

Lakeshore residential development and growth of largemouth bass (*Micropterus salmoides*): a cross-lakes comparison

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Abstract – Lakeshore residential development is associated with changes in littoral habitat, riparian habitat, and ecosystem function with potential impacts ramifying through aquatic food webs. Effects of these changes on economically important game fishes may vary with fish size. We investigated largemouth bass (*Micropterus salmoides*) size-specific growth rates across 16 lakes spanning the range of lakeshore residential development in Wisconsin's Northern Highland Lake District using a longitudinal multilevel model. Growth rates of small fish had a strong positive relationship with lakeshore residential development. The strength of the relationship decreased with length and became increasingly negative for fish longer than 210 mm. This pattern may be driven by a release from density-dependent growth, shifts in available prey sources, reduced macrophyte cover, or angling-induced selection pressures. Regardless of the mechanism, our results indicate, relative to undeveloped lakes, largemouth bass in highly developed lakes take 1.5 growing seasons longer to enter the fishery (356 mm).

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Key words: largemouth bass; *Micropterus salmoides*; fish growth; lakeshore residential development; longitudinal multilevel model; longitudinal hierarchical model

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Introduction

Critical lake littoral habitat, riparian habitat, and ecosystem function are altered as a result of lakeshore residential development (LRD) (Engel & Pederson 1998; Francis & Schindler 2009). Fallen trees in lake littoral zones, for instance, serve as an important refuge for fish (Sass et al. 2006; Roth et al. 2007), a substrate for invertebrate prey production (Vander Zanden & Vadeboncoeur 2002; Roth et al. 2007), and as fish nesting habitat (Hunt & Annett 2002), but this coarse woody habitat is negatively correlated with LRD (Christensen et al. 1996; Jennings et al. 2003; Francis & Schindler 2006). Future inputs of coarse woody habitat into the littoral zone are greatly reduced by reductions in riparian vegetation associated with LRD (Francis & Schindler 2006; Marburg et al. 2006). LRD is inversely correlated with littoral macrophyte richness (Bryan & Scarnecchia 1992) and cover of

floating leaf and emergent vegetation (Jennings et al. 2003; Radomski 2006). Shifts in macroinvertebrate communities (Brauns et al. 2007; Rosenberger et al. 2008) and reduced organic sediments in the littoral zone (Francis et al. 2007) are also associated with LRD. Likewise, exploitation rates of game fishes are expected to increase with LRD (NRC 1992). These changes associated with LRD have the potential to ramify through both aquatic and terrestrial food webs (Engel & Pederson 1998).

Altered habitat structure and ecosystem function associated with LRD may drive changes in fish ecology. A fish diet survey by Francis & Schindler (2009) found a negative correlation between LRD and energetically favourable food sources, likely due to altered riparian habitat. Within developed lakes, black crappie (*Pomoxis nigromaculatus*) nest adjacent to undeveloped sections of shoreline and associate with macrophytes, which were less abundant adjacent to

developed shorelines (Reed & Pereira 2009). The same trend was identified for largemouth bass (*Micropterus salmoides*) although a mechanism was not identified. Reductions in littoral habitat are the suspected driver of the negative correlation between LRD and small fish (≤ 100 mm) aggregations (Scheurell & Schindler 2004). Bluegill (*Lepomis macrochirus*) growth rates negatively correlate with LRD (Schindler et al. 2000). Schindler et al. (2000) also identified a marginally significant negative relationship between LRD and growth rates of the largest size class (400 mm) of largemouth bass but did not identify a conclusive relationship for smaller size classes. These shifts in behaviour and growth associated with LRD may have implications for recreational fisheries.

In many areas of the United States, such as Wisconsin's Northern Highland Lake District (NHLD), recreational fisheries are a pillar of the regional economy (Penalzo 1991; Postel & Carpenter 1997; Peterson et al. 2003). Therefore, understanding and quantifying whether humans alter these important fisheries is essential. We investigated the relationship between largemouth bass growth rate across both fish size and LRD. Our study built upon the findings of Schindler et al. (2000) by nearly doubling the sample size of lakes and fish, spanning a larger gradient of LRD, avoiding potential confounding effects of coarse woody habitat, and employing a more sensitive hierarchical analysis method.

We performed a cross-lakes comparison of 16 lakes spanning the full regional gradient of LRD (0–45.8 buildings·km⁻¹) in the NHLD to test for a relationship between LRD and largemouth bass growth across fish size. We used a longitudinal,

multilevel approach to estimate growth responses across a range of fish sizes and found that growth rates of both small and large largemouth bass were significantly related to LRD.

Methods

Study area

We surveyed largemouth bass size-specific growth rates among 16 lakes spanning the known gradient of lakeshore residential development in Wisconsin's NHLD (Fig. 1). The NHLD is a formerly glaciated, lake-rich region spanning about 5330 km² with approximately 7600 lakes (Peterson et al. 2003; Carpenter et al. 2007) and is vegetated by upland conifer-hardwood forests (Stearns 1951; Brown & Curtis 1952). Human population densities in the region have increased nearly fivefold in the last half century (Carpenter et al. 2007), and since the 1960s, the majority of that development has occurred on lake shorelines (Schnaiberg et al. 2002). In the early 2000s, Vilas County, the county of our study lakes, had nearly 16,500 buildings within 100 m of lake shorelines (Riera et al. 2001).

Lakeshore residential development of our study lakes ranged from 0 to 45.8 buildings·km⁻¹ within 100 m of lake shorelines (Table 1). Predators of largemouth bass from the Esocidae family (e.g., muskellunge *Esox masquinongy* or northern pike *Esox lucius*) were common or abundant in all but three lakes in our study: Camp Lake, Little Rock Lake, and Day Lake (Wisconsin Department of Natural Resources 2005). Study lakes were selected for low coarse woody habitat densities (0–125 logs·km⁻¹) and

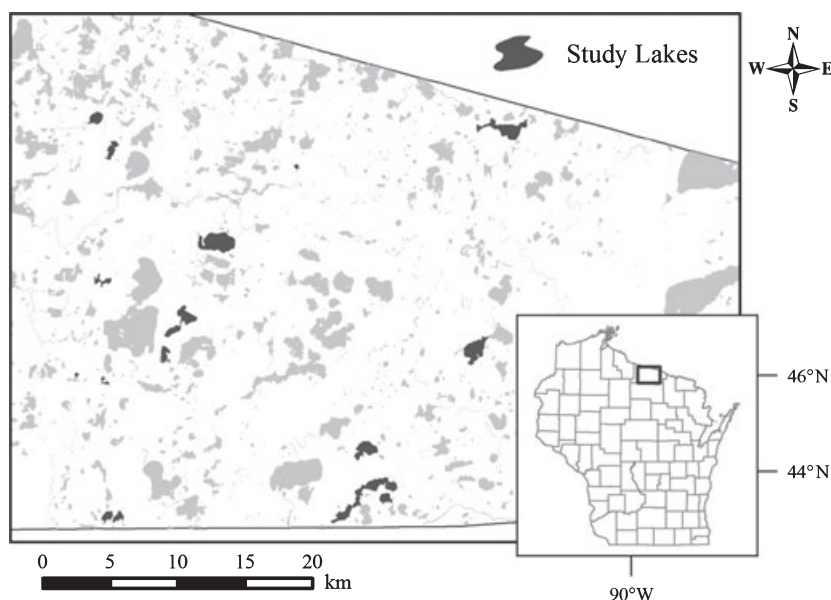


Fig. 1. Map of study lakes in the Northern Highlands Lake District located in Vilas County, Wisconsin, USA.

Table 1. Summary of physical lake characteristics and largemouth bass (*Micropterus salmoides*) sample size (N ; young-of-the-year fish removed).

| Lake | Lake Code | Perimeter (km) | Area (ha) | Maximum Depth (m) | Building Density (no. km ⁻¹) | Largemouth Bass (N) |
|--------------------|-----------|----------------|-----------|-------------------|--|-------------------------|
| Allequash | AL | 10.2 | 165.3 | 7.3 | 0.0 | 30 |
| Arrowhead | AR | 3.5 | 40.1 | 13.1 | 45.8 | 30 |
| Black Oak | BO | 12.0 | 230.1 | 25.9 | 18.0 | 30 |
| Brandy | BR | 3.5 | 45.1 | 13.4 | 30.1 | 30 |
| Camp | CP | 2.9 | 17.6 | 9.4 | 0.0 | 30 |
| Day | DY | 5.5 | 47.3 | 14.6 | 0.2 | 30 |
| Found | FD | 6.4 | 139.3 | 6.4 | 16.6 | 30 |
| Johnson | JN | 3.6 | 34.7 | 12.8 | 26.2 | 30 |
| Little Crooked | LC | 4.8 | 63.8 | 6.1 | 5.5 | 30 |
| Little John | LJ | 5.3 | 63.4 | 5.8 | 2.1 | 30 |
| Little Rock | LR | 1.4 | 8.1 | 6.5 | 0.0 | 30 |
| Little St. Germain | LSG | 23.3 | 402.2 | 16.2 | 19.8 | 28 |
| Moon | MN | 3.4 | 54.4 | 11.6 | 15.0 | 28 |
| Round | RD | 3.7 | 71.5 | 7.6 | 0.3 | 30 |
| Upper Buckatabon | UB | 13.2 | 211.4 | 14.3 | 12.6 | 30 |
| White Sand | WS | 9.3 | 304.6 | 21.6 | 5.8 | 27 |

spanned only 13% of the observed regional coarse woody habitat gradient (Christensen et al. 1996) to reduce potential confounding effects of coarse woody habitat and lakeshore residential development.

Fish sampling

We sampled largemouth bass between June and August of 2006 primarily via electrofishing along the lake perimeter. Fish were collected via angling when lake conductivity was not suitable for electrofishing. Thirty fish were collected from each lake to determine size-specific growth rates. Fish length (total length; mm) was recorded, and 5 to 10 scales were collected from each fish from the area posterior to a depressed pectoral fin. We removed young-of-the-year fish from the analysis owing to the lack of annuli, and as a result, sample size varied between lakes (Table 1). Scales from yearling fish and older were sonicated and pressed between two slides. Nonregenerated scales were read into a digital imaging system. Annual growth rates (mm·year⁻¹) were determined using Fraser-Lee's method of back calculation with Carlander's recommended constant of 20 mm for largemouth bass (Carlander 1982) as used in Schindler et al. (2000). It is possible that LRD could have changed during the lifetimes of the longer-lived bass in our study, especially because LRD boomed during the 1990s but slowed substantially during the 2000s (Carpenter et al. 2007). To eliminate any potential effects of changing LRD levels, only the annual growth estimates from 2001 to 2005 were included as repeated measures of annual growth for each fish.

Estimating ages from hard structures such as scales and otoliths is challenging (Buckmeier & Howells 2003) especially for older largemouth bass (Maraldo & Maccrimmon 1979); however, largemouth bass have been successfully aged up to 16 years (Buckmeier & Howells 2003). We acknowledge that back-calculated growth rates from any structure must be recognised as estimates with inherent errors (Maceina et al. 2007), and for that reason, we used relatively large sample sizes ($N = 27-30$ per lake) to evaluate growth responses in our study.

Statistical analysis

Our data were hierarchically structured with repeated measures of annulus-specific growth observations (mm) nested within individual fish growth rates (mm·year⁻¹), individual fish nested within lakes, and each lake with a unique set of lake characteristics, such as LRD. We designed our analysis around the hierarchical nature of the data and tested for a relationship between LRD and largemouth bass growth rate using a longitudinal (repeated measures) multilevel model (Goldstein 1995; Ai 2002; Wagner et al. 2006). Unlike least squares regression methods more commonly used to determine size-specific growth rates, the longitudinal multilevel model approach allows us to account for repeated measures of annuli and to quantify, rather than lose, variation in growth at multiple levels (among fish and lakes).

We performed all analyses in R-Cran statistical package (R Development Core Team 2010; package: 'lme4' version 0.999375-33). Multilevel modelling methods followed procedures outlined in Gelman & Hill (2008). Growth rates were log_e-transformed prior to analysis. Likewise, fish length was log_e-transformed and grand-mean-centred prior to analysis. We allowed both slopes and intercepts to vary as random effects.

Based on sample design, we expected our model to include fish length and LRD; however, we performed forward stepwise selection with a suite of additional covariates to account for unexplained variance. The covariates included in the stepwise selection process were LRD, coarse woody habitat, conductance, maximum lake depth, Secchi depth, chlorophyll a concentration, dissolved organic carbon, area, and an index of shoreline morphometry (Wetzel 2001). The initial model defined growth only as a function of length. At every step, model fit was assessed as each covariate as well as the interaction of the covariate with fish length was systematically added to the initial model as a fixed effect. Models were fit by maximizing the log likelihood. At each step, the covariate or interaction with the greatest change in deviation information criterion (DIC) of four or more was included, as

suggested by Burnham & Anderson (1998) for AIC and by Spiegelhalter et al. (2002) for DIC. All covariate data, including LRD, were previously surveyed during the summers of 2001–2004 and archived in the North Temperate Lakes Long-Term Ecological Research online database (Carpenter & Kratz 2001).

Model structure

The multilevel model was composed of three levels: (1) the lowest measurement level in which annulus-specific observations of fish length were used to model variation in growth (2032 annuli observations); (2) the fish level in which the intercepts and slopes of individual fish growth trajectories were allowed to vary (473 individual fish); and (3) the lake level in which among-lake variation in growth was modelled using lake characteristics (16 lakes).

Level 1: Annulus level: within fish, within lake

$$y_i \sim N(\beta_{0j[i]} + \beta_{1j[i]}x_i, \sigma_y^2), \quad (\text{Model 1.1})$$

for $i = 1, \dots, n$ observations

Here, y_i is the growth for observation i in fish j at length x_i , $\beta_{0j[i]}$ is the intercept (or growth at the centred or average length) of fish j , $\beta_{1j[i]}$ is the slope parameter (or growth–length relationship) of fish j , and σ_y^2 is the residual variance of y_i (growth) of observation i in fish j at length x_i . The notation $N(\mu, \sigma^2)$ refers to a normal (or, below, a multivariate normal) distribution with mean vector μ and covariance matrix σ^2 . In the case of Eq. (1.1), the model is a linear regression of \log_e -transformed growth rate on \log_e -transformed centred body size.

Level 2: Fish level: among fish, within lake

$$\begin{pmatrix} \beta_{0j} \\ \beta_{1j} \end{pmatrix} \sim N\left(\begin{pmatrix} \gamma_{0k[j]} \\ \gamma_{1k[j]} \end{pmatrix}, \begin{pmatrix} \sigma_{0\beta}^2 & \rho\sigma_{0\beta}^2\sigma_{1\beta}^2 \\ \rho\sigma_{0\beta}^2\sigma_{1\beta}^2 & \sigma_{1\beta}^2 \end{pmatrix}\right), \quad (\text{Model 1.2})$$

Here, $\gamma_{0k[j]}$ is the mean intercept (or growth at average or centred length) for lake k , $\gamma_{1k[j]}$ is the mean growth rate (or growth–length relationship) for lake k , $\sigma_{0\beta}^2$ and $\sigma_{1\beta}^2$ are the variation among fish-specific slopes and intercepts, respectively, and $\rho\sigma_{0\beta}^2\sigma_{1\beta}^2$ is the covariance among $\sigma_{0\beta}^2$ and $\sigma_{1\beta}^2$ where β_{0j} and β_{1j} have correlation ρ . Equation (1.2) relates growth parameters β_{0j} and β_{1j} of an individual fish to the lake means and the covariance matrix among fish within a lake.

Level 3: Lake level: among fish, among lakes

$$\begin{pmatrix} \gamma_{0k} \\ \gamma_{1k} \end{pmatrix} \sim N\left(\begin{pmatrix} \delta_{00k} + \delta_{01k}z_{01k} + \dots + \delta_{0nk}z_{0nk} \\ \delta_{10k} + \delta_{11k}x_{i1k} + \dots + \delta_{1nk}x_{i1k}z_{1nk} \end{pmatrix}, \begin{pmatrix} \sigma_{0\gamma}^2 & \rho\sigma_{0\gamma}^2\sigma_{1\gamma}^2 \\ \rho\sigma_{0\gamma}^2\sigma_{1\gamma}^2 & \sigma_{1\gamma}^2 \end{pmatrix}\right), \quad \text{for } k = 1, \dots, K \text{ lakes} \quad (\text{Model 1.3})$$

Here, δ_{00k} is the overall intercept (or grand mean growth at average or centred length over all lakes) with $\sigma_{0\gamma}^2$ as the variance among lake intercepts, and δ_{0nk} is the effect of covariate n with a value of z_{0nk} on the intercept. δ_{10k} is the overall growth rate (or grand mean growth–length relationship) with $\sigma_{1\gamma}^2$ as the variation in growth rates (or slopes) among lakes; δ_{1nk} is the effect of the interaction of fish length x_i and covariate n with a value of z_{1nk} on the overall growth rate. $\rho\sigma_{0\gamma}^2\sigma_{1\gamma}^2$ is the covariance between $\sigma_{0\gamma}^2$ and $\sigma_{1\gamma}^2$ where $\gamma_{0,k}$ and $\gamma_{1,k}$ have correlation ρ . Equation (1.3) is a bivariate regression of lake-specific growth parameters γ_{0k} and γ_{1k} on the fixed effects of the added covariates.

The relationship between LRD and the growth rate of a fish of a given length, henceforth referred to as the building density effect, was calculated as the derivative of model-predicted growth rate with respect to LRD with units of $\ln(\text{mm}\cdot\text{year}^{-1})/\text{building}\cdot\text{km}^{-1}$. The standard deviation of the building density effect was calculated from the covariance matrix of model parameters using standard error propagation formulae (Meyer 1975). The building density effect can be interpreted as the average change in growth rate of fish of a given length with the addition of 1 $\text{building}\cdot\text{km}^{-1}$ of shoreline.

Results

A total of 2032 annulus observations from 473 fish were made from 16 lakes in the NHLD. The total number of bass represented in each lake ranged from 27 to 30 (Table 1), and fish lengths from 57 to 408 mm were represented in our data set (Fig. 2). The mean \log_e length, or length on which the data were centred, was 5.3 \log_e mm. The maximum growth rate observed was 133.8 $\text{mm}\cdot\text{year}^{-1}$ at annulus (age) one from a fish in Little St. Germain Lake (LSG). The lowest growth rate observed was 5.8 $\text{mm}\cdot\text{year}^{-1}$ at annulus 12 in a fish from Camp Lake (CP).

Although growth at length varied greatly within a lake, an apparent trend at small sizes (approximately 90 mm or -0.85 centred \log_e mm) was observed in all lakes (Fig. 3). This trend, however, is an artefact of how growth was calculated. The growth rate at annulus one, or how much a fish grew in the first year, is equal to the fish length at annulus one, thus

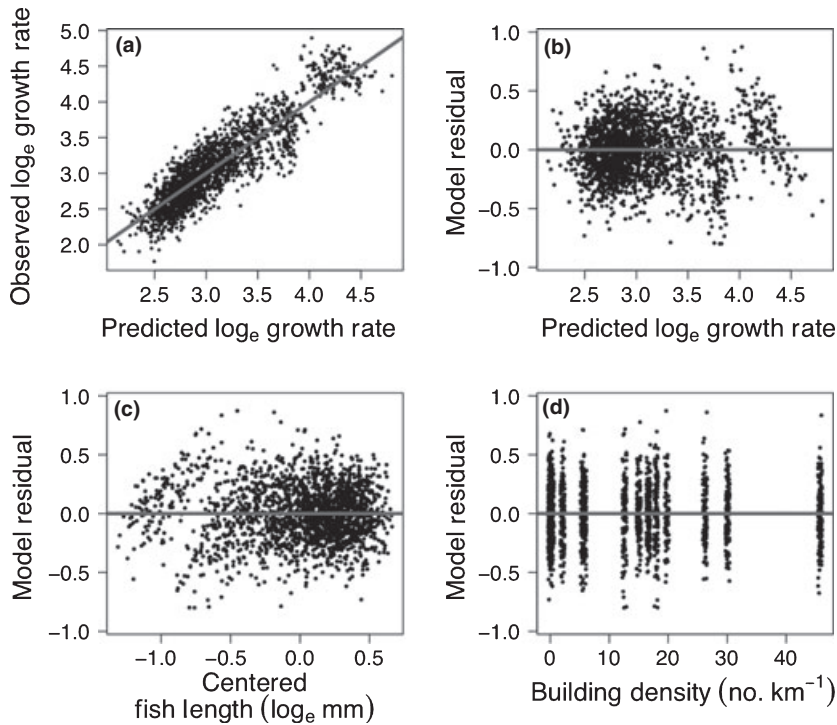


Fig. 2. Longitudinal multilevel model fit. (a) Observed \log_e growth rate ($\text{mm}\cdot\text{year}^{-1}$) plotted against predicted \log_e growth rate ($\text{mm}\cdot\text{year}^{-1}$). Model residuals plotted against (b) predicted \log_e growth rate ($\text{mm}\cdot\text{year}^{-1}$), (c) centred fish length ($\log_e\text{mm}$), and (d) building density (no. km^{-1}). Residuals were jittered when plotted against building density.

producing a 1:1 relationship between growth rate and length for observations at annulus one.

Most lakes had annulus-specific observations spanning the entire range of fish lengths (Fig. 3). After young-of-the-year fish were removed from the analysis, we captured fish from a range of over 300 mm and 15 years. The average maximum size at capture was 371 mm across all lakes. Two lakes had a sparse sample of large individuals; the largest individuals from Little John and Little Crooked Lakes were a 249-mm 8-year-old and a 310-mm 11-year-old largemouth bass, respectively.

Model selection

The forward stepwise selection process considered both the interaction of fish length and LRD and the interaction of fish length and maximum depth as candidate predictors. The initial model fitted growth as a function of length and had a DIC of 752.4. Adding the interaction of LRD and length at step one improved the DIC by 5.3, and adding the interaction of length and maximum depth at step two improved the DIC by 5.8. No covariate improved model fit by the minimum cut-off of 4 at step three, based on criteria proposed for the AIC (Burnham & Anderson 1998; Spiegelhalter et al. 2002). When compared to the initial model, unconditional at levels 2 and 3, all the standard deviations of the random effects of the final stepwise-selected model were within 0.001 or 1% of the initial model except for the slope at level 3. The

addition of the interactions of LRD and maximum depth with length improved model fit and reduced the standard deviation of the slope at level 3 by 0.116 or 37%.

Model fit

Largemouth bass growth rate was successfully modelled as a function of fish length, the interaction of fish length and LRD, and the interaction of fish length and maximum depth. Predicted growth rates were closely clustered around observed growth rates (Fig. 2a). Residuals were evenly distributed across predicted growth rate (Fig. 2b) and across fish length (Fig. 2c). Model fit was also unbiased across the regional gradient of building density (Fig. 2d). As an unavoidable consequence of how growth rates are calculated, growth rate and length at annulus one are equal creating a conspicuous trend for observations at annulus one (clustered observations in the upper right of Fig. 2a, on the right side of Fig. 2b, and on the left side of Fig. 2c). Nonetheless, growth calculations at annulus one did not affect model results for later annuli.

Model results

Our analysis identified a significant relationship between LRD and largemouth bass size-specific growth rate that varied across fish length (Table 2). In general, we observed a more negative slope

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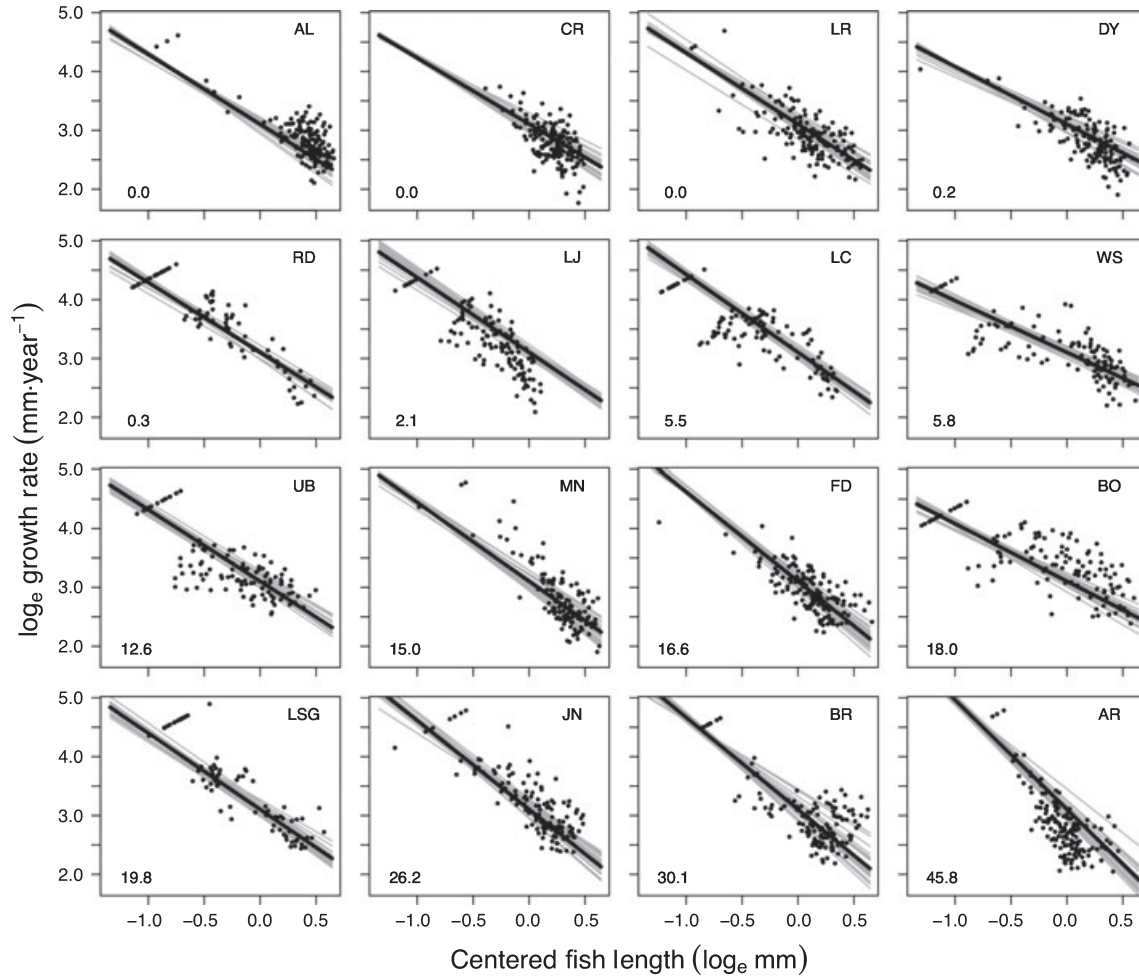


Fig. 3. Lake-specific longitudinal multilevel model fit. Largemouth bass (*Micropterus salmoides*) annulus-specific \log_e growth rate ($\text{mm}\cdot\text{year}^{-1}$) across centred fish length ($\log_e\text{-mm}$) per lake (points) is shown with lake-specific model-predicted growth trajectories (black line) and random effects (grey lines). Lake codes are shown in upper right (refer to Table 1 for lake name and characteristics) with LRD ($\text{buildings}\cdot\text{km}^{-1}$) in bottom left.

Table 2. Longitudinal multilevel model results. Parameter standard deviations (SD), correlations between the intercepts and slopes (corr), coefficients estimates (coef est), and coefficient standard errors (coef SE) of fixed and random effects at each level of the model. Parameter symbols in parenthesis correlate with parameter symbols in Models 1.1–1.3.

| Model Details | | | Random Effects | | | Fixed Effects | | |
|---------------|-------------|-------------|----------------|------------------------------|------------------|-----------------------|---------------------------|---------|
| Model Level | Sample Unit | Sample Size | Parameter | SD | Corr | Coef Parameter | Coef Est | Coef SE |
| Level 1 | Annuli | 2032 | Residual | 0.259 (σ_ν) | | | | |
| Level 2 | Fish | 473 | Intercept | 0.126 ($\sigma_{0\beta}$) | 0.496 (ρ) | | | |
| | | | Slope | 0.169 ($\sigma_{1\beta}$) | | | | |
| Level 3 | Lake | 16 | Intercept | 0.145 ($\sigma_{0\gamma}$) | 0.060 (ρ) | Intercept | 3.105 (δ_{00k}) | 0.038 |
| | | | Slope | 0.197 ($\sigma_{1\gamma}$) | | Length | -1.402 (δ_{10k}) | 0.129 |
| | | | | | | LRD: length | -0.018 (δ_{11k}) | 0.005 |
| | | | | | | Maximum depth: length | 0.029 (δ_{12k}) | 0.010 |

between growth and length as LRD increased (Fig. 3), although this relationship was dampened with greater maximum depth (Table 2; Fig. 3). The relationship between LRD and growth across fish length was

illustrated by taking the derivative of the model with respect to LRD (Fig. 4). This identified the average change in growth rate at a given length with the addition of 1 $\text{building}\cdot\text{km}^{-1}$, or the building density

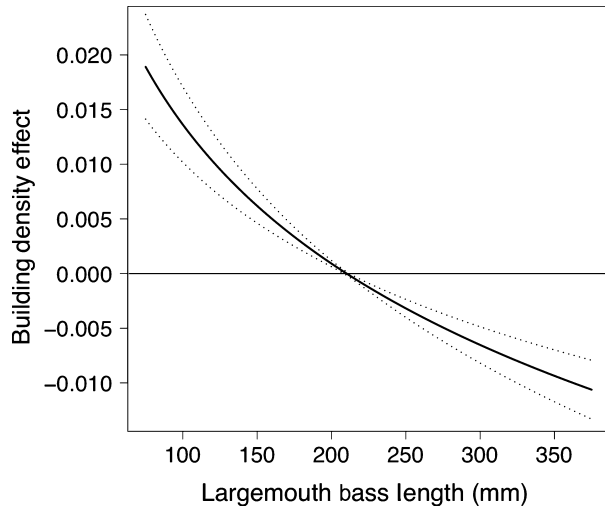


Fig. 4. The effect of building density on growth rate across the observed gradient of largemouth bass (*Micropterus salmoides*) length (black line). A value above zero (grey line) indicates a positive relationship between building density and growth rate; a value below zero indicates a negative relationship. Dotted lines are \pm one standard deviation calculated from the covariance matrix of model parameters using standard error propagation formulae. The building effect is interpreted as the average change in the growth rate of fish of a given length if 1 building \cdot km $^{-1}$ is added to the shoreline; units are ln (mm year $^{-1}$)/building km $^{-1}$.

effect. The model indicated that largemouth bass growth rate was positively correlated with building density for largemouth bass sizes smaller than 210 mm and was negatively correlated for all larger sizes. Growth rates showed the largest changes across the gradient of building densities for the largest and smallest size classes.

Discussion

The relationship between largemouth bass growth rate and LRD across fish length was determined using a longitudinal multilevel model. This innovative approach allowed us to account for repeated measures of annuli observations, include the hierarchical nature of the sample design, and incorporate variance between hierarchical levels. We found a strongly significant negative relationship between LRD and the growth rate of large sizes (>210 mm) of largemouth bass. Intriguingly, the opposite outcome was observed at smaller body sizes: a significant positive relationship was observed between LRD and the growth rate of small sizes (<210 mm) of largemouth bass. The results for small sizes of largemouth bass appear to be new. The findings for large sizes of largemouth bass corroborate trends reported by Schindler et al. (2000). Furthermore, our sample design and statistical methods showed that the negative relationship of LRD and growth rates of large sizes of largemouth bass is

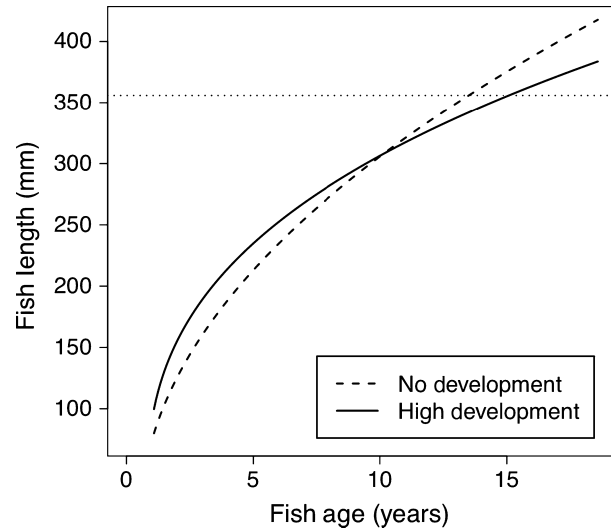


Fig. 5. Model-predicted growth trajectories for the average largemouth bass in a lake without development and a lake with high development (45.8 buildings \cdot km $^{-1}$). Simulations were initiated at the mean observed length at age 1 in the three least and most developed lakes, 80.0 and 99.7 mm, respectively. Simulations were performed using the average maximum lake depth (12 m). Grey dotted line shows the legal length limit in the NHLD, 356 mm (14 inches).

statistically robust. Thus, our findings confirm the trends reported by Schindler et al. (2000).

Comparative studies such as ours are powerful for testing patterns or associations across lakes, but inferences about mechanisms must be cautious (Cole et al. 1991). Nonetheless, we have identified an ecologically important pattern that suggests LRD alters largemouth bass growth. The mechanisms driving this relationship are likely complex and highly variable. For instance, release from density-dependent growth, shifts in available prey sources, reduced macrophyte cover, and angling-induced selection pressures are all potential mechanisms that could be acting independently or concurrently to drive the observed trends in largemouth bass growth.

The observed trend of increased growth rates of smaller largemouth bass with LRD (Fig. 4) could be driven by several mechanisms. For instance, reductions in lake-wide aggregations of small fish (≤ 100 mm) associated with LRD (Scheuerell & Schindler 2004) may release young-of-the-year and yearling largemouth bass from negative density-dependent growth responses (Olson et al. 1995; Post et al. 1998), resulting in increased growth rates of these small sizes with LRD. Reductions in vegetation, similar to those associated with LRD (Jennings et al. 2003; Radomski 2006), have also been shown to result in increased growth rates of small largemouth bass (Bettoli et al. 1992; Olson et al. 1998). Likewise, shifts in macroinvertebrate abundance associated with

LRD (Rosenberger et al. 2008) could result in an increased availability of energetically beneficial food sources with LRD for smaller largemouth bass in highly developed lakes. An increase in energetic food sources could potentially result in greater growth rates for small fish and induce earlier ontogenetic shift to piscivory with LRD (Olson 1996). Earlier ontogenetic shifts to piscivory would promote a rapid growth divergence along a LRD gradient for small sizes of largemouth bass that would likely diminish with size as individuals in undeveloped lakes undergo ontogenetic shift later in the season, similar to the growth trends we observed (Fig. 4).

Angling has also been shown to act as a strong selection pressure not only resulting in an increase in growth rate of smaller size classes, as seen in our model (Fig. 4), but also causing a shift in maturity towards smaller sizes and younger ages (Reznick et al. 2001; Reznick & Ghalambor 2005; Lewin et al. 2006). Reductions in size and age at maturity result in a reallocation of energy from somatic to reproductive growth of mature individuals causing reduced growth rates of larger sizes, similar to our results (Fig. 4). Furthermore, angling can impact populations by sparing the less-vulnerable, slower-growing individuals. Vulnerability to angling has been correlated with growth rate (Biro & Post 2008), and a quarter-century-long experiment showed that largemouth bass vulnerability is heritable and recreational fisheries can select towards a less-vulnerable population (Philipp et al. 2009). This suggests that exploitation of largemouth bass associated with LRD (NRC 1992) could result in reduced growth rates. However, the selection for slower-growing individuals is not limited to harvested populations.

Faster-growing individuals are likely more vulnerable to angling, as mentioned above (Biro & Post 2008; Philipp et al. 2009), and largemouth bass are particularly vulnerable while nesting (Suski & Philipp 2004). Therefore, catch-and-release practices during spawning have the potential to promote egg loss and thereby reduce fecundity of these more vulnerable and faster-growing individuals owing to rapid nest predation (Uusi-Heikkilä et al. 2008) and nest abandonment after being handled by anglers (Siepkner et al. 2009), resulting in the removal of faster growth rates from the population (Philipp et al. 2009). An increase in angling associated with LRD, therefore, has the potential to alter growth rates through harvesting or catch-and-release practices.

Regardless of the mechanism, the observed pattern of largemouth bass size-specific growth rate versus LRD has implications for fish ecology and management. To determine how the observed growth pattern might impact largemouth bass fisheries across LRD, we used our model to predict the growth

trajectories of an average individual in both a lake without development and a lake with high development ($45.8 \text{ buildings}\cdot\text{km}^{-1}$) given the mean maximum depth (Fig. 5). We initiated the model at the average length at age 1 in the three lakes with the lowest LRD and the three lakes with the highest LRD or 80.0 and 99.7 mm, respectively. We found that the length at age is greater for individuals in highly developed lakes until around age 9 or a length of 300 mm. Above this size, the length at age of individuals in lakes without LRD is greater than that of individuals in highly developed lakes. As a result, individuals in highly developed lakes take about 1.5 growing seasons longer to reach the legal length limit of 356 mm. If individuals in lakes without LRD follow this growth trajectory, they will reach trophy lengths several years before individuals in high-LRD lakes will reach.

Ages at length for adult largemouth bass in our study are greater than those observed in some other regions (Bennett 1937; Jackson et al. 2008). However, long-term research on tagged largemouth bass populations in the Northern Highland Lake District is consistent with our findings. For example, tagged largemouth bass have been observed growing at rates similar to our model in both Little Rock Lake, Vilas Co. WI (e.g., 304 mm in 2001, 337 mm in 2005; 201 mm in 2001, 330 mm in 2009; Gaeta, J.W. unpublished data), and Paul Lake, Gogebic Co. MI (e.g., 150 mm in 1988, 312 mm in 1997; 188 mm in 1986, 342 mm in 1997; J.F. Kitchell, B. Weidel, J. Hodgson, T. Cline and S. Carpenter, unpublished data). Largemouth bass adults appear to persist despite rather slow growth rates in some lakes of the Northern Highland Lake District. Regional differences in largemouth bass growth rates in relation to habitat and other factors are an important topic for further research.

We determined that growth rates of small largemouth bass (<210 mm) are positively correlated with LRD, while growth rates of large individuals (>210 mm) are inversely related to LRD as they grow (Fig. 4). Future work investigating potential mechanisms of the observed pattern should study the timing of ontogenetic shifts as well as the diets of young-of-the-year and yearling largemouth bass across LRD. Likewise, quantifying both species-specific retention and catch-and-release rates across the NHLD and between the NHLD and other regions could provide invaluable insight into this potential driver of growth. Researchers should also attempt to establish the relationship between growth rate and vulnerability of largemouth bass to angling. Humans may choose to develop lakes with inherent characteristics, such as fish community structure, that drive the observed pattern of largemouth growth versus LRD. Nonetheless, we have identified an ecologically important pattern of largemouth bass growth versus LRD.

Fisheries' managers should note that largemouth bass in highly developed lakes take longer to enter the fishery and may reach trophy lengths more rapidly in undeveloped systems.

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