Ecosystems (2000) 3: 229–237
DOI: 10.1007/s100210000022

ECOSYSTEMS

# Patterns of Fish Growth along a Residential Development Gradient in North Temperate Lakes

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## ABSTRACT

Residential development of lakeshores is expected to change a variety of key lake features that include increased nutrient loading, increased invasion rate of nonnative species, increased exploitation rates of fishes by anglers, and alteration of littoral habitats. All of these factors may alter the capacity of lakes to support productive native fish populations. Fourteen north temperate lakes were surveyed to examine how growth rates of two common fish species (bluegill sunfish, *Lepomis macrochirus*; largemouth bass, *Micropterus salmoides*) varied along a residential development gradient. Size-specific growth rates for both species were negatively correlated with the degree of lakeshore residential development, although this trend was not statistically significant for largemouth bass. On average, annual growth rates for bluegill sunfish were 2.6 times lower in heavily developed lakes than in undeveloped lakes. This effect of lakeshore development on fish growth was not size specific for bluegills between 60 and 140 mm in total length. An index of population production rate that accounted for both the size-specific growth rate and the size distribution of fishes showed that bluegill populations were approximately 2.3 times less productive in highly developed lakes than in undeveloped lakes. Our results suggest that extensive residential development of lakeshores may reduce the fish production capacity of aquatic ecosystems.

**Key words:** bluegill sunfish; largemouth bass; coarse woody debris; riparian management; littoral habitat; lakeshore development; fish production; fish growth.

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## INTRODUCTION

Key ecosystem processes and features of lakes may be altered as a result of residential development in watersheds. For example, increased nutrient loads that result from watershed disturbance, inefficient sewage systems, and agriculture commonly are cited as important problems that lead to eutrophication of lakes (NRC 1992; Carpenter and others 1998). Residential development of lakeshores may increase exploitation rates of fish populations, degrade littoral zone productivity through increased siltation (NRC 1992), and decrease littoral zone habitat complexity through removal of coarse woody debris (CWD; Christensen and others 1996) and mechanical/chemical removal of macrophytes. Introduction of exotic species also may have tremendous effects on the growth and population dynamics of native fishes (Hrabik and others 1998). Despite the host of problems linked to residential encroachment on watersheds, we have a very poor understanding of whether these impacts alter the capacity of lakes to support productive fish populations.

The potential effects of lakeshore residential development on growth rates of fishes are numerous. For example, increased nutrient loading to lakes may

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Received 29 April 1999; Accepted 26 October 1999.
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increase fish production by increasing primary production (Hanson and Leggett 1982). Increased exploitation rates of fishes in developed lakes may increase growth rates of fishes by relaxing density-dependent constraints on growth (Goedde and Coble 1981) or decrease growth rates by causing shifts in life-history strategies of exploited populations (Ehlinger 1997). Lakeshore residential development may reduce fish growth rates through alterations in littoral habitat productivity and complexity. For example, reduction of CWD (dead trees that become part of the littoral habitat of lakes) density in littoral habitats of developed lakes (Christensen and others 1996) may represent critical losses of predation refuges and foraging habitats for fishes. If development of lakeshores increases species introductions to lakes, growth rates of native fishes also may be depressed through interspecific competition with introduced species. It is likely that several of the mechanisms listed above interact in complex ways to alter fish growth and production rates as lakeshores become developed for residential purposes.

In a survey of 14 lakes from Northern Wisconsin and the Upper Peninsula of Michigan, Christensen and others (1996) showed that the amount of littoral zone habitat provided by CWD was negatively correlated with the density of human dwellings on the lakeshore (Figure 1; Christensen and others 1996). In this study, we resurveyed the lakes examined by Christensen and others (1996) to determine whether growth rates of two common fish species (bluegill sunfish, *Lepomis macrochirus;* largemouth bass *Micropterus salmoides)* changed systematically along this residential development gradient. The purpose of this study was to compare the evidence to support the hypotheses that predict that lakeshore development will increase fish growth rates (that is, eutrophication, exploitation) versus the evidence to support the hypothesis that fish growth rates are reduced as lakeshores become developed (that is, littoral habitat degradation). Our results showed that growth rates of bluegill sunfish decreased substantially as the intensity of lakeshore development increases. A similar but weaker trend was observed for largemouth bass. Although we are unable to determine the mechanisms that determine this pattern in growth rate, the direction of the effect runs counterintuitive to expectations that would derive entirely from nutrient loading impacts. Our results suggest that extensive residential development may be altering the potential of lakes to support fish production across the Upper Midwest of the US through littoral zone habitat degradation.

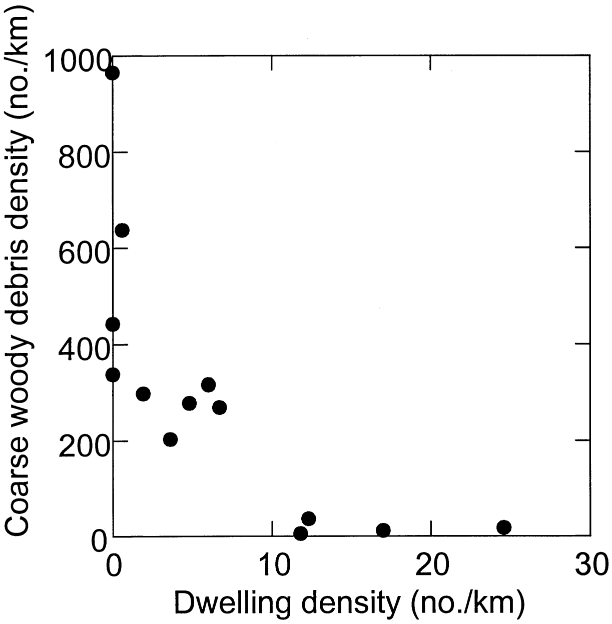

Figure 1. The density of CWD found in littoral habitats as a function of the intensity of lakeshore residential development in lakes in Northern Wisconsin and Michigan. Data were taken from Christensen and others (1996).

# METHODS

## Study Area

We surveyed the fish communities in the 14 lakes sampled by Christensen and others (1996) that varied along a residential development gradient (Table 1). The primary goal used in choosing these lakes was to produce a balanced distribution of systems that were distributed along a residential development gradient but that had similar geologic features (Christensen and others 1996). Biological features such as fish community composition, lake productivity, and woody debris density were not used as criteria in lake selection. All lakes are located in Vilas County in Northern Wisconsin and in Gogebic County in the Upper Peninsula of Michigan. Lakes varied in surface area from 9 ha to 254 ha and were surrounded by a forest of mixed hardwood-conifer trees (Stearns 1951; Brown and Curtis 1952; Curtis 1959). Three of the lakes sampled had no development, seven had low dwelling densities, and four had high dwelling densities. The low development category was assigned to lakes where some of the shoreline remained undeveloped. The high development category included only lakes that had close to 100% of their shorelines developed and represents lakes that were among the most densely developed in this region. Lakes with no development were located at the University of Notre Dame

**Table 1.** Summary of the Location, Physical Characteristics, and Total Species, and the Number of Bluegills and Largemouth Bass Caught for Each Lake

| Lake | Surface Area (ha) | Maximum Depth (m) | Shoreline Convolution | Secchi Depth (m) | Dwelling Density (no./km) | Total Fish (*n*) | Total Species (*n*) | Bluegill (*n*) | Largemouth Bass (*n*) |
|---|---|---|---|---|---|---|---|---|---|
| Bay (MI) | 69 | 13.7 | 2.64 | 4.3 | 0.0 | 321 | 5 | 122 | 31 |
| Bergner (MI) | 9 | 11.9 | 1.39 | 2.4 | 0.0 | 811 | 3 | 436 | 31 |
| Crampton (WI/MI) | 24 | 14.0 | 1.42 | 4.3 | 0.0 | 708 | 4 | 20 | 60 |
| Tenderfoot (WI/MI) | 175 | 10.1 | 1.91 | 1.3 | 0.6 | 344 | 11 | 3 | 0 |
| Palmer (WI) | 254 | 4.0 | 1.7 | 1.9 | 1.9 | 336 | 12 | 5 | 0 |
| Street (WI) | 22 | 6.7 | 1.8 | 5.1 | 3.6 | 96 | 4 | 3 | 15 |
| Laura (WI) | 240 | 13.1 | 1.5 | 7.4 | 4.1 | 160 | 6 | 2 | 0 |
| Annabelle (WI) | 85 | 9.1 | 2.3 | 1.7 | 4.8 | 219 | 9 | 84 | 0 |
| Joyce (WI) | 12 | 10.1 | 1.3 | 6.3 | 6.0 | 404 | 7 | 262 | 45 |
| Lake-Hills (WI) | 25 | 3.0 | 1.2 | 1.2 | 6.7 | 306 | 7 | 65 | 21 |
| Towanda (WI) | 58 | 8.2 | 2 | 2.3 | 11.8 | 213 | 9 | 53 | 0 |
| Black Oak (WI) | 234 | 25.9 | 2.2 | 5.1 | 12.3 | 217 | 9 | 101 | 27 |
| Johnson (WI) | 31 | 12.8 | 1.8 | 1.8 | 17.0 | 199 | 10 | 81 | 23 |
| Arrowhead (WI) | 40 | 13.1 | 1.4 | 3.2 | 24.6 | 331 | 10 | 80 | 18 |

*Dwelling density numbers refer to the density of lakeshore cabins and houses as reported in Christensen and others (1996).*

Environmental Research Center (UNDERC; Carpenter and Kitchell 1993) whereas the remaining lakes were in Vilas County.

## Fish Sampling

Sampling to characterize the fish populations in the study lakes was performed during June and July of 1996. Within each lake, two randomly selected lakeshore sites were chosen as starting points for boat electroshocking transects. Electroshocking commenced approximately 30 minutes after sunset and followed the 1-m depth contour of the lake for 30 minutes on each transect. The total distance sampled along the shoreline was approximately 750 m for all lakes. All fish collected were identified to species, and their lengths were measured to the nearest 1 mm. If more than 100 individuals of one species were caught in a lake, lengths of the first 100 individuals were recorded and the remaining fish were simply counted.

We focussed our analyses on growth in total length of bluegill sunfish and largemouth bass. Both of these species are common to water bodies throughout the continental US and support valuable sport fisheries (Becker 1983). Largemouth bass and bluegills often occur sympatrically in lakes and represent a well-described predator–prey system (Werner and others 1983; Werner and Gilliam 1984; Guy and Willis 1990; Olson and others 1995).

Weight measurements and scale samples were taken from most bluegill and largemouth bass caught on each lake. Weights to the nearest gram were recorded for the first five fish in each 10-mm size/length category (for example, 50–59 mm, 60–69 mm, etc.). Several scales behind the pectoral fin were collected for age determination on every fish whose weight was recorded. Bluegill scales were mounted on glass slides, and largemouth bass scales were pressed onto acetate strips, and at least one nonregenerated scale from each fish sampled was read on an Optimas (Media Cybernetics, Bothell, WA, USA) optical imaging system to determine the individuals growth rate in the previous year. All bluegill and largemouth bass growth rates (in mm/year) were determined with the Fraser-Lee method by taking the back-calculated length from the most recently completed annulus and subtracting the back-calculated length of the previous year (Carlander 1982). Thus, we derived only one age-specific growth rate from each individual fish.

## Statistical Analyses

We tested whether there was an effect of lakeshore dwelling density on the growth rate of bluegills and largemouth bass. Because the ecological roles of these species are dependent on their relative size (Werner and Gilliam 1984; Mittelbach and Osenberg 1993; Olson 1996a, 1996b), we also tested whether the potential effect of dwelling density on fish growth was size specific. An important statistical consideration in the analysis of the effect of residential development on fish growth is to avoid artificial inflation of the degrees of freedom. In our study, each lake is an experimental unit that represents an independent combination of fish growth and lakeshore development. However, in this analysis we had to account for changes in growth rate as a function of fish size. We also wanted to be able to test for size-specific effects of residential development on fish growth. To achieve these goals and avoid pseudoreplication, least squares regression was first used to determine the dependence of growth in length ($\log_{10}$ transformed) on length of the fish for each lake and fish species. The mean slope of the growth ($\log_{10}$ transformed) versus length relationships was –0.0035 (standard deviation 0.001), the mean intercept was 1.74 (standard deviation 0.167), and $r^2$ values ranged from 0.19 to 0.72, for lakes where these regressions were statistically significant ($P \leq 0.05$). For lakes where there was no statistically significant effect of length on growth rate ($P > 0.05$), the mean growth rate across all sampled individuals was determined.

Lake-specific growth versus length regressions then were used to estimate the growth rate of fish of several distinct sizes that span much of the variation in observed sizes from the field (60, 100, and 140 mm total length for bluegills; 100, 200, 300, and 400 mm total length for largemouth bass) for each lake in the study. For each size class, predicted growth rate ($\log_{10}$ transformed) in each lake then was regressed against dwelling density ($\log_{10}+1$ transformed) to determine whether size-specific growth rate varied systematically with the degree of lakeshore residential development. We compared the slopes of functions that characterized the effect of dwelling density on growth rate to determine whether this effect was size specific. For all regressions reported in this article, residuals were homoscedastic and approximately normally distributed.

We also calculated an aggregated index of the population production rate for bluegills in each of the lakes. This was accomplished by applying each of the lake-specific growth versus length models to the size distribution of fishes sampled in the field. The aggregated production index then was calculated as the mean of all the predicted growth rates for all individuals in the sample (that is, this is simply a weighted average growth rate). Least squares regression also was used to test for an effect of dwelling density on the production index.

## RESULTS

In total, over 4500 fish from 16 different species were caught in the 14 lakes from this study (Table 1). The total number of fish caught in each lake ranged from 96 to 811, and the total numbers of species present in each lake ranged from three to 12. Bluegills were caught in all 14 lakes, whereas largemouth bass were caught from only nine lakes. Numbers of bluegill caught in each lake varied from two to 436 whereas largemouth bass numbers varied between 0 and 60. Sizes of bluegill ranged from 30 mm to 236 mm whereas largemouth bass sizes ranged from 40 mm to 510 mm. Scales from 452 bluegills and 216 largemouth bass were collected for growth rate determination. Ages of both bluegill and largemouth bass ranged from 1 to 10 years, but fish older than 9 years were dropped from growth rate analyses because of the difficulty in accurately assessing annuli and the subsequent age of the scale/fish. We also removed Laura Lake from the analyses because only two bluegills were caught there.

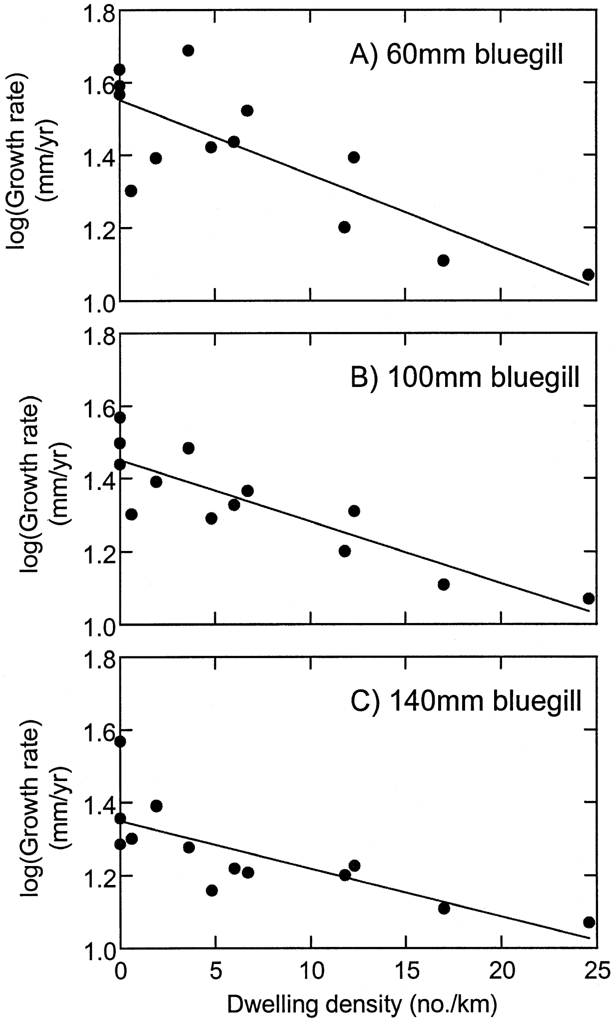

Figure 2. Average annual growth rates (mm/y) for bluegill at specific sizes (60, 100, and 140 mm) in each lake plotted against the residential development gradient. The least squares fits of linear regressions are shown in each panel.

**Table 2.** Summary Statistics from Linear Regressions of the Effects of Lakeshore Development on Annual Growth Rate[a]

| Size Class (mm) | Intercept $B_0$ | Slope $B_1$ | $P$ | $r^2$ | Standard Error of Estimate |
|---|---|---|---|---|---|
| All lakes with bluegills | | | | | |
| 60 | 1.60 (0.070) | −0.12 (0.036) | 0.008 | 0.49 | 0.15 |
| 100 | 1.50 (0.041) | −0.11 (0.022) | 0.0005 | 0.68 | 0.086 |
| 140 | 1.40 (0.037) | −0.093 (0.020) | 0.0007 | 0.67 | 0.078 |
| Lakes where ≥20 bluegills were sampled | | | | | |
| 60 | 1.63 (0.059) | −0.14 (0.028) | 0.001 | 0.76 | 0.106 |
| 100 | 1.51 (0.038) | −0.117 (0.018) | 0.000 | 0.84 | 0.068 |
| 140 | 1.40 (0.046) | −0.093 (0.022) | 0.003 | 0.69 | 0.003 |

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*The regressions take the form of* $\log_{10}$ *(growth rate)* $= B_0 + B_1 \log_{10}$ *(dwelling density* $+ 1) +$ *error. Standard errors of the parameters are given in parentheses.*

[a] *Shown in millimeter total length.*

Growth rates of bluegill sunfish decreased with body size (Figure 2 and Table 2). Bluegill growth rates were significantly reduced as the intensity of lakeshore residential development increased (Figure 2). The strength of this negative effect of residential development on bluegill growth (that is, the slopes) was statistically indistinguishable for 60-, 100-, and 140-mm size classes of bluegill sunfish (Table 2). Thus, there was no significant interaction between the intensity of lakeshore residential development and body size in determining the growth rates of bluegill sunfish. Despite the fact that CWD densities are estimated with modest measurement error and dwelling densities are estimated with essentially no measurement error (Christensen and others 1996), regressions of bluegill growth rates as a function of CWD density ($\log_{10}$ transformed) explained approximately as much variation in growth rates as dwelling density did.

The age distribution of bluegills was shifted to emphasize more old individuals as lake development increased (Figure 3). However, there were no apparent patterns in the size structure of bluegill populations that were found along the residential development gradient (Figure 3). An index of population production rate that incorporated both the size structure and the size-specific growth rates of bluegills was strongly and negatively correlated with lakeshore residential development (Figure 4).

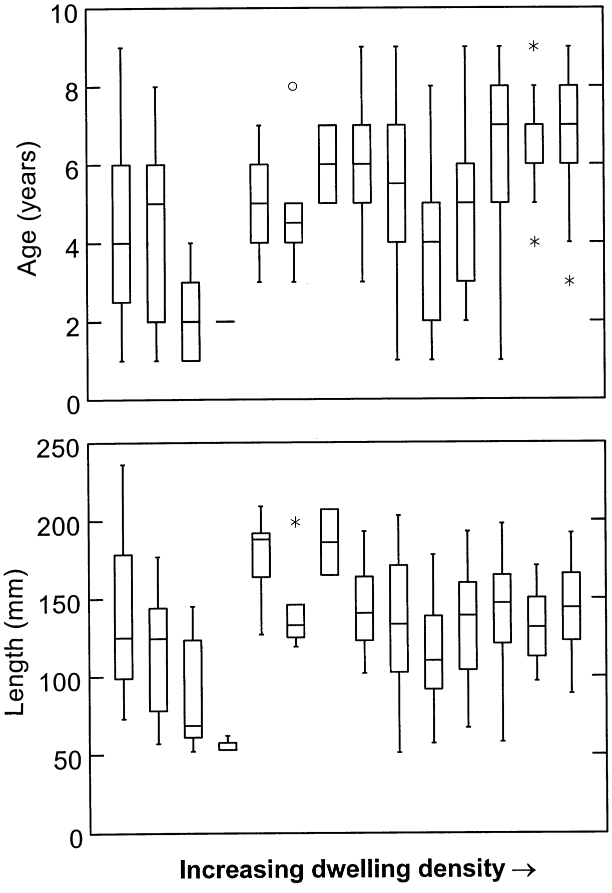

Figure 3. Boxplots of the age and length distributions of bluegills sampled in each of the lakes. Lakes are ordered from low to high dwelling density (left to right). Open circles and asterisks are outliers; single horizontal dash is the length of a single fish.

Growth rates of largemouth bass from 100 to 300 mm in length did not exhibit any significant and consistent change across the gradient of lakeshore residential development ($P > 0.1$). Growth of the largest size class of largemouth bass exhibited a marginally significant negative correlation with lakeshore residential development ($P < 0.10$, not shown). The size structure of largemouth bass populations did not show any consistent pattern of change across the development gradient. However, we aggregated the nine lakes where bass were captured into the classes of no-, low-, and high-development that were established by Christensen and others (1996). Although not statistically significant ($P > 0.1$), a plot of the average largemouth bass

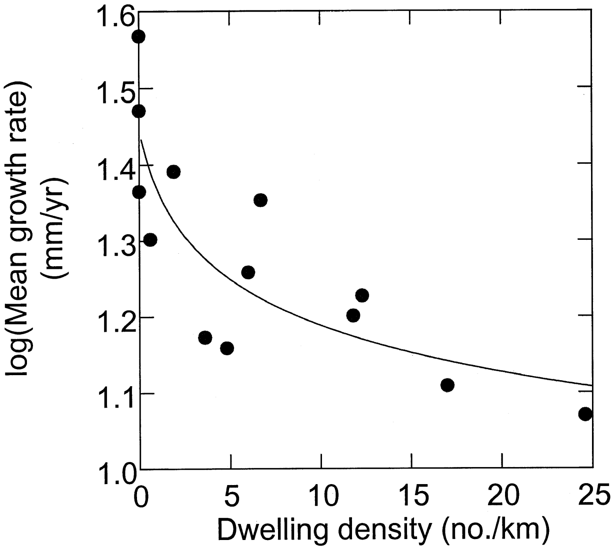

Figure 4. An index of population production rates for bluegill sunfish as a function of the degree of lakeshore residential development. The production rates for each lake were calculated by applying the size-specific growth rates of bluegills in each lake to the size distribution of fish caught in each lake. The mean growth rate for each of the populations is plotted. The best fitting model [$\log_{10}$(growth)=1.45*(dwelling density+1)$^{-0.082}$] to describe the effect of lakeshore development on bluegill population production rate is shown.

growth rate versus the average density of CWD in each of these groups is suggestive of a systematic reduction in largemouth bass growth in lakes with high residential development and low CWD densities (Figure 5). A similar plot for bluegills also showed a distinct correlation between bluegill growth rates and the density of CWD in the littoral habitats of lakes (Figure 6).

Bluegill growth rates and largemouth bass growth rates were poorly correlated with each other for all pairwise comparisons between the three size classes of bluegills and the four size classes of bass; correlation coefficients ranged from –0.15 to 0.18. Growth rates of bluegills and largemouth bass also were not significantly related ($P > 0.10$) to their catch per unit effort (CPUE), which we used as an index of abundance for these fish, suggesting that the reduction in growth with increased lakeshore residential development was not merely a density-dependent response to changes in population size. Growth estimates for 140-mm bluegills and 300- and 400-mm largemouth bass were positively related ($P < 0.02$) with the total CPUE of all fish caught in each of the lakes.

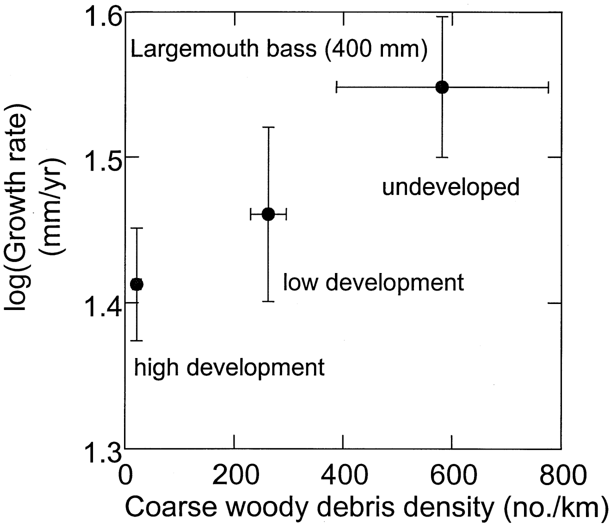

Figure 5. Average annual growth rates of largemouth bass (400 mm total length) plotted against the density of littoral zone CWD density. Lakes are assigned to the undeveloped, low development, and high development groups described in Christensen and others (1996). Symbols show the average growth rates and CWD density in each of these lake groups. Error bars are one standard deviation for both the $\log_{10}$ of the growth rates and for CWD density.

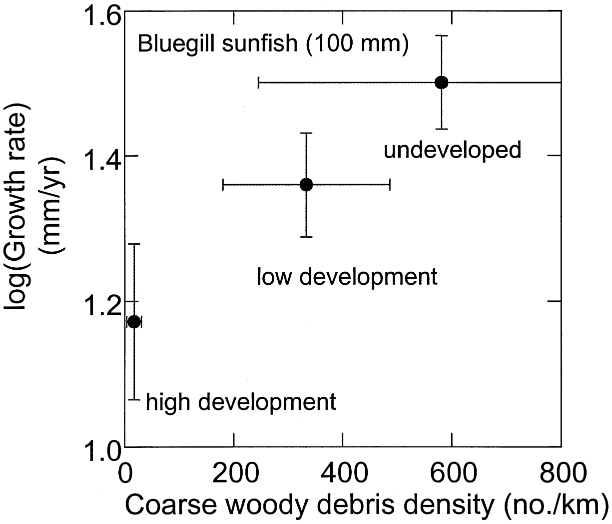

Figure 6. Average annual growth rates of bluegill sunfish (100 mm total length) plotted against the density of littoral zone CWD density. Lakes are assigned to the undeveloped, low development, and high development groups described in Christensen and others (1996). Symbols show the average growth rates and CWD density in each of these lake groups. Error bars are one standard deviation for both the $\log_{10}$ of the growth rates and for CWD density.

To test for effects of lake morphometry and potential productivity on bass and bluegill growth rates, we regressed growth rates against lake area, lake maximum depth, the degree of shoreline convolution, and Secchi depth (Table 1). This analysis detected no significant effects of any of the morphometric ($P > 0.2$) or water transparency ($P > 0.2$) variables on the growth rates of bluegills or largemouth bass.

## DISCUSSION

We used a comparative approach to explore how the growth rates of two common fish species varied with the degree of lakeshore residential development in north temperate lakes. Our results showed that the growth rates of bluegill sunfish were negatively correlated with the degree of lakeshore residential development, and that this effect was not size specific across a relatively broad range of fish sizes. We did not detect a statistically significant effect of residential development on growth rates of largemouth bass. Although this study design does not allow us to identify the mechanisms that cause this growth rate depression of fishes in highly developed lakes, the results nonetheless demonstrate an ecologically important pattern that suggests that residential development of lakeshores may reduce the fish production capacity of lakes.

Models that have been developed to characterize the impact of residential development on lakes have focussed on pelagic processes in these systems. For example, total phosphorus concentration has been shown to increase with increases in the degree of residential development (Dillon and Rigler 1975; Dillon and others 1994). Total phosphorus concentrations are positively correlated with lake primary productivity (Schindler 1978) and fish production and biomass (Hanson and Leggett 1982). Because lakeshore development should increase nutrient loading to lakes, we expected that fish growth rates would increase with increases in residential development. The fact that fish growth rates decreased with residential development suggests that factors other than eutrophication were important to the observed pattern in fish growth. Our analysis of the relationship between fish growth rate and water transparency suggested that these two variables were independent. However, it is important to note that water transparency may not be an accurate indicator of pelagic productivity due to the contributions to light attenuation by dissolved organic matter in lakes (Elser 1987). This study did not allow us to identify the mechanism through which fish growth apparently is reduced in lakes with substantial residential development.

Christensen and others (1996) showed that the density and volume of CWD decreased with increases in residential development in the 14 lakes we surveyed in this study. CWD serves several important functions in littoral zone habitats that may affect the profitability of this habitat to fish populations. One possible explanation for the changes in growth rates along a residential density gradient may be the loss of littoral habitat for fishes by the removal of CWD. The significant decline in CWD as residential development increases (Christensen and others 1996) may reduce the quantity and quality of littoral habitat that is used by bluegill and largemouth bass for foraging on aquatic invertebrates and as refugia from predators. The effects of increased littoral habitat complexity on centrarchid foraging and growth rates are relatively well established for macrophyte-dominated habitats (for example, Crowder and Cooper 1982). However, the effects of CWD on fish growth rates and species interactions in lakes remain relatively unexplored. In general, we should expect that increases in the surface area of underwater structure increases both the biomass of aquatic invertebrates and fish growth rates (Pardue 1973).

The presence or absence of other species in a lake may affect growth rates by influencing competition of bluegill and largemouth bass with other species. Lakes with no residential development had only three to five species present, whereas low and high dwelling density lakes had an average of 10 species (Table 1). Although lake size may explain variations in the number of species found in each lake (Magnuson and others 1994), it is possible that species introductions are more prevalent in highly developed lakes. Several of the species found in highly developed lakes are potential competitors with bluegills (for example, *Ambloplites rupestris*, *Perca flavescens*, *Lepomis gibbosus*). Interspecific competition can substantially decrease the density of aquatic invertebrates and cause declines in bluegill growth (Mittelbach 1988). Interspecific competition also may be more influential on growth rates of juvenile sunfishes (*Lepomis* spp.) before ontogenetic diet shifts occur (Mittelbach 1984; Osenberg and others 1992). Therefore, growth rates of bluegill in lakes with residential development may be reduced because of increased competition with other species.

Our sampling protocol was primarily designed for analyses of the growth rates of bluegills and largemouth bass. The data collected from the two electroshocking transects in the littoral zone of each lake have limited utility to characterize fish community composition and density of each species, especially for species that reside in pelagic habitats. As a result, we treated the CPUE estimates merely as rough approximations of relative fish density and community composition. Future studies designed to evaluate community composition and density effects on bass and bluegills growth rates will benefit from a greater variety of sampling methods to characterize composition (for example, Magnuson and others 1994) and mark-recapture methods to characterize absolute densities.

Increased angling rates in highly developed lakes may reduce average growth rates of sunfish by causing a shift in reproductive strategies in exploited populations. Angling may preferentially exploit large, parental male sunfish when they are guarding nests in the spring and increase the relative proportion of small, early-maturing males in the population (Beard and others 1997; Drake and others 1997; Ehlinger 1997). Because early-maturing males direct a larger proportion of the energy budgets to reproduction rather than somatic growth, selective exploitation of large males can decrease average growth rates in the population. Although this study was not specifically designed to test this mechanism, we have weak evidence to suggest that shifts in reproductive strategies in response to selective exploitation were not important in determining bluegill growth rate responses to development. If increased development resulted in higher exploitation that was selective on large and old individuals, then we would expect that the age distributions of bluegill populations would be shifted to younger and smaller individuals with increased development. Our data suggest the opposite trend (Figure 3). The age distributions of bluegill populations were shifted to older individuals as lakeshore development increased. A substantial component of this age distribution shift appeared to be due to reduced representation by young individuals (less than or equal to 4 years) in the populations (Figure 3). The age distributions of bluegills sampled in this study do not support a life-history mechanism to explain reduced growth in developed lakes. However, these data are suggestive of a mechanism that reduces the growth and survival of young fish.

There are several possibilities that may explain why we did not detect a statistically significant, systematic change in the growth rate of largemouth bass as lakeshore residential development increased in lakes, as was detected for bluegills. First, we had lower statistical power to detect significant effects of lakeshore development on bass growth due to the fact that bass were caught in only nine of the 14 study lakes. The errors in our estimates of lake-specific growth rates also may have been substantial because fewer bass scales were collected for growth rate determination as compared with bluegill scales in each lake. Increases in the intensity and the extent of our study may have shown stronger effects of lakeshore development on bass growth. It is also possible that lakeshore development affects bass growth via several confounding mechanisms. For example, increasing angling pressure on largemouth bass may increase growth rates by decreasing density-dependent interactions (Goedde and Coble 1981; Eder 1984, Gabelhouse1987), and bass growth rates may increase with P loading that increases with residential development. It is possible that these positive effects of residential development on bass growth rate are offset by the negative effects of loss of CWD from littoral habitats. An interesting avenue for future research is to determine the mechanisms through which residential development of lakeshore alters patterns of growth in fishes and evaluate whether these mechanisms are species and size specific.

Our comparative study of growth rates of fish in lakes that are distributed along a residential development gradient showed that bluegill sunfish growth was negatively correlated with the intensity of residential development. The negative correlation between bluegill growth and lakeshore development does not necessarily imply that lakeshore development is reducing the productivity of fish populations. For example, humans may preferentially develop lakes with desirable water quality conditions (that is, low primary productivity). However, given that littoral zone habitat degradation also has been documented along this same human impact gradient (Christensen and others 1996), we suggest that development of lakeshores that results in alterations to riparian and littoral habitats may reduce the capacity of lakes to maintain productive fish populations. The recent changes in land-use patterns that have resulted from extensive residential development in Northern Wisconsin (WI–Department of Natural Resources 1996) may be having important detrimental impacts on the ecological integrity of lake ecosystems. Increasing human pressures on aquatic resources are occurring throughout the United States (NRC 1992). Although future research may elucidate the mechanisms that drive the negative association between fish growth and lakeshore development, we urge that lake and land managers develop proactive management plans to protect littoral and riparian habitats in lakes.

## ACKNOWLEDGMENTS

We are grateful to the staff of the University of Wisconsin, Center for Limnology–Trout Lake Laboratory for support and logistical help, to the University of Notre Dame Environmental Research Center for assistance and access to their lakes, and to Steve

Carpenter and Jim Kitchell for advice throughout this study. Tom Frost and Kathy Webster provided invaluable assistance in accessing background limnological data on the study lakes. Mark Olson, Tony Ives, Tim Kratz, and Doug Beard provided many helpful suggestions, and Tim Essington and Mark Olson reviewed earlier versions of the manuscript. The field work for this study was only possible because of the assistance from the students and staff of the Trout Lake Laboratory. This study was supported in part by the National Science Foundation.

## REFERENCES

Beard TD Jr, Drake MT, Breck JE, Nate NA. 1997. Effects of simulated angling regulations on stunting in bluegill populations. North Am J Fisheries Manage 17:525–32.

Becker GC. 1983. The fishes of Wisconsin. Madison, WI: University of Wisconsin Press. 1052 p.

Brown RT, Curtis JT. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecol Monogr 22:217–34.

Carlander KD, 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. Trans Am Fisheries Soc 111:332–6.

Carpenter SR, Kitchell JF. 1993. The trophic cascade in lakes. Cambridge: Cambridge University Press.

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol Appl 8:559–68.

Christensen DL, Herwig BJ, Schindler DE, Carpenter SR. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. Ecol Appl 6:1143–9.

Crowder LB, Cooper WE. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–13.

Curtis JT. 1959. The vegetation of Wisconsin. Madison, WI: University of Wisconsin Press.

Dillon PJ, Rigler FH. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J Fisheries Res Board Can 32:1519–31.

Dillon PJ, Scheider WA, Reid RA, Jeffries DS. 1994. Lakeshore capacity study: part 1—test of effects of shoreline development on the trophic status of lakes. Lake Reservoir Manage 8:121–9.

Drake MT, Claussen JE, Philipp DP, Pereira DL. 1997. A comparison of bluegill reproductive strategies and growth among lakes with different fishing intensities. North Am J Fisheries Manage 17:496–507.

Eder S. 1984. Effectiveness of an imposed slot length limit of 12.0–14.9 inches on largemouth bass. North Am J Fisheries Manage 4:469–78.

Ehlinger TJ. 1997. Male reproductive competition and sex-specific growth patterns in bluegill. North Am J Fisheries Manage 17:508–15.

Elser JJ. 1987. Evaluation of size-related changes in chlorophyll-specific light extinction in some north temperate lakes. Arch Hydrobiol 111:171–82.

Gabelhouse DW Jr. 1987. Responses of largemouth bass and bluegills to removal of surplus largemouth bass from a Kansas pond. North Am J Fisheries Manage 7:81–90.

Goedde LE, Coble DW. 1981. Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin lakes. Trans Am Fisheries Soc 110:594–603.

Guy CS, Willis DW. 1990. Structural relationships of largemouth bass and bluegill populations in South Dakota ponds. North Am J Fisheries Manage 10:338–43.

Hanson JM, Leggett WC. 1982. Empirical prediction of fish biomass and yield. Can J Fisheries Aquatic Sci 39:257–63.

Hrabik TR, Magnuson JJ, McLain AS. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research in two lakes. Can J Fisheries Aquatic Sci 55:1364–71.

Magnuson JJ, Benson BJ, McLain AS. 1994. Insights on species-specific richness and turnover from long-term ecological research: fishes in North temperate lakes. Am Zool 34:437–51.

Mittelbach GG. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499–513.

Mittelbach GG. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69:614–23.

Mittelbach GG, Osenberg CW. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology 74:2381–94.

[NRC] National Research Council. 1992. Restoration of aquatic ecosystems. Washington, DC: National Academy Press.

Olson MH. 1996a. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179–90.

Olson MH. 1996b. Predator-prey interactions in size-structured fish communities: implications of prey growth. Oecologia 108:757–63.

Olson MH, Mittelbach GG, Osenberg CW. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76: 1758–71.

Osenberg CW, Mittelbach GG, Wainwright PC. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology 73:255–67.

Pardue GB. 1973. Production response of the bluegill sunfish, *Lepomis macrochirus* Rafinesque, to added attachment surface for fish-food organisms. Trans Am Fisheries Soc 102:622–6.

Schindler DW. 1978. Factors regulating phytoplankton production and standing crop in the world's lakes. Limnol Oceanogr 23:478–86.

Stearns F. 1951. The composition of the sugar maple-hemlock-yellow birch association in northern Wisconsin. Ecology 32: 245–65.

Werner EE, Gilliam JF. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–426.

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 62:1540–8.

WI–Department of Natural Resources. 1996. Northern Wisconsin's Lakes and Shorelines: a report examining a resource under pressure. Technical Report.