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A Multilevel Modeling Approach to Assessing Regional and Local Landscape Features for Lake Classification and Assessment of Fish Growth Rates

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Abstract The ecoregion and watershed frameworks are landscape-based classifications that have been used to group waterbodies with respect to measures of community structure; however, they have yet to be evaluated for grouping lakes for demographic characteristics of fish populations. We used a multilevel modeling approach to determine if variability in mean fish length at age could be partitioned by ecoregions and watersheds. For the ecoregions analysis, we then examined if within-ecoregion variability could be explained by local water quality and lake morphometry characteristics. We used data from agency surveys conducted during 1974–1984 for age 2 and 3 fish of seven common warm and coolwater fish species. Variance in mean length at age between ecoregions for all species was not significant, and between-watershed variance estimates were only significant in 3 out of 14 analyses; however, the total amount of variation between watersheds was very small (ranging from 1.8% to 3.7% of the total variance), indicating that ecoregions and watersheds were ineffective in partitioning variability in mean length at age. Within ecoregions, water quality and lake morphometric characteristics accounted for 2%–23% of the variation in mean length at age. Measures of lake productivity were the most common significant covariates, with mean length at age increasing with increasing lake productivity. Much of the variability in mean length at age was not accounted for, suggesting that other local factors such as biotic interactions, fish density, and exploitation are important. The results indicate that the development of an effective regional framework for managing inland lakes will require a substantial effort to understand sources of demographic variability and that managers should not rely solely on ecoregions or watersheds for grouping lakes with similar growth rates.

Keywords Ecoregion · Watershed · Classification · Fish growth · Mean length at age · Water quality

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1 Introduction

Over past decades, many state and federal agencies have moved toward a regional approach for biological assessment and monitoring. This approach often entails delineating an area of land into discrete management units, which are based on physical geographical features. In the United States, two approaches dominate how agencies divide land into management units: basinwide or watershed approaches and ecoregion classification (Brown & Marshall, 1996). An ecoregion is defined as a unit of land that is homogenous with respect to multiple landscape characteristics such as geology, soil characteristics, natural vegetation, and climate. A watershed is defined as the topographical area which drains water into a waterbody (Omernik & Bailey, 1997). In the United States, however, the use of hydrologic units (HUs) as proxies for watersheds has increased since the development of digital HU maps by the United States Geological Survey (Seaber, Kapinos, & Knapp, 1987). Hydrological units may or may not overlap with a waterbody's topographical watershed (Omernik, 2003); however, they represent a valuable and accessible framework for classifying waterbodies. Hydrologic units are classified into several levels and are identified based on a unique hydrological unit code (HUC). Spatial scales of HUCs range from 'regions' (2-digit HUC) to 'subwatersheds' (14-digit HUC).

Although watershed-based approaches are still used in many states, the ecoregion framework is becoming increasingly popular as ecoregion delineations are becoming available for most states and from multiple sources, including the US Environmental Protection Agency (e.g., Bailey, 1983; Omernik, 1987; Albert, 1995). The use of watershed and ecoregion frameworks is not limited to the United States, as several European countries have also adopted these approaches for regional environmental management (Sandin & Johnson, 2000; Santoul, Soulard, Figuerola, Céréghino, & Mastrorillo, 2004). The underlying assumption behind the use of ecoregions and watersheds is that classification of surface waters will reduce natural within-class variation of ecological data (Gerritsen, Barbour, & King, 2000). If so, then the grouping of lakes that are ecologically similar will facilitate the identification of reference conditions, allow for more precise assessment of aquatic communities, and provide the opportunity to extrapolate biological information to other lakes within a relatively homogenous landscape (Gerritsen et al., 2000).

Although ecoregions or watersheds are often adopted as a framework for classifying aquatic systems, several limitations exist regarding their ability to group waterbodies (Johnson, 2000; Van Sickle & Hughes, 2000). First, the delineation of ecoregion boundaries is subjective at some level. Second, as mentioned above, the delineation of HUs does not always overlap with topographical watersheds and thus defining a HU is not simple (Omernik, 2003). Third, one of the primary assumptions of the ecoregion and watershed approaches to classifying aquatic systems is that the spatial variability of the abiotic features constrains important properties of aquatic ecosystems. If the properties of aquatic systems that are being measured are not constrained spatially, for example, if properties vary independently over the landscape, then these frameworks will be ineffective at partitioning variance (Hawkins & Vinson, 2000). This highlights the need to determine how well ecoregions and watersheds (i.e., HUs) actually partition variability prior to their implementation for ecosystem management (Johnson, 2000; Omernik, 2003).

To date, most investigations into the effectiveness of ecoregions and watersheds as frameworks for ecosystem management have focused on streams (Newall & Magnuson, 1999; Pan, Stevenson, Hill, & Herlihy, 2000), with fewer studies examining lakes (but see Johnson, 2000; Jenerette, Lee, Waller, & Carlson, 2002). Furthermore, the emphasis of these investigations has often focused on measures of community structure, such as species richness or diversity and results from these studies often conflict. For example, Newall and Magnuson (1999) demonstrated fish community structure was not related to ecoregions in Wisconsin streams. Conversely, Van Sickle and Hughes (2000) found that stream fish and amphibian assemblages were more similar within ecoregions than between ecoregions in Oregon streams and that ecoregions performed better in grouping similar stream vertebrate assemblages as compared to watersheds. Studies have yet to investigate if ecoregions or watersheds are effective at partitioning variability in demographic characteristics of aquatic organisms. An understanding of both the spatial patterns of species assemblages and the spatial variability in demographic characteristics is necessary for the conservation and management of aquatic populations.

Although many demographic characteristics are difficult to measure, growth rates of fishes are relatively easy to determine and often readily available from state and federal management agencies. Fish growth rates are of great importance to ecological interactions in aquatic systems (Weatherley, 1972) and of particular interest to fisheries management agencies because they can be used to assist management decisions regarding stocking programs and size and bag limits for sport fishes (e.g., Shuter, Jones, Korver, & Lester, 1998). Furthermore, fish growth rates are inherently variable among lakes, making regional management difficult (Shuter et al., 1998). Therefore, fish growth data represent an opportunity to assess the ability of the ecoregion and watershed frameworks to partition variance of demographic data.

Many studies evaluating the ecoregion and watershed approaches have focused primarily on how well the framework maximizes between-class variability, without exploring factors that explain within-class variability. However, factors that regulate the structure and function of aquatic communities operate at multiple spatial scales (Roth, Allan, & Erickson, 1996; Jackson, Peres-Neto, & Olden, 2001). Identifying whether local or regional controlling factors explain the most variability among waterbodies will greatly assist the development of regional management plans. For instance, there is a paucity of information on the relative importance of local factors such as lake morphometry and water quality *versus* regional factors in explaining variability in fish growth rates and whether potential relationships vary among ecoregions (or watersheds). The use of multilevel mixed models, as employed in this study, is a novel approach for the evaluation of the ecoregion and watershed frameworks that allows for the investigation of factors (covariates) that operate at multiple spatial scales in a single statistical model.

Elucidation of relationships between physical and chemical lake properties and growth of fishes can lead to the development and/or refinement of lake classification tools to be used independently or conjointly with existing frameworks. Therefore, the objectives of this study were to: (1) Examine how variability in inland lake fish growth rates is partitioned within and between ecoregions and major river watersheds in Michigan, (2) determine what aspects of ecoregions or watersheds can explain between-class variation, if it does exist, and (3) determine what lake morphometric and water quality characteristics can predict within-class variability in fish growth rates. Due to data restrictions, we limited our analysis of factors explaining within-class variation to the ecoregion analysis (see Section 2). We analyzed data for seven fish species including the warmwater species bluegill *Lepomis macrochirus*, pumpkinseed *Lepomis gibbosus*, largemouth bass *Micropterus salmoides*, and the coolwater species smallmouth bass *Micropterus dolomieu*, yellow perch *Perca flavescens*, walleye *Sander vitreus*, and northern pike *Esox lucius*.

1.1 Hypotheses

Our model-building process was driven by *a priori* hypotheses, in that covariates were selected for inclusion in the model-building process based on hypothesized relationships between the covariate and the growth of fishes. As a framework for selecting potential covariates, we considered fish growth to be a function of consumption and metabolic costs, which is similar to many bioenergetics models (Hansen et al., 1993). We restricted our analysis of within-class variation to ecoregions, because sample sizes were larger than those associated with watersheds. Within this bioenergetics framework, we hypothesized the following water quality and landscape characteristics to be important factors influencing the growth of fishes within and between ecoregions and between watersheds.

1.1.1 Consumption

We hypothesized that water quality and landscape characteristics would influence fish consumption through three mechanisms, and that these characteristics would show similar effects at the local lake scale and the regional watershed/ecoregion scale. The three mechanisms are: (1) prey availability, (2) prey diversity, and (3) predator–prey overlap. Because species density and diversity (richness) tend to increase with increasing productivity (Waide et al., 1999), we hypothesized that measures of productivity (e.g., chlorophyll *a* and total phosphorus) would be positively associated with fish growth rates. The diversity–productivity relationship in lakes is often considered unimodal, with diversity decreasing under hypereutrophic conditions. However, given the relatively low nutrient status of our study lakes, we expected a positive linear relationship.

Species diversity of both fishes and zooplankton is related to local landscape characteristics (e.g., basin morphology), with diversity increasing with increasing lake size and depth (Barbour & Brown, 1974; Dodson, 1992). We did not expect, however, that larger and deeper lakes would necessarily be associated with faster fish growth rates because shallower lakes may increase the amount of foraging habitat for species that depend primarily on littoral prey (but see Mittelbach & Chesson, 1987; Mittelbach & Osenberg, 1992). Therefore, because the species we included in our analyses all utilize the littoral regions of lakes for foraging, we hypothesized that large shallow lakes with extensive littoral areas would be associated with faster growth. Accordingly, we also hypothesized that lakes with a high shoreline development factor (SDF), which is a measure of shoreline complexity, would be positively associated with fast fish growth. A lake's hydrologic position in the landscape is also related to fish species richness (Kratz, Webster, Bowser, Magnuson, & Benson, 1997). For example, lakes that are isolated from other sources of surface waters (e.g., seepage lakes) have lower species richness as compared to lakes that are connected to other lakes and streams (Riera, Magnuson, Kratz, & Webster, 2000). The isolation of seepage lakes may result in lower richness due to lower invasion probabilities. Therefore, we hypothesized that isolated lakes would have fish with slower growth rates compared to lakes connected to streams and other lakes.

1.1.2 Metabolic costs

Temperature influences rates of fish metabolism, consumption, and growth (Power & van den Heuvel, 1999; Zweifel, Hayward, & Rabeni, 1999). Growth increases as temperature increases to a maximum point (i.e., growth plateaus), beyond which growth decreases as metabolic costs exceed energy intake at higher temperatures (Kitchell, Stewart, & Weininger, 1977). Because Michigan is located in the northern portion of the country and therefore has relatively mild summers, and because we examined data for warm and coolwater fish species, we predicted the growth–temperature relationship to be linear and not parabolic, as temperatures exceeding the thermal optimum for an extended length of time are unlikely.

We also hypothesized that a lake's morphometry would indirectly influence fish metabolic rates by affecting the amount of thermally optimal habitat by influencing thermal stratification and growing season length. Because warm and coolwater species are included in our analysis, we predicted that deep lakes would have slower growth rates compared to shallower lakes. Furthermore, large, shallow lakes are predicted to have highest growth rates due to potentially higher prey diversity and warmer temperatures. For all species, we also predicted that a large amount of variability in fish growth rates would remain unexplained, as biotic interactions and fish density can substantially influence fish growth rates (Mittelbach, 1988; Pazzia, Trudel, Ridgway, & Rasmussen, 2002; Werner & Hall, 1977). The specific covariates we included in the analyses and their sources are described in detail below.

2 Materials and Methods

2.1 Datasets

Growth data (mean length at age) for seven warm and coolwater fish species (Table I) were obtained from historical fish growth surveys conducted by the Fisheries Division of the Michigan Department of Natural Resources. Species used in analyses included the warmwater species bluegill *L. macrochirus*, pumpkinseed *L. gibbosus*, largemouth bass *M. salmoides*, and the coolwater species smallmouth bass *M. dolomieu*, yellow perch *P. flavescens*, walleye *S. vitreus*, and northern pike *E. lucius*. Mean length at age data from surveys conducted during 1974–1984 were used in the analyses because they coincide with years during which water quality was also sampled. In each survey, fish growth was recorded as the mean length at age for a given species and age. The corresponding number of fish that contributed to the mean was also reported; however, data for individual fish were not reported. Other data contained in the surveys included the season of sampling (categorized as spring, summer, fall, or winter) and the sampling year. The gear type used to collect the fish was sometimes reported; however, often multiple gear types were used or no gear type was reported. Due to the inconsistencies in reporting gear types and the fact that multiple gear types were often used, we were

Table I Sample size ranges (number of lakes per ecoregion or eight digit hydrologic unit (HU)) and the number of HUs used in the analysis of each species and age combination

Species (age)	Ecoregion section	8-digit HUs	Number of HUs
Bluegill (2)	10–90	3–21	21
Bluegill (3)	13–102	3–26	24
Pumpkinseed (2)	10–35	3–8	13
Pumpkinseed (3)	13–49	3–10	16
Largemouth bass (2)	3–49	3–23	21
Largemouth bass (3)	4–96	3–23	22
Smallmouth bass (2)	9–35	3–7	10
Smallmouth bass (3)	9–33	3–7	9
Yellow perch (2)	22–74	3–19	22
Yellow perch (3)	22–69	3–19	23
Walleye (2)	6–28	3–6	7
Walleye (3)	4–24	3–8	8
Northern pike (2)	11–65	3–15	19
Northern pike (3)	9–69	3–16	19

The number of ecoregions used in the analyses was always four.

unable to control for this potentially important covariate. Historically, the Fisheries Division did not randomly sample lakes. However, the fish growth surveys used in this analysis represent a large sample of public lakes (surface area >20 ha) distributed across the entire state (Figure 1). We restricted our analyses to mean length at age 2 and 3 for each species because the reliability of fish aging decreases with increasing age (Ricker, 1975) and because the growth of early age classes of fishes is an important factor in determining predator–prey and competitive interactions, which can affect species distributions, size–structure, and population dynamics (Diehl & Eklöv, 1995; Eklöv & Hamrin, 1989; Persson, Andersson, Wahlström, & Eklöv, 1996).

Water quality data were obtained from the US Environmental Protection Agency's data storage and retrieval system (STORET). All data were collected by the Michigan Department of Environmental Quality from public lakes greater than 20 ha during 1974–1984. We extracted from the database those variables we hypothesized would affect fish growth rates, including Secchi depth, water color, total phosphorus, total nitrogen, chlorophyll *a*, and alkalinity (Table II). All data are summer (July, August, and September) values collected from the epilimnion. Growing degree days (GDD) were also calculated for each lake as the sum of the amounts that daily average air temperature exceeded a base of 10°C (MDNR, 2003). Growing degree days are based on 30 year average (1951–1980) air temperature records (http://www.climatesource.com) and calculated as an area-weighted average for each lake to represent a proxy for the thermal conditions experienced by aquatic organisms throughout the state. Air temperature was used instead of water temperature because it was more readily available and is correlated with fish growth (McCauley & Kilgour, 1990).

Landscape data consisted of measures of lake morphometry and lake connectedness (i.e., landscape position, Riera et al., 2000). Lake morphometry data were obtained from a lake polygon coverage for the state of Michigan (MDNR, 2003) and include lake area, perimeter and SDF, which is defined as the ratio of the length of the shoreline to the circumference of a circle of area equal to that of the lake (Wetzel, 2001) and is an indicator of lake shoreline complexity (Table II). Lake mean depth was calculated by overlaying a grid of points on bathymetric lake maps and calculating the average depth as the average depth value of all points (Omernik & Kinney, 1983). This approach was verified by comparing values to those calculated by measuring the volume of each depth contour for a sub-sample of lakes (Cheruvelil, unpublished data). Each lake was classified according to its hydrologic connectivity as visible on 1:100,000 scale maps as (1) a seepage lake, with no connections to other surface waters, (2) a lake connected only to streams, or (3) a lake connected to lakes and streams. We calculated ecoregion and watershed averages of the covariates listed in Table II, which were measured at the local lake scale. These averages were then used as covariates to explain any significant between-class variance in fish growth. Therefore, we had water quality and morphometric covariates representative of both local and regional scales. We used ecoregion sections in the analysis as defined by Albert (1995) which are primarily based on long-term climate records. We used eight-digit HUs for our major river watershed delineation (Seaber et al., 1987; Figure 1).

2.2 Statistical analysis

In our analyses, lakes comprised the units of analysis and each lake was represented once within the 10 year period. If a lake was sampled in multiple years, the sampling year with the most data was retained in the analysis. If a lake was sampled more than once in a season within a year (e.g., sampled twice in the spring), the average of the mean length at age was calculated and the total number of fish contributing to the mean was recorded. However this rarely occurred; less than 5% of the lakes in each dataset were sampled more than once per year.

To accommodate possible dependency among lakes within ecoregions and watersheds, we employed a multilevel mixed modeling approach which enabled us to partition the variance in mean length at age within and between ecoregion sections and watersheds and to examine the importance of water quality and landscape features in predicting mean length at age within ecoregion sections (Raudenbush & Bryk, 2002). A separate analysis was performed for each species/age combination. For each analysis, mean length at age was the dependent variable and the number of fish contributing to the mean was used as the weighting factor.

2.2.1 Model building

Because each dataset consisted of a somewhat different suite of lakes (and watersheds for the watershed analyses; Table I), a general model building strategy was followed for each species/age dataset. First, descriptive statistics were generated to examine each dataset for outliers and for collinearity among covariates. The assumption of normality was assessed for each covariate by examining normal probability plots. Non-normally distributed covariates

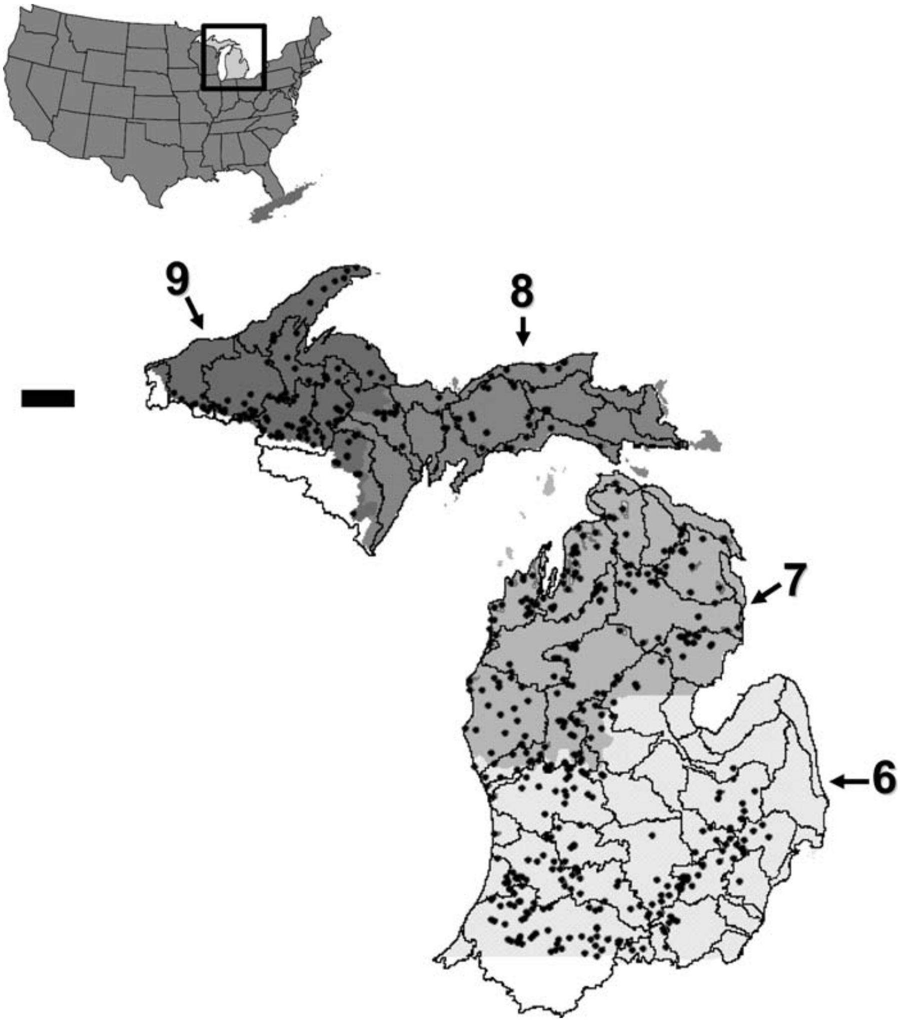


Figure 1 Map illustrating the four ecoregion sections and eight-digit hydrologic units (Seaber et al. 1987) in Michigan. Ecoregion sections defined by Albert (1995) are numbered six through nine. *Black circles* represent lakes used in the analyses.

were log-transformed to accommodate the assumptions of normality and homogeneity of variance. Second, an unconditional means model was fitted to provide baseline variance estimates which were used to calculate an intraclass correlation coefficient, which measures the proportion of variance in mean length at age that is between ecoregion sections and watersheds (the level-2 units). The unconditional means model can be viewed as a two-level model as follows, using ecoregions as the level-2 unit:

$$\text{Level-1 model}: Y_{ij} = \beta_{0j} + r_{ij} \tag{1}$$

where Y_{ij} is the mean length at age for a species in lake i in ecoregion j, β_{0j} is the mean outcome for the jth ecoregion, r_{ij} is the level-1 error, where $r_{ij} \sim N(0, \sigma^2)$, and σ^2 represents the within-ecoregion variability in mean length at age.

$$\text{Level-2 model}: \beta_{0j} = \gamma_{00} + u_{0j} \tag{2}$$

Where γ_{00} represents the grand mean of mean length at age for all ecoregions, u_{0j} is the random effect associated with ecoregion j, and $u_{0j} \sim N(0, \tau_{00})$, and τ_{00} represents the between-ecoregion variability in mean length at age. The combined unconditional model is therefore:

$$Y_{ij} = \gamma_{00} + u_{0j} + r_{ij} \tag{3}$$

The intraclass correlation coefficient can then be calculated as follows:

$$\widehat{\rho} = \widehat{\tau}_{00} / \left(\widehat{\tau}_{00} + \widehat{\sigma}^2\right) \tag{4}$$

As a third step, because the sampling season will affect mean length at age estimates, we controlled for season by including dummy variables for fish collected in the spring, summer, fall, and winter. Each level-1 covariate was then added separately as a fixed effect (covariates were added as fixed effects because of small sample sizes within ecoregions) to the model that controlled for the season to identify significant covariates (α-level = 0.05). After significant, non-correlated level-1 covariates were identified, those covariates were included in a single model. With the addition of each covariate, the more complex model was compared to the simpler model using a likelihood ratio test. Furthermore, all continuous covariates were grand-mean centered to aid in model interpretability. The general form of the final models is as follows, using ecoregions as the level-2 unit:

$$\begin{aligned} \text{Level-1}: Y_{ij} = {} & \beta_{0j} + \beta_{1j}(\text{summer}) + \beta_{2j}(\text{fall}) \\ & + \beta_{3j}(\text{winter}) \\ & + \sum_{q=1}^{Q} \beta_{qj} X_{qij} + r_{ij} \end{aligned} \tag{5}$$

where summer, fall, and winter are dummy variables for sampling season (spring is the reference category) and Q is the number of level-1 covariates. If X_{qij} was a continuous variable, it was grand mean centered by subtracting it from the grand mean of all observations $\left(X_{qij} - X_{Q..}\right)$.

$$\begin{aligned} \text{Level}-2: \ \beta_{0j} = {} & \gamma_{00} + \sum_{s=1}^{S} \gamma_{0s} \mathrm{W}_{sj} + \mathrm{u}_{0j}, \beta_{1j} \\ & = \gamma_{10}, \ldots \beta_{qj} = \gamma_{q0} \end{aligned} \tag{6}$$

where γ_{0s} is the effect of ecoregion-level covariates (W_{sj}) on the adjusted mean (β_{0j}) after controlling for season of sampling and any differences among lakes due to X_1 ... X_Q. Thus, the level-1 model models mean length at age as a function of lake-level covariates and the level-2 model models the average mean length at age of each ecoregion as a function of ecoregion-level covariates. For example, if the significant variation in mean length at age occurred among ecoregions, then ecoregion attributes (e.g., ecoregion average lake total phosphorus) were used to try to explain that variation. The unconditional model [Equations (1) and (2)] and the two-level model described above [Equations (5) and (6)] were also used for the watershed analyses. However, because the analysis of within-class variation was restricted to ecoregion analyses, Equation (5) only included the covariates to control for season of sampling (i.e., we were interested in determining which watershed-level covariates could explain between-watershed variability in mean length at age after controlling for season of sampling at level-1). After the final model was selected, homogeneity of variance was assessed by examining scatter plots of the residuals against predicted values and histograms of the residuals. All analyses were performed using the SAS MIXED procedure (SAS Institute Inc., 2000).

3 Results

3.1 Explaining between-ecoregion/watershed variation

Mean length at age for all species varied considerably (Figure 2). For all ecoregion analyses, between-ecoregion variance estimates in mean length at age were not significant (Table III). For those analyses where the between-ecoregion variability was not estimated as zero, the intraclass correlation coefficients ranged from 0.04%–8.4%, with most <2% (Table III). Because the between-ecoregion variance estimates were nonsignificant, all models were unconditional at level-2. For the watershed analyses, there were significant between-watershed variance estimates for ages 2 and 3 northern pike and age-2 yellow perch; however, the total variation between watersheds was small, ranging from 1.8%–3.7% of the total variance (Table IV). Therefore, conditional level-2 models were constructed for these three datasets to determine which watershed-level attributes could explain between-watershed variance in mean length at age. All other between-watershed variance estimates were nonsignificant (Table IV).

Watershed average chlorophyll *a* explained all of the variance between watersheds for ages 2 and 3 northern pike (Table V). Contrary to our predictions, for age-2 and age-3 northern pike, as watershed average lake chlorophyll *a* increased, watershed average mean length at age decreased. No watershed-level covariates were significant for predicting between-watershed variance in age-2 yellow perch mean length at age.

3.2 Explaining within-ecoregion variation

After controlling for the effects of sampling season, water quality and landscape covariates explained between 2%–23% of the variability in mean length at age within ecoregions (Table VI). However, we were unable to explain any variation in mean length at age for age-2 largemouth and smallmouth bass and age-3 walleye. The estimated intercepts can be interpreted as the mean length at age for fish sampled in the spring from a lake with characteristics equal to the grand mean of the significant covariates. For example, the $\widehat{\gamma}_{00}$ estimate for age-2 northern pike is 466 mm. This is the estimated mean length at age-2 for northern pike sampled in the spring from a lake with total nitrogen equal to 577 μg l^{-1}, water color of 13.7 platinum–cobalt units, and a mean depth and lake area of 4.6 m and 404.6 ha, respectively (values from Table II).

3.3 Consumption

We hypothesized that fish mean length at age would increase with measures of lake productivity and shoreline complexity, and would be highest in large, shallow lakes, and lowest in isolated seepage lakes. Consistent with our initial hypothesis, mean length at age increased with increasing lake productivity (e.g., total nitrogen, total phosphorus, Chl *a*); significant, positive relationships existed for age-2 and 3 bluegill, age-3 smallmouth bass, age-2 yellow perch, and ages-2 and 3 northern pike (Table VI).

Lake area and mean depth were significant for several species; however, the sign of the coefficient varied among analyses. When lake area was significant, mean length at age generally increased with increasing lake area (e.g., for age-2 pumpkinseed, ages-2 and 3 northern pike). However, mean length at age decreased with increasing lake area for age-2 bluegill. Also consistent with our hypotheses, mean length at age for ages-2 and 3 pumpkinseed decreased with increasing mean depth. However, mean length at age for age-2 northern pike increased with increasing mean depth. Shoreline development factor was only significant in one analysis (age-2 yellow perch), with mean length at age decreasing with increasing shoreline complexity. A lake's hydrologic position was not significant in predicting mean length at age for any analysis.

3.4 Metabolic costs

We hypothesized that direct and indirect effects of temperature would be a primary influence on metabolic processes and subsequently on growth. We specifically hypothesized that mean length at age would be positively correlated with GDD and negatively correlated with mean depth due to a larger volume of cooler water and a potentially shorter growing season in deep lakes. Contrary to our predictions, GDD was negatively correlated with mean

Table II List of water quality and landscape covariates used in the analyses

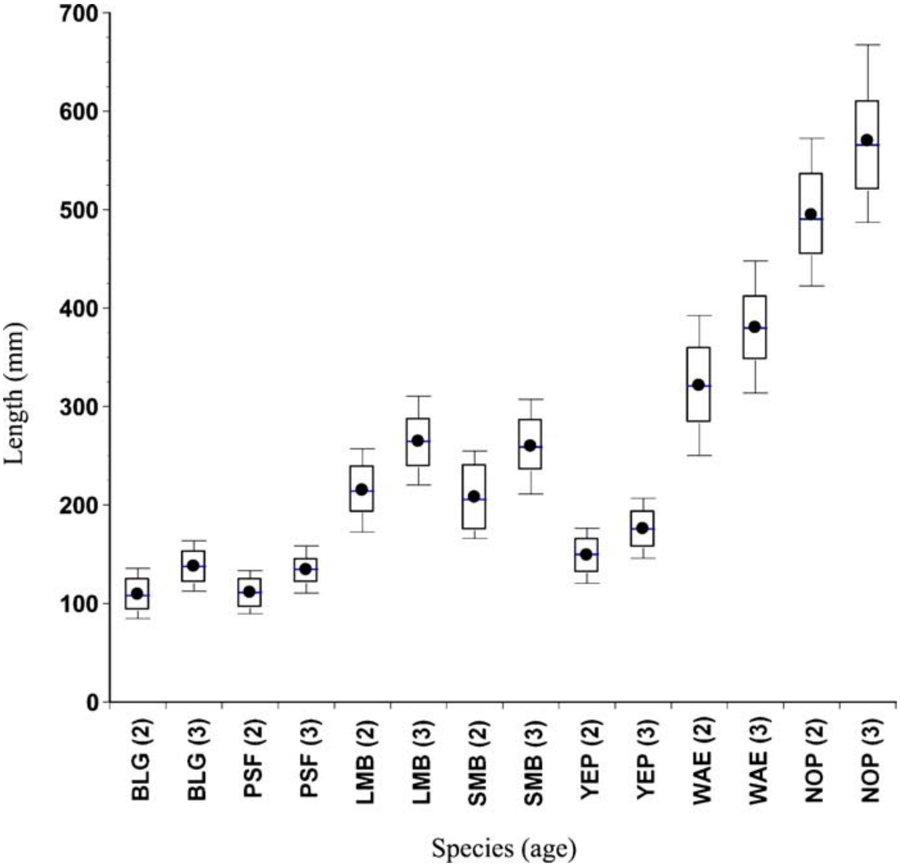
Species (age)	Secchi depth (m)	Color[a] (platinum-cobalt units)	Total nitrogen[a] (μg l^{-1})	Total phosphorus[a] (μg l^{-1})	Chlorophyll *a*[a] (μg l^{-1})	Alkalinity (mg l^{-1} as CaCO3)	GDD[a]	SDF[a]	Mean depth[a] (m)	Lake area[a] (ha)
Bluegill (2)	2.9 (0.5–7.3)	12.0 (1.0–54.0)	644.7 (112.0–2,756)	20.1 (1.0–155.0)	6.3 (0.5–66.0)	105.9 (4.0–197.0)	2,344 (1,451–3,121)	2.2 (1.0–6.3)	4.8 (1.2–18.0)	210.7 (20.9–6,988)
Bluegill (3)	3.0 (0.5–7.3)	11.8 (1.0–54.0)	640.3 (112.0–2,756)	21.1 (1.0–155.0)	6.4 (0.2–66.0)	103.5 (2.0–66.0)	2,354 (1,451–3,121)	2.2 (1.0–6.3)	4.7 (0.9–18.0)	243.4 (20.8–6,988)
Pumpkinseed (2)	2.8 (0.5–7.3)	13.8 (2.0–61.0)	611.4 (112.0–2,756)	21.2 (1.0–155.0)	6.5 (0.7–35.0)	89.6 (4.0–190.0)	2,105 (1,416–2,891)	2.2 (1.1–4.7)	4.4 (1.2–18.0)	270.6 (20.8–6,988)
Pumpkinseed (3)	2.9 (0.5–7.3)	13.2 (1.0–61.0)	592.3 (112.0–2,756)	19.9 (1.0–155.0)	5.8 (0.2–35.0)	88.5 (1.0–190.0)	2,122 (1,416–2,902)	2.2 (1.1–6.5)	4.4 (1.2–18.0)	321.6 (20.8–1,988)
Largemouth bass (2)	3.0 (0.5–7.8)	11.5 (1.0–75.0)	645.3 (112.0–1,717)	19.7 (1.0–155.0)	6.4 (0.5–66.0)	109.8 (1.0–197.0)	2,413 (1,539–3,121)	2.2 (1.1–6.3)	4.7 (1.2–11.6)	188.2 (20.8–3,545)
Largemouth bass (3)	3.0 (0.5–7.0)	11.7 (1.0–75.0)	650.0 (130.0–2,756)	21.0 (1.0–155.0)	6.6 (0.5–66.0)	107.5 (1.0–197.0)	2,390 (1,539–3,121)	2.2 (1.1–6.3)	4.6 (1.2–11.6)	183.4 (20.8–1,848)
Smallmouth bass (2)	3.4 (0.9–7.3)	11.4 (1.0–80.0)	439.2 (92.0–850)	14.1 (10–73.0)	4.3 (0.2–32.0)	86.3 (2.0–166.0)	1,919 (1,488–2,747)	2.1 (1.1–5.4)	5.7 (1.5–20.4)	619.6 (31.7–7,039)
Smallmouth bass (3)	3.5 (0.6–7.3)	13.0 (1.0–80.0)	454.8 (92.0–1,130)	17.0 (1.0–118.0)	5.3 (0.2–60.0)	85.3 (2.0–166.0)	1,971 (1,500–2,747)	2.2 (1.1–5.4)	6.4 (1.5–42.4)	668.6 (31.7–7,576)
Yellow perch (2)	3.1 (0.6–7.8)	12.7 (1.0–80.0)	572.0 (112.0–1,430)	18.5 (1.0–127.0)	6.3 (0.5–66.0)	97.9 (2.0–186.0)	2,197 (1,416–3,121)	2.1 (1.0–6.5)	5.3 (1.2–42.4)	373.9 (20.8–7,576)
Yellow perch (3)	3.1 (0.5–7.8)	12.6 (1.0–80.0)	579.1 (111.0–2,756)	19.4 (1.0–155.0)	6.1 (0.5–66.0)	98.1 (1.0–190.0)	2,184 (1,451–3,121)	2.2 (1.0–6.45)	5.3 (1.2–42.4)	370.0 (20.8–7,576)
Walleye (2)	3.1 (0.6–7.3)	14.3 (1.0–80.0)	484.5 (112.0–1,406)	21.0 (2.0–118.0)	7.3 (0.2–60.0)	93.2 (2.0–197.0)	1,937 (1,451–2,820)	2.2 (1.2–4.7)	5.3 (1.5–18.0)	786.8 (30.0–7,039)
Walleye (3)	2.9 (0.6–7.3)	15.3 (1.0–80.0)	515.7 (112.0–1,406)	22.0 (2.0–118.0)	8.2 (0.2–60.0)	83.2 (2.0–197.0)	1,897 (1,451–2,670)	2.1 (1.1–5.4)	4.7 (1.5–12.8)	662.5 (31.7–7,039)
Northern pike (2)	2.8 (0.5–5.8)	13.7 (1.7–80.0)	577.1 (130.0–2,756)	21.1 (1.0–127.0)	7.4 (0.5–66.0)	94.7 (1.0–197.0)	2,123 (1,416–3,121)	2.1 (1.1–6.5)	4.6 (1.5–18.0)	404.6 (20.8–7,039)
Northern pike (3)	2.9 (0.5–7.0)	12.9 (1.0–80.0)	570.6 (130.0–2,756)	21.0 (1.0–127.0)	6.6 (0.5–60.0)	96.1 (1.0–197.0)	2,139 (1,451–3,121)	2.2 (1.1–6.5)	4.8 (1.2–18.0)	396.4 (20.9–7,039)

[a] Variables were log-transformed prior to analyses to accommodate the assumptions of normality and homogeneity of variance.

Means for each species/age combination are followed by ranges in parentheses.

SDF Shoreline development factor, *GDD* growing degree days (see Section 2 for description).

Figure 2 Mean length at age box and whisker plots for ages 2 and 3 of three warmwater species: bluegill (*BLG*), pumpkinseed (*PSF*), largemouth bass (*LMB*), and four coolwater species: smallmouth bass (*SMB*), yellow perch (*YEP*), walleye (*WAE*), and northern pike (*NOP*) for all seasons combined. The lowest, second lowest, middle, second highest, and highest box points represent the 10th, 25th, median, 75th, and 90th percentiles, respectively. The mean is shown as a *circle*.



length at age for age-2 bluegill and age-3 pumpkinseed. However, mean length at age for age-3 yellow perch was positively correlated with GDD. Our hypothesis with regards to mean depth was supported in two of the three analyses (age-2 and 3 pumpkinseed) in which mean depth was a significant covariate (see above, Table VI).

4 Discussion

4.1 Explaining between-ecoregion/watershed variation

Variance in mean length at age between ecoregion sections for all species was not significant, while between-watershed variance estimates were only significant in three analyses. These results indicate that ecoregions and HUC8 watersheds were ineffective in partitioning variability in mean length at age. Other geographic grouping factors should be investigated to determine their effectiveness in classifying lakes based on demographic data.

Although it is difficult to hypothesize causal mechanisms for the unexpected significant negative relationship between watershed average chlorophyll *a* and watershed average age-2 and 3 northern pike mean length at age, it is likely due to the spatial distribution of this covariate in the landscape (i.e., spatial autocorrelation). For example, watersheds with higher average lake chlorophyll *a* levels are located in the southern portion of the Lower Peninsula of Michigan, while watershed averages for chlorophyll *a* are lower in the northern Lower and Upper Peninsulas. This suggests that on average, watersheds in the northern Lower Peninsula and Upper Peninsula of Michigan have larger mean length at age-2 and 3 northern pike as compared to the southern part of the state. Therefore, the watershed groupings may be identifying a latitudinal gradient in pike mean length at age. The actual mechanism behind this relationship cannot be determined; however, other unmeasured variables that potentially vary from south to north could be responsible, such as fish density. Nonsignificant between-watershed variance estimates for other

Table III Fixed effects and variance estimates for ecoregion unconditional models

Species (age)	$\widehat{\gamma}_{00}$ (95% Confidence interval)	$\widehat{\sigma}^2$	$\widehat{\tau}_{00}$[a]	$\widehat{\rho}$[b]
Bluegill (2)	108.7 (105.7, 111.7)*	5,820*	0.0	NA
Bluegill (3)	136.0 (132.5, 139.5)*	6,596*	2.3	0.04
Pumpkinseed (2)	111.6 (107.2, 116.0)*	2,748*	3.4	0.12
Pumpkinseed (3)	135.6 (130.0, 141.2)*	2,947*	19.4	0.65
Largemouth bass (2)	214.1 (208.9, 219.3)*	12,014*	0.0	NA
Largemouth bass (3)	260.1 (242.3, 277.9)*	9,939*	204.6	2.02
Smallmouth bass (2)	203.8 (190.9, 216.7)*	9,898*	89.1	0.89
Smallmouth bass (3)	245.4 (218.7, 272.1)*	7,175*	659.5	8.42
Yellow perch (2)	154.0 (145.1, 162.9)*	7,108*	64.1	0.89
Yellow perch (3)	171.4 (162.2, 180.6)*	5,182*	72.5	1.38
Walleye (2)	330.3 (318.9, 341.6)*	22,765*	0.0	NA
Walleye (3)	379.9 (354.4, 405.4)*	32,326*	402.3	1.23
Northern pike (2)	480.9 (455.2, 506.6)*	37,108*	483.3	1.28
Northern pike (3)	545.3 (505.8, 584.8)*	34,098*	1,377	3.88

NA Not available.

* Variance estimate significantly different from zero ($P<0.05$).

[a] $\widehat{\tau}_{00}$ of zero represents variance estimates of near zero.

[b] Intraclass correlation coefficient was not calculated when $\widehat{\tau}_{00}$ was estimated near zero.

$\widehat{\gamma}_{00}$, grand mean of mean length at age for all ecoregions (mm), $\widehat{\sigma}^2$ represents the within-ecoregion variability in mean length at age; $\widehat{\tau}_{00}$ represents the between-ecoregion variability in mean length at age; and $\widehat{\rho}$ is the intraclass correlation coefficient [%, $\widehat{\rho} = \widehat{\tau}_{00}/(\widehat{\tau}_{00} + \widehat{\sigma}^2)$].

species–age combinations are likely partly due to small sample sizes. For example, once all watersheds with less than three lakes were excluded from analysis the sample sizes were often reduced substantially.

The ecoregion analyses suggest that the use of ecoregions as a framework to manage fish populations, especially with respect to mean length at age, is not appropriate. Our watershed analyses also suggest that HUC8 watersheds are of limited use as a spatial framework for classifying lakes based on mean length at age. Although significant between-watershed variance estimates were obtained for three analyses, the proportion of the total variance that was between watersheds was less than 4% in all cases. Van Sickle and Hughes (2000) examined the ability of watersheds to group aquatic vertebrate assemblages in western Oregon streams and concluded that watersheds did have utility for classifying stream vertebrates; however, their ability to classify assemblages was likely due to spatial autocorrelation effects, as was evident in our watershed analysis. Van Sickle and

Table IV Fixed effects and variance estimates for watershed unconditional models

Species (age)	$\widehat{\gamma}_{00}$ (95% Confidence interval)	$\widehat{\sigma}^2$	$\widehat{\tau}_{00}$[a]	$\widehat{\rho}$[b]
Bluegill (2)	110.1 (104.6, 115.5)*	5,890*	57.8	0.97
Bluegill (3)	137.1 (132.9, 141.3)	11,628*	0.0	NA
Pumpkinseed (2)	106.1 (99.1, 113.2)	1,566*	70.9	4.33
Pumpkinseed (3)	134.3 (128.7, 139.8)	2,608*	45.4	1.71
Largemouth bass (2)	215.9 (208.5, 223.4)	14,440*	37.4	0.26
Largemouth bass (3)	266.2 (253.7, 278.7)	27,648*	264.9	0.94
Smallmouth bass (2)	214.6 (196.8, 232.4)	29,264*	0.0	NA
Smallmouth bass (3)	266.5 (246, 287)	35,321*	0.0	NA
Yellow perch (2)	152.9 (144.9, 161.0)*	5,578*	214.6*	3.70
Yellow perch (3)	172.1 (166.1, 178)	8,954*	49.8	0.55
Walleye (2)	318.9 (291.3, 346.6)	19,479*	335.6	1.69
Walleye (3)	395.0 (344, 446.0)	190,944*	0.0	NA
Northern pike (2)	490.4 (470.4, 510.3)*	28,422*	1,046*	3.55
Northern pike (3)	544.8 (526.9, 562.7)*	31,298*	561.6**	1.80

NA Not available.

* Variance estimate significantly different from zero ($P<0.05$).

** $P=0.074$, however after controlling for season of sampling there was significant between-watershed variation to model ($\widehat{\tau}_{00} = 635.48$, $P=0.04$).

[a] $\widehat{\tau}_{00}$ of zero represents variance estimates of near zero.

[b] Intraclass correlation coefficient was not calculated when $\widehat{\tau}_{00}$ was estimated near zero.

$\widehat{\gamma}_{00}$, grand mean of mean length at age for all watersheds (mm), $\widehat{\sigma}^2$ represents the within-watershed variability in mean length at age, $\widehat{\tau}_{00}$ represents the between-watershed variability in mean length at age, and $\widehat{\rho}$ is the intraclass correlation coefficient (%, $\widehat{\rho} = \widehat{\tau}_{00}/(\widehat{\tau}_{00} + \widehat{\sigma}^2)$.

Table V Final multilevel mixed model parameter estimates for the watershed analysis

Species (age)	Coefficient	df	*t*-value	*P*-value	Between-watershed variance explained (%)
Northern pike (2)					100*
Intercept	456.8	17	48.11	<0.0001	
Summer	25.5	89	1.97	0.052	
Fall	45.6	89	3.31	0.001	
Winter	73.0	89	4.31	<0.0001	
Chlorophyll *a*	−7.8	89	−2.55	0.013	
Northern pike (3)					100^*
Intercept	508.9	17	62.46	<0.0001	
Summer	42.3	91	3.28	0.0015	
Fall	51.9	91	4.04	0.0001	
Winter	80.1	91	3.90	0.0002	
Chlorophyll *a*	−10.1	91	−3.86	0.0002	

*Variance estimates were not significantly different from zero ($P > 0.05$).

Summer, fall, and winter are dummy variables for sampling season (reference category is spring). No significant between-watershed variance remained in either northern pike models after watershed average chlorophyll *a* was included in the models.

Hughes also concluded that geographic classifications can be expected to account for only a small portion of the total variance in stream vertebrate communities, which is in agreement with our results regarding fish mean length at age data.

Studies that have evaluated the ecoregion framework using lake ecosystems have been equivocal to date. Jenerette et al. (2002) concluded that ecoregions were relatively ineffective at minimizing variability in lake water quality in the northeast United States. In contrast, Johnson (2000) found that ecoregions performed relatively well when discriminating between measures of species richness and diversity in littoral macroinvertebrate assemblages in Swedish lakes. The ecoregions used in the study by Johnson spanned a larger geographic region, from arctic-alpine to nemoral regions characterized by deciduous forests, compared to those used by Jennerette et al. and those used in our study. This broad geographic range likely contributed to the differences found in invertebrate assemblages. In fact, most differences occurred between the ecotone that delineated northern and southern forests types (Johnson, 2000). It could be argued that if our analysis were performed using a landmass equal in size and geographic diversity to that used by Johnson, we would detect significant between-ecoregion and between-watershed variability due to large differences in growing conditions over such a broad geographical area. At smaller scales, however, such as the state-level, ecoregions and HUC8 watersheds are of limited use in partitioning variance in fish mean length at age.

The poor performance of ecoregions in our study is partly due to the fact that each ecoregion is composed of a relatively large land area relative to the entire study area of Michigan. Therefore, even though an ecoregion is defined as a relatively homogenous landscape, in our case there was still substantial variability in growing degree days, geology, soils, etc. within ecoregions, which may have contributed to the relatively large amount of variability within ecoregions in fish mean length at age. Watersheds were of a smaller area as compared to ecoregions; however, they were also relatively ineffective at grouping similar lakes, further demonstrating the need to better understand sources of variability in fish growth. Another contributing factor to large within-ecoregion and within-watershed variability is the alteration of these lake ecosystems by anthropogenic disturbances and activities that may have removed any or a substantial amount of spatial patterns in fish growth rates that may have previously existed (McCormick, Peck, & Larsen, 2000). Given this large amount of variability within these classification systems, future research should focus on alternative ways to classify lakes, perhaps at a smaller spatial scale or by using different grouping criteria, in order to group ecologically similar lakes for management and conservation purposes.

4.2 Explaining within-ecoregion variability

We explained 2%–23% of the variability in mean length at age within ecoregions using lake morphometry and water quality variables. This amount of

Table VI Final multilevel mixed model parameter estimates for the ecoregion analysis

Species (age)	Coefficient	df	*t*-value	*P*-value	Total variance explained (%)	Variance explained after controlling for season (%)
Bluegill (2)						
Intercept	107.2	3	30.0	<0.0001	37	14
Summer	−8.1	154	−1.89	0.06		
Fall	10.0	154	2.03	0.044		
Winter	12.5	154	3.01	0.003		
TP	6.6	154	2.98	0.003		
Lake area	−3.1	154	−1.97	0.050		
GDD	−22.5	154	−2.98	0.003		
Bluegill (3)						
Intercept	135.3	3	25.64	0.0001	11	2
Summer	−3.0	180	−0.77	0.44		
Fall	9.1	180	2.17	0.032		
Winter	10.5	180	2.61	0.010		
TN	7.7	180	1.99	0.048		
Pumpkinseed (2)						
Intercept	116.2	3	22.13	<0.001	39	18
Summer	0.7	82	0.15	0.88		
Fall	14.3	82	3.18	0.002		
Winter	33.5	82	4.78	<0.0001		
Mean depth	−11.1	82	−2.70	0.009		
Lake area	5.5	82	3.70	0.0004		
Pumpkinseed (3)						
Intercept	134.9	3	26.28	0.0001	27	9
Summer	−8.88	111	−2.22	0.028		
Fall	3.1	111	0.80	0.42		
Winter	8.3	111	1.00	0.32		
Mean depth	−8.0	111	−2.78	0.006		
GDD	−37.7	111	−2.43	0.017		
Largemouth bass (2)	NS					
Largemouth bass (3)						
Intercept	250.8	3	22.31	0.0002	9	4
Summer	7.9	158	1.25	0.21		
Fall	14.1	158	1.65	0.10		
Winter	22.7	158	3.38	0.009		
Color	10.5	158	2.84	0.005		
Smallmouth bass (2)	NS					
Smallmouth bass (3)						
Intercept	224.6	3	15.47	0.0006	26	6
Summer	13.1	53	1.23	0.22		
Fall	41.2	53	3.72	0.005		
Winter	33.7	53	2.31	0.025		
Chla	9.8	53	2.03	0.048		
Yellow perch (2)						
Intercept	136.5	3	19.55	0.0003	18	5
Summer	15.7	175	2.89	0.004		
Fall	23.5	175	3.91	0.0001		
Winter	30.7	175	5.07	<0.0001		
TN	9.5	175	2.08	0.039		
SDF	−13.3	175	−2.91	0.004		

Table VI (Continued)

Species (age)	Coefficient	df	*t*-value	*P*-value	Total variance explained (%)	Variance explained after controlling for season (%)
Yellow perch (3)						
Intercept	164.5	3	36.18	<0.0001	19	6
Summer	5.8	179	1.41	0.16		
Fall	10.8	179	2.21	0.028		
Winter	20.0	179	4.14	<0.0001		
GDD	30.9	179	2.35	0.019		
Walleye (2)						
Intercept	317.7	3	27.33	0.0001	17	7
Summer	−0.6	48	−0.04	0.97		
Fall	32.6	48	1.24	0.22		
Winter	30.5	48	2.00	0.052		
Alkalinity	−0.3	48	−2.15	0.037		
Walleye (3)	NS					
Northern pike (2)						
Intercept	466.5	3	56.56	<0.0001	35	23
Summer	6.7	124	0.62	0.54		
Fall	43.0	124	3.26	0.001		
Winter	67.1	124	4.49	<0.0001		
TN	56.6	124	5.03	<0.0001		
Color	−16.0	124	−2.28	0.025		
Mean depth	21.1	124	2.42	0.017		
Lake area	16.4	124	4.43	<0.0001		
Northern pike (3)						
Intercept	512.5	3	26.58	0.0001	12	6
Summer	36.9	128	2.83	0.005		
Fall	32.3	128	2.36	0.020		
Winter	68.1	128	3.30	0.001		
Lake area	11.8	128	2.58	0.011		
TN	34.2	128	2.50	0.013		

Summer, fall, and winter are dummy variables for sampling season (reference category is spring).

TN total nitrogen, *TP* total phosphorus, *Chla* chlorophyll *a*, *GDD* growing degree days, *SDF* shoreline development factor, *NS* no significant covariates.

variation lies within the range found in other studies. For example, Tomcko and Pierce (2001) were able to explain 16%–33% of the variation in bluegill growth using lake morphometry and water quality variables in Minnesota lakes.

5 Consumption

In 6 of 14 analyses, mean length at age was positively associated with measures of lake nutrient status. Tomcko and Pierce (2001) also found bluegill length at ages one to six be positively correlated with lake productivity. Greene and Maceina (2000) found the growth of age-zero largemouth bass was faster in eutrophic as compared to less productive reservoirs in Alabama. Although causal mechanisms cannot be identified from these studies, these patterns are likely due to higher prey abundance or production in more productive systems.

Morphometric characteristics were important for predicting mean length at age for several species. The relationship between mean length at age and lake area and depth for age-2 pumpkinseed was consistent with our hypothesis that mean length at age would be highest in large, shallow lakes. This species spends a majority of its time in nearshore waters, using these areas for foraging on littoral prey such as gastropods

(Huckins, 1997). Therefore, a potential mechanism for this relationship is with increasing mean depth, pumpkinseeds experience a decrease in the amount of foraging habitat, resulting in slower growth rates in deeper lakes. Mean length at age for age-3 pumpkinseed also showed a negative relationship with mean depth; however, lake area was not a significant covariate. Contrary to our predictions, mean length at age for age-2 yellow perch was negatively associated with SDF. It is unclear what mechanism is responsible for this relationship.

Northern pike length at ages-2 and 3 was positively related to lake area. Contrary to our initial hypothesis, mean length at age for age-2 northern pike also was positively related to mean depth. As northern pike grow, their depth preference changes, with older fish utilizing deeper water and larger individuals using a wider range of depths compared to smaller individuals (Casselman & Lewis, 1996). Therefore, large lakes and lakes with a variety of depth habitats may provide conditions conducive to faster growth.

5.1 Metabolic costs

Contrary to our predictions, mean length at age was negatively related to GDD for age-2 bluegill and age-3 pumpkinseed. The reasons for these negative relationships are unknown. However, because GDD was only significant in three models (positively associated with mean length at age-3 yellow perch) it may indicate that the GDD data did not accurately represent the thermal conditions experienced by the fish populations. The GDD data used in these analyses were a 30-year average and because annual temperature variability can be high, this long-term average may have attenuated any affect of temperature on fish growth rates.

Also consistent with our initial hypothesis, a large amount of within-ecoregion variability in mean length at age was unaccounted for by water quality and morphometric characteristics. Other factors such as fish density and exploitation, which can greatly influence growth of fishes, were unaccounted for in this analysis and may prove useful in predicting fish growth rates in future studies. For example, Drake, Claussen, Philipp, and Pereira (1997) found higher growth of brood-guarding bluegill in lakes with low angling effort as compared to lakes with higher angling effort. Pierce, Tomcko, and Margenau (2003) found that northern pike density explained 36%–57% of the variation in mean back-calculated lengths at ages 2 to five for northern pike populations in north-central Minnesota lakes. This suggests that classifying lakes based on demographic characteristics may be more difficult compared to classifying lakes based on species assemblages or water quality variables, especially when using landscape characteristics to build the classification scheme. For example, variance in lake water chemistry variables was partitioned for Michigan inland lakes using HUC8 watersheds, with significant among-watershed variance estimates ranging from 6% to 67% of the total variance. Landscape features were then able to explain significant variation in water quality variables at both the local and watershed scales (Cheruvelil, 2004). Furthermore, the classification of waterbodies should be based on multiple demographic characteristics; however, this will not be possible until such data are routinely collected and become widely available. The identification of lakes with similar demographic properties would facilitate regional management of aquatic populations.

5.2 Study limitations

Although we can learn much from the results in our study, there are some limitations due to the use of existing historic data. For example, the lack of standardized sampling protocols and often incomplete or summary records limited the scope of our analyses and clouded the interpretation of our results. The mean length at age data were collected over a 10 year period, which allowed us to expand the spatial scale of our analyses, but also added temporal variability to our analyses. To determine if temporal trends influenced our findings, we ran the models with sampling year as a covariate. The parameter estimates for sampling year were rarely significant and when they were, they did not account for much additional variability, nor did they change the results presented here. Also, the clear identification of mechanisms and processes responsible for the observed patterns is not possible in our study (Peters et al., 1991). Given these limitations, however, we were still able to account for significant within-ecoregion variation in mean length at age using lake morphometry and water quality characteristics in 11 out of 14 analyses, suggesting that the use of data collected from a statistically valid sampling program

(Hayes et al., 2003) will likely provide further insight into the effects of lake morphometry and water quality on fish growth. Although there are limitations to the use of historic data, this approach also has advantages. For example, the ability to examine patterns at such a large spatial scale would likely not be possible otherwise. This approach is also useful in generating new hypotheses and prioritizing research questions to address in future research (Peters et al., 1991).

5.3 Conclusions

We determined that local lake characteristics can explain a significant amount of variation in mean length at age; however, the relative importance of abiotic factors *versus* biotic interactions remains unclear. A better understanding of the importance of abiotic and biotic factors and how they affect fish populations is needed if the classification of lakes based on demographic properties is going to be successfully implemented for regional aquatic conservation and management. The relative importance of these factors in affecting demographic properties of aquatic communities is species- and scale-dependent. Therefore, it will be necessary for management agencies to have well defined goals with respect to the target species and the spatial scale of management prior to the development of a classification system. Furthermore, for regional management to be effective, agencies must design and implement statistically valid sampling programs with standardized sampling protocols (Hayes et al., 2003). Our analysis also demonstrates that ecoregions or watersheds (i.e., HUs), are not effective in grouping lakes with similar fish growth rates.

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