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The Relationships Between Several Limnological Factors and Bluegill Growth in Michigan Lakes

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The Relationships Between Several Limnological Factors and Bluegill Growth in Michigan Lakes.

by

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ABSTRACT

Thirty lakes in southern Michigan were studied to determine if food availability, chemical and physical factors and habitat type influenced the growth rate of bluegills (Lepomis macrochirus). The lakes studied spanned a continuum of bluegill growth rates which allowed for comparisons of the relative importance of several limnological factors. The limnological factors considered were; benthic biomass from discrete lake zones, zooplankton size and density, macrophyte density, algal concentration, nutrients (nitrates, ammonia, orthophosphate and total phosphorus),secchi disk transparency, chlorophyll, dissolved oxygen, alkalinity and morphometric variables (lake area, area of discrete lake zones and maximum depth). Data on the growth rate of bluegill were available from the Michigan Department of Natural Resources (MDNR) and were ranked according to the growth index for Michigan fishes.

Few variables differed for lakes with good or poor growth. Macrophyte density correlated negatively and zooplankton size correlated positively with bluegill growth rate. The multiple linear regression model developed in the final analysis used bluegill growth rate as the dependent

variable and macrophyte density, zooplankton size and profundal benthos as the independent variables (r^2 = 0.598, alpha = 0.05).

A number of relationships among the variables studied were noted. Macrophytes played a key role in the size distribution and abundance of zooplankton. Lake morphology, similarily, played a key role in the distribution of macrophytes.

INTRODUCTION

The bluegill (Lepomis macrochirus) is one of the most common fish in southern Michigan. Some lakes consistently produce populations of fast-growing bluegills while many others consistently produce slow-growing bluegills. This study, a cooperative effort between the Michigan Department of Natural Resources (MDNR) and the University of Michigan, School of Natural Resources, examines limnological factors such as; food availability, physical and chemical factors and habitat type, that may be affecting the growth of bluegills.

The growth rate of bluegills, young and adult, is typically density dependent (Grice 1957; Parker 1958; Gerking 1962; Cooper et al. 1971; Latta and Merna 1977; Beard 1982). Larval bluegills must initiate exogenous feeding about four days after birth. Beard (1982) states that the fate of the year-class is determined in the first four days. In addition, he states that larval survival appears to be a key to controlling the fate of fish populations. Both density dependent and density independent factors are important determinants of reproductive success. The time of spawning is temperature dependent and occurs when water temperatures reach 21^{0}C (Beard 1982). At this time of year (May and June in southern Michigan),

food items of the appropriate size (copepod nauplii and immature cladocera) are usually abundant (Lemly and Demmick 1982). Thus spawning usually occurs when biotic and abiotic factors, barring extreme shifts in temperature, are optimal for the survival of young. Large year classes of bluegills and the abundance of other animals feeding on the same food items can, however, deplete food resources (Engel 1985). This density-related reduction in food can lead to low rates of larval survival and reduced growth rates of the surviving individuals (Gerking 1962; Cooper et al. 1971; Latta and Merna 1977; Beard 1982; Weiner and Hanneman 1982). Latta and Merna (1977) identified an optimal density of larval bluegills at 41fry/m^3 of water in research ponds.

Adult bluegill growth can also be density dependent. Early investigators conducted removal experiments, and growth rates of bluegills improved after fish removal (Grice 1957; Parker 1958; Gerking 1962). Later investigators manipulated fish densities, as well as macrophyte and predator densities, in ponds. Fish from low density populations under similar environmental conditions showed faster growth than high density populations (Werner and Hall 1977; Crowder and Cooper 1979,1982). Wiener and Hanneman (1982) found density dependent factors to be so critical to growth that it masked pH-related factors affecting

growth.

Habitat use by bluegills is determined by physiological needs, feeding habits and predator avoidance behavior. They are found in shallow water during the spawning season and afterwards are widely distributed in all but anoxic areas of lakes (Werner et al. 1977; Werner 1979). Their feeding habits are generalized. They can be found feeding on zooplankton, benthos, terrestrial insects and plants (Laarman and Schneider 1972; Beard 1982; Engel 1985) as environmental conditions may dictate (Werner and Hall 1977, 1979; Mittelbach 1981; Werner and Mittelbach 1981). This generalized feeding accounts for their wide distribution in lakes (Werner 1977). Many times, however, their foraging is restricted by their predator avoidance behavior (Werner et al. 1983; Savino and Stein 1979, 1982, 1989). Savino and Stein (1979, 1982,1989) found that small bluegills can avoid predation in dense vegetation. Restricted movement and successful predation avoidance can lead to overcrowding of the littoral zone and subsequent resource depletion (Werner and Hall 1977; Keast 1978; Crowder and Cooper 1979, 1982; Werner et al. 1983; Engel 1985).

The growth rate of bluegills is obviously dependent on numerous factors. Biotic and abiotic factors combine to produce conditions which are favorable to or detrimental to rapid growth of bluegills (Beard 1982).

In many lakes environmental conditions exist which favor development of dense bluegill populations which show slow growth (Gerking 1962; Cooper et al. 1971). The variables studied included benthic invertebrate biomass from discrete lake zones, zooplankton density and size distribution, macrophyte density in the littoral zone as an index and throughout the lake as percent surface area coverage, water chemistry and nutrient content, chlorophyll concentration, secchi disk transparency and lake morphology.

The objective of this study was to observe several environmental factors in a group of lakes, exposed to similar climatic fluctuations, to produce a model which might be used to predict bluegill growth performance in a typical fishery (Laarman and Schneider 1972, Ryder 1974; Gailbraith 1975, Schneider 1975a, 1975b,1978; Mills et al. 1978; Mills and Schiavone 1982). Thirty lakes, in southern Michigan, were chosen for study and bluegills in these lakes exhibited a continuum of growth rates (Schneider 1981b). The continuum of growth rates allowed for comparisons among the lakes of relative importance of the limnological variables being investigated. The comparative approach is a powerful tool for field biologists in that it provides for a "natural experiment" (Diamond 1978). It allows biologists to observe systems in nature for which the variable of interest differs, thus avoiding the need

for manipulation by the investigator. This approach is appropriate in field ecology in that it avoids time consuming, manipulation of variables in the field and it can provide the significant amount of data necessary for ecological generalization. One drawback to this method is that it allows for, in this case, only one sampling effort on each of the sampling sites. The lack of multiple sampling can miss important ecological shifts such as changes in zooplankton distribution, benthic emmergence, or chemical changes. The purpose of this study was to test the following hypotheses:

1. The biomass of benthic invertebrate food items influences the growth rate of bluegills.

2. The density and size distribution of zooplankton influences the growth rate of bluegills.

3. The density of aquatic macrophytes influences the growth rate of bluegills.

4. Algal productivity of the lake influences the growth rate of bluegills.

5. The lake nutrient status influences the growth rate of bluegills.

6. Lake morphology influences the growth rate of bluegills.

METHODS

Thirty lakes for which the MDNR had bluegill growth data were chosen by the following criteria:

1. Bluegills were the predominant (> 50% by weight) of all centrarchid species.

2. The lake had a history of consistently fast- or slow-growing bluegill populations based on at least two MDNR surveys over the past forty years.

3. The lake had a fish community free from extensive manipulation by fishery managers.

4. The lake received average fishing pressure (reported by district managers).

5. The lake had a relatively small surface area (< 180 hectares).

An effort was made to include equal numbers of lakes with slow and fast growth (Table 1).

Benthos was sampled during the winter (January-February) of 1988. A stratified systematic design was used to minimize sampling error and to insure that most habitat types were sampled. Strata were chosen to represent major zones of the lakes. The first stratum included the littoral

Table 1. Locations, growth index (deviation in inches from the Michigan average) and classification ("good" = G, "poor" = P) of the study lakes.

Lake	County	Location	Growth index	Classi-fication
Algonquin	Barry	T2N,R9W,Sec.1-2	-1.25	P
Baptist	Newago	T11N,R11W,Sec.23-24	-1.6	P
Bass	Kent	T10N,R1E,Sec.9	-1.0	P
Bear	Hillsdale	T7S,R3W,Sec.8,17	0.06	G
Big Brower	Kent	T9N,R10W,Sec.34	-0.9	P
Big Pine Island	Kent	T8N,R9W,Sec.3,10	-0.95	P
Big Seven	Oakland	T5N,R7E,Sec.19,30	-1.6	P
Big Silver	Washtenaw	T15S,R4E,Sec.3	0.6	G
Blueberry	Livingston	-	0.5	G
Carter	Barry	T3N,R8W,Sec.6	-0.9	P
Cassidy	Washtenaw	T1S,R3E,Sec.33	0.0	G
Crispell	Jackson	T4S,R1W,Sec.20	-0.05	P
Crooked	Washtenaw	T1S,R3E,Sec.5	-0.2	G
Dead	Washtenaw	T1S,R6E,Sec.6	0.3	G
Dickinson	Oakland	T5N,R7E,Sec.29	-1.4	P
Eagle	Allegan	T1N,R14W,Sec.35	-0.5	P
Gilead	Branch	T8S,R7W,Sec.7	0.9	G
Halfmoon	Washtenaw	T1S,R4E,Sec.6	0.9	G
Hall	Barry	T2N,R8W,Sec.2	-1.2	P
Long[1]	Kent	T10N,R11W,Sec.31	-1.0	P
Long[2]	St. Joseph	T6S,R12W,Sec.7	-0.6	P
Loon[1]	Oakland	T3N,R9E,Sec.11	0.6	G
Loon[2]	Oscoda	T25N,rE,Sec.36	1.8	G
Muskellunge	Montcalm	T11N,R9W,Sec.26	-0.9	P
Sand[1]	Lenawee	T5S,R3E,Sec.12	0.5	G
Sand[2]	Newago	T11N,R13W,Sec.19	-0.4	P
Strawberry	Washtenaw	T1N,R5E,Sec.27	1.7	G
Sugarloaf	Washtenaw	T1S,R3E,Sec.31	-0.6	G
Townline	Montcalm	T12N,R7W,Sec.6	-0.5	P
Turk	Montcalm	T10N,R8W,Sec.10	-1.25	P

zone (0 - 3 m). The second stratum included the sublittoral zone (3 - 9 m). The third stratum was to represent the profundal zone (> 9 m). To increase sampling efficiency, strata were sampled unevenly. The littoral strata were allotted ten samples due to habitat heterogeneity characteristic of the littoral zone of lakes. The sublittoral and profundal strata were allotted six samples each due to the more homogeneous habitat types found in deeper waters. Sampling locations were chosen by randomly picking a starting point on bathymetric maps, then spacing samples evenly around the lake. In the profundal stratum samples were evenly spaced in a line through the center of the strata.

Benthic samples were obtained using a 15X15 cm Ekman dredge. Stations were located using landmarks on maps which could be identified from the lake. Holes for the dredge were made with a chain saw or by augering by hand.

The dredge was lowered slowly to the bottom, with care taken not to disturb the substrate. The dredge was then triggered and retrieved to the surface where samples were placed in plastic bags, labeled, sealed and returned to the lab for ellutriation.

An ellutriator was used to rinse the samples through a 500 μm mesh net and into a collecting jar. These samples were preserved in 10%

formalin. Samples were sorted by sugar flotation and hand sorting. The sugar flotation method was abandoned due to inefficient separation of benthic organisms from plant material. Hand picking was done under a binocular dissecting scope at 7X magnification. Material in jars were subsampled when the grab sample was large or animal density was high.

Taxonomic identification was done to a level which allowed determination of the general size of the animal (Appendix 1). Insects were identified to genera except for chironomids and ceratopogonids which were identified to the family level. Dry-weight biomass estimates were made using length-weight regressions developed for this study and from the literature (Table 2). The invertebrates, excluding worms, were measured using a computer-aided video analysis system (JAVA 1988). The animals were placed under a video camera where there lengths were digitized and sent directly to computer files. Subsamples of thirty animals were measured when a particular taxon was extremely numerous. Taxa commonly subsampled for measurement included chironomids, amphipods, caenid mayflies and molluscs. Invertebrates were removed as they were encountered for use in the development of the length-weight regressions. Animals saved for regression estimates were remeasured, dried 24 hours at 105 ^{o}C and weighed on a Cahn model 4700 digital

electrobalance.

The length-weight regressions were computed using the formula:

$$\ln \text{weight} = a + \ln \text{length}\ (b)$$

where a= the intercept and b= the slope of the regression between the natural log transformed length and dry weight of the animals (Table 2). BASIC programs were written to convert length to weight and to produce biomass estimates for each stratum and for the entire lake. To facilitate analysis for this project, invertebrates were categorized as either "food items" or "large food items" (Table 2). Food items included all benthic invertebrates found in the study except for molluscs and worms. Large food items included those invertebrates which were known to reach a large size (odonates, Hexagenia sp., Sialis sp., ect.) and chironomids over 10 mm long. The biomass estimates were expressed as mg dry weight per square meter.

Zooplankton was sampled in summer (July - August) of 1988. Vertical tows were made at cardinal compass points around the deepest point of the lake. A 159 µm-mesh plankton net, fitted with a one-pint mason jar, was lowered to a depth at which the oxygen was below 0.5 mg/l or to the bottom. The net was retrieved vertically, slowly to prevent back pressure, to the surface where the sides were washed to collect all

organisms. Samples were preserved in 10% fomalin in the field. In the laboratory, samples were stained with Eosin Y to aid identification and counting. Samples were rinsed of formalin and concentrated to a volume of 400 ml. Subsamples of 5 or 10 ml were counted in a gridded Petrie dish under 40X magnification. Zooplankton taxa were identified to major groups (copepods, Daphnia sp. and other cladocera). Counts from subsamples were converted to number of plankters per cubic meter. Densities from the four samples taken were averaged to give lake-wide density estimates.

Zooplankton size distribution was determined by measuring random subsamples of 50 zooplankters from each sample (200 per lake). The subsamples were measured and recorded using JAVA (JAVA 1988). Daphnia sp. were measured from the anterior of the head to the base of the terminal spine along the line bisecting the eye spot. Other Cladocera were measured from head to posterior end along a line bisecting the eye spot. Copepods were measured from anterior of the head to end of the abdomen. Copepodites were measured similarly and recorded as copepods.

A BASIC program was written to produce size-frequency histograms, summary statistics (mean, minimum, maximum, and standard deviation) and quartile plots for each group and for the groups pooled. The sizes exceeded by 10% and 90% of the population, and the mean size of the

Table 2. Benthic invertebrates in food item and large food item categories, and the regression coefficients used to estimate dry weight (mg) from lengths (mm). All large food items were considered as food items as well.

Taxa	Category	N	r^2	Size range (mm)	Intercept	Slope
Planaria [a]	food	23			0.359	--
Hirudinea	food	36	0.823	3-44	0.048	1.759
Hydracarina	food	42	0.475	0.5-3	0.007	1.752
Isopod	lg. food	23	0.735	6-13	0.003	2.963
Amphipod	food	98	0.672	2-15	0.008	2.112
Diptera						
Chaoborus [b]	food				0.003	1.721
sm. Chironomidae [c]	food				0.0003	3.07
lg. Chironomidae [c]	lg. food				0.0003	3.07
Ceratopogonidae [b]	food				0.007	1.473
Trichoptera						
Hydroptilidae	food	50	0.756	1-4	0.008	2.027
Polycetropodidae	lg. food	42	0.803	3-14	0.005	2.225
Leptoceridae	food	37	0.750	2-11	0.006	2.271
(Nectopsyche) [d]	lg. food				0.006	2.271
Helicopsychidae [d]	food				0.006	2.271
Molannidae [d]	lg. food				0.006	2.271
Phryganeidae [a]	lg. food	2			40.97	--
Ephemeroptera						
Heptageniidae	food	60	0.805	2-12	0.006	2.340
Leptophlebiidae [e]	food				0.006	2.340
Oligoneuridae [e]	food				0.006	2.340
Ephemerellidae [e]	lg. food				0.006	2.340
Baetidae [e]	food				0.006	2.340
Ephemeridae	lg. food	31	0.942	3-25	0.002	2.715
Caenidae [b]	food				0.029	1.837
Odonata						
Zygoptera						
Coenagrionidae	lg. food	59	0.891	3-14	0.002	2.567
Anisoptera						
Corduliidae [f]	lg. food	43	0.755	2-28	0.008	2.498
Libellulidae [f]	lg. food				0.008	2.498
Macromiidae [f]	lg. food				0.001	2.498
Gomphidae	lg. food	7	0.945	4-23	0.007	2.064
Coleoptera (larvae)	food	20	0.650	3-7	0.002	2.593
Hemiptera						
Naucoridae [a]	lg. food	5		13.4	--	
Megaloptera						
Sialis	lg. food	28	0.935	8-23	0.002	2.827

Table 2 continued.

a= Too few animals were found to develop a regression so mean weights were used.

b= Regression developed from data in Hall et al. (1970).

c= Regression from Wiley (1981).

d= Families combined due to similar body forms.

e= Families combined due to similar body forms.

f= Families combined due to similar body forms.

population, were used to represent the size distribution of zooplankton. In this manuscript the 10% exceedence size is termed large zooplankton, the 90% exceedence size is termed small zooplankton.

Macrophyte densities were measured using two methods. The littoral macrophyte density index involved circling the lake in a boat and assigning a macrophyte density rank. The range was 1 - 5 with 1 = no plants and 5 = complete cover. The percent coverage was determined by mapping the bottom with a Si-Tex depth sounder and chart recorder adjusted to distinguish plants from the bottom. Six evenly spaced transects were run on each lake. The percent of each transect containing plants was determined and the results of the transects were averaged to give a whole lake estimate. Some lakes had emergent plants so dense in the littoral zone that it was impossible to run transects. For these lakes, the percent coverage was estimated from maps assuming that plants covered 100% of the area under 4 m deep.

Water quality sampling was done in summer (July-August) of 1988. A temperature profile was constucted from measurements at 1-meter intervals using a thermister. An approximation of an oxygen profile was constructed from water samples taken at the; surface, mid epilimnion, thermocline, mid hypolimnion and bottom. Dissolved oxygen content was

measured using the Winkler method. Dissolved oxygen was ranked as follows for analysis; 1 = oxygen to bottom > 2 ppm, 2 = oxygen to mid hypolimnion > 2 ppm, 3 = oxygen only to thermocline > 2 ppm. Alkalinity was measured at surface and mid hypolimnion. Dissolved nutrients were sampled from four depths; surface, mid epilimnion, thermocline and mid hypolimnion. Nutrients analyzed included; total phosphorus (total P), nitrates (NO_3), ammonia (NH_4) and orthophosphate (PO_4). Water samples for nutrient analysis were stored in plastic bottles in a cool, dark cooler in the field. Upon return to the lab, samples were filtered through 0.45 μm membrane filters. Nutrient analysis was done using a Technicon Autoanalyzer II at the University of Michigan Great Lakes Research Division (Davis and Simmons 1979). Secchi disk transparencies and water samples for chlorophyll analysis were taken at the deepest part of the lakes. chlorophyll samples were obtained from the filters used to filter epilimnetic nutrient samples. Filters were dissolved in 10 ml of acetone in amber glass vials and kept frozen until analysis (Davis and Simmons 1979).

Data on growth of bluegills was provided by MDNR. The data were obtained from routine fisheries surveys, during surveys for other projects and in some cases specifically for this project. Some of the lakes had been

surveyed as early as the 1940's. Fish samples were obtained by a variety of methods; trap nets, fyke nets, gill nets, seines and electroshocking. Due to the variety of gear used and the lack of consistent sampling efforts population size and fish community composition were difficult to estimate.

A growth index developed by MDNR (Schneider 1981b) was used to summarize growth characteristics of fish. The growth index is a measure of deviation in mean size of a particular bluegill population from the state's mean bluegill size. Growth index is calculated by comparing mean total length at each age for a fish population, measured at one of four times of the year, to the state mean total length at each age for that species. The lakes were classified as "good" or "poor" based on this growth index. "Good" lakes had bluegills greater than eight inches and the growth index was greater than -1.0 inch. "Poor" lakes had no bluegills greater than eight inches and the growth index was below the state average.

Statistical analysis was done using SYSTAT software on an IBM personal computer. Exploratory analysis included one - way analysis of variance (ANOVA) and Pearson correlation matrices. One - way ANOVAs were done on each variable measured. Lakes were classified as "good" (n = 13) or "poor" (n = 17) using bluegill growth as the classification factor.

The Pearson correlation matrix of all variables was used to explore relationships between variables and bluegill growth as well as among variables themselves (N = 30, alpha = 0.05).

Multiple linear regression (MLR) was used in the final analysis to produce a model which would use several limnological variables as independent variables to explain variance in bluegill growth rates. Stepwise MLR (alpha for inclusion = 0.15) was used to aid in development of the model.

RESULTS

There were no significant correlations between any nutrients measured and bluegill growth performance (Table 3). Ammonia ranged from 10 µg/l to 510 µg/l, with a mean concentration of 148 µg/l. Nitrates ranged from nondetectable levels to 1.31 mg/l, with a mean concentration of 0.167 mg/l. Orthophosphate ranged from 2 µg/l to 18 µg/l, with a mean concentration of 6 µg/l. Total phosphorus ranged from 11 µg/l to 27 µg/l, with a mean concentration of 17 µg.

There were no significant relationships between dissolved oxygen rank or alkalinity (Table 4) and bluegill growth. Dissolved oxygen varied among the lakes; shallow, unstratified lakes had oxygen to the bottom while deeper lakes with highly organic substrates occassionally had oxygen depletion in the hypolimnion. The lakes were primarily hardwater lakes; $CaCO_3$ concentrations ranged from 62 mg/l to 227 mg/l, with a mean of 147.7 mg/l.

There were also no significant correlations between bluegill growth and secchi disk depth or chlorophyll *a*. concentration (Table 4). Secchi transparencies ranged from 1.3 m to 4.6 m with a mean of about 3 m.

Table 3. Mean nutrient concentrations for each study lake. Lakes are listed in rank by bluegill growth rate with the slowest growth first.

Lake	NO_3 (mg/l)	NH_3 (µg/l)	PO_4 (µg/l)	Total P (µg/l)
Baptist	0.01	10.7	5.6	13.7
Big Seven	0.73	77.6	5.0	13.7
Dickinson	0.47	57.0	4.1	11.3
Algonquin	0.02	19.0	3.2	24.5
Turk	0.06	325.6	3.5	16.8
Hall	0.04	39.1	4.1	27.3
Bass	0.02	51.2	5.3	14.7
Long[1]	0.02	51.5	3.4	13.6
Big Pine Is.	0.00	19.3	5.3	15.6
Big Brower	0.00	163.7	5.4	12.7
Carter	0.03	452.1	17.6	22.3
Muskellunge	1.15	115.0	4.7	16.2
Long[2]	0.01	265.3	5.8	19.1
Sugarloaf	0.06	479.7	5.0	13.2
Eagle	0.01	51.4	6.4	21.5
Townline	0.02	180.6	6.4	21.4
Sand[2]	0.00	15.2	7.7	21.5
Crooked	0.02	153.7	2.0	13.4
Crispell	0.01	25.5	4.5	--
Cassidy	--	--	--	19.4
Bear	0.03	325.6	2.3	14.8
Dead	0.02	224.2	1.6	14.6
Blueberry	0.04	25.3	3.4	21.7
Sand[1]	0.06	129.2	13.5	21.5
Big Silver	0.06	46.3	4.2	14.5
Loon[1]	0.47	133.9	8.6	12.2
Gilead	0.05	164.8	5.2	15.8
Halfmoon	1.31	157.6	5.2	15.0
Strawberry	0.07	510.3	16.6	14.7
Loon[2]	0.06	37.8	4.2	12.8

Chlorophyll *a* concentrations ranged from nondetectable to 0.034 mg/l, with a mean concentration of 0.005 mg/l. Chlorophyll *a* concentrations are lower than would be expected for the types of lakes in this study. The low values may be due to chlorophyll degradation during 60 days storage in the freezer before analysis, however, there was still a significant relationship between chlorophyll *a* and secchi disk depth ($r = -0.480$, alpha = 0.05, indicating the inverse relationship between secchi disk depth and algal density).

The correlation between the two macrophyte density measurements was also strong and significant ($r = .750$, alpha = 0.05) (Table 5). Macrophyte ranks ranged from 1 = very few plants to 5 = complete coverage of the littoral zone. The percent surface area coverage ranged from 8.5% to 100%, with a mean of 48.8%.

There was a significant negative correlation between the macrophyte density and bluegill growth performance (Figure 1). This correlation was significant using either measurement of macrophyte abundance (littoral rank: $r = -0.443$, alpha = 0.05), percent surface area coverage: $r = -0.431$, alpha = 0.05). The relationship between macrophyte density and growth is not linear, (Figure 1) and fish growth was highly

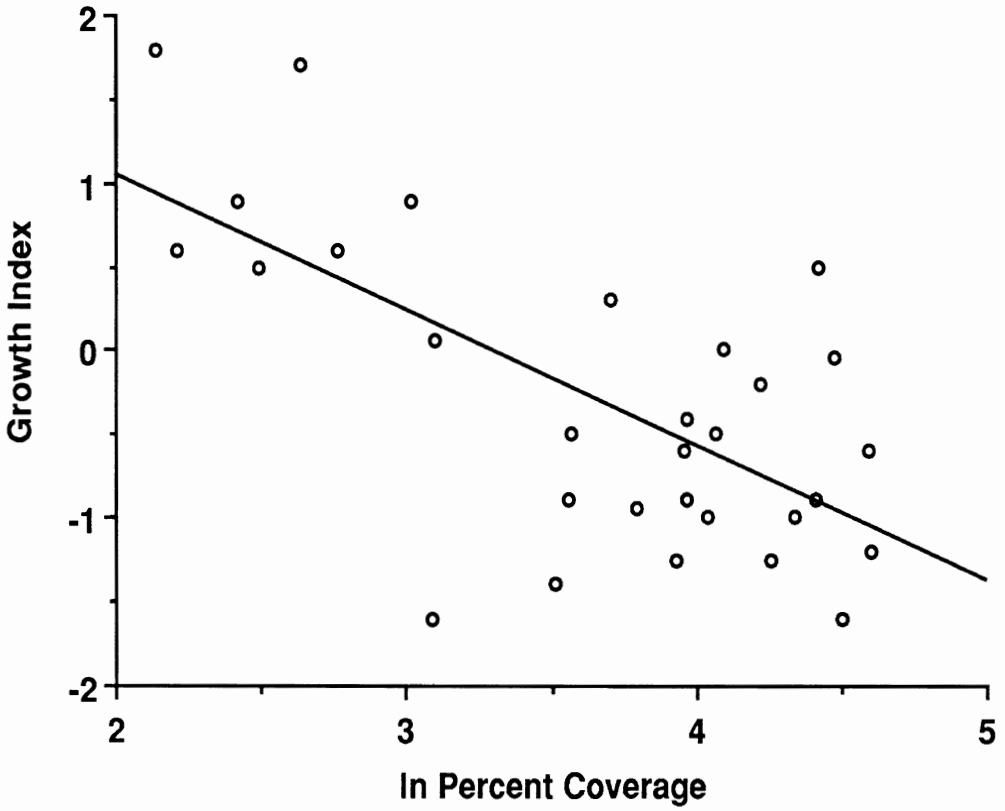

Figure 1. The relationship between plant percent coverage (natural log) and growth index of bluegills for each study lake.

variable for plant densities of 30 - 100%.

There was considerable variation in the size distribution of the zooplankton in the lakes studied (Table 6). Small zooplankton (size exceeded by 90% of the population) size ranged from 0.26 mm to 0.72 mm, with a mean of 0.43 mm. The average size of zooplankton ranged from 0.49 mm to 1.15 mm, with a mean of 0.76 mm. Large zooplankton (size exceeded by 10% of the population) size ranged from 0.73 mm to 1.86 mm in the lakes with a mean of 1.15 mm.

There was a significant positive correlation between the average size of large zooplankton and bluegill growth performance (Figure 2, $r = 0.622$, alpha = 0.05).

Zooplankton densities ranged from 5900/m^3 to 212,000/m^3 in the lakes, with a mean density of 51,566/m^3. There was a significant negative relationship between zooplankton density and bluegill growth performance ($r = -0.361$, alpha = 0.05).

Surprisingly, there was only one significant correlation between bluegill growth and any benthic biomass variable (Appendix 7). This correlation was for large food items from the profundal stratum ($r = 0.444$, alpha = 0.05). There was high variability among lakes' benthic

Table 4. Secchi disk transparency, chlorophylll *a*, dissolved oxygen rank and average alkalinity for the study lakes. Lakes are in rank order as in Table 3.

Lake	Secchi depth (meters)	Chlorophyll *a* (mg/l)	Dissolved oxygen rank	Alkalinity (mg $CaCO_3$/l)
Baptist	2.7	0.002	2	62
Big Seven	3.5	0.002	3	170
Dickinson	3.5	0.000	2	208
Algonquin	1.9	0.007	2	174
Turk	1.2	0.011	3	142
Hall	1.8	0.004	1	148
Bass	3.2	0.001	1	125
Long[1]	3.2	0.002	1	106
Big Pine Island	2.4	0.004	2	144
Big Brower	1.8	0.010	3	142
Carter	1.8	0.010	3	221
Muskellunge	1.6	0.003	1	158
Long[2]	2.6	0.002	3	113
Sugarloaf	2.0	0.015	1	186
Eagle	4.5	0.002	3	149
Townline	2.9	0.003	3	153
Sand[2]	1.8	0.005	1	73
Crooked	2.9	0.000	1	103
Crispell	2.3	0.002	2	153
Cassidy	2.4	0.002	1	124
Bear	3.2	0.002	3	147
Dead	3.0	0.003	3	114
Blueberry	2.0	0.034	3	105
Sand[1]	3.7	0.001	3	149
Big Silver	2.6	0.000	2	152
Loon[1]	3.5	0.001	3	201
Gilead	2.7	0.001	3	161
Halfmoon	2.6	0.006	3	189
Strawberry	1.4	0.004	3	227
Loon[2]	3.7	0.001	1	137

Table 5. Macrophyte densities expressed as littoral density index and as percent surface area coverage. Lakes are in rank as in Table 3.

Lake	Macrophyte littoral density index	Macrophyte percent cover
Baptist	4.5	21.9
Big Seven	5	89.9
Dickinson	3	33.6
Algonquin	5	70.3
Turk	4	50.8
Hall	5	100
Bass	3.5	56.8
Long[1]	5	76.6
Big Pine Island	4	44.4
Big Brower	1	35.2
Carter	5	82.2
Muskellunge	5	53.0
Long[2]	5	52.3
Sugarloaf	4	98.3
Eagle	4.5	35.4
Townline	4	58.5
Sand[2]	4	52.9
Crooked	4	67.8
Crispell	4	88.1
Cassidy	3	60.0
Bear	3	22.1
Dead	5	40.7
Blueberry	5	82.8
Sand[1]	2	12.0
Big Silver	2	9.1
Loon[1]	2	15.8
Gilead	3	20.4
Halfmoon	1.5	11.2
Strawberry	2	13.9
Loon[2]	1	8.5

Table 6. Zooplankton sizes for three categories (all zooplankters, large zooplankters and small zooplankters) and total densities (no./m^3). Large and small zooplankton represent the size exceeded by 10% and 90% of the population, respectively. Lakes are in rank as in Table 3.

Lake	Mean size (mm)	Large size (mm)	Small size (mm)	Density X10^3 (no./m3)
Baptist	0.65	0.88	0.30	57.8
Big Seven	0.84	1.22	0.48	77.7
Dickinson	0.83	1.22	0.50	11.1
Algonquin	0.77	1.15	0.41	54.5
Turk	0.60	0.81	0.38	74.6
Hall	0.49	0.76	0.28	85.5
Bass	0.49	0.73	0.26	51.7
Long[1]	0.63	0.85	0.43	44.4
Big Pine Island	0.65	0.87	0.38	59.9
Big Brower	0.53	0.77	0.29	107.8
Carter	0.81	1.15	0.43	34.2
Muskellunge	0.79	1.20	0.53	73.6
Long[2]	0.70	0.92	0.43	51.7
Sugarloaf	0.54	0.80	0.28	211.7
Eagle	0.95	1.72	0.49	15.4
Townline	0.66	0.86	0.43	45.3
Sand[2]	0.50	0.74	0.27	129.6
Crooked	1.00	1.37	0.72	49.9
Crispell	0.72	0.96	0.42	47.9
Cassidy	0.77	0.99	0.52	19.0
Bear	0.84	1.85	0.27	24.9
Dead	0.86	1.33	0.49	16.9
Blueberry	0.78	1.15	0.41	5.9
Sand[1]	0.90	1.29	0.68	28.3
Big Silver	0.98	1.59	0.40	9.6
Loon[1]	0.86	1.54	0.45	22.3
Gilead	0.74	1.29	0.41	48.4
Halfmoon	0.77	1.18	0.49	20.2
Strawberry	0.93	1.46	0.52	52.8
Loon[2]	1.15	1.86	0.52	14.4

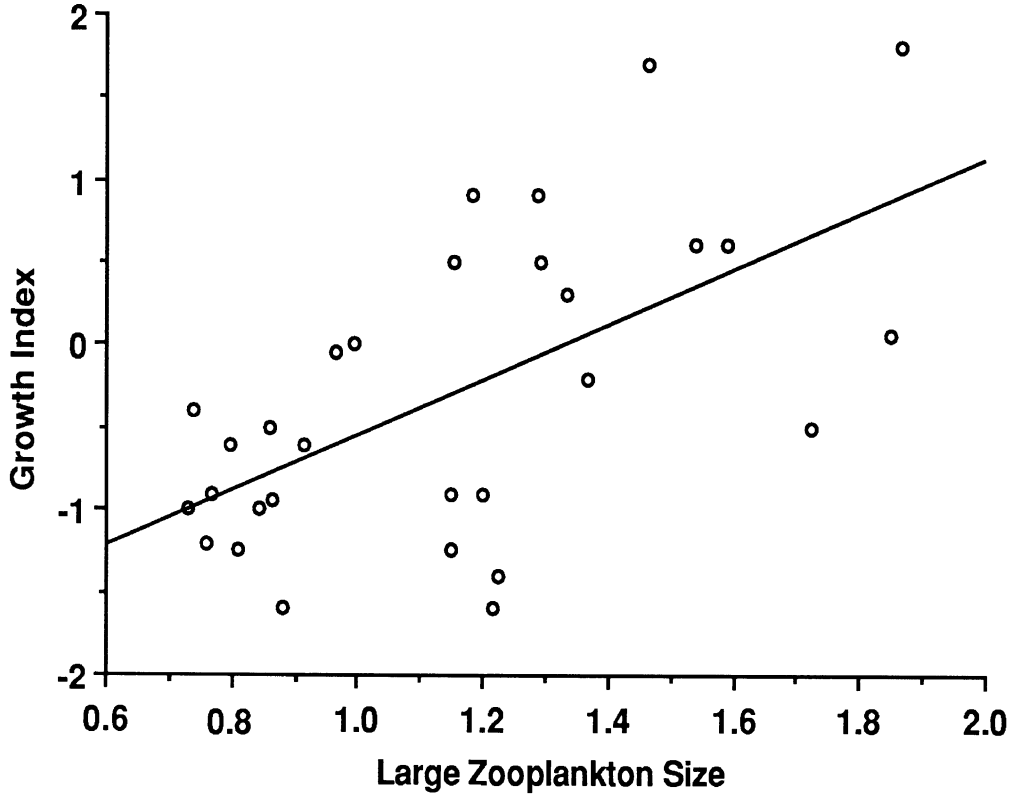

Figure 2. The relationship between large-size zooplankton and growth index of bluegills for each study lake.

populations (Tables 7 - 8) as might be expected, but there were no trends noted such as high benthic biomass in dense vegetation. The littoral stratum consistently had the highest biomass of benthos (703 mg/m^2) while the profundal stratum consistently had the lowest biomass (190 mg/m^2). The food-item category contributed the bulk of benthic biomass. Since benthic sampling and the other sampling was done at different times of the year, one must use caution in relating benthos to other variables, and this may be the reason for the lack of association between variables.

The morphological measurements (strata sizes as percent of the total area, total area and maximum depth) varied among lakes (Table 9). Total lake area ranged from 10.1-178.1 ha, with a mean size of 60 ha. The percent of area within each specific stratum was variable; some lakes were entirely littoral zone while others had large sublittoral and profundal areas. The size of each stratum was a function of the basin morphology and maximum depth (which ranged from 3.4 - 25 m). There were no significant correlations between the morphological variables and bluegill growth performance.

In addition to the relationships between each variable measured and bluegill growth, the relationships among the variables were examined

through the use of a Pearson correlation matrix (Appendices 2 - 7). Algal standing crops correlated negatively with size of zooplankton and maximum depth. Algal density was positively correlated with abundance of zooplankton, macrophyte cover and littoral strata size (Appendices 3 - 4).

Macrophyte densities were positively correlated with the size of the littoral zone ($r = 0.683$, alpha = 0.05) and negatively correlated with the size of the profundal zone ($r = -0.646$, alpha = 0.05) and maximum depth ($r = -0.676$, alpha =0.05). Another significant positive correlation was found between macrophytes and total phosphorus concentration.

There were several significant correlations between zooplankton and other variables (Appendices 4-7). Generally algal content, size, morphology and macrophyte density of the lake determined size distribution of zooplankton. Zooplankton mean and large size classes were negatively correlated with both macrophyte density and the littoral strata size and positively correlated with the algal content, the size of profundal strata and the maximum depth. Zooplankton densities were negatively correlated with zooplankton size (mean size: $r = -0.631$, large zooplankton size $r = -0.595$, small zooplankton size $r = -0.447$, alpha = 0.05).

Table 7. Benthic invertebrate biomass for food items from the study lakes. Lakes are in rank as in Table 3. (--) indicates no profundal stratum. Benthic invertebrate biomass (mg/m^2).

Lake	Littoral	Sublittoral	Profundal	Whole lake
Baptist	607.1	188.4	409.0	376.7
Big Seven	109.8	96.9	18.3	102.3
Dickinson	616.8	699.7	213.1	418.7
Algonquin	765.3	62.4	12.9	481.1
Turk	804.1	95.8	--	780.4
Hall	372.4	164.7	--	303.5
Bass	461.8	258.3	--	389.7
Long[1]	299.2	215.3	--	263.7
Big Pine Island	768.5	603.9	1188.3	664.1
Big Brower	456.4	359.5	--	429.5
Carter	2300.2	153.9	--	1657.6
Muskellunge	1099.0	392.9	185.1	589.9
Long[2]	1610.3	92.6	167.9	586.6
Sugarloaf	1364.9	102.3	--	1362.7
Eagle	1928.9	442.4	557.6	920.3
Townline	297.1	455.3	582.3	371.4
Sand[2]	129.2	64.6	--	117.3
Crooked	607.1	329.4	--	543.6
Crispell	241.1	148.5	--	194.8
Cassidy	550.0	81.8	--	527.4
Bear	1103.3	1022.6	204.5	845.0
Dead	622.2	306.8	--	526.4
Blueberry	360.6	173.3	--	292.8
Sand[1]	883.7	418.7	727.6	722.3
Big Silver	226.0	216.4	494.1	268.0
Loon[1]	298.2	89.3	119.5	195.9
Gilead	1202.3	394.0	265.9	711.5
Halfmoon	318.6	43.1	20.5	130.2
Strawberry	141.0	39.8	25.8	59.2
Loon[2]	554.3	297.1	517.7	405.8

Table 8. Benthic invertebrate biomass for large food items from the study lakes. Lakes are in rank as in Table 3. (--) indicates no profundal stratum. Benthic invertebrate biomass (mg/m^2).

Lake	Littoral	Sublittoral	Profundal	Whole lake
Baptist	115.2	76.4	0.0	63.5
Big Seven	5.4	0.0	0.0	3.2
Dickinson	345.5	15.1	0.0	103.3
Algonquin	104.4	0.0	0.0	64.6
Turk	334.8	0.0	--	323.0
Hall	94.8	0.0	--	63.5
Bass	4.3	16.1	--	8.6
Long[1]	47.4	31.2	--	40.9
Big Pine Island	159.3	1.1	0.0	65.7
Big Brower	239.0	21.6	--	179.8
Carter	1080.7	22.6	--	773.9
Muskellunge	350.9	43.1	1.5	139.9
Long[2]	72.1	9.7	0.0	28.0
Sugarloaf	271.2	0.0	--	271.2
Eagle	808.4	5.4	0.0	265.9
Townline	26.9	9.7	0.0	18.3
Sand[2]	65.7	0.0	--	52.7
Crooked	164.7	109.8	--	152.8
Crispell	35.5	0.0	--	22.6
Cassidy	162.5	7.5	--	155.0
Bear	253.0	0.0	0.0	110.9
Dead	144.2	11.8	--	105.5
Blueberry	155.0	10.8	--	117.3
Sand[1]	523.1	20.5	14.0	315.4
Big Silver	76.4	0.0	0.0	35.5
Loon[1]	33.4	14.0	0.0	18.3
Gilead	431.6	1.1	0.0	187.3
Halfmoon	42.0	5.4	0.0	16.1
Strawberry	49.5	6.5	0.0	14.0
Loon[2]	274.5	93.6	17.2	152.8

Table 9. Depth and area (as percent of the total) of the littoral (0-3m), sublittoral (3-9m) and profundal (>9m) zones, as well as whole lake area and maximum depth for the study lakes. Lakes are in rank as in Table 3.

Lake	Littoral (%)	Sublittoral (%)	Profundal (%)	Whole lake (ha.)	Maximum depth (m)
Baptist	29.9	37.7	32.4	34.8	19.8
Big Seven	74.6	19.6	5.8	68.8	16.1
Dickinson	29.3	17.8	52.9	17.8	20.7
Algonquin	62.0	28.2	9.8	97.1	13.7
Turk	51.0	49.0	0.0	64.3	6.1
Hall	75.1	24.9	0.0	17.0	3.7
Bass	66.0	34.0	0.0	74.5	6.2
Long[1]	58.3	41.7	0.0	19.4	8.2
Big Pine Island	40.6	48.8	10.6	90.2	13.7
Big Brower	72.5	27.5	0.0	34.4	8.2
Carter	71.0	29.0	0.0	28.3	7.6
Muskellunge	32.8	57.9	9.3	54.2	11.3
Long[2]	32.8	50.2	17.0	85.4	12.5
Sugarloaf	98.3	1.7	0.0	72.8	5.5
Eagle	32.6	36.6	30.8	91.1	18.0
Townline	52.7	41.7	5.6	100.0	14.9
Sand[2]	81.0	19.0	0.0	23.5	4.6
Crooked	79.1	20.9	0.0	45.7	6.1
Crispell	64.8	35.2	0.0	33.2	7.6
Cassidy	71.0	29.0	0.0	17.4	3.4
Bear	44.1	34.7	21.2	47.3	15.2
Dead	71.3	28.7	0.0	23.1	9.8
Blueberry	74.2	25.8	0.0	10.1	6.7
Sand[1]	65.2	23.7	11.1	178.1	16.2
Big Silver	45.9	33.7	20.4	82.6	14.3
Loon[1]	46.2	20.5	33.3	98.3	22.3
Gilead	43.3	32.4	24.3	52.6	14.9
Halfmoon	34.6	26.8	38.6	95.5	25.0
Strawberry	24.7	33.5	41.8	105.2	15.8
Loon[2]	36.5	55.0	8.5	36.4	15.2

Correlations with other variables showed relationships opposite those shown for zooplankton size. Zooplankton densities were positively correlated with algal density and macrophyte density. They were negatively correlated with profundal stratum size and maximum depth.

Relationships between benthic invertebrate biomass and other variables measured are difficult to distinguish in this study since they were measured at different times of the year (Appendices 5 - 7). One unexpected negative correlation was between invertebrate biomass and macrophyte density. This result is opposite of expectations from a review of the literature (Hayne and Ball 1956; Pardue 1973; Crowder and Cooper 1979, 1982; Gilinsky 1984; Wiley et al. 1984). These results may be due to benthic invertebrates distributing differently when plants die back in the fall and recolonize macrophyte beds again in spring (Gilinsky 1984). Sampling benthos in winter and plants in summer would not account for such invertebrate migrations and the relationship between invertebrates and plants could be biased. A second significant correlation was a positive relationship between size of zooplankton and biomass of the large-sized benthic invertebrates.

There were several significant correlations between lake morphology and variables affecting bluegill growth (as noted above) but no

direct correlations with growth (Appendices 2 - 7).

One-way analysis of variance (ANOVA) was used to examine differences observed among the variables between "good" and "poor" lakes. Bluegill growth performance was the classification factor used to separate the two lake types by criteria described above (Table 10). Only two variables were significantly different between the two lake types (macrophytes and zooplankton) and these were examined more closely using regression analysis.

Stepwise regression using all variables (alpha for inclusion = 0.15) was also used to aid development of the final multiple linear regression (MLR) model. As in the previous analysis, stepwise techniques identified plant cover and large-sized zooplankton as variables which should be included in the model for bluegill growth.

In an effort to produce a better model, each of the other variables was forced into the model. Several variables improved the fit of the model but were difficult to explain biologically or introduced too much multicollinearity. The final equation was:

$$Y = 1.362 - 0.685\ (X1) + 1.005\ (X2) + 0.083\ (X3),$$

where: Y = bluegill growth index (deviation in inches from state avgerage).

X1 = natural log of percent surface area coverage by macrophytes.

X2 = size exceeded by 10% of the zooplankton population (mm).

X3 = biomass of the large size benthic invertebrates from the profundal stratum.

(r^2 = 0.589).

Analysis of Variance

Source	Sum of Squares	df	Mean Square	F-ratio	p
regression	14.544	3	4.848	12.290	<0.0005
residual	10.256	26	0.394		

The assumptions of homogeneity of variance and normality were tested and met. There were no problems with multicollinearity among variables included in the model. Macrophytes contribute most to the variance explained by the model (75%), large-size zooplankton 10% and large profundal benthos contribute 15% despite there being only three data points with non-zero values.

DISCUSSION

The regression model developed here is consistent with bluegill biology as it is currently understood. Macrophytes contribute greatly to the variance explained by the model, and they play a key role in structuring bluegill population density (Beard 1982; Lemly and Demmick 1982; Engel 1985) and growth (Crowder and Cooper 1979, 1982). The contribution of macrophytes is, presumably, through their role in providing refuge from predation for small bluegills (Mittelbach 1981; Savino and Stein 1982, 1989; Werner et al. 1983; Engel 1985). When small fish engage in this behavior, and successfully avoid predation, their populations grow to a point where they may overexploit their food resources (Grice 1957; Parker 1958; Gerking 1962).

Zooplankton are an easily obtained food resource in lakes. They are distributed into fairly discrete zones with larger zooplankton found predominantly in open water areas while smaller zooplankton concentrate in littoral areas (Brooks and Dodson 1965; Pennak 1978). Among the study lakes, large zooplankton were common in lakes with large open water areas and small zooplankters were common to lakes consisting predominantly of littoral habitat. Bluegills forage optimally by

Table 10. Results of One-way ANOVAs for each variable measured and its relation to bluegill growth. The classification factor is bluegill growth performance (good or poor) alpha = 0.05, d.f. = 1.

Variable	N	Relation to growth	Mean square	F	p
nitrates	30	NS	0.004	0.032	0.860
ammonia	30	NS	44001.863	2.161	0.153
orthophosphate	30	NS	0.833	0.057	0.813
total phosphorus	30	NS	21.966	1.282	0.267
dissolved oxygen rank	31	NS	0.979	1.223	0.278
alkalinity	31	NS	581.048	0.378	0.544
secchi disk transparency	31	NS	25.236	3.643	0.066
chlorophylll *a*	31	NS	0.0	0.119	0.732
macrophyte density index	31	-	11.715	8.481	0.007
percent coverage	31	-	5664.980	7.984	0.008
zooplankton					
mean size	31	+	0.332	18.122	<0.0005
large size	31	+	1.585	26.066	<0.0005
small size	31	+	0.067	5.901	0.022
density	31	NS	0.86e+10	3.587	0.068
benthic invertebrate biomass					
stratum 1	31	NS	422.998	0.161	0.691
stratum 2	31	NS	129.693	0.194	0.592
stratum 3	31	NS	141.152	0.194	0.663
whole lake	31	NS	418.603	0.367	0.550
large benthic invertebrate biomass					
stratum 1	31	NS	242.683	0.478	0.495
stratum 2	31	NS	2.346	0.347	0.561
stratum 3	31	NS	0.304	2.406	0.132
whole lake	31	NS	31.777	0.155	0.697
size stratum 1	31	NS	105.582	0.242	0.627
stratum 2	31	NS	140.959	0.790	0.382
stratum 3	31	NS	490.529	2.204	0.148
whole lake	31	NS	14404.375	1.683	0.205
max. depth	31	NS	735.823	0.490	0.171

selecting large zooplankton when zooplankton density is high (Werner and Hall 1974; Mittelbach 1981; Werner et al. 1983). When zooplankton density is low or large zooplankters are rare, bluegills feed on items as they are encountered or switch food items. This pattern has been observed in all bluegills when predators are absent but only in large (> 100 mm) bluegills when predators are present. Small bluegills in the presence of predators confine themselves to the cover provided by macrophytes (Werner and Hall 1976; Werner et al. 1983; Osenburg et al. 1988), a behavior which may limit their growth by reducing foraging opportunities.

Large immature insects (primarily Chironomus) in the profundal zone of lakes provide a valuable food resource for bluegills when the insects emerge. It is unlikely that these insects are utilized extensively in their profundal habitat due to anoxic conditions which occur during large portions of the year; some bluegills, however, are taken at depths >10 m in the winter (J. C. Schneider, personal communication). Insects emerging from the profundal zone may provide a valuable, though seasonally distributed, food resource (Wiley, personal communication). The seasonal distribution of profundal insects emerging is similar to the seasonal distribution, shown by occurrence in gut samples, of terrestrial insects in the diet (Laarman and Schneider 1972; Beard 1982; Engel 1985).

Anecdotally, this is also consistent with high success rates of anglers fishing with dry flies and surface baits.

Macrophyte density, zooplankton abundance and size, and profundal benthic biomass were significantly related to bluegill growth performance. These variables were, similarly, related to other limnological variables sampled in this study. Although there were not strong correlations between depth or the size of the lake zones and bluegill growth I believe that these factors are important in the structuring bluegill populations because of their influence on distribution and abundance of macrophytes, zooplankton and benthic invertebrates.

Lake morphology was correlated to the density of macrophytes (Appendix 2). Macrophyte distribution is largely, though not entirely, limited by the depth of light penetration (Wetzel 1985). Large, deep (>10 m) lakes with small littoral areas and extensive profundal zones had few macrophytes while shallow, unstratified lakes had dense macrophyte cover. Macrophyte distribution is a key component in the ecology of freshwater lakes (Wetzel 1985). Macrophyte distribution influences zooplankton species diversity (Brooks and Dodson 1965; Pennak 1978), nutrient concentrations in water (Wetzel 1985), algal densities and distribution (Wetzel 1985) and benthic invertebrate species diversity,

abundance and distribution (Gilinsky 1984). Lakes included in this study, as most lakes in the region, are of glacial origin whose sediments are rich in organic matter after 10,000 years of existence. They commonly have macrophytes ringing the shoreline to the depth at which light penetration becomes limiting, indicating a rich supply of nutrients in the sediments.

Zooplankton size distribution and abundance were also related to lake morphology (Appendix 4). The size of zooplankton was positively correlated with size of the profundal stratum and depth and were negatively correlated with size of the littoral strata. Abundance of zooplankton was positively correlated with size of the littoral stratum and negatively to size of the profundal stratum and depth. Littoral zooplankton are often small and commonly occur in large numbers (Brooks and Dodson 1965; Pennak 1978), but the small size class did not correlate significantly with the morphologic variables.

Benthic invertebrate species diversity and abundance can be affected by lake morphology. Many benthic animals have strict habitat requirements which can only be met in certain areas of a lake. For example, many odonates cling to vegetation, some mayflies (Hexagenia sp.) require firm sediments for burrowing and other insects (Chironomidae) can live virtually anywhere (Merrit and Cummins 1984). The invertebrates

correlated with the growth of bluegills, in this study, were profundal animals not commonly found in shallow regions of lakes. Their distribution is undoubtedly limited by the amount of profundal habitat available.

The results of this study identify several variables which influence growth of bluegills. One factor, not studied here, which may be as important as all others combined is density of the bluegill population and structure of the entire fish population. Schneider (1981a) identified "good" lakes as having 50 - 78% fish biomass comprised of bluegills while "poor" lakes had > 78% of the fish community comprised of bluegills. He also determined a predator biomass at 20% of the total fish biomass as being correlated with good bluegill growth.

Mechanisms determining year-class strength of bluegills have been studied extensively. It appears that most eggs laid will produce larvae and that year-class strength may be determined during the first four days of life (Beard 1982; Engel 1985). Lakes with extensive littoral zones and dense macrophytes are likely to produce large year-classes. Food for larval bluegills (small zooplankton) may be abundant in the littoral habitat and there is protection from predation in the macrophytes. Lakes with small littoral habitats and few macrophytes are likely to produce

small year-classes due to high rates of predation on small bluegills. It is unlikely that food for small bluegills in these lakes would be much less abundant because they can feed on the limited number of littoral zooplankton or on immature members of pelagic zooplankton.

The processes by which large populations of bluegills can limit their own food resources have been identified. Bluegills have been shown to reduce benthic invertebrate size, species abundance and morphology (Hayne and Ball 1956; Gerking 1962; Werner and Hall 1974; Crowder and Cooper 1979, 1982; Gilinsky 1984; Butler 1988; Pierce 1988). In cases where zooplanktivores are size selective in their feeding habits, they can alter size and species composition of the zooplankton community (Brooks and Dodson 1965; Gailbraith 1975; Hall et al. 1976; Mills et al. 1978; Zaret 1980; Mills and Schiavone 1982). Thus, large populations of bluegills feeding in the limnetic region of lakes could cause species changes in the zooplankton community towards smaller species and thus limit this food resource. This effect would be most pronounced in small lakes with high densities of planktivores.

One goal of fishery managers is to provide an ample supply of harvestable fish for anglers. To accomplish this goal for bluegills the manager must consider many factors. Sufficient cover must be available

for some young fish to survive but not so much that most survive. Habitat for important food types, as mentioned above, must be available. Finally, piscivorous fish and forage fish populations must be balanced so the piscivores can control bluegill population abundance.

Plant management can be an effective tool for fishery managers. Using chemicals, fertilizers and mechanical control, they can keep macrophyte density low which may promote good growth of bluegills. Low plant density should provide habitat for large zooplankton species and keep bluegill recruitment low through higher rates of predation.

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Appendix 1. Benthic invertebrates found in the study lakes.

Class	Order	Family	Genus
Turbellaria	Tricladida	Planariidae	
Annelida	Oligochaeta		
	Hirudinea		
Crustacea	Isopoda		
	Amphipoda	Taltridae	Hyalella
		Gammaridae	Gammarus
Arachnoidea	Hydracarina		
Insecta	Ephemeroptera	Baetidae	Baetis
			Calibaetis
		Ephemeridae	Ephemera
			Hexagenia
		Heptageniidae	Stenacron
		Oligonueridae	Isonychia
		Caenidae	Caenis
		Ephemerellidae	Eurylophella
	Odonata	Coenagrionidae	Argia
			Enallagma
			Nehalennia
		Corduliidae	Cordulia
			Epitheca
			Neurocordulia
			Stomatochlora
		Gomphidae	Arigomphus
			Gomphus
			Stylurus
		Libellulidae	Celethimis
			Erythemis
			Ladona
			Leucorrhinia
			Libellula
			Pachydiplax
		Macromiidae	Didymops
			Macromia
	Hemiptera	Naucoridae	Pelocoris
	Megaloptera	Sialidae	Sialis

Appendix 1. continued

Trichoptera	Polycentropodidae	
		Neuroclipsis
		Nyctiophylax
		Polycentropus
	Hydroptilidae	Hydroptila
		Orthotrichia
		Oxyethira
	Helicopsychidae	
		Helicopsyche
	Leptoceridae	Ceraclea
		Leptocerus
		Nectopsyche
		Oecetis
		Triaenodes
	Molanidae	Molanna
	Phryganeidae	Fabria
		Agrypnia
Lepidoptera	Pyralidae	
Coleoptera (larvae)	Dytiscidae	
	Haliplidae	
	Elmidae	Stenelmis
Diptera	Ceratopogonidae	
	Chaoboridae	Chaoborus
	Chironomidae	
	Tabanidae	Chrysops

Appendix 2. Correlations between macrophyte density and other variables. (N=30, alpha=.05). NS = not significant.

Variable	Littoral index	% Coverage
nitrate	NS	NS
ammonia	NS	NS
orthophosphate	NS	NS
total phosphorus	0.449	0.394
dissolved oxygen	NS	NS
alkalinity	NS	NS
macrophyte density		
index	--	0.750
% coverage	0.750	- -
size		
stratum 1	NS	0.683
stratum 2	NS	NS
stratum 3	-0.401	-0.646
whole lake	NS	-0.360
maximum depth	-0.428	-0.676

Appendix 3. Correlations between algal standing crop and other variables. (N=30, alpha=.05). NS = not significant.

Variable	Secchi disk	chlorophyll *a*
secchi disk depth	----	-0.480
chlorophyll *a*	-0.480	----
nitrate	NS	NS
ammonia	-0.372	NS
orthophosphate	NS	NS
total phosphorus	NS	NS
dissolved oxygen	NS	NS
alkalinity	NS	NS
macrophyte density		
index	NS	NS
% s.a. coverage	NS	0.436
size		
stratum 1	NS	0.409
stratum 2	NS	NS
stratum 3	NS	NS
whole lake	NS	NS
maximum depth	0.501	-0.394
growth index	NS	NS

Appendix 4. Correlations between zooplankton and other variables. (N=30, alpha= .05). NS = not significant.

Variable	Mean size	Large size	Small size	Density
secchi disk depth	0.450	0.486	0.326	-0.478
chlorophyll *a*	NS	NS	NS	NS
nitrates	NS	NS	NS	NS
ammonia	NS	NS	NS	NS
orthophosphate	NS	NS	NS	NS
total phosphorus	NS	NS	NS	NS
dissolved oxygen	NS	NS	NS	-0.390
alkalinity	NS	NS	NS	NS
macrophyte				
index	NS	-0.376	NS	NS
% s.a. coverage	-0.464	-0.543	NS	0.487
size				
stratum 1	-0.369	-0.398	NS	0.539
stratum 2	NS	NS	NS	NS
stratum 3	0.364	0.436	NS	-0.403
whole lake	NS	NS	NS	NS
maximum depth	0.478	0.504	NS	-0.504
growth index	0.582	0.622	NS	-0.361

Appendix 5. Correlations between food items and other variables. (N=30, alpha= .05). NS = not significant.

Variable	Littoral	Sublittoral	Profundal	Whole lake
secchi disk depth	NS	0.402	0.381	NS
chlorophyll *a*	NS	NS	NS	NS
nitrate	NS	NS	NS	NS
ammonia	0.401	NS	NS	0.521
orthophosphate	NS	NS	NS	NS
total phosphorus	NS	NS	NS	NS
dissolved oxygen	NS	NS	NS	NS
alkalinity	NS	NS	NS	NS
macrophyte				
index	NS	NS	NS	NS
% s.a. coverage	NS	NS	NS	-0.417
size				
stratum 1	NS	NS	NS	NS
stratum 2	NS	NS	NS	NS
stratum 3	NS	NS	NS	NS
whole lake	NS	NS	NS	NS
maximum depth	NS	NS	NS	NS
zooplankton				
mean size	NS	NS	NS	NS
large size	NS	NS	NS	NS
small size	NS	NS	NS	NS
density	NS	NS	NS	NS
growth index	NS	NS	NS	NS

Appendix 6. Correlations between large food items and other variables. (N=30, alpha= .05). NS = not significant.

Variable	Littoral	Sublittoral	Profundal	Whole lake
secchi disk depth	NS	NS	NS	NS
chlorophyll *a*	NS	NS	NS	NS
nitrate	NS	NS	NS	NS
ammonia	NS	NS	NS	0.455
orthophosphate	0.483	NS	NS	0.472
total phosphorus	NS	NS	NS	NS
dissolved oxygen	NS	-0.416	NS	NS
alkalinity	NS	NS	NS	NS
macrophytes				
index	NS	NS	NS	-0.443
% s.a. coverage	NS	NS	NS	-0.362
size				
stratum 1	NS	NS	NS	NS
stratum 2	NS	NS	NS	NS
stratum 3	NS	NS	NS	NS
whole lake	NS	NS	NS	NS
maximum depth	NS	NS	NS	NS
zooplankton				
mean size	NS	NS	NS	0.389
large size	NS	NS	0.367	NS
small size	NS	0.437	0.412	NS
density	NS	NS	NS	NS
growth index	NS	NS	0.444	NS

Appendix 7. Correlation between growth index and other variables. (N=30, alpha= .05). NS = not significant.

Variable	Growth performance
secchi disk depth	NS
chlorophyll a	NS
nitrate	NS
ammonia	NS
orthophosphate	NS
total phosphorus	NS
dissolved oxygen	NS
alkalinity	NS
macrophytes	
index	-0.443
% s.a. coverage	-0.431
zooplankton	
mean size	0.582
large size	0.622
small size	NS
density	-0.361
benthic invertebrate biomass	
stratum 1	NS
stratum 2	NS
stratum 3	NS
whole lake	NS
large benthic invertebrate. biomass	
stratum 1	NS
stratum 2	NS
stratum 3	0.444
whole lake	NS
size	
stratum 1	NS
stratum 2	NS
stratum 3	NS
whole lake	NS
maximum depth	NS