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DEVELOPING DECISION TOOLS FOR INLAND LAKE MANAGEMENT THROUGH FIELD SAMPLING AND STATISTICAL MODELS

BY

TYLER WAGNER

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ABSTRACT

DEVELOPING DECISION TOOLS FOR INLAND LAKE MANAGEMENT THROUGH FIELD SAMPLING AND STATISTICAL MODELS

BY

Tyler Wagner

My research encompasses several aspects of fisheries management, ranging from the use of historical databases to help guide monitoring programs to a field study examining the effects of natural and anthropogenic factors on largemouth bass nest success. A common feature of my research is the use of mixed models and generalized linear mixed models to partition variance in ecological response variables and to account for hierarchical data structures. Because the use of mixed models is not commonly employed in fisheries research, where hierarchical data structures are common, my first chapter is an instructional paper on the advantages of using mixed models versus general linear models and how to implement mixed model analyses in a common statistical package, SAS. My other chapters use mixed models to address specific questions and hypotheses. For my second chapter, the specific research question was: are the ecoregion and watershed frameworks for lake classification useful approaches for grouping lakes with regards to fish growth rates (i.e., can mean fish length at age be partitioned by ecoregions and watersheds)? For the ecoregions analysis, I also examined if within-ecoregion variability could be explained by local water quality and lake morphometry characteristics. 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, indicating that ecoregions and watersheds were ineffective in partitioning variability in mean length at age. The results suggest that managers should not rely solely on ecoregions or watersheds for grouping lakes with similar growth rates. For my third chapter, I examined if habitat alteration and spring angling could explain variability in largemouth bass nest success. In 2004, we monitored nest distribution and success and quantified local nest habitat features, lakewide angler effort, and lakeshore development in five Michigan lakes to determine the extent to which habitat alteration and/or fishing limit the number of successful nests. Surprisingly, local habitat characteristics were not important determinants of the probability of a nest producing swim-up fry ($P > 0.05$). At the whole-lake scale, however, nest success was negatively related to dwelling density, with the probability of a nest producing swim-up fry declining from 0.77 in the lowest dwelling density lake to 0.45 in the highest dwelling density lake ($P = 0.018$). These results demonstrate that knowledge of the magnitude of anthropogenic effects and the spatial scale at which they operate is integral for black bass management. For my fourth chapter I examined statewide trends, and the statistical power to detect trends, in mean length at age for seven fish species in Michigan and Wisconsin inland lakes. Of the 42 datasets examined, only four demonstrated significant regional trends. The structure of variation differed substantially among datasets and these differences had a strong effect on the power to detect trends. To maximize trend detection capabilities, fisheries management agencies should consider variance structures prior to choosing indices for monitoring and realize that trend detection capabilities are species-specific. Through the use of historical data analysis, field sampling, statistical modeling, my research informs monitoring efforts, quantifies anthropogenic effects on an important demographic parameter for largemouth bass, and helps understand the underlying variation among lakes.

DEDICATION

I dedicate this dissertation to my parents, Gordon and Sandy Wagner.

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PREFACE

Chapter 1 is in press in the American Fisheries Society journal Fisheries as:

Wagner, T., Hayes, D. B., and Bremigan, M. T. In Press. Accounting for multilevel data structures in fisheries data using mixed models.

Chapter 2 has been submitted for publication in the journal Environmental Monitoring and Assessment and is currently under review as:

Wagner, T., Bremigan, M. T., Spence Cheruvelil, K., Soranno, P. A., Nate, N. A., and Breck, J. E. A multilevel modeling approach to assessing regional and local landscape features for lake classification and assessment of fish growth rates.

Chapter 3 is in press in the journal Transactions of the American Fisheries Society as:

Wagner, T. Jubar, A. K., and Bremigan, M. T. Can habitat alteration and spring angling explain largemouth bass nest success?

Chapter 4 will be submitted for publication to the Canadian Journal of Fisheries and Aquatic Sciences as:

Wagner, T., Bence, J. R., Bremigan, M. T., Hayes, D. B., and Wilberg, M. J. Regional trends in fish mean length at age: components of variance and the power to detect trends.

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INTRODUCTION

Freshwater ecosystems and inland lake ecosystems in particular, are important and valued resources, providing services that are essential for the sustainability of both aquatic and terrestrial life. These services include the direct use of water and aquatic organisms by humans and other ecosystem services, including nutrient cycling and enhanced biological production (Lubchenco 1998). Over the foreseeable future there will be an increasing demand on this finite resource due to increasing global population growth. For example, the global human population is estimated to be growing at a rate of 1.2% per year, resulting in an increase of 80 million people annually (PRB 2005). Also, the uncertain effects of global climate change and its interactions with human population growth on aquatic ecosystems (Vörösmarty et al. 2000), further demonstrate the need for sustainable management of freshwater ecosystems. The sustainable management of freshwater ecosystems includes ensuring that they are functionally intact and biologically diverse. Maintenance of the structure and function of aquatic ecosystems is necessary not only to retain the integrity and diversity of natural ecosystems, but also to ensure that humans benefit from these systems well into the future (Baron et al. 2002).

Sustainable management of inland lake ecosystems requires an understanding of how factors, both natural and anthropogenic, affect the structure and/or function of these ecosystems. Implicit in this understanding is the need to identify the role of scale, both spatial and temporal, in identifying the most important controlling factors of variables and processes of interest, such as water clarity and fish production. Because lakes are strongly linked to terrestrial environments, this also means that studying lakes within a landscape context is critical to identifying factors that affect lake structure and function. Therefore, in my research I use a multiple spatial scale approach to identifying important drivers of in-lake processes and I examine the temporal dynamics of lake systems while estimating the magnitude of several spatial and temporal sources of variation. Collectively, this research provides insight into the sustainable management of inland lake ecosystems, with an emphasis on the design of monitoring programs, which is an essential component of aquatic resource management.

Research questions.-Through the use of historical data, statistical and simulation modeling, and field sampling, my research addresses the following questions and challenges faced by ecologists. (1) How do we account for the spatial structure/hierarchy inherent in ecological data? (2) How do we monitor and manage many aquatic systems over large geographic regions? (3) How can we quantify the effects of anthropogenic and natural features, at multiple spatial scales, that affect within-lake processes?

Synthesis and applications

The hierarchical structure of ecological data (e.g., a hierarchical data structure may consist of measurements taken on individual fish (lower level) that are nested within lakes or streams (higher level)) along with inherently high variability makes studying and managing aquatic ecosystems difficult. With methodological advancements and advances in computing over the past several decades, we are better able to meet these analytical challenges. For example, statistical methods (e.g., mixed effect models) can assist with the management of aquatic systems by allowing for the analysis of patterns across spatial and temporal scales. Thus I use mixed models extensively in my dissertation research.

To address question 1, I explain how multilevel models (i.e., mixed models), that account for multilevel (hierarchical) data structures in fisheries data, can be used to test hypotheses, and discuss how the analytical approach (accounting for versus ignoring multilevel data structures) affects hypothesis testing and inferences. To accomplish these goals I provide two examples using simulated data similar in structure to published studies and contrast the findings obtained using mixed models with those obtained using traditional ordinary least squares methods. This paper also provides examples of how to implement the analyses in a commonly used statistical software package. This research will provide fisheries scientists and professionals with an accessible example of how to analyze data using mixed models.

Because environmental policy is developed over broad spatial scales, regional (e.g., statewide) management of aquatic systems is a necessity. A common first step in the development of regional management plans involves dividing the landscape into management units that, ideally, group waterbodies that are ecologically similar. In my second chapter, through the use of historical datasets, I address question 2 by examining how variability in inland lake fish growth rates is partitioned within and between ecoregions and major river watersheds in Michigan. In the United States, these two approaches (ecoregions and watersheds) to regional management dominate how agencies divide land into management units (Brown and Marshall 1996); however, they have yet to be evaluated for fish growth. The goal of this research was to determine if commonly used classification frameworks, ecoregions and major river watersheds, are useful for grouping lakes based on fish growth. The results of this analysis indicate that both ecoregions and watersheds are ineffective at partitioning variability in fish mean length at age and therefore are not useful regionalization frameworks for this metric. Thus, although ecoregions and watersheds have partitioned variability in some stream and lake water quality and aquatic invertebrate diversity metrics, these frameworks need to be further evaluated prior to wide-scale implementation for multiple metrics, especially in lakes.

Also during this analysis, I determined what lake morphometric and water quality characteristics can predict within-ecoregion variability in fish growth rates. The results of this study indicate that relatively little of the total variance in fish mean length at age can be accounted for by lake morphometry and water quality characteristics (accounting for 2 – 23% of the total variance). However, this study provides insight into what variables might be useful in future efforts to develop a lake classification scheme that facilitates monitoring of mean length at age as a monitoring metric.

To further explore issues related to regional lake management, in my fourth chapter, I used historical time series data on fish growth (mean size at age), mixed models, and simulations, to examine regional (statewide) temporal trends of growth for seven fish species in Michigan and Wisconsin inland lakes, quantify the structure of the total variation in the time series, and explore how the variance structure affects the statistical power to detect temporal trends (question 2). This research, along with the research examining the ability of ecoregions and watersheds to partition variability in mean length at age, has implications for the design and implementation of regional ecological monitoring programs for inland lake fisheries. For example, the ability to detect regional (e.g., statewide) temporal trends is crucial for the evaluation of many management actions and to examine responses to natural or anthropogenic perturbations. Furthermore, the early detection of regional changes is important in many cases to allow time for managers and policy-makers to respond and take appropriate action (Vaughan et al. 2001). Through the use of a components of variance analysis (decomposing the total variance into several spatial and temporal components, including (1) lake-to-lake (spatial) variation, (2) coherent (year-to-year) variation affecting all lakes in a similar manner, (3) ephemeral temporal variation (e.g., lake-by-year interaction) corresponding to independent yearly variation at each lake, (4) trend variation where each lake is allowed to have its own trend, and (5) residual variation (variation due to sampling error)), I demonstrate that the partitioning of variance differed substantially among species, ages, and states and that the variance structure greatly influences the power to detect regional temporal trends in mean length at age. For example, the power to detect a trend in age 4 walleye size at age was greatly reduced compared to Michigan age 4 walleye due to the influence of a significant coherent temporal variation component for the Wisconsin data. This illustrates the importance of evaluating metrics for monitoring prior to implementation of the monitoring program.

Both studies examining the regional management of fish mean length at age (dissertation chapters 2 and 4) pose the question of whether or not fish mean length at age is a "good" metric to monitor from a fisheries management perspective. I show that it will likely be difficult to partition variability in mean length at age, especially at the state level, and that the power to detect trends is greatly reduced if coherent temporal variation is present. Fisheries management agencies measure and monitor mean length at age because it is understood that it is important both ecologically and from a management perspective (e.g., Shuter et al. 1998). However, if regional management is the goal, then other potential metrics should be evaluated to determine if a different metric is more informative for fisheries monitoring and management. So, if fish size at age is not a very informative metric, then other aspects of fish population size structures should be considered and evaluated.

How "useful" a metric is, however, depends on the specific management and monitoring objectives. Furthermore, metrics should meet the following requirements (Graedel and Allenby 2002):

1. They must be related to underlying causal relationships within the systems being monitored, and must aggregate as much information as possible into a meaningful composite measure. Metrics should also be easy to understand.
2. They must accurately reflect a trend within an appropriate timescale.
3. They must link to existing management objectives.
4. They must be clear and understandable to the public.

Other metrics, besides fish mean length at age, have been identified for marine fisheries that are simple and easy to understand. These metrics also give insight into population dynamics as well as to the effects of the fishery on the fish population(s). Some of these metrics include, (1) the percentage of mature fish in catch, (2) percent of fish with optimum length in catch (optimum length is often larger than length at first maturity), and (3) percentage of "mega-spawners" in catch (i.e., the percentage of old, large fish in the catch; Froese 2004). Indicator 1 can be described as "let them spawn", indicator 2 as "let them grow", and indicator 3 as "let mega-spawners live" (Froese 2004). These metrics, if they help meet the objectives of an inland lake fisheries management agency, might represent more reliable, useful metrics to monitor over time compared to fish mean length at age. However, because fish growth data can be useful (e.g., Shuter et al. 1998), new metrics could be monitored in conjunction with fish length at age to better inform regional management of inland lake fisheries. I would recommend that alternative metrics, such as those identified by Froese (2004) be evaluated for inland lake monitoring and assessment.

Finally, in my third chapter I examine the importance identifying controlling factors of within lake processes. It is well established that both natural and anthropogenic factors, acting at different spatial scales, can be important in driving lake processes. So, through the use of a multi-lake field study and the application of a generalized linear mixed model, I examine the importance of local nest habitat features and lake-wide features, such as dwelling density and angling effort, in determining largemouth bass nest success (question 3). This research also provides another demonstration of the hierarchical nature of ecological data. In this case, bass nests (lower level) are nested within lakes (higher level), and there are covariates measured at each level.

Largemouth bass are keystone predators and a valued sport fish in North American lakes. They also possess life history characteristics that make them vulnerable to within-lake habitat conditions and perturbations associated with human development of lake shorelines. Because of their ecological and socioeconomic importance and life history characteristics, largemouth bass populations represent an opportunity to quantify the effects of habitat conditions and anthropogenic activities, at multiple spatial scales, on important demographic properties of fishes. Our results indicated that nest success was negatively related to lakeshore dwelling density, with the probability of a nest producing swim-up fry declining from 0.77 in the lowest dwelling density lake to 0.45 in the highest dwelling density lake. Examining covariates at multiple spatial scales (e.g., local nest-level and lake-wide) allowed for the identification of a covariate (i.e., dwelling density) important to nest success that would have been overlooked if a multiple spatial scale approach had not been used. Furthermore, this research is rather new, as most studies examining factors affecting nest success focus on single lakes and ignore the hierarchical nature of the data. This study helps illustrate that knowledge of the magnitude of anthropogenic effects and the spatial scale at which they operate is integral for black bass management.

My dissertation research is an example of combining multiple approaches to address ecological and lake management issues. The use of historical data can provide valuable information to address research questions and to provide information to help guide future management decisions and design statistically powerful monitoring programs. The use of multilevel models provides a useful framework to not only account for hierarchical data structures often encountered in ecology, but also to examine questions that span multiple spatial and temporal scales. The design of statistically powerful monitoring programs, as well as implicitly accounting for the spatial and temporal variation in ecological data, provides researchers and managers with some of the necessary information for the sustainable management of aquatic ecosystems.

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CHAPTER 1: ACCOUNTING FOR MULTILEVEL DATA STRUCTURES IN FISHERIES DATA USING MIXED MODELS

Abstract

Multilevel data structures are those that have a hierarchical structure, in which response variables are measured at the lowest level of the hierarchy and modeled as a function of predictor variables measured at that level and higher levels of the hierarchy. For example, a multilevel data structure may consist of measurements taken on individual fish (lower level) that are nested within lakes or streams (higher level). Multilevel data structures are a common feature in fisheries research. We provide simulated fisheries data examples, similar in structure to other published studies, to illustrate the application of multilevel models and discuss how hypothesis testing and inferences can be incorrect if multilevel data structures are ignored. Ignoring multilevel data structures has implications for the use of commonly-used ordinary least squares (OLS) approaches to test hypotheses and to make inferences. Multilevel models are an alternate approach that circumvents problems associated with traditional OLS methods and allows valid inferences to be made.

Introduction

Aquatic systems are often viewed as being hierarchically organized, with lower levels of organization nested within higher levels (e.g., Frissell et al. 1986; Imhof et al. 1996). For example, a hierarchy may consist of headwater streams nested within subwatersheds that are nested within larger watersheds, or lakes nested within ecoregions. This hierarchical organization provides a conceptual basis for testing hypotheses, often leading to sampling designs that are also hierarchically organized. A common feature of such sampling designs is that the response variable is measured at the lowest level (i.e., finest scale) of the hierarchy and is modeled as a function of predictors measured at that level as well as one or more higher levels. This hierarchical organization leads to multilevel data structures for which traditional methods of statistical inference are often inappropriate (Raudenbush and Bryk 2002).

The fisheries literature is replete with examples of studies that have collected data with a multilevel structure. Despite this prevalence, the hierarchical structure of the data is often ignored during statistical analysis. A fundamental problem with ignoring the multilevel structure during analyses is that observations measured within a higher level (e.g., measurements made within the same stream) are likely to be more similar to each other compared to observations between levels (e.g., measurements made in different streams). Therefore, analyses that ignore the multilevel structure of the data violate a critical assumption to commonly-used analyses, namely the assumption of independence. Although the importance of accounting for the correlation structure of repeated measurements on individuals has received attention in the fisheries literature, especially with respect to laboratory studies and analyzing size-at-age data obtained from scales and otoliths of fishes (e.g., Jones 2000; Schaalje et al. 2002; Pedersen and Malte 2004), multilevel data structures in field settings have been largely ignored.

The goals of this article are (1) to explain how to use multilevel models that account for multilevel data structures in fisheries data to test hypotheses and (2) to discuss how the analytical approach affects hypothesis testing and inferences. To accomplish these goals we provide two examples using simulated data similar in structure to published studies. We illustrate the analysis of these data with a commonly used statistical package, SAS®. The first example uses data with a two-level data structure to emphasize how hypothesis testing and inferences are affected depending on the statistical approach used, while the second example provides a detailed example of how to model data with a three-level data structure.

Example 1: Examining the effects of in-stream barriers on fish density

To introduce a simple multilevel data structure we present the following example. Data were generated to emulate a commonly-used field study design to examine the effects of instream barriers on fish density. The simulated dataset contains sample sites (level 1) nested within streams (level 2; Figure 1). We used these data to test the null hypothesis that fish densities do not differ between sites above and below barriers or between streams with or without barriers. The dataset contains measurements for eight streams: four "treatment" streams that contain instream barriers and four "control" streams that lack instream barriers. For each treatment stream, fish density measurements were generated for three sites below the barrier and three sites above the barrier (or "reference line" for control streams; Figure 1; Table 1). The data were then analyzed two ways—using a general linear model (GLM) and a multilevel model (MIXED) in

Statistical Analysis System (SAS), and using the GLM and MIXED procedures, respectively (Littell et al. 1996; SAS Institute Inc. 2000; Littell et al. 2002). The data were generated to represent a case where mean fish densities were reduced in treatment streams as a whole relative to control streams, and with a greater reduction in sites above the barriers in the treatment streams. In the control streams, mean fish density was similar in sites above and below the reference line.

Contrasting traditional and multilevel models

Traditional approaches – Two ordinary least squares (OLS) approaches are commonly used to analyze multilevel data: an aggregating and a disaggregating approach. For the aggregated approach, observations within each higher level group are combined (analysis is performed at the higher level). For our stream barrier example, aggregation would occur if mean densities were calculated for each stream based on the six sample sites within each stream (Figure 1). When this approach is used, within-group variation is ignored (e.g., within stream), which may be a large proportion of the total variance, resulting in a loss of information and statistical power. For the disaggregated approach, all observations are used, but the higher level grouping factor (e.g., stream) is not factored into the analysis. For our stream barrier example, disaggregation would occur if each measurement of fish density was treated as an independent replicate sample from each stream. This approach is inappropriate however, because the experimental unit is actually the stream, not individual sites, and because the between-group variation is ignored (analysis is performed at the lower level). When this occurs "replicate" samples from a higher level grouping factor are assumed to be independent, which is often an invalid assumption and results in pseudoreplication (Hurlbert 1984). This approach can underestimate standard errors and thus increase the probability of type I errors, i.e., finding a significant difference when one does not actually exist. Furthermore, groups with the largest sample size may dominate the coefficient estimates.

Multilevel models – Multilevel models have received much attention in the past several years, especially in the social and behavioral sciences. Their increase in popularity is partly due to methodological advances and advances in statistical computing over the past several decades. As a result, several excellent references on the theory and application of multilevel models in the social and behavioral sciences are available; we refer readers to these references for more detailed information (e.g., Hox 2002; Raudenbush and Bryk 2002; Duan and Reise 2003).

Multilevel models are represented in the literature under a variety of names including mixed-effects models, hierarchical linear models, random-effects models, and random coefficient regression models. Multilevel models circumvent the problems described above associated with using OLS approaches. For example, multilevel models estimate standard errors correctly and result in improved estimation of fixed effects when multilevel data structures exist. Furthermore, both continuous and categorical variables can be specified to have fixed or random effects. A factor is fixed if it represents all possible levels of a factor for which inferences are to be made. For the instream barrier example, if the streams used in the analysis were the only streams for which inferences were to be made (e.g., if the researchers did not want to generalize their results to other streams) then stream would be specified as a fixed effect. A factor is random if it represents a random sample of a larger set of potential factors. For the instream barrier example, if the study streams represented a sample of streams from a larger population of streams with and without barriers, stream would be specified as a random effect. Another way to illustrate the difference between fixed and random effects was presented by Bennington and Thayne (1994). Their definition is presented in terms of the null hypothesis being tested for each effect. "Consider two effects, A and B, where A is fixed, B is random, and there is an interaction (A × B) possible between them. For a given dependent variable, the null hypothesis concerning A is that there is no difference in means among the levels of A in the experiment. For B, the null hypothesis is that there is no variability among all possible levels of B (including those not sampled), not that there are no differences among levels of that effect included in the experiment. For the interaction term (A × B), the null hypothesis is that variability among levels of B is the same for all levels of A. This differs from the case for fixed effects in that the null hypothesis for an interaction between two fixed effects (A and C) is that the response of the dependent variable is not different among specific levels of A depending upon the particular level of C."

Analysis of Example 1

Ordinary least squares – We first analyzed the simulated stream data assuming all factors are fixed effects (we assumed streams were not randomly selected from a larger population of streams) while ignoring the fact that sites are nested within streams. This is equivalent to using a disaggregated OLS approach, and was performed using the GLM procedure in SAS. An aggregated approach could also be implemented with these data, but for illustration purposes we restrict our analysis and discussion to the disaggregated approach, which is a common approach used in the analysis of fisheries data. Fish density was the response variable and site position (above or below a barrier) and stream type (barrier or no barrier) were fixed effects. The general form of this model is as follows:

$$Y_{ijk} = u + Position_i + Stream\_Type_j + (Position \times Stream\_Type)_{ij} + e_{ijk} \qquad (1)$$

Where Y_{ijk} is the k^{th} measurement on the i^{th} position, in the j^{th} stream, u is the overall mean, $(Position \times Stream\_Type)_{ij}$ is the interaction effect, and errors (e_{ijk}) are assumed independent and $e_{ijk} \sim N(0, \sigma^2)$. An example of the data structure needed for analyzing the dataset in SAS is given in Appendix I. The SAS code for performing the GLM analysis is as follows.

```
PROC GLM DATA = barrier_data;
CLASS stream stream_type position;
MODEL density = stream_type position stream_type*position / SOLUTION;
LSMEANS stream_type position stream_type*position / STDERR PDIFF ADJUST =
tukey;
RUN;
```

For a detailed description of the SAS syntax, see Littell et al. (2002). Briefly, the CLASS statement contains the classification variables (categorical independent variables), the MODEL statement defines the model to be fit, and the SOLUTION option requests the parameter estimates. The LSMEANS statement requests that the least-squares (LS) means be calculated for each classification variable listed in the statement. Least-squares means are within-group means adjusted for other effects in the model and are also known as the population marginal means (Searle 1987). The PDIFF option reports the results of the hypothesis test of the differences between LS means (H_o: LS mean$_i$ = LS mean$_j$). The ADJUST = tukey statement requests a multiple comparison test with adjusted *P*-values and confidence limits for the LS means using the Tukey-Kramer method. This adjustment controls for the overall experiment-wise error rate (e.g., controls for type I error rate). Note that PROC GLM allows for random terms; however, the standard errors from the LSMEANS statement are usually not computed correctly (Littell et al. 1998). The GLM procedure in this example was run with only fixed effects.

The Type III sums of squares tests for the significance of the fixed effects, which account for the other effects in the model, are as follows, stream type $F = 58.31$, $P = <0.0001$, position $F = 1.01$, $P = 0.319$, stream type×position interaction $F = 1.71$, $P = 0.197$. The analysis indicates there is a significant difference in mean fish density between stream types, with barrier streams having significantly lower mean density levels compared to control streams (barrier stream $\overline{X} = 26.8$ fish/m^2, standard error (SE) = 2.92; control stream $\overline{X} = 58.4$ fish/m^2, SE = 2.92). Table 2 contains the LS means and standard error estimates for each stream type and site position. The analysis did not detect any interaction between site position and stream type, although we had simulated an interaction effect in the dataset.

Multilevel model – Because multilevel models have received more attention in the social and behavioral sciences and thus references are not available specifically for the natural sciences, we use symbols consistent with Raudenbush and Bryk (2002) in our description of multilevel models. For this analysis, the dependent variable was the same as in the GLM analysis; however, we took into account the nested structure of the data (sites nested within streams) and analyzed the data using the MIXED procedure in SAS with random effects. Position, above or below the barrier, was the site-level (level 1) predictor and stream type (with or without a barrier) was the stream-level predictor (level 2). Stream was regarded as a random effect. Typically, it is likely that measurements of fish density from the same stream are correlated (i.e., lack statistical independence); one way to model this correlation is by treating each stream as having a random effect. Furthermore, we assumed that streams used in the study represented a random sample of a larger population of streams; therefore, we can generalize our results to other similar systems.

The model can also be viewed in two levels and in a combined form as follows:

Level 1 model: $Y_{ij} = \beta_{0j} + \beta_{1j}(Position) + r_{ij}$ (2)

where Y_{ij} is the density of fish in site i in stream j, β_{0j} is the mean outcome for stream j, β_{1j} is the coefficient for the fixed effect of site position on fish density, r_{ij} is the level-1 error, where $r_{ij} \sim N(0,\sigma^2)$, and σ^2 is the variance at level 1 after controlling for the effects of position.

Level 2 model: $\beta_{0j} = \gamma_{00} + \gamma_{01}(Stream\_Type) + u_{0j}$, and

$$\beta_{1j} = \gamma_{10} \tag{3}$$

where γ_{00} is the grand mean density, γ_{01} is the estimated coefficient for the fixed effect of stream type (i.e., barrier or control) on stream mean fish density, γ_{10} is a fixed effect representing the coefficient for the effect of position on fish density, and u_{0j} is the residual, where $u_{0j} \sim N(0,\tau_{00})$ and τ_{00} is the conditional variance (the stream-level variance after controlling for stream type). The combined model can then be written to contain the site position×stream type interaction as follows:

$$Y_{ij} = \gamma_{00} + \gamma_{10}(Position) + \gamma_{01}(Stream\_Type) + \gamma_{11}(Position \times Stream\_Type) + u_{0j} + r_{ij} \tag{4}$$

where γ_{11} is the estimated coefficient for the interaction term and all other variables are defined as above. The model can be implemented using the following code:

```
PROC MIXED COVTEST DATA= barrier_data;
CLASS stream stream_type position;
MODEL density = stream_type position stream_type*position / SOLUTION;
RANDOM intercept / SUBJECT = stream;
LSMEANS stream_type position stream_type*position / PDIFF ADJUST = tukey;
RUN;
```

For an extensive explanation of the PROC MIXED syntax, see Littell et al. (1996). The syntax is similar to that used in the GLM procedure; however, important differences exist. The COVTEST statement produces asymptotic standard errors and Wald Z-tests for the covariance parameter estimates, $\hat{\sigma}^2$ and $\hat{\tau}_{00}$. The CLASS statement is the same as described for the GLM procedure, while the MODEL statement lists the dependent variable and only the fixed effects. The SOLUTION option after the MODEL statement requests the parameter estimates and their standard errors for the fixed effects. The RANDOM statement specifies the random effects in the model. The intercept is designated as random in this model because it is assumed that the stream-level intercepts are from a larger population of stream-level intercepts. The SUBJECT option identifies the subject(s) in the multilevel model. Specifying a subject is equivalent to nesting all effects in the RANDOM statement within the subject effect (Littell et al. 1996). Therefore, the above syntax is modeling fish density while accounting for the data being clustered (grouped) by streams. As in the GLM procedure, the LSMEANS statement requests the LS means estimates for the specified fixed effects and the PDIFF option for the LSMEANS statement requests the differences between the LS means.

The analysis indicated that there was a significant position × stream type interaction. The overall Type III tests for the fixed effects are as follows: stream type, $F = 9.44$, $P = 0.0039$; position, $F = 5.56$, $P = 0.024$; and position × stream type interaction, $F = 9.39$, $P = 0.004$. Note that because PROC MIXED uses a likelihood-based approach to estimation it does not directly compute or display the sums of squares; however, the Type III tests are equivalent to those produced by PROC GLM. Table 2 contains the LS means estimates and standard errors for each stream type and site position. In treatment streams, sites located above the barrier had significantly lower mean fish density estimates compared to sites below the barrier; whereas, in control streams mean fish density did not differ between sites located above or below the barrier reference line. Treatment streams had lower fish density estimates compared to control streams, regardless of position, but considering only sites below the barriers, treatment and control streams did not differ significantly in mean fish density estimates.

Both the traditional (OLS) and multilevel analyses resulted in the same LS means point estimates and they were equal to the arithmetic means of the values outlined in Table 1. Least-squares means will be equivalent to arithmetic means for cases with balanced designs, as in this example. However, for unbalanced designs, which are common in ecological studies, the LS means estimates will typically not equal the arithmetic means.

There are two major differences between the traditional and multilevel analyses that have implications for hypothesis testing and inferences: (1) the difference in standard error estimates and (2) the specification of random versus fixed effects. In the multilevel analysis, the standard error estimates of the means are about two times larger compared to the OLS estimates. This difference is due to the fact that the standard error in the traditional analysis is calculated using only the residual variance (the residual variance is the only variance component in fixed effects models); whereas, the standard error in the multilevel analysis is calculated using two variance components: the residual variance and a between-stream variance. The smaller standard errors estimated using the traditional approach can lead to increased probabilities of type I error rates, i.e., finding a significant difference when one does not actually exist.

The second major difference between our two analyses is the specification of stream as a random effect in the multilevel analysis. The specification of random effects has implications for what inferences can be made based on the results of the analyses. For the traditional approach, with stream as a fixed effect, results can not be generalized to streams that were not used in the analysis and must be restricted to the eight streams used in the study. For the multilevel analysis, where stream was specified as a random effect, inferences can be generalized to a larger population of barrier and no-barrier streams. Often a goal of a study is the ability to generalize results found from a subset of study streams or lakes to a larger population of streams or lakes of interest. The use of random effects allows for such inference whereas purely fixed effects models do not.

Example 2: Examining the relationship between aquatic macrophyte percent cover and stomach fullness of yellow perch (*Perca flavescens*) in inland lakes

For this example, we focus our analysis on the multilevel modeling approach to demonstrate how to analyze and interpret datasets with three levels. As a result, we do not compare this multilevel analysis with a traditional OLS analysis. The limitations of using traditional OLS approaches as discussed previously, however, do exist for analyzing these data. We realize that some of the following model details are fairly dense; however, it is our goal that these details will aid in the understanding and interpretation of the model.

Data were generated to emulate a field study designed to examine the effects of macrophyte cover on percent stomach fullness of yellow perch in inland lakes. The dataset contains individual fish (level 1), nested within sampling sites (level 2), nested within lakes (level 3). In this example, sample sites were assumed to be randomly chosen within lakes and lakes were randomly selected from a larger population of lakes. The data were used to test the null hypothesis that percent stomach fullness is not related to percent macrophyte cover while controlling for the effect of individual fish weight on stomach fullness. The dataset contains measurements of percent stomach fullness and weight (g) for individual fish sampled from eight sample sites within each of four lakes. Sample sizes of individual fish varied among sites and lakes, ranging from 0 – 46 fish per site and from 160 – 245 fish per lake for a total of 751 observations. Weight and percent stomach fullness of individual fish ranged between 110 – 293 g and 14.4 – 42.2%, respectively. Percent macrophyte cover was generated for each sample site and ranged from 2 – 97%.

We introduced complexity to this dataset by not only introducing a third level to the hierarchy, but by also including predictors at multiple levels: the predictor at level 1 (the individual fish level) is fish weight and the predictor at level 2 (the site level) is percent macrophyte cover. Because of this complexity, we are going to view this analysis as a two-stage process.

Stage 1 – The first stage involves obtaining initial estimates of the total variance, how the variation is partitioned (i.e., obtain variance estimates that describe how much variation in stomach fullness there is due to individual differences of fish within sites nested within lakes, among sites nested within lakes, and among lakes). These variance estimates are also used, along with variance estimates obtained in stage 2, to determine the percent variation explained at each level of the model by the predictor variables. The model that produces these estimates is a one-way ANOVA with random effects and is also referred to as an unconditional model because it does not contain any predictor variables. This one-way ANOVA with random effects can be viewed as a three-level model as follows:

Level 1 model: $Y_{ijk} = \pi_{0jk} + e_{ijk}$ (5)

where Y_{ijk} is the percent stomach fullness of fish *i* in site *j* and lake *k*, π_{0jk} is the mean stomach fullness of site *j* in lake *k*, and e_{ijk} is the random "fish effect", and $e_{ijk} \sim N\left(0, \sigma^2\right)$, where σ^2 is the residual variance component due to individual differences of fish within sites nested within lakes.

Level 2 model: $\pi_{0jk} = \beta_{00k} + r_{0jk}$ (6)

where β_{00k} is the mean fullness in lake *k*, r_{0jk} is the random "site effect", and $r_{0jk} \sim N(0, \tau_\pi)$, where τ_π is the variance between sites nested within lakes.

Level 3 model: $\beta_{00k} = \gamma_{000} + u_{00k}$ (7)

where γ_{000} is the overall grand mean fullness, u_{00k} is the random "lake effect", and $u_{00k} \sim N(0, \tau_{\beta})$, where τ_{β} is the variance between lakes. The combined unconditional model, therefore, has a fixed effect (γ_{000}) and three random effects (u_{00k}, r_{0jk}, and e_{ijk}) and is as follows:

$$Y_{ijk} = \gamma_{000} + u_{00k} + r_{0jk} + e_{ijk} \tag{8}$$

Examining the initial variance estimates provides information regarding how much total variation there is at each level that can subsequently be modeled with predictor variables. The code required for performing the one-way ANOVA with random effects for this example is:

```
PROC MIXED COVTEST DATA = lake_data;
CLASS lake site;
MODEL fullness = / SOLUTION;
RANDOM intercept / SUBJECT = lake;
RANDOM intercept / SUBJECT = site(lake);
RUN;
```

The syntax for this unconditional model is similar to that described in example 1; however, there is an additional RANDOM statement which specifies that sites are nested within lakes.

Results from the one-way ANOVA with random effects show that the grand mean ($\hat{\gamma}_{000}$) stomach fullness over all lakes is 24% and the estimates of variance among-fish-within-sites-nested-within-lakes ($\hat{\sigma}^2$), among-sites-within-lakes ($\hat{\tau}_{\pi}$), and among-lakes ($\hat{\tau}_{\beta}$) are 8.67 (SE = 0.46, $P < 0.0001$), 7.44 (SE = 2.18, $P = 0.0003$), and 2.18 (SE

= 2.6, $P = 0.202$), respectively. The percent variance among fish within sites nested within lakes, among sites within lakes, and among lakes is 47%, 41%, and 12%, respectively. We now have information on how the variance is partitioned in our dataset and a conditional model can be specified in stage 2.

Stage 2 – The predictor of interest in this study is percent macrophyte cover. However, we also need to account for the effect of individual fish weight on stomach fullness in the model. Therefore, our two predictors are fish weight, modeled at level 1, and percent macrophyte cover, modeled at level 2. Level 3 (the lake level) is left unconditional, with no predictor variables (covariates). Again, the model can be viewed as three levels and in a combined form as follows:

Level 1 model: $Y_{ijk} = \pi_{0jk} + \pi_{1jk}(Weight)_{ijk} + e_{ijk}$ (9)

where Y_{ijk} is the stomach fullness for fish *i* in site *j* in lake *k*, π_{0jk} is the intercept for site *j* in lake *k*, π_{1jk} is the estimated coefficient for the fixed effect of fish weight on stomach fullness, and e_{ijk} is the level-1 random effect.

Level 2 model: $\pi_{0jk} = \beta_{00k} + \beta_{01k}(Percent\_Cover)_{jk} + r_{0jk}$

$$\pi_{1jk} = \beta_{10k} \qquad (10)$$

where β_{00k} is the intercept for lake *k*, β_{01k} is the estimated coefficient for the fixed effect of percent macrophyte cover, β_{10k} is a fixed effect representing the coefficient for the effect of fish weight on stomach fullness, and r_{0jk} is the level-2 random effect.

Level 3 model: $\beta_{00k} = \gamma_{000}, \beta_{10k} = \gamma_{100}, \beta_{01k} = \gamma_{010}$ (11)

where γ_{000} represents the coefficient for the level 2 intercept, γ_{100} represents the coefficient for the fixed effect of fish weight on stomach fullness, and γ_{010} represents the coefficient for the fixed effect of percent macrophyte cover on stomach fullness. The combined model is as follows:

$$Y_{ijk} = \gamma_{000} + \gamma_{100}(Weight) + \gamma_{010}(Percent\_Cover) + \gamma_{110}(Weight \times Percent\_Cover) + u_{00k} + r_{0jk} + e_{ijk} \tag{12}$$

where γ_{110} is the estimated coefficient for the interaction term and all other variables are defined as above. The model can be specified using the following code:

```
PROC MIXED COVTEST DATA = lake_data;
CLASS lake site;
MODEL fullness = weight cover weight*cover / SOLUTION;
RANDOM intercept / SUBJECT = lake;
RANDOM intercept / SUBJECT = site(lake);
RUN;
```

The syntax is similar to that described in the unconditional model; however, we now have specified the full model in the MODEL statement.

The analysis indicated that both fish weight and percent macrophyte cover were significantly and positively associated with percent stomach fullness and that there was not a significant interaction effect (Table 3). Variance estimates obtained from the final model (full model) can be used along with the variance estimates from the unconditional model to determine how much variation was explained at each level as follows:

$$\text{Percent variance explained} = \frac{Variance_{unconditional} - Variance_{full}}{Variance_{unconditional}} \tag{13}$$

where $Variance_{unconditional}$ is an estimate of $\hat{\sigma}^2$, $\hat{\tau}_{\pi}$, or $\hat{\tau}_{\beta}$ from the unconditional model and $Variance_{full}$ is an estimate of $\hat{\sigma}^2$, $\hat{\tau}_{\pi}$, or $\hat{\tau}_{\beta}$ from the full model. For example, to determine how much of the variation in stomach fullness among fish within sites nested within lakes was explained by fish weight we perform the following calculation:

$$\frac{8.67(\hat{\sigma}^2{}_{unconditional}) - 1.07(\hat{\sigma}^2{}_{full})}{8.67(\hat{\sigma}^2{}_{unconditional})} = 0.88 \tag{14}$$

thus, fish weight explained 88% of the among-fish-within-site-nested-within-lake (level 1) variation in stomach fullness. Using equation 13, we can determine that percent macrophyte cover explained 31% of the variation in fish stomach fullness among sites within lakes (level 2). Because we did not have predictors at the lake-level (level 3), we do not need to calculate percent variation explained at this level. However, if predictors were included at level 3, the same calculation could be performed to determine percent variation explained.

In this example, the multilevel model accounted for the fact that fish were nested within sample sites within lakes and sample sites were nested within lakes. As in example 1, the specification of random effects allowed us to account for the lack of independence of observations within sites and lakes with similar implications for inferring (e.g., the ability to generalize to a larger population of lakes). The analysis also allowed for the partitioning of variance among the three levels. Variance partitioning provides valuable information on how much variation is contained at each level. Knowledge of how much variation exists at each level can also help guide future data collection efforts by allowing researchers to focus data collection at the level (e.g., spatial scale) that contains much of the variability that needs to be explained.

Conclusion

Multilevel models provide several advantages over the more commonly-used OLS approaches when analyzing data with a hierarchical structure. Because hierarchical structures are common to both experimental and field (observational) studies in fisheries research, we encourage the use of multilevel models where appropriate. Some other examples of where hierarchical data structures may arise in fisheries research, where multilevel models would be applicable, include investigations of fishing tournament related mortality, where fish are nested within tournaments and tournaments are nested within lakes, and investigations of landscape features on lake or stream attributes, where waterbodies are nested within watersheds and watersheds are nested within ecoregions. Furthermore, due to statistical computing advances, multilevel models can be implemented in widely available statistical software packages. These approaches provide better estimation of fixed effects, allow for the partitioning of variance components across levels, and allow for generalizations beyond the particular groups (e.g., streams or lakes) used in the study.

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Table 1. Simulated dataset used for example 1. Numbers represent simulated fish densities (fish/m^2) for sites nested within treatment (barrier) and control (no barrier) streams and for sample sites above or below the barrier or reference line. Values used to calculate within group means are shown outlined in a dashed line.

		Barrier				Control			
Stream		A	B	C	D	E	F	G	H
Site	Position								
1	Above	15	49	14	12	46	67	45	74
2	Above	14	47	15	9	41	70	45	67
3	Above	7	39	25	18	42	82	57	72
4	Below	38	45	21	20	49	76	39	66
5	Below	13	50	31	24	50	76	37	64
6	Below	24	50	33	30	55	74	35	72

Table 2. Least-squares means (LSM) and standard error (SE) estimates for example 1 analyzed in SAS using a general linear model (PROC GLM) and a multilevel model (PROC MIXED). For each analysis (column) least-squares means with different superscripted letters are significantly different ($P < 0.05$ using Tukey-Kramer multiple comparison test). Least-squares means correspond to the arithmetic within group means which can be calculated using the values in Table 1.

		General linear model		Multilevel model	
Stream type	Position	LSM	SE	LSM	SE
Barrier	Above	22.0^{a}	4.14	22.0^{a}	7.38
Barrier	Below	31.6^{a}	4.14	31.6^{b}	7.38
Control	Above	59.0^{b}	4.14	59.0^{b}	7.38
Control	Below	57.8^{b}	4.14	57.8^{b}	7.38

Table 3. Final parameter and variance estimates, standard errors (SE) and P – values for example 2.

Parameter	Estimate	SE	P – value
Intercept ($\hat{\gamma}_{000}$)	5.92	1.31	0.02
Weight ($\hat{\gamma}_{100}$)	0.10	0.003	<0.0001
Percent cover ($\hat{\gamma}_{010}$)	5.02	1.26	<0.0001
Weight × percent cover ($\hat{\gamma}_{110}$)	-0.005	0.004	0.24
Variance components			
Among fish within sites nested within lakes ($\hat{\sigma}^2$)	1.07	0.05	<0.0001
Among sites within lakes ($\hat{\tau}_{\pi}$)	5.15	1.48	0.0002
Among lakes ($\hat{\tau}_{\beta}$)	1.71	1.95	0.19

Figure 1

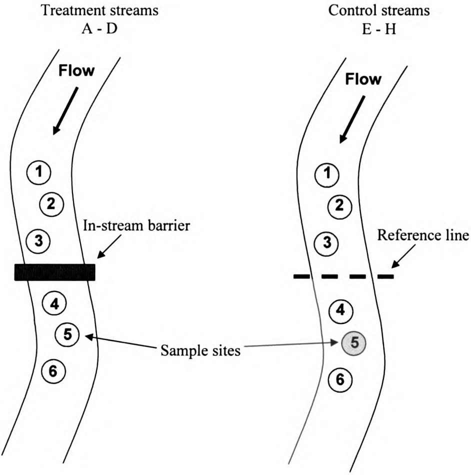
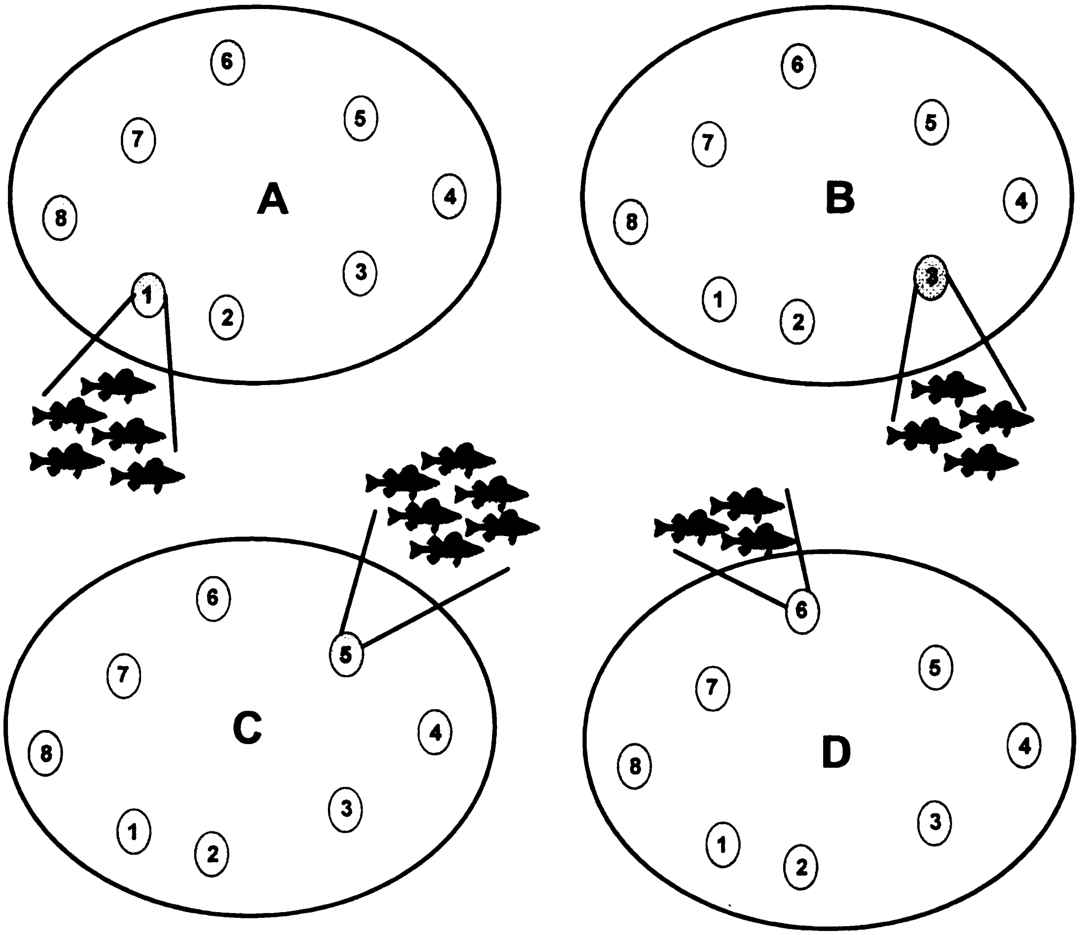

Treatment streams
A - D
Control streams
E - H
Flow
Flow
1
2
3
In-stream barrier
4
5
6
1
2
3
Reference line
4
5
6
Sample sites

Figure 2



Appendix I. An example of the data structure required to analyze the stream barrier dataset (example 1) using SAS. The DATA statement specifies the name of the dataset that is generated. The INPUT statement specifies the variables that are read from the program editor window and the "$" designates variables as character variables. The data corresponding to the variables listed in the INPUT statement are entered after the DATALINES statement.

```
DATA barrier_data;
INPUT density stream $ site stream_type $ position $;
DATALINES;
15  A  1   Barrier  Above
14  A  2   Barrier  Above
7   A  3   Barrier  Above
49  B  1   Barrier  Above
47  B  2   Barrier  Above
39  B  3   Barrier  Above
14  C  1   Barrier  Above
15  C  2   Barrier  Above
25  C  3   Barrier  Above
.
.
.
72  E  6   Control  Below
;
```

CHAPTER 2: A MULTILEVEL MODELING APPROACH TO ASSESSING REGIONAL AND LOCAL LANDSCAPE FEATURES FOR LAKE CLASSIFICATION AND ASSESSMENT OF FISH GROWTH RATES

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.

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 and 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 and 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 *et al.,* 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 U.S. Environmental Protection Agency (e.g., Bailey, 1983; Omernick, 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 and Johnson, 2000; Santoul *et al.,* 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 *et al.,* 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 and 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 and 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 and Magnuson, 1999; Pan *et al.,* 2000), with fewer studies examining lakes (but see Johnson, 2000 and Jenerette *et al.,* 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 *et al.,* 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 *et al.,* 1996; Jackson *et al.,* 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 Methods). We analyzed data for seven fish species including the warmwater species bluegill *Lepomis macrochirus*, pumpkinseed *L. gibbosus*, largemouth bass *Micropterus salmoides*, and the coolwater species smallmouth bass *M. 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 and 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 and Chesson, 1987; Mittelbach and Osenberg, 1992). Therefore, because the species we included in our analyses all utilize the littoral regions of lakes for foraging (see below), 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 *et al.,* 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 *et al.,* 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 and van den Heuvel, 1999; Zweifel *et al.,* 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 *et al.,* 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 (Werner and Hall, 1977; Mittelbach, 1988; Pazzia *et al.,* 2002). The specific covariates we included in the analyses and their sources are described in detail below.

2. 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 *Lepomis macrochirus*, pumpkinseed *L. gibbosus*, largemouth bass *Micropterus salmoides*, and the coolwater species smallmouth bass *M. dolomieu*, yellow perch *Perca flavescens*, walleye *Sander vitreus*, and northern pike *Esox 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 (see below). 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 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 (Eklöv and Hamrin, 1989; Diehl and Eklöv, 1995; Persson *et al.,* 1996).

Water quality data were obtained from the U.S. 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 yr 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 and 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 and 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 (Spence 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 8-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 yr 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 and 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 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:

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

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.

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

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:

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

The intraclass correlation coefficient can then be calculated as follows:

(4) $\hat{\rho} = \hat{\tau}_{00} /(\hat{\tau}_{00} + \hat{\sigma}^2)$

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:

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

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 $(X_{qij} - X_{Q..})$.

(6) Level-2: $\beta_{0j} = \gamma_{00} + \sum_{s=1}^{S} \gamma_{0s} W_{sj} + u_{0j}, \beta_{1j} = \gamma_{10}, \ldots \beta_{qj} = \gamma_{q0}$

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 $X_1 \ldots X_Q$. 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 $\hat{\gamma}_{00}$ 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 $\mu g \bullet L^{-1}$, 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 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 age-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 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 3 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 Hughes (2000) 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 (2000) spanned a larger geographic region, from arctic-alpine to nemoral regions characterized by deciduous forests, compared to those used by Jennerette *et al.* (2002) 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 (2000), 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 *et al.,* 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 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.

4.3 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 1 – 6 to be positively correlated with lake productivity. Greene and Maceina (2000) found the growth of age-0 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. Also, deeper lakes warm up at a slower rate as compared to shallower lakes; thus pumpkinseed in deeper lakes may experience a shorter growing season as compared to shallower lakes that warm up more rapidly in the spring. 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. One possibility is that SDF covaries with another controlling factor. However, in this analysis SDF was not significantly correlated with any other lake morphometry or water quality covariate, suggesting that SDF may be correlated with a covariate that was not used in this study. Alternatively, because this study relies on variables that are surrogates for hypothesized mechanisms, there is an increased probability of chance correlations (Peters *et al.,* 1991), which may explain the significance of SDF in this analysis.

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 and Lewis, 1996). Therefore, large lakes and lakes with a variety of depth habitats may provide conditions conducive to faster growth. Also, prey diversity and abundance may be higher in these larger, more productive lakes providing a wider forage base for northern pike.

4.4 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-yr average and because annual temperature variability can be high, this long-term average may have attenuated any affect of temperature on fish growth rates. Alternatively, lakes with high GDD may differ in angling pressure or other biotic or abiotic factors we were unable to measure as compared to lakes with lower GDD.

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 *et al.* (1997) found higher growth of brood-guarding bluegill in lakes with low angling effort as compared to lakes with higher angling effort. Pierce *et al.* (2003) found that northern pike density explained 36 – 57% of the variation in mean back-calculated lengths at ages 2 – 5 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 (Spence 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.

4.5 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 ten 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).

4.6 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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TABLE I

Sample size ranges (number of lakes per ecoregion or 8 digit hydrologic unit (HU)) and the number of HUs used in the analysis of each species and age combination. The number of ecoregions used in the analyses was always four

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

TABLE II

List of water quality and landscape covariates used in the analyses. Means for each species/age combination are followed by ranges in parentheses. SDF = shoreline development factor, GDD = growing degree days (see Methods for description)

Species (age)	Secchi depth (m)	Color^1 (platinum-cobalt units)	Total nitrogen^1 (μg•L^{-1})	Total phosphorus^1 (μg•L^{-1})	Chlorophyll *a*^{1} (μg•L^{-1})
Bluegill (2)	2.9	12.0	644.7	20.1	6.3
	(0.5-7.3)	(1.0-54.0)	(112.0-2756)	(1.0-155.0)	(0.5-66.0)
Bluegill (3)	3.0	11.8	640.3	21.1	6.4
	(0.5-7.3)	(1.0-54.0)	(112.0-2756)	(1.0-155.0)	(0.2-66.0)
Pumpkinseed (2)	2.8	13.8	611.4	21.2	6.5
	(0.5-7.3)	(2.0-61.0)	(112.0-2756)	(1.0-155.0)	(0.7-35.0)
Pumpkinseed (3)	2.9	13.2	592.3	19.9	5.8
	(0.5-7.3)	(1.0-61.0)	(112.0-2756)	(1.0-155.0)	(0.2-35.0)
Largemouth bass (2)	3.0	11.5	645.3	19.7	6.4
	(0.5-7.8)	(1.0-75.0)	(112.0-1717)	(1.0-155.0)	(0.5-66.0)
Largemouth bass (3)	3.0	11.7	650.0	21.0	6.6
	(0.5-7.0)	(1.0-75.0)	(130.0-2756)	(1.0-155.0)	(0.5-66.0)
Smallmouth bass (2)	3.4	11.4	439.2	14.1	4.3
	(0.9-7.3)	(1.0-80.0)	(92.0-850)	(10-73.0)	(0.2-32.0)
Smallmouth bass (3)	3.5	13.0	454.8	17.0	5.3
	(0.6-7.3)	(1.0-80.0)	(92.0-1130)	(1.0-118.0)	(0.2-60.0)
Yellow perch (2)	3.1	12.7	572.0	18.5	6.3
	(0.6-7.8)	(1.0-80.0)	(112.0-1430)	(1.0-127.0)	(0.5-66.0)
Yellow perch (3)	3.1	12.6	579.1	19.4	6.1
	(0.5-7.8)	(1.0-80.0)	(111.0-2756)	(1.0-155.0)	(0.5-66.0)
Walleye (2)	3.1	14.3	484.5	21.0	7.3
	(0.6-7.3)	(1.0-80.0)	(112.0-1406)	(2.0-118.0)	(0.2-60.0)
Walleye (3)	2.9	15.3	515.7	22.0	8.2
	(0.6-7.3)	(1.0-80.0)	(112.0-1406)	(2.0-118.0)	(0.2-60.0)
Northern pike (2)	2.8	13.7	577.1	21.1	7.4
	(0.5-5.8)	(1.7-80.0)	(130.0-2756)	(1.0-127.0)	(0.5-66.0)
Northern pike (3)	2.9	12.9	570.6	21.0	6.6
	(0.5-7.0)	(1.0-80.0)	(130.0-2756)	(1.0-127.0)	(0.5-60.0)

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

TABLE II CONTINUED

List of water quality and landscape covariates used in the analyses. Means for each species/age combination are followed by ranges in parentheses. SDF = shoreline development factor, GDD = growing degree days (see Methods for description)

Species (age)	Alkalinity (mg•L^{-1} as CaCO3)	GDD^1	SDF^1	Mean depth^1 (m)	Lake area^1 (ha)
Bluegill (2)	105.9 (4.0-197.0)	2344 (1451-3121)	2.2 (1.0-6.3)	4.8 (1.2-18.0)	210.7 (20.9-6988)
Bluegill (3)	103.5 (2.0-66.0)	2354 (1451-3121)	2.2 (1.0-6.3)	4.7 (0.9-18.0)	243.4 (20.8-6988)
Pumpkinseed (2)	89.6 (4.0-190.0)	2105 (1416-2891)	2.2 (1.1-4.7)	4.4 (1.2-18.0)	270.6 (20.8-6988)
Pumpkinseed (3)	88.5 (1.0-190.0)	2122 (1416-2902)	2.2 (1.1-6.5)	4.4 (1.2-18.0)	321.6 (20.8-1988)
Largemouth bass (2)	109.8 (1.0-197.0)	2413 (1539-3121)	2.2 (1.1-6.3)	4.7 (1.2-11.6)	188.2 (20.8-3545)
Largemouth bass (3)	107.5 (1.0-197.0)	2390 (1539-3121)	2.2 (1.1-6.3)	4.6 (1.2-11.6)	183.4 (20.8-1848)
Smallmouth bass (2)	86.3 (2.0-166.0)	1919 (1488-2747)	2.1 (1.1-5.4)	5.7 (1.5-20.4)	619.6 (31.7-7039)
Smallmouth bass (3)	85.3 (2.0-166.0)	1971 (1500-2747)	2.2 (1.1-5.4)	6.4 (1.5-42.4)	668.6 (31.7-7576)
Yellow perch (2)	97.9 (2.0-186.0)	2197 (1416-3121)	2.1 (1.0-6.5)	5.3 (1.2-42.4)	373.9 (20.8-7576)
Yellow perch (3)	98.1 (1.0-190.0)	2184 (1451-3121)	2.2 (1.0-6.45)	5.3 (1.2-42.4)	370.0 (20.8-7576)
Walleye (2)	93.2 (2.0-197.0)	1937 (1451-2820)	2.2 (1.2-4.7)	5.3 (1.5-18.0)	786.8 (30.0-7039)
Walleye (3)	83.2 (2.0-197.0)	1897 (1451-2670)	2.1 (1.1-5.4)	4.7 (1.5-12.8)	662.5 (31.7-7039)
Northern pike (2)	94.7 (1.0-197.0)	2123 (1416-3121)	2.1 (1.1-6.5)	4.6 (1.5-18.0)	404.6 (20.8-7039)
Northern pike (3)	96.1 (1.0-197.0)	2139 (1451-3121)	2.2 (1.1-6.5)	4.8 (1.2-18.0)	396.4 (20.9-7039)

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

TABLE III

Fixed effects and variance estimates for ecoregion unconditional models. $\hat{\gamma}_{00}$ =grand mean of mean length at age for all ecoregions (mm), $\hat{\sigma}^2$ represents the within-ecoregion variability in mean length at age, $\hat{\tau}_{00}$ represents the between-ecoregion variability in mean length at age, and $\hat{\rho}$ is the intraclass correlation coefficient ($\%, \hat{\rho} = \hat{\tau}_{00} / (\hat{\tau}_{00} + \hat{\sigma}^2)$)

Species (age)	$\hat{\gamma}_{00}$ (95% confidence interval)	$\hat{\sigma}^2$	$\hat{\tau}_{00}$ [a]	$\hat{\rho}$ [b]
Bluegill (2)	108.7(105.7, 111.7)*	5820*	0.0	na
Bluegill (3)	136.0 (132.5, 139.5)*	6596*	2.3	0.04
Pumpkinseed (2)	111.6 (107.2, 116.0)*	2748*	3.4	0.12
Pumpkinseed (3)	135.6 (130.0, 141.2)*	2947*	19.4	0.65
Largemouth bass (2)	214.1 (208.9, 219.3)*	12014*	0.0	na
Largemouth bass (3)	260.1 (242.3, 277.9)*	9939*	204.6	2.02
Smallmouth bass (2)	203.8 (190.9, 216.7)*	9898*	89.1	0.89
Smallmouth bass (3)	245.4 (218.7, 272.1)*	7175*	659.5	8.42
Yellow perch (2)	154.0 (145.1, 162.9)*	7108*	64.1	0.89
Yellow perch (3)	171.4 (162.2, 180.6)*	5182*	72.5	1.38
Walleye (2)	330.3 (318.9, 341.6)*	22765*	0.0	na

Walleye (3)	379.9 (354.4, 405.4)*	32326*	402.3	1.23
Northern pike (2)	480.9 (455.2, 506.6)*	37108*	483.3	1.28
Northern pike (3)	545.3 (505.8, 584.8)*	34098*	1377	3.88

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

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

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

TABLE IV

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

Species (age)	$\hat{\gamma}_{00}$ (95% confidence interval)	$\hat{\sigma}^2$	$\hat{\tau}_{00}$[a]	$\hat{\rho}$[b]
Bluegill (2)	110.1 (104.6, 115.5)*	5890*	57.8	0.97
Bluegill (3)	137.1 (132.9, 141.3)	11628*	0.0	na
Pumpkinseed (2)	106.1 (99.1, 113.2)	1566*	70.9	4.33
Pumpkinseed (3)	134.3 (128.7, 139.8)	2608*	45.4	1.71
Largemouth bass (2)	215.9 (208.5, 223.4)	14440*	37.4	0.26
Largemouth bass (3)	266.2 (253.7, 278.7)	27648*	264.9	0.94
Smallmouth bass (2)	214.6 (196.8, 232.4)	29264*	0.0	na
Smallmouth bass (3)	266.5 (246, 287)	35321*	0.0	na
Yellow perch (2)	152.9 (144.9, 161.0)*	5578*	214.6*	3.70
Yellow perch (3)	172.1 (166.1, 178)	8954*	49.8	0.55
Walleye (2)	318.9 (291.3, 346.6)	19479*	335.6	1.69

Walleye (3)	395.0 (344, 446.0)	190944[*]	0.0	na
Northern pike (2)	490.4 (470.4, 510.3)[*]	28422[*]	1046[*]	3.55
Northern pike (3)	544.8 (526.9, 562.7)[*]	31298[*]	561.6[**]	1.80

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

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

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

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

TABLE V

Final multilevel mixed model parameter estimates for the watershed analysis. 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

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 ($P > 0.05$).

TABLE VI

Final multilevel mixed model parameter estimates for the ecoregion analysis. 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

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		
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

Figure 1

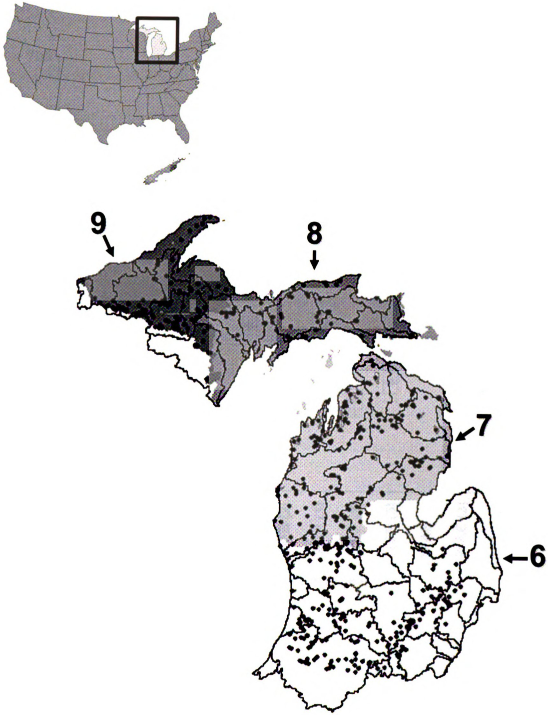
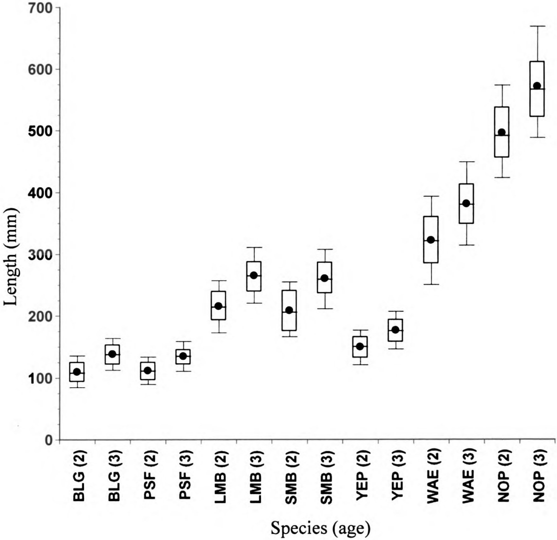


Figure 2


700
600
500
400
300
200
100
0
Length (mm)
BLG (2)
BLG (3)
PSF (2)
PSF (3)
LMB (2)
LMB (3)
SMB (2)
SMB (3)
YEP (2)
YEP (3)
WAE (2)
WAE (3)
NOP (2)
NOP (3)
Species (age)

CHAPTER 3: CAN HABITAT ALTERATION AND SPRING ANGLING EXPLAIN LARGEMOUTH BASS NEST SUCCESS?

Abstract

Largemouth bass *Micropterus salmoides* nest in shallow littoral areas, making them vulnerable to negative effects of habitat alteration due to development of lake shorelines and fishing during the spring nesting period. For instance, alteration of shorelines may reduce the quality and abundance of nesting habitat, and the high visibility of nests and the aggressive guarding behavior of nesting males increase their vulnerability to fishing. In 2004, we monitored nest distribution and success, and quantified local nest habitat features and lakewide angler effort and lakeshore development patterns, in five Michigan lakes in an effort to determine the extent to which habitat alteration and/or fishing limit the number of nests that produce swim-up fry. Lakes spanned a range of lakeshore dwelling density (8 – 22 dwellings/km), allowing us to determine the extent to which nest success varies within and among lakes due to local (e.g., substrate and cover) and lakewide (e.g., dwellings/km and fishing effort) factors. Surprisingly, local habitat characteristics were not important determinants of the probability of a nest producing swim-up fry ($P > 0.05$). At the whole-lake scale, however, nest success was negatively related to dwelling density, with the probability of a nest producing swim-up fry declining from 0.77 in the lowest dwelling density lake to 0.45 in the highest dwelling density lake ($P = 0.018$). Lakewide estimates of angling effort could not explain this difference among lakes, indicating the likely importance of quantifying angling at finer spatial scales. Knowledge of the magnitude of anthropogenic effects and the spatial scale at which they operate is integral for black bass management.

As keystone predators and a valued sport fish in North American lakes, black bass — specifically largemouth *Micropterus salmoides* and smallmouth *M. dolomieui* — possess life history characteristics that make them vulnerable to perturbations associated with human development of lake shorelines. These species spawn in the spring when water temperatures are near or above 15°C. Males construct nests in the substrate of relatively shallow, littoral areas often in close proximity to physical structure (Annett et al. 1996; Hunt and Annett 2002; Wills et al. 2004). After attracting and mating with a female, male bass guard the eggs and developing fry until the brood disperses (Ridgway 1988; Ongarato and Snucins 1993; Philipp et al. 1997). This period of parental care by males may last more than a month (Brown 1984), during which time the male bass are highly active and guard offspring aggressively, while feeding only opportunistically (Ridgway 1988; Hinch and Collins 1991).

Events occurring during these early life stages are important for first year recruitment of bass (Ludsin and DeVries 1997). Therefore, an understanding of anthropogenic factors affecting black bass early life history is necessary to further our knowledge of their biology and effectively manage them. Nest success, often defined as the occurrence of a nest producing swim-up fry (Philipp et al. 1997), is considered to be an important event in the recruitment process that may affect the abundance of age-0 bass that will ultimately survive to the first winter (Ridgway and Shuter 1997). Although compensatory mortality may occur, neither the magnitude of the effect on nesting success, nor the capacity of bass populations to compensate, is fully understood.

Because bass typically nest in shallow littoral areas, human development of lake shorelines (i.e., lakeshore dwelling density) and associated activities may negatively affect nesting success in two ways. First, removal of structure (i.e., rooted vegetation or coarse woody material) and alteration of littoral substrate may increase risk of predation and/or siltation (Christensen et al. 1996; Radomski and Goeman 2001; Jennings et al. 2003). For instance, Hunt and Annett (2002) concluded that male largemouth bass selected nest-building sites near physical structure such as woody debris compared to habitats that lacked structure, suggesting that removal of structure, through activities such as lakeshore development (LSD), may alter bass nest distributions and ultimately negatively affect nest success. Second, the high visibility of black bass nests and the aggressive guarding behavior of nesting males increase their vulnerability to angling (Ridgway 1988). Removing male bass from the nest, even for short periods of time, reduces the male's ability to guard the nest, which ultimately increases predation risk on bass eggs and larvae, and increases the likelihood that the male will pre-maturely abandon the nest, thereby negatively affecting production of successful nests (Philipp et al. 1997; Ridgway and Shuter 1997; Suski et al. 2003).

Most studies of nesting black bass have been conducted in ponds or on a single lake or reservoir, with the focus often on smallmouth bass (but see Philipp et al. 1997). There is therefore a paucity of information on the potential impacts and relative importance of LSD (and associated habitat modification) and angling for patterns of nest distribution and nesting success of largemouth bass within and across lakes. Furthermore, because most previous studies examining factors affecting nesting success have only been performed at one spatial scale, that of the local nest, it is unclear as to whether these assorted factors operate at the local nest scale (i.e., through factors measured at the nest-scale such as the depth of the nest), lakewide scale (i.e., through factors measured at the lake-scale such as lake productivity), or both. The goals of this study were to determine whether largemouth bass nest success varies with both local and lakewide features, and to explore the relative importance of habitat modification versus spring angling to patterns of nest success. To accomplish these goals we conducted a study examining largemouth bass reproductive success at multiple spatial scales in six southeast Michigan lakes with a wide range of lakeshore dwelling density (8 – 22 dwellings/km). Our primary objective was to determine the extent to which residential LSD and habitat variables, at both local and lakewide scales, and lakewide angling pressure affect the probability of largemouth bass producing successful nests. As a secondary objective, we sought to gain further insight into our nest success findings by evaluating the spatial distribution of bass nests relative to natural and anthropogenic lakeshore habitat characteristics. We also highlight the use of generalized linear mixed models, which have properties that make them useful in the analysis of fisheries data (Venables and Dichmont 2004), but have not been widely applied in fisheries to date.

Methods

Study area.—We monitored six lakes located in Washtenaw and Livingston counties in southeast Michigan, USA during May and June 2004 to assess the importance of local nest and lakewide- scale habitat characteristics to largemouth bass reproductive success (Figure 1). We selected lakes that were similar morphometrically but that spanned a wide range of lakeshore dwelling densities from 7.8 – 22.3 dwellings/km (Table 1). All lakes were mesotrophic, stratified, and accessible to public fishing.

Lake characteristics.—We viewed nest success as a function of lakewide and local characteristics. We included three whole-lake features: lakeshore dwelling density (lakewide LSD), angler effort, and total phosphorus (TP; Table 2). Lakeshore dwelling density was determined using visual observations by boat to quantify the number of riparian dwellings within 50 m of each lake, and then dividing the number of dwellings by lake perimeter (km). We sampled for TP using integrated epilimnetic water samples collected using a tube sampler during the month of July. TP was measured using a persulfate digestion (Menzel and Corwin 1965) followed by standard colorimetry (Murphy and Riley 1962). We determined angler effort separately for May and June by conducting two instantaneous angler counts per week in each lake (once per randomly chosen week day and weekend day). We randomly selected (without replacement) time of day (morning, mid-day, or evening) for each survey, and surveyed lakes in haphazard order. During each survey, we visually assessed fishing activity for all boats on the lake from the vantage of a boat and using binoculars. We recorded the number of anglers per boat, the location of the boat (near the shoreline or open water), and the gear type used when possible. Following Philipp et al. (1997), we recorded an angler as potentially targeting black bass if he/she was using tactics (fishing near the shoreline and using appropriate lures or jigs) that could potentially catch nesting bass. We followed the methods of Lockwood et al. (1999) to expand each survey count to an estimate of the total number of angler hours, using the equation:

(1) $\hat{E}_{pdj} = F_p A_{dj}$

where E = estimated angler hours, F = number of fishable hours during the entire period, p (e.g. weekends or weekdays during May or June), A = number of anglers, d = day, and j = count. We calculated two estimates of lakewide angling effort (total hours/km shoreline): all anglers and just anglers potentially targeting nesting black bass. We generated separate estimates for May 8 – 28, and May 29 – June 27 because it is illegal to target or harvest bass in Michigan lakes prior to the Saturday of Memorial Day weekend (May 29 in 2004). Within each month, we averaged weekend estimates and also weekday estimates, and then summed those means to generate the final estimates for each month. We calculated variance separately for weekend and weekday estimates (as per equation 58 in Lockwood et al. 1999) and then summed the two values.

Nest location and reproductive success.—We surveyed the littoral area for largemouth bass nests using boats powered by electric trolling motors. We conducted surveys at least biweekly for new nests and to examine the status of previously located nests. Once a new nest was located, we marked it with a numbered marker and recorded its location using a differentiated global positioning system (GPS; Trimble GeoExplorer ®). After marking the nest, we observed local nest characteristics (see below), the presence/absence of a male bass, eggs, larvae, and/or fry, with either an aqua-scope or by snorkeling. We considered a nest successful if fry were observed actively swimming above the nest (Philipp et al. 1997).

Nest characteristics.—Once a nest was located, we recorded the dominant substrate type (e.g., silt, sand, etc.) and the presence of cover (boulders, woody debris, macrophytes) within a 1 m radius of the nest, along with the depth of the nest. We also recorded the development type of the nearest shoreline (local LSD type) as either undeveloped, developed maintained (developed, but with no retaining wall, e.g., a shoreline with a maintained lawn), or developed retained (a shoreline with riprap or a retaining wall). Using the GPS locations, we calculated distance to shore. Also, we determined wind exposure for each nest from existing GIS coverages. We classified each nest as having high or low wind exposure based on the location of the nest in relation to the prevailing SW winds (Table 2). In addition, we used the existing GIS coverages to quantify the total amount of spawning habitat with regards to local LSD type and wind exposure.

Statistical analyses

Nest success.— We omitted nests from our analysis if their fate could not be determined. We only included predictor variables in our analysis for which we had mechanistic hypotheses regarding their likely effects on bass nest success. We recognized two general mechanisms through which local habitat features and/or angling pressure could affect nest success. First, habitat features may directly affect nest success through physical and chemical constraints on egg survival. Second, local habitat features and angling pressure, in combination, may indirectly influence the vulnerability of nests to failure through parental male abandonment and nest predation. Two additional factors potentially affecting nest success must also be factored into the analysis. First, nest site features not subject to anthropogenic alteration may influence nest success. Second, attributes at the whole-lake scale may affect the average probability of nest success for a given lake.

We used a generalized linear mixed model to determine if local nest site characteristics or whole-lake characteristics affected the probability of a largemouth bass nest successfully producing swim-up fry (Table 2). Generalized linear mixed models (GLMMs) are extensions of generalized linear models (GLMs) with the inclusion of random effects. Fixed effects models (e.g., GLMs) assume that all observations are independent of each other, and thus are not appropriate for analysis of hierarchical or correlated data structures (see Wagner et al. in press). In our analysis, GLMMs are used to accommodate dependence among observations within lakes and to accommodate the hierarchical nature of the data (e.g., bass nests nested within lakes). Both GLMs and GLMMs are extensions of the general linear model that allow response variables to follow any probability distribution in the exponential family (e.g., normal, binomial, and Poisson). GLMMs are composed of three model components including: (1) a linear predictor that is a linear combination of regression coefficients; (2) a link function that relates the mean of the response data to the linear predictor; and (3) a response distribution from the exponential family of distributions. For a more detailed overview of the theory and use of GLMs and GLMMs in fisheries research see Venables and Dichmont (2004).

To begin, we built separate models of nest success as a function of each covariate hypothesized to affect nest success. After significant, uncorrelated predictors were identified we then included them in a single model. The model can be described as a two level model, with the first level modeling the probability of a nest succeeding as a function of local nest characteristics and the second level modeling the average probability of nest success for each lake as a function of lake characteristics. The probability of success was assumed to be Bernoulli distributed. The response variable (Y_{ij}) is binary, where $Y_{ij} = 1$ if nest i in lake j was successful and $Y_{ij} = 0$ if nest i in lake j failed. The probability of success of nest i in lake j is defined as $\varphi_{ij} = Pr(Y_{ij} = 1)$. The general form of the two-level model is as follows.

Level 1 model:

$$(2)\ \eta_{ij} = \beta_{0j} + \sum_{q=1}^{Q} \beta_{qj} X_{qij}$$

where η_{ij} is the log odds of success for nest i in lake j, η_{ij} is the level 1 link function (logit link), $\eta_{ij} = \log\left(\frac{\varphi_{ij}}{1-\varphi_{ij}}\right)$, β_{0j} is the mean log odds of success for lake j, β_{qj} is the effect of covariate X_{qij} on the log odds of success, $q = 1$ to Q, with Q equaling the total number of level 1 covariates.

Level 2 model:

$$(3)\ \beta_{0j} = \gamma_{00} + \sum_{s=1}^{S} \gamma_{sj} W_{sj} + u_{0j}\ , \beta_{1j} = \gamma_{10}, \ldots \beta_{qj} = \gamma_{q0}$$

where γ_{00} is the average log odds of success when all level 2 covariates (W_{sj}) are equal to zero ($s = 1$ to S, with S equaling the total number of level 2 covariates) and represents a grand mean value, γ_{sj} is the effect of covariate W_{sj} on the average log odds of success, u_{0j} is the random effect associated with lake j, and $u_{0j} \sim N(0, \tau_{00})$, where τ_{00} is the variance between lakes in lake-average log odds of success. A predicted log odds of success can then be converted to a probability by calculating

$$(4)\ \varphi_{ij} = \frac{1}{1+\exp\{-\eta_{ij}\}}$$

To provide further illustration of the model structure, assume that we are interested in modeling nest success as a function of a single nest level covariate (level 1), nest depth and a single lake level covariate (level 2), lakeshore development (LSD). The model can be viewed in two levels and in combined form as follows, with parameters and subscripts defined as above:

Level 1:

$$(5)\ \eta_{ij} = \beta_{0j} + \beta_{1j}(nest\_depth)_{ij}$$

Level 2:

$$(6)\ \beta_{0j} = \gamma_{00} + \gamma_{01}(LSD)_j + u_{0j},\ \beta_{1j} = \gamma_{10}$$

Combined form:

$$(7)\ \eta_{ij} = \gamma_{00} + \gamma_{10}(nest\_depth)_{ij} + \gamma_{01}(LSD)_j + u_{0j}$$

We performed generalized linear modeling using the GLIMMIX macro of the MIXED procedure in SAS (SAS Institute Inc. 2000). When using many generalized linear models, there is a possibility that the conditional variance of the errors may differ from theory. The GLIMMIX macro allows for the possibility that the conditional error variance differs from theory by adding an additional parameter to the conditional variance, the extra-dispersion parameter $(\hat{\phi})$. If $\hat{\phi} < 1$, the distribution of the conditional errors is said to be underdispersed and if $\hat{\phi} > 1$ the distribution is overdispersed. If $\hat{\phi}$ is close to 1, the variance is consistent with the assumed distribution (Littell et al. 1996). Underdispersion can lead to inflated standard errors, while overdispersion can lead to underestimated standard errors and thus inflated type I error rates. Therefore, we assessed the final model for over- or under-dispersion by examining the extra-dispersion parameter.

Nest habitat features.—Because we hypothesized that nest depth, substrate type, and the presence/absence of cover would be influenced by anthropogenic effects associated with LSD, we modeled these nest attributes as a function of local LSD type and lakewide LSD. For nest depth, we used a two-level mixed model, with lake as a random effect and local LSD type and lakewide LSD as fixed effects. Local LSD type was included in the model by designating developed maintained and developed retained shorelines as dummy variables (undeveloped shorelines were reference cells). For substrate type and the presence/absence of cover, we used a generalized linear mixed model, with predictor variables designated as above. The analyses were preformed using the GLIMMIX macro and MIXED procedure in SAS (SAS Institute Inc. 2000).

Nest distribution.—To explore if patterns of nest distribution relative to available habitat, we used a chi-square goodness of fit test to determine if habitat used for constructing nests was significantly different from the distributions of available habitat. We reasoned that if most nests were located in a relatively rare habitat type, it would be indicative of high nest site selectivity and potential limitation of preferred nesting habitat. Habitat was categorized into proportions of each development type and wind exposure combination. The analysis was performed for each lake individually.

Results

A total of 178 largemouth bass nests were located during the study period (Table 3). The number of largemouth bass nests located in each lake ranged from 0 (in Blind Lake) to 51 (in North Lake). Because largemouth bass did not spawn in Blind Lake it was excluded from further analyses. Largemouth bass initiated nest building in early May, with the number of nests peaking in all lakes in mid-May. Both the last, new nest and the last successful nest were located on 8 June.

Nest success.—To determine the magnitude of variation among lakes in the probability of nest success, we estimated an unconditional model, with no predictors at either the nest or lakewide level. The average log-odds of success across lakes was $\hat{\gamma}_{00} =$

0.26. Therefore, the probability of success in an "average" lake, with a random effect of $\hat{u}_{0j} = 0$, was 0.56. The variance between lakes in lake-average log odds of success was estimated as $\hat{\tau}_{00} = 0.193$; thus we would expect that 95% of the lakes in our study have a probability of nest success between 0.35 and 0.75.

Surprisingly, no nest-scale habitat characteristics were significantly associated with the probability of a nest successfully producing swim-up fry ($P \geq 0.10$). At the whole-lake scale, however, the probability of a nest producing swim-up fry decreased markedly with increasing LSD (intercept $(\hat{\gamma}_{00})$ = 1.96, standard error (s.e.) = 0.748, $P = 0.078$; slope, effect of LSD $(\hat{\gamma}_{01})$ = -0.096, s.e. = 0.04, $P = 0.018$). The predicted probability of success ranged from 0.77 in Bruin Lake, the lowest LSD lake to 0.45 in Patterson Lake, the highest LSD lake (Figure 2). No other lakewide covariates were significant (all $P >$ 0.20). Over or underdispersion were not evident in our analysis, with the extra-dispersion parameter estimated very close to 1 ($\hat{\phi}$ = 1.02, Littell et al. 1996).

Angling effort.—Our estimate of total fishing effort (total angler hours per km of shoreline) were quite variable among lakes, but did not vary predictably with LSD in May or June (May, $P = 0.75$; June, $P = 0.21$). Estimated total angler hours were much lower during the May period (ranging 0 – 227 hrs/km; standard deviations ranged 0 – 64.5), when the majority of nesting occurred, than in June (ranging 65 – 453 hrs/km; standard deviations ranged 29.3 – 158.3), when the legal season for bass fishing was open. Anglers using techniques likely to target bass represented a substantial component of total angling effort both before and after opening of the legal season for targeting bass (35% and 42% of angling effort in May and June, respectively). Thus, even though the predominance of angling that potentially targets nesting bass increased in June, it still occurred in May to a substantial degree despite the fishing regulations.

Nest habitat features.—Nest depth was the only nest habitat feature that differed significantly among shoreline development types. Local LSD type explained 8.5% of the variation in depth of largemouth bass nests. According to our model, on average, if a largemouth bass nest was constructed near an undeveloped shoreline it was shallower compared to nests constructed near developed shorelines, and nests constructed near retaining walls were, on average, constructed in yet deeper water (intercept = 0.845, s.e. = 0.065, $P = 0.002$; fixed effect of developed maintained shoreline = 0.135, s.e. = 0.047, $P = 0.004$; fixed effect of developed retained shoreline = 0.197, s.e. = 0.058, $P = 0.0009$). The grand-mean depth at which largemouth bass nests were constructed was 0.92 m (95% confidence interval = 0.83, 1.01) and did not vary significantly among lakes (between lake variance estimate = 0.008, $P = 0.12$). Surprisingly, substrate type and the presence/absence of cover did not significantly differ among either local LSD types or among lakes according to lakewide LSD.

Nest distribution.—Largemouth bass used shoreline habitats to construct nests in different proportions compared to what was available in 4 of 5 lakes (Figure 3), although patterns of selection varied among lakes. The only lake in which largemouth bass used habitat in proportion to what was available was Bruin Lake (7.8 dwellings/km), with the majority of habitat, and nest sites, comprised of undeveloped shoreline. For East Crooked (14.6 dwellings/km) and Patterson (22.3 dwellings/km) lakes, largemouth bass selected undeveloped shorelines for nest construction, as we had expected. In East Crooked, bass utilized undeveloped sites that were both exposed to low and high wind, whereas bass in

Patterson Lake primarily used undeveloped sites that were located in low wind exposure sites in greater proportion compared to what was available. Contrary to our expectations, in both Halfmoon (17.7 dwellings/km) and North lakes (21.5 dwellings/km), largemouth bass primarily used developed maintained shorelines in low wind exposure areas for nesting. In Halfmoon Lake, in particular, largemouth bass nests were located in undeveloped sites less than expected given the available proportion of this habitat type.

Discussion

We expected local and lakewide features to influence the distribution and success of largemouth bass nests. In particular, we hypothesized that nests would be concentrated along undeveloped shorelines within lakes, and that these nests would have a higher probability of success than nests located along developed shorelines. We thought that availability of cover and visibility to anglers (i.e., nest depth) would explain, in large part, differences in nest success between developed and undeveloped shorelines. We also expected nest success to vary predictably among lakes, with nest success declining with increasing lakewide LSD, due to higher levels of angling pressure and generally lower availability of preferred nesting habitat. As expected, at the whole-lake scale, nesting success declined with increasing lakewide LSD; but surprisingly, whole-lake angling effort could not explain the differences in nest success among lakes. Further, we saw no evidence that local nest features, such as availability of cover or nest depth, could explain variability in success among nests. Patterns of nest distribution relative to available habitat varied among lakes, with some indication that preferred habitat becomes limiting at high LSD, but also that additional refinement of habitat categories is required (see nest distribution, below).

Nest success.—Contrary to our expectations, neither nest depth, nor other local nest features, could explain a significant amount of variation in nest success. Although this is consistent with findings by Gross and Kapuscinski (1997), where local habitat characteristics such as nest depth and dominant substrate type could not predict reproductive success of smallmouth bass in Lake Opeongo, Ontario, Canada, we view these findings as somewhat surprising given the attention in the literature on local nest habitat features and the documented habitat preferences of black bass (Hunt and Annett 2002; Saunders et al. 2002; Wills et al. 2004). Why did we detect no local effects on nest success? The answer may be in part that a more detailed quantification of structure is needed. In our field observations, available structure was treated as a categorical variable (presence/absence), such that we failed to consider varying degrees of cover. For example, an extensive stand of vegetation and a few sprigs of macrophytes in close proximity to nests were both considered equal vegetative cover, when they may, in fact, influence the fate of an individual nest differently. Also, angling may need to be observed at a finer (i.e., local) spatial scale (see below), and/or variation in the abundance and spatial distribution of nest predators (a factor that we did not quantify), both within and across lakes, may play a predominant role in determining variation in nest success. In fact the interaction between fishing pressure and nest predator abundance may be important, as the removal of guarding male bass during fishing, even for a brief period of time, increases the probability of nest failure due to predation (Kieffer et al. 1995; Phillipp et al. 1997).

Contrary to our expectations, fishing effort did not increase with lake dwelling density. Hence, fishing pressure could not account for the ~35% decline in probability of nest success across lakes. Fishing pressure may not increase with dwelling density in our lakes because they all have public access. Therefore, a large component of the anglers likely do not reside on the lake. Still, we were initially surprised that fishing effort could not explain the variation in nest success because the effects of fishing on nest success have been investigated in ponds and sections of lakes, with convincing evidence that fishing negatively affects the success of individual nests (Neves 1975; Ridgway 1988; Kieffer et al. 1995). This reduction in nest success is often due to nest predation either while the male bass is off the nest, or even after the male bass has returned, because such males show decreased ability to defend the nest and increased likelihood of abandoning the nest (Philipp et al. 1997; Suski et al. 2003).

Our working hypothesis for why fishing effort did not explain a significant amount of variation in nest success is that the spatial distribution of angling, relative to nest distribution, is a critical factor to observe. Our angling surveys may have been conducted at too broad of a scale. For example, anglers in Patterson Lake were observed to be using methods that targeted nesting bass in a small cove with a high number of bass nests. Nest predators also appeared to be particularly abundant in this cove. Nest failure rate in this cove was particularly high. It is likely that the spatial distributions of fishing and of nest predators interact to influence nest success, such that both factors should be observed at finer spatial scales to be able to determine their combined effect on nest success. It may be that high levels of shoreline development result in concentration of nesting bass and potential nest predators, such as other centrarchid species.

Finally, although we chose our lakes to be similar morphometrically, we cannot conclusively rule out the possibility that other unmeasured features of our study lakes, either natural or due to human activities, covaried with LSD, and provided the mechanism driving the observed negative relationship between nest success and LSD. For example, it is possible that some feature of a lake, such as an unmeasured indicator of littoral habitat quality, which makes it unfavorable for bass reproduction also makes it preferable for human development. Future studies examining the relative importance of LSD on nest success that include more study lakes and contain more detailed measurements of habitat will help address such questions.

Nest habitat features.—We hypothesized that nest habitat features (e.g., nest depth, substrate type, and presence/absence of cover) would vary predictably among local LSD types and lakewide LSD. Nest depth was the only variable that varied, differing among local LSD types. The construction of retaining walls, and to some extent maintained shorelines, apparently reduced the availability of shallow-water spawning habitat, resulting in bass constructing nests in deeper water. However, because neither nest depth nor local LSD type were significant in predicting nest success, the difference in nest depth among local LSD types does not appear to have substantive effects on nesting success. Research has demonstrated that local modification affects substrate type, vegetation cover, and course woody material abundance in these lakes and others in Wisconsin and Minnesota (Radomski and Goeman 2001; Jennings et al. 2003; Jubar 2004). Therefore, the fact that these factors did not vary predictably among nest sites according to modification type indicates that bass effectively seek out these features, even if they are relatively less abundant at developed sites.

Nest distribution.—Habitat availability may affect the overall outcome of nesting for a population through altering the number of nests, the distribution of those nests, and/or the success of those nests in producing swim up fry. The number of largemouth bass nests that we detected ranged from 0 – 51 across lakes, with 5 of the 6 lakes having at least 21 largemouth bass nests. We can not decisively discern the influence of the abundance of adult male bass on nest number across lakes; however, bass catch per effort ranged from 47 – 92 largemouth bass per hour and was not correlated with the number of nests located in each lake ($r = 0.28$, $P = 0.59$), nor was it related to the average probability of success in each lake ($P = 0.30$; A. K. Jubar and M. T. Bremigan, unpublished data). Determining the potential influence of male bass abundance on the number of nests and nest success is further complicated by the fact that not all adult males breed each year (Raffetto et al. 1990).

We reasoned that if nests were disproportionately abundant along undeveloped shorelines and rare along developed shorelines, that this would be an indication that local LSD influences nest site choice (or the very early success or failure of nests, i.e., failure before we detected them). Although local habitat features of nest sites have been studied (Gross and Kapuscinski 1997; Rejwan et al. 1999), to our knowledge, the distribution of nest sites relative to local LSD status has not been evaluated. Given the propensity of bass to select nest sites with nearby structure (Bozek et al. 2002; Hunt and Annett 2002), one would expect fewer nests to occur along developed shorelines, due to the reduction in coarse woody material that occurs due to residential LSD, which has been documented in northern Wisconsin lakes (Christensen et al. 1996) and our study lakes (Jubar 2004).

There was substantial variation among lakes with regards to the distribution of nests relative to development type. Overall, patterns appeared to roughly correspond to lakewide LSD. For example, Bruin Lake, our lowest development lake with bass nests, was the only lake in which nest distribution did not differ from random, with respect to development type and wind exposure. From this pattern we infer that strong selection for development status or wind exposure did not occur. The majority of nests in Bruin Lake were located along undeveloped shoreline, indicating that strong "selection" was not necessary because the majority of available shoreline was of this type. In contrast, in Patterson Lake, our highest development lake, strong selection for nesting along undeveloped shoreline with low wind exposure was evident. The majority (~65%) of nests were located in this category that comprised only ~10% of the shoreline. In the remaining three lakes, we saw intermediate results, generally with selection for undeveloped and developed maintained shoreline, and avoidance of developed retained shoreline. In fact, developed retained shoreline was avoided in all but one lake (Halfmoon). It may be that additional habitat features need to be taken into account to explain the distribution of bass nests in lakes. For example, in Halfmoon Lake, where nests were concentrated along developed maintained shorelines with low wind exposure, much of the undeveloped shoreline was of poor habitat quality for nesting, consisting of shallow (< 0.5 m) depths, and consolidated, compacted substrates with little cover. Poor "natural" habitat likely also explains the lack of nests in Blind Lake, where most of the littoral substrate consisted of consolidated clay (A. K. Jubar, pers. observation). Although the observed patterns did roughly correspond to LSD patterns, we cannot rule out other factors that may influence nest distribution. For example, Rejwan et al. (1999) identified a positive relationship between smallmouth bass nest densities and temperature and shoreline reticulation in Lake Opeongo, Canada.

Conclusions.—Elucidating the spatial scale at which controlling factors operate is a challenge in ecological studies. The use of multilevel models, however, as were used in our study, allows for the investigation of potential controlling factors (i.e., covariates) at multiple spatial scales in a single statistical model. We determined that, although local habitat characteristics are likely important factors affecting nesting success, lakewide features of lakes are also important (actually more important in our study) and they help explain large-scale patterns in nesting success that would be missed if only local habitat characteristics or single lakes were considered.

Understanding the ecology and management of black bass is challenged by the disconnect between the effects of fishing and habitat on individual nests, and the ultimate population level effects. Certainly events after nesting are also important contributors to recruitment. To date, most research on black bass nesting success has been done in ponds or sections of lakes, in an experimental context. Such work is important, but it does not quantify the magnitude of anthropogenic and natural effects at the whole-lake scale. Our findings demonstrate that dwelling density warrants more attention. It provides valuable information for modelers by quantifying the scope of the response and hence it begins to define the compensatory capacity (in subsequent life stages) needed to nullify negative effects of lakeshore dwelling density on nest success. This constitutes a critical step in ultimately determining the population level effects of habitat modification and fishing on black bass recruitment.

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TABLE 1.—Lake morphometry and water quality characteristics for the six study lakes surveyed for black bass reproductive success. Shoreline complexity 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.

Lake	Dwelling density (dwellings/km)	Lake area (ha)	Mean depth (m)	Total phosphorus (µg/L)	Shoreline Complexity
Bruin	7.8	52.7	3.74	15.3	1.20
Blind	9.5	28.8	4.05	12.5	1.32
East Crooked	14.6	100.5	3.97	19.9	1.84
Halfmoon	17.7	97.4	6.77	13.1	2.12
North	21.5	90.5	3.53	16.6	1.67
Patterson	22.3	64.1	5.58	22.0	1.79

TABLE 2.— List of covariates used in the analysis of largemouth bass nest success using a generalized linear mixed model. Level 1 covariates are those measured at the nest-scale; level 2 covariates are those measured at the lake scale.

Level 1 covariates	Level 2 covariates
Dominant substrate type	Lakeshore development (dwellings/km)
Presence/absence of cover (boulders, woody debris, macrophytes)	Angler effort (hrs/km)
Depth (m)	Total phosphorus levels (μg/L)
Lakeshore development type	
Distance to shore (m)	
Wind exposure (high, low)	

TABLE 3.—The total number of largemouth bass nests and the number of successful and failed nests located at each study lake. The sum of the numbers of successful and failed nests is less than the total number of nests because the total number of nests includes those nests for which the fate could not be determined. Lakes are ordered according to increasing dwelling density.

Lake	Total number of nests	Successful nests	Failed nests
Blind	0	-	-
Bruin	21	12	5
East Crooked	48	23	9
Halfmoon	24	9	9
North	51	19	18
Patterson	34	10	16

Figure 1

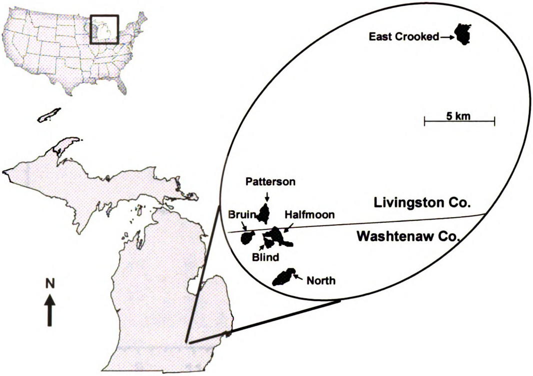

East Crooked
5 km
Patterson
Bruin
Halfmoon
Livingston Co.
Washtenaw Co.
Blind
North
N

Figure 2

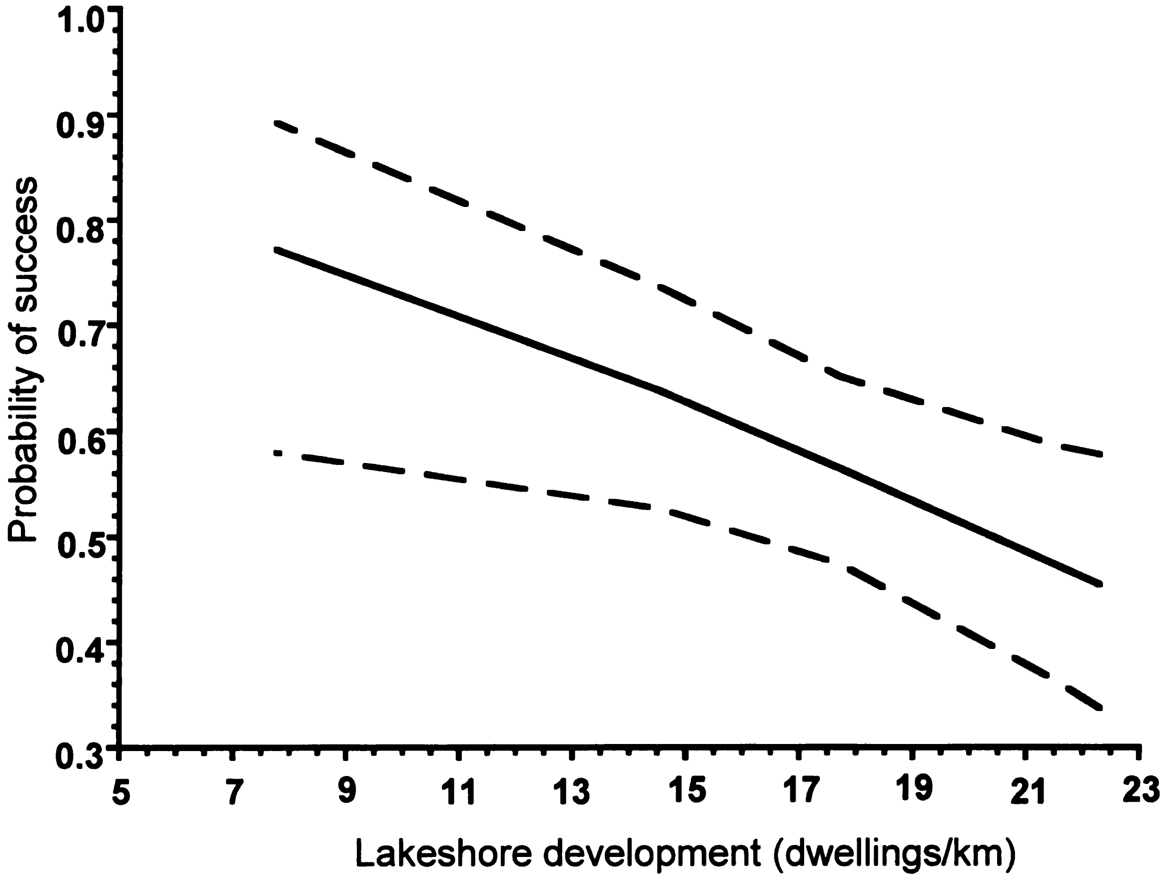
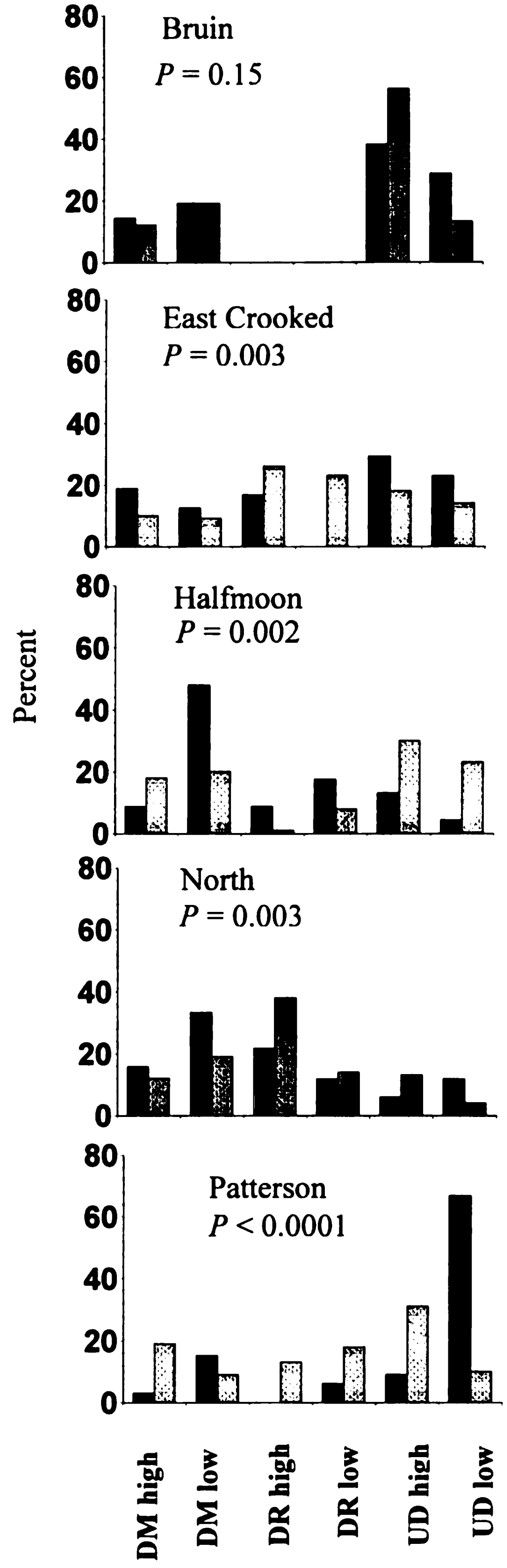

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Probability of success
5
7
9
11
13
15
17
19
21
23
Lakeshore development (dwellings/km)

Figure 3


Bruin
P = 0.15
East Crooked
P = 0.003
Halfmoon
P = 0.002
North
P = 0.003
Patterson
P < 0.0001
Percent
80
60
40
20
0
DM high
DM low
DR high
DR low
UD high
UD low

CHAPTER 4: REGIONAL TRENDS IN FISH MEAN LENGTH AT AGE: COMPONENTS OF VARIANCE AND THE POWER TO DETECT TRENDS

Abstract

We examined statewide time-series (1940s – 2002) of mean length at ages 2, 3, and 4 for seven fish species sampled from Michigan and Wisconsin inland lakes for temporal trends. We also used a components of variance approach to examine how total variation in mean length at age was partitioned into five components, including several sources of spatial and temporal variation. Using these estimated variance components, we simulated the effects of different variance structures on the power to detect trends in mean length at age. Of the 42 datasets examined, only four demonstrated significant regional (statewide) trends. The slope estimate for age 4 largemouth bass from Wisconsin lakes was significant, with an increase of about 0.7 $mm \cdot yr^{-1}$ in mean length at age. In contrast, ages 2, 3, and 4 walleye from Wisconsin lakes showed a negative trend, decreasing between 0.5 and 0.9 $mm \cdot yr^{-1}$. The structure of variation differed substantially among datasets and these differences strongly affected the power to detect trends. To maximize trend detection capabilities, fisheries management agencies should consider variance structures prior to choosing indices for monitoring and realize that trend detection capabilities are species-specific.

Introduction

Knowledge of trends in fish growth rates is important ecologically, as growth rates influence ecological interactions and population dynamics, and are often used along with recruitment and mortality information to assist management decisions (Trippel 1993). Furthermore, growth rates are influenced by environmental conditions and can represent an integrative measure of conditions experienced by a fish over its lifetime. Consequently, one goal of many fishery monitoring programs is to determine whether growth of fish populations (e.g., mean size at age) is changing with time and if so, if such changes are consistent across species and across systems. Most work on evaluating trends in fish growth have focused on individual populations (e.g., Reckahn 1986). There have been some regional evaluations of trends in fish demographics, although most have emphasized abundance (McDonough and Buchanan 1991; Beard and Kampa 1999; Maceina and Bayne 2001; Grant et al. 2002), the majority of aquatic work evaluating trends has emphasized single systems and water quality across rivers (Antonopoulos et al. 2001), lakes (Jassby et al. 1999), and seas (Sandén and Håkansson 1996). Although investigations into temporal trends within individual systems provide valuable information, the ability to detect regional (e.g., statewide) temporal trends is crucial for the evaluation of many management actions and to examine responses to natural or anthropogenic perturbations. Furthermore, the early detection of regional changes is important in many cases to allow time for managers and policy-makers to respond and take appropriate action (Vaughan et al. 2001). This said, detection of regional trends in fish growth (or other parameters) is a challenge, both because available data are often limited, and because regional trends can become obscured by the large amount of temporal variation common to the region and unique to particular populations within a region. In this study we provide one approach to evaluating regional trends in fish growth (mean size at age), and then use the estimated structures of variance to evaluate the statistical power of different sampling designs for detecting regional trends in fish growth to lend insight into design and feasibility of reliable monitoring programs.

Trends and components of variance

A components of variance approach has been advocated to address the issue of variability in ecological data when evaluating regional temporal trends and monitoring of ecological systems (Urquhart et al. 1998; Larsen et al. 2001; Kincaid et al. 2004). Under this framework, total variance is partitioned into four components including, (1) site-to-site (spatial) variation, (2) coherent (year-to-year) variation affecting all sites (e.g., lakes) in a similar manner, (3) ephemeral temporal variation (e.g., site-by-year interaction) corresponding to independent yearly variation at each site, and (4) residual variation (Larsen et al. 2001; Kincaid et al. 2004). A fifth component can be included in this framework. In this approach, each site has its own trend (i.e., trend variation: allowing the slope of the response variable versus time at each site to be a draw from a distribution and estimate the variance of the distribution of slopes).

Although the total variance of the data is one of the primary factors affecting the ability to detect trends (Stow et al. 1990), the partitioning of the total variance among these sources also influences statistical power. Power analysis is a useful tool for evaluating the performance of ecological monitoring programs (Peterman 1990; Fairweather 1991; Hatch 2003) and in particular for investigating how specific variance components affect the power to detect trends. Ideally, a monitoring program should have high statistical power, the ability to detect a specific deviation from the null hypothesis. More formally, power is defined as $1 - \beta$, where β is the probability of a type II error (failing to reject the null hypothesis when it is actually false).

To our knowledge, a components of variance approach has not been applied to fish growth data (i.e., mean length at age data) within the context of trend detection over a large spatial region (although random effects models have been used to partition variability in fish growth data to test other hypotheses; e.g., Osenberg et al. 1988), even though fisheries agencies are collecting fish growth data through time to monitor regions of lakes and streams (e.g., Hayes et al. 2003). The specific objectives of this study were to (1) determine if trends are evident in mean length at age for seven fish species in Michigan and Wisconsin inland lakes, (2) quantify the components of variance for mean length at age and (3) perform power analyses to investigate the effects of the different components of variance on the statistical power to detect trends, and to evaluate alternative sampling designs.

Methods

Datasets

We obtained mean length at age data for seven fish species from fish growth surveys of inland lakes conducted by the Fisheries Division of the Michigan Department of Natural Resources and the Wisconsin Department of Natural Resources. We included bluegill *Lepomis macrochirus*, pumpkinseed *L. gibbosus*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, yellow perch *Perca flavescens*, walleye *Sander vitreus*, and northern pike *Esox lucius* because of their prevalence in the historical data. In each lake survey, fish growth had been 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 recorded along with the day of year that sampling occurred. We restricted our analyses to mean length at ages 2, 3, and 4 for each species because the reliability of fish aging decreases with increasing age (Ricker 1975) and because these ages had adequate sample sizes.

Mean length at age time series were available beginning in the early 1960s to the early 2000s for fish collected in Michigan and from the late 1940s or late 1950s to the early 2000s for fish collected in Wisconsin (Table 1). Fish were collected using a variety of gear types over the time series. Thus, in an effort to reduce potential biases introduced by using different sampling gear, we only retained fish collected using the same gear type in the analyses for each species, age, state combination (Table 1). For nets, however, (e.g., trap nets and fyke nets) the mesh size was not recorded over time; thus we could not control for any potential changes in mesh size. Historically, fish were not sampled in a truly random design by the state agencies. However, the fish growth surveys used in this analysis represent a large sample of public lakes broadly distributed throughout both states, thus reducing the likelihood of substantial bias.

Temporal trend statistical analysis

A weighted mixed model was used to assess the presence of regional (statewide) linear trends in mean length at age for each species, similar to that suggested by Piepho and Ogutu (2002). Although we restricted our analysis to the investigation of linear trends, if a monotonic increase or decrease is present then a linear trend will be present (Urquhart and Kincaid 1999). Each state, species/age dataset was analyzed separately. States were analyzed separately to reduce potential biases introduced by differences in sampling methodologies between agencies. Each data point (mean length at age) was weighted by the number of fish that contributed to each mean for each lake. To account for potential biases introduced by fish being sampled during different times of the year (i.e., seasonal trends in mean length at age), seasonal trends were examined prior to the interannual analysis by fitting linear and quadratic least-squares regression models (Grant et al. 2004). For each species/age combination with a significant seasonal trend, the regression equation was used to adjust mean length at age to the median sample date.

Because we could not estimate the lake × year interaction effect for most datasets (e.g., the data sets did not contain sufficient data on lakes sampled multiple times within a year or overall sample size was small), we used a simpler model to examine temporal trends that excludes the estimation of the variance due to lake × year interaction. In this case the variance due to the lake × year interaction is contained within the residual error term. Not estimating this parameter, however, does not affect the estimate of the slope. The mixed model fit to detect interannual trends was

(1) $Y_{ij} = \mu + a_i + y(\lambda + t_i) + b_j + e_{ij}$

where Y_{ij} is the mean length at age for lake i in year j, μ and λ are the fixed intercept and slope (fixed regional trend), respectively, y is the j^{th} year minus the mean year used in the analysis. This standardization of year was performed to provide numerical stability. a_i is a random effect for lake i, representing lake-to-lake variability, iid as $N(0, {\sigma_a}^2)$, b_j is a random effect for the j^{th} year (coherent temporal variability), iid as $N(0, {\sigma_b}^2)$, t_i is a random effect for the trend for lake i, iid as $N\left(0,\sigma_t^2\right)$, and e_{ij} is the unexplained error (residual error), iid as $N\left(0,\sigma_e^2\right)$.

Components of variance

To partition the total variance among the various components, where possible, we also fit a mixed model identical to equation 1, except that an additional random effect for the lake × year interaction $\left(c_{ij}\right)$ was added to the model, yielding

(2) $Y_{ij} = \mu + a_i + y\left(\lambda + t_i\right) + b_j + c_{ij} + e_{ij}$

where all parameters are defined as in equation 1 and c_{ij} is the random effect for lake × year interaction (ephemeral temporal variability). Note that e_{ij} represents sampling error that influences the observed mean and its variance and its variance is inversely related to sample size. In practice this means that the model was fit by weighting observations (means for a year and age) by their sample sizes. We estimated variance components using restricted maximum likelihood and P-values were estimated using a likelihood ratio test (Self and Liang 1987). We considered all analyses significant at $P < 0.05$.

Power analysis

We used a simulation approach to examine the statistical power to detect temporal trends using the variance components estimated from equation 2. For each simulation, one thousand datasets were generated containing species specific mean length at age data for a population of lakes (50 or 1,000 lakes, see below) over 25 years. First, a 'true' mean length at age for each lake in the population was generated over the 25 year time period. A trend of known magnitude (e.g., a decease of 1 mm•yr^{-1}) was also incorporated into the dataset. Using the 'true' mean lengths at ages for each lake, an 'observed' mean length at age was then generated for each lake. The observed mean length at age was created by randomly generating lengths for a pre-specified number of fish (ranging from 5 – 30) for each of the lakes from a normal distribution with a mean equal to the "true" mean and variance equal to the estimated residual (sampling) variance from equation 2. From these 1,000 datasets, a user-specified number of lakes (ranging from 10 – 40) were then randomly sampled from the population 50 or 1,000 lakes each year. When the number of fish sampled per lake was held constant, we used the mean number of fish sampled per age class from our surveys $(\bar{x} = 10)$. Thirty lakes sampled per year were used as a realistic number of lakes that could be sampled per year by a management agency when the number of lakes sampled per year was held constant (K. Wehrly, Michigan Department of Natural Resources Fisheries Division, Institute of Fisheries Research, Pers. Comm.). Lakes were sampled without replacement within a year, but all lakes were available for selection each year. Data were analyzed for different sampling durations from 5 up to 25 years and analyzed for the presence of a trend. The model specified in equation 1 was used to test the null hypothesis that $\hat{\lambda} = 0$ for each dataset and the test statistic was calculated and compared to a critical value ($\alpha = 0.05$). Because the data generated depict a situation in which we know the null hypothesis is false (i.e., a trend of known magnitude was incorporated into the data), power was estimated as the percentage of trials (out of 1,000) that rejected the null hypothesis.

We investigated the extent to which the following factors affected the ability to detect a trend (1) increasing trend magnitude (λ ranged from -0.5 – 2.0 mm•yr^{-1}), (2) increasing number of fish sampled per lake (ranging from 5 – 30 fish per lake), (3) increasing the number of lakes sampled per year (ranging from 10 – 40 lakes per year), (4) decreasing lake effect variance, and (5) sampling from a population of 50 or 1,000 lakes. We address factor 1 to provide information on the effects of trend magnitude on power. We address factors 2 and 3 because the number of fish and lakes sampled is an important consideration for sampling designs with respect to allocating personnel and fiscal time and money resources. We address factor 4 to understand how power would increase if lake-to-lake variance was reduced, for example, by using a lake classification scheme. To this end, we reduced lake-to-lake variance by 50% and then reduced it to zero. Finally, we examined factor 5 to examine how the proportion of lakes sampled each year influences statistical power. For simulations for which sampling from a population of 50 or 1,000 lakes did not change the general patterns observed, we report only those results for sampling from a 50 lake population, unless otherwise stated.

Results

Temporal trend

Not all datasets contained enough information to fit model 1. Of 42 datasets examined (7 species × 3 ages × 2 states), we were able to examine temporal trends for only 26 datasets (Table 2). Of the 26 analyses, only four demonstrated significant temporal trends. The slope estimate for age 4 largemouth bass from Wisconsin lakes was significant, with an increase of about 0.7 $\text{mm}\cdot\text{year}^{-1}$ in mean length at age. Ages 2, 3, and 4 walleye from Wisconsin lakes showed a negative trend, decreasing between 0.5 and 0.9 $\text{mm}\cdot\text{year}^{-1}$ in mean length at age (Table 2). For all other analyses, estimates of the slope for the fixed regional trend had absolute values of 0.43 or less, which were not significantly different from zero ($P > 0.05$).

Variance components

We could not estimate the lake$\times$year interaction effect for 20 of 26 of the datasets used in trend estimation. For the datasets where estimation was possible, the structure of variation differed substantially among datasets (Figure 1). Mean residual variation $\left(\hat{\sigma}_e{}^2\right)$ was 54%, and ranged from 18.1 – 75.7% of the total variation. Mean ephemeral temporal variation $\left(\hat{\sigma}_c{}^2\right)$ was 17.2% and ranged from 4.9 – 30.6% of the total variation. The mean percent of total variation attributed to coherent temporal variation $\left(\hat{\sigma}_b{}^2\right)$ was 3.5% and ranged from 0.5% to 8.7%. The mean percent of total variation attributed to lake-to-lake differences $\left(\hat{\sigma}_a{}^2\right)$ was 25.4% and ranged from 5.5 – 50.5%. The mean percent of the total variation due to trend variation $\left(\hat{\sigma}_t{}^2\right)$ was small (mean = 0.1%), ranging from 0.01% to 0.24%.

Power analysis

We investigated the effects of variance structures on statistical power by contrasting two carefully chosen datasets, which had strikingly different variance structures, namely age 4 walleye sampled in Michigan and Wisconsin (Figure 1). Because the slope estimates for the significant analyses of temporal trends ranged from -0.5 to -0.9, we used $\lambda = -1.0$ mm•year^{-1} for simulations in which λ was held constant. Trends less than this would likely not be considered biologically "significant" in the short-term.

The power to detect trends in mean length at age increased, as expected, with increasing trend magnitude (Figure 2). For example, after 15 years of sampling, the power to detect a trend increased from 0.2 – 1.0 as λ decreased from -0.5 – -2.0 mm•year^{-1} for age 4 walleye sampled from Michigan lakes. For age 4 walleye sampled from

Wisconsin lakes, power also increased with trend magnitude, but power at a given number of years and trend magnitude was markedly lower in Wisconsin as compared to Michigan, demonstrating the influence of states' different variance structure.

In an effort to visualize the trade-offs between sampling more fish per lake versus sampling more lakes per year, we plotted power curves for both Michigan and Wisconsin walleye across 10 and 25 year sampling periods (Figure 3). For walleye sampled in Michigan, the greatest increase in power at 10 years of sampling was gained by increasing the number of lakes sampled each year, with only a slight gain in power achieved by increasing the number of fish sampled in each lake. For example, if 30 lakes were sampled per year, increasing the number of fish sampled from 5 – 30 increased power by only 0.05. In contrast, assuming 10 fish were sampled from each lake, increasing the number of lakes sampled from 10 – 40 increased power by 0.3. A similar pattern was observed at 25 years; however, relatively high power (ranging from 0.85 – 1.0) was obtained regardless of the number of lakes or fish sampled (Figure 3).

A different pattern was observed for walleye sampled from Wisconsin (Figure 3). At a 10 and 25 years of sampling, although increasing the number of lakes sampled each year from 10 – 20 increased power, power leveled off and remained relatively low even as the number of lakes increased from 20 – 40. Increasing the number of fish sampled from each lake did increase power; however, this increase was quite small.

Decreasing lake-to-lake variance did not have a noticeable effect on power for either walleye sampled in Michigan or Wisconsin when 60% of the total population of lakes was sampled each year (sampling 30 out of 50 lakes each year). Rather, power remained similar at all sampling durations (Figure 4), but was consistently higher for Michigan compared to Wisconsin lakes. Under the scenario in which 3% of the lakes were sampled each year (sampling 30 out of 1,000 lakes each year), decreasing lake-to-lake variance resulted in an increase in power for walleye sampled in Michigan where lake-to-lake variance comprised 51% of the total variance; however, this pattern of increasing power with decreasing lake-to-lake variance was not observed with the walleye sampled in Wisconsin lakes, where lake-to-lake variance was smaller, comprising 15% of the total variance (Figure 4). Furthermore, when sampling a small percentage (e.g., 3%) of the population of lakes, some models were not estimable over short sampling durations (< 10 yrs) because there were not sufficient data on individual lakes sampled repeatedly over time. Thus, power estimates reported for sampling from the 1,000 lake scenario are only for models that were estimable (i.e., the number of trials was < 1,000).

Discussion

Temporal trend

We detected four significant regional trends out of the 26 datasets analyzed, all of which were from inland lakes sampled in Wisconsin. Of these, one was positive (age 4 largemouth bass) and three were negative (ages 2, 3, and 4 walleye). The magnitude of the trends ranged from 0.5 – 0.9 mm•year^{-1}. No significant regional trends in mean length at age were detected from Michigan inland lakes. Although we detected four significant regional trends, any inference regarding causation is difficult (Stow et al. 1998); however, potential mechanisms can be hypothesized. For instance, potential causal factors of increasing trends in mean length at age could be due to effective regional harvest regulations or increases in regional temperatures resulting in increased growth rates. However, if increases in regional temperature were responsible for the observed increasing trend, then we would expect that more of our datasets would demonstrate such a trend. Thus, temperature alone is likely not responsible for the observed trend. Decreases in mean length at age for walleye could be due to effects of anglers or stocking programs. For example, if stocking rates increased over time or if fish numbers increased for some other reason, then increasing competition for resources could lead to reduced growth rates. This mechanism was also proposed by Li et al. (1996) to explain reduced mean weights of walleye in stocked lakes in Minnesota. However, the observed trends could be due to interactions of changing biotic and abiotic conditions over time, which make it difficult to attribute causality to any single source.

Components of variance

Variance structures (i.e., the proportion of total variance attributed to each component) varied considerably among the six datasets we examined. Across all six datasets, residual variation (variation due to sampling error) comprised the largest proportion ($\bar{x}$ = 54%) of the total variance, while lake-to-lake and ephemeral temporal averaged 25% and 17% of the total variation, respectively. In contrast, coherent temporal variation and trend variation averaged only 3% and 0.1%, respectively. Furthermore, coherent temporal variation was only significantly different from zero in three out of six analyses, while slope variation was only significant in two analyses. However, our variance estimates are within the percentages reported by Osenberg et al. (1988). Osenberg et al. (1988) partitioned variance in growth rates of bluegill and pumpkinseed sunfish into four components, residual error, lake, year, lake×year. On average, residual error variance comprised 69% of the total variance, whereas, lake-to-lake variability and lake×year variation comprised an average of 20% of the total variance. They found that year effects (coherent variation) did not explain any of the variance. For our analyses, the relatively high residual variation is likely due to measurement error (e.g., errors made during the reading of scales for age determination), errors in data processing, crew effects, and collection protocol sampling errors that may have occurred over the time period we examined.

Examining variance structures of monitoring indices has been performed for several lake indicators, primarily using data obtained from the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) in the northeastern U.S.A. The EMAP collected data on a wide range of chemical and biological data, including water chemistry measures of conservative and nonconservative ions and biological measures such as fish and zooplankton species richness (Stemberger et al. 2001; Kincaid et al. 2004). The variance structures in our analysis of fish mean length at age were within the ranges for zooplankton abundance indicators from the EMAP described by Stemberger et al. (2001), although these authors did not estimate slope variation in their study. For zooplankton abundance indicators, percent lake-to-lake variation ranged from 0 – 69%, coherent temporal variation was "small or negligible", ephemeral temporal ranged from 0 – 16%, and residual variation ranged from 14 – 43% (Stemberger et al. 2001).

For some biological indicators, such as fish mean length at age in our study and zooplankton abundances and species richness estimated for the EMAP data, the proportion of residual variance is much higher compared to conservative chemical indicators, such as calcium and magnesium (Kincaid et al. 2004). For conservative chemical indicators, lake-to-lake variation comprises a majority of the total variation and there is relatively low residual variance (Kincaid et al. 2004). The high spatial variation among lakes and low residual variation for conservative ions likely reflects the relative stability of these indicators within lakes over time and space compared to nutrients and biological measurements that are controlled more by within-lake processes and which are more prone to sampling biases (e.g., have higher within-lake spatial and temporal variation). These differences between conservative chemical indicators and biological indicators need to be acknowledged and incorporated into the expectations of monitoring programs. For example, detecting a pre-specified trend for a biological indicator with a large residual variance component will require a longer sampling period compared to indicators with lower residual variances to detect the same trend, all else being equal. Furthermore, agencies should take steps to reduce sampling errors associated with biological indicators in order to improve trend detection. All other sources of variation, with the exception of coherent temporal variation, can also be reduced by manipulating certain aspects of the sampling design (see Larsen et al. 2001 and Urquhart et al. 1998 for details).

Trend detection

We observed the expected increase in power with increasing trend magnitude and sample duration for both the Michigan and Wisconsin analyses. This pattern was also demonstrated using the EMAP data (Urquhart et al. 1998). A striking difference between the Michigan and Wisconsin power analyses, however, was the overall low power observed for the Wisconsin data. Although, we expected power to be lower for the Wisconsin analyses due to the higher proportional and absolute value of the estimated coherent temporal and residual variation compared to the Michigan analyses (see below), we were not certain as to the relative affects of each component (coherent temporal or residual) was on power. Furthermore, because Urquhart et al. (1998) demonstrated the importance of coherent temporal variance in reducing trend detection, we wanted to examine its relative affect compared to the much greater proportion of variance attributed to sampling error. To examine this in more detail, we performed a sensitivity analysis using the Wisconsin data. Again, because the Wisconsin variance components that differed most from the Michigan dataset were the residual variance (comprising 76% if the total variation for WI $(\hat{\sigma}_e{}^2 = 4936)$ versus 18% for MI $(\hat{\sigma}_e{}^2 = 550)$ and coherent temporal variance (comprising 4% of the total variation for WI $(\hat{\sigma}_b{}^2 = 261)$ versus nonsignificant for MI), we concentrated our sensitivity analysis on these two components. We set the residual and coherent temporal variance to 50 and 25% of the estimated values while holding all other variance components at their estimated values. We then reduced them simultaneously while holding all other variances at their estimated values and calculated the mean percent increase in power compared to the "baseline" situation when only estimated values were used. We report the mean percent power increase representing the average percent increase in power over the sampling period (5 – 25 years) compared to a situation using the estimated variance components. The mean percent change was calculated as

$$(3)\quad \frac{\sum_{i=5}^{25}((power\_reduced_i - power\_full_i)/(power\_full_i)\times 100}{21}$$

Where $power\_reduced_i$ is the power to detect a -1.0 mm•year^{-1} trend under the scenario of reduced residual or coherent temporal variation (or both) in year i and $power\_full_i$ is the power to detect the same trend under the scenario using the estimated variance components from equation 2 in year *i*.

The sensitivity analysis revealed that the coherent temporal variation had a large effect on the power to detect trends (Table 4). Reducing the coherent temporal variation to 50 and 25% of the estimated value led to an average percent increase in power of 35 and 95%, respectively. Conversely, setting the residual variance to 50 and 25% of estimated values led to only 3 and 5% increases in power, respectively. Thus, even though coherent temporal variation comprised only 4% of the total variation for Wisconsin and residual variation comprised 75% of Wisconsin's the total variation; coherent temporal variation had a disproportionately large influence on the power to detect trends. However, once the coherent temporal variance was set to 25% of estimated value, setting the residual variance to 25% of estimated value did lead to a slightly larger increase in power, a further 8% increase over the baseline estimates when compared to just setting coherent temporal variance to 25% of estimated value. The strong effect of temporal coherent variation to reduce trend detection capabilities was also demonstrated by Urquhart et al. (1998). Because this source of temporal variation cannot be reduced by changing the design of a monitoring program, only an increased sampling duration will lead to an increase in statistical power (Urquhart et al. 1998; Kincaid et al. 2004). This example illustrates the importance of examining variance components of potential monitoring indices, because even a small (as estimated as percent of the total variation) coherent temporal variation component can reduce trend detection capabilities over the short-term.

Although coherent temporal variation can greatly reduce power, the power to detect trends can also be affected by the allocation of resources to either sample more lakes per year or sample more fish per lake. The effect of increasing the number of lakes sampled each year versus increasing the number of fish sampled from each lake on the power to detect trends is important from a management perspective because this issue represents a trade-off between resource allocations. Should resources be allocated towards sampling more fish from each lake (e.g., obtaining a more precise estimate of each lake's status) or on sampling more lakes within the region? In our analysis of the age 4 walleye Michigan data, obtaining a more precise estimate of a lake's status did not improve trend detection as much as increasing the number of lakes sampled each year. For the age 4 walleye Wisconsin data, again relatively high coherent temporal variation resulted in relatively low power regardless of the sampling design used.

High lake-to-lake (spatial) variance has been shown to reduce the power to detect trends (e.g., Urquhart et al. 1988). However as we show here, the relative importance of lake-to-lake variance is dependent on the proportion of lakes sampled from the population of lakes each year. For example, in our analysis of the age 4 walleye Michigan data, we were able to obtain a better estimate of lake-to-lake variance when we sampled 60% of the lakes each year compared to sampling 3% of the lakes each year. Consequently a reduction in lake-to-lake variance did not have an appreciable effect on power under the 60% sampling scenario. However, when sampling only 3% of the population of lakes each year, lake-to-lake variation became more important and reductions in this source of variation led to an increase in power. Thus, in situations with a large lake-to-lake variance component, it may be advisable to sample some lakes

repeatedly (e.g., sample fixed sites) in order to obtain a better estimate of lake-to-lake variance to increase power. However, as illustrated with the Wisconsin analysis, if coherent temporal variation is present, even a large reduction in other sources of variance may not lead to an improvement in power.

Furthermore, the statistical model used to estimate trends should be considered during the design stage of a monitoring program. In our analyses, some models were not estimable over a short sampling duration when only 3% of the population of lakes were sampled each year. This illustrates how the sampling design (e.g., a simple random sample in our analyses) can affect what kind of statistical model can be used for trend detection. If detecting trends over a short time period is of interest, then having fixed sites in addition to randomly selected sites is desirable. The use of fixed sites will ensure that some lakes are sampled repeatedly over time and thus allow some models to be estimable. Although it was not within the scope of this paper to explore the many alternative sampling designs, the type of sampling design employed, such as the use of fixed sites in combination with a random selection of lakes each year, can affect power to detect trends (Urquhart et al. 1988). With information on the components of variance for desired monitoring indices, management agencies can explore alternate designs in an effort to maximize power.

Conclusions

The use of historical data from state and federal agencies provides one source of data that can be used to investigate the presence of trends in fisheries data for multiple populations (e.g., this study, Reckahn 1986; Beard and Kampa 1999). Much of the historical data, however, were not collected following probability sampling methods, in which every sampling unit has a known probability of being sampled (Olsen et al. 1999). Rather, waterbodies were often sampled based on expert choice (i.e., judgment sampling; Olsen et al. 1999), selected by convenience, or in response to local or regional political concerns (e.g., convenience sampling; Olsen et al. 1999). Although it must be acknowledged that the non-probability based sampling associated with the historical data we used has implications when making statistical inference to the population of lakes or streams as a whole, these data provide a unique opportunity to examine regional trends. Furthermore, because the implementation of probabilistic sampling designs is only now becoming more prevalent, historical data often represent the only source of information that can be used to inform the development of monitoring programs designed to describe the status and to detect trends of aquatic indices.

Although the statistical power to detect trends is important to consider when developing a monitoring program, there are other components of a monitoring program that should also be considered. For example, the costs and benefits of implementing a monitoring design should be considered along with the uncertainties associated with alternative designs (MacGregor et al. 2002). Thus, power analysis represents one source of information to be used in the processes of designing an ecological monitoring program. Examining variance components of desired indices, power analysis, and other quantitative analyses that take into account uncertainties and expected benefits of monitoring programs, represents powerful tools that will help guide fisheries management agencies develop effective monitoring programs.

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Table 1. Fish species, age, sample size (*N*, number of observations used in the analyses), gear type used to collect fish, and sampling years used in the trend analysis for Michigan and Wisconsin inland lakes. MI = Michigan, WI = Wisconsin, BLG = bluegill, PSF = pumpkinseed sunfish, LMB = largemouth bass, SMB = smallmouth bass, YEP = yellow perch, NOP = northern pike, WAE = walleye, EF = electrofishing, TN = trap net, FN = fyke net.

	N		Gear type		Sampling years	
Species (age)	MI	WI	MI	WI	MI	WI
BLG (2)	261	162	EF	EF	1961-2002	1959-2003
BLG (3)	265	216	EF	EF	1962-2002	1958-2003
BLG (4)	261	245	EF	EF	1963-2002	1958-2003
PSF (2)	51	66	TN	EF	1960-2002	1959-2003
PSF (3)	120	132	TN	EF	1960-2003	1959-1992
PSF (4)	143	146	TN	EF	1958-2003	1959-1992
LMB (2)	277	227	EF	EF	1961-2002	1958-2003
LMB (3)	275	285	EF	EF	1963-2002	1959-2003
LMB (4)	243	273	EF	EF	1963-2002	1959-2002
SMB (2)	93	52	EF	EF	1963-2001	1957-2003
SMB (3)	74	47	EF	EF	1963-2001	1957-2003
SMB (4)	61	44	EF	EF	1963-1999	1956-2003
YEP (2)	266	167	EF	EF	1961-2002	1958-2003
YEP (3)	229	203	EF	EF	1961-2002	1958-2003
YEP (4)	185	187	EF	EF	1961-2002	1958-2003

NOP (2)	157	166	FN	FN	1960-2002	1947-2002
NOP (3)	161	176	FN	FN	1957-2002	1947-2002
NOP (4)	151	183	FN	FN	1957-2002	1947-2002
WAE (2)	236	303	EF	FN	1967-2002	1946-2001
WAE (3)	210	401	EF	FN	1967-2002	1946-2001
WAE (4)	176	434	EF	FN	1967-2002	1946-2001

Table 2. Parameter estimates for the fixed effect of sampling year (fixed regional trend (mm•year^{-1}),$\hat{\lambda}$) followed by standard error (s.e.) in parentheses, F-value, and P-value for mean length at age of seven warm and coolwater fish species in Michigan and Wisconsin inland lakes. Significant regional trends are shown in bold (α =0.05). MI = Michigan, WI = Wisconsin, BLG = bluegill, PSF = pumpkinseed sunfish, LMB = largemouth bass, SMB = smallmouth bass, YEP = yellow perch, NOP = northern pike, WAE = walleye, n.e. = not estimable.

	$\hat{\lambda}$ (s.e.)		F-value		P-value	
Species (age)	MI	WI	MI	WI	MI	WI
BLG (2)	-0.176 (0.160)	n.e.	1.20	n.e.	0.282	n.e.
BLG (3)	-0.012 (0.173)	-0.425 (0.195)	0.01	4.73	0.944	0.118
BLG (4)	0.004 (0.198)	-0.413 (0.196)	0.00	4.43	0.983	0.059
PSF (2)	n.e.	n.e.	n.e.	n.e.	n.e.	n.e.
PSF (3)	-0.046 (0.262)	n.e.	0.03	n.e.	0.873	n.e.
PSF (4)	0.066 (0.237)	-0.381 (0.242)	0.08	2.48	0.788	0.176
LMB (2)	-0.221 (0.265)	n.e.	0.69	n.e.	0.412	n.e.

LMB (3)	-0.390	0.306	2.13	0.95	0.157	0.338
	(0.267)	(0.314)				
LMB (4)	-0.292	**0.672**	1.05	**4.59**	0.326	**0.045**
	(0.285)	**(0.313)**				
SMB (2)	-0.202	n.e.	0.23	n.e.	0.655	n.e.
	(0.425)					
SMB (3)	-0.392	n.e.	0.28	n.e.	0.626	n.e.
	(0.743)					
SMB (4)	n.e.	n.e.	n.e.	n.e.	n.e.	n.e.
YEP (2)	-0.077	n.e.	0.19	n.e.	0.665	n.e.
	(0.176)					
YEP (3)	-0.271	n.e.	1.69	n.e.	0.213	n.e.
	(0.210)					
YEP (4)	0.165	n.e.	0.40	n.e.	0.545	n.e.
	(0.260)					
NOP (2)	-0.430	n.e.	0.33	n.e.	0.577	n.e.
	(0.753)					
NOP (3)	n.e.	n.e.	n.e.	n.e.	n.e.	n.e.
NOP (4)	n.e.	-0.036	n.e.	0.01	n.e.	0.947
		(0.435)				
WAE (2)	0.096	**-0.917**	0.05	**10.52**	0.831	**0.002**
	(0.448)	**(0.283)**				
WAE (3)	0.074	**-0.530**	0.01	**4.26**	0.936	**0.042**

	(0.918)	**(0.257)**				
WAE (4)	0.138	**-0.676**	0.03	**8.13**	0.867	**0.005**
	(0.816)	**(0.237)**				

Table 3. Estimated variance components followed by standard error in parentheses from a weighted mixed model examining mean length at age over time for Michigan and Wisconsin inland lakes. Variance components significantly different from zero are shown in bold (α =0.05). YEP = yellow perch, LMB = largemouth bass, WAE = walleye.

Species (age)	Lake-lake $(\hat{\sigma}_a^2)$	Coherent temporal $(\hat{\sigma}_b^2)$	Ephemeral temporal $(\hat{\sigma}_c^2)$	Trend variation $(\hat{\sigma}_t^2)$	Residual error $(\hat{\sigma}_e^2)$
Michigan					
YEP (2)	59.1	**31.6**	**227.1**	0.4	**765.9**
	(91.4)	**(23.5)**	**(100.4)**	(0.43)	**(200.4)**
LMB (3)	**240.9**	32.8	**455.4**	1.4	**1145.0**
	(108.8)	(40.1)	**(121.4)**	(1.1)	**(261.0)**
WAE (3)	**1526.4**	95.5	**533.7**	**8.2**	**1238.8**
	(368.8)	(101.6)	**(168.8)**	**(4.7)**	**(315.4)**
WAE (4)	**1531.8**	16.1	**928.4**	4.9	**549.9**
	(402.0)	(88.4)	**(268.2)**	(4.2)	**(216.1)**
Wisconsin					
WAE (3)	**833.5**	**313.2**	**225.6**	0.4	**2230.9**
	(139.9)	**(179.1)**	**(63.9)**	(0.4)	**(504.9)**
WAE (4)	**1001.8**	**260.7**	**319.3**	**0.8**	**4936.2**
	(167.6)	**(155.6)**	**(87.9)**	**(0.5)**	**(1063.9)**

Table 4. Mean percent increase in statistical power due to setting the estimated residual and coherent yearly variance to 50 and 25% of estimated values. The power estimates correspond to a temporal trend of -1.0 mm•year^{-1} in mean length at age for age 4 walleye sampled in Wisconsin inland lakes. The mean percent increase reported is the average percent increase in power over the sampling period (5 – 25 years) compared to a situation using the estimated variance components from historical data (see Table 3 for variance estimates; population of lakes = 50, 30 lakes sampled each year for 25 years, 10 fish sampled per lake).

	50% of residual variance	25% of residual variance	50% of coherent temporal variance	25% of coherent temporal variance	25% of coherent temporal and residual variance
Mean percent increase	3	5	35	95	103

Figure 1.

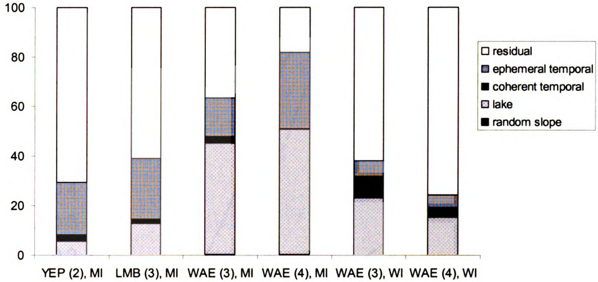

100
80
60
40
20
0
YEP (2), MI
LMB (3), MI
WAE (3), MI
WAE (4), MI
WAE (3), WI
WAE (4), WI
☐ residual
▦ ephemeral temporal
■ coherent temporal
▨ lake
■ random slope

Figure 2.

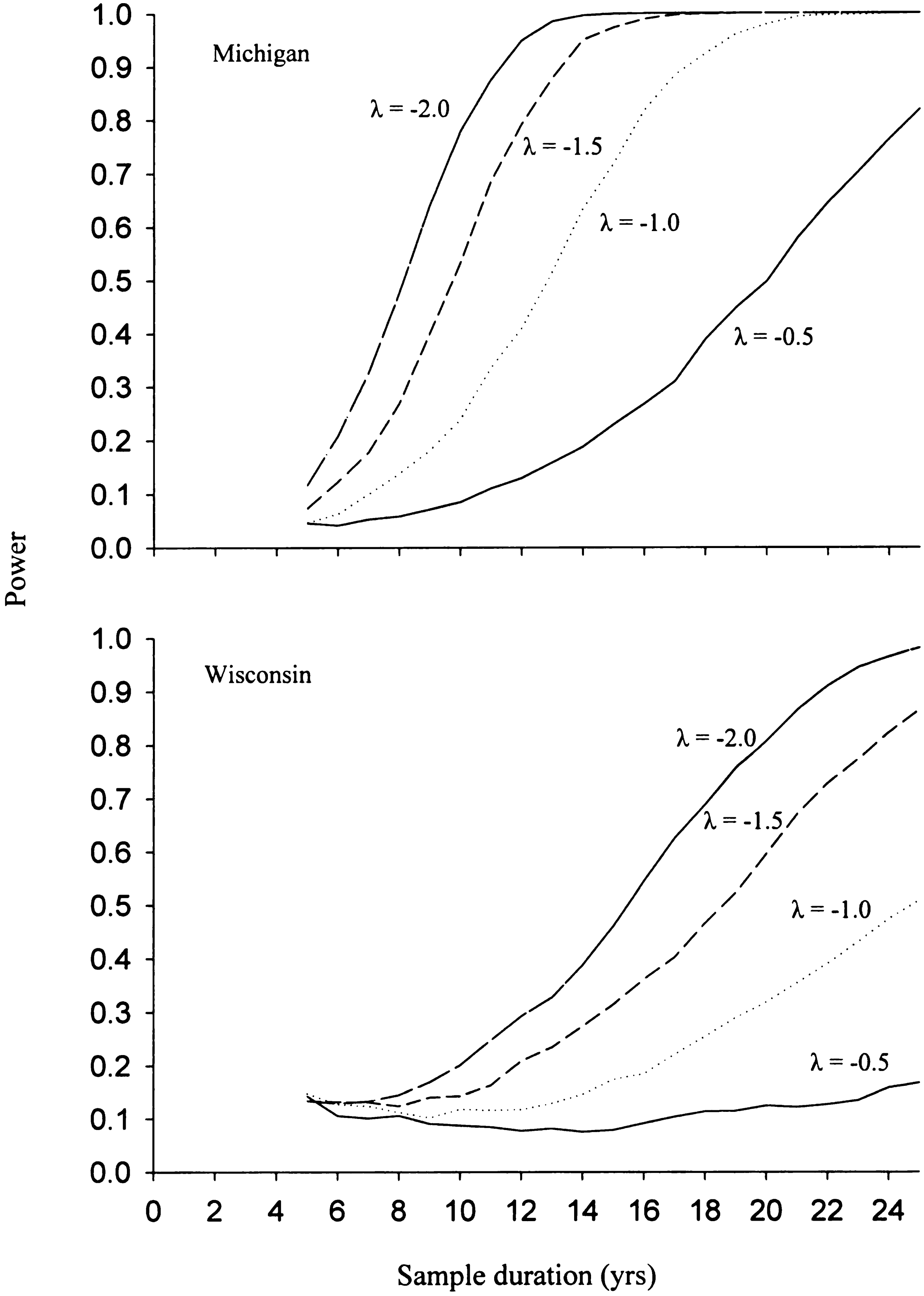
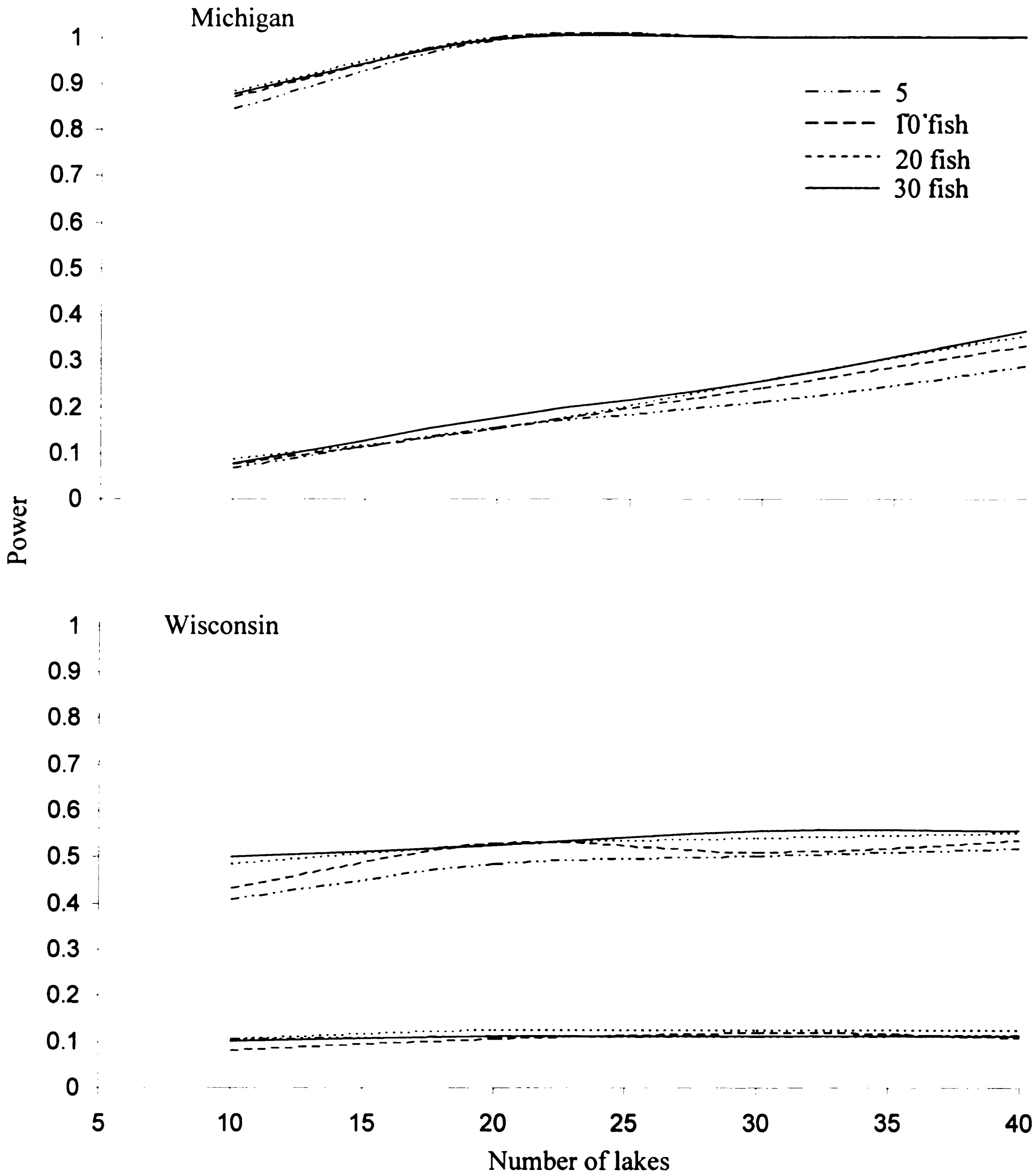
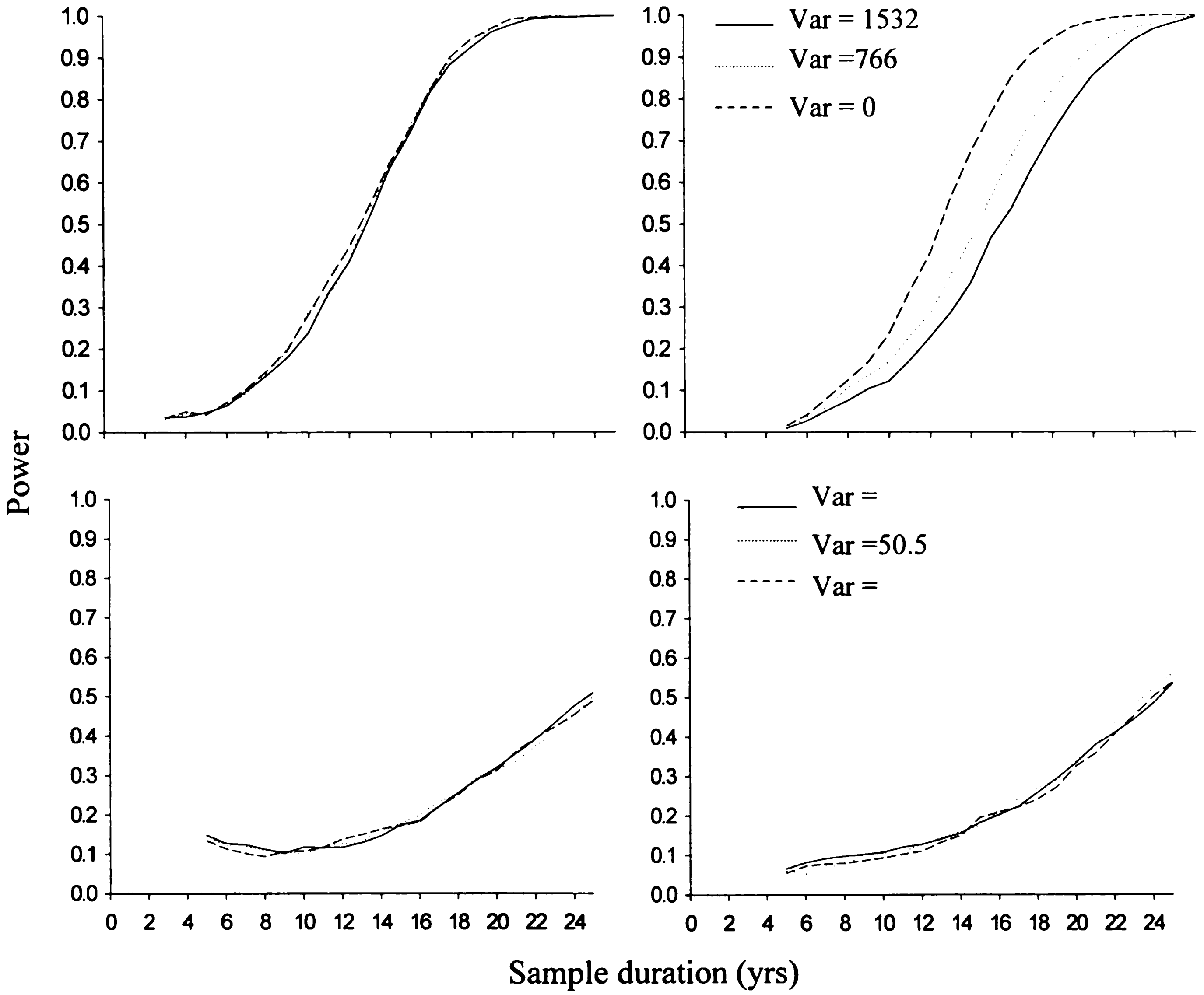

Power
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Michigan
λ = -2.0
λ = -1.5
λ = -1.0
λ = -0.5
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Wisconsin
λ = -2.0
λ = -1.5
λ = -1.0
λ = -0.5
0
2
4
6
8
10
12
14
16
18
20
22
24
Sample duration (yrs)

Figure 3.


Michigan
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10 fish
20 fish
30 fish
Power
Wisconsin
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
35
40
Number of lakes


Power
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Var = 1532
Var =766
Var = 0
Var =
Var =50.5
Var =
0
2
4
6
8
10
12
14
16
18
20
22
24
Sample duration (yrs)