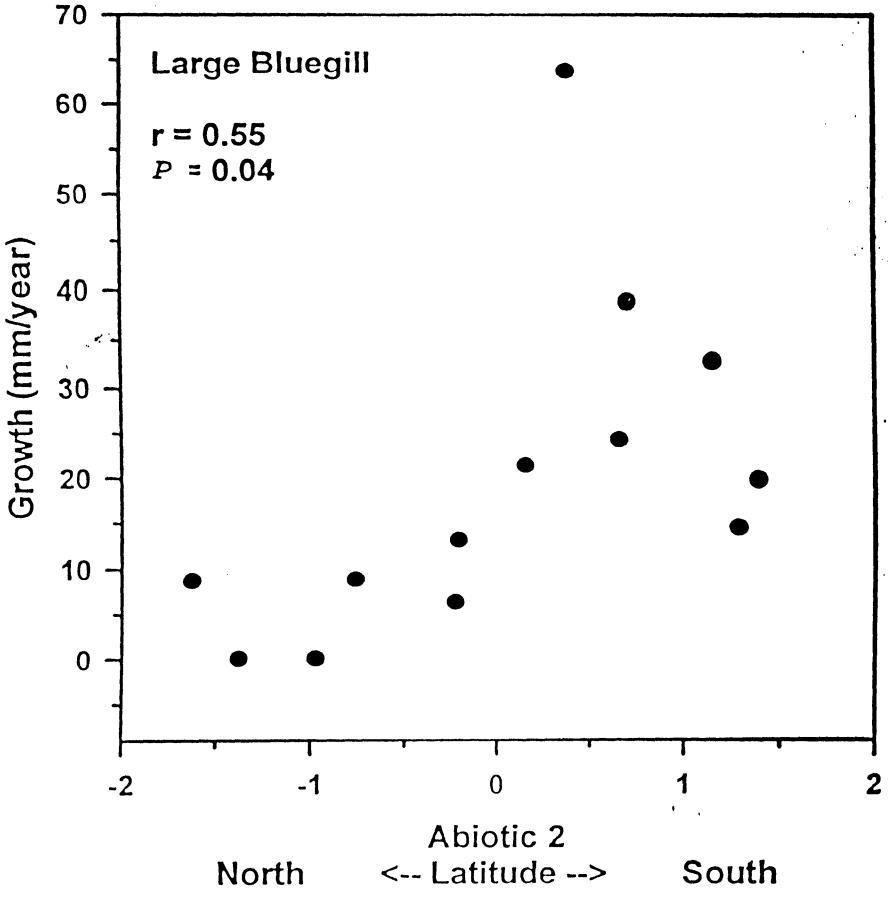
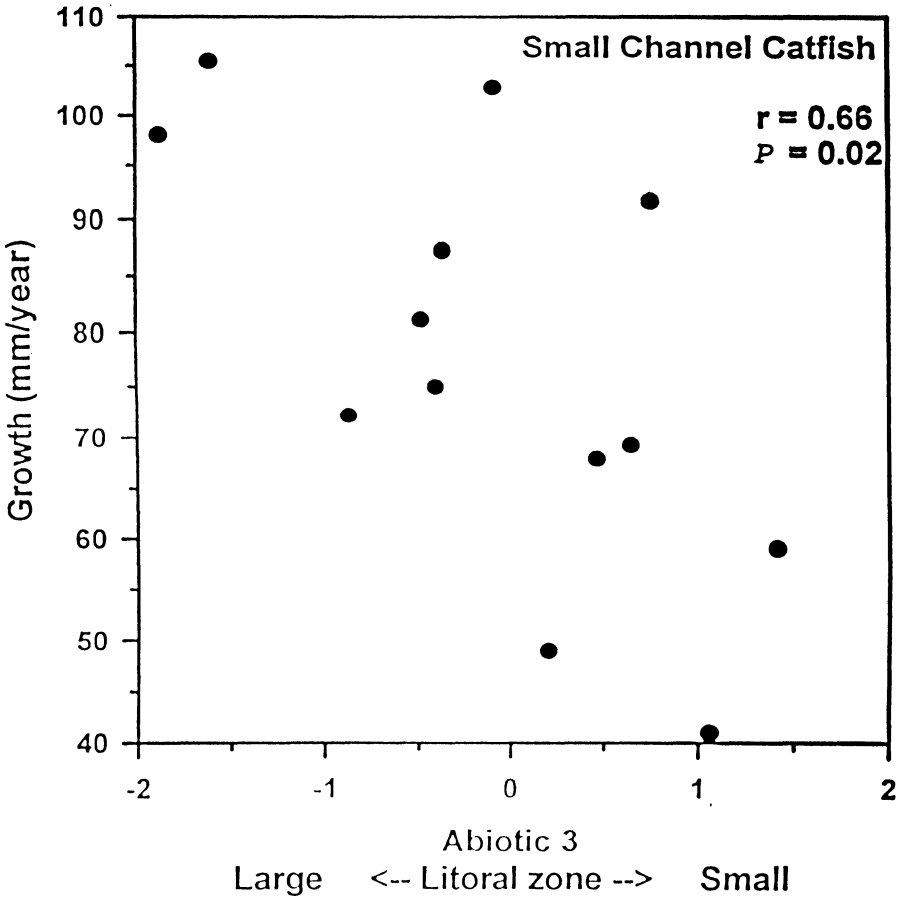

Large Bluegill
r = 0.55
P = 0.04
Growth (mm/year)
70
60
50
40
30
20
10
0
-2
-1
0
1
2
Abiotic 2
North
<-- Latitude -->
South

Figure 7


Small Channel Catfish
r = 0.66
P = 0.02
Growth (mm/year)
110
100
90
80
70
60
50
40
-2
-1
0
1
2
Abiotic 3
Large <-- Litoral zone --> Small