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VARIABILITY IN FISH GROWTH RATES IN RELATION TO PHYSICAL AND LANDSCAPE CHARACTERISTICS OF MICHIGAN AND WISCONSIN INLAND LAKES

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VARIABILITY IN FISH GROWTH RATES IN RELATION TO PHYSICAL AND LANDSCAPE CHARACTERISTICS OF MICHIGAN AND WISCONSIN INLAND LAKES

By

Nancy Ann Nate

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ABSTRACT

VARIABILITY IN FISH GROWTH RATES IN RELATION TO PHYSICAL AND LANDSCAPE CHARACTERISTICS OF MICHIGAN AND WISCONSIN INLAND LAKES

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The goal of this research was to explore the use of historic fisheries survey information to explain variability in fish growth rates in relation to physical and landscape characteristics of Michigan and Wisconsin inland lakes. First, estimates of fish mean length at age, and of von Bertalanffy growth parameters estimated from mean length at age, can be biased if based only on age information collected from length-stratified sub-samples. To evaluate the potential for using historic length-stratified sub-samples to compare the average growth of fishes across Michigan lakes, I quantified the sub-sample bias in estimates of mean lengths at ages 2–4 and von Bertalanffy growth parameters for bluegill, largemouth bass, and yellow perch. In regression analysis of sub-sample based estimates versus sample based estimates, only 4 of 15 possible tests indicated significant bias in sub-samples relative to samples, however the magnitude of the variability in bias around von Bertalanffy estimates across lakes was large for all species tested. Therefore, historic growth data sets that lack complete sampling information (e.g., sample length frequencies) can still provide meaningful comparisons of growth among lakes or over time if comparisons are limited to mean lengths at ages.

Next, I evaluated a lake classification scheme consisting of 6 lake classes differing in landscape position, connectivity, and maximum depth for use in managing angling fisheries in inland lakes. I used analysis of variance to determine if lake classes accounted for variability in fish species richness in 256 Wisconsin lakes and in mean lengths at age 4 of bluegill, largemouth bass, walleye, and yellow perch in 358 Michigan and 410 Wisconsin lakes. Fish species richness and mean lengths of age 4 bluegill, largemouth bass, and walleye varied among lake classes, but not all lake class pairs differed. Map-based variables related to temperature and habitat area were then evaluated using regression tree analyses to refine the classification for each response variable. Lake surface area was an important predictor of fish species richness, and mean lengths of age 4 bluegill and largemouth bass, whereas latitude was an important predictor of mean lengths of age 4 yellow perch and walleye. Regression tree results revealed species-specific separation points for identifying categories of lake size (large and small lakes), and for stratifying the region into northern and southern zones.

Finally, to evaluate the lake classification scheme developed in Chapter 2 for use in management, I determined expected ranges of bluegill growth and mortality for different lake classes in Wisconsin from existing survey data to determine the best combination of minimum length limits (152, 178, 203, and 229 mm) and daily creel limits (25, 10, 5) to maximize yield per recruit and number of bluegill harvested per 100 individuals for each lake class. For each combination of minimum length limit and daily creel limit, yield per recruit increased with lake size, from the smallest lake class to the largest lake class, and ranged 4–30 grams per recruit among regulation scenarios. My results provide ranges of bluegill growth, natural mortality, and fishing mortality for lake classes that may be used to evaluate future regulation proposals and to identify candidate lakes for experimental regulations.

DEDICATION

For my husband Michael J. Hansen.

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INTRODUCTION

Individual lakes, within and across broad geographic areas, differ greatly in inherent internal physical, chemical, and biological attributes, local and regional landscape settings, and fish community assemblages. Within individual lakes, fish population levels may fluctuate over time due to biotic and abiotic factors, such as food availability, predation, competition, lake level, drought, and storm events (Van Den Avyle 1993). The complex forces that continually shape fish populations operate at different spatial and temporal scales, which can add to management uncertainty and risk when setting fisheries management policy for an entire state.

Often fisheries management policies relating to angling regulations are established for large geographic areas (e.g., states or regions within states), so factors that affect fish populations across large geographic areas need to be understood. However, most investigations of fish populations and community dynamics in inland lakes tend to be small scale, either following populations in one lake through time (e.g. Forney 1977; Hansen et al. 1998), or multiple populations in several lakes in a small geographic area (e.g. Tonn and Magnuson 1982, Carpenter and Kitchell 1993). These studies provide insight into the temporal dynamics and current status and trends of fish populations in close geographic proximity, but may not sufficiently explain spatial variability among lakes, status and trends of a statewide resource, or the impact of a statewide fisheries management strategy. Many ecosystem patterns and processes only emerge at larger scales (Levin 1992). Further, variability of fish population growth, recruitment, or mortality may be erroneously attributed to spatial variability among lakes if considered separately and independently from temporal changes (Wiley et al. 1997). Therefore, 00studies that are large both in spatial and temporal scale are needed to accurately partition fish population variability into its respective components. Through this integration, underlying processes that affect survival, growth, and recruitment may be more easily and accurately identified.

Large-scale research in time and space is not common because of the time and expense involved in data collection. However, Michigan Department of Natural Resources Fisheries Division and Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection personnel have conducted fisheries surveys on lakes throughout the states of Michigan and Wisconsin. Historic survey data collected as part of routine surveys across two states were not collected as part of a standardized or organized sampling program, but due to the large spatial and temporal coverage, may still provide insights into patterns and processes that operate at large spatial and temporal scales. With some careful investigation of potential biases, historic fisheries survey data may be used to classify lakes to account for lake-to-lake variability in fish populations, explore long-term changes, characterize the scope of inter-annual variability, and ultimately generate statewide management strategies. Ideally, the classification scheme could then be used to predict the productive potential and sustainability of fish populations in lakes for which recent survey information is lacking.

Many lake classification schemes have been developed to explain patterns in fish community assemblages and species abundance by exploring relationships with measured within-lake physical, chemical, or biological characteristics at the local scale (Schneider 1975; Johnson et al. 1977; Tonn et al. 1983; Matuszek and Beggs 1988; Dolman 1990; Schupp 1992). In fact, a large portion of variability in species assemblages and abundance among lakes has been explained through classification based on measured lake habitat characteristics. Part of the variability in species assemblages or abundance left unexplained in these classification schemes may be attributed to temporal changes in fish population dynamics or to processes operating at larger spatial scales (but not included in the classification). These confounding factors may cloud our ability to see clear relationships between fish population characteristics and habitat variables. Therefore, by including temporal changes in population dynamics within the context of a classification scheme that accounts for spatial variability among lakes at several spatial scales, factors that affect fish population dynamics may be more accurately identified. Further, classification schemes that account for variability in ecological processes like growth or life history strategies, which indirectly may influence abundance, are less prevalent but may provide additional framework for making management decisions or for research into causal mechanisms (Shuter et al. 1998). Ecologically similar lakes are expected to respond similarly to management actions (Emmons et al.1999).

The goal of this research was to explore the use of historic fisheries survey information to explain variability in fish growth rates in relation to physical and landscape characteristics of Michigan and Wisconsin inland lakes. To do so, I focused on three main objectives 1) to determine if von Bertalanffy growth parameters and mean lengths at age estimated from length-stratified sub-samples were biased in relation to parameters estimated from full samples for game fishes surveyed routinely in Michigan lakes, 2) to determine if an existing lake classification scheme explained variability in fish species richness and mean length at age from historic survey data collected on Michigan and Wisconsin lakes, and 3) to demonstrate how lake classification may be used in management by estimating how bluegill yield per recruit and number harvested varied as a function of minimum age entering the fishery and fishing mortality rate among four classes of Wisconsin inland lakes.

CHAPTER 1

COMPARISON OF GROWTH PARAMETERS FROM LENGTH STRATIFIED SUB-SAMPLES AND SAMPLES IN MICHIGAN LAKES

Abstract. — Estimates of mean length at age, and of von Bertalanffy growth parameters estimated from mean length at age, can be biased if based only on age information collected from length-stratified sub-samples. To evaluate the potential for using historic length-stratified sub-samples to compare the average growth of fishes across Michigan lakes, I quantified the sub-sample bias in estimates of mean lengths at ages 2–4 and von Bertalanffy growth parameters for bluegill, largemouth bass, and yellow perch. In regression analysis of sub-sample based estimates versus sample based estimates, only 4 of 15 possible tests indicated significant bias in sub-samples relative to samples. Von Bertalanffy growth parameters indicated that yellow perch early growth (ω) tended to be higher when estimated from sub-samples than from samples, but indicated no bias for bluegill L_∞ and for largemouth bass ω and L_∞. While regression tests showed that sub-sample estimates were generally linearly related to estimates from samples, the magnitude of the variability in bias around von Bertalanffy estimates across lakes was large for all species tested. My findings suggest that mean lengths at ages 2–4 for bluegill, largemouth bass, and yellow perch estimated from length-stratified sub-samples were not generally biased, but that the large variation in von Bertlanffy parameter estimates limits their utility for use in among-lake comparisons. Therefore, historic growth data sets that lack complete sampling information (e.g., sample length frequencies) can still provide meaningful comparisons of growth among lakes or over time if comparisons are limited to mean lengths at ages 2–4.

Introduction

Fish growth affects many aspects of fish population dynamics. Body size influences age at maturity (Trippel 1995), fecundity (Baccante and Reid 1988), recruitment (Madenjian et al. 1996), and mortality (Madenjian and Carpenter 1991). Growth rates during early life stages can directly affect size-dependent mortality by determining the timing and duration of vulnerability to predators (Osenberg and Mittelbach 1988; Olson 1996), and size at the end of the first growing season can influence over-winter survival in some species (Madenjian and Carpenter 1991; Ludsin and DeVries 1997).

Fish growth can be an important indicator of environmental conditions within lakes (Diana 1995), so growth may be useful for classifying variability in fish populations among lakes for the purpose of management. Lakes that are ecologically similar should support populations with similar growth rates, and therefore respond similarly to management actions such as angler regulations. The success of many angler regulations that seek to increase the size structure or numbers of large fish in lakes depends largely on the growth potential of the population. For example, for minimum size limits to be effective, growth potential should be sufficiently high for fish to reach the minimum size vulnerable to harvest (Van Den Avyle 1993). If growth potential is low and abundance of small fish is high, preventing juvenile harvest with minimum size limits may exacerbate poor size structure.

Fish growth is often estimated from mean length at age and fisheries biologists often sub-sample a fixed number of fish per length category for estimating mean length at age for a population (Murphy and Willis 1996). Sub-sampling a fixed number of fish per length category and using the sub-sample to estimate the mean length and variance at age may result in biased estimates of mean length, because the distribution of lengths around any one age is often skewed (Goodyear 1995; Bettoli and Miranda 2001). Biased estimates of mean length at age will inflate standard error estimates, thereby leading to an increase in type II errors (failure to detect an effect; Bettoli and Miranda 2001). Bias is more likely for ages that are not well represented in the sample, often the youngest or oldest ages (Haddon 2001). Further, growth parameter estimates from the von Bertalanffy growth equation are greatly influenced by the youngest and oldest ages in the sample, which tend to be the least well represented (Ricker 1975; Haddon 2001). The use of length-stratified sub-sample mean lengths at age to estimate von Bertalanffy growth parameters for comparative analyses among lakes should be evaluated.

My objective was to determine if mean lengths at age and von Bertalanffy growth parameters estimated from length-stratified sub-samples were biased in relation to parameters estimated from full samples for game fishes surveyed routinely in Michigan lakes. I quantified the bias between estimates of mean lengths at age and von Bertalanffy growth parameters from length-stratified sub-samples of fish and sample mean lengths at age reconstructed using an age-length key. My goal was to evaluate the potential for using historic mean length at age summaries from length-stratified sub-samples to characterize average growth of fishes and to compare growth parameters among lakes.

Methods

Lake Selection Criteria

Fisheries survey data were obtained from the Michigan Department of Natural Resources, Fish Collection System (FCS) in June 2003. Fishery surveys were conducted on Michigan lakes between 1993 and 2002. Fishery surveys were included if (1) the data entry and results were approved through an established quality assurance protocol, (2) the full sample length frequency included ≥ 100 fish, (3) at least five age classes were present in the sub-sample, and (4) the sub-sampling was length-stratified (i.e. a specified number of fish per length class were sub-sampled for age estimation). Surveys from 126 lakes satisfied these criteria, including 111 surveys for bluegill *Lepomis macrochirus*, 22 surveys for largemouth bass *Micropterus salmoídes*, and 24 surveys for yellow perch *Perca flavescens*.

Statistical Analysis

To quantify bias in estimates of mean lengths at age 2, 3, and 4, and von Bertalanffy growth parameters from length-stratified sub-samples and samples, mean length at age was estimated directly from sub-samples of fish, and from samples of fish using age-length keys (Ricker 1975; Haddon 2001). Age length keys were constructed from length-stratified sub-sample length and age information and were used to reconstruct the age distribution from the length frequency of each sample (Ricker 1975). Sample mean lengths at age were then calculated from the new age frequency distribution. Mean length at age for the sample was taken as the sum of products between mid-point lengths of each length interval and the number of that age in each length interval, divided by the total number of fish in the age class. Mean length at age from the sub-sample was taken as the arithmetic mean of the lengths at each age. Ages 2–4 were selected because these ages were likely to be estimated correctly for all species and to make explicit comparisons to results from Betolli and Miranda (2001). Length-stratified sub-samples were collected during the same survey, thereby avoiding potential bias in using an age-length key to estimate age-frequency when sub-sample information was not collected during the same period (Westrheim and Ricker 1978).

The Gallucci and Quinn (1979) modification of the von Bertalanffy growth equation was used to estimate early growth rate (ω) and the mean asymptotic length (L_∞) for each species in each lake from mean lengths at age for sub-samples and samples:

$$L_t = L_\infty \left(1 - e^{-\left(\omega / L_\infty\right)\left(t - t_0\right)} \right)$$

The modified von Bertalanffy model describes how length (L) at age (t) increases from the hypothetical age at zero length (t_0) toward the average asymptotic length (L_∞) at rate ω. The modified von Bertalanffy model reduces the correlation between the traditional von Bertalanffy parameters K and L_∞, provides a rate of growth in tangible units (e.g., ω = inches per year), and provides a superior fit to growth data (Chen et al. 1992). Parameters and their asymptotic standard errors were estimated using nonlinear regression, with additive errors. Parameter estimates were excluded if the estimated asymptotic length exceeded the state record by 10%.

I tested for differences in growth indices (mean length at ages 2, 3, and 4, and von Bertalanffy growth parameters ω and L_∞) between sub-samples and full samples using geometric mean functional regression (GM regression; Sokal and Rohlf 1995). Geometric mean functional regression is appropriate when the independent variable is subject to natural variability (Ricker 1975). The t statistic was adjusted to test whether the slope differed significantly from one by taking (1 – slope)/SE. Bias was inferred if the slope of the regression was significantly greater than or less than one or if the intercept was significantly less than or greater than zero ($P \leq 0.05$).

Because I was interested in using sub-sample growth indices for among-lake comparisons, I quantified the magnitude of the bias in growth indices from sub-samples relative to the actual variation in unbiased growth indices from samples, across all surveys as the "relative sub-sample bias":

$$\frac{\sum\limits_{surveys}(G_{sub} - G_{full})^2}{\sum\limits_{surveys}(G_{full} - \overline{G}_{full})^2}$$

In this equation, G_{sub} is the growth index from the sub-sample (mean length at ages 2, 3, and 4, and von Bertalanffy growth parameters ω and L_∞), G_{full} is the growth index from the sample, and $\overline{G}_{full}$ is the mean of the growth index for samples. If the relative sub-sample bias was greater than 10%, we considered the growth index to be unreliable for among-lake comparisons.

Results

Regression tests indicated little bias in mean lengths at ages 2–4 estimated from sub-samples. Mean lengths at age estimated from sub-samples and samples did not differ for bluegill of ages 3–4, largemouth bass of ages 2–4, or yellow perch of ages 2–4 (slope = 1 and intercept = 0; Table 1 Figure 1). In contrast, bluegill mean length at age 2 was overestimated for small fish from sub-samples and underestimated for larger fish from sub-samples (slope < 1 and intercept > 0; Table 1; Figure 1). Absolute differences between mean lengths at age from sub-samples and samples ranged from 0.0 to 0.9 in for bluegill, from 0.0 to 0.7 in for largemouth bass, and from 0.0 to 1.0 in for yellow perch.

Similarly, regression tests indicated little bias in von Bertalanffy growth parameters estimated from sub-samples. For bluegill, L_∞ did not differ between sub-samples and samples, and for largemouth bass, ω and L_∞ did not differ significantly between sub-samples and samples (Figure 2). In contrast, ω for bluegill and L_∞ for yellow perch were lower when estimated from sub-samples than when estimated from samples, and the absolute bias increased with the magnitude of the sample parameter estimate from a y-intercept that was not different from zero (Table 2; Figure 2). In addition, ω for yellow perch was consistently over-estimated from sub-samples, because the y-intercept was greater than zero and the slope was not significantly different from 1.0 (i.e., absolute bias was constant and positive; Table 2). Absolute differences in L_∞ from sub-samples and samples ranged from 0.003 to 3.755 in for bluegill, from 0.057 to 6.751 in for largemouth bass, and from 0.012 to 4.748 in for yellow perch.

While regression tests indicated little overall bias in growth indices from sub-samples (i.e., significant linear relationships), relative sub-sample bias was large for some growth indices. Relative sub-sample bias in mean lengths at age were less than 10% for all species and ages except for yellow perch mean length at age 3 (Table 3). In general, relative sub-sample bias in mean length at age was small and ranged from 3.1% to 14.1% (Table 3). In contrast, relative sub-sample bias in von Bertalanffy growth parameters was large and ranged from 16.9% to 51.1% (Table 3). Estimates of L_{∞} were more variable than ω for all species (Table 3).

Discussion

I found that mean lengths at age and von Bertalanffy growth parameters estimated from length-stratified sub-samples were linearly related to parameters estimated from full samples for bluegill, largemouth bass, and yellow perch. Only 4 of 15 possible tests indicated significant bias in sub-samples relative to samples. In general, when evident, bias was larger for von Bertalanffy estimates than for mean length at age estimates. For largemouth bass, mean length at age and von Bertalanffy growth parameters estimated from sub-samples were not significantly biased, whereas for bluegill and yellow perch, some mean length at age and von Bertalanffy growth parameters estimated from sub-samples were biased. For example, bluegill mean length at age-2 tended to be overestimated from sub-samples for small age-2 bluegill, and underestimated from sub-samples for larger age-2 bluegill. Bluegill ω and yellow perch L_{∞} were underestimated from sub-samples (regression slope < 1), whereas yellow perch ω was consistently overestimated from sub-samples.

I found that mean lengths at age of bluegill, largemouth bass, and yellow perch from sub-samples were generally no different than mean lengths at age from samples (highly correlated 1:1 relationships), in contrast to studies by Betolli and Miranda (2001) and Goodyear (1995) who found that mean lengths at age from length-stratified sub-samples were biased in relation to random samples. Bettoli and Miranda (2001) showed that mean size at age 2 for a single largemouth bass population was less when estimated from a length-stratified sub-sample than when estimated from the full sample, whereas the mean size at age 4 was greater when estimated from the sub-sample than when estimated from the full sample. Similarly, Goodyear (1995) used computer simulations to evaluate the effect of sub-sampling on estimates of mean length at age of red grouper *Epinephelus morio*, and found that mean length of young grouper was underestimated and mean length of older grouper was overestimated by sub-samples. Bettoli and Miranda (2001) cautioned against using mean lengths at age from non-random stratified sub-samples to estimate mean length at age for a population because of an increased risk of type II error or failure to detect an effect. My approach differed in that I evaluated the bias between sub-samples and samples across numerous populations using existing surveys (not simulations). Although individual survey differences between sub-sample and sample estimates were occasionally large, I found few consistent biases across surveys, so comparisons among lakes may provide meaningful relative comparisons.

I found that von Bertalanffy growth parameters estimated from sub-samples for bluegill, largemouth bass, and yellow perch were linearly related to estimates from samples, though highly variable. The similarities between sub-sample and sample von Bertalanffy growth parameters estimated from mean length at age data were unexpected because length-stratified sub-sampling of ages may lead to biased estimates of mean length at age (Goodyear 1995; Betolli and Miranda 2001). Since the age-length key was first introduced by Fredriksson (1934), the usefulness of non-random and random sub-sampling has been debated without resolution (Ketchen 1949; Kimura 1977; Goodyear 1995; Betolli and Miranda 2001). Random sub-sampling may provide similar estimates of mean lengths at age to samples, whereas non-random sub-sampling may be problematic in this regard (Kimura 1977; Goodyear 1995; Betolli and Miranda 2001). However, the extent of the problem has not been thoroughly evaluated. Non-random or length-stratified sub-sampling is a common practice and ensures that relatively rare size classes are represented. In my analyses of mean length at age estimated from length-stratified sub-samples, I excluded rare age classes that were most likely to be biased by limiting the analyses to ages 2–4. Mean lengths at other ages from length-stratified sub-samples may be more biased; therefore von Bertalanffy growth parameters estimated from biased mean lengths at age may also be biased. The effect of including mean lengths at age from all age classes in my estimation of von Bertalanffy growth parameters from length-stratified sub-samples and samples may have contributed to high variability in parameter estimates.

I did not consistently detect bias when comparing a large number of von Bertalanffy growth parameter estimates from sub-samples and samples from multiple lakes, though the variability in growth parameter estimates was large enough to warrant caution. While my results differ from those of other studies, I do not suggest that bias caused by non-random sub-sampling does not exist. Rather, the application of growth information should dictate whether length-stratified sub-sample data should be used. Here, I was interested in using length-stratified sub-sample data for statewide comparisons of growth potential across lakes and assessing the degree to which relative comparisons were possible. Because of the high variability in of von Bertalanffy growth parameter estimates from sub-samples and samples, the use of these estimates for among-lake comparisons is problematic.

Estimates of mean length at age and associated growth parameters can also be biased by non-random samples of the population, age estimation error, gear selectivity, and size-selective mortality. Age estimation error results in biased estimates of growth and mortality (Campana 2001). Young and especially old ages are usually the most difficult to estimate accurately, and are also the most influential on estimates of growth, mortality, or longevity (Campana 2001). If the age of older fish is underestimated, mortality will be overestimated and the importance of strong year-classes can be masked (Beamish and McFarlane 1983). For example, age estimation error resulted in overestimation of abundance of younger ages, overestimation of mean weight at age, and up to 19% overestimation of yield per recruit (Tyler et al. 1989). Gear selectivity also biases estimates of growth and mortality (Ricker 1975). If large fishes are more vulnerable to capture, older and larger fish will be over-represented, thereby resulting in over-estimation of survival and growth (Ricker 1975). Size-selective mortality biases estimates of growth, mortality, and yield, because larger individuals in each age class often suffer higher mortality than smaller individuals in each age class (Ricker 1969).

Understanding growth potential is important for fishery management, but collecting fish growth information is expensive and time consuming (Murphy and Willis 1996). In many states, growth data have not been readily accessible for large numbers of lakes across large geographic scales, thereby limiting the potential for use in lake classification. Recently, management agencies have begun to compile historic fisheries survey information in large databases, thereby facilitating access to growth information such as mean length at age (Hayes et al. 2003). Use of historic growth information for purposes other than the intent of the original data collection has not been thoroughly tested. Often, historic records are limited to summary information such as mean length at age, rather than lengths and ages of all individual fish that are needed for constructing age-length keys. Differences in sampling methods and other sources of potential bias should be evaluated before historic data of this type are used. If shown to be unbiased, historic growth data such as mean length at age summaries may be useful for developing large-scale lake classification schemes that could ultimately be used as a basis for developing fishery regulations. For Michigan lakes, I found that relative comparisons among lakes using mean length at ages 2–4 estimated from sub-sample data are robust.

Table 1. Regression parameters for bluegill, largemouth bass, and yellow perch mean lengths at ages 2–4 from sub-samples (dependent) and samples (independent) in Michigan lakes during 1993–2002. *N* represents the number of surveys. Lengths were measured in inches.

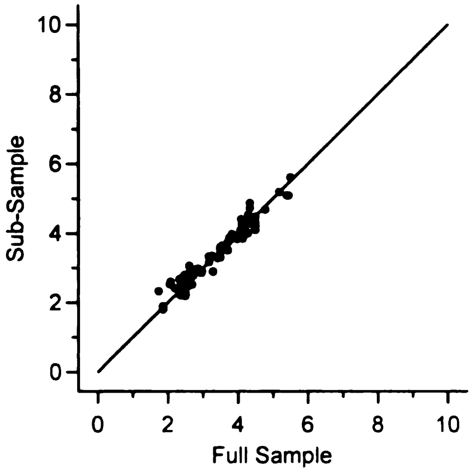
Species and age	**Coefficient**	**SE**	***t***	***P***
Bluegill Age 2 *(N = 78; R = 0.971)*				
Intercept	0.245	0.088	2.786	0.007
Mean Length Sample	0.937	0.025	-2.493	0.015
Bluegill Age 3 *(N = 104; R = 0.955)*				
Intercept	0.001	0.141	0.008	0.994
Mean Length Sample	0.992	0.029	-0.275	0.784
Bluegill Age 4 *(N = 110; R = 0.958)*				
Intercept	0.157	0.158	0.991	0.324
Mean Length Sample	0.962	0.027	-1.436	0.154
Largemouth Bass Age 2 (*N = 22; R = 0.986*)				
Intercept	-0.303	0.280	-1.080	0.293
Mean Length Sample	1.037	0.039	0.942	0.357
Largemouth Bass Age 3 (*N = 22; R = 0.986*)				
Intercept	0.231	0.343	0.673	0.509
Mean Length Sample	0.970	0.036	-0.828	0.418
Largemouth Bass Age 4 (*N = 22; R = 0.974*)				
Intercept	0.359	0.549	0.654	0.520
Mean Length Sample	0.970	0.495	-0.060	0.953
Yellow Perch Age 2 (*N = 20; R = 0.965*)				
Intercept	0.448	0.302	1.481	0.156
Mean Length Sample	0.923	0.057	-1.341	0.197
Yellow Perch Age 3 (*N = 22; R = 0.929*)				
Intercept	0.468	0.519	0.901	0.378
Mean Length Sample	0.938	0.078	-0.791	0.438
Yellow Perch Age 4 (*N = 22; R = 0.971*)				
Intercept	0.735	0.389	1.889	0.074
Mean Length Sample	0.917	0.049	-1.696	0.105

Table 2. Regression parameters for bluegill, largemouth bass, and yellow perch von Bertalanffy growth parameters L_∞ (in) and ω (in/year) from sub-samples (dependent) and samples (independent) in Michigan lakes during 1993–2002. N represents the number of surveys.

Parameter	**Coefficient**	**SE**	***t***	***P***
Bluegill ω *(N = 111 ; R = 0.806)*				
Intercept	0.248	0.141	1.757	0.082
Sample ω	0.871	0.049	2.610	0.010
Bluegill $L\infty$ *(N = 111 ; R = 0.729)*				
Intercept	0.807	0.629	1.284	0.202
Sample $L\infty$	0.930	0.061	1.153	0.251
Largemouth Bass ω *(N = 22 ; R = 0.893)*				
Intercept	0.379	0.385	0.984	0.337
Sample ω	0.903	0.091	1.065	0.300
Largemouth Bass $L\infty$ *(N = 22 ; R = 0.794)*				
Intercept	2.537	2.340	1.084	0.291
Sample $L\infty$	0.868	0.118	1.121	0.275
Yellow Perch ω *(N = 24; R = 0.933)*				
Intercept	0.517	0.217	2.377	0.027
Sample ω	0.897	0.069	1.494	0.149
Yellow Perch $L\infty$ *(N = 24 ; R = 0.915)*				
Intercept	1.843	0.974	1.893	0.072
Sample $L\infty$	0.818	0.070	2.597	0.016

Table 3. Relative sub-sample bias for bluegill, largemouth bass, and yellow perch mean length at ages 2–4 (in) and von Bertalanffy growth parameters L_∞ (in) and ω (in/year) from sub-samples and samples in Michigan lakes during 1993–2002.

Species	Growth Index	Relative Sub-sample Bias Across Surveys (%)
Bluegill	Mean Length Age 2	5.8
	Mean Length Age 3	9.1
	Mean Length Age 4	8.8
	von Bertalanffy ω	36.1
	von Bertalanffy L_∞	51.1
Largemouth Bass	Mean Length Age 2	3.3
	Mean Length Age 3	3.1
	Mean Length Age 4	5.3
	von Bertalanffy ω	20.4
	von Bertalanffy L_∞	37.4
Yellow Perch	Mean Length Age 2	7.4
	Mean Length Age 3	14.1
	Mean Length Age 4	6.5
	von Bertalanffy ω	16.9
	von Bertalanffy L_∞	20.0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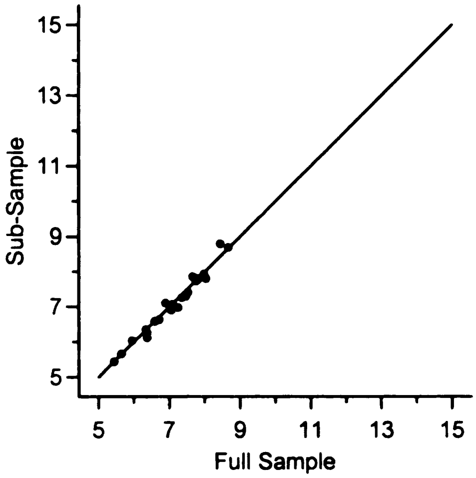
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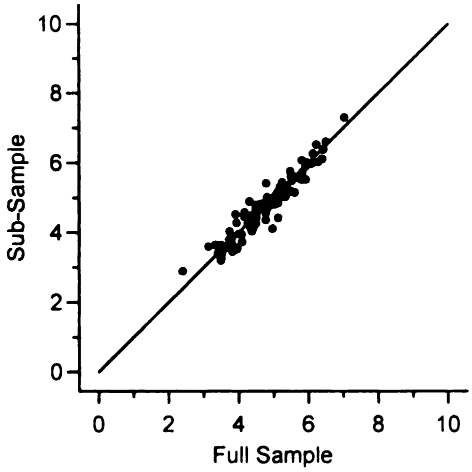
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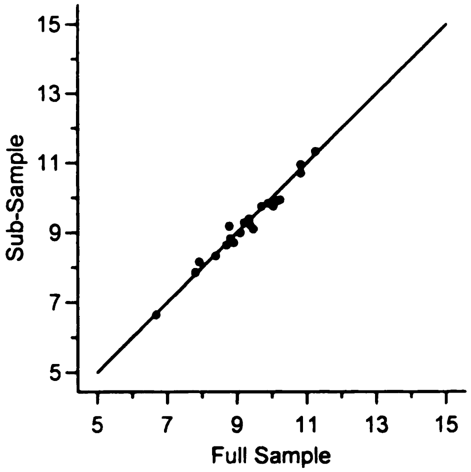
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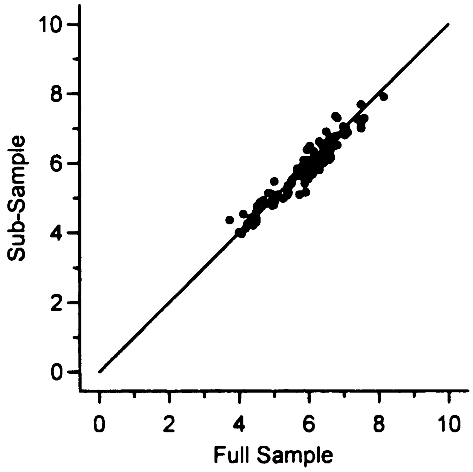
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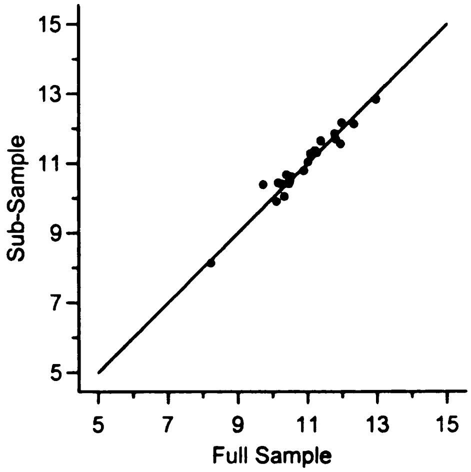
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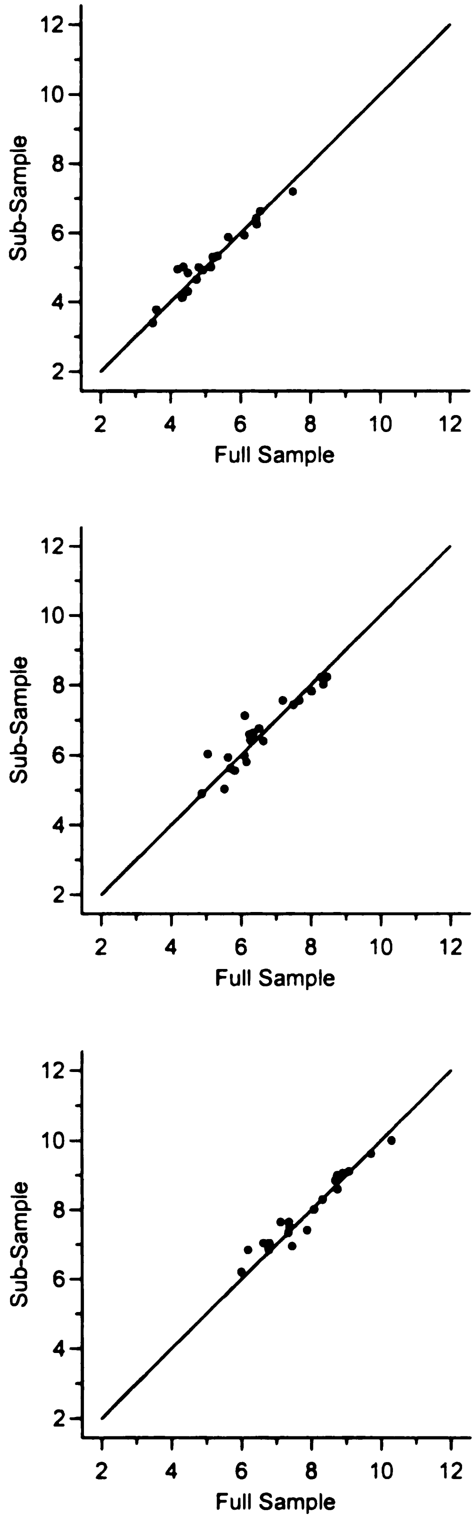

Figure 1. Sub-sample and sample mean length (inches) at ages 2 (top), 3 (middle) and 4 (bottom) for bluegill (BLG, left panel), largemouth bass (LMB, middle panel) and yellow perch (YEP, right panel) in Michigan lakes during 1993–2002.

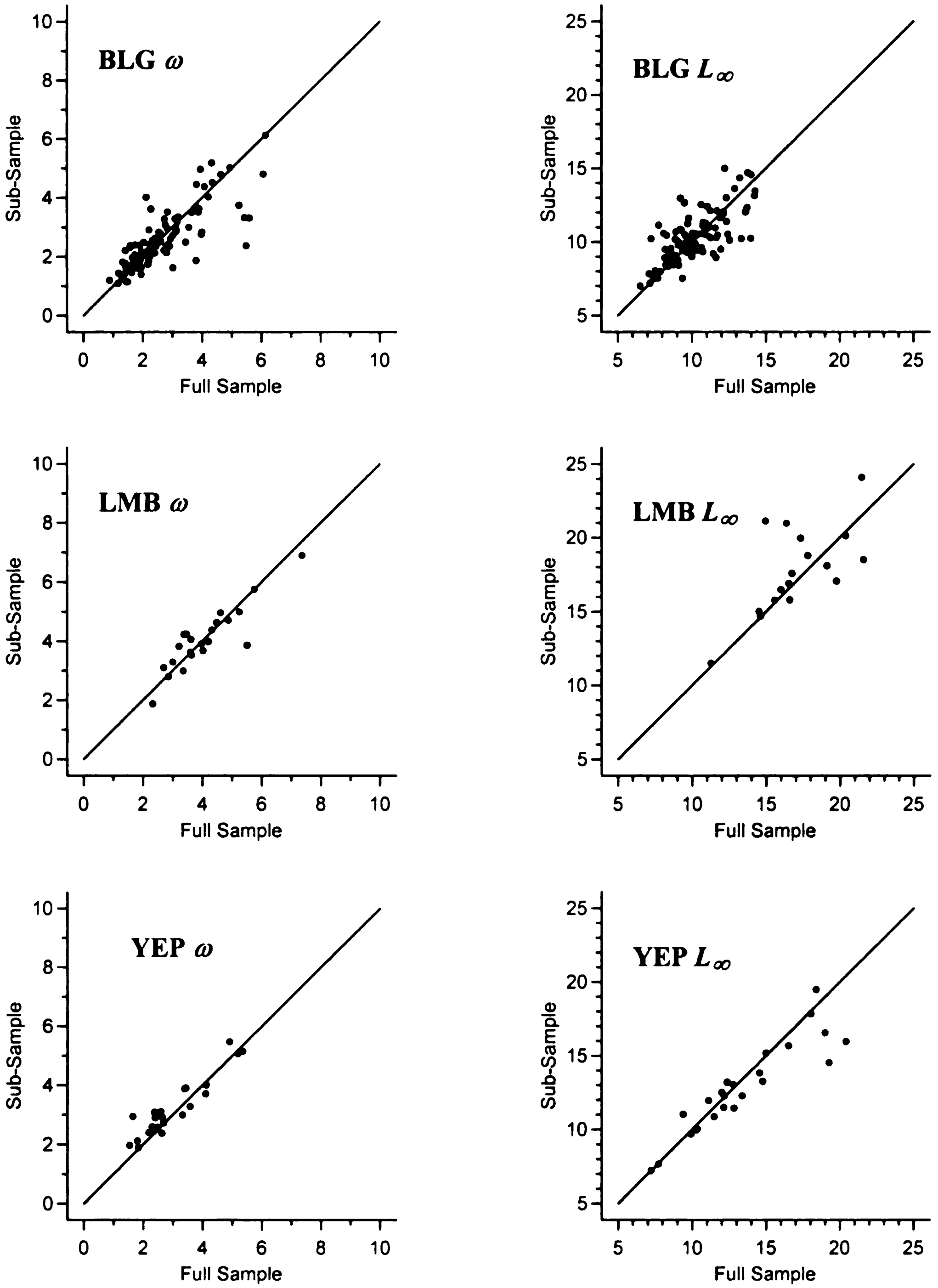

Figure 2. Sub-sample and sample von Bertalanffy parameter estimates ω (in/year) [left side] and L_∞(in) [right side] for bluegill (BLG top), largemouth bass (LMB middle) and yellow perch (YEP bottom) in Michigan lakes during 1993–2002.

CHAPTER 2

A LAKE CLASSIFICATION SCHEME FOR FISH SPECIES RICHNESS AND FISH GROWTH IN MICHIGAN AND WISCONSIN LAKES

Abstract. — Lake classification schemes can account for diversity in physical, chemical, or biological attributes of lakes, and so may be useful in managing fisheries in inland lakes. I evaluated a lake classification scheme consisting of 6 lake classes differing in landscape position, connectivity, and maximum depth using analysis of variance to determine if lake classes accounted for variability in fish species richness in 256 Wisconsin lakes and in mean lengths at age 4 of bluegill, largemouth bass, walleye, and yellow perch in 358 Michigan and 410 Wisconsin lakes. Fish species richness and mean lengths of age 4 bluegill, largemouth bass, and walleye varied among lake classes, but not all lake class pairs differed. Map-based variables related to temperature and habitat area were then evaluated using regression tree analyses to refine the classification for each response variable. Lake surface area was an important predictor of fish species richness, and mean lengths of age 4 bluegill and largemouth bass, whereas latitude was an important predictor of mean lengths of age 4 yellow perch and walleye. Regression tree results revealed species-specific separation points for identifying categories of lake size, and for stratifying the region into northern and southern zones. The revised classifications demonstrate the importance of incorporating regional, lake-type, and local spatial scales for explaining variation among lakes. These classifications can serve as a statewide framework for management, based on patterns of ecological similarity among lakes. Angling regulations could be established for lake classes, rather than individual lakes, thereby reducing the complexity of angling regulations.

Introduction

Lakes are inherently diverse in their physical, chemical, and biological characteristics because internal and external forces continually shape lake ecosystems and the processes that lead to predictable patterns. Lakes, particularly in the upper mid-western United States, are not only diverse in character and origin, but are also numerous and extend across a broad geographic extent. For example, Wisconsin has nearly 15,000 lakes that range in surface area from 0.04 to 55,730 ha (Lillie and Mason 1983) and Michigan has over 35,000 lakes that range in surface area from < 2.47 to 51,891 ha (Humphrys and Colby 1962; Schneider 1975). Given the complexity and broad spatial scale of lake resources, monitoring the status and trends of lake ecosystem health (e.g. documenting temporal change in fish communities or water quality) or fisheries is challenging. Monitoring ecosystem integrity and fisheries are not mutually exclusive objectives, but are often tackled independently by different branches of management agencies (e.g., water quality versus fisheries management). Monitoring all lakes in a single year is impossible, even if many agencies are involved. Therefore, monitoring programs should incorporate statistically rigorous sampling designs that stratify lakes according to ecological similarity to obtain unbiased samples of the populations of lakes (Hayes et al. 2003; Lester et al. 2003).

In this paper, I seek to evaluate and improve on an existing classification scheme, developed and used in Wisconsin for use in monitoring, that is based on habitat characteristics. I assume that ecologically similar lakes should respond similarly to management actions or environment stressors (Marshall and Ryan 1987; Emmons et al. 1999). By first accounting for variability in physical, chemical, or biological characteristics of lakes, detection of change brought on by environmental stress or management actions should be more easily identified because expected conditions are known (Hawkins et al. 2000). Classifications should account for sufficient natural variation in an indicator of interest (e.g., fish abundance, species richness, or fish growth rates) that a comparison between observed and expected conditions will reveal subtle changes, thereby minimizing type I and II errors (Hawkins et al. 2000). For example, stratification based on a habitat classification model for Texas reservoirs decreased the statewide variance in electro-fishing relative abundance estimates up to 43% for bluegill *Lepomis macrochirus* and 23% for largemouth bass *Micropterus salmoides* (Dolman 1990).

Classification schemes that explicitly account for variability in ecological processes such as growth or life history strategies, which may indirectly influence fish abundance, are less prevalent, but can provide a framework for management decisions or for research into causal mechanisms of variation in fish population demographics (e.g., Shuter et al. 1998). Understanding factors that affect fish growth, in particular, is important in fisheries management because growth can respond to changes in population size (e.g., Diana 1983; Healey 1980), so therefore may be an important indicator of change brought on by environmental stress, environmental change, or angling pressure (Trippel 1995). In addition, fish growth underlies, in large part, the response of fish populations to management regulations, such as minimum size limits (Noble and Jones 1993). The role of regulations in fisheries management will increase in the future, as the demand on fisheries increases as the number of licensed-anglers increases (Noble and Jones 1993).

Fish growth is an important indicator of environmental and physiological conditions in lakes (Diana 1995). The environment primarily regulates fish growth through temperature and food availability (Magnuson et al. 1979; Diana 1995). Therefore, fish growth should vary among lakes according to physical features that dictate temperature, and the physical and environmental forces that influence nutrients, productivity, and ultimately food availability. Factors that influence food availability, such as predation and competition, tend to be highly variable, more difficult to measure, less easily predicted, and therefore less desirable for use in classification. Factors that influence temperature in lakes, such as latitude, surface area, and depth, are less variable. By accounting for physical features that determine temperature in a classification scheme, I seek to build a template for understanding the more dynamic biological interactions such as predation and competition that influence food availability. To do so, I test the ability of an existing lake classification scheme, developed for northern Wisconsin lakes, to explain variation in fish species composition and growth among Wisconsin and Michigan lakes, and evaluate the ability of factors that influence temperature in lakes (latitude and surface area) to improve the explanatory power of the classification.

Ideally, variables used to develop classification schemes should be available for a large number of lakes, capture the full range of variability in lake characteristics in the population of lakes of interest, and enable the establishment of a classification scheme for an entire state or region (Hawkins et al. 2000). Use of temporally stable or map-based attributes in classification minimizes the need to visit the site to classify new lakes, and enables the classification of a large number of lakes at one time. For example, the lake classification scheme currently used in Wisconsin classifies lakes according to landscape position, connectivity and depth. The classification distinguishes lakes that are connected to other lakes in a drainage network from lakes that are land-locked. Connected lakes are further separated by their general landscape position (high or low) in the drainage network. Lakes that are deep and potentially stratified are separated from lakes that are shallow. Each of these characteristics is known or easily estimated for all lakes in the state from existing data sources.

The literature contains support for using landscape position, connectivity and lake depth to group similar lakes. The basis for the landscape position component of the Wisconsin classification scheme was based on research that suggests that a lake's position in the landscape constrains its physical, chemical, and biological attributes (Kratz et al. 1997; Riera et al. 2000; Soranno et al. 1999; Webster et al. 1996, 2000). For example, lake surface area, ionic concentrations, and fish species richness have been shown to vary predictably with landscape position, with lakes lower in the drainage network typically being larger and having higher surface area, ionic concentration, and fish species richness than lakes higher in the drainage network in northern Wisconsin (Kratz et al. 1997; Riera et al. 2000; Webster et al. 1996, 2000). Connectivity can also explain variation among lakes. For example, Tonn and Magnuson (1982) differentiated two fish assemblage types primarily on the basis of connectedness and minimum oxygen conditions in 18 northern Wisconsin lakes. Presence of an inlet or outlet may provide a winter refuge from low oxygen concentrations or large piscivores, thereby supporting greater species diversity (Tonn and Magnuson 1982). Finally, thermal stratification, which is largely determined by lake area and depth, may influence fish species distribution, the amount of species-specific suitable habitat and interactions in lakes, and nutrient cycling (MacLean and Magnuson 1977; Magnuson et al. 1979; Crowder and Magnuson 1983; Fee et al. 1994). Therefore, a classification scheme with landscape position, depth, and connectivity is likely to explain variability in a biological response like fish species richness.

Many recent landscape position studies were conducted in northern Wisconsin lake districts within a homogeneous geomorphologic and land-use setting (e.g., Riera et al. 1997; Webster et al. 1996). However, across the Upper Great Lakes region, geology, climate, and land-use factors are more variable. Larger-scale, regional filters like climate may constrain species richness or other patterns at the local or lake-district scale (Barbour and Brown 1974; Tonn 1990; Minns and Moore 1995). Therefore, when considering a biological response like fish growth across the Upper Great Lakes region, the amount of length attained in one growing season may vary with latitude because the length of the growing season tends to vary along a latitudinal gradient (Colby et al. 1979; Colby and Nepszy 1981; Beverton 1987; Quist et al. 2003). In addition, lake surface area, a factor not explicitly accounted for in the current classification, has been linked to fish species richness in many studies (Barbour and Brown 1974; Matuszek and Beggs 1988; Minns 1989; Magnuson et al. 1998), and affects solar radiation input and circulation patterns within lakes (i.e., the thermal structure;Wetzel 1975; Lampert and Sommer 1997). Therefore, before using a classification scheme based solely on landscape position, connectivity, and maximum depth as the basis for a larger statewide or regional management and monitoring framework, the extent to which biological attributes vary with existing lake classes across a larger spatial area should be determined, and additional map-based factors that have been shown to influence biological patterns should be explored as potential grouping variables.

My objectives were to determine: (1) if the current Wisconsin lake classification scheme explains variability in fish species richness in Wisconsin lakes, (2) if the current Wisconsin lake classification scheme explains variability in fish growth in Michigan and Wisconsin lakes, (3) if additional map-based variables influencing climate, habitat volume, and habitat complexity can further refine the existing classification scheme, and (4) if a refined classification scheme explains more variability in fish species richness and fish growth. Given the large spatial scale of this study, I expected that mean length at age would vary with latitude, and that surface area would be an important additional predictor of fish species richness. The over-arching goal of this research is to develop the foundation for building a sampling, monitoring, and management framework that can be used at the statewide or regional level.

Methods

Study Area

The study area includes 358 inland lakes in Michigan and 410 inland lakes in Wisconsin between 42 and 47 degrees north latitude (Figure 3). The states of Michigan and Wisconsin share a similar geologic history, with landscapes shaped primarily by glaciers 10,000–12,000 years ago (Scheider 1975; Becker 1983). Surface topology and soils in the glaciated regions of both states are complex and range from areas of thick glacial till to bedrock outcrops (Scheider 1975; Becker 1983).

Lake Morphometry and Landscape Features

Lakes were assigned to Wisconsin lake classes based on landscape position, connectivity, and maximum depth (Table 4). Landscape position, connectivity, and maximum depth were obtained from the Michigan Landscape Context GIS database (Cheruvelil 2004) for Michigan lakes, and the Surface Water Inventory File (Wisconsin Department of Natural Resources, 1967-1983) and Lakes Book (Wisconsin Department of Natural Resources) for Wisconsin lakes. Water body type designations (e.g., seepage, drainage, drained, and spring) were used to determine connectivity for Wisconsin lakes (Wisconsin Department of Natural Resources, 1995). Drained, drainage, and spring lakes had either an inlet or outlet, so were considered connected and grouped under the general connectivity category of drainage lakes. Seepage lakes had no inlet or outlet, so were grouped under the general connectivity category of seepage lakes. For Wisconsin lakes, landscape position was quantified using watershed area. Lakes with watershed areas < 1,036 ha were considered high in the landscape, while lakes with watershed areas $\geq$ 1,036 ha were considered low in the landscape. Because watershed areas were not available for all Michigan lakes, landscape position and connectivity were obtained from the Michigan Landscape Context GIS database. Michigan and Wisconsin lakes were categorized as deep (> 5.5 m maximum depth) or shallow (< 5.5 m maximum depth) to roughly separate mixed from thermally-stratified lakes (Lillie and Mason 1983).

Fish Species Richness

Fish species richness estimates were not available for Michigan lakes, so I limited this analysis to Wisconsin lakes. In Wisconsin lakes, species richness was estimated from summer mini-fyke net and fall electro-fishing surveys in which all species were targeted during 1998–2004. Because the effort was standardized among lakes, relative comparisons of estimates of species richness are possible. Fish species richness was defined as the number of unique species caught in a particular lake for a given year from both sampling events combined.

Fish Growth

Fish mean length at age summaries from inland lake sampling programs were compiled from historic and current databases in Michigan and Wisconsin. To standardize for sampling season, I limited the analyses to surveys that occurred between January and May, before the start of the growing season. For lakes with more than one survey, a single survey was randomly selected from all surveys for that lake, so each lake was represented once in the final dataset. The final dataset included surveys conducted during 1953–2003 for Michigan lakes and during 1947–2003 for Wisconsin lakes.

Various sampling gears and combinations were used in both Michigan and Wisconsin lakes to sample fish during these periods. Approximately 62% of all surveys were from single gear types, 28% were from multiple gears, and 10% were unknown gear types. Of the surveys in which a single gear type was used, most were fyke-netting surveys (50%), electro-fishing surveys (20%), or trap-netting surveys (15%). I used all gear types and combinations in the analysis because I sought to obtain a large sample on a broad spatial scale.

I chose mean length at age 4 for bluegill, largemouth bass, walleye, and yellow perch as a growth index because age 4 was fully recruited to the sampling gears used in both states and was the most commonly encountered age class in surveys for all species. Age 4 is also likely to be an age that is accurately estimated, thereby minimizing age-estimation error. Principal components analysis of surveys with mean lengths at ages 3-6 revealed that the first principal component explained 79-89 % of the variability in mean lengths at age for all species, thereby making the first principle component a good descriptor of overall growth among lakes. For all species, the first principal component was highly correlated with mean lengths at age 4 (Pearson correlation coefficients ranging from 0.92 – 0.96). Therefore, to ensure large sample sizes, mean length at age 4 was selected (instead of principal component factor scores) as a growth index for analysis because there were many more surveys with mean length at age 4, then had a complete matrix of ages 3–6 (as would be required for principle components analyses). The four species were selected because they were commonly present in samples, represented warm water and cool water species, and were important to angling fisheries in both states.

Statistical Analysis

To determine if the Wisconsin lake classification scheme explains variability in fish species richness and fish growth, I tested for differences in fish species richness and fish growth among lake classes using one-way analysis of variance (ANOVA) with lake class as the factor. In lakes where the results of the ANOVA indicated significant differences among lake classes, Bonferroni multiple comparison tests were used to determine which lake classes differed from one another in the response variable. The Bonferroni method is applicable for unequal sample sizes and when all pair-wise comparisons are of interest (Neter et al. 1996). General patterns in significant pair-wise comparisons were examined across all responses tested to infer the relative importance of each categorical component of the classification scheme (i.e. connectivity, landscape position, or depth categories).

Regression tree analysis was used to determine if additional map-based variables, likely related to lake thermal regime, such as latitude and lake surface area could refine the existing classification scheme. Latitude and lake surface area were obtained from the Michigan Landscape Context GIS database (Cheruvelil 2004) for Michigan lakes, and the Surface Water Inventory File (Table 5; Wisconsin Department of Natural Resources, 1967-1983) for Wisconsin lakes. Regression tree analysis is a flexible nonparametric multivariate analysis method that allows categorical, ratio, and continuous or threshold data types, accounts for interactions among explanatory variables, and does not assume linearity among variables (Breiman et al. 1984; Magnuson et al. 1998). The least-squares loss function with Automatic Interaction Detection (AID) was used because AID incorporates interactions among predictor variables. The AID algorithm begins with a single cluster of cases and searches the explanatory variables for a way to split the cluster into two clusters with the smallest overall within-cluster sum of squares (Morgan and Sonquist 1963; Wilkinson 2000). By repeatedly splitting the explanatory variables, in this case latitude, surface area, and maximum depth, into pairs of subsets, the AID algorithm produces a dichotomous key (Wilkinson 2000). Interactions are represented by branches from the same node with different predictors splitting further down the tree (Wilkinson 2000).

In the regression tree analyses, maximum depth was included as a continuous variable to allow for interactions among latitude, lake surface area, and maximum depth, and because poorer fits are likely to result when continuous predictor variables are categorized prior to analysis (Wilkinson 2000). First, lake types were included, regardless of connectivity or landscape position. Then, based on findings from the initial

ANOVAs, regression tree analyses were conducted separately for all seepage and then for all drainage lakes. Proportional reduction in error (PRE), analogous to a squared-multiple correlation coefficient, was used to judge the overall fit of the regression tree models (Wilkinson 2000). Refined lake classes were then developed based on the outcomes of the regression tree analyses. Differences in fish species richness and fish growth among lake classes were tested using one-way analysis of variance (ANOVA) with new lake class as the factor, followed by Bonferroni multiple comparison tests.

Results

Fish Species Richness

Fish species richness varied among lake classes in 256 Wisconsin lakes (Table 6), but not all pair-wise comparisons of lakes classes were significantly different (Table 7). The number of fish species ranged from 3 to 30 species across all lake classes. Fish species richness in seepage lakes was lower than in deep drainage lakes, either high or low in the landscape (Figure 4). The mean number of species in seepage lake classes was 10, while the mean number of species in drainage classes (classes 1–4) was 14. Fish species richness was lower in high, shallow drainage lakes than in low, deep drainage lakes (Figure 4). Overall, comparisons indicate that depth and connectivity may be more important than landscape position in determining species richness. Of 15 possible multiple comparison tests, only 1 test involving landscape position (contrasting a high drainage class to a low drainage class) revealed a significant difference (Table 7). The significant contrast involved both landscape position and depth categories. In contrast, 4 of 15 multiple comparison tests contrasting shallow or deep seepage and deep drainage categories were significantly different (Table 7).

For all lakes regardless of connectivity or landscape position category, regression tree analyses of latitude, maximum depth, and surface area revealed that fish species richness was lower in lakes smaller than 226 ha, and small lakes had fewer species south of 45.4°N latitude than small lakes north of 45.4°N latitude based on regression tree analyses (Table 8; Figure 6). However, the low proportion reduction in error in the overall regression tree model (PRE = 0.277) suggested that much of the variability in fish species numbers was unexplained (Table 8).

Because landscape position did not emerge strongly in the ANOVA, I evaluated connectivity categories (e.g. seepage versus drainage) in the next expanded regression tree analyses for species richness. For seepage lakes, fish species richness was lower in lakes smaller than 81 ha than in lakes larger than 81 ha (Table 9). For small seepage lakes (< 81 ha), another split at 38 ha separated medium from small-sized lakes, with mean species numbers being lowest in the smallest lake group (Table 9). Larger seepage lakes (≥ 81 ha) had more species in deep lakes than in shallow lakes (Table 9), suggesting that habitat volume may be important in determining species richness patterns. For drainage lakes, fish species richness was lower in lakes shallower than 13 m than in lakes deeper than 13 m (Table 9). The proportion reduction in error in the separate regression tree models for seepage and drainage lakes ranged from 0.113–0.401, with more of the variability in fish species numbers being explained in some connectivity lake types than in the model of all lake types combined (Table 9).

Fish Growth

Mean length at age 4 varied among lake classes for bluegill, largemouth bass, and walleye (Table 6), but not all pair-wise comparisons of lake classes differed (Table 7).

For bluegill, mean length at age 4 was greater in deep drainage lakes low in the landscape (class 4) than in deep drainage lakes high in the landscape (class 2) or deep and shallow seepage lakes (classes 5 and 6; Table 7; Figure 5). For largemouth bass, mean length at age 4 was greater in deep drainage lakes low in the landscape (class 4) than in shallow drainage lakes high in the landscape or deep seepage lakes (class 6; Table 7; Figure 5). For walleye, mean length at age 4 was lower in deep and shallow drainage lakes low in the landscape (classes 3 and 4) than in deep drainage lakes high in the landscape (class 2) or deep and shallow seepage lakes (classes 5 and 5; Table 7; Figure 5). For yellow perch, mean length at age 4 did not differ among lake classes (Table 6). Bluegill, yellow perch, and largemouth bass were most frequently sampled in deep seepage lakes (class 6), where sizes at age were also relatively low, whereas walleye were most frequently sampled in deep lowland drainage lakes (class 4), where sizes at age were relatively low. In general, shallow drainage lakes high in the landscape were least represented (fewest surveys) for all tests. Only 11 of 60 possible multiple comparison test were significant (Table 7). Of the 11 significant comparisons, 2 clearly separated high (class 2) versus low (classes 3 and 4) landscape categories, 2 contrasted deep and shallow as well as high and low landscape classes (i.e., differences can be attributed to either depth or landscape position), and 5 separated seepage from drainage classes (Table 7).

Based on regression tree analyses for all lakes regardless of connectivity or landscape position category, mean lengths at age 4 for bluegill, largemouth bass, walleye, and yellow perch were best predicted by latitude or lake surface area. For bluegill, mean length at age 4 was higher in lakes larger than 446 ha than in lakes smaller than 446 ha (Table 8). For largemouth bass, mean length at age 4 was higher in lakes larger than 528 ha than in lakes smaller than 528 ha (Table 8). For walleye, mean length at age 4 was higher in lakes south of 45.2°N latitude than in lakes north of 45.2°N latitude (Table 8). For yellow perch, mean length at age 4 was higher in lakes south of 42.4°N latitude than in lakes north of 42.4°N latitude and in lakes north of 45.4°N latitude (Table 8). The low proportion reduction in error in the regression tree models for bluegill, largemouth bass, walleye and yellow perch (PRE = 0.10–0.32) suggested that much of the variability in fish growth was unexplained (Table 8).

Because landscape position did not emerge as strongly as connectivity in the ANOVA, I evaluated connectivity categories (e.g. seepage versus drainage) in the next expanded regression tree analyses for mean length at age. For lakes of different connectivity categories, mean length at age 4 exhibited similar patterns (as in the previous analysis including all lake connectivity categories), with either lake surface area or latitude emerging at the primary split for all responses tested (Table 9). Maximum depth also emerged at secondary or tertiary splits in several models, including walleye in seepage and high drainage lakes, and yellow perch in seepage and low drainage lakes (Table 9). While lake surface area or latitude were consistently important in explaining variation in mean length at age 4 for each fish species, the separation points varied between each connectivity model and among species. For both bluegill and largemouth bass, when lake surface area entered at the first split, the separation point was typically lower for seepage lakes than for drainage lakes (Table 9). For walleye and yellow perch, the separation point for latitude was typically farther south for yellow perch than for walleye, except for drainage lakes (Table 9). The proportion reductions in error were higher (PRE = 0.05–0.48) for 5 of 8 models that distinguished among connectivity lake categories (Table 9) than for four models that did not distinguish among lake categories (Table 8). Therefore, revised lake classes were created in the next step based on the outcomes of the expanded regression tree analyses by connectivity category (Table 9).

New Lake Classes

New lake classes were created based on the separation points identified in the regression tree analyses for species richness and bluegill, largemouth bass, walleye, and yellow perch mean lengths at age (Table 9). Species richness and mean length at age varied among new lake classes (Table 10; Figures 7 and 8), but not all lake class pairs differed (Table 11). Of 58 possible multiple comparison tests, 32 were significantly different. In all cases, the amount of variation explained by the new lake classes was greater than the amount of variation explained by the Wisconsin lake classes (Table 6; Table 10). The new lake classification scheme for species richness still resulted in 6 classes, but rather than landscape position, surface area and maximum depth were used to separate seepage and drainage lakes respectively (Table 9; Figure 7). The new lake classifications for bluegill, largemouth bass, walleye, and yellow perch mean length at age resulted in between 4 and 7 lake groups depending on the species.

Discussion

Fish Species Richness

I found that the Wisconsin classification scheme based on landscape position, connectivity, and maximum depth explained a moderate about of variability in fish species richness in 256 Wisconsin lakes. The largest differences in fish species richness were between seepage lakes and deep lowland drainage lakes, which correspond to the extreme ends of the Riera et al. (2000) lake-order scheme. My results suggest that connectivity may be a particularly important determinant of fish species richness. My results may also suggest that lake area affects fish species richness, because seepage lakes tended to have small surface areas, and lakes low in a drainage are larger in surface area than seepage lakes or drainage lakes high in a drainage (Kratz et al. 1997; Riera et al. 2000).

The fact that landscape position did not consistently emerge as a strong predictor of fish species richness may suggest the importance of explicitly considering lake surface area when evaluating fish species richness patterns among lakes. Lake surface area has been strongly associated with species richness in several studies (Barbour and Brown 1974; Rahel and Magnuson 1983; Matuszek and Beggs 1988; Minns1989; Minns and Moore 1995; Magnuson et al. 1998). Local extinction variables like lake area, conductivity, pH, and depth were more important than isolation variables related to connectivity in predicting species richness and community composition in Wisconsin and Finnish lakes (Magnuson et al. 1998). Riera et al. (2000) detected significant differences in lake surface area among lake order classes (i.e., landscape position determined lake surface area), but surface areas for each lake order class were highly variable..

The relative importance of isolation and extinction variables in Wisconsin and Finnish lakes differed based on the local geomorphic setting (Magnuson et al. 1998). Similarly, Webster et al. (2000) studied landscape controls on lake chemical responses to drought in four lake districts in Wisconsin and Ontario ranging between 45 and 51° N latitude. The degree to which chemical properties of individual or small groups of lakes responded to drought varied with local hydrologic setting (groundwater versus surface-water dominated) and landscape position. Therefore, local and landscape position variables alone may not explain all variability in physical, chemical, or biological characteristics of lakes. Consideration of the hydrologic and geomorphologic setting is also important, which could account for my inability to differentiate species richness among all lake class pairs in the ANOVA of the Wisconsin lake classification scheme, the relatively low predictive power of the Wisconsin classification scheme, and the emergence of latitude as an important predictor in the later regression tree analyses.

The Wisconsin lake classes used in this analysis were derived using general approximations for landscape position (high and low) and connectivity (seepage and drainage), based on watershed area for Wisconsin lakes and visual inspection of maps for Michigan lakes. The lake order classes used by Riera et al. (2000) were based on the type and strength of connections between a lake and the surface drainage network, and were determined from stream order designations from stream network information. However, Riera et al. (2000) presented convincing evidence that lakes higher in the landscape consistently had smaller catchments. Therefore, the watershed area approximation of less than 1036 ha used in this analysis for Wisconsin lakes is likely to be useful in separating lakes high in the landscape from lakes low in the landscape. Still, more accurate determinations of landscape position could help to further refine the Wisconsin classification scheme. Whether approximated or measured directly, landscape position is thought to constrain not just physical attributes of lakes, such as lake surface area, but also chemical attributes of lakes such as concentrations of ions (Kratz et al. 1997; Riera et al. 2000; Soranno et al. 1999; Webster et al. 1996, 2000). Because water chemistry data are important, but less available for large numbers of lakes, the use of map-based variables such as landscape position to characterize lake productivity is appealing from a classification perspective.

Fish Growth

I found that the Wisconsin classification scheme based on landscape position, connectivity, and maximum depth explained a moderate amount of variability (R^2 0.02–0.12) mean length at age 4 of bluegill, largemouth bass, and walleye. As with species richness, deep seepage lakes were consistently different than lowland drainage lakes for bluegill, largemouth bass, and walleye growth. Largemouth bass and bluegill growth was lower in deep seepage lakes than in low drainage lakes. In contrast, walleye growth was higher in deep or shallow seepage lakes than in low drainage lakes. Walleye prefer cool water, whereas largemouth bass and bluegill prefer warm water. Seepage lakes such as kettle lakes in glaciated areas like Michigan and Wisconsin, are typically bowl shaped, and may lack expansive warm littoral areas typically used by centrarchids. Seepage lakes in Wisconsin tend to have greater water clarity, lower nutrients, lower alkalinity, and are less eutrophic than drainage lakes (Lillie and Mason 1983).

The distribution of lakes surveyed was not even among lake classes in my analysis. Of all lakes included in my analysis, only 16 percent of shallow lakes (classes 1, 3, and 5) had survey information, which is likely due to the tendency of resource management agencies to focus sampling efforts on large, deep lakes, or to the fact that the distribution of lake types within the region is uneven. Except for species richness and walleye growth in shallow lowland drainage lakes, other shallow Wisconsin lake classes had sample sizes less than 30 for each variable tested. Because sampling was typically not randomly distributed and the targeted species were unknown, inferences about statewide patterns in species presence or absence by lake class are not possible.

New Lake Classes

Lake surface area and latitude explained significant amounts of variation in species richness and fish growth. The consistent emergence of latitude and lake area in regression tree analyses suggests that both local lake-type and regional factors influenced fish species richness and growth in my study lakes. Barbour and Brown (1974) found that latitude explained 64% of the variation in species numbers in 14 lakes across North America, a much larger spatial scale than my study. In my study, for all lake types, latitude was an important predictor of walleye and yellow perch growth, but did not emerge as a predictor of bluegill or largemouth bass growth. Many studies have shown that fish growth varies with latitude (Colby et al. 1979; Colby and Nepszy 1981; Beverton 1987; Quist et al. 2003). Because fish species differ in their thermal requirements, growth potential, production potential, and presence in a lake may be directly related to thermal structure of that lake, which is largely determined by lake morphometry and climate (Wetzel 1975; Johnson et al. 1977; Tonn et al. 1983; Marshall and Ryan 1987; Christie and Regier 1988). In this region, temperature may be a more important driver for percid growth, than for centrarchid growth.

In addition to setting up the thermal properties of lakes, lake morphometry also influences nutrient cycling in lakes and primary productivity. Annual rates of phytoplankton photosynthesis per unit of lake surface area have been shown to increase as a function of lake size (Fee et al. 1992). Nutrient recycling may be more efficient in large lakes because the intensity of turbulence within the mixed layer and the depth of the mixed layer increase with increasing lake size (Fee at al. 1994). Through these processes, the mixed layer retains particles longer, thus increasing the likelihood of phytoplankton uptake and minimizing nutrient loss to the sediments. Because of increased nutrient recycling efficiency, large lakes may be more productive than smaller stratified lakes, which would also influence growth potential. Likewise, lakes that do not stratify and continually mix may have different nutrient cycling than lakes that stratify (Lillie and Mason 1983). Stratification patterns are a function of lake surface area, fetch, and maximum depth (Wetzel 1977). Fish yield, a response variable not included in this analysis, has been linked to measures of primary productivity (Ogelsby 1977; Ogelsby et al. 1987), but has also been linked to thermal habitat volume (Christie and Regier 1988). Fish abundance and harvest have been predicted from lake surface area in several studies (Hansen 1989; Baccante and Colby 1996; Nate et al. 2000; Nate et al. 2001). Therefore, including latitude and lake surface area in the classification scheme may expand the utility of the classification scheme beyond monitoring of species richness to management of fish populations.

Ricklefs (1987) suggested that ecology should focus on macro-scale explanations for local phenomena. Here, I used regional, lake-type (in the sense of Tonn 1990), and local features to explain two local phenomena, species richness and fish growth, of interest to inland lake resource management agencies. The importance of lake-type variables was demonstrated because the influence of latitude, lake surface area, and maximum depth varied with lake connectivity. Forces that influence species richness and fish population dynamics in inland lakes occur at multiple spatial and temporal scales (Minns 1986; Minns and Moore 1995; Hershey et al. 1999; Beard et al. 2003; Lester et al.

2003), therefore multiple scales should be considered when developing classification schemes for monitoring or management programs. Multiple spatial scale classifications and monitoring programs not only help us to understand the present condition, but also aid in monitoring the status and trends of aquatic ecosystems in the face of future environmental stressors. For example, changes in species distributions as a result of global climate change will be most evident at the regional scale because species ranges shift in response to warmer climates, changes in precipitation patterns, changes in soil moisture content, and frequency of fire (Minns and Moore 1995). In a synthesis of classification papers presented to the North American Benthological Society, Hawkins et al. (2000) suggested that a tiered approach to classification, where local habitat features form the foundation of the classification and large-scale features are used to refine the classification, should lead to greater precision and accuracy in predicting biological conditions. The approach is supported by the fact that local extinction factors like lake surface area and depth were found to be more important than isolation factors like connectivity in determining species richness in northern Wisconsin and Finnish lakes (Tonn and Magnuson 1982; Magnuson et al. 1998).

When interpreting biological patterns among lakes such as fish species richness or growth among species, each measure includes among-site spatial, within-site spatial, temporal, and measurement error components of total variability. In classification, we seek to explain among-site spatial variability, which can only be successful if among-site spatial variability is the largest component of the total variability (Hawkins et al. 2000). My study was unique in that it encompassed a large geographic scale, and incorporated data from an approximate 60-year time period. Patterns and processes affecting aquatic ecosystems operate at various spatial and temporal scales (O'Neill 1989; Roughgarden 1989; Tonn 1990). By expanding the temporal scale, more variability in time is introduced, which typically should reduce our ability to classify among-site variability (Hawkins et al. 2000). However, because the number of lake surveys was large, I had the statistical power to see the underlying spatial pattern. By confining my analyses to available, temporally stable, map-based variables, I evaluated a classification that could be implemented for most lakes in the region with minimal effort. Because the predictor variables were stable in time, they could be used to predict biological attributes across large time periods, thereby increasing my sample of lakes and expanding the spatial scale, which ultimately revealed an underlying spatial pattern.

My research did not explicitly account for chemical or biological differences among lake classes, which may also explain the relatively low predictive ability of some of my models. Other variables not tested here are likely to be important predictors of species richness or mean length at age, and could be used to further enhance the classification schemes if they become available for a large number of lakes or can be predicted from map-based variables like landscape position. For example, species richness has been shown to vary with pH (Matuszek and Beggs 1988; Minns 1989) and alkalinity (Rahel 1984), and bluegill mean lengths at age have been correlated with Secchi depth and alkalinity (Tomcko and Pierce 2001). More research is needed to quantify the effects of other factors on species richness, fish growth, and other biological responses, and to expand our ability to extrapolate aspects of nutrient status to un-sampled lakes using map-based or remote sensing technologies. Because my classification does not currently contain a water chemistry variable to indicate lake productivity or nutrient status, landscape position may still provide an important indicator of ionic concentrations (Webster et al. 1996; Kratz et al. 1997; Soranno et al. 1999; Riera et al. 2000; Webster et al. 2000).

Management Implications

My overall goal was to develop a management tool for inland lakes that may ultimately be used to generate statewide or regional management frameworks for sampling and managing fish populations and for monitoring aquatic ecosystem health. The new classification scheme developed herein is more complex (increasing from from 6 to 26 lake classes), but shows a marked improvement over the existing Wisconsin classification scheme (i.e., more variability is explained by the new lake classes). By accounting for inherent differences among lakes through a classification scheme that incorporates physical and landscape features at multiple spatial scales, we provide a template for understanding lake-to-lake variability in fish species richness and growth of fish populations. Through an improved understanding of the "expected state" for a given lake type, underlying processes that affect survival and recruitment of fish populations may also be more easily and accurately identified. Ideally, the classification scheme could then be used to 1) predict the productive potential and sustainability of fish populations in lakes for which recent survey information is lacking, 2) serve as a basis for stratifying organized, statewide random sampling efforts, 3) serve as a basis for experimental regulations, and 4) refine stocking practices.

A common focus of state fisheries resource management agencies has been to conduct intensive surveys of game fish populations on individual lakes, while ignoring non-game-fishes (Hayes et al. 2003). Lake surveys are often conducted in response to public complaints of poor fishing, rather than as part of an organized, statistically-based sampling design that seeks to obtain information on all aspects of the fish community in a comparable manner. Local fisheries managers often focus on responding to the public, while placing less emphasis on larger-scale statewide issues such as reporting on the status and trends of the fishery (e.g., monitoring), stocking and regulation evaluations, or the status and trends of aquatic ecosystem health. Nonetheless, larger-scale, statewide issues are part of the mission of fisheries management agencies (Hayes et al. 2003). Standardized statewide monitoring strategies, should enable both local and statewide questions to be addressed with a single sampling effort, but are often met with resistance, primarily because these programs supposedly "compete" with local management needs (Bonar and Hubert 2002; Hayes et al. 2003). However, standardized random sampling can provide a means to extrapolate to lakes that have not been sampled, thereby providing tools to address local management issues (e.g., Hansen et al. 1989) and a sound basis for comparing conditions among similar lake types (Bonar and Hubert 2002). The new lake classification scheme presented here defines lake types, thereby providing a sound basis for comparisons for both monitoring and management activities.

Table 4. Wisconsin lake classification scheme based on maximum depth (deep: ≥ 5.5 m, shallow <5.5 m), landscape position (high: watershed area < 1036 ha, low: watershed area ≥ 1036 ha), and connectivity (drainage: inlet or outlet present, seepage: no inlet or outlet present).

Wisconsin Classification	**Description**
1	Shallow, High, Drainage
2	Deep, High, Drainage
3	Shallow, Low, Drainage
4	Deep, Low, Drainage
5	Shallow, Seepage
6	Deep, Seepage

Table 5. Summary of lake morphology and latitude used in regression tree analyses to predict fish species richness in 256 Wisconsin lakes during 1998-2004 and mean length at age 4 for bluegill, largemouth bass, walleye, and yellow perch in 358 Michigan and 410 Wisconsin lakes during 1947–2003.

	Species Richness			**Mean Length at Age 4**		
	N	**Minimum**	**Maximum**	**N**	**Minimum**	**Maximum**
Latitude	256	42.5082	46.5801	768	41.7772	47.4636
Maximum Depth (m)	256	1	30	768	1	37
Surface Area (ha)	256	4	9324	768	6	8124

Table 6. Analysis of variance of species richness and mean length at age 4 for bluegill, largemouth bass, walleye, and yellow perch among six classes of Michigan and Wisconsin lakes during 1947–2003.

Response	**N**	**F**	**P**	**R^2**
Species Richness	256	12.783	$\leq$ 0.001	0.204
Bluegill	412	4.309	0.001	0.050
Largemouth Bass	370	5.712	$\leq$ 0.001	0.073
Walleye	376	9.995	$\leq$ 0.001	0.119
Yellow Perch	368	2.189	0.0549	0.029

Table 7. Bonferonni matrix of pairwise comparison probabilities for species richness and mean length at age 4 for bluegill, largemouth bass, walleye, and yellow perch among the six classes of Michigan and Wisconsin lakes during 1947–2003. Bold indicates significant difference.

Lake Class	**1 High Shallow**	**2 High Deep**	**3 Low Shallow**	**4 Low Deep**	**5 Seepage Shallow**	**6 Seepage Deep**
Fish Species Richness						
1	1					
2	0.840	1				
3	1	0.904	1			
4	**0.041**	1	**0.006**	1		
5	1	**0.006**	0.556	**≤ 0.001**	1	
6	1	**≤ 0.001**	0.384	**≤ 0.001**	1	1
Bluegill						
1	1					
2	1	1				
3	1	1	1			
4	1	**0.004**	1	1		
5	1	1	0.414	**0.002**	1	
6	1	1	1	**0.006**	1	1
Largemouth Bass						
	1	2	3	4	5	6
1	1					
2	0.403	1				
3	0.203	1	1			
4	**0.006**	0.064	1	1		
5	1	1	1	0.161	1	
6	1	0.656	0.674	**≤ 0.001**	1	1
Walleye						
1	1					
2	1	1				
3	1	**0.038**	1			
4	1	**≤ 0.001**	1	1		
5	1	1	**0.008**	**0.002**	1	
6	1	1	**0.010**	**≤ 0.001**	1	1
Yellow Perch*						

* ANOVA not significant

Table 8. Regression tree results using latitude (decimal degrees), surface area (ha) and maximum depth (m) to predict fish species richness and mean length at age 4 for bluegill, largemouth bass, walleye, and yellow perch for 358 Michigan and 410 Wisconsin lakes during 1947–2003. PRE = proportional reduction in error, Values = back-transformed hectares or meters, and latitude in decimal degrees, Means = the mean value (number of species or length at age 4) for each split (group), N = the number of lakes in each group, and New Class = the new response-specific class assignment based on regression tree results.

PRE	**Split**	**Variable**	**Value**	**Mean**	**Number of Lakes**
		Species Richness			
0.277	1	Surface Area	< 228	12	196
	2	Latitude	< 45.4046	10	72
	2	Latitude	> 45.4046	13	124
	3	Surface Area	< 57	10	40
	3	Surface Area	> 57	14	84
	1	Surface Area	> 228	16	60
		Bluegill			
0.101	1	Surface Area	< 446	146	373
	1	Surface Area	> 446	174	39
		Largemouth Bass			
0.077	1	Surface Area	< 528	287	341
	1	Surface Area	> 528	327	29
		Walleye			
0.316	1	Latitude	< 45.1999	442	74
	1	Latitude	> 45.1999	359	48
		Yellow Perch			
0.150	1	Latitude	< 42.3858	208	53
	1	Latitude	> 42.3858	181	315
	2	Latitude	< 45.8479	186	204
	2	Latitude	> 45.8479	171	111

Table 9. Regression tree results using latitude (decimal degrees), Log_e surface area (ha) and Log_e maximum depth (m) to predict fish species richness in 256 Wisconsin lakes and fish mean length at age 4 for Michigan and Wisconsin lakes during 1947–2003. PRE = proportional reduction in error, Values = back-transformed hectares or meters, and latitude in decimal degrees, Means = the mean value (number of species or length at age 4) for each split (group), N = the number of lakes in each group, and New Class = the new response-specific class assignment based on regression tree results.

Connectivity Category	PRE	Split	Variable	Value	Mean	N	New Class
			Fish Species Richness				
Seepage	0.401	1	Surface Area	< 81	8	46	
		2	Surface Area	< 38	6.9	22	A
		2	Surface Area	≥ 38	9.3	24	B
		1	Surface Area	≥ 81	12	24	
		2	Maximum Depth	< 11	10	14	C
		2	Maximum Depth	≥ 11	15	10	D
Drainage	0.113	1	Maximum Depth	< 18	13	161	E
		1	Maximum Depth	≥ 18	18	25	F
			Bluegill				
Seepage	0.081	1	Surface Area	< 12	112	8	G
		1	Surface Area	≥ 12	147	184	H
Drainage	0.177	1	Surface Area	< 446	147	189	I
		1	Surface Area	≥ 446	177	31	J
			Largemouth Bass				
Seepage	0.052	1	Surface Area	< 19	246	9	K
		1	Surface Area	≥ 19	284	157	L
Drainage	0.115	1	Surface Area	< 686	292	186	M
		1	Surface Area	≥ 687	338	18	N
			Walleye				
Seepage	0.475	1	Latitude	< 45.3646	377	74	
		2	Surface Area	< 53	480	11	O
		2	Surface Area	≥ 53	430	20	P
		1	Latitude	≥ 45.3646	448	31	
		2	Surface Area	< 30	420	9	Q
		2	Surface Area	≥ 30	371	65	
		3	Maximum Depth	< 5	428	5	R
		3	Maximum Depth	≥ 5	366	60	S
Drainage	0.324	1	Latitude	< 45.1055	439	45	T
		1	Latitude	≥ 45.1055	352	226	U
			Yellow Perch				

Seepage	0.180	1	Latitude	< 43.3319	201	50	V
		1	Latitude	≥ 43.3319	177	124	
		2	Maximum Depth	< 5	155	15	W
		2	Maximum Depth	≥ 5	180	109	X
Drainage	0.137	1	Latitude	< 42.2289	216	23	Y
		1	Latitude	≥ 42.2289	181	171	Z

Table 10. Analysis of variance of species richness and fish mean length at age 4 among new lake classes developed from regression tree analyses for Michigan and Wisconsin lakes during 1947–2003.

Response	***df***	***F***	***P***	R^2
Species Richness	5;250	20.553	≤ 0.001	0.291
Bluegill	3;408	19.931	≤ 0.001	0.128
Largemouth Bass	3;366	15.810	≤ 0.001	0.115
Walleye	6;269	39.230	≤ 0.001	0.389
Yellow Perch	4;363	15.351	≤ 0.001	0.145

Table 11. Bonferonni matrix of pairwise comparison probabilities for species richness and fish mean length at age 4 among new classes developed from regression tree analyses for Michigan and Wisconsin lakes during 1947–2003. Bold indicates significant difference.

Lake Class	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Fish Species Richness							
1	1.000						
2	1.000	1.000					
3	0.591	1.000	1.000				
4	**≤ 0.001**	**0.004**	0.066	1.000			
5	**≤ 0.001**	**0.001**	0.150	1.000	1.000		
6	**≤ 0.001**	**≤ 0.001**	**≤ 0.001**	1.000	**≤ 0.001**	1.000	
Bluegill							
1	1.000						
2	**0.007**	1.000					
3	**0.008**	1.000	1.000				
4	**≤ 0.001**	**≤ 0.001**	**≤ 0.001**	1.000			
Largemouth Bass							
1	1.000						
2	**0.015**	1.000					
3	**0.002**	0.333	1.000				
4	**≤ 0.001**	**≤ 0.001**	**≤ 0.001**	1.000			
Walleye							
1	1.000						
2	0.466	1.000					
3	0.368	1.000	1.000				
4	1.000	1.000	1.000	1.000			
5	**≤ 0.001**	**≤ 0.001**	**0.029**	0.094	1.000		
6	0.998	1.000	1.000	1.000	**≤ 0.001**	1.000	
7	**≤ 0.001**	**≤ 0.001**	**≤ 0.001**	**0.007**	0.689	**≤ 0.001**	1.000
Yellow Perch							
1	1.000						
2	**≤ 0.001**	1.000					
3	**≤ 0.001**	0.194	1.000				
4	0.321	**≤ 0.001**	**≤ 0.001**	1.000			
5	**≤ 0.001**	0.093	1.000	**≤ 0.001**	1.000		

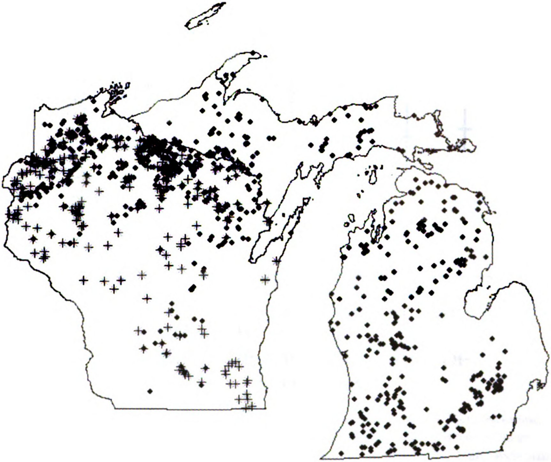

Figure 3. Locations of 256 Wisconsin lakes used to examine variability in species richness (asterisks) and 358 Michigan and 410 Wisconsin lakes used to examine variability in bluegill, largemouth bass, walleye and yellow perch mean length at age 4 (solid diamonds).

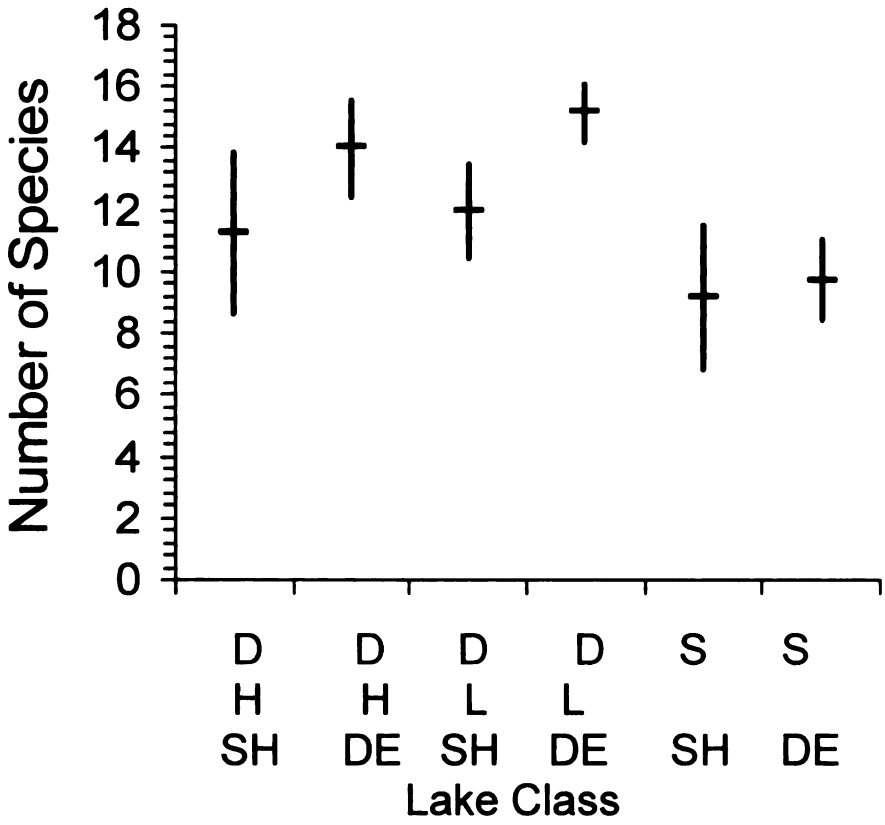

Figure 4. The mean number of species (± 95% confidence interval) by Wisconsin lake class in summer mini-fyke net and fall electrofishing surveys on 256 Wisconsin lakes during 1998–2004. X axis labels include D = drainage, S = seepage, H = high landscape position, L = low landscape position, SH = shallow, and DE = Deep.

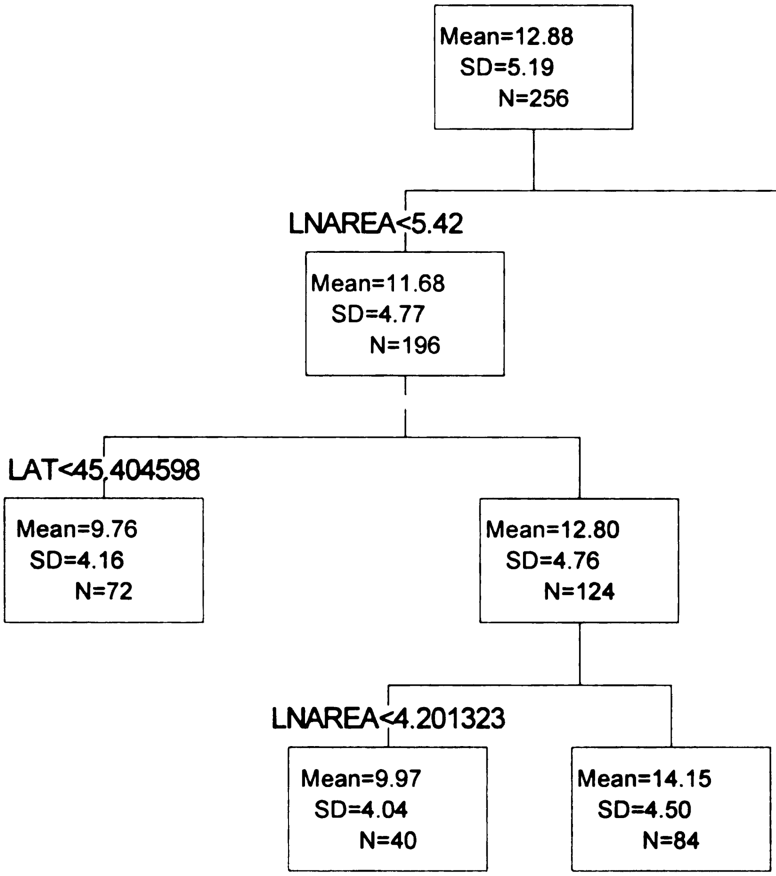

Figure 5. Regression tree mobile diagram example predicting the number of species by Log_e Surface Area, Log_e Maximum Depth, and Latitude for 256 Wisconsin lakes during 1998-2004. Results from regression tress analyses are presented in tabular format rather than mobile diagrams.

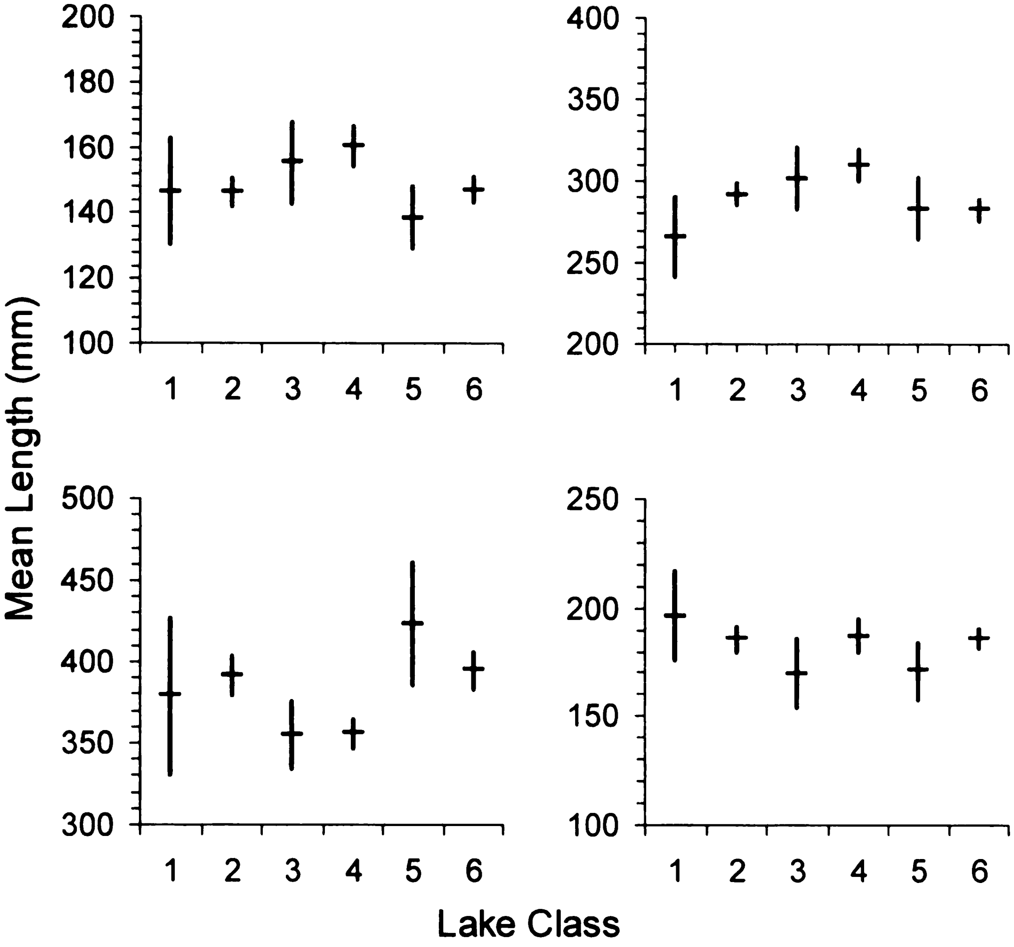

Figure 6. Bluegill (upper left panel), largemouth bass (upper right panel), walleye (lower left panel), and yellow perch (lower right panel) mean length at age 4 (mm; ± 95% confidence interval) for six Wisconsin lake classes.

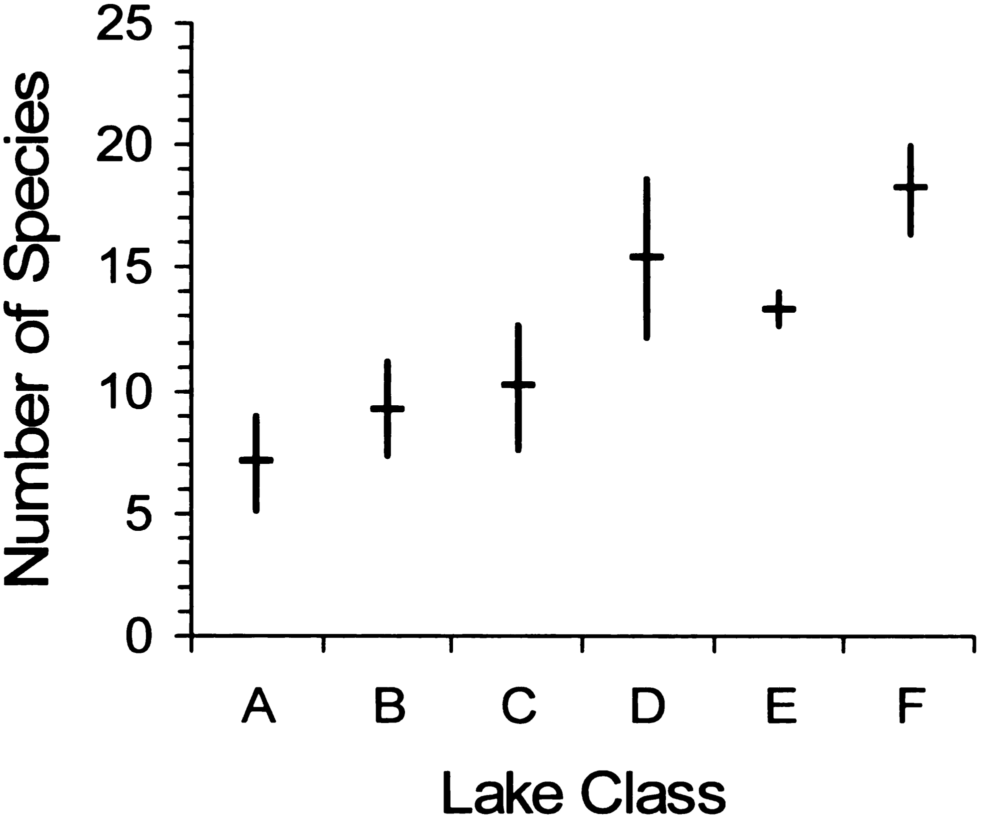

Figure 7. The mean number of species (± 95% confidence interval) by new lake class in summer mini-fyke net and fall electrofishing surveys on 256 Wisconsin lakes during 1998–2004.

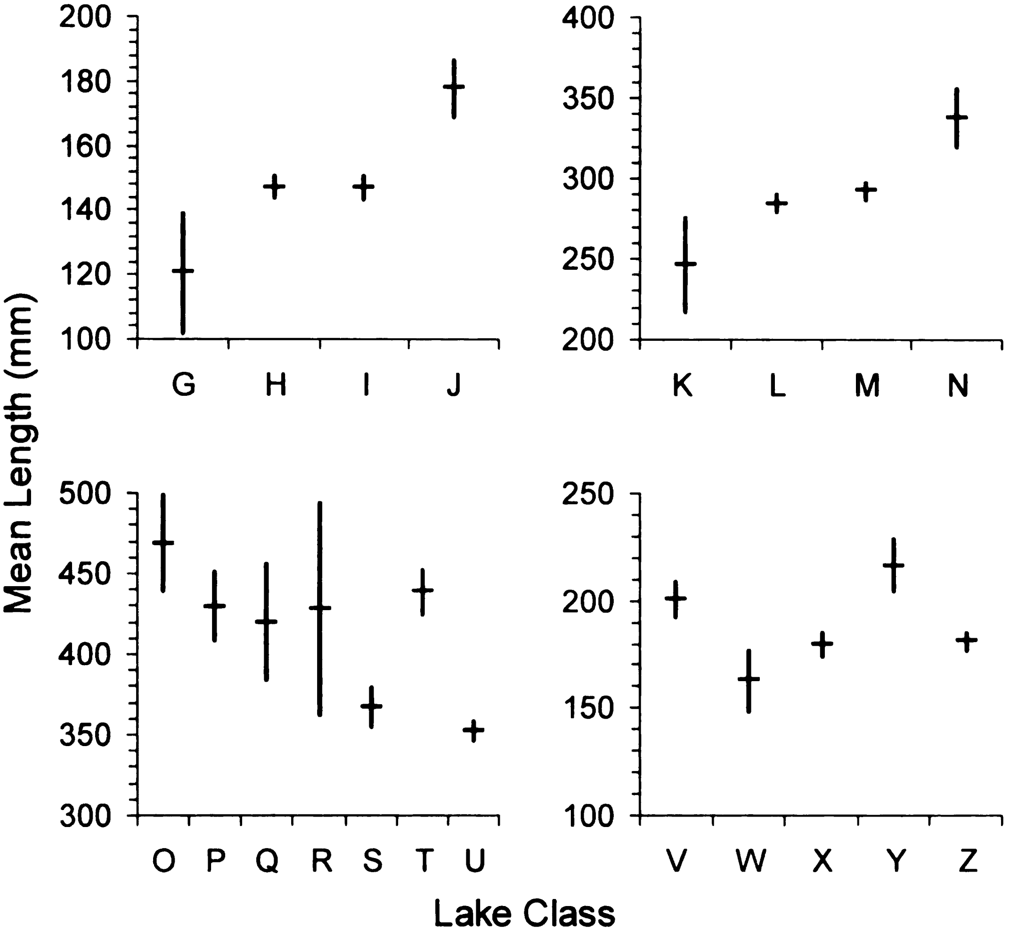

Figure 8. Bluegill (upper left panel), largemouth bass (upper right panel), walleye (lower left panel), and yellow perch (lower right panel) mean length at age 4 (mm; ± 95% confidence interval) for new lake classes.

CHAPTER 3

EVALUATING ANGLING REGULATIONS FOR BLUEGILL IN WISCONSIN

Abstract. — I determined expected ranges of bluegill growth and mortality for different lake classes in Wisconsin from existing survey data to determine the best combination of minimum length limits (152, 178, 203, and 229 mm) and daily creel limits (25, 10, 5) to maximize yield per recruit and number of bluegill harvested per 100 individuals for each lake class. For each combination of minimum length limit and daily creel limit, yield per recruit increased with lake size, from the smallest lake class to the largest lake class, and ranged 4–30 grams per recruit among regulation scenarios. Under a 25-fish daily creel limit, a 152-mm minimum length limit produced the highest yield per recruit for small and large seepage lakes and small drainage lakes, whereas a 178-mm minimum length limit produced the highest yield per recruit for large drainage lakes. With the exception of large drainage lakes, higher minimum length limits (203 or 229 mm) at the 25 daily creel limit yielded fewer grams per recruit than reduced daily creel limits at smaller minimum length limits (152 or 178 mm). The number of fish harvested at or above quality length (152 mm) ranged 7–31 per 100 among lake classes. Higher minimum length limits under the 25 daily creel limit often yielded similar numbers of quality-sized fish as reduced daily creel limits under 152 or 178 mm minimum length limits. My results provide ranges of bluegill growth, natural mortality, and fishing mortality for lake classes that may be used to evaluate future regulation proposals and to identify candidate lakes for experimental regulations. Regulations like minimum length limits may be more effective in increasing the number of quality-sized fish harvested in lake classes (e.g. New Lake Classes I or J) that have the highest growth and exploitation.

Introduction

Bluegill (*Lepomis macrochirus*) are among the most highly sought fish species by anglers in Wisconsin (McClanahan 2003) and are typically managed with liberal seasons, no minimum length limit, and high daily creel limits (Becker 1983; Coble 1988). Bluegill are prolific and rarely limited by recruitment, so angling is generally not perceived to have long-term impact on bluegill populations (Coble 1988). However, angling can directly affect bluegill population size structure through selective removal of large fish (Goedde and Coble 1981;Coble 1988; Beard and Kampa 1999), which indirectly shifts life history strategies to favor early maturation, decreased growth, and reduced maximum size (Drake et al.1997; Jennings et al 1997). Typically, high daily creel limits such as 25 per day are intended to distribute harvest among anglers, but are not intended to directly address poor population size structure caused from angling or life history changes (Noble and Jones 1993).

In contrast, minimum length limits have recently been evaluated as a means to improve size structure of bluegill populations (Beard et al. 1997a; Paukert et al. 2002). Minimum length limits prevent harvest of fish shorter than a specified length, and thereby may reduce mortality on vulnerable populations at low abundance, or reduce exploitation of immature fish before they spawn (Noble and Jones 1993). Minimum length limits may be ineffective where harvest has little effect on total mortality (Noble and Jones 1993). Minimum length limits have been implemented as a means to increase size structure for other centrarchids such as largemouth bass *Micropterus salmoides* (Wilde 1997; Newman and Hoff 2000) and black crappie *Pomoxis nigromaculatus* or white crappie *Pomoxis annularis* (Maceina et al. 1998; Hale et al. 1999) with mixed results.

For example, minimum length limits were most likely to improve crappie size structure and yield in North American lakes if growth was fast and natural mortality was low (Allen and Miranda 1995). Paukert et al. (2002) suggested that natural mortality was more important than growth for determining success of a 200-mm minimum length limit for bluegill in 18 Nebraska lakes. Delaying harvest is not likely to increase size structure for populations with high natural mortality (Coble 1988). Overall, the relative importance of growth, natural mortality, and fishing mortality in determining the success of minimum length limits should depend on the species, and on the growth and mortality experienced by the population.

The growth and mortality experienced by a fish population likely vary among lakes, because lakes vary greatly in morphometry, fish assemblages, and productivity. Consequently, regulation changes are often proposed for individual lakes, or small numbers of lakes, after analysis of time-series data or simulations of population dynamics in response to a proposed set of regulations (e.g., Maceina et al. 1998). The weakness of this approach is that the number of experimental units is usually small (e.g., one to a few lakes), and the methods used for data collection and analyses are typically not standardized among lakes. Therefore, the information obtained from studying individual lakes before and after regulation changes cannot be extrapolated to other potential candidate lakes for the same regulations, or for studying the effects of state- or region-wide regulation of fish populations. Lake classification provides a means to account for natural variation among lakes, and thereby provides a framework for implementing large-scale management actions, such as minimum length limits or daily creel limits, on many lakes at the same time.

When evaluating length limits, lake classes based on growth potential may provide a framework for understanding other dynamic rates such as natural and fishing mortality, age-at-maturity, fecundity, and recruitment, because growth is linked to all of these rates and processes. For example, growth parameters and environmental temperature are strongly related to the rate of natural mortality among many fish stocks (Pauly 1980; Beamesferder and North 1995). High fishing mortality may lead to decreased density, increased growth, decreased age and size at maturity, and decreased fecundity (Trippel 1995). Large parents may spawn earlier and produce offspring that experience a longer growing season and therefore may have higher over-winter survival (Miranda and Muncy 1987; Ridgway et al. 1991). Therefore, growth can influence recruitment. Decreased age at maturity and increased growth rates as a result of high exploitation, have been shown for northern pike *Esox lucius* (Diana 1983), brown trout *Salmo trutta* (Hegge et al. 1991), Atlantic cod *Gadus morhua* (Beacham 1983), and arctic char *Salvelinus alpinus* (Hegge et al. 1991). Size at maturity is often positively related to asymptotic size (Charnov 1993), estimated from the von Bertalanffy growth equation (von Bertalanffy 1938), so early growth rates may affect population size structure. Consequently, growth, which is relatively easy to estimate from data collected during routine fisheries surveys, may be more useful for categorizing lakes for fishery regulation than other fish population attributes, such as recruitment, mortality, or density, which are more difficult to estimate.

My objective was to estimate how bluegill yield per recruit and number harvested varied as a function of minimum age entering the fishery and fishing mortality rate among four classes of Wisconsin inland lakes. I used these estimates to determine the minimum length and daily bag limits that maximize yield per recruit and number of quality-sized or larger bluegill harvested per 100 recruits for each lake class. Lake classes for bluegill were developed based on growth and habitat characteristics of lakes in Wisconsin and Michigan as part of a previous study (Chapter 2), but had not been evaluated as a framework for regulating bluegill fisheries. First, I determined expected ranges of bluegill growth and mortality for each lake class. Next, I estimated yield per recruit and number of bluegill harvested across four minimum length limits and three daily creel limits, based on the expected ranges of growth and mortality for each lake class. Given the strong linkage between growth and other population characteristics, such as recruitment and mortality, I expected that lake classes would provide a useful framework for setting angling regulations, especially minimum length limits, for bluegill fisheries in Wisconsin. I also expected that regulations that maximized yield per recruit or number of fish harvested might vary among lake classes due to differences in growth and mortality rates among lake classes.

Methods

Study Area and Data Sources

My study area was the population of all inland lakes in Wisconsin, because my interest was in using lake classification as a basis for evaluating potential angling regulations for bluegill on the state's inland lakes. Lake classes based on bluegill growth potential were established for Wisconsin lakes as part of a previous study, based on categories of connectedness (seepage and drainage) and lake surface area (Table 12; Chapter 2). The lake classification scheme was developed based on analysis of patterns in bluegill mean length at age 4 for inland lakes in Wisconsin and Michigan (Chapter 2), but has not been evaluated as a basis for setting regulations, or for its ability to explain variation in other population characteristics, such as mortality, which should be considered when setting regulations.

My interest was in using the lake classification scheme to evaluate bluegill regulation strategies that could be set on a statewide basis for a class of lakes, so data requirements for fisheries population information were large (e.g. statewide) and different from the previous study (Chapter 2) in that I focused on Wisconsin lakes only. I used existing fisheries survey data from Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection databases to develop new datasets specific to this analysis. Lakes were typically sampled as part of regional or local sampling priorities, so final datasets were not comprised of randomly selected lake surveys. However, sampling was extensive in both space and time, so I assumed that lakes sampled provided a representative sample of bluegill population characteristics in inland lakes in Wisconsin (Figure 9).

To identify expected ranges of bluegill growth and mortality among classes of Wisconsin lakes, I identified subsets of lakes in the database with fyke-netting and electrofishing surveys that included mean length at age and weight-length data. From mean length at age data, I estimated growth parameters, age frequency, total mortality, and natural mortality. From weight-length data, I estimated weight-length relationships and asymptotic average weight (W_{∞}) for yield/recruit models. Most surveys did not contain all information needed (e.g., length, weight, and age), so I developed separate datasets for length-age, weight-length, and age structure (Figure 9) and assumed that each dataset was a representative sample of each population attribute for each lake class. I tested for differences in growth and mortality parameters among lake classes. However, because my intent was to demonstrate how lake classification could be used in management and not all lake classes had large sample sizes for each parameter, I proceeded with minimum length limit and daily creel limit analyses by lake class, regardless of the outcome of the tests for differences in growth or mortality estimates among lake classes.

Growth

Growth parameters were estimated for the von Bertalanffy growth model using non-linear regression (von Bertalanffy 1938):

$$L_t = L_\infty (1 - e^{(-K(t-t_0))});$$

where L_t = the mean length at age t, L_∞ = the asymptotic average length, K = the instantaneous rate at which L_t approaches L_∞, and t_0 = the hypothetical age at which length is zero (Haddon 2001). Von Bertalanffy growth parameters were estimated from mean lengths at ages 1–7 for each lake survey, and then parameter estimates were averaged for each lake class. Growth parameters and their asymptotic standard errors were estimated using nonlinear regression, with additive errors. Parameter estimates were excluded if the estimated asymptotic length exceeded the state record by 10%. Weight-length relationships were estimated for the allometric weight-length model to obtain an estimate of W_∞ for the yield per recruit model:

$$W_i = \alpha L_i^{\beta};$$

where W_i = the mean weight at length L_i, α is a scaling constant, and β is the allometric shape parameter (Haddon 2001). Parameters of weight-length relationships were estimated for each lake survey from the log-transformed equation, and then averaged across all lake surveys within each lake class. Asymptotic average weight W_∞ was estimated by substituting L_∞ into the averaged weight-length model. The assumption that growth parameters differed by lake class was tested with analysis of variance with lake class as the factor.

Mortality

Age frequencies were estimated using age-length keys and catch curves were then used to estimate instantaneous total mortality (Z) from the age frequency (Ricker 1975). Survival (S) was estimated from e^{-Z}, and total annual mortality (A) equaled $1 - S$. Natural mortality (M) was estimated using the Pauly equation (1980):

$$Log_e M = -0.0152 - 0.279 Log_e L_\infty + 0.6543 Log_e K + 0.4634 Log_e T\ ;$$

where L_∞ and K are von Bertalanffy growth parameters, and T = the mean annual temperature (^{o}C) experienced by the stock. Because mean annual water temperature was not available, mean annual air temperature was obtained from the National Oceanic and Atmospheric Administration website (http://climvis.ncdc.noaa.gov/). Mean annual air temperature roughly corresponds to mean annual surface water temperature for freshwater systems (Pauly 1980; Shuter et al. 1983). Statewide mean annual air temperatures were averaged for a 60-year period corresponding to the period of fishery survey information. Instantaneous fishing mortality (F) was estimated by subtracting instantaneous natural mortality (M) from instantaneous total mortality ($Z = F + M$). Exploitation was estimated from F, A, and Z using Baranov's equation ($u = F*A/Z$). In Wisconsin, the aggregate panfish bag limit was reduced from 50 to 25 in 1998. Differences in mortality rates between periods (pre–1988 and post–1988) were tested with analysis of covariance to determine if mortality rates could be combined, and averaged across periods with $\log_e$ number at age as the dependent variable, age as the (covariate) independent variable, and period (pre or post) as the treatment variable. The assumption that total instantaneous mortality estimates differed by lake class was tested with analysis of variance with lake class as the factor.

Exploitation

Harvest limit reductions were incorporated into the yield per recruit model by estimating the percent reduction in exploitation for each of two reduced creel-limit scenarios (from 25 to 10 bluegill per day and from 25 to 5 bluegill per day) using angler interviews from recent creel surveys (1998–2002). Creel surveys for northern Wisconsin lakes were conducted during the angling season (first Saturday in May through March 1 of the following year) as part of a larger random set of northern Wisconsin walleye lakes using a random stratified roving access design (Pollack et al. 1994; Beard et al. 1997b). The current creel limit in Wisconsin is an aggregate panfish limit that includes bluegill, pumpkinseed *Lepomis gibbosus,* black crappie, white crappie, yellow perch *Perca flavescens*, green sunfish *Lepomis cyanellus*, warmouth *Lepomis gulosus*, and orangespotted sunfish *Lepomis humilis*, so I used panfish rather than bluegill to estimate reduced exploitation levels. First, the number of panfish harvested per interview was divided by the number of anglers in the party to derive the number of panfish harvested by each individual (e.g., if two anglers in a party harvested 10 panfish, they were treated as if each angler harvested 5 panfish). Second, the total number of anglers who harvested panfish at each level of harvest per angler was tabulated across all creel surveys (i.e., for all creel surveys, the number of anglers who harvested 1, 2, 3, ... *n* panfish). Third, the frequency of individual anglers who harvested each number of panfish was multiplied by the number harvested to derive the total harvest for each harvest limit across all surveys. For reduced creel limits of 5 and 10 fish per day, harvest numbers were reduced to 5 for any number harvested that exceeded 5, or to 10 for any number harvested that exceeded 10, respectively, and then the total harvest was recalculated. The percent reduction in total harvest was estimated as the reduced total harvest divided by the initial total harvest (under the current regulation). I assumed the reduced panfish harvest would be representative of reduced bluegill harvest.

Yield per Recruit and Number Harvested

To estimate how bluegill yield per recruit varied among ages vulnerable to harvest and fishing mortality rates, I used a Beverton Holt yield per recruit model (Ricker 1975):

$$\frac{Y_t}{N_0} = Fe^{-M(t_r - t_0)}W_\infty\left(\frac{1}{Z} - \frac{3e^{-K(t_r - t_0)}}{Z+K} + \frac{3e^{-2K(t_r - t_0)}}{Z+2K} - \frac{e^{-3K(t_r - t_0)}}{Z+3K}\right);$$

where yield per recruit, Y_i/N_0, is a function of growth and mortality estimates for each lake class (defined above), across a range of hypothetical fishing mortality rates, F, and ages of vulnerability to harvest, t_r. The Beverton Holt yield per recruit model examines yield as a function of growth, age at first capture, and fishing mortality to evaluate trade-offs in biomass harvested per individual recruited, between capturing a large number of young fish and capturing a smaller number of fish later in their life-span (King 1995). For each lake class, yield per recruit was estimated for minimum length limits of 127 mm (5 in), 152 mm (6 in), 178 mm (7 in), 203 mm (8 in), and 229 mm (9 in) and daily creel limits of 25, 10, and 5 representing a range of exploitation rates ($u = FA/Z$). Quality length for bluegill was defined as 152 mm (6 inches; Willis et al.1993), so I used 152 mm as the lower end of the minimum length limits evaluated, but provided a smaller minimum length limit (127 mm) as a means to assess yield per recruit and number harvested per 100 in the absence of a minimum length limit.

The number of bluegill reaching a minimum length limit that were harvested by anglers was estimated as the difference between the number present with and without fishing:

$$C_t = N_0 e^{-M(t-t_0)} - N_0 e^{-Z(t-t_0)};$$

where C_t = the number estimated to be harvested at age t, N_0 = the number of recruits entering the population at age 0, and M and Z are as defined above. For simulating the number of bluegill that would be harvested under each combination of minimum length limit and daily creel limit, I set $N_0 = 100$. The number harvested was analogous to the biomass harvested from the yield per recruit analysis, except that the number harvested was numbers per 100 recruits rather than grams per individual recruit.

Results

Growth

Bluegill grew at different rates both within and among lake classes, but generally, average asymptotic average length (L_∞) and instantaneous growth rate (K) increased as lake size increased from small seepage lakes (Class G) to large drainage lakes (Class J). Based on 170 lake surveys during 1948–2003, the asymptotic average length (L_∞) ranged 255–281 mm and did not differ among lake classes ($F = 1.29$; $df = 3, 166$; $P = 0.28$). The average instantaneous growth rate (K) ranged 0.247–0.255/year and did not differ among lake classes ($F = 0.01$; $df = 3, 166$; $P = 1.00$; Table 13). Based on 43 lake surveys during 1944–2002, the allometric shape parameter (β) ranged 2.99–3.14 and did not differ among lake classes ($F = 0.22$; $df = 3, 39$; $P = 0.88$). The asymptotic average weight (W_∞) ranged 312–549 grams across lake classes, and both parameters tended to increase with increasing lake size (Table 13).

Mortality

Based on 34 surveys during 1954–2003, total mortality of bluegill varied greatly among lake classes, whereas natural mortality of bluegill varied little among lake classes. Instantaneous total mortality did not differ significantly between periods, before or after the 1998 creel-limit reduction ($F = 3.68$; $df = 1, 163$; $P = 0.06$), so I combined estimates between the two periods for each lake class. Estimates of instantaneous total mortality (Z) ranged 0.26–1.61 and did not differ among lake classes ($F = 0.42$; $df = 3, 30,$; $P = 0.74$). Instantaneous fishing mortality (F) estimates were lowest in small seepage lakes and highest in small drainage lakes (Table 14). Instantaneous natural mortality (M) did not vary as much as total or fishing mortality, but were highest in small and large seepage lakes and lowest in large drainage lakes (Table 14). In all lake classes, instantaneous fishing mortality (*F*) was higher than instantaneous natural mortality. Average exploitation (*u*) ranged 0.27–0.47 (Table 14).

Exploitation

Panfish species were harvested from 105 lakes where creel surveys were conducted during 1998–2003. Of 8,447 anglers interviewed, less than 3% of anglers harvested their daily creel limit of 25 fish or more (Table 15; Figure 10). Under the current 25 fish daily creel limit, 50,131 panfish were harvested, whereas a reduced daily creel limit of 10 fish (a 60% reduction in creel) would reduce harvest by 21% (39,728 panfish), and a reduced daily creel limit of 5 fish (an 80% reduction in creel) would reduce harvest by 45% (27,788 panfish).

Yield per Recruit and Number Harvested

For each combination of minimum length limit and daily creel limit, estimated yield per recruit increased with lake size, from the smallest lake class (G) to the largest lake class (J), and ranged 4–30 grams per recruit across regulation scenarios (Table 16; Figure 11). Under a 25-fish daily creel limit, a 152-mm minimum length limit produced the highest yield per recruit for small and large seepage lakes and small drainage lakes, whereas a 178-mm minimum length limit produced the highest yield per recruit for large drainage lakes. For all lake classes, yield per recruit declined as the daily creel limit was reduced from 25 fish to 5 fish, which was expected because creel limits were directly related to the fishing mortality rate. With the exception of large drainage lakes (J), higher minimum length limits (203 or 229 mm) at the 25 daily creel limit yielded fewer grams per recruit than reduced daily creel limits at smaller minimum length limits (152 or 178 mm). The number of fish harvested at or above the minimum length limit ranged 7–31 per 100 for all lake classes (Table 16; Figure 11). Higher minimum length limits under the 25 daily creel limit often yielded similar numbers of quality-sized fish (>152 mm)than reduced daily creel limits under 152 or 178 mm minimum length limits, though the fish would be larger under the higher minimum length limits.

For small seepage lakes (G), yield per recruit was maximized by a 25-fish daily creel limit and a 152-mm minimum length limit (Table 16; Figure 11). However, at low exploitation rates, such as the current lake class average of 16.7%, the difference in yield per recruit between the 152-mm minimum length limit and the 178-mm or 203-mm minimum length limits for the 25 fish daily creel limit was small (1-4 g). Under lower exploitation rates (10 or 5 fish daily creel limits), the 152-mm and 178-mm minimum length limits produced similar yields, and the 203-mm and 209-mm minimum length limits produced the lowest yield per recruit. Numbers harvested ranged 7–17 fish, and was maximized by a 25-fish daily creel limit and 152-mm minimum length limit (17 fish per 100 recruits; Table 16; Figure 12).

For large seepage lakes (H) under a 25-fish daily creel limit, yield per recruit was slightly higher under a 152-mm minimum length limit than under a 178-mm minimum length limit, and a 10 fish daily creel limit and 152-mm minimum length limit produced the second highest yield per recruit (Table 16; Figure 11). Under reduced daily creel limits of 10 fish and 5 fish, yield per recruit was highest under a 152-mm minimum length limit, slightly lower under a 178-mm minimum length limit, and lowest under 203-mm and 229-mm minimum length limits. Numbers harvested ranged 9–25 fish, and was maximized by a 25-fish daily creel limit and 152-mm minimum length limit (25 fish per 100 recruits; Table 16; Figure 12). A 203-mm minimum length limit and 25-fish daily creel limit produced similar numbers of fish as a 5-fish daily creel limit and 152-mm or 178-mm minimum length limits.

For small drainage lakes (I) under a 25-fish daily creel limit, yield per recruit was slightly higher with a 152-mm minimum length limit than a 178-mm minimum length limit, and much higher than 203-mm or 229-mm minimum length limits (Table 16; Figure 11). Under reduced daily creel limits of 10 fish and 5 fish, yield per recruit was highest for 152-mm and 178-mm minimum length limits. The decline in yield per recruit was larger under higher minimum length limits (203–229 mm) than under reduced daily creel limits (10 or 5 fish). Number harvested ranged 15–31, and was maximized by a 25-fish daily creel limit and 178-mm minimum length limit (31 fish per 100 recruits; Table 16; Figure 12). Similarly, the decline in numbers harvested under higher minimum length limits (203–229 mm) was greater than under lower daily creel limits (10 or 5 fish).

For large drainage lakes (J) under a 25-fish daily creel limit, yield per recruit was maximized by 152-mm and 178-mm minimum length limits, slightly lower (3 g) for a 203-mm minimum length limit, and lowest (9 g) for a 229-mm minimum length limit (Table 16; Figure 11). Under a 10 fish daily creel limit, a 152-mm minimum length limit produced the highest yield per recruit, but yield per recruit under 152-mm or 178-mm minimum length limits was slightly greater than under a 25-fish daily creel limit with 203-mm or 229-mm minimum length limits. At a 5-fish daily creel limit, a 229-mm minimum length limit produced the lowest yield per recruit, whereas 152-mm and 178-mm minimum length limits produced the highest yield per recruit. Numbers harvested were highest for a 25-fish daily creel limit and 152-mm or 178-mm minimum length limits, and lowest for a 5-fish daily creel limit and 229-mm minimum length limit (Table 16; Figure 12). A reduced daily creel limit of 10 fish yielded similar numbers of fish as higher minimum length limits (203 or 229 mm) at the current 25-fish daily creel limit.

Discussion

Growth

I found that von Bertalanffy asymptotic average length and instantaneous growth rate (*K*) tended to increase as lake size increased from small seepage lakes to large drainage lakes. Lake class average asymptotic length (L_∞ = 255–281 mm) and instantaneous growth rate (K = 0.247–0.255/year) were similar to those reported by Beard et al. (1997a), who found that L_∞ ranged between 213 and 268 mm and K ranged between 0.24 and 0.29/year for slow and fast growing bluegill populations in northern Wisconsin. Beard et al. (1997a) did not provide the number of lake surveys for their estimates, or describe physical characteristics of lake types used, which may limit comparisons to my findings obtained from 170 lake surveys in southern and northern Wisconsin. Ranges in growth parameters for bluegill in 18 Nebraska lakes were 213–311 mm for L_∞ and 0.21–0.46/year for K during 1998-1999, similar to my L_∞ estimates, but much larger than my range in growth (Paukert et al. 2002). However, my range in growth parameters was the range among 4 lake class averages, whereas Paukert et al. 2002 reported ranges across lakes.

Mortality

My natural mortality estimates were similar among lake classes, despite differences in mean asymptotic weights and instantaneous growth rates for bluegill among lake classes. The Pauly equation used for estimating instantaneous natural mortality (M) was developed through a meta-analysis of 175 different freshwater and marine fish stocks, including 84 species, though bluegill was not among the species included in the analysis (Pauly 1980). However, Beamesderfer and North (1995) found that natural mortality was correlated with latitude, air temperature, and degree-days for another centrarchid, largemouth bass, across 40 populations in North America. My use of statewide mean annual air temperature averaged across a 60-year period likely diminished the sensitivity of the estimate, and therefore could be improved by estimating regional mean annual air temperature or by measuring surface water temperature on lakes. Another approach would be to estimate yield across a range of natural mortality rates (e.g., Maceina et al. 1998). My estimates of M were similar among lake classes, so natural mortality was nearly constant and therefore did not strongly influence predicted differences in yield per recruit or numbers harvested among lake classes.

My estimates of average annual mortality obtained from catch curves were lower than others reported in the literature. For example, Ricker (1945) studied three Indiana bluegill populations and estimated annual mortality between 60% and 87%, whereas my annual mortality estimates were between 43% and 61%. Mean annual air temperature in Wisconsin is likely lower than in Indiana, so my estimates of natural mortality, and presumably annual mortality, should be lower than for more southerly states like Indiana. Snow (1978) reported bluegill annual mortality in Murphy Flowage Wisconsin to be

59%, and Paukert et al. (2002) reported annual mortality rates in 18 Nebraska lakes between 15 and 53%, similar to my estimates. Mortality estimates derived from catch curves may be inaccurate when survival rate is not constant with age, the population is not sampled randomly, or recruitment fluctuates greatly (Ricker 1975; Allen 1997). However, Maceina et al. (1998) compared total annual mortality estimated from catch curves to four other methods for estimating total annual mortality and found that all five methods provided consistent estimates of total annual mortality for crappie in Weiss Lake, Alabama.

Exploitation

I found that exploitation rates ranged 17–39% and increased with lake size for small and large seepage lakes and small drainage lakes, which has also been shown for other fisheries. For example, angler harvest was positively related to lake size for lake trout *Salvelinus namaycush namaycush* (Goddard et al. 1987), walleye *Stizostedion zander* (Baccante and Colby 1996), and panfish (Wisconsin Department of Natural Resources *unpublished data*), so lake classes that are descriptive of lake size may be useful for evaluating harvest regulation strategies that depend on exploitation rates. Exploitation rates in my study were similar to those reported for Indiana lakes (*u* = 20-45%; Ricker 1945) and Murphy Flowage Wisconsin (*u* = 3–35%; Snow 1978). In a literature review of 46 different studies, Coble (1988) estimated an average bluegill exploitation rate of 27%.

Yield per Recruit and Number Harvested

High minimum length limits for bluegill generally reduced yield per recruit and number harvested, similar to results of other studies of panfish. Paukert et al. (2002)

evaluated a 200-mm length limit to increase bluegill size structure for Nebraska lakes and found that anglers would have to sacrifice yield and number harvested to gain a small increase in numbers of fish longer than 8 inches. Minimum length limits were more successful for increasing crappie size structure in lakes where growth was high, natural mortality was low, and angler exploitation was high (Allen and Miranda 1995). In Wisconsin lakes, natural mortality was not high and did not differ greatly among lake classes. Growth rates did not differ greatly among lake classes and may not have been high enough overall for a minimum length limit to drastically increase numbers of large fish in most lakes. Large seepage and small drainage lakes had the highest exploitation rates, so may be the best candidate lakes for minimum length limits, but exploitation rates were not as high as those reported by Allen and Miranda (1995) for southern crappie populations. In fact, current exploitation rates may not be sufficiently high enough to maximize yield per recruit or numbers harvested for any of the lake classes I examined for Wisconsin.

Reduced daily creel limits at the lowest minimum length limit often produced similar or greater yield per recruit than high minimum length limits (e.g. 229 mm) at a higher daily creel limit, indicating that at least in some cases, reduced daily creel limits may be more effective for increasing yield per recruit of quality-sized or larger bluegill than high minimum length limits. Similarly, numbers harvested per 100 recruits under a 5 fish daily creel limit and 152-mm minimum length limit were greater than numbers harvested under a 25 fish daily creel limit and 229-mm minimum length limit for three of the four lake classes. However, reducing the daily creel limit means reducing exploitation from current levels, which generally did not maximize yield per recruit or numbers harvested.

Reduced daily creel limits in combination with minimum length limits may be effective for decreasing fishing mortality on spawning adult bluegill, which may be more necessary in small seepage lakes than in large drainage lakes. Daily creel limit reductions are often proposed for protection of bluegill in small lakes, which are assumed to be more vulnerable to over-exploitation in Wisconsin. If exploitation is excessive in small lakes, then growth is likely to be high and age at maturity is likely to be low, especially in seepage lakes where immigration is not possible. I did not see evidence of high exploitation in two small seepage lakes for which total mortality could be estimated, and age to reach 152-mm was higher (3.6 years) than all other lake classes. However, my sample size was small, so more detailed studies of small lakes should identify representative ranges of growth and mortality to justify a reduced daily creel limit.

Changes in bluegill angling regulations require support from the angling public. For example, Reed and Parsons (1999) found that most anglers (61%) on four Minnesota lakes supported a proposed daily creel limit reduction from 30 to 20 fish, but would not support further reduction. My results suggest that reduced creel limits (from the current 25 to 10 or 5 fish) would not increase yield per recruit or numbers harvested per 100 recruits, and that reduced daily creel limits may not reduce harvest as much as anglers perceive. Reed and Parsons (1999) also found that 56% of anglers opposed the idea of bluegill length limits, but that the most acceptable minimum length limit was 6 inches. Among the four minimum length limits I evaluated, a 152-mm (6-inch) minimum length limit generally increased yield per recruit and numbers harvested per 100 recruits at current levels of estimated exploitation in Wisconsin. Paukert et al. (2002) reported that 67% of anglers interviewed on a Nebraska lake during 1998–2001 were there to harvest bluegill to eat and were not concerned with catching large bluegill. Therefore, increasing size structure may not be a concern to most bluegill anglers. However, in Minnesota, anglers interested in catching larger bluegill may make more trips if size structure increased, suggesting that some anglers are interested in catching quality-sized bluegill (Reed and Parsons 1988). In general, I found that benefits of minimum length limits (e.g., higher yield per recruit or numbers available for harvest) were more pronounced at higher levels of exploitation, as was found by Allen and Miranda (1995) for crappie in North America.

Management Implications

My results provide ranges of bluegill growth, natural mortality, and fishing mortality for lake classes that may be used to evaluate future regulation proposals. My estimates of yield per recruit and numbers harvested may be used to predict the effects of proposed regulation changes on angling harvest of bluegill. My estimates of yield per recruit and numbers harvested should be refined as more data become available, to improve our understanding of the trade-offs between growth and mortality in managing bluegill fisheries.

The impact of statewide angling regulations such as creel and size limits on fish populations requires analyses on a statewide scale. Ideally, information used in modeling angling regulations would be collected using standard methods and a statistically rigorous study design. More frequently, the only long-term information on a large spatial scale is collected using non-standard methods and non-random sampling, which often minimizes the utility of the information (Bonar and Hubert 2002; Hayes et al. 2003). However, using historic fisheries survey and creel survey data, Beard and Kampa (1999) were able to convincingly demonstrate a decline in the mean size and proportion of large bluegill in fyke net surveys in Wisconsin during 1967–1991. While these historic datasets are often fraught with challenges, large statewide datasets may offer the only information available, and through their use, may reveal obvious shortcomings in statewide sampling or data capture efforts, as was the case with this analysis. For example, most historic age-length information was limited to summary information, such as mean length at age summaries, rather than individual fish lengths and ages. Consequently, I was only able to construct age frequencies and estimate mortality on 34 lakes, even though I queried all existing databases over a 60-year period. Individual age-length data probably exist for more lakes in field office files, but unless such data are archived in a centralized database, it remains largely inaccessible and therefore cannot be used for retrospective analyses. Estimating the correct range in mortality rates is critical when evaluating regulations. In addition, I was able to estimate von Bertalanffy growth parameters for 170 surveys from summary, length-stratified, sub-sampled mean lengths at age, but these estimates may be biased because length-stratified sub-sampled mean lengths at age do not constitute a random sample of lengths at age (Betolli and Miranda 2001, Chapter 1). Complete raw data, rather than summary data, should be entered into centralized statewide databases.

Table 12. Lake classification criteria for predicting bluegill mean length at age 4 (Chapter 2).

Connectivity Category	**Surface Area (ha)**	**Lake Class**
Seepage	< 12	G
	≥ 12	H
Drainage	< 446	I
	≥ 446	J

Table 13. Minimum, maximum, and average Von Bertalanffy growth parameters estimated for bluegill in four classes of Wisconsin inland lakes surveyed during 1948–2003, where N = number of lake surveys, L_∞ = the asymptotic average length (mm), K = the instantaneous rate at which L_t approaches L_∞ (1/year), t_0 = the hypothetical age at which length is zero (years), and average weight–length coefficients estimated for bluegill in four classes of Wisconsin inland lakes surveyed during 1944–2002, where N = number of lake surveys, $\text{Log}_e (\alpha)$ = a scaling constant, and β = the allometric shape parameter. W_∞ = the asymptotic average weight (grams) was estimated from average-lake class L_∞, α, and β so there were no minumum and maximum values.

Lake Class	Parameter	N	Min	Max	Average
G	L_∞	10	163	365	269
	K	10	0.074	0.764	0.247
	t_0	10	-2.673	1.573	0.085
	$Log_e (a)$	2	-10.985	-10.982	-10.984
	b	2	2.979	3.001	2.990
	W_∞	2			312
H	L_∞	66	158	361	255
	K	66	0.069	0.678	0.250
	t_0	66	-2.942	1.333	-0.227
	$Log_e (a)$	15	-13.346	-8.618	-11.291
	b	15	2.520	3.455	3.09
	W_∞	15			342
I	L_∞	80	162	382	269
	K	80	0.084	0.715	0.251
	t_0	80	-3.049	1.950	-0.067
	$Log_e (a)$	19	-14.393	-7.739	-11.434
	b	19	2.417	3.728	3.137
	W_∞	19			451
J	L_∞	14	210	354	281
	K	14	0.134	0.583	0.255
	t_0	14	-1.823	1.067	-0.532
	$Log_e (a)$	7	-13.027	-9.349	-11.304
	b	7	2.733	3.457	3.123
	W_∞	7			549

Table 14. Average mortality estimates by lake class from 34 Wisconsin lakes during 1954–2003. The table includes the average, minimum and maximum instantaneous total mortality (*Z*) from catch curves of the age frequency, survival (*S*) estimated from e^{-Z}, total annual mortality (*A*) estimated from 1 – *S*, natural mortality (*M*) estimated from Pauly's equation (Pauly 1980), instantaneous fishing mortality (*F*) estimated from *Z* – *M*, and exploitation (u) estimated from *F***A*/*Z*.

Lake Class	***N***	***Z***	***Min Z***	***Max Z***	***S***	***A***	***M***	***F***	***u***
G	2	0.566	0.256	0.876	0.568	0.432	0.347	0.219	0.167
H	17	0.792	0.423	1.253	0.453	0.547	0.347	0.445	0.308
I	13	0.932	0.289	1.606	0.394	0.606	0.340	0.592	0.385
J	2	0.670	0.564	0.777	0.512	0.488	0.338	0.332	0.242

Table 15. Estimated harvest under 25, 10, and 5 daily creel limits estimated from 8,447 creel survey interviews where panfish species were harvested from 106 northern Wisconsin lakes during 1998–2002. Because angler interviews were divided by the number in the angling party to arrive at number per angler, there were instances where between 0–1 fish were harvested (i.e., Number of Fish Harvested = 0).

Number of Fish Harvested	***Frequency of anglers***	***Percent***	***25 Harvest Limit***	***10 Harvest Limit***	***5 Harvest Limit***
0	900	0.1065	900	900	900
1	1234	0.1461	1234	1234	1234
2	1315	0.1557	2630	2630	2630
3	606	0.0717	1818	1818	1818
4	754	0.0893	3016	3016	3016
5	452	0.0535	2260	2260	2260
6	542	0.0642	3252	3252	2710
7	272	0.0322	1904	1904	1360
8	398	0.0471	3184	3184	1990
9	210	0.0249	1890	1890	1050
10	356	0.0421	3560	3560	1780
11	99	0.0117	1089	990	495
12	221	0.0262	2652	2210	1105
13	101	0.0120	1313	1010	505
14	108	0.0128	1512	1080	540
15	131	0.0155	1965	1310	655
16	102	0.0121	1632	1020	510
17	61	0.0072	1037	610	305
18	69	0.0082	1242	690	345
19	45	0.0053	855	450	225
20	112	0.0133	2240	1120	560
21	38	0.0045	798	380	190
22	38	0.0045	836	380	190
23	34	0.0040	782	340	170
24	38	0.0045	912	380	190
25	161	0.0191	4025	1610	805
26	16	0.0019	416	160	80
27	3	0.0004	81	30	15
28	3	0.0004	84	30	15
29	1	0.0001	29	10	5
30	8	0.0009	240	80	40
31	1	0.0001	31	10	5

32	3	0.0004	96	30	15
33	3	0.0004	99	30	15
37	1	0.0001	37	10	5
40	4	0.0005	160	40	20
41	2	0.0002	82	20	10
43	1	0.0001	43	10	5
45	1	0.0001	45	10	5
50	3	0.0004	150	30	15
Total	8447	1	50131	39728	27788

Table 16. Yield per recruit (g) and number harvested per 100 bluegill under varying minimum length and daily creel limits for Wisconsin lakes. Maximum yield per recruit and number harvested per 100 for the minimum length limits and daily creel limits evaluated for each lake class are indicated in **bold**. The 127 mm length limit represents the yield per recruit and number harvested in the absence of a minimum length limit. Age is the estimated time (years) to reach each minimum length limit.

			Yield per Recruit			**Number Harvested per 100**		
Lake Class	**Length**	**Age**	**25 Creel**	**10 Creel**	**5 Creel**	**25 Creel**	**10 Creel**	**5 Creel**
G	127	2.7	13.8	12.5	10.3	18	15	11
	152	3.5	**13.5**	**12.0**	**9.8**	**16**	**14**	**10**
	178	4.5	12.2	10.7	8.6	14	12	9
	203	5.8	9.6	8.4	6.7	10	9	7
	229	7.8	6.0	5.2	4.1	6	5	4
H	127	2.5	18.7	17.9	16.1	27	24	19
	152	3.4	**18.9**	**17.7**	**15.5**	**23**	**20**	**17**
	178	4.6	17.0	15.7	13.4	17	16	13
	203	6.1	12.9	11.8	10.0	10	10	9
	229	8.8	6.4	5.8	4.8	4	4	4
I	127	2.5	25.9	25.4	23.9	33	29	24
	152	3.3	**27.4**	**26.4**	**24.1**	**28**	**25**	**21**
	178	4.3	26.6	25.1	22.4	21	20	17
	203	5.6	22.5	21.0	18.4	14	14	12
	229	7.5	15.0	13.9	12.0	8	7	7
J	127	1.8	29.8	28.2	24.7	24	21	16
	152	2.5	**30.6**	**28.4**	**24.4**	**23**	**20**	**15**
	178	3.4	29.4	26.9	22.7	19	17	14
	203	4.5	25.7	23.3	19.3	15	13	11
	229	6.1	19.1	17.1	14.0	10	9	8

Figure 9. Locations of surveys used in this study. Different symbols represent each type of estimate (mortality estimates (triangles), creel surveys (circles), weight-length estimates (asterisks), and von Bertalanffy growth parameter estimates from mean lengths at age (plus).

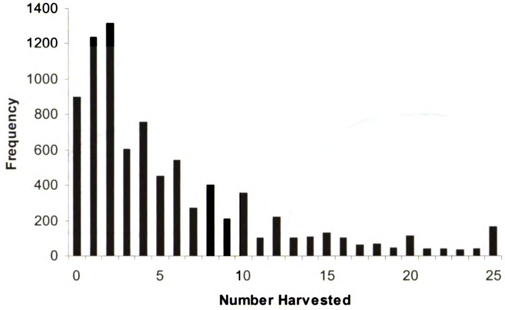

Figure 10. The frequency of anglers harvesting between 1 and 25 panfish in Wisconsin lakes during 1998–2003.

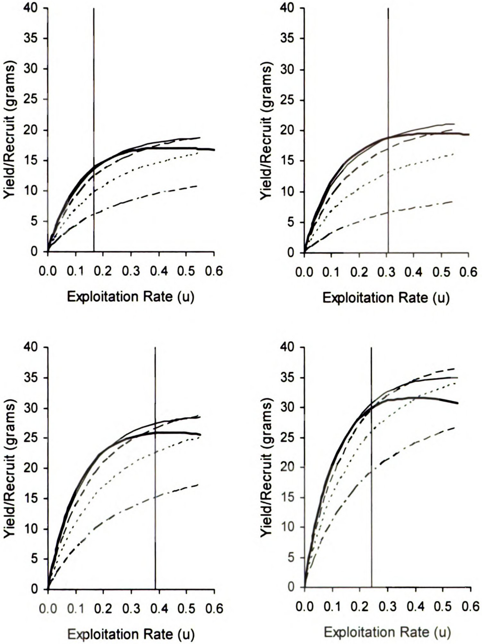

Figure 11. Yield per recruit (g) by lake class under 5 minimum length limit scenarios (127 mm (heavy —), 152 mm (—), 178 mm (– – –), 203 mm (- - -), and 229 mm (– - –). Vertical solid line indicates average exploitation rate (u) for the lake class. Lake class G upper left), lake class H (upper right), lake class I (lower left), and lake class J (lower right).

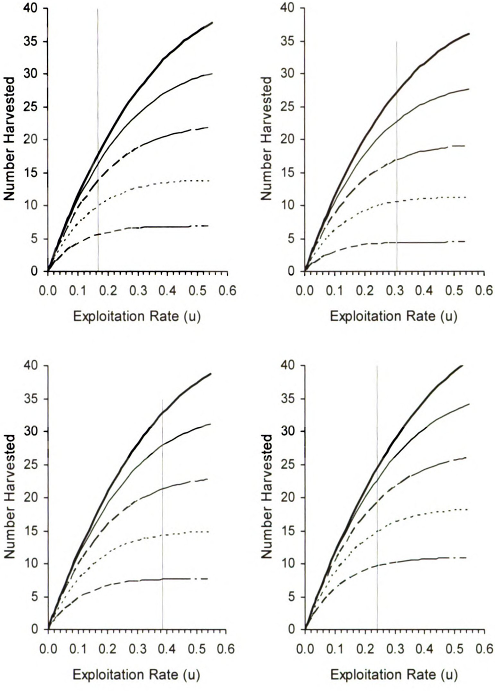

Figure 12. Number harvested per 100 by lake class under 4 minimum length limit scenarios (127 mm (heavy —),152 mm (—), 178 mm (– – –), 203 mm (- - -), and 229 mm (– - –). Vertical solid line indicates average exploitation rate (u) for the lake class. Lake class G (upper left), lake class H (upper right), lake class I (lower left), and lake class J (lower right).

SUMMARY AND CONCLUSIONS

The goal of this research was to explore the use of historic fisheries survey information to explain variability in fish growth rates in relation to physical and landscape characteristics of Michigan and Wisconsin inland lakes. I focused on three main objectives: (1) to determine if von Bertalanffy growth parameters and mean lengths at age estimated from length-stratified sub-samples were biased in relation to parameters estimated from full samples for game fishes surveyed routinely in Michigan lakes, (2) to determine if an existing lake classification scheme explained variability in fish species richness and mean length at age from historic survey data collected on Michigan and Wisconsin lakes, and (3) to demonstrate how lake classification may be used in management by estimating how bluegill yield per recruit and number harvested varied as a function of minimum age entering the fishery and fishing mortality rate among four classes of Wisconsin inland lakes.

In Chapter 1, I found that historic length-stratified sub-sample summary data could be used to compare the average growth of fishes across Michigan lakes. Bluegill, largemouth bass, and yellow perch mean lengths at age 4 estimated from length-stratified sub-samples were generally not biased compared to samples. Regression tests showed that length-stratified sub-sample von Bertalanffy growth parameter estimates were generally linearly related to estimates from samples, but the magnitude of the variability between sub-sample and sample across lakes was large for all species tested. Large variation in von Bertalanffy parameter estimates from length-stratified sub-sample summary data may limit their utility for use in among-lake comparisons. Historic growth data sets that lack complete sampling information (e.g., sample length frequencies) can still provide useful information for among lake comparisons, but mean length at age may be a better growth index than von Bertalanffy growth parameters. Based on these conclusions, I used mean lengths at age 4 as my index of growth for Chapter 2.

In Chapter 2, I found that an existing lake classification scheme consisting of 6 lake classes differing in landscape position, connectivity, and maximum depth explained variation in fish species richness and mean lengths of age 4 bluegill, largemouth bass, and walleye, but not all lake class pairs differed and overall, little variation was explained by the classification. Seepage lake classes, regardless of depth category differed from lowland deep drainage lakes for most responses tested, so drainage type was retained as I refined the classification. Additional map-based variables related to temperature and habitat area changed the classification in different ways for each response variable tested. Based on regression tree results, lake surface area was an important predictor of fish species richness, and mean lengths of age 4 bluegill and largemouth bass, whereas latitude was an important predictor of mean lengths of age 4 yellow perch and walleye. Regression tree results revealed species-specific separation points for identifying categories of lake size (large and small lakes), and for stratifying the region into northern and southern zones. The revised classifications may have the potential to serve as a statewide framework for management recreational fisheries, based on patterns of ecological similarity among lakes. I tested this claim in Chapter 3, where I used lake classification criteria specific to bluegill and developed in Chapter 2, as the basis for angling regulation simulations.

Finally, in Chapter 3, to evaluate the lake classification scheme developed in Chapter 2 for use in management, I determined expected ranges of bluegill growth and mortality for different lake classes in Wisconsin from existing survey data to determine the best combination of minimum length limits (152, 178, 203, and 229 mm) and daily creel limits (25, 10, 5) to maximize yield per recruit and number of bluegill harvested per 100 individuals for each lake class. For each combination of minimum length limit and daily creel limit, yield per recruit increased with lake size, from the smallest lake class to the largest lake class, and ranged 4–30 grams per recruit among regulation scenarios. Under a 25-fish daily creel limit, a 152-mm minimum length limit produced the highest yield per recruit for small and large seepage lakes and small drainage lakes, whereas a 178-mm minimum length limit produced the highest yield per recruit for large drainage lakes. My results provide ranges of bluegill growth, natural mortality, and fishing mortality for lake classes that may be used to evaluate future regulation proposals and to identify candidate lakes for experimental regulations. With additional data, my estimates of yield per recruit and numbers harvested could be refined to improve our understanding of the trade-offs between growth and mortality in managing bluegill fisheries.

In conclusion, the integration of historic and current fisheries data provided a means to expand the spatial and temporal scale of my research. By developing large datasets from two states for an approximate sixty year period, I was able to increase the statistical power to detect patterns amidst the many sources of error and potential bias. Examining potential bias in historic datasets continues to be important, but through the use of historic data, we can illucidate weaknesses in sampling strategies and develop research questions that may be more formally tested.

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