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QUANTIFYING EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT ON LITTORAL FISHES AND HABITAT: TOWARD A FRAMEWORK FOR LAKE ECOSYSTEM CONSERVATION

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of the requirements for the

M.S. degree in Fisheries and Wildlife

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QUANTIFYING EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT ON LITTORAL FISHES AND HABITAT: TOWARD A FRAMEWORK FOR LAKE ECOSYSTEM CONSERVATION

By

Aaron Kenneth Jubar

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ABSTRACT

QUANTIFYING EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT ON LITTORAL FISHES AND HABITAT: TOWARD A FRAMEWORK FOR LAKE ECOSYSTEM CONSERVATION

By

Aaron Kenneth Jubar

Extensive alterations to north temperate lakes due to residential lakeshore development (LSD) and associated activities have the potential to negatively affect habitat features in the littoral zones of lakes. To quantify the effects of residential LSD, I surveyed littoral habitat features of six Michigan lakes that varied primarily in their degree of LSD measured in dwellings per kilometer. Undeveloped sites had significantly greater abundance of coarse woody material and submersed macrophyte cover compared to developed sites. Substrate particle size was significantly larger at retaining wall sites compared to undeveloped and maintained sites. In order to assess the indirect effects of LSD on lakewide response variables, I examined whole-lake macrophyte cover, water chemistry, and growth rates of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in 15 Michigan lakes representing a gradient of LSD. Whole-lake littoral floating macrophyte cover decreased with increasing amount of LSD, but other macrophyte growth forms and water chemistry showed no significant response to LSD. Bluegill growth increased while largemouth bass growth showed a marginally significant decrease with increasing LSD. The effects of LSD on fish growth also depended upon growth year (for bluegill), and fish size (for both species). Collectively, these findings demonstrate the importance of investigating both local and lakewide (i.e., cumulative) effects of LSD on lake ecosystems.

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INTRODUCTION

As the demand for waterfront property increases, lakeshore owners are extensively developing riparian areas adjacent to north temperate lakes. Human alterations do not cease at the land-water interface, but often extend into the nearshore littoral areas of the lake. There is a growing body of literature examining the effects of residential lakeshore development (LSD) on nearshore habitat (Christensen *et al.* 1996, Radomski and Goeman 2001, Jennings *et al.* 1996, Jennings *et al.* 2003, Hatzenbeler *et al.* 2004) and fish (Jennings *et al.* 1999, Schindler *et al.* 2000, Scheuerell and Schindler 2004). Many of these studies, however, consider lakes from northern regions of Minnesota and Wisconsin, USA, which may have different limnology and food web ecology compared to lakes from other north temperate regions, and thus differ in their response to LSD. To date, no research has examined the effects of LSD on aquatic ecosystems in southern Michigan. Riparian lake owners in southern Michigan have caused extensive development in recent decades, as many seasonal cottages have been built, and subsequently converted to or replaced with year-round residences. Additionally, rapid suburban development in this area over the past few decades has forced many residences on these lakes to convert from septic to sewer waste disposal systems.

My research examined lakes located in one major river watershed (Huron River) in southeast Michigan. This study area provided me with a unique opportunity to examine habitat and fish responses to LSD for lakes ranging from low development (located in some of the many recreation areas) to extremely high development (due to the relatively close proximity of these lakes to the urban areas of Ann Arbor and Detroit, Michigan).

As the human population increases in southeast Michigan, boaters and anglers have increasingly used lakes in this area for recreational purposes. Lakeshore development and associated activities have the potential to negatively affect lake littoral habitat, which may, in turn, affect fish populations with close linkages to the littoral environment of lakes.

I studied multiple attributes of lake ecosystems to identify the response of various lake ecosystem components to LSD at local and lakewide scales. This research will contribute to our understanding of how lake ecosystems respond to changes caused by human perturbation, particularly in southeast Michigan. The knowledge gained through this research will aid managers by identifying components of the lake ecosystem most influenced by LSD. My hope is that this study will stimulate further research, as well as provide a starting point for aquatic ecosystem managers seeking to quantify and potentially mitigate the effects of loss or alteration of critical lake habitat through proactive management strategies in north temperate lakes.

CHAPTER 1: LOCAL EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT ON LITTORAL HABITAT

Introduction

The loss of natural habitat in lakes has become an area of concern for fisheries and wildlife managers. For north temperate lakes, the ever-increasing residential development of lake riparian zones is a major factor driving habitat loss. Fish and plant species in the littoral zone of north temperate lakes can be adversely affected by lakeshore modification and development (Jennings *et al.* 1999; Schindler *et al.* 2000; Hatzenbeler *et al.* 2004; Scheuerell and Schindler 2004), in part because residential development of lakes often does not end where the land meets the water. Rather, developers and homeowners typically modify their shoreline and the related littoral zone of the lake for recreational and aesthetic purposes. Although small amounts of lakeshore development (LSD) may benefit aquatic organisms by diversifying littoral habitat, extensive and uniform development along shorelines may be detrimental to aquatic biota (Jennings *et al.* 1999). Because individual lake-dwellers modify their nearshore areas to varying degrees, and such modifications contribute to and are confounded with cumulative LSD, it is still uncertain what spatial scale (i.e., lakewide development versus development type for individual stretches of shoreline) is most important in assessing habitat loss in lakes.

Littoral fish species may be particularly vulnerable to effects of habitat loss given their use of near-shore habitat for nesting, foraging, and refuge. A reduction of complex littoral habitat may affect fish assemblages in complex ways because specific habitat requirements or preferences vary among littoral fish species, and within fish species, habitat requirements vary with life stage. For example, juvenile, non-nesting adult, and nesting adult largemouth bass (*Micropterus salmoides*) exhibit significantly different patterns of habitat use (Annett *et al.* 1996). Bluegill (*Lepomis macrochirus*) habitat use is also dependent upon size (Mittelbach 1984). However, the degree to which LSD compromises littoral habitat, and associated fish assemblages and life stages, is poorly understood.

Lakeshore development may affect available habitat structures in the littoral zone including coarse woody material (CWM) abundance, macrophyte cover, and substrate particle size. Coarse woody material is an important physical structure contributing to habitat diversity in both riverine and lake ecosystems. In lotic systems, CWM provides habitat for invertebrates (Phillips and Kilambi 1994) and numerous fish species (Cunjak and Power 1987; Neumann and Wildman 2002). The loss or removal of CWM from rivers can be detrimental to aquatic organisms by reducing suitable in-stream habitat (Gurnell *et al.* 1995). Impacts of CWM in lakes, however, are poorly understood. Coarse woody material located in the littoral zone of lakes may provide important refuges for prey fish from predators (Savino and Stein 1989*a*) and may also promote substrate habitat for macroinvertebrates which serve as prey for some fish species (Bowen *et al.* 1995). For example, age-0 fish may benefit from the interstitial spaces and invertebrate prey found among or associated with CWM. Further, the findings of Schindler *et al.* (2000) suggest a positive relationship between growth rates of bluegill and largemouth bass and density of CWM. Christensen *et al.* (1996) determined that LSD in northern Wisconsin and Michigan lakes had strong negative effects on abundance of CWM not only at the whole-lake scale, but also at the local scale. Specifically, forested (or undeveloped) sites had greater amounts of CWM than developed sites, and lakes with more highly developed shorelines had lower CWM (Christensen *et al.* 1996).

The impacts of LSD on macrophyte communities may be more complex than those on CWM. Residential development of lakes may indirectly increase aquatic plant abundance through increased inputs of nutrients important for plant growth. Conversely, LSD and associated activities may directly reduce macrophyte abundance through chemical treatments, mechanical removals, or increased wave action due to boating activity. Specific types of macrophytes may be particularly vulnerable to LSD. For example, increased LSD has been found to reduce abundance of emergent and floating-leaf vegetation (Radomski and Goeman 2001; Hatzenbeler *et al.* 2004). Further, increased recreational use of lakes resulting from LSD has been associated with declines in emergent plants (Ostendorp *et al.* 1995). Lakeshore development can potentially affect macrophytes on both individual site and whole-lake levels.

Substrate composition determines the quality of spawning habitat and cover for many fish species and influences benthic macroinvertebrate and periphyton composition and production (McMahon *et al.* 1996). In lakes, some littoral fish species, such as those of the family Centrarchidae, exhibit strong preferences for specific substrata for nest construction (Balon 1975). For example, Hunt *et al.* (2002) found spawning male largemouth bass frequently construct nests in sites dominated by sand or gravel substrata. Similarly, smallmouth bass (*M. dolomieu*) nest success and nest density in four Au Sable River reservoirs, Michigan, were highest in areas with gravel substrate (Wills *et al.* 2004). Residential development of lake shorelines may alter the substrate composition in areas critical for bass nest construction. Suitable spawning habitat may be reduced by shoreline modifications which remove rocks and gravel (e.g., for aesthetic purposes), add fine sand or silt (e.g., through building of beaches), or disrupt natural sedimentation (e.g., through construction of retaining walls). For example, Jennings *et al.* (2003) found littoral sediments at developed sites contained more fine particles compared to undeveloped sites within the same lake.

The effects of human development on lakes have typically been examined at local spatial scales with a focus on LSD effects on particular habitat characteristics, with the exception of a few studies examining lakewide habitat response to LSD. Radomski and Goeman (2001) used aerial photography to quantify the effects of LSD on floating-leaf and emergent vegetation. Christensen *et al.* (1996) studied coarse woody debris in relation to amount of LSD and type of development. However, studies generally have failed to investigate the effects of specific lakeshore modifications on substrate composition of the littoral zone within a lake (but see Jennings *et al.* 1996); and few studies have examined the direct effects of riparian development and lakeshore modifications on littoral habitat or identified the indirect effects of such LSD on littoral fishes. In this study, I quantified littoral habitat features along lake shorelines composed of different modification types in southeast Michigan lakes that are limnologically similar, but differ according to overall level of LSD. Human development patterns and habitat characteristics may be influenced by natural features as well. Therefore, my main objectives were to answer two questions: Is development randomly distributed in relation to natural features? And, how does development at the local and lakewide scale affect lake littoral habitat? Based on previous research examining the effects of LSD on littoral habitat, I generated a number of expectations. First, CWM in the littoral zone of southeast

Michigan lakes will be lower along developed shorelines and decrease with increasing LSD, similar to lakes in northern Wisconsin (although overall abundance of CWM may be lower, due to differences in land cover and vegetation between regions). Second, macrophyte cover will be lower along developed shorelines and decrease as overall LSD increases. Third, substrate particle size will be smaller in littoral areas adjacent to residential development and decrease in size as overall LSD increases.

Methods

Study lakes

I selected 15 lakes within a single ecoregion and within a single major river watershed, in southeastern Michigan, USA (Figure 1), in order to control as much as possible for differences in climate, geology, lake morphology and aquatic flora and fauna. The Huron River watershed contains lakes with a wide range of LSD, thus providing a mix of highly developed, moderately developed, and undeveloped lakes. I used visual observations by boat to quantify the number of riparian dwellings within 50 m of each lake, and then divided number of dwellings by lake perimeter (km) to calculate LSD (dwellings$\cdot$km^{-1}). Lakes were chosen to have similar composition of land use types in their watershed (< 70% of either agricultural, forested, or urban land use within a 500 m buffer). In doing so, I aimed to select lakes that were biologically and physically similar and that differed primarily in the extent of their LSD (Table 1). To standardize lake size, and assure that all lakes were of sufficient depth for summer stratification, I selected a subset of six study lakes that ranged 29 to 100 hectares and had a mean depth

>3m. The six lakes represent a gradient of LSD based on dwellings·km^{-1}, ranging from 7.76 to 22.31 dwellings·km^{-1}.

Site Selection

I used a differential GPS unit (Trimble GeoExplorer®) to record length of different features. At each site, I recorded natural feature attributes, and modification type of shoreline segments along the perimeter of the six study lakes. I classified three types of shoreline modifications: undeveloped (including unaltered or natural shoreline), developed maintained (including beach, lawn, or groomed shoreline), and developed retaining wall (including seawall and rip-rap). I recorded slope of the riparian area within 30 m of shore as low grade (<30°), or high grade (>30°), and determined wind exposure based on shoreline exposure to the region's prevailing southwesterly wind (shoreline facing SE, E, NE, N, and NW = high wind, all other shoreline = low wind).

I then entered these lakeshore attribute data into a Geographic Information System (GIS). Although lakeshore frontage depends on local zoning ordinances, typical residential lot size for the study lakes is roughly 40 m of shoreline. Therefore, using GIS, I separated continuous stretches of each shoreline modification type into 40m increments. Due to relatively flat topography in the study area, I only considered sites with low terrestrial slope in sample site selection because high slope sites were so rare. I randomly selected study sites within each lake, with three replicates per modification*wind exposure combination for a total of 18 sites per lake. This design allowed me to examine littoral habitat variation both within and among lakes.

Field methods

I sampled study lakes and subsequent sites within each lake in random order. In order to determine the effects of shoreline modification type at different wind exposures and across a gradient of LSD, I quantified natural habitat features at each site. I quantified CWM using transect-intercept methods similar to Christensen *et al.* (1996). I conducted sampling transects along the 0.5 m depth contour once at each sampling site during May and June 2003. I used a caliper to identify CWM >5 cm in diameter, and counted the number of intersections per meter of transect to provide a relative measure of CWM abundance.

I visually measured substrate composition at each sampling site using a modified Wentworth scale (adapted from Cummins 1962) and then classified substrate as one of four groups based on particle size: silt (<0.0625mm), sand (0.0625-2mm), gravel (2-32mm), or cobble (>32mm). During May and June 2003, I recorded substrate using a 1 m quadrat placed every 5 meters along the 0.5 m and 1 m depth contours at each site, and calculated mean substrate size along each contour at each site.

Macrophyte composition and cover at each site was recorded during August 2003, by an observer from a boat along the 0.5 m and 1 m depth contours. I surveyed emergent, floating, and submersed vegetation every 5 m along each contour (0.5 m and 1 m) and assigned a qualitative value for cover (0, 1, 2, or 3; where 0 = <5% cover, 1 = 5-33%, 2 = 34-66% cover, and 3 = 67-100% cover). For each depth contour for each site I then calculated the mean for each vegetation type.

Statistical analyses

I analyzed all data using SAS version 8.0 (SAS Institute Inc. 2000). When appropriate, I transformed data to meet the necessary distributional assumptions. In order to determine if residential LSD was randomly distributed in relation to natural features, I conducted a Chi-square analysis for each modification type comparing expected (percent of shoreline in each natural feature of slope-wind combinations) versus observed (percent distribution of modification type in each natural feature category; SAS Institute 2000) patterns of LSD relative to natural lake features. For example, if a particular development type is distributed randomly with respect to natural shoreline features, then the percent of lake shoreline in each natural feature category (expected values) will equal the percent of shoreline with the development type in each natural feature category (observed values). To examine littoral habitat response to shoreline development at local and lakewide scales, I used a mixed-effect analysis of covariance (ANCOVA, SAS Institute 2000). For each natural habitat feature (CWM abundance, substrate composition, and macrophyte cover), I used the ANCOVA model to determine if habitat varied predictably among sites as a function of site modification type, overall LSD, or their interaction. For all mixed-effect models, I treated shoreline modification type and wind exposure as fixed effects. Lakeshore development was treated as the covariate. To be conservative, I used two-tailed statistical tests, with rejection criterion set at α=0.05 for all analyses.

Results

Is lakeshore development distributed evenly relative to natural shoreline features?

The proportions of shoreline composed of different combinations of wind exposure and terrestrial slope varied among the six study lakes (Figure 2). With the exception of one lake (North Lake: 62% high slope) the study lake shorelines were dominated by low terrestrial slope (range 38 to 91%). Predominance of low slope was to be expected given the relatively flat topography in the study area. As LSD increased, there was a general increase in the proportion of retaining wall shoreline along with a decrease in the proportion of undeveloped shoreline. The distribution of each shoreline modification type relative to slope and wind features, however, was not consistent across the six study lakes and varied with increasing LSD (Table 2, Figure 3). Nearly all of the Chi-square comparisons yielded significant differences, indicating that the proportion of lake shoreline in each wind-slope combination differed from the proportion of a given modification type in each wind-slope combination. However, patterns differed among lakes. For example, in East Crooked Lake, retaining wall shoreline was disproportionately prevalent along high wind-high slope, whereas in Halfmoon Lake, retaining wall shoreline was disproportionately prevalent along low wind-low slope. In only two cases did the Chi-square indicate even distribution of shoreline modification relative to natural features (East Crooked and Patterson Lake maintained shorelines; Table 2).

What are the effects of local and lakewide lakeshore development on littoral habitat?

Coarse woody material

Coarse woody material abundance along 0.5 m depth study site transects ranged from 0 to 0.53 intersections•$m^{-1}$and varied predictably among shoreline modification types (Table 3). In all study lakes, mean coarse woody material abundance was higher at undeveloped sites (mean = 2.91 intersections•m^{-1}) compared to maintained (mean = 0.43) and retaining wall sites (mean = 0.20; ANCOVA, F = 6.48 p = 0.0024; Figure 4a).

Although not significant, there were negative trends for LSD and also for the interaction between modification type and LSD (ANCOVA, $F = 2.61$ $p = 0.079$; Table 3), indicating that differences in CWM abundance among modification types are smaller in high LSD lakes (Figure 4a), due primarily to a reduction in CWM at undeveloped sites with increasing LSD.

Macrophyte cover

Macrophyte cover of study sites was typically dominated by submersed vegetation. Submersed cover ranged from 0 to ~70% among study sites. Submersed macrophyte cover along the 0.5 m depth contour varied among modification types (ANCOVA, $F = 6.88$ $p = 0.0017$) and along the gradient of LSD (ANCOVA, $F = 34.74$ $p < 0.0001$; Table 3, Figure 4b). Mean submersed cover did not differ between undeveloped and maintained sites, but both modification types had greater submersed cover than retaining wall sites as determined by pairwise comparisons ($p < 0.001$, and $p = 0.027$ respectively). This finding did not meet my expectations. Submersed macrophyte cover along the 1 m depth contour resulted in findings similar to macrophyte cover along the 0.5 m depth contour (Table 3). Similar to the 0.5 m contour, mean submersed cover at the 1 m contour did not significantly differ between undeveloped and maintained sites, but both modification types had greater submersed cover than retaining wall sites ($p = 0.005$, and $p = 0.019$ respectively). Also, submersed cover at 1 m study sites increased with LSD (ANCOVA, $F = 26.87$ $p < 0.0001$) for all modification types (ANCOVA, $F = 4.47$ $p = 0.0142$).

Floating macrophyte cover along the 0.5 m depth contour varied among modification types (ANCOVA, $F = 7.33$ $p = 0.0011$) and along the gradient of LSD

(ANCOVA, $F = 12.44$ $p = 0.0007$; Table 3, Figure 5a). Mean floating cover did not significantly differ between undeveloped and maintained sites, but both modification types had greater floating cover than retaining wall sites as determined by pairwise comparisons ($p = 0.0005$, and $p = 0.0022$ respectively). Contrary to my expectations, floating cover increased with LSD. Additionally, I noted a trend that as LSD increases, floating vegetation at retaining wall sites appears to respond differently than at undeveloped and maintained sites, but this interaction was not significant (ANCOVA, $F = 1.21$ $p = 0.3033$). Floating macrophyte cover along the 1 m depth contour varied among modification types and along the gradient of LSD. Similar to submersed cover, effects of modification type and LSD on floating cover were comparable along both the 0.5 and 1 m depth contours (Table 3). As with the 0.5 m depth contour, mean floating cover at the 1 m depth contour was not significantly different between undeveloped and maintained sites, but both modification types had higher floating cover than retaining wall sites ($p = 0.0018$, and $p = 0.01$ respectively). Lakeshore development as a covariate was also significant in explaining additional variation of floating macrophyte cover among study sites at the 1 m depth contour (ANCOVA, $F = 9.9$ $p = 0.0023$), indicating that as LSD increased, floating macrophyte cover generally increased. Although floating macrophyte cover was low at retaining wall sites regardless of LSD (Figure 5a), the interaction between modification type and LSD was not significant in explaining additional variation in floating macrophyte cover among study sites (ANCOVA, $F = 1.15$ $p = 0.3203$).

Emergent macrophyte cover along the 0.5 m depth contour varied among modification types, but not along the gradient of LSD (Table 3, Figure 5b). Mean emergent cover did not significantly differ between maintained and retaining wall sites, but undeveloped sites had higher emergent macrophyte cover than both ($p < 0.0001$, and $p < 0.0001$ respectively). LSD as a covariate was not significant in explaining additional variation in emergent macrophyte cover at study sites (ANCOVA, $F = 1.96$ $p = 0.165$). Similar to the 0.5 m contour, emergent macrophyte cover along the 1 m depth contour varied among modification types, but not along the gradient of LSD. Mean emergent cover at the 1 m depth contour was not significantly different between maintained and retaining wall sites, but both of these types had lower emergent cover than undeveloped sites ($p < 0.001$, and $p = 0.0029$ respectively). As with the 0.5 m depth contour, LSD as a covariate was not significant in predicting emergent macrophyte cover along the 1 m depth contour of study sites.

Substrate composition

Substrate size along the 0.5 m depth contour varied as a function of modification type, but not LSD (Table 3, Figure 6). Mean substrate size was not significantly different between undeveloped and maintained sites, but both of these types had smaller substrate size than retaining wall sites ($p = 0.0024$, and $p = 0.024$ respectively), contrary to expectations. LSD as a covariate was not significant in explaining additional variation in substrate size of study sites (ANCOVA, $F = 1.16$ $p = 0.285$). Substrate size along the 1 m depth contour resulted in findings similar to substrate size along the 0.5 m depth contour (Table 3). Mean substrate size did not significantly differ between undeveloped and maintained sites, but both of these types had smaller substrate size than retaining wall sites ($p = 0.0045$, and $p = 0.09$ respectively). As with substrate size at the 0.5 m depth contour, LSD as a covariate did not explain a significant amount of variation among sites at the 1 m depth contour (ANCOVA, $F = 0.26$ $p = 0.615$).

Discussion

Although LSD was not distributed evenly relative to natural features (wind exposure and terrestrial slope) of the shoreline, consistent patterns in its distribution relative to natural features were not evident. I expected retaining wall structures to be more prevalent along high wind exposed shorelines, but this was not the case as only three out of 10 observations across lakes had a higher proportion of retaining wall along high wind shoreline than expected. In only two instances was the observed modification type distributed evenly with regards to amount of available shoreline. The inconsistencies among the significant Chi-square tests indicate that natural features of the shoreline are not driving lakeshore modification in any consistent pattern. All six study lakes had at least some shoreline adjacent to public land that is not available for riparian development. Thus, the pattern of public versus private shoreline might constrain my findings. For example, a high amount of public land (not developed) along high wind exposure shorelines could influence the lakewide patterns that were documented. Although natural features of the shoreline did not explain variation in location of riparian development, wind exposure and terrestrial slope were still included in the habitat sampling study design to control for potential abiotic differences between sites that may influence littoral habitat variables.

My results indicate that shoreline modification type at the site-level significantly affected all littoral habitat variables quantified (CWM, substrate composition, and submersed, floating and emergent macrophyte cover). Overall lakewide LSD was significant in explaining variation in submersed and floating macrophyte cover only, while other littoral habitat variables were not significantly correlated with LSD. In all cases, littoral habitat was significantly correlated with modification type along both the

0.5 and 1 m depth contours, indicating that effects of residential lakeshore modifications on littoral habitat extend well beyond the land-water interface (at least to 1m depth for plants and substrate, and at least to 0.5 m depth for CWM). In general, interaction terms were not significant, indicating that site-level effects of development did not depend on the lakewide level of development.

The importance of CWM as a habitat feature utilized by fish and aquatic invertebrates in lotic systems is well documented. Research in riverine systems has examined the negative impacts of CWM removal on aquatic organisms (Gurnell *et al.* 1995), but analysis of CWM as a habitat feature in lakes is lacking. Reduction of CWM in north temperate lakes due to LSD has been documented in 16 Wisconsin and northern Michigan lakes (Christensen *et al.* 1996). In a similar analysis of 34 northern Wisconsin lakes, Jennings *et al.* (2003) also found less CWM with increasing LSD, as well as less CWM at undeveloped sites compared to developed sites within lakes. My results from CWM analyses in six southeastern Michigan lakes are consistent with findings from these other studies; however, the relative abundance of CWM in my lakes is substantially lower. Christensen *et al.* (1996) found CWM density at forested sites to be 0.38 logs•m^{-1}, while developed sites had 0.057 logs•m^{-1}. In my study, undeveloped sites contained 0.0773 logs•m^{-1}, and developed sites (both maintained and retaining wall) had only 0.0078 logs•m^{-1}. Because efforts were made to control for natural differences among modification types, my results combined with others indicate that riparians remove CWM from the nearshore areas adjacent to their dwellings, but that differences in land cover or geographic location also influence lakewide levels of CWM. On the lakewide scale, CWM relative abundance decreased with increasing LSD, particularly at undeveloped sites. This reduction in CWM at undeveloped sites may be due to removal by riparian lakeshore owners in close proximity to such sites, but this scenario is unlikely. A more plausible explanation for decreased abundance of CWM with increasing LSD involves the generation and transport of CWM within a lake. If CWM is generated along undeveloped shoreline and then is transported within a lake due to wind or wave action to a different shoreline, the chance that CWM will end up settling along a developed shoreline (where it is likely to be removed by riparians) increases with LSD. This explanation, however, requires two assumptions: that developed shorelines do not generate substantial amounts of CWM; and that lakeshore owners remove CWM from their nearshore areas rather expeditiously. Higher amounts of CWM at undeveloped sites compared to other modification types and decreased relative abundance of CWM with increasing LSD met my expectations concerning woody material in the littoral zones of north temperate lakes.

Human development of lake shorelines may include the removal or reduction of aquatic vegetation in order to establish swimming areas or meet lakeshore owners' aesthetic goals. With a few notable exceptions (Radomski and Goeman 2001; Jennings *et al.* 2003, Hatzenbeler *et al.* 2004), the response of littoral vegetation to LSD of north temperate lakes has not been examined. In a study of 44 Minnesota lakes, Radomski and Goeman (2001) documented a decrease in the amount of floating-leaf and emergent vegetation present at developed sites compared to undeveloped lakeshore. In a more recent study, Jennings *et al.* (2003) found that not only were floating-leaf and emergent vegetation reduced at developed sites compared to undeveloped sites, but also in relation to lakewide LSD. While Jennings *et al.* (2003) did not find submersed vegetation to be affected by site level differences, I found submersed, floating-leaf, and emergent macrophyte cover were greater at undeveloped sites compared to sites with retaining walls. These results might be explained due to my characterization of three separate modification types that may represent a gradient of disturbance (with retaining wall shoreline having a higher disturbance to the littoral habitat than maintained shoreline). I also found emergent macrophyte cover to be greater at undeveloped sites compared to both developed modification types. Based on these results, I surmise two possible explanations for the observed patterns in macrophyte cover. First, submersed and floating macrophyte assemblages as a whole are perhaps more resistant than emergent vegetation in response to disturbance caused by maintained shorelines, but all cover types are still reduced by retaining wall shorelines. Second, the modification types I examined may indicate a gradient of disturbance in which undeveloped, maintained, and retaining wall shorelines represent low, intermediate, and high disturbance respectively. In contrast to the findings of Jennings *et al.* (2003), I found a positive correlation between macrophyte cover (submersed, floating-leaf, and emergent) and LSD, which did not meet my expectations. Although I did not assess specific mechanisms, one possible explanation for this observation would be increased non-point nutrient inputs due to increases in cumulative LSD that could lead to higher incidence of macrophytes in the littoral zone. This is a plausible explanation considering that the total phosphorus values for the six lakes in this study increased, although not significantly ($p = 0.149$), with increasing LSD (see Chapter 2).

Substrate size and composition have often been identified as critical habitat features for many stream-dwelling organisms. Alteration in the size and structure of substrata due to anthropogenic stressors has rarely been studied in lakes (but see Jennings *et al.* 2003). My results indicate larger substrate size along retaining wall sites, compared with both undeveloped and maintained sites, but no relationship was detected between substrate and LSD. The larger substrate along retaining wall sites may be due to reduced sediment transport from land to water caused by the shoreline structure. I expected substrate at undeveloped sites to be larger than at developed sites reflecting greater siltation at developed sites, but this was not the case in my study. Currently, it is unclear how changes in substrate caused by LSD will affect nesting fish. The fish communities of the six study lakes are dominated by black crappie *Pomoxis nigromaculatis*, bluegill, largemouth bass, pumpkinseed *Lepomis gibbosus*, rock bass *Amblopites rupestris*, and smallmouth bass (Jubar, unpublished data), which construct nests in nearshore littoral areas (Balon 1975) where the effects of LSD are most apparent. Understanding the direct effects of modification type and LSD on substrate composition of north temperate lakes should lend insight to the mechanisms influencing fish nesting and nest distribution.

CHAPTER 2: LAKEWIDE EFFECTS OF RESIDENTIAL LAKESHORE DEVELOPMENT ON WATER CHEMISTRY, MACROPHYTE COVER, AND LITTORAL FISH GROWTH

Introduction

The alteration of lake shorelines by humans has increasingly become an area of concern for aquatic ecosystem managers throughout North America. The impacts of activities associated with lakeshore development (LSD) can affect littoral habitat features, such as abundance of coarse woody material (Christensen *et al.* 1996), aquatic macrophyte cover (Bryan and Scarnecchia 1992, Radomski and Goeman 2001), substrate particle size and composition (Jennings *et al.* 1996, Jennings *et al.* 2003) and also species composition and spatial distribution of fishes (Jennings *et al.* 1999, Scheuerell and Schindler 2004). Studies contrasting developed and undeveloped lakeshore sites have focused on the local effects of LSD on fishes and aquatic habitat, and such studies and their applicability to management have recently been emphasized in the primary literature. Fewer studies have examined the cumulative impacts of LSD, which may affect lake habitat and associated biota on a broader scale. Such cumulative impacts of LSD may indirectly affect water chemistry, whole-lake macrophyte cover, and fish growth, although these effects remain poorly understood. The alteration or loss of littoral habitat in nearshore areas due to incremental LSD may combine with changes in vegetative cover and water chemistry at the whole-lake scale to negatively affect littoral fish species. However, much remains unknown regarding fish response to LSD as few studies have addressed this issue (but see Jennings *et al.* 1999, Schindler *et al.* 2000, Scheuerell and Schindler 2004).

The effects of various land uses on nutrient concentrations in streams and rivers have been well documented (Omernik 1976, Roth et al. 1996), as have more localized effects of riparian influences on lotic systems (Roth et al. 1996, Nakamura et al. 2000). Similar to riverine ecosystems, lake interactions with riparian and land use changes are potentially complex. However, lake research has emphasized the broader watershed scale. At the watershed scale, research has examined the effects of human land use on lake productivity and fish habitat (Evans *et al.* 1996, Siver *et al.* 1996, Gunn and Sein 2000). For example, increased phosphorus levels due to increased fertilizer use or other non-point nutrient inputs can lead to decreased dissolved oxygen and increased mean temperature of lakes (Evans *et al.* 1996) causing eutrophication. Such a shift in trophic status may reduce suitable habitat for some fish species. Relatively little is known regarding the cumulative effects of residential LSD on water chemistry and plankton in lakes, although in a study of New England lakes, Stemberger and Lazorchak (1994) determined that percentage of disturbed lakeshore may be important in explaining variability in zooplankton assemblages among lakes. Overall, LSD is likely to result in higher nutrient input into lakes, due to increased fertilizer use by riparian landowners and increased sediment transport across the land-water interface resulting from lakeshore degradation and reduced riparian vegetation.

Lakeshore development can potentially affect macrophyte communities on both individual site and whole-lake levels, in potentially complex manners. Lakeshore development may indirectly increase aquatic plant abundance through increased inputs of nutrients important for plant growth. For example, in a study of six southeast Michigan lakes, I noted an increase in submersed vegetation at developed sites with increasing *et al.* 1992) because bass foraging success is higher at moderate as opposed to high plant abundance. Sparse amounts of vegetation, however, may constrain bass diet composition and growth, because relatively few macroinvertebrates and prey fishes may persist (Crowder and Cooper 1979, Anderson 1984). In addition to aquatic macrophytes, other littoral habitat features, such as coarse woody material, also provide important refuge and foraging areas for many aquatic organisms (Savino and Stein 1989*b*, Bowen *et al.* 1995). In a study of 14 northern Wisconsin and Michigan lakes, Christensen *et al.* (1996) showed that CWM was negatively correlated with LSD, with a similar pattern noted in southeast Michigan lakes (see Chapter 1). In a more recent study on the 14 northern lakes, Schindler *et al.* (2000) recorded a decrease in bluegill growth rates as LSD increased, and saw a similar though weaker trend in bass. To date, however, no study has examined the response of macrophyte cover to cumulative increases in LSD and the subsequent effects on growth of littoral fishes.

In order to quantify the effects of residential LSD on water chemistry, whole-lake macrophyte cover, and growth of littoral fishes, I used a comparative approach of lakes along a gradient of residential development. I measured water chemistry, macrophyte cover, and growth rates of bluegill and bass in 15 southeast Michigan lakes that have similar morphometry and watershed land use, but differ according to overall amount of LSD. Based on results of previous studies, I expected total phosphorus to increase and Secchi disk depth to decrease in response to increasing LSD. I expected whole-lake macrophyte cover to decrease with increasing LSD, particularly for emergent and floating-leaf cover types which are more likely to be negatively affected by activities associated with LSD. Finally, I also expected bluegill growth rates to decrease *et al.* 1992) because bass foraging success is higher at moderate as opposed to high plant abundance. Sparse amounts of vegetation, however, may constrain bass diet composition and growth, because relatively few macroinvertebrates and prey fishes may persist (Crowder and Cooper 1979, Anderson 1984). In addition to aquatic macrophytes, other littoral habitat features, such as coarse woody material, also provide important refuge and foraging areas for many aquatic organisms (Savino and Stein 1989*b*, Bowen *et al.* 1995). In a study of 14 northern Wisconsin and Michigan lakes, Christensen *et al.* (1996) showed that CWM was negatively correlated with LSD, with a similar pattern noted in southeast Michigan lakes (see Chapter 1). In a more recent study on the 14 northern lakes, Schindler *et al.* (2000) recorded a decrease in bluegill growth rates as LSD increased, and saw a similar though weaker trend in bass. To date, however, no study has examined the response of macrophyte cover to cumulative increases in LSD and the subsequent effects on growth of littoral fishes.

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Methods

Study lakes

I selected 15 lakes within a single ecoregion and within a single major river watershed, in southeastern Michigan, USA (Figure 7), in order to control as much as possible for differences among lakes in climate, geology, morphometry and aquatic flora and fauna. Study lakes were selected to exhibit similar surface areas (29 to 106 hectares) and sufficient depth for summer stratification (mean depth >3m, with the exception of two lakes). Additionally, lakes were chosen to have similar composition of land use types in their watershed (< 70% of either agricultural, forested, or urban land use within a 500 m buffer). In doing so, I aimed to select lakes that were biologically and physically similar so that lakes differed primarily in the extent of their LSD (Table 4). The Huron River watershed contains lakes with a wide range of LSD, thus providing a mix of highly developed, moderately developed, and undeveloped lakes. Visual observations by boat were used to quantify the number of riparian dwellings within 50 m of each lake. Number of dwellings for each lake was then divided by lake perimeter (km) to calculate LSD ($dwellings \cdot km^{-1}$).

Water chemistry

To evaluate the effects of LSD on lake productivity, I sampled water chemistry and clarity of the 15 study lakes during August and September of 2003 and 2004. Secchi disk depth, a measurement of water clarity, was surveyed from the shaded side of the boat. For each lake, the epilimnion depth was estimated from a temperature profile at the deepest area of the lake. I measured total phosphorus and total alkalinity using epilimnetic water samples collected using a tube sampler. Total alkalinity ($mg \cdot L^{-1}$ $CaCO_3$) was measured immediately with a titration test kit (LaMotte). Total phosphorus samples were frozen for later analysis. In the lab, total phosphorus was measured using a persulfate digestion (Menzel and Corwin 1965) followed by standard colorimetry (Murphy and Riley 1962).

Macrophyte sampling

Whole-lake macrophyte sampling was conducted in the 15 study lakes during August and September of 2003. I sampled lakes in mid-late summer because the lakes are likely to be well stratified during that time, and macrophytes typically are at or near maximum growth. To assess macrophyte cover at the whole-lake scale, I used a modification of the point-intercept method (Madsen 1999, Spence Cheruvelil 2004). I used a Geographic Information System (GIS) to overlay a grid of sample points on each lake. The sample points, each with a corresponding latitude and longitude, were located 40 or 50 m apart, depending on lake surface area (40 m for lakes with a surface area <65 ha, or 50 m for lakes with a surface area >65 ha). A handheld global positioning system (GPS) unit was used to locate each sample point in the field. At each sample point, water depth was recorded, and macrophyte cover was assessed either by visual inspection (sites where macrophytes were visible below the water surface) or by 2-sided rake (deeper sites, where macrophytes were less visible). Areal cover estimates at each site were assigned for three macrophyte categories: submersed macrophytes, floating leaf macrophytes and emergent macrophytes. Cover estimates were based on qualitative density of each macrophyte category, and were given a cover score ranging from 0 to 3 (0 = 0-5%, 1 = 5-33%, 2 = 33-67%, 3 = 67-100% cover) with a cover score of 2 or 3 indicating dense cover. The presence or absence of the invasive Eurasian watermilfoil (*Myriophyllum spicatum*) was also noted at each site. From the whole-lake surveys, I calculated eight macrophyte metrics: percent cover (lake), percent cover (littoral), percent dense cover (lake), percent dense cover (littoral), percent submersed cover (littoral), percent floating leaf cover (littoral), percent emergent cover (littoral), and percent Eurasian watermilfoil cover (littoral) (Table 5).

Littoral fish sampling

To quantify the effects of LSD on littoral fish growth, I collected scales from bluegill and bass in summer 2003 and 2004. Fish were sampled using nighttime electrofishing (7 amps pulsed D.C., 120hz) transects conducted along the 1 m depth contour at haphazardly selected sites within each lake. Transects averaged ten minutes and were conducted along both developed and undeveloped stretches of lakeshore. In 2003, sampling on all lakes began at dusk and continued until at least 50 bluegill (>80mm total length) and 50 bass (>100mm total length) were captured; however, 8 of the sampling surveys produced fewer than 50 bass. To supplement sample sizes, additional nighttime electrofishing was conducted during summer 2004 until more than 50 bass were collected per lake. Approximately ten scales were taken from posterior to the pectoral fin and just above the lateral line from at least 50 bluegill and 50 bass ranging the entire size distribution of fish captured. Lengths of all bluegill and bass captured were recorded to the nearest millimeter. In order to collect smaller bluegill and bass, supplemental sampling including beach, purse, and bag seining was conducted in all lakes during summer 2004.

Fish growth analysis

In the lab, fish scales were mounted on slides for use in age determination and growth analysis. I measured scale incremental growth distances using an Optimas 6.5 image analysis system and a Nikon Eclipse E600 compound microscope and camera at 20x magnification.

For the bluegill and bass collected, I back-calculated lengths at previous ages using three different methods: Fraser-Lee method (Carlander 1982), body proportional hypothesis (BPH), and scale proportional hypothesis (SPH; Francis 1990). For the Fraser-Lee back-calculations, a common intercept ("*a*" below, representing fish total length at the onset of scale formation) was estimated separately for bluegill and bass sampled from all 15 lakes, and then back-calculated lengths estimated using the formula:

$$L_t = a + \left[\frac{L_C - a}{S_C} \right] \times S_t$$

where a is the intercept of the relationship $L_C = a + b(S_C)$ obtained by linear regression, S_C and S_t are scale size at capture and for the year of back-calculation, respectively, and L_C and L_t are total length at capture and for the year of back-calculation, respectively. The BPH method assumes a constant proportional deviation in fish length from mean fish length expected for a fish throughout life. To back-calculate length for a given scale size, I used the formula:

$$L_t = \left[\frac{a + bS_t}{a + bS_C} \right] \times L_C$$

where a, S_C, S_t, L_C, and L_t are as defined above for the Fraser-Lee method. The SPH method assumes a constant proportional deviation in scale size from mean scale size for a fish throughout life. To back-calculate length based on the assumptions of the SPH method, I used the formula:

$$L_t = -\left[\frac{c}{d}\right] + \left[L_C + \frac{c}{d}\right] \times \left[\frac{S_t}{S_C}\right]$$

where c and d are the intercept and slope of the relationship $S_C = c + d(L_C)$ obtained by linear regression. For each bluegill and bass, I used all three methods to estimate back-calculated total length (mm) at each scale annulus and determined growth increments (mm/yr) from the difference in estimated total lengths between consecutive annuli.

In order to test for Lee's phenomenon, wherein younger fish from a sample would appear to be exhibiting greater growth than fish of the same age from an earlier year-class, I used conventional qualitative methods (DeVries and Frie 1996). Lee's phenomenon appears evident in my bluegill data (Table 6). Therefore, to minimize possible error that would be associated with back-calculated lengths, I restricted bluegill growth analysis to back-calculated lengths from fish during the 2001 and 2002 growth years. A qualitative analysis of bass back-calculated total lengths did not clearly indicate evidence of Lee's phenomenon (Table 7). However, in order to minimize possible errors associated with back-calculating lengths of older fish (and possible errors associated with recent growth years) I restricted bass growth analysis to back-calculated lengths of fish for the 1998 to 2001 growth years.

Statistical analyses

All data were analyzed using SAS version 8.0 (SAS Institute Inc. 2000). When appropriate, data were transformed to meet the necessary distributional assumptions. In order to determine if residential LSD affected whole-lake macrophyte cover, each macrophyte metric was regressed against dwellings•km^{-1} (PROC REG, SAS Institute 2000). I conducted similar analyses to determine if water chemistry (total phosphorus, total alkalinity) and water clarity (Secchi disk depth) were correlated with LSD. To determine if littoral fish growth varied predictably as a function of LSD, I compared mean back-calculated total length estimates for bluegill and bass for the 15 study lakes (PROC MIXED, SAS Institute 2000). To account for the effects individual lakes may have on fish within that lake, I used a model which nested fish within lakes. For the mixed-effect models, I treated back-calculated total length and growth year as fixed effects. Because multiple growth increments were calculated from a single individual, and thus these observations were not statistically independent, I included individual fish as a random effect in the model. Lakeshore development was treated as the covariate. To determine if littoral fish growth varied predictably as a function of macrophyte cover or water chemistry, separate analyses were conducted with macrophyte cover metrics or water chemistry as covariates (PROC MIXED, SAS Institute 2000). Rejection criterion was set at $\alpha = 0.05$ for all analyses.

Results

Water chemistry

Total phosphorus in the 15 study lakes was regressed against LSD and year, resulting in a non-significant LSD*year interaction ($p > 0.5$). Therefore, I calculated the mean total phosphorus between the two samples years and used the values for subsequent analyses. Mean total phosphorus in the 15 study lakes in the summers of 2003 and 2004 ranged from 10.7 – 21.3 $\mu g \cdot l^{-1}$ (Table 4), with Secchi disk depth varying from 0.7 – 3.25 m in 2003 and 1.6 – 5.15 m in 2004. Total phosphorus levels and water clarity indicate the trophic state of the study lakes to be predominantly mesotrophic, with some lakes leaning towards oligo-mesotrophic and others meso-eutrophic in condition (Wetzel 2001). Although Secchi disk depth tended to decrease with increasing total phosphorus during 2003 and 2004, I detected no significant correlation for either year (p-values > 0.05). Mean total phosphorus did not vary predictably with LSD ($r^2 = 0.05$, $p > 0.39$), nor did Secchi disk depth in 2003 ($p > 0.77$) or 2004 ($p > 0.36$).

Whole-lake macrophyte cover

Total plant cover in the 15 study lakes varied from 13 – 94% (Table 5). Total dense cover of macrophytes ranged from 1 – 89%, and littoral plant cover in the 15 lakes ranged from 19 – 96%. Because emergent and floating macrophytes only occurred in relatively shallow regions of the study lakes, I only calculated littoral cover for these plant types, which ranged from 2 – 40% and 3 – 80% for emergent and floating plants, respectively (Table 5). Because multiple macrophyte growth form categories can occur at the same location (e.g. emergent and floating cover present at the same site), the macrophyte categories are not mutually exclusive; therefore percent cover across growth forms for an individual lake does not sum to 100. Contrary to my expectations, only littoral floating macrophyte cover was negatively correlated with LSD ($r^2 = 0.27$, $p = 0.045$; Figure 8*a*). Emergent macrophyte cover exhibited a similar, though not significant response to LSD. All other macrophyte metrics did not vary predictably with LSD (p-values > 0.05; Figure 8*b-d*). Additionally, mean total phosphorus did not explain a significant amount of variation in whole-lake plant cover ($p > 0.51$).

Littoral fish growth

Back-calculated total lengths of bluegill and bass derived from the three separate analyses (Fraser-Lee, body-proportional hypothesis, and scale-proportional hypothesis) were quite similar (for all comparisons $r^2 > 0.97$, with slope not significantly different from 1). Because I sampled fish using multiple gear types and scales collected represent a wide range of body sizes (35 – 260 mm for bluegill, 84 – 505 mm for largemouth bass), the BPH method of back-calculating total length is appropriate for my study (Francis 1990). Growth increments used in statistical analyses are thus calculated from the BPH method.

Although annual growth increment generally declined with increasing fish size, as would be expected, fish size explained relatively little variation in growth increments, which ranged broadly among bluegill (Figure 9) and bass (Figure 10) for any given fish size. The analysis resulted in a significant three-way interaction of bluegill back-calculated total length*growth year*LSD ($p < 0.0001$), indicating that the effect of LSD on growth increment varies with fish size and growth year. The interaction of bluegill back-calculated total length*LSD was also significant ($p < 0.036$), indicating that the effect of LSD on growth increment varies with fish size. Lakeshore development as a main effect was significant ($p < 0.004$) in predicting bluegill growth among lakes, and contrary to my expectations, showed a trend to increase (positive parameter estimate) with increasing LSD. For bass growth among the 15 lakes, the three-way interaction of back-calculated total length*growth year*LSD and the interactions of back-calculated total length*growth year and growth year*LSD were not significant, therefore I removed those interactions from the mixed-model in SAS. Following appropriate statistical adjustments, bass growth among the study lakes resulted in a significant interaction between back-calculated total length*LSD ($p < 0.006$; positive parameter estimate) indicating that effects of LSD on bass growth vary depending on fish size. When examined as a main effect, bass growth was marginally significant and negatively correlated with LSD (negative value for parameter estimate, $p = 0.094$) indicating decreased bass growth with increasing LSD, which met my expectations. In order to facilitate interpretation of the bluegill and bass growth data, I constructed plots (Figures 11 and 12) comparing annual growth increment and back-calculated total length for both fish species, while accounting for three levels of LSD (low development <13 dwellings•km^{-1}, medium development 13-20 dwellings•km^{-1}, and high development >20 dwellings•km^{-1}). Whole-lake macrophyte cover, dense cover, and total phosphorus did not explain variation in growth among lakes for either bluegill or bass (p-values > 0.05).

Discussion

I show that cumulative amount of LSD does not significantly affect lake water chemistry and water clarity variables (total phosphorus and Secchi disk depth). I expected to note an increase in total phosphorus and a decrease in Secchi disk depth with increasing LSD, similar to results of studies examining riparian and land use changes on the watershed-scale (Evans *et al.* 1996, Siver *et al.* 1996). The lack of variation in water chemistry among lakes of differing LSD may be due to mechanisms extending beyond the scale of my study. For example, watershed-scale effects on water chemistry have been well documented in lakes, but I only controlled for extreme proportions of individual land use within 500 m of each study lake. A more quantitative analysis of individual lake watershed features (such as land use, surface water flow, etc.) may shed insight into mechanisms controlling water chemistry within lakes. I expected water clarity to be correlated with total phosphorus (Wetzel 2001), but although I found a negative trend between Secchi disk depth and total phosphorus, the relationship was not significant. The lack of a significant correlation between total phosphorus and Secchi depth may be due to the relatively small number of lakes sampled in this study and the relatively narrow range of total phosphorus values involved. Also, I sampled water chemistry and water clarity only once during the summers of 2003 and 2004, and samples obtained for one survey date may not be representative of the seasonal averages for each lake. Finally, differences among lakes with regards to prevalence of septic versus sewer waste disposal might also prevent a straightforward relationship between LSD and nutrient levels.

Whole-lake plant cover in the 15 study lakes did not vary significantly with LSD for most macrophyte forms surveyed, with only littoral floating macrophyte cover negatively correlated with LSD. My findings are consistent with other studies which failed to detect a response in submersed macrophyte cover (Jennings *et al.* 2003), but found significant declines in floating and emergent cover (Radomski and Goeman 2001; Jennings *et al.* 2003) in relation to increasing LSD. The general lack of response of macrophyte cover types to LSD may be due to contrasting effects to lakes resulting from activities associated with LSD. For example, while riparian alteration of the lakeshore may contribute to increased nutrient inputs contributing to macrophyte growth, activities associated with LSD (such as chemical or mechanical harvest of plants, or increased lakeshore degradation due to recreational activities) may act to reduce macrophyte cover or otherwise inhibit aquatic plant growth. Regardless of the possibility of increased nutrients positively affecting macrophyte growth, one consequence of LSD remains relatively certain, that being the reduction of floating and emergent vegetation (see Chapter 1). This may be due to the fact that many emergent and floating macrophyte assemblages are composed of plant species intolerant to environmental degradation (Hatzenbeler *et al.* 2004). Additionally, the spatial distribution of emergent and floating macrophytes (generally associated with nearshore areas) brings these plants in closer proximity to residential lakeshore alterations, whereas some submersed plants may be able to inhabit regions of the lake bottom that are relatively isolated from the immediate effects of LSD and associated human activities.

The indirect effects of LSD on growth of littoral fishes are potentially complicated, because productivity of fish populations is often influenced by such factors as lake surface area, water chemistry, fish population density, predator-prey interactions, and angler harvest (Shuter *et al.* 1998; Tomcko and Pierce 2001). By selecting lakes of similar size, morphometry, and presumed angling pressure (all study lakes were public access), but which differed primarily in amount of LSD, I attempted to control for inherent variation among lakes that might influence fish growth. More than 50 bluegill and 50 bass were collected from each lake, and these species comprised the vast majority of fishes caught while electrofishing, indicating their predominance in all study lakes. The results of my study indicate that bluegill growth is dependent upon LSD, but the response varied with back-calculated total length of the fish and growth year. When considering only LSD, bluegill growth was positively correlated with LSD, which is contrary to the findings of Schindler *et al.* (2000) that indicated a negative relationship between LSD and bluegill growth. Bass growth in my study lakes declined with increasing LSD, but the slope of the relationship varied with growth year. This is similar to the findings of Schindler *et al.* (2000), who found a marginally significant negative relationship between growth of the largest size class of bass and LSD. The study of Schindler *et al.* (2000), however, only examined bass growth in nine lakes, with five of the lakes represented by relatively small sample sizes ($n < 30$). The findings of my study and Schindler *et al.* (2000) are qualitatively similar, but because we included more lakes and larger sample sizes per lake, we likely had greater statistical power to detect an effect of LSD. Also, there may be habitat differences between my study lakes and the lakes examined by Schindler *et al.* (2000), with respect to macrophyte cover, substrate composition, and particularly coarse woody material (see Chapter 1), which may underlie why we detected a stronger response.

The finding that bluegill growth increases while bass growth decreases along the LSD gradient was an unexpected result in my study. One reason for the opposite effects of LSD on growth may be due to the strong predator-prey interactions between bluegill and bass (Savino and Stein 1982, 1989*a*). In a study of seven Wisconsin lakes, Olson (1996) found bluegill growth has strong effects on the structure of bass populations, due to the influence of growth rate on bluegill population size-distributions. For example, in lakes with slow bluegill growth, bass growth was strongly size-dependent (small bass had low growth, while larger bass had higher growth). In lakes with high bluegill growth rates, bass growth rates were more uniform across all bass sizes. Such strong predator-prey interactions may explain why I found bluegill and bass growth responded differently to LSD.

Determining the cumulative effects of LSD on lakes is difficult because time lags may exist between disturbance to the ecosystem and the response, and because the type of development differs among lakes and over time. Numerous instances regarding river and stream system response to riparian disturbance over time exist in the primary literature. For example, Nakamura *et al.* (2000) believe the network structure of stream and riparian systems may lend resilience in response to major disturbances by providing widely distributed refuges. In contrast, lakes with relatively closed systems may not exhibit similar resilience to disturbance. For example, Christensen *et al.* (1996) conclude that 200 years would be required for natural coarse woody material in northern WI and MI lakes to return to pre-settlement levels. The relatively low resilience of lakes compared to lotic systems may be more apparent in such habitat characteristics as coarse woody material and substrate composition. Aquatic vegetation, however, may exhibit relatively high resilience to disturbance due to the relatively short life histories of macrophytes. Degradation of water quality as a result of long-term changes to watersheds due to human activity has been documented (e.g., Siver *et al.* 1996), but little is known regarding the long-term effects of LSD on aquatic ecosystems.

Conclusion

I quantified the lakewide response of water chemistry, macrophyte cover, and fish growth to a gradient of LSD. Ideally, a study of this nature would seek to identify aquatic ecosystem responses both before and after shoreline alteration. Due to restraints imposed by time and resources, such experimental studies are not feasible at present. The 15 lakes comprising the gradient of LSD used in this study represent a wide range of disturbance levels, from virtually undeveloped lakes, to nearly complete lakeshore development. If conditions in low to moderately developed lakes on this gradient are considered to be representative of conditions that may have once been found in more highly developed lakes, then studies of this nature provide a glimpse of what many lakes were like prior to extensive human development. Furthermore, ecosystem conditions in highly developed lakes can be viewed as the result of development should low development lakes experience increased levels of human lakeshore modification. I feel this approach is important for aquatic ecosystem managers seeking to determine past (and predict future) responses of lake habitat and biota to residential LSD.

APPENDIX

Tables and Figures

Table 1. Physical characteristics, lakeshore development (LSD), water chemistry and land cover of the 6 study lakes.

Lake	Surface area (hectares)	Lake perimeter (meters)	Mean depth (meters)	SDF[1]	#dwellings	LSD (#dwellings •km^{-1})	TP[2]	ALK[3]	Secchi[4]	% Agr[5]	% For[5]	% Urb[5]
Bruin	53	3091	3.74	1.2	24	7.76	13.4	171	3.0	69.5	12.8	1.1
Blind	29	2520	4.05	1.32	24	9.52	12.5	176	2.0	55.2	22.0	1.0
East Crooked	100	6528	3.97	1.84	95	14.55	14.8	157	3.3	33.3	28.0	23.6
Halfmoon	97	7399	6.77	2.12	131	17.71	13.4	200	2.4	63.2	15.3	1.8
North	91	5635	3.53	1.67	121	21.47	14.6	106	3.1	35.4	32.5	27.1
Patterson	64	5066	5.58	1.79	113	22.31	21.3	186	2.3	5.0	48.7	17.5

[1]SDF is the shoreline development factor calculated from the formula SDF = lake perimeter / (2*(√pi*lake area)). Increasing values indicate greater irregularity of the lake shoreline.

[2]TP is the mean total phosphorus (μg/L) of two samples taken during summers of 2003 and 2004.

[3]ALK is the mean alkalinity (mg/L CaCO3) of two samples taken during summers of 2003 and 2004.

[4]Secchi is the mean Secchi disk depth (m) of two surveys conducted during summers of 2003 and 2004.

[5]Percent land use within a 500 m buffer surrounding each lake (Agr = agricultural; For = forested; and Urb = urban)

Table 2. Percentages of expected and observed shoreline for each modification type (retaining wall, maintained, and undeveloped) in each of the six study lakes. Percent (%) expected indicates the amount of shoreline in a lake for each combination of natural features (high/low wind, and high/low slope). Percent (%) observed indicates the amount of shoreline within a particular combination of natural features that is made up of each modification type. Even distribution of modification types relative to available natural features would be indicated by observed percentages equal to expected percentages. P-values are derived from a Chi-square analysis. Bold indicates the higher value for comparisons that were significantly different. Lakes are ordered according to increasing lakeshore development.

		High wind, high slope		High wind, low slope		Low wind, high slope		Low wind, low slope		
Modification type	**Lake**	% Observed	% Expected	% Observed	% Expected	% Observed	% Expected	% Observed	% Expected	**P-value**
Retaining wall	Bruin	0	0	0	67.33	0	9.11	0	23.16	N/A*
	Blind	0	**12.39**	0	**41.44**	**60.5**	12.18	**39.5**	33.97	< 0.0001
	East Crooked	**34.36**	15.29	31.61	**43.88**	**26.75**	13.77	7.27	**27.06**	< 0.0001
	Halfmoon	0	**12.96**	12.43	**36.17**	0	**6.13**	**87.57**	44.75	< 0.0001
	North	38.07	**42.87**	**34.79**	19.12	**23.66**	19.31	3.48	**18.7**	< 0.0001
	Patterson	**22.59**	10.62	18.63	**52.42**	0	**4.04**	**58.78**	32.92	< 0.0001
Maintained	Bruin	0	0	38.28	**67.33**	**29.99**	9.11	**31.72**	23.16	< 0.0001
	Blind	**15.96**	12.39	**48.58**	41.44	0	**12.18**	**35.46**	33.97	0.0023
	East Crooked	8.14	15.29	44.48	43.88	16.34	13.77	31.04	27.06	0.2198
	Halfmoon	**19.25**	12.96	17.17	**36.17**	**26.53**	6.13	37.04	**44.75**	< 0.0001
	North	33.95	**42.87**	3.73	**19.12**	**22.72**	19.31	**39.6**	18.7	< 0.0001
	Patterson	13.29	10.62	55.32	52.42	0	4.04	31.39	32.92	0.1761
Undeveloped	Bruin	0	0	**80.58**	67.33	0	**9.11**	19.42	**23.16**	0.0064
	Blind	8.43	**12.39**	29.08	**41.44**	**42.36**	12.18	20.12	**33.97**	< 0.0001
	East Crooked	0	**15.29**	**55.52**	43.88	0	**13.77**	**44.48**	27.06	< 0.0001
	Halfmoon	**40.04**	12.96	32.02	**36.17**	5.81	**6.13**	22.13	**44.75**	< 0.0001
	North	**73.56**	42.87	0	**19.12**	0	**19.31**	**26.44**	18.7	< 0.0001
	Patterson	0	**10.62**	**75.32**	52.42	**9.74**	4.04	14.94	**32.92**	< 0.0001

*P-values could not be calculated because Bruin Lake lacked retaining wall shoreline.

Table 3. Within-lake variable P-values and associated degrees of freedom (in parentheses) derived from ANCOVA for sampling transects conducted along 0.5 m and 1 m depth contours. Main effects in the model include shoreline modification type (undeveloped, maintained, and retaining wall) and lakeshore development (LSD; #dwellings/km). Modification*LSD refers to the interaction between modification type and lakeshore development. Significant P-values are in bold.

	0.5 m depth contour				1 m depth contour			
Variable	**Overall Model**	**Modification**	**LSD**	**Modification *LSD**	**Overall Model**	**Modification**	**LSD**	**Modification* LSD**
Coarse woody material	**<0.0001** (5, 84)	**0.0024** (2)	0.057 (1)	0.079 (2)	N/A*	N/A*	N/A*	N/A*
Submersed macrophyte cover	**<0.0001** (3, 87)	**0.0017** (2)	**< 0.0001** (1)	NS	**<0.0001** (3, 87)	**0.0142** (2)	**< 0.0001** (1)	NS
Floating macrophyte cover	**0.0002** (3, 87)	**0.0011** (2)	**0.0007** (1)	NS	**0.0013** (3, 87)	**0.0053** (2)	**0.0023** (1)	NS
Emergent macrophyte cover	**< 0.0001** (3, 87)	**<0.0001** (2)	0.165 (1)	NS	**0.0028** (3, 87)	**0.0011** (2)	0.796 (1)	NS
Substrate composition	**0.021** (3, 87)	**0.0085** (2)	0.285 (1)	NS	**0.0246** (3, 86)	**0.0171** (2)	0.615 (1)	NS

*Coarse woody material sampling was only conducted along the 0.5 m depth contour.

Table 4. Physical characteristics, lakeshore development (LSD), water chemistry and land cover of the 15 study lakes.

Lake	Surface area (hectares)	Lake perimeter (meters)	Mean depth (meters)	SDF[1]	#dwellings	LSD (#dwellings $\cdot km^{-1}$)	TP[2]	ALK[3]	Secchi[4]	% Agr[5]	% For[5]	% Urb[5]
Crooked	46	4189	3.05	1.74	5	1.19	11.6	172	3.4	32.2	19.2	26.8
South	82	5370	5.51	1.67	13	2.42	12.0	162	3.1	11.9	18.6	51.0
Bruin	53	3091	3.74	1.2	24	7.76	13.4	171	3.0	69.5	12.8	1.1
Blind	29	2520	4.05	1.32	24	9.52	12.5	176	2.0	55.2	22.0	1.0
Woodburn	31	4804	3.39	2.43	61	12.70	20.1	213	1.2	14.4	30.7	22.1
West Crooked	77	11033	3.03	3.57	153	13.87	10.7	140	2.9	59.1	24.7	7.9
East Crooked	100	6528	3.97	1.84	95	14.55	14.8	157	3.3	33.3	28.0	23.6
Joslin	79	3855	1.53	1.22	68	17.64	16.3	131	3.3	15.2	6.7	66.1
Halfmoon	97	7399	6.77	2.12	131	17.71	13.4	200	2.4	63.2	15.3	1.8
Hiland	46	10427	1.89	4.34	194	18.61	12.2	190	1.6	8.1	24.6	19.6
North	91	5635	3.53	1.67	121	21.47	14.6	106	3.1	35.4	32.5	27.1
Strawberry	106	7183	5.64	1.97	159	22.18	13.9	191	3.3	7.2	16.2	57.8
Patterson	64	5066	5.58	1.79	113	22.31	21.3	186	2.3	5.0	48.7	17.5
Baseline	99	5875	6.71	1.67	134	22.83	13.1	204	4.2	2.4	62.4	11.3
Zukey	60	5108	3.29	1.86	147	28.77	12.0	175	3.1	20.2	23.0	42.0

[1]SDF is the shoreline development factor calculated from the formula SDF = lake perimeter / (2*(√pi*lake area)). Increasing values indicate greater irregularity of the lake shoreline.

[2]TP is the mean total phosphorus (μg/L) of two samples taken during summers of 2003 and 2004.

[3]ALK is the mean alkalinity (mg/L CaCO3) of two samples taken during summers of 2003 and 2004.

[4]Secchi is the mean Secchi disk depth (m) of two surveys conducted during summers of 2003 and 2004.

[5]Percent land use within a 500 m buffer surrounding each lake (Agr = agricultural; For = forested; and Urb = urban)

Table 5. Macrophyte assemblage characteristics of the 15 study lakes in southeast Michigan. Cover refers to the percentage of sampled points at which plants were present. Total plant cover indicates the percent occurrence of plants sampled over the entire lake, whereas littoral plant cover is the percentage of sampled points at which plants were present in the littoral zone. Littoral zone is defined as the area from shore to the depth at which plants consistently occurred. Dense cover indicates the percent occurrence of sites with macrophyte cover scores of 2 or 3 for any macrophyte category. Plant data were collected during August and September 2003.

Lake	County	Dwellings/ km	Total Plant Cover (%)	Total Dense Cover (%)	Littoral Plant Cover (%)	Littoral Dense Cover (%)	Littoral Submersed Cover (%)	Littoral Emergent Cover (%)	Littoral Floating Cover (%)	Littoral EWM Cover (%)
Crooked	Washtenaw	1.19	76	69	87	79	69	38	80	0
South	Washtenaw	2.42	48	24	93	46	92	18	12	18
Bruin	Washtenaw	7.76	31	9	63	17	52	27	7	12
Blind	Washtenaw	9.52	13	1	19	2	17	10	5	1
Woodburn	Livingston	12.70	36	13	71	28	54	40	48	0
West Crooked	Livingston	13.87	93	78	96	81	80	12	20	53
East Crooked	Livingston	14.55	49	24	82	40	82	8	9	41
Joslin	Washtenaw	17.64	94	89	94	90	94	4	6	24
Halfmoon	Livingston	17.71	19	5	60	17	56	22	14	7
Hiland	Livingston	18.61	53	34	70	45	63	21	41	7
North	Washtenaw	21.47	59	54	80	73	80	3	6	32
Strawberry	Livingston	22.18	26	13	69	34	66	31	24	14
Patterson	Livingston	22.31	26	14	71	38	58	28	21	32
Baseline	Livingston	22.83	26	11	87	36	86	2	3	11
Zukey	Livingston	28.77	35	12	48	17	45	7	7	5

Table 6. Back-calculated lengths (as determined by the body-proportional hypothesis) for bluegill from all study lakes by year-of-capture (2003-2004) and year class. Lee's phenomenon would be indicated when the estimated size at a particular age declines within a year class with increasing year of capture or within a year of capture with decreasing year class. Because Lee's phenomenon appears evident, I only used back-calculated lengths for bluegill from 2001 and 2002 year classes.

Year Class	**Age 1**		**Age 2**		**Age 3**	**Age 4**	**Age 5**	**Age 6**	**Age 7**
	03	04	03	04	03	03	03	03	03
2003	.	42.6	.	.	.	.	.	.	.
2002	58.3	42.3	.	59.3	.	.	.	.	.
2001	47.9	.	77.5	.	.	.	.	.	.
2000	50.9	.	80.8	.	106.9	.	.	.	.
1999	48.4	.	75.8	.	107.3	134.5	.	.	.
1998	47.1	.	71.4	.	96.7	122.6	142.6	.	.
1997	46	.	66.8	.	91.3	115.9	138.5	155.8	.
1996	44.2	.	65.7	.	87.1	112.9	138.7	159.1	173.9

Table 7. Back-calculated lengths (as determined by body-proportional hypothesis method) for largemouth bass from all study lakes by year-of-capture (2003-2004) and year class. Lee's phenomenon would be indicated when the estimated size at a particular age declines within a year class with increasing year of capture or within a year of capture with decreasing year class. Because Lee's phenomenon appears evident, I only used back-calculated lengths of largemouth bass from 1998 to 2001 year classes.

Year Class	**Age 1**		**Age 2**		**Age 3**		**Age 4**		**Age 5**		**Age 6**		**Age 7**		**Age 8**	
	03	04	03	04	03	04	03	04	03	04	03	04	03	04	03	04
2003	.	95.3	.	.	.		.		.		.		.			
2002	97.4	90.9	.	150.5	.		.		.		.		.			
2001	100.8	98.2	171.4	156.7	.	198.6	.		.		.		.			
2000	100.7	90.9	179.5	157.4	233.8	213.4	.	257.5	.		.		.			
1999	92.6	89	168.8	149.4	233.9	201.9	279.4	248.3	.	285.5	.		.			
1998	86.9	92.1	164.9	156.1	228.3	213.6	279.2	261.2	316.9	301.7	.	339.1	.			
1997	80.7	94.7	151.2	150.6	214.9	196.7	264.1	243.1	305	296.6	336.9	340.4	.	380.7		
1996	81.3	103.6	141.7	171.9	195.4	238.2	252.4	280.9	292.1	327.9	339	364.9	369.8	397.7		428.16
1995	83.6	92.1	133.2	146	187.8	194.6	222.4	253.9	268.9	303.1	310.5	342.3	343.5	379.5	378.15	428.4

Figure 1. Map illustrating the location of the six study lakes. The six study lakes are located within the Huron River Watershed, southeast Michigan.

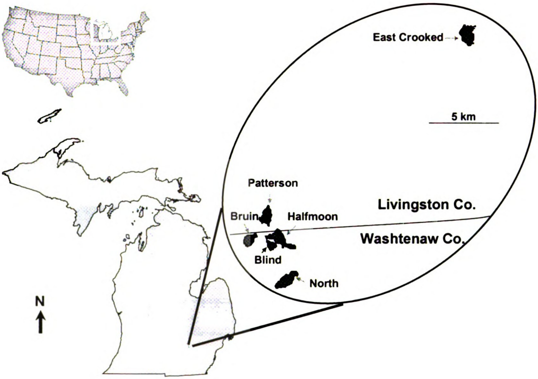


Figure 2. Percentages of the four combinations of natural features along the shorelines of the six study lakes. Lakes are presented from lowest LSD (Bruin = 7.76 dwellings•km^{-1}) to highest LSD (Patterson = 22.31 dwellings•km^{-1}). Note: wind exposure is not evenly distributed due to differences in lake morphometry.

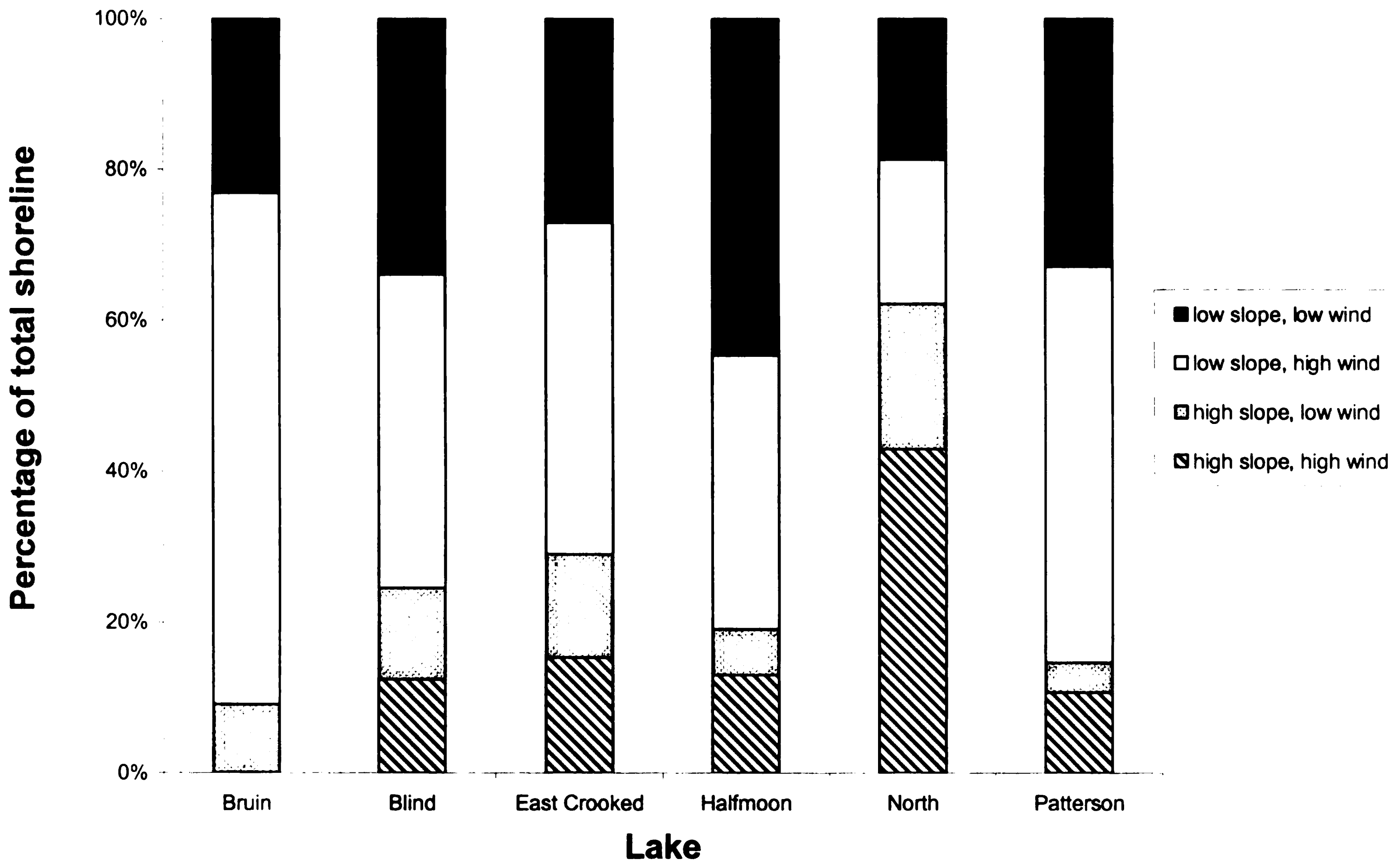


Figure 3. Percentages of the three different modification types along the shorelines of the six study lakes. Lakes are presented from lowest LSD (7.76) to highest LSD (22.31).

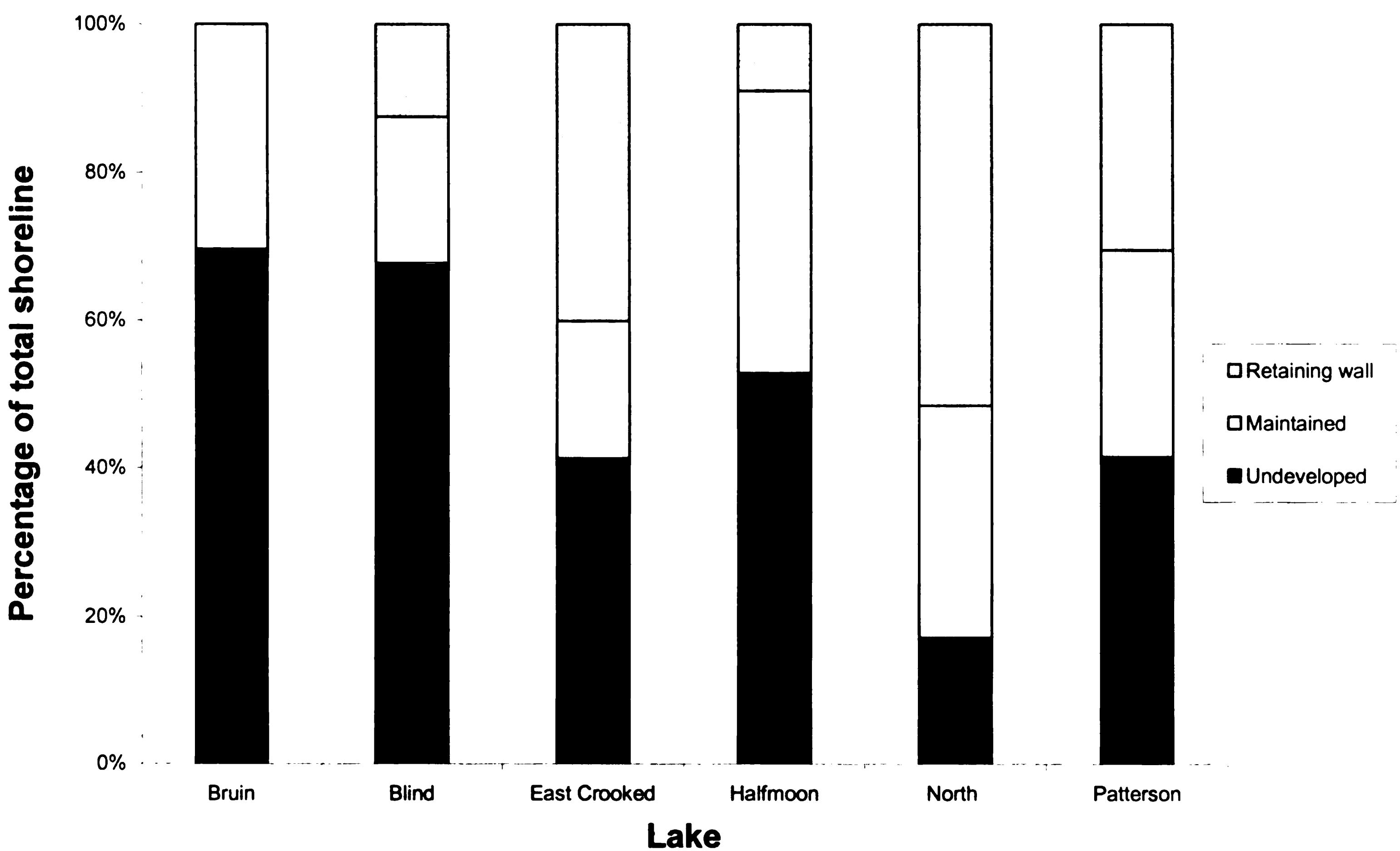


Figure 4. Relationship between lakeshore development (#dwellings/km) and coarse woody material abundance (mean intersections per meter, a.), and submersed macrophyte cover (cover score, b.), ±1 SE, along the 0.5 m depth contour for the three shoreline modification types: undeveloped, maintained, and retaining wall. Note difference in y-axes between coarse woody material abundance and submersed cover.

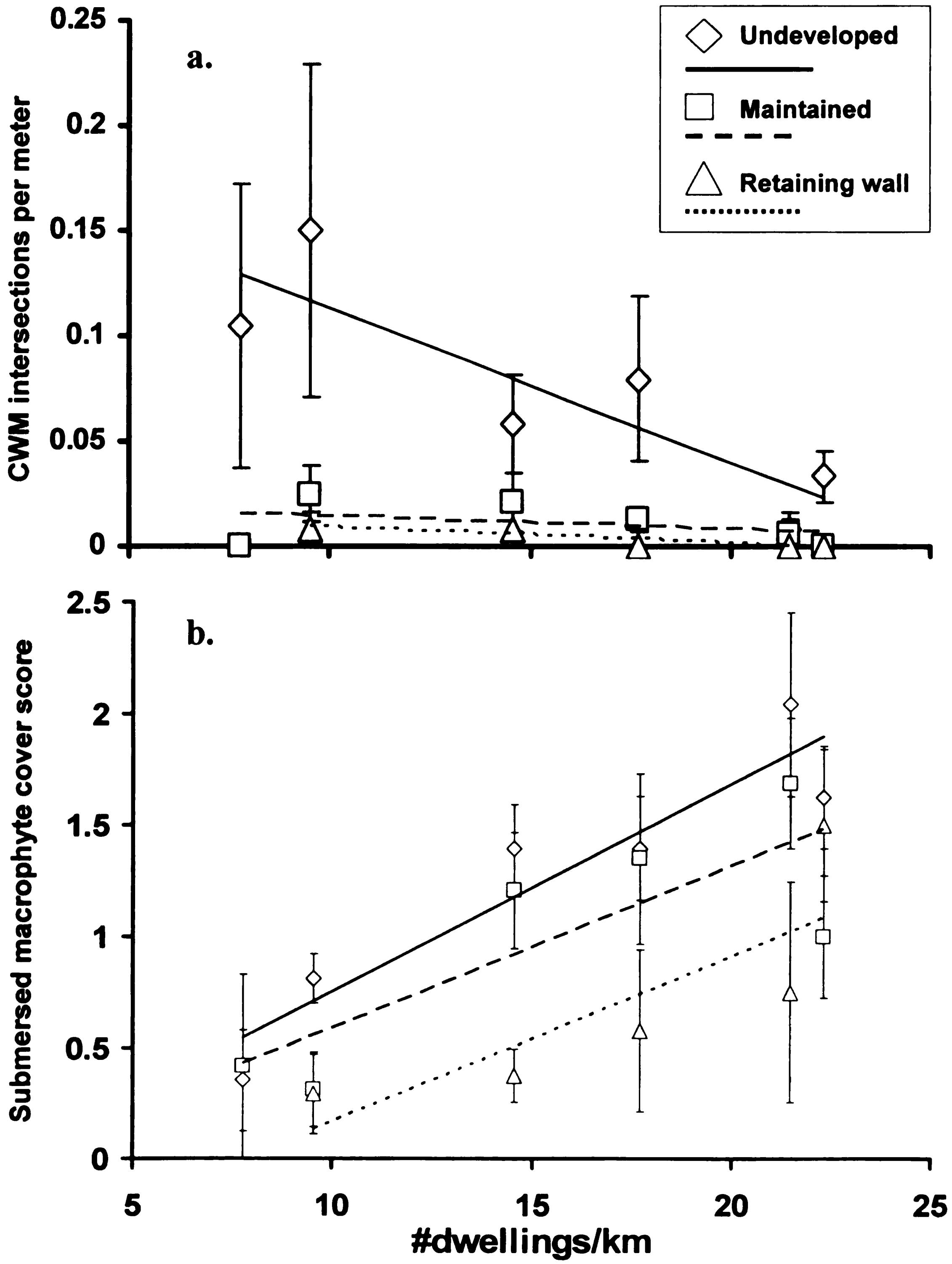


Figure 5. Relationship between lakeshore development (#dwellings/km) and floating macrophyte cover (cover score, a.), and emergent macrophyte cover (cover score, b.), ±1SE, along the 0.5 m depth contour for the three shoreline modification types: undeveloped, maintained, and retaining wall. Note difference in y-axes between floating macrophyte and emergent macrophyte cover.

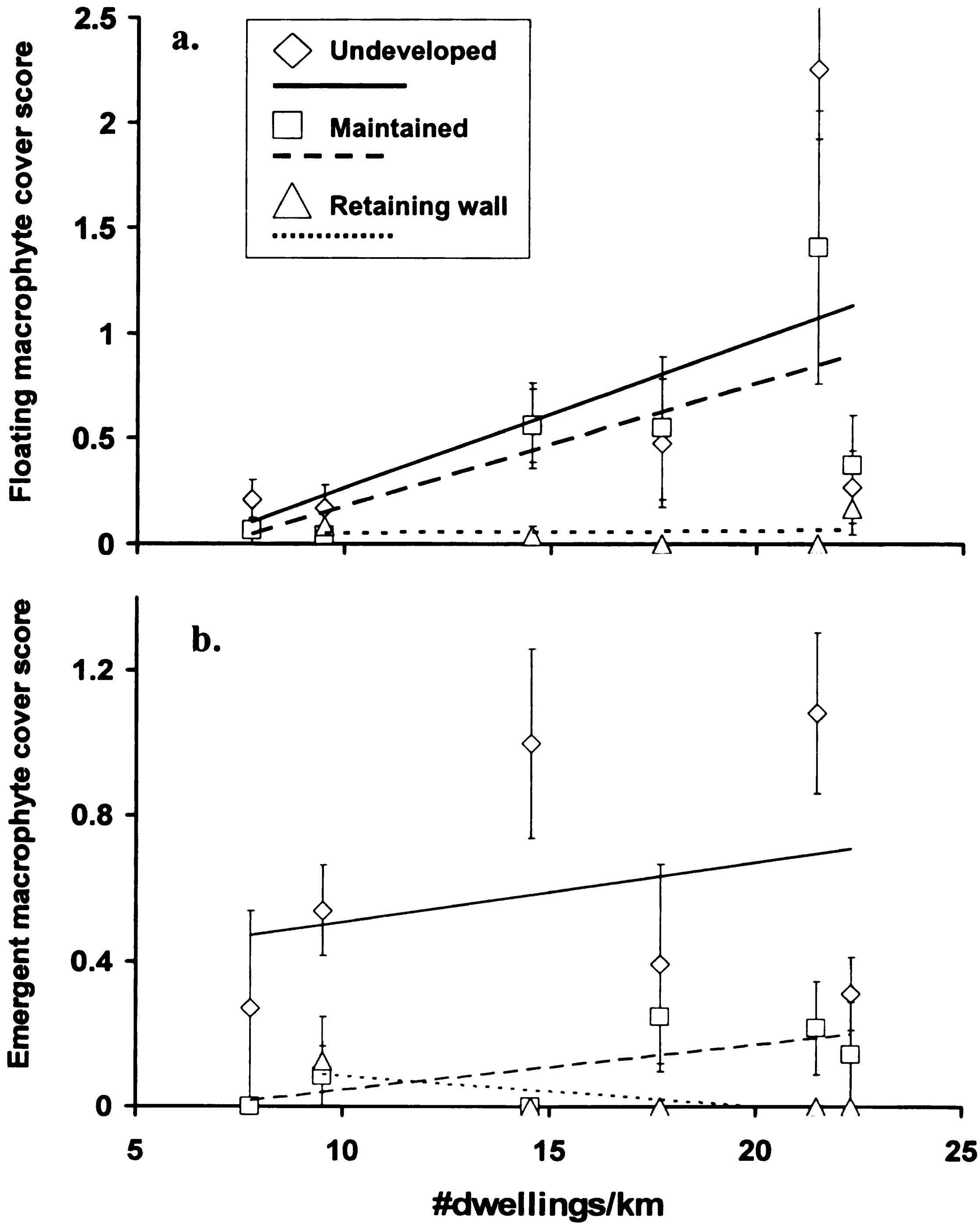


Figure 6. Relationship between lakeshore development (#dwellings/km) and mean substrate particle size, ±1SE, along the 0.5 m depth contour for the three shoreline modification types: undeveloped, maintained, and retaining wall.

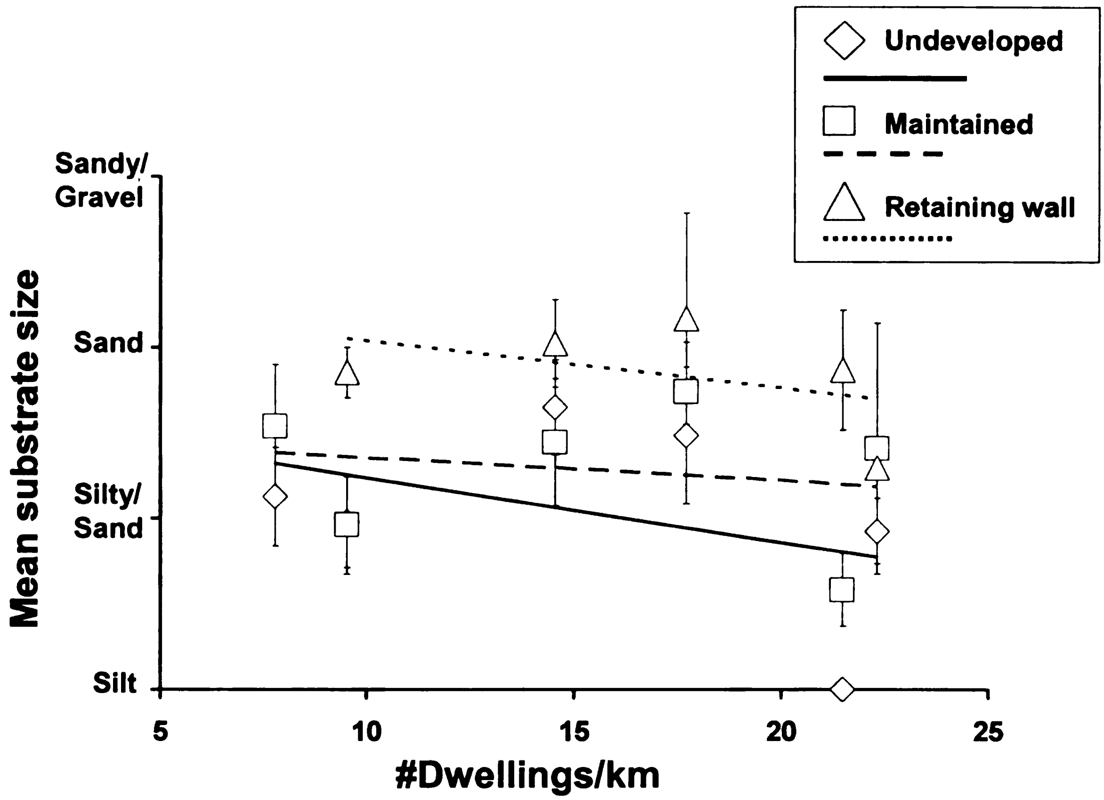


Figure 7. Map illustrating the location of the fifteen study lakes. The fifteen study lakes are located within the Huron River Watershed, southeast Michigan.

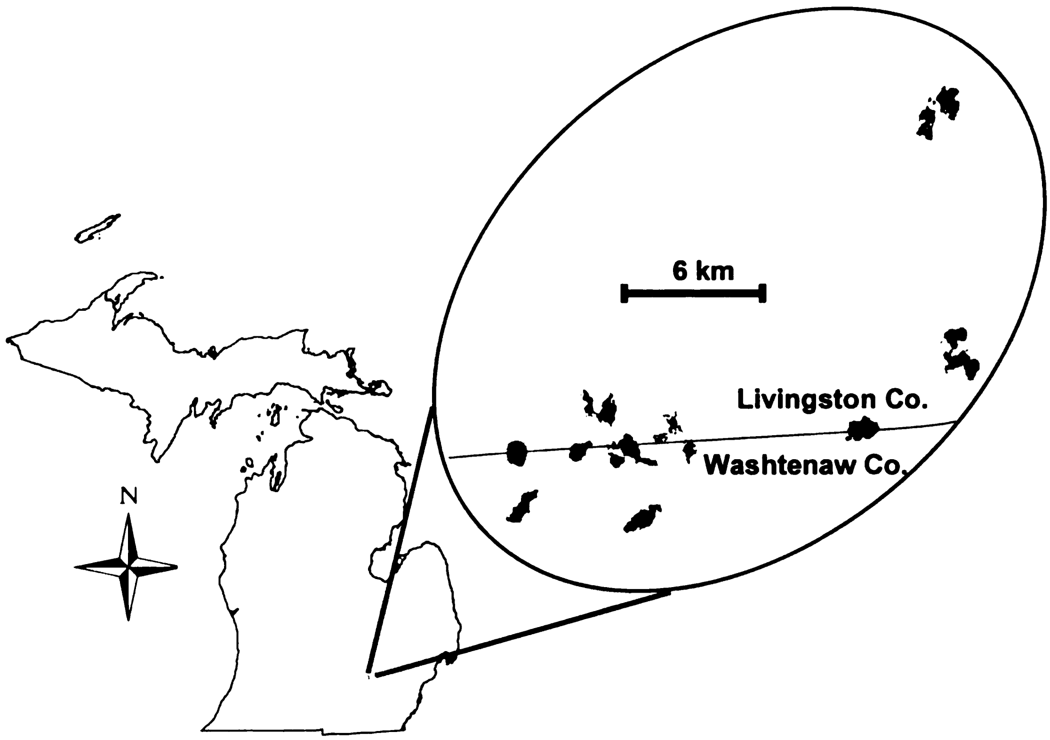


Figure 8. Whole-lake macrophyte response to LSD for littoral floating cover (A), whole-lake macrophyte cover (B), littoral emergent cover (C), and littoral submersed cover (D). Data presented are actual values. Statistical values are based upon transformed data (when appropriate).

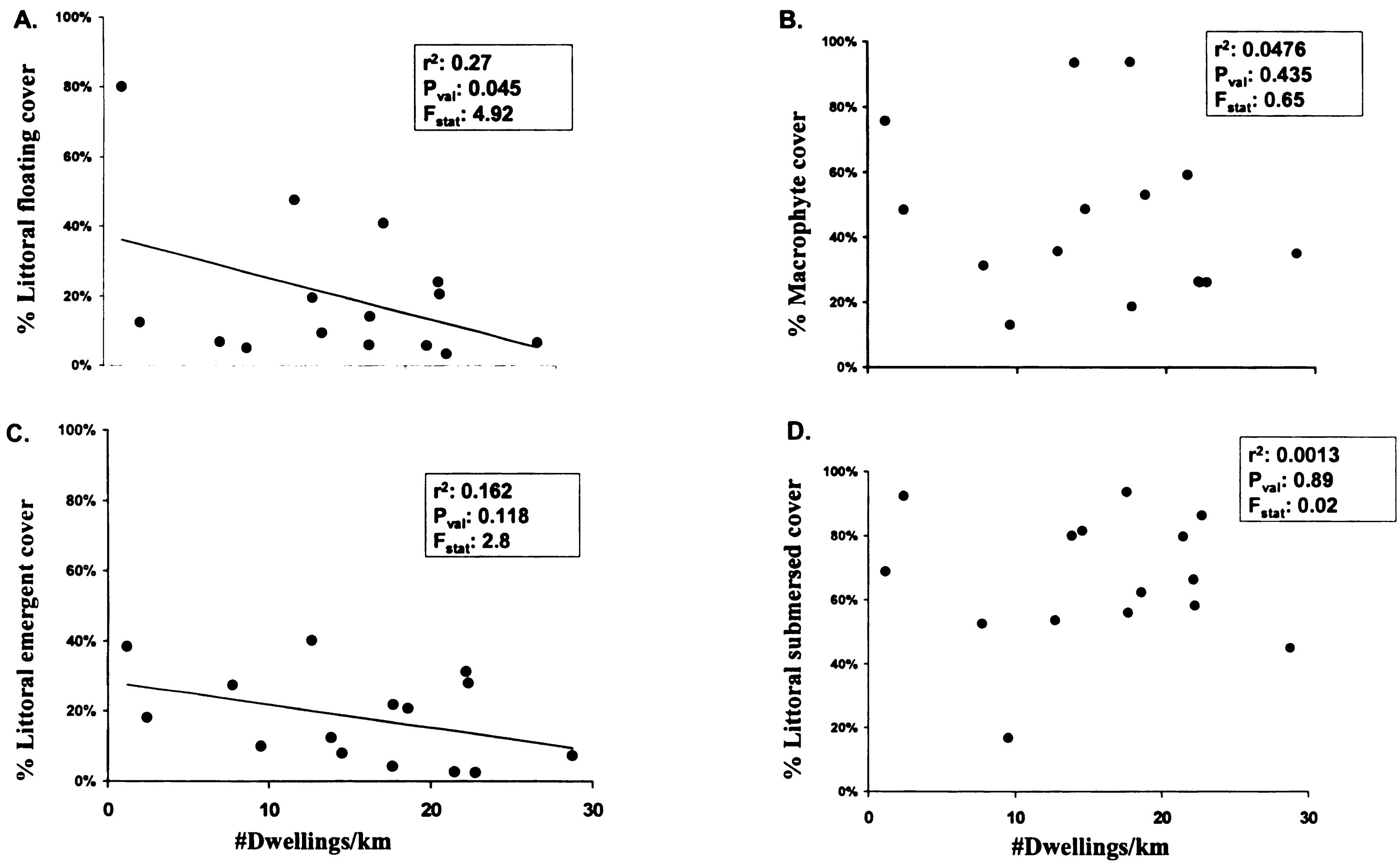


Figure 9. Annual growth increment (mm) relative to fish size (back-calculated total length, mm) of bluegill collected in 2003 and 2004 in the 15 study lakes. Data points on far left indicate size at hatching (3mm, Carlander 1977).

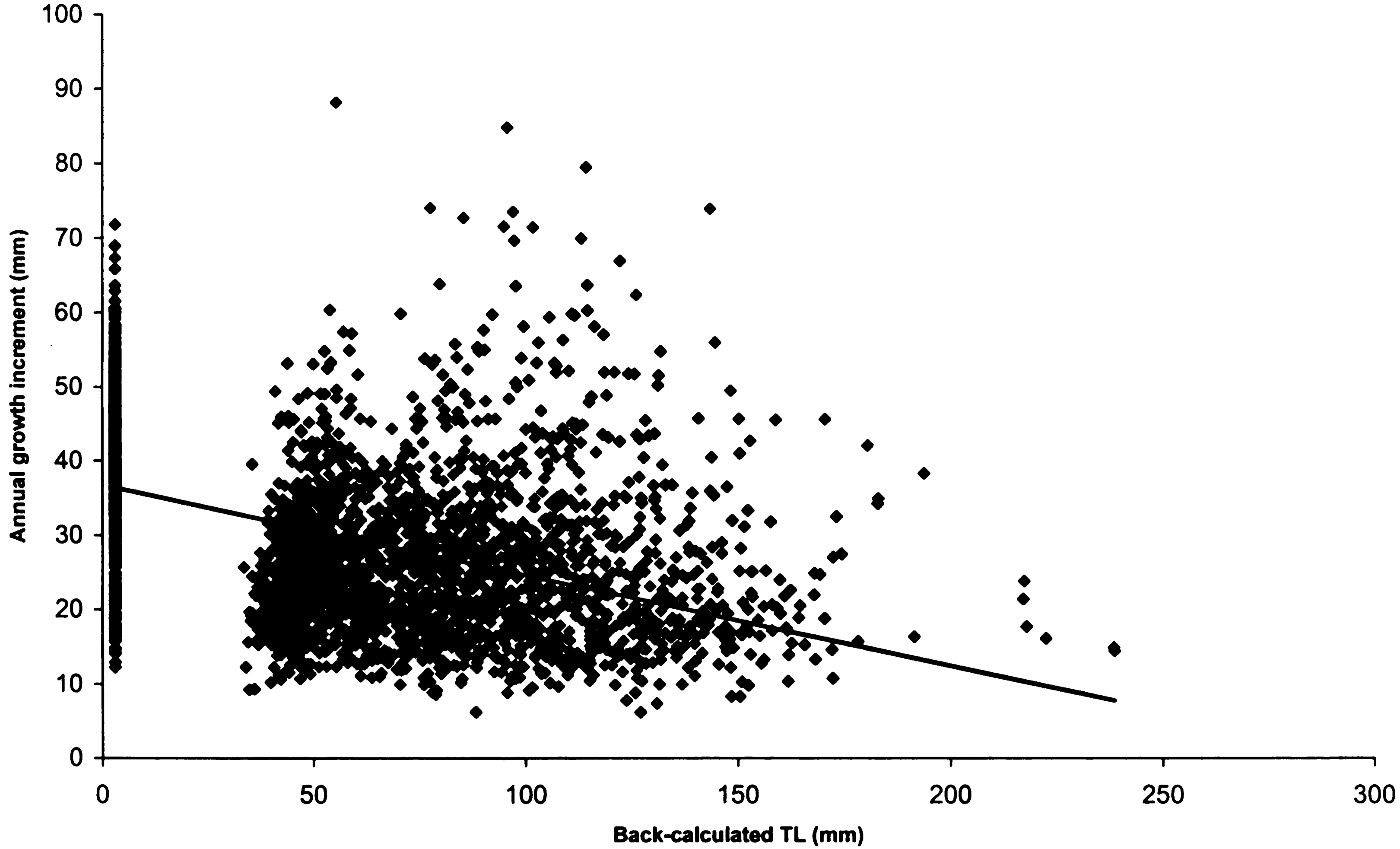


Figure 10. Annual growth increment (mm) relative to fish size (back-calculated total length, mm) of largemouth bass collected in 2003 and 2004 in the 15 study lakes. Data points on far left indicate size at hatching (3mm, Carlander 1977).

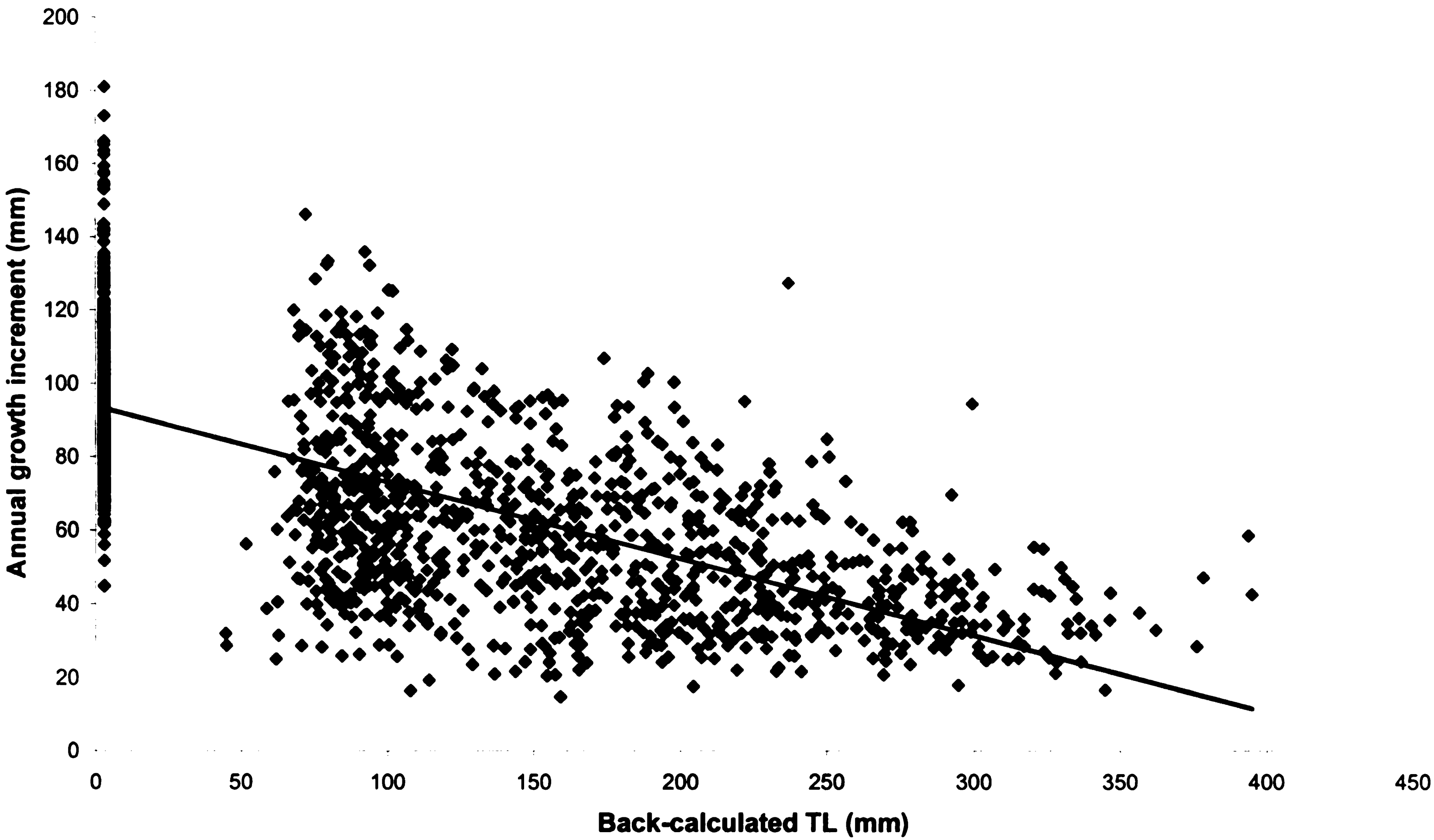


Figure 11. Annual growth increment for bluegill (growth years 2001 and 2002) as a function of back-calculated total length. Low development lakes (<13 dwellings•km^{-1}) are represented by the solid line, medium development lakes (13-20 dwellings•km^{-1}) are represented by the wide-dashed line, and high development lakes (>20 dwellings•km^{-1}) are represented by the short-dashed line.

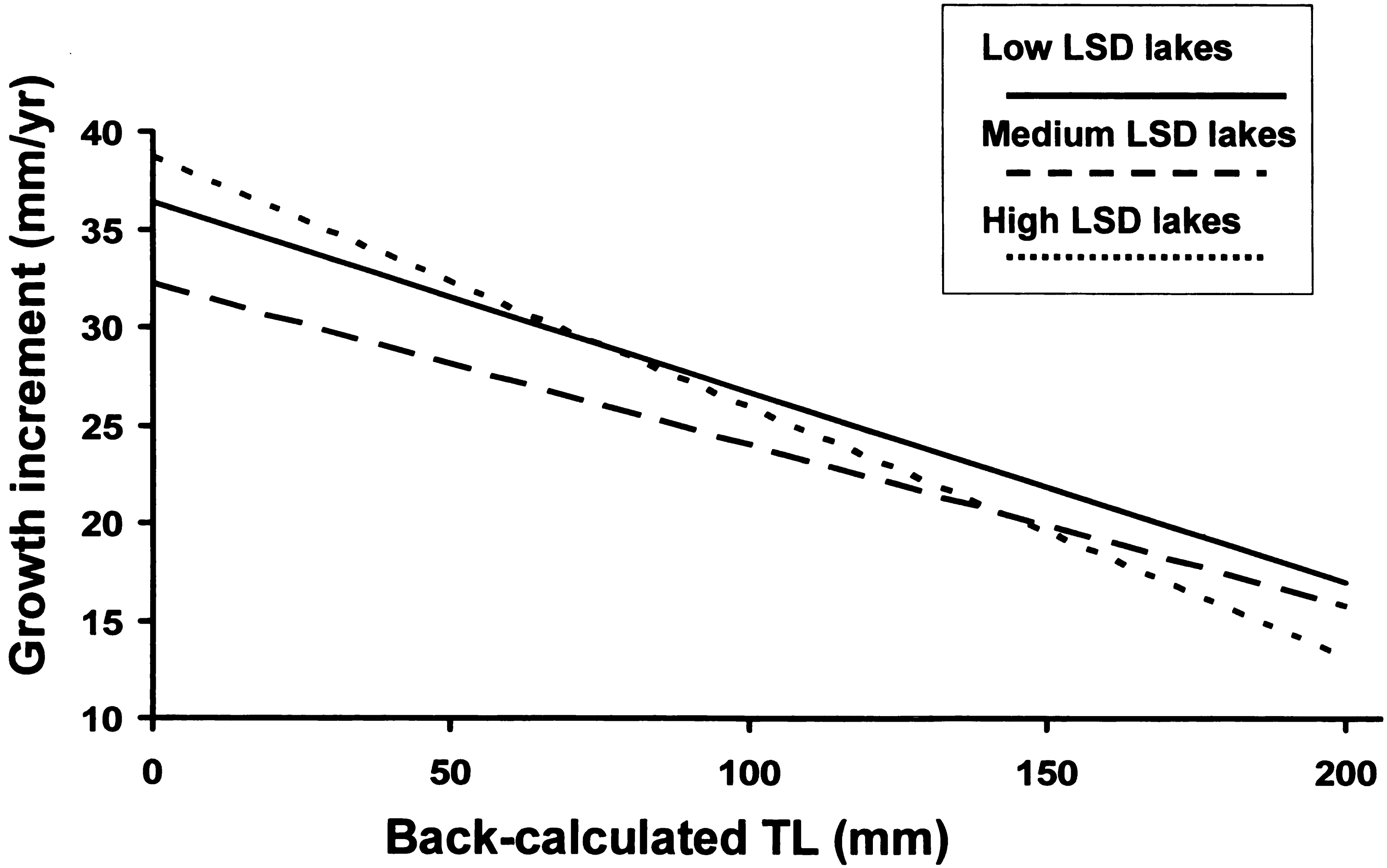
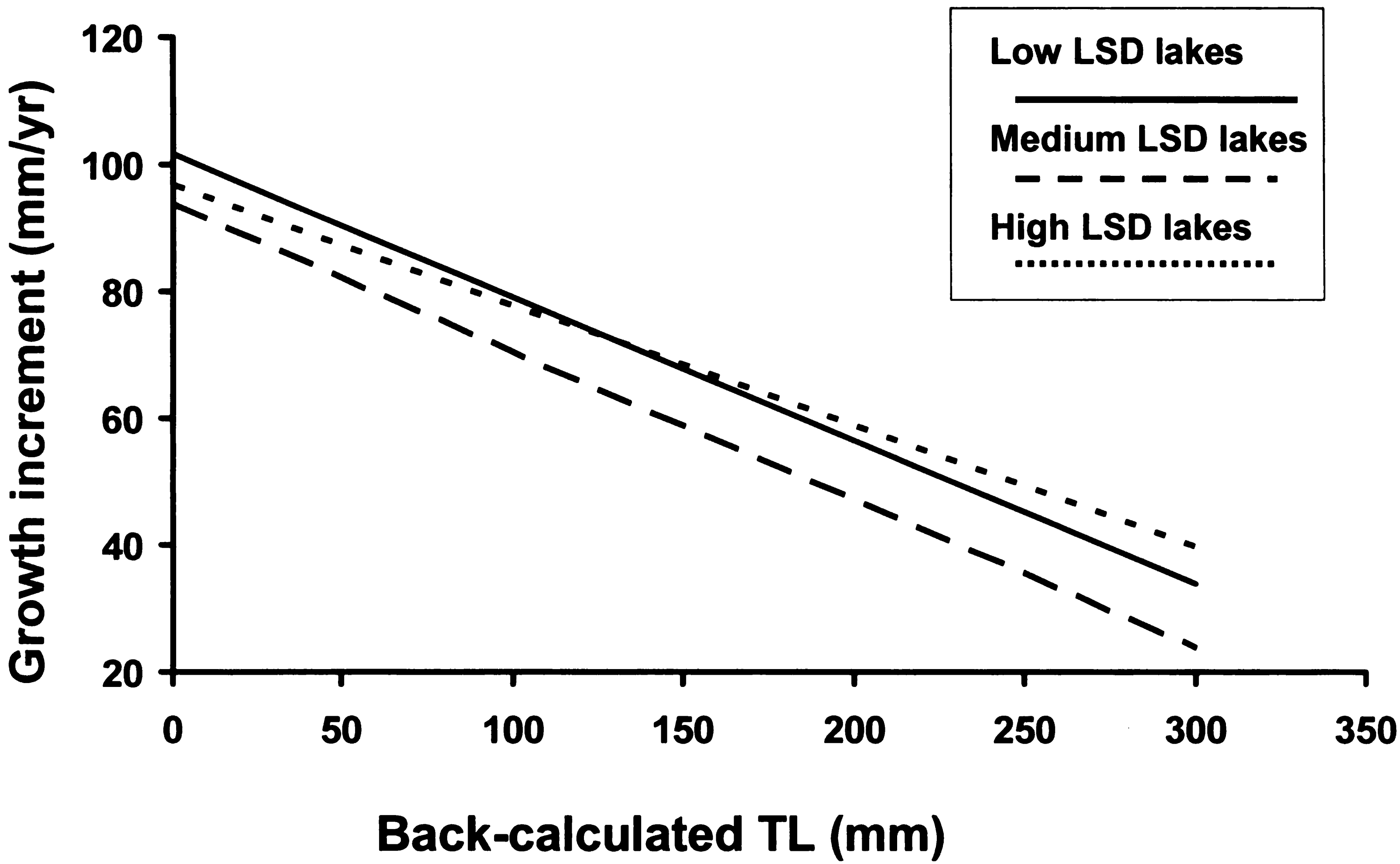


Figure 12. Annual growth increment for largemouth bass (growth years 1998 and 2001) as a function of back-calculated total length. Low development lakes (<13 dwellings•km^{-1}) are represented by the solid line, medium development lakes (13-20 dwellings•km^{-1}) are represented by the wide-dashed line, and high development lakes (>20 dwellings•km^{-1}) are represented by the short-dashed line.



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