Climate and Dynamics of Walleye

(*Sander vitreus*, formerly *Stizostedion vitreum vitreum*)

Populations in North America

By

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Abstracts

Climatic conditions significantly influenced growth of walleye in North America. Genetically distinct walleye populations appear to have developed their own adaptation strategies to respond to their regional climatic conditions. Walleye early growth rate showed a significant latitudinal trend: the populations at low latitudes, experiencing high thermal input, had a high early growth rate (ω) and a high value for k, the rate of approaching asymptotic length (L_∞) as defined in the von Bertalanffy growth model. However, the impact of climatic conditions on walleye growth in later life, as characterized by L_∞, was not significant.

In Lake Erie, three walleye sub-populations (i.e. the western basin, Van Buren Bay, and Grand River) showed distinct demographic characteristics. The western basin walleye had a lower early growth rate than the eastern basin walleye. The differences in early growth rate among these walleye subpopulations were associated with the differences in thermal regimes experienced by each sub-population during the growing season. The overheated western basin provided the worst growth habitat for walleye during summer/fall. Younger fish cannot avoid these overheated conditions and thus may be exhibiting reduced growth rates because of the unsuitable growth habitat in the western basin. The survival rates of adult walleye in the eastern basin were higher than the lakewide average, but the abundance was less than one percent of the lakewide adult walleye abundance. The warmer and clearer water conditions in 1998 created more walleye habitat than in 1993. The increases in water temperature and decreases in water level that may result from climate change will have different impacts on the habitat suitable for walleye among the three basins, with the greatest effect in the western basin. A simulation study showed that density-dependent early survival

and density-dependent adult growth and egg production significantly affect the dynamics of the walleye metapopulation in Lake Erie. Walleye early survival (i.e. recruitment) could be a bottleneck, setting the overall sizes of the western basin and eastern basin sub-populations. This bottleneck would be sensitive to the changes in habitat expected from climate change.

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General Introduction

The walleye is a North American freshwater fish, belonging to the perch family (the Percidae), the second largest freshwater fish family in North America after the Cyprinidae (e.g. minnows, carps) (Wood and Mayden 1997). Two subfamilies, i.e. Percinae and Luciopercinae, were initially recognized by fish taxonomists (Collette 1963, Collette and Banarescu 1977), however, recent DNA studies have led to the division of the Percidae into three subfamilies and 10 genera (Craig 2000), i.e. Etheostomatinae (*Ammocrypta, Crystallaria, Etheostoma,* and *Percina*), Percinae (*Perca, Percarina* and *Gymnocephalus*), and Luciopercinae (*Stizostedion, Zingel,* and *Romanichthys*). Together with their three European cousins, the North American walleye (*S. vitreum*) and sauger (*S. canadense*) together make up the genus *Stizostedion* of the subfamily Luciopercinae. This genus is characterized by weak anal spines, no enlargement of the anterior interhaemal bones and full extension of the lateral line to the tail. The name "Walleye" was given to *Stizostedion vitreum* in recognition of its smoky, silver appearance of its eyes, a product of the reflective nature of the retinal tapetum lucidum. This reflective material is one of several retinal adaptations to dim light environment exhibited by this genus (Ali and Anctil 1977). Recently, the name of the genus *Stizostedion* has been changed to *Sander*, a name used for their European cousins for many years (Kottelat 1997, Nelson et al 2003). This change in name does not reflect a change in taxonomy but simply recognizes the fact that use of the term '*Sander'* pre-dates use of the term '*Stizostedion'* (Gill 1903, Eschmeyer and Bailey 1990, Reshetnikov et al 1997, Kottelat 1997). The orthography of the species name for walleye has also been changed from *vitreum* to *vitreus*, and the authorship of this name is "Mitchill,

1818" instead of "Smith, 1834". In this thesis, I will use *Sander vitreus* as the scientific name for walleye.

Walleye is an ecologically and economically important fish species in many North American freshwater ecosystems. As a top predator, walleye has the ability to structure the temperate fish community in mesotrophic environments by top-down trophic cascade effects (McQueen et al 1986, Carpenter and Kitchell 1988, Ryan et al 1999). Walleye has been one of the first fish species to support a significant commercial fishery in North America since 1795 (Regier et al 1969) and it continues to provide food and entertainment to mankind. Its ecological and commercial importance has made walleye a focus of many research projects in the past, and it is a primary reason why I selected it for my doctoral research.

This thesis is organized into two parts, consisting of four chapters. The first part of the thesis consists of two chapters that explore how the walleye has adapted to environmental conditions it experiences across North America. The second part of the thesis focuses on the walleye in Lake Erie with the aim of describing the present dynamics of walleye meta-populations and its future dynamics, given the changes in the lake environment that are likely to result from climate change.

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Part I. Regional Adaptation of Walleye to North American Climate

Introduction

Paleontological and ichthyological studies revealed that the ancestors of the walleye lived in Europe (Sychevskaya and Devyatkin 1960, Yakovlev 1960, Svetovidov and Dorofeeva 1963, Craig 2000). Walleye and some other species from the genera *Perca* and *Sander* invaded North America by two routes, the north Pacific route across the Bering land bridge (Billington et al 1990, 1991, Song 1995) and the Eurasia to North America route, across the Atlantic via the band of brackish water bounding the edge of the receding ice sheet during the late Pleistocene glacial Wurm period, 13000-15000BP (Cihar 1975, Craig 2000). After postglacial re-colonization, the walleye occupied many of the coolwater habitats in rivers and lakes of North America. Its northern boundary is at the mouth of the Mackenzie River at the Arctic Ocean. Its southern limit is at the Gulf Coast in Alabama (Regier et al 1969, Colby et al 1979, Scott and Crossman 1973). It is generally believed that the Rocky and Appalachian Mountains stopped the advance of the walleye's distribution in the west and the east, respectively (Craig 2000, Berra 2001). Due to its financial importance as a primary sport and commercial fish species, walleye has been widely introduced outside of its native range, particularly in western reservoirs (Goodson 1966) and along the Atlantic sea-board and southern United States in North America (Whitworth et al 1968, Munger 2002). After nearly ten thousand years, walleye has had the opportunity to develop its own characteristic adaptations to the climatic conditions of North America. The following two chapters will focus on such adaptations, particularly adaptations in their lifetime growth pattern.

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Chapter 1. Concordance between environmental factors and life-history traits revealing fish genetic variations

Abstract

I used multivariate statistical approaches (Procrustes Analysis and Canonical Correlation Analysis) to explore the association between climate conditions (frost frequency, precipitation, air temperature, solar radiation, and cloud cover) and growth characteristics of walleye (*Sander vitreus*) from 89 populations in North America. I found significant concordance between climatic conditions and walleye growth, however the pattern of concordance differed among populations that originated from different glacial refugia. This suggests that contemporary differences in the walleye populations may have been shaped by evolutionary divergence that occurred among refugia during the last glaciations. Individual climate variables play different roles in shaping walleye growth pattern. Walleye in areas with high thermal input (higher air temperature, solar radiation and lower frost frequency) have high growth rates in the first and second years of life. This is consistent with the fact that walleye growth is positively associated with temperature over a broad range. Populations in areas of higher precipitation also have higher early growth rates, perhaps reflecting higher nutrient input from increased watershed run-off and hence higher productivity.

Introduction

Fish growth can be viewed as an integration of several physiological processes involving food consumption, metabolism and other activities (Pitcher and Hart 1983). All these processes are influenced by environmental factors, such as temperature and food availability. Therefore, the study of fish growth cannot be comprehensively examined without explicit considerations of the environmental variables that characterize the ecosystems where the fish live. Climatic conditions are a major driving force in shaping ecological conditions.

Walleye (*Sander vitreus*) is a cool-water species (Hokanson 1977) and one of the most economically important fish species in the north-temperate freshwaters of North America. The optimal temperature range for walleye growth is from 18 to 22 degrees Celsius (Christie and Regier 1988). Due to its negative phototactic retinal response after the first year of life, walleye prefer feeding in a low-light environment (Ryder 1977). Therefore, both light conditions and temperature are expected to shape the growth pattern of walleye.

The native distribution of walleye in North America extends northward to the mouth of the Mackenzie River at the Arctic coast, and southward to the Gulf Coast in Alabama (Fig 1). Its eastern and western boundaries are marked by the Rocky Mountains and Appalachian Mountains, respectively (Regier et al 1969). Due to its financial importance as a primary sport and commercial fish species, walleye has been widely introduced outside of its native range, particularly in western reservoirs (Goodson 1966) and along the Atlantic sea-board and southern United States in North America (Whitworth et al 1968, Munger 2002). Therefore, the present zoogeographic distribution of walleye is very broad and covers several climatic zones. There is wide variation in growth over this range, and strong statistical

associations between growth differences and climatic differences have been discovered (Colby et al 1979, Colby and Nepszy 1981).

Growing-degree-days has been successfully used as an index of the energy available for crop plants (Swan et al 1987), and Colby and Nepszy (1981) found that growing degree days above 5 degrees Celsius (GDD5) explained 72 % of the variation in body length of first-year walleye from 78 populations with GDD5 ranging from around 1000 to 6000. Walleye populations with higher GDD5 values have a shorter life span, but tend to mature at younger ages. Beverton (1987) explained this phenomenon as a reproductive strategy for walleye to stabilize the value of lifetime egg production per female recruit over different climatic conditions and concluded that walleye is a species whose reproductive strategy is well adapted to climatic conditions in North America. In addition, he put forward the hypothesis that temperature and food supply have divergent effects on walleye life-history parameters: walleye growth rate, age at maturity and longevity are more influenced by temperature whereas length at maturity and asymptotical size are shaped mainly by food supply. This hypothesis was supported by studies of other species, such as brown trout (*Salmo trutta*), guppies (*Lebistes reticulates*), pupfish (*Cyprinodon macularias*) and Atlantic cod (*Gadus morhua*) (Beverton 1987).

Using mitochondrial DNA markers, Billington et al (1992) found that the three major haplotypes, dominant in walleye populations in North America, showed distinct geographic distributions. This spatial distribution pattern reflected the postglacial recolonization of North America by walleye from three different refugia: the Missouri refugium (MS), the Mississippi refugium (MP) and the Atlantic refugium (AT) (Fig 1). After analyzing additional samples, especially for populations in the Mobile drainage basin, Billington (1996)

and Billington & Strange (1995) provided evidence for the existence of five genetically and geographically distinct groups of walleye populations in North America. In addition to the first three groups from the three refugia described above, the fourth walleye group (HB, located in the south-eastern states of Tennessee and Kentucky) was identified as a hybrid of stocked fish from the Atlantic (AT) and Mississippi (MP) refugia (Fig 1). Gulf Coast walleye were found to be genetically distinct from other groups and were classified as a fifth group, the Mobile Basin drainage group (MB in Fig 1) (Billington 1996). The inclusion of walleye populations in western Ontario and Minnesota into the Missouri refugium (Billington 1996) is debatable, however, because there were few samples from western Ontario and because both haplotypes 4 and 10 (the genotypes of populations from the Mississippi and Missouri refugia, respectively) appeared in Minnesota populations (Billington et al 1992).

To summarize: walleye populations in North America can be separated into two large groups based on their recent history: one composed of all populations in the native range of the species and the other composed of introduced populations, located outside the native range. The populations in the native ranges can be further subdivided into five genetically distinct groups. In this chapter, using published size-at-age data for walleye in North America, I (1) assess the association between somatic growth and climate conditions; (2) explore the spatial pattern of the concordance between somatic growth and climate conditions; (3) investigate whether such concordance patterns between life-history traits and environmental factors reflect the genetic divergence associated with membership in different glacial refugia ; and (4) identify the impact of individual climate variables on the growth of walleye at different life stages.

Methods

A. Data Collection

Walleye length-at-age

Data on walleye length-at-age were compiled by searching the published scientific literature for the period from 1933 to present. A total of 89 walleye populations were included in the data base. These populations cover a latitudinal range from about 33° N to 59° N and a longitudinal range from about 75 °W to 111° W (Fig 1, Appendix 1). The data covers both native populations and introduced populations. For the native group, we were unable to obtain data for the populations belonging to the Mobile Basin Drainage (MB) refugium. Most length-at-age data were estimated from scales using back calculation methods. Data from both sexes were combined to give overall average size at age values. The longest series of length-at-age data collected for the analysis was from age 1 to age 14, and the shortest series was from age 1 to 5. Sexual dimorphism of older fish was evident for many walleye populations and such differences in the growth rates between male and female walleye were population specific and increased with age. The accuracy of scale ages also tends to decline with older fish. Therefore, we chose to work only with fish aged 5 and less in order to minimize estimation problems associated with missing data, sexual dimorphism and aging errors (Colby et al 1979, Craig 2000, Munger 2002). Because length at older age is not independent of length at younger age (i.e. length at older age = length at younger age + growth increment), we only used age-specific estimates of annual incremental growth in our analyses.

Climate Data

The following climate variables, averaged for the period from 1960 to 1990, were obtained from the IPCC (Intergovernmental Panel on Climate Changes) global climate data

web site (http://ipcc-ddc.cru.uea.ac.uk/ipcc_ddc.html): ground frost frequency (days), precipitation ($cm \cdot d^{-1}$), mean air temperature (degree Celsius), cloud cover (percentage) and solar radiation ($W \cdot m^{-2}$). The data sets consist of monthly mean values for the five variables at a resolution of 0.5 degree latitude by 0.5 degree longitude. The values for each variable were interpolated from weather station data using thin-plate splines (New et al 1999). An annual mean for each variable at each population location in the walleye database was calculated and used in the following analyses.

B. Statistical analysis of data

Incremental growth-at-age and climate data sets were standardized to z-scores before carrying out any further analysis in order to remove the effects of different scales of variables. Principal Component Analysis (PCA) was applied to increment-at-age and climate data sets to characterize the main trends of variation of the observations with respect to both and growth and climate. A Procrustean Randomization Test (PROTEST; Jackson and Harvey 1993; Jackson 1995) was applied on the first two principal components from each dataset. In order to find the maximum concordance between the two data matrices (i.e. relationship between the climate and the growth), PROTEST carries out rescaling, rotating and/or reflecting operations on the configurations of original data (the first two principal components from both data matrices in this study) to identify the closest fit between two matrices. It then tests to see whether this match is significantly different from random using a randomization test, and then generates a standardized residual for each individual observation that permits that observation to be ranked in terms of the match between its two sets of multivariate data (Jackson 1995; Olden et al 2001).

Comparison of the direction and magnitude of the residual vectors from the Procrustes analysis can identify groups of observations that exhibit similar deviations from the best matching pattern generated by PROTEST. In this study, each residual vector was produced by subtracting the observed growth vector for each population in the space determined by the first two principal components growth axes from the corresponding growth vector predicted by its climatic conditions. The 4 quadrants of the two-dimensional ordination plot, based on the first two growth principal component axes, were used to classify each individual observation into one of 4 groups depending on the quadrant where the residual vector for the observation was located. The quadrant classification was assigned in a counter-clockwise manner. For example, a population with its residual vector in quadrant 1 would have two positive components, indicating that the climate-based predicted values for its two growth principal components exceed both observed values; similarly, a population with two negative components to its residual vector would be in quadrant 3, indicating that climate-based predicted values for its two growth principal components are both less than its observed values. A two-sample t-test was used to compare the magnitude of residual vector between different population groupings, such as between native and introduced populations. Chi-square test was applied to each group to test for a non-random distribution of residual vectors amongst the 4 quadrants in the growth ordination plot. Finally, a Procrustean superimposition plot was used to illustrate how the observed growth for each group differed from the expected growth based on the PROTEST 'best match' pattern (Peres-Neto and Jackson 2001).

Simulation studies have shown that PROTEST is superior to the Mantel test in assessing the association between two multivariate data matrices (Peres-Neto and Jackson

2001). The standard PROTEST is based on the least-squares criteria, which is adversely affected by atypical observations (i.e. outliers) (Olden et al 2001) as in standard linear regression analyses. Therefore, a resistant-fit approach, using the repeated-medians algorithm, was applied to reduce the influence of atypical observations in the data set (Siegel and Benson 1982, Olden et al 2001).

To quantify the relationship between walleye growth increments at different ages and climate variables, a Canonical Correlation Analysis (CCorA) was applied to these two sets of variables for all 89 populations and a separate analysis for only the 74 native populations. A Chi-square test proposed by Bartlett (1947) was used to determine which pair of canonical variates from CCorA analysis was statistically significant.

Result

Bi-variate plots (appendix 2) of variables within each of the increment-at-age and climate data sets, and between variables from each data set, showed approximately linear relationships supporting the applicability of PCA and CCorA as being appropriate approaches for carrying out multivariate analysis on the two sets of variables (Legendre and Legendre 1998).

For the growth data set, the first principal component represents walleye average growth rate after age 1 because the principal component coefficients of standardized increment-at-age variables for ages 2-5 were similar to one another in sign and magnitude (Table 1). Age 1 growth was generally unrelated to this first component (Table 1). However, for the second principal component, the coefficients of increment at age 1 and age 2 were more than twice as large as others, which implied that the second principal component was

most influenced by the early growth rate of walleye and provides a general summary of this phenomenon. Therefore, we can conclude that walleye early growth rate and average young adult growth rate summarize 60.6% (24.9% and 35.8%, respectively) of total variation in annual increment-at-age of walleye in North American lakes.

For the climate data set, the first principal component contrasted frost frequency with precipitation, temperature, and solar radiation. Cloud cover had little association with this component given its low coefficient in the component (0.036) (Table 2). The second principal component was a contrast between solar radiation and both precipitation and cloud cover. The first two components accounted for about 92.13% of total variation in climate data, i.e. 65.02% for climate PCA1 and 27.11% for climate PCA2. The first component can be interpreted as a measure of thermal input to the waterbodies, and the second component can be considered as an index the light intensity conditions for each location in the database: high values for both temperature and radiation produce a large score on the first component whereas low values for both cloud cover and precipitation or high value for radiation produce a large score for the second component. The climatic conditions for introduced walleye populations exhibited extreme or close to extreme values for at least one of the climate principal components and effectively bounded the climate PCA space inhabited by the native populations (Fig 2).

Results from the resistant-fit PROTEST analysis showed the walleye increment-at-age ordination was significantly associated with the ordination of the climatic conditions (m^2=0.800, P=0.002). The vector residuals from the analysis can be used to assess the degree to which each population ‘fit’ the overall association between walleye increment-at-age and climatic conditions. The population with the largest residual (e.g., the population in Lake

Meridith of Texas) indicated the weakest association between two data sets, and the smallest residual (e.g. the population in Attawapiskat Lake of Ontario) indicated the closest match between walleye growth and climate conditions. The residual obtained for Lake Meridith was so different from all others that it is considered independently of the other populations. For more detailed consideration, the other 88 walleye populations were divided into 4 groups with 22 populations in each group based on their rank-ordered residuals. Groups 3 and 4 were the populations with the poorest match, whereas Groups 1 and 2 had the best-match. The Lake Meridith population from Texas was assigned as Group 5 (Fig 3). Most populations that exhibit a good match between growth and climate are located in the central region of North America: western South Dakota, Iowa and Minnesota and north-western Ontario. Regions surrounding the well-matched groups exhibited relatively poor match between walleye growth pattern and climate conditions (Fig 4). Among them, the populations in Texas, Pennsylvania, and Montana produced the three largest residuals. Populations with a high degree of concordance (small residuals) between walleye increment-at-age and climatic conditions are mainly located in the central areas of walleye native range. There exists a significant difference in the degree of concordance, i.e. residual magnitudes, between walleye native distribution and the introduced populations (t_{15}=-3.96, p-value=0.001). This finding suggests that the system describing the relationship between climatic conditions and walleye growth patterns for populations in its native range may not apply to those introduced populations.

For walleye native distribution range, comparing with the results from genetic studies carried out by Billington (1996), the populations exhibiting a better walleye climate-growth relationship, i.e. those from groups 1 and 2, are nearly half from the Mississippi refugium

(MP in Fig 5) and half from Minnesota and western Ontario populations (MS2 in Fig 5) which were arguably classified into Missouri refugium by Billington (1996). A majority of populations from the Atlantic refugium (AT in Fig 5), the remainder of the Missouri refugium (MS1 in Fig 5), and the hybrid group (HB in Fig 5) did not follow the same walleye climate-growth relations shaped by MP and MS2 populations and therefore created large residuals (in groups 3,4) from fitting the relationship. Two-sided t-test showed the residuals for a group composed of MP populations and MS2 population are significantly different from the ones for the group combining AT, MS1 and HB groups (t_{48}=-4.96, p-value<0.001).

The directions of the residuals showed that Atlantic (AT) origin populations had a dominant direction in the first quadrant whereas most of vector residuals for hybrid (HB) populations between Atlantic (AT) and Mississippi (MP) refugia were in the second quadrant (Fig 5). Missouri (MS1) origin populations had most vector residuals in the third and fourth quadrants (Fig 5). The null hypothesis of a uniform distribution of residual vector on each group was rejected for the Missouri (χ_3^2 =8.67, p-value=0.03) and hybrid (χ_3^2 =9.57, p-value=0.02) groups. The null hypothesis was not rejected for the Atlantic group (χ_3^2 =4.4, p-value=0.22). However, power of this test was low due to small sample size (total 10 populations). Given such small sample size, the power to detect 20% departure from the null hypothesis is only 0.075 (i.e. with a sample of size of 10, at the 5% significance level, there is a 7.5% probability of detecting a difference of this magnitude). The distribution of the residuals for this group was evident to skew to the first quadrant (Fig 6). There seems to be no dominant direction for the Mississippi (MP) populations (Fig 6) (χ_3^2 =3.53, p-value=0.32) nor to populations in north-western Ontario and Minnesota (MS2) (χ_3^2 =2.91, p-value=0.41) and the introduced populations (χ_3^2 =1.27, p-value=0.73). In addition, the populations in

north-western Ontario and Minnesota (MS2) showed a better overall climate-growth match and smaller residuals much like the Mississippi (MP) populations (Fig 5).

The superimposition plots demonstrated how observed growth deviated from expectations based on the climate conditions. For example, the residuals (a) in Fig 7 (Demo) indicates that the populations exhibited smaller observed adult growth rate (mostly on age 3 ,4,and 5) than the expected one given that the residual was almost parallel to eigenvectors of adult growth rates but perpendicular to the first year growth rate. Similarly, residual (b) suggested that the population had smaller observed early growth rate than the expected one. The populations in the Mississippi (MP) refugium and western Ontario and Minnesota (MS2) produced random residuals (Fig. 7). The other three refugia, however, produced specific patterns of residuals (Fig 7). Most populations in the Atlantic (Fig 7 (AT)) refugium grew faster in adult stages than expected from their climate conditions, but some showed smaller growth rates for young age walleye. In contrast, a majority of populations in hybrid group from Atlantic and Mississippian refugia showed smaller young growth rates, especially for the second year growth rate given that those residuals were parallel to the eigenvector of the second year growth rate (Fig 7 (HB)). A larger observed early growth rate (i.e. the first and second year growth rate) than expected one seems to dominate the growth pattern in Missouri refugium (Fig 7 (MS1)).

Among five pairs of canonical variates from canonical correlation analysis on all eighty nine populations, only the first two pairs were significantly correlated with the correlation coefficients of about 0.81 (χ_{25}^2 =137.13,p<0.0001) and 0.58 (χ_{16}^2=47.05,p=0.0001), respectively (Table 3). Because the individual variables were significantly correlated within each data set (Appendix 2), the coefficients associated with

variables in each canonical variate may not provide an accurate measure of their importance or association (Table 4, Table 5). Given these conditions, the correlation coefficient between each variable and canonical variate was a better measure for interpreting each canonical variate (Manly 1986). The first growth canonical variate (*Size 1*) was positively correlated to the first and second year growth rate, meaning that *Size 1* emphasizes walleye early growth rate (Table 6). The first climate canonical variate (*Climate 1*) was positively correlated to temperature (r = 0.987), solar radiation (r = 0.882) and precipitation (r = 0.551), but highly negatively correlated to annual mean frost frequency (r = -0.963; Table 7), which suggested that *Climate 1* summarized net thermal input to the waterbodies. A significant correlation (r = 0.81) between the pair of first canonical variates indicated that walleye had a high early growth rate in the areas with a high net thermal input.

The second size canonical variate (*Size 2*) was negatively related to the first year growth but positively correlated to walleye growth after age 1, in particular year 2 and 5 (Table 6), suggesting that a high first year growth could produce a small score on canonical variate *Size 2*. For the second climate variate (*Climate 2*), a high annual mean of precipitation results in a small value of *Climate 2* (Table 7), but high mean cloud cover and frost frequency produce large values of *Climate 2*. The correlation of the second pair of canonical variates (r = 0.58; Table 3) suggests that walleye in the areas with high annual precipitation tends to have a high first-year growth, and the growth rate for older walleye could benefit from a high cloud cover (i.e. low light intensity measurement in the surface of water bodies).

After excluding the 15 introduced populations, the canonical correlation analysis based on the populations in the native range also produced only two pairs of significantly

correlated canonical variates between walleye length increments and climate conditions. The correlation coefficients for first and second pairs of canonical variates were 0.8 (χ_{25}^2 =135.39, p<0.0001) and 0.59 (χ_{16}^2 =50.08, p=0.0001), respectively (Table 8). The results were similar to the results from the analyses with all 89 populations involved, the highly correlations among the variable for each data set make the interpretation of standardized coefficients of each canonical variate difficult and thus the correlations between each variable and their canonical variates should be adopted to describe each canonical variate (Table 9, Table 10). The significant correlation between first pair of canonical variates indicated that a high thermal input resulted in a high early growth rate (Table 11, Table 12). However, the second pair of canonical variates produced different interpretation from the analysis on the all 89 populations, especially for the climate variate. The second growth variate again measured the growth in walleye late life stages, i.e. after age 2, but for the second climate variate, the precipitation played overwhelmingly dominant role with the negative correlation coefficient of -0.533 which is more than twice as large as the second largest coefficient (i.e. radiation) in their absolute values. Hence, this canonical variate essentially indicated the precipitation. The significant correlation between the second pair of canonical variates indicated that a high precipitation producing a small second climate variate should predict a small second growth variate resulted from either a large first year growth rate or small growth rate after age 2 (Table 12, Table 13).

Discussion

Significant relationships between life-history traits and environmental factors are caused by phenotypic plasticity, responding to the environmental gradients, and/or by natural selection changing the characteristics of the phenotypic plasticity (Pigliucci 2001). Such

relationships should apply equally across the geographic distribution of a species as long as the phenotypic values predicted by the relationship for the species in any area of its distribution are within the range of such plasticity. The lack of concordance between somatic growth and climate in introduced populations suggests that either the introduced populations have not been established long enough to adapt to the new environments, or the extreme environmental conditions in those areas are beyond the response range of walleye plasticity, or both. The hypothesis of effect of extreme climatic conditions was supported by some of those introduced populations. In addition, if all introduced populations are consider as one group due to my inability to identify the source of each introduced population, and then a random distribution of their residual vectors from PROTEST analysis would be expected because they were most likely introduced from the different groups.

The decreasing concordance between climate and walleye growth, from the center of its native distribution to the edges of its current distribution, may indicate that walleye climate-growth reaction norms vary across the current range; such differences could be caused by genotypic variation. In our study, the reaction norm of walleye climate-growth was shaped by the populations originating from Mississippi refugium and western Ontario and Minnesota populations, therefore, the large deviations of other three genetic distinct populations from the reaction norm are most caused by the genotype differences. This argument is supported by the results showing the same directions of vector residuals from different populations having similar origins in this study. The variation in response (reaction norm) of fish life-history traits to environmental factors due to the genotype variation was also observed in Atlantic silverside (*Menidia menidia*) (Yamahira and Conover 2003). By studying the effect of water temperature on growth rates of this species from two different

geographical locations, i.e. the northern stock and southern stock, Yamahira & Conover (2003) showed that differentiation of growth rate responding to temperature changes between two populations was due to differences in their genotype.

Both our study and other studies mentioned above demonstrated that the matched pattern between environmental factors and growth could reveal fish genetic variations. The finding of similar vector residuals (both in direction and magnitude) of the population in western Ontario and Minnesota (MS2) with the populations from Mississippi (MP) refugium suggests that the populations in western Ontario and Minnesota (MP2) could be from Mississippi (MP) refugium, or at least the hybrid with the Mississippian genotype dominant in the populations, which is contrast to Billington (1996)'s conclusion. Confirming such results will require more genetic work to be done on the populations in those areas.

Walleye growth is significantly influenced by environmental factors. Water temperature is positively related to walleye growth for all ages (Huh et al 1976, Ostazeski and Spangler 2001). A high level of light intensity decreases walleye feeding rate and food consumption rate (Swenson 1977, Ryder 1977). An increase in growing degree days above 5 °C results in an increase in walleye early growth rate (Baccante and Colby 1996). Air temperature also shows a positively relationship with walleye growth (Ostazeski and Spangler 2001, Cyterski and Spangler 1996). In this study, climate variables in addition to air temperature, such as the frost frequency, precipitation, cloud cover and radiation, showed significant association with walleye growth patterns. These environmental factors can modify the physical habitat of walleye in their ecosystem through their impacts on temperature and light levels.

Walleye growth can be clearly divided into two stages by the different habitat requirements, i.e. the growth of the pelagic, planktivorous stage during the first year of life and growth of the benthic, piscivorous stage during the late years of life (Smith and Pycha 1960). By the end of their first summer of life, walleye change their retinal response from positive phototaxis to negative phototaxis (Houde and Forney 1970, Ryder 1977). This physiological change induces a significant habitat shift, i.e. from a pelagic mode to an inshore, demersal mode (Forney 1976, Colby et al 1979). I suggest that these two types of habitat can respond differently to the climate variables, with the effect that the different climate variables impose the different influence on the two stages. Both our PCA and CCorA results provide empirical evidence supporting this hypothesis.

A positive relationship between air temperature and walleye growth rates has been reported by other studies (Ostazeski and Sprangler 2001, Cysteski and Sprangler 1996, Colby and Nepszy 1981). In this study, I found that the annual net thermal input of lakes, as indicated by a combination of air temperature, radiation and frost frequency, represents one overall important factor determining walleye early growth. This result is consistently applicable for both the populations in native range and the current distribution range. Therefore, when assessing the impacts of climate change on walleye or other species, one should consider the combined effects of various climate variables, instead of only air temperature.

The difference in the interpretation on the second pair of canonical variates between native populations and all the populations in the current distribution range confirmed the Procrustes results which showed that interaction between introduced populations and their climatic conditions is beyond predictability based on the native populations. Cloud cover and

radiation both participate in shaping the optical habitat for walleye. Therefore, these variables are expected to impact the growth of adult walleye given their sensitivity to light conditions. Denser cloud cover that reduces the level of light intensity at the surface of a lake can increase adult walleye feeding activities in the lake (Ryder 1977) and thus adult walleye growth rate. However, this conclusion was only supported by the analysis of all the populations across broad distribution range and not by the native populations alone. This is likely caused by the reduction in the range of environmental variables considered (Jackson et al 2001) and high correlation among the variables in the climate data set. The other explanation is the climatic conditions cannot provide enough information to capture fish adult growth pattern. As shown in Beverton (1987)'s hypothesis, food supply and/or density effect should be considered when modeling fish adult growth rates. The significant positive relationship between precipitation and walleye early growth rate consistently discovered in this study has not been reported before, yet this study includes a large number of populations and a greater geographic range. Increased precipitation increases inflows to the lakes which may carry more nutrients and chemicals essential for the photosynthesis. A higher rate of photosynthesis results in a large scale of blooming of phytoplankton and zooplankton, which provide more food for young walleye growth. Therefore, impacts of individual climate variables on walleye growth are life-stage specific.

In conclusion, climate conditions significantly influence walleye growth patterns across their geographic range; however, the response in walleye growth to the climate conditions differs among the populations due to the genetic variations. These differences in the growth patterns relative to climate can indicate potential differences in their genetic origins and this finding was supported from published genetic relationships. However, some

of the factors (e.g. physical characteristics of the waterbodies in the study, such as morphometry) can introduce uncertainty into the relationship between air temperature and radiation (the climate factors) and water temperature (the environmental factors the fish can respond to) and thus create similar match pattern discovered in this study if some waterbodies with the similar physical characteristics happen to occupy the same refugium. In addition, the regional deviation in "match pattern" could also stem from regional differences in the kinds of environments (e.g. rivers vs lakes: the same air temperature and radiation could create thermal habitat in river that were quite different from what they could create in lakes). However, this effect is less likely to be the cause of match pattern found in this study because a majority of the waterbodies were lakes and a small number of river populations were randomly distributed among the refugia (Appendix I).

By modeling the concordance between two multivariate data set (fish life-history traits and the environmental conditions), PROTEST provides an optional approach to identify groups of populations that have common responses within the group but differ among the groups. Such differences may indicate populations suitable for more detailed genetic comparisons or other types of study (e.g. common garden experiments). Because of multivariate characteristics of PROTEST, more life-history traits and relevant environmental conditions can be included in the analysis, and the more informative and integrated are the results. Walleye growth pattern can be explicitly divided by two stages: early stage (i.e. age 1 or 2) and older ages. Individual climate variables, such as frost frequency, precipitation, air temperature, and solar radiation, cloud cover play different roles in shaping walleye growth in the two stages. Walleye in the areas with high net thermal condition, i.e. high temperature and solar radiation over frost frequency, have an increased early growth rate, as do walleye in

the areas with high precipitation rate, whereas high cloud cover has the potential to favour adult walleye feeding and growth due to enhanced optical habitat.

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Table 1. The eigenvector coefficients and eigenvalues from principal component analysis (PCA) on walleye growth data for 89 walleye populations (including both introduced and native populations) in North America

		Principal Components				
		PCA1	**PCA2**	**PCA3**	**PCA4**	**PCA5**
Eigenvector (Coefficient of)	**Increment at Age 1**	0.082	0.792	0.185	0.029	0.574
	Increment at Age 2	-0.437	0.549	-0.007	-0.202	-0.682
	Increment at Age 3	-0.536	0.016	-0.386	0.736	0.142
	Increment at Age 4	-0.545	-0.152	-0.311	-0.638	0.419
	Increment at Age 5	-0.466	-0.216	0.848	0.093	0.088
Eigenvalues		1.789	1.243	0.754	0.665	0.548
Percentage (%)		35.79	24.86	15.09	13.30	10.96
Cumulative (%)		35.79	60.64	75.73	89.04	100.00

Table 2. The eigenvector coefficients and eigenvalues from principal component analysis (PCA) on climate data for 89 walleye populations (including both introduced and native populations) in North America

		Principal Components				
		PCA1	**PCA2**	**PCA3**	**PCA4**	**PCA5**
Eigenvector (Coefficient of)	**Frost Frequency**	0.543	0.080	0.128	0.682	0.466
	Precipitation	-0.406	-0.439	0.778	0.161	0.101
	Temperature	-0.541	0.033	-0.357	-0.026	0.761
	Radiation	-0.496	0.352	-0.144	0.663	-0.413
	Cloud Cover	0.036	-0.822	-0.479	0.263	-0.154
Eigenvalues		3.251	1.355	0.330	0.054	0.009
Percentage (%)		65.02	27.11	6.61	1.08	0.19
Cumulative (%)		65.02	92.13	98.74	99.82	100.00

Table 3. Correlations of five pairs of canonical variates between walleye growth and climate conditions for 89 walleye populations (including both introduced and native populations) in North America

Canonical Vairates	**Canonical Correlation**	**Squared Canonical Correlation**	**Bartlett's Chi-Square**	***DF***	***P-value***
1	0.81	0.66	137.13	25	<0.0001*
2	0.58	0.34	47.05	16	0.0001*
3	0.35	0.12	12.35	9	0.19
4	0.11	0.01	1.68	4	0.79
5	0.09	0.01	0.84	1	0.35

* significant correlation at the level of 0.05.

Table 4. Standardized canonical coefficients of individual growth variables for walleye growth canonical variates for 89 walleye populations (including both introduced and native populations) in North America

Individual Variables	Growth Canonical Variates				
	Size 1	**Size 2**	**Size 3**	**Size 4**	**Size 5**
Increment at age 1	0.790	-0.405	0.580	-0.084	-0.162
Increment at age 2	0.441	0.553	-0.808	-0.021	0.328
Increment at age 3	0.010	0.230	0.101	0.568	-0.909
Increment at age 4	0.021	0.150	0.710	0.463	0.711
Increment at age 5	-0.014	0.436	0.390	-0.870	-0.201

Table 5. Standardized canonical coefficients of individual climate variables for climate canonical variates for 89 walleye populations (including both introduced and native populations) in North America

Individual Variables	Climate Canonical Variates				
	Climate 1	**Climate 2**	**Climate 3**	**Climate 4**	**Climate 5**
Frost Frequency	-0.350	3.172	0.640	4.108	-2.133
Precipitation	-0.125	-0.350	-0.222	1.516	-1.052
Temperature	1.157	4.140	3.269	2.920	-4.978
Radiation	-0.491	-0.910	-3.022	0.216	4.041
Cloud Cover	-0.228	0.339	-1.751	-0.487	1.248

Table 6. Correlations between individual growth variables and individual climate variables, and walleye growth canonical variates for 89 walleye populations (including both introduced and native populations) in North America.

Individual Variables	Growth Canonical Variates				
	Size 1	**Size 2**	**Size 3**	**Size 4**	**Size 5**
Increment at age 1	0.901	-0.357	0.206	-0.077	-0.107
Increment at age 2	0.649	0.624	-0.386	0.088	0.178
Increment at age 3	0.091	0.567	0.172	0.504	-0.622
Increment at age 4	0.011	0.549	0.558	0.418	0.462
Increment at age 5	-0.038	0.682	0.399	-0.593	-0.154
Frost Frequency	-0.785	0.100	0.068	0.004	0.006
Precipitation	0.449	-0.247	-0.182	0.026	-0.041
Temperature	0.804	0.021	-0.044	0.010	0.003
Radiation	0.719	-0.041	0.013	0.035	0.032
Cloud Cover	-0.083	0.177	-0.254	-0.043	-0.044

Table 7. Correlations between individual growth variables and individual climate variables, and climate canonical variates for 89 walleye populations (including both introduced and native populations) in North America.

Individual Variables	Climate Canonical Variates				
	Climate 1	**Climate 2**	**Climate 3**	**Climate 4**	**Climate 5**
Increment at age 1	0.735	-0.210	0.071	-0.009	-0.010
Increment at age 2	0.529	0.366	-0.134	0.010	0.016
Increment at age 3	0.074	0.332	0.060	0.057	-0.058
Increment at age 4	0.009	0.322	0.193	0.048	0.043
Increment at age 5	-0.031	0.400	0.138	-0.068	-0.014
Frost Frequency	-0.963	0.170	0.195	0.034	0.065
Precipitation	0.551	-0.442	-0.526	0.230	-0.434
Temperature	0.987	0.036	-0.126	0.091	0.029
Radiation	0.882	-0.070	0.037	0.305	0.350
Cloud Cover	-0.102	0.302	-0.732	-0.373	-0.472

Table 8. Correlations of five pairs of canonical variates between walleye growth and climate conditions for 74 walleye populations in walleye native distribution range in North America

Canonical Vairates	Canonical Correlation	Squared Canonical Correlation	Bartlett's Chi-Square	*DF*	*P-value*
1	0.80	0.64	135.39	25	<0.0001*
2	0.59	0.35	50.08	16	<0.0001*
3	0.37	0.14	14.36	9	0.11
4	0.14	0.01	2.06	4	0.72
5	0.07	0.01	0.41	1	0.52

* significant correlation at the level of 0.05.

Table 9. Standardized canonical coefficients of individual growth variables for walleye growth canonical variates for 74 walleye populations in walleye native distribution range in North America.

Individual Variables	Growth Canonical Variates				
	Size 1	**Size 2**	**Size 3**	**Size 4**	**Size 5**
Increment at age 1	0.723	-0.327	0.644	0.316	-0.048
Increment at age 2	0.482	0.400	-0.820	-0.266	-0.191
Increment at age 3	0.029	0.241	0.161	-0.170	1.026
Increment at age 4	0.014	0.502	0.590	-0.541	-0.409
Increment at age 5	-0.076	0.434	0.023	0.943	-0.277

Table 10. Standardized canonical coefficients of individual climate variables for climate canonical variates for 74 walleye populations in walleye native distribution range in North America

Individual Variables	Climate Canonical Variates				
	Climate 1	**Climate 2**	**Climate 3**	**Climate 4**	**Climate 5**
Frost Frequency	0.395	1.151	-0.933	6.057	3.699
Precipitation	0.238	-1.217	-0.043	1.499	1.348
Temperature	2.347	1.733	0.285	8.867	0.610
Radiation	-1.193	0.441	-1.066	-4.359	2.191
Cloud Cover	-0.354	0.142	-1.295	-1.18	0.313

Table 11. Correlations between individual growth variables and individual climate variables, and walleye growth canonical variates for 74 walleye populations in walleye native distribution range in North America

Individual Variables	Growth Canonical Variates				
	Size 1	**Size 2**	**Size 3**	**Size 4**	**Size 5**
Increment at age 1	0.889	-0.240	0.347	0.176	0.006
Increment at age 2	0.721	0.416	-0.535	-0.136	-0.056
Increment at age 3	0.153	0.518	0.145	0.015	0.829
Increment at age 4	-0.001	0.672	0.530	-0.414	-0.310
Increment at age 5	-0.071	0.677	0.062	0.729	-0.046
Frost Frequency	-0.796	0.043	0.017	0.047	-0.002
Precipitation	0.653	-0.333	-0.044	-0.023	0.017
Temperature	0.797	0.074	-0.026	-0.033	0.009
Radiation	0.698	0.126	0.060	-0.057	0.024
Cloud Cover	0.153	-0.108	-0.383	0.006	-0.017

Table 12. Correlations between individual growth variables and individual climate variables, and climate canonical variates for 74 walleye populations in walleye native distribution range in North America.

Individual Variables	Climate Canonical Variates				
	Climate 1	**Climate 2**	**Climate 3**	**Climate 4**	**Climate 5**
Frost Frequency	-0.966	0.069	0.041	0.243	-0.036
Precipitation	0.792	-0.533	-0.106	-0.119	0.250
Temperature	0.967	0.119	-0.062	-0.173	0.128
Radiation	0.848	0.202	0.147	-0.294	0.364
Cloud Cover	0.185	-0.173	-0.933	0.032	-0.254
Increment at age 1	0.733	-0.143	0.143	0.034	0.001
Increment at age 2	0.594	0.259	-0.220	-0.026	-0.004
Increment at age 3	0.126	0.323	0.060	0.003	0.055
Increment at age 4	-0.006	0.420	0.218	-0.080	-0.021
Increment at age 5	-0.059	0.422	0.026	0.141	-0.003

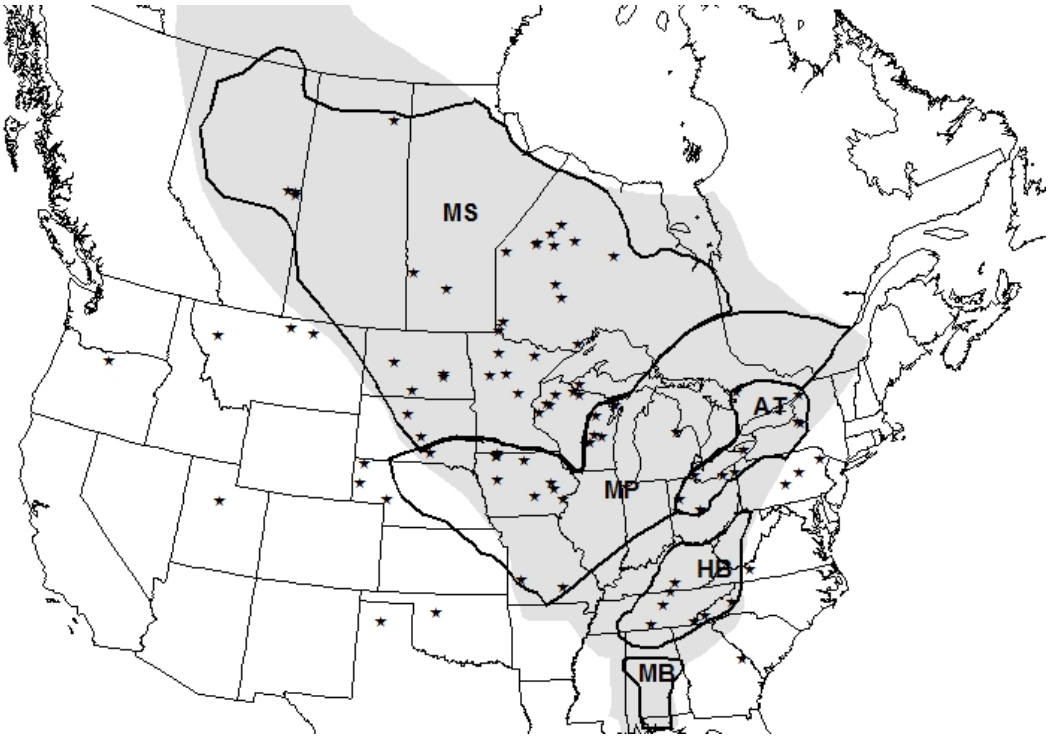


Figure 1. A map showing the locations of eighty nine (*****) walleye populations collected in this study, the native distribution (shaded area) of walleye populations in North America (redrawn from Colby et al 1979) and five genetically distinct groups (polygons enclosed by thick lines—redrawn from Billington 1996).
Note: AT—Atlantic refugium; MS—Missourian refugium; MP—Mississippian refugium; HB—Hybrids from MS and MP; MB—Mobile drainage basin.

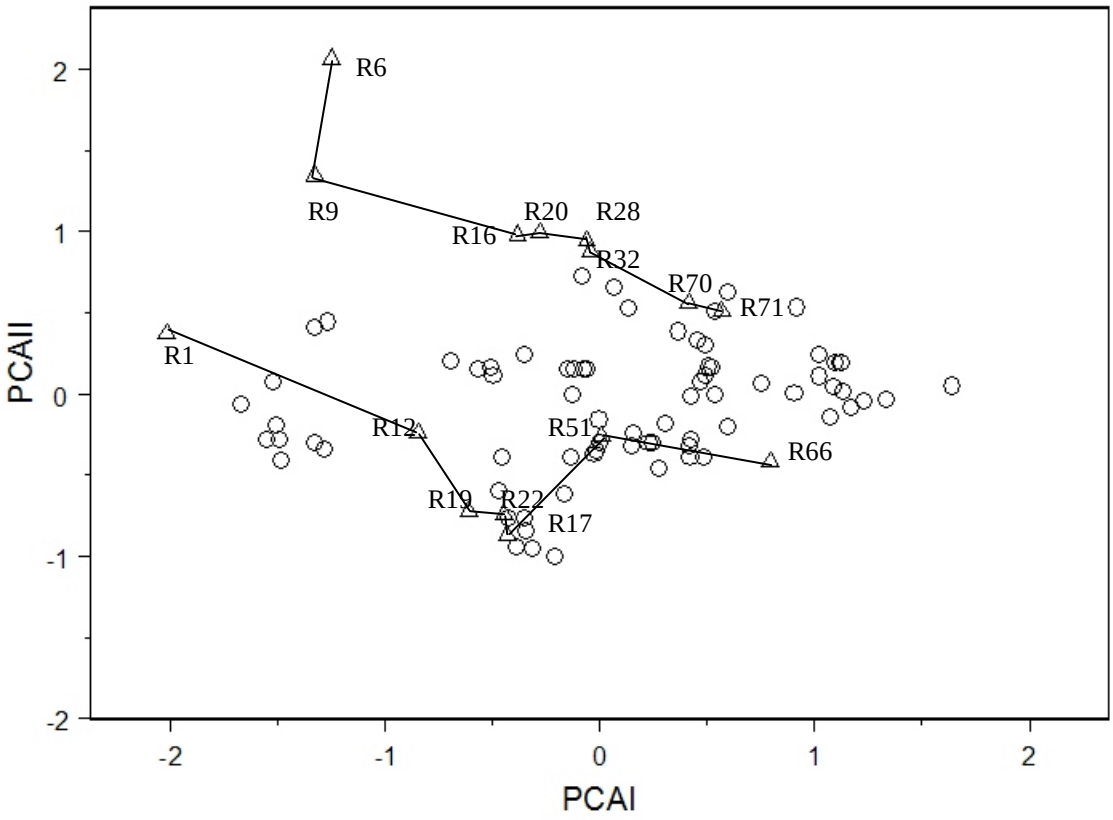


Figure 2. Bi-plot of the first two PCA scores for climate conditions showing difference of climate conditions for the introduced populations (triangles) and the native populations (circles) .
Note: the labels in the figure are the population IDs in Appendix I; lines connecting the adjacent introduced populations

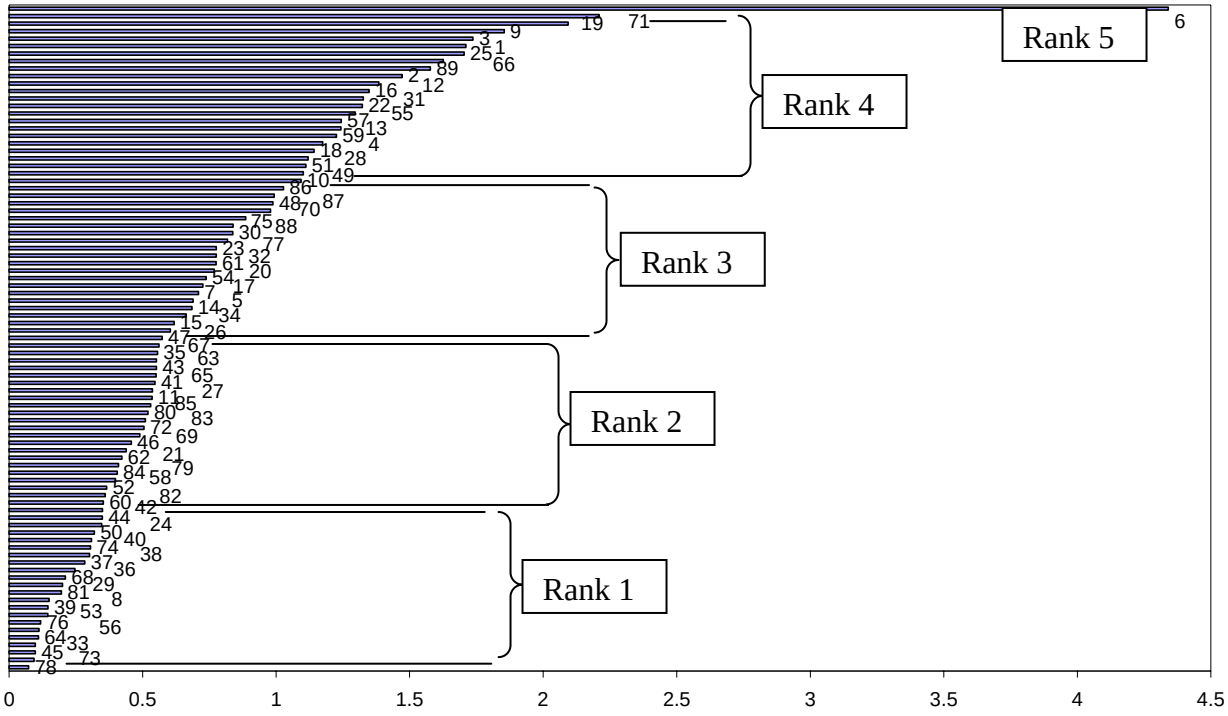


Figure 3. Magnitude of standardized vector residuals from PROTEST analysis and the groups assigned based on their rank orders.
Note: (1) The number beside the bar indicates the populations ID in Appendix 1; (2) Low ranks indicate the better match between climate conditions and walleye growth.

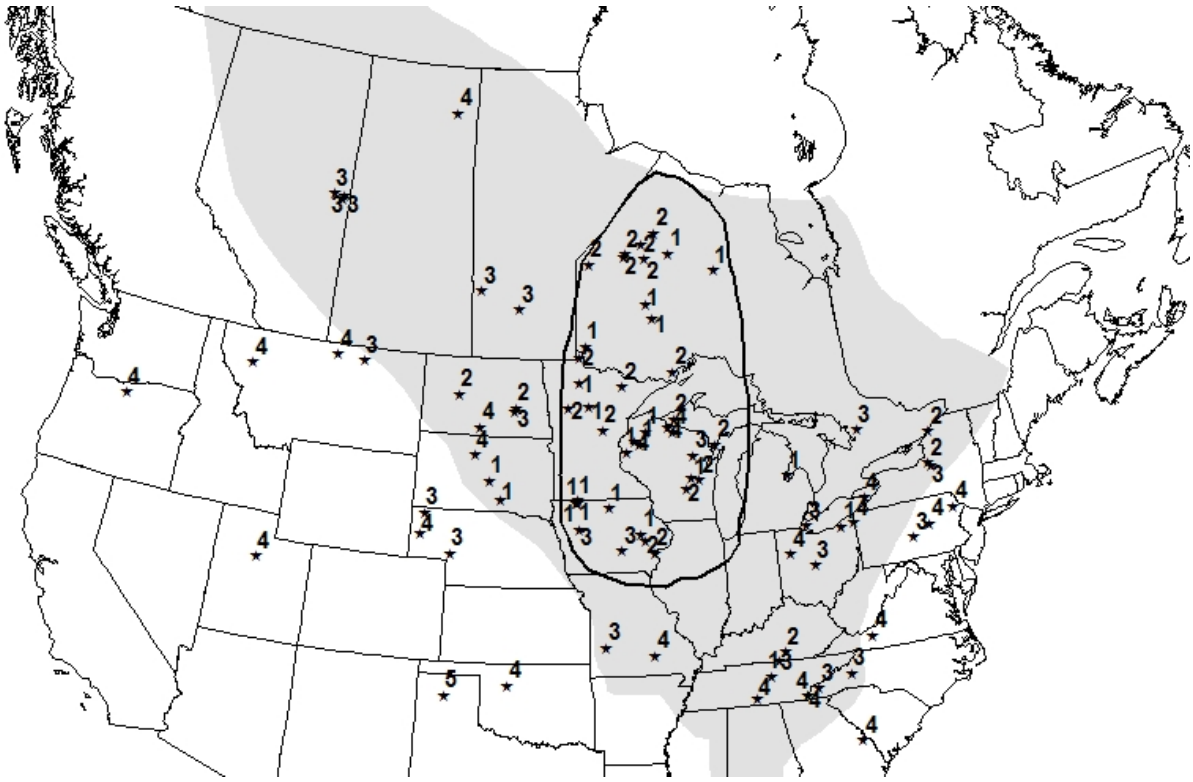


Figure 4. A map of rank groups of residuals of individual walleye populations from PROTEST analysis.
Note: Numbers showing the rank groups in Figure 3; The lower the rank groups (for example, 1,2), the better the concordance between climate conditions and walleye growth; shaded area showing walleye native distribution (redrawn from Colby et al 1979); the populations enclosed by the thick line showing the good march between the growth and climate.

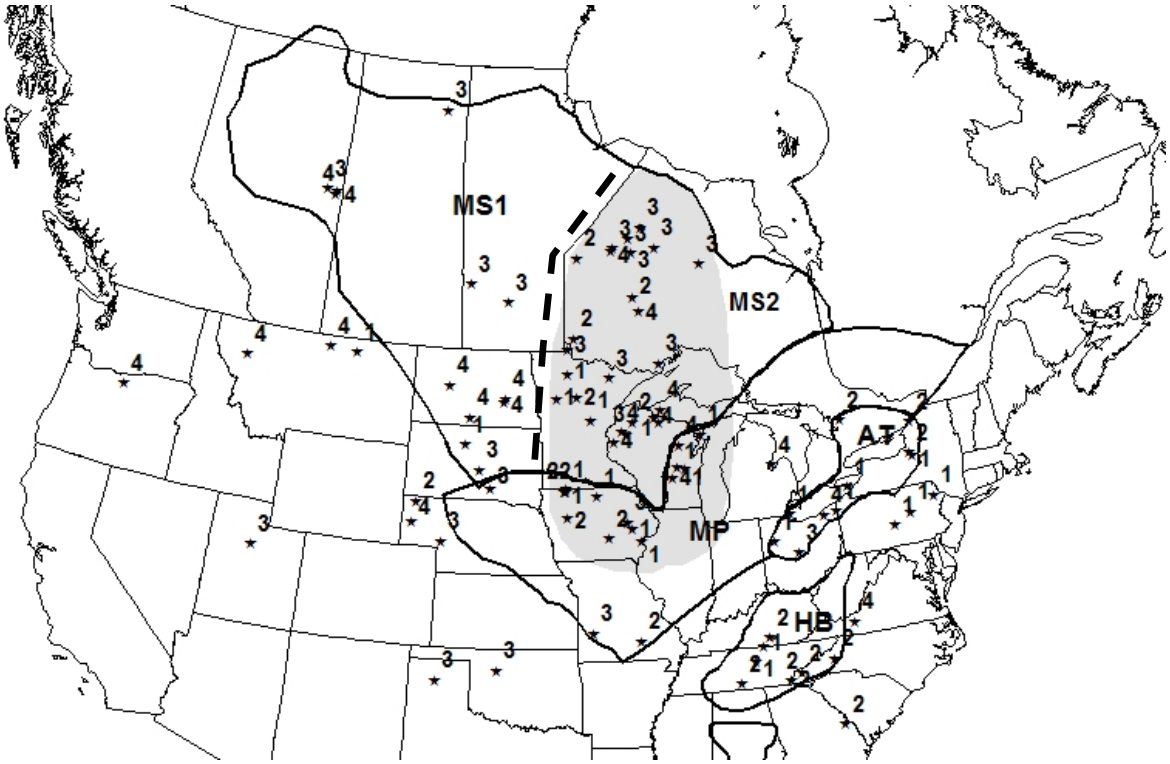
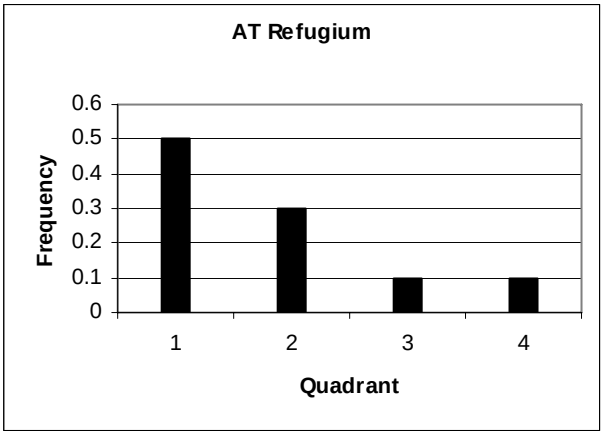
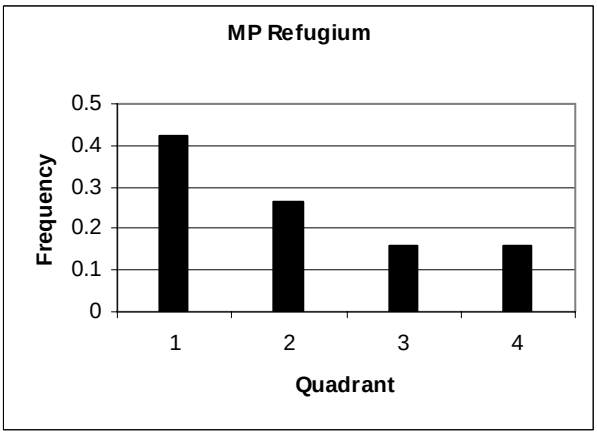
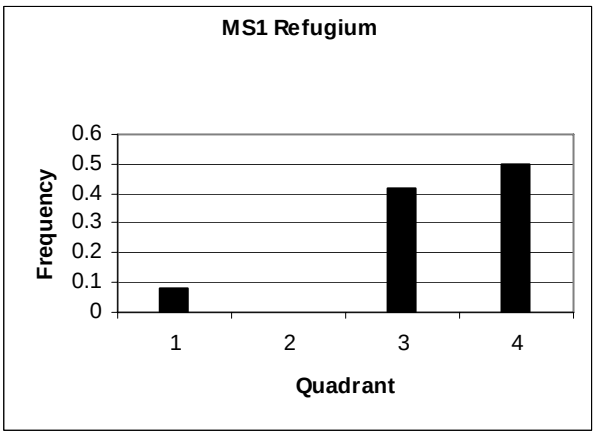
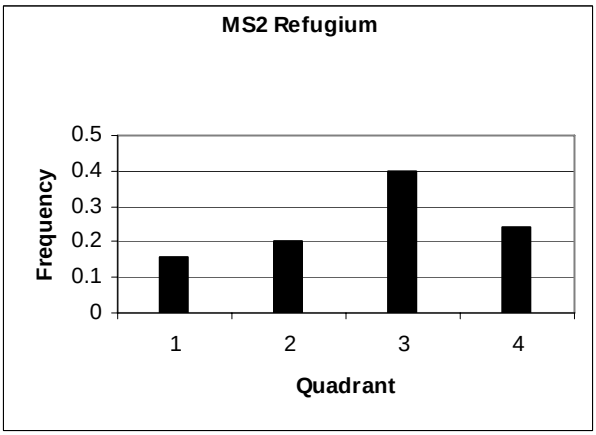


Figure 5. A map of directions of residuals of individual walleye populations from PROTEST analysis and five genetically distinct groups.
Note: Number (1,2,3,4) showing quadrants where the residuals are located beginning with quadrant 1 being the top-right quadrant and progressing counter-clockwise; the polygons closed by dashed lines showing groups of genetic distinct populations; the dotted line is a proposed separating line of Missouri refugium based on this study.









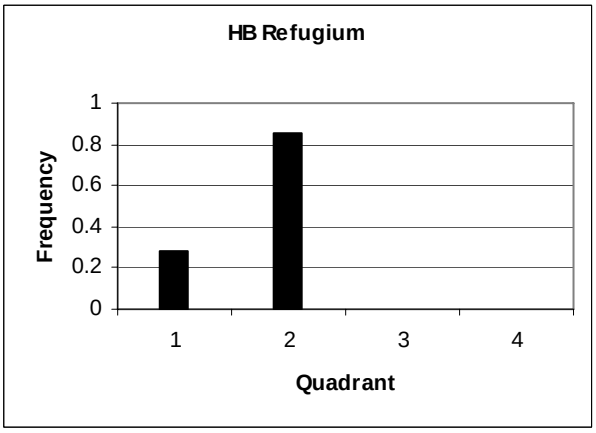


Figure 6. The frequency of directions of residuals from PROTEST analysis from each genetically distinct group (i.e. AT, MP, MS1, MS2, HB in Figure 5) showing distinct characteristics of the vector directions within each group.

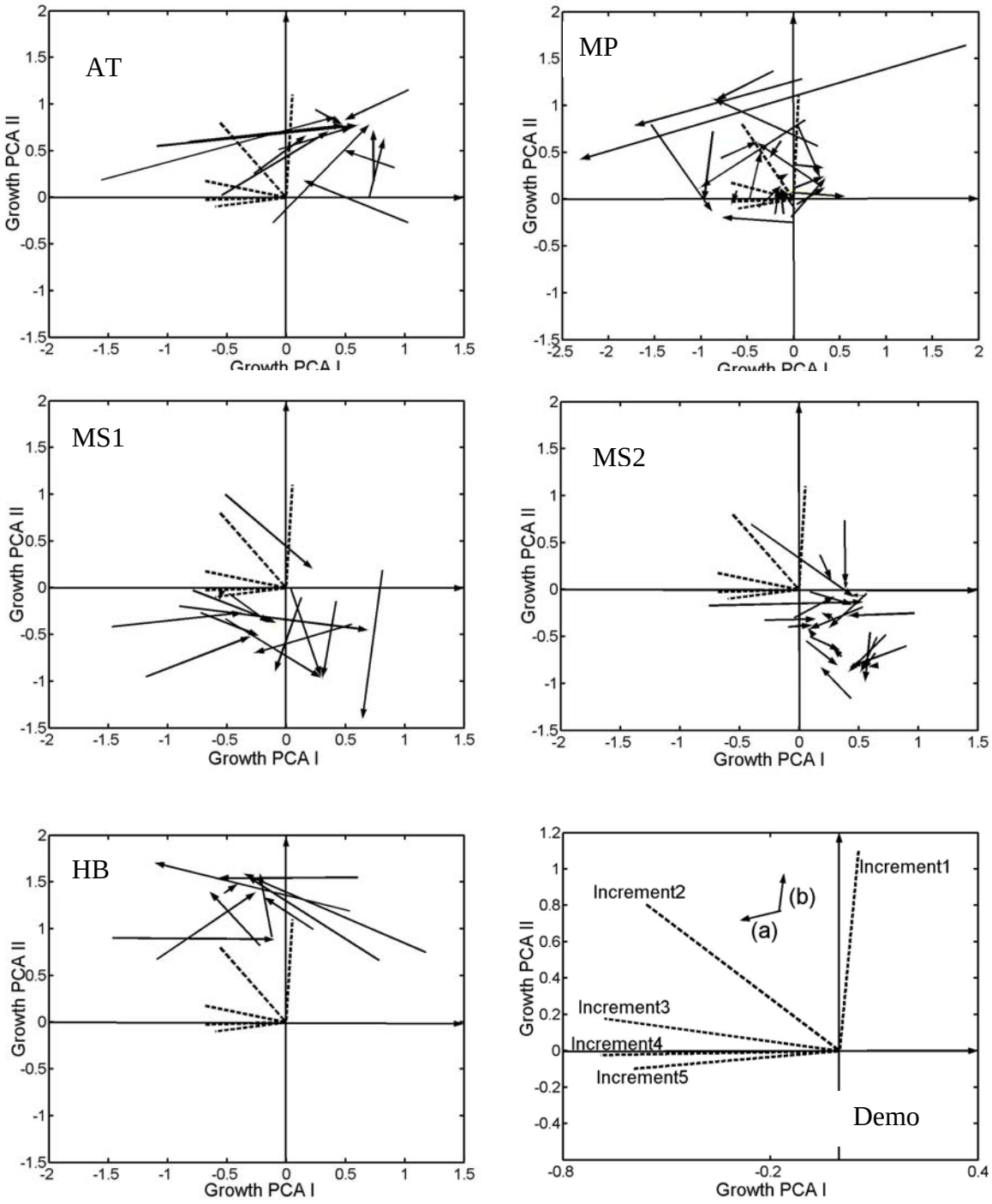


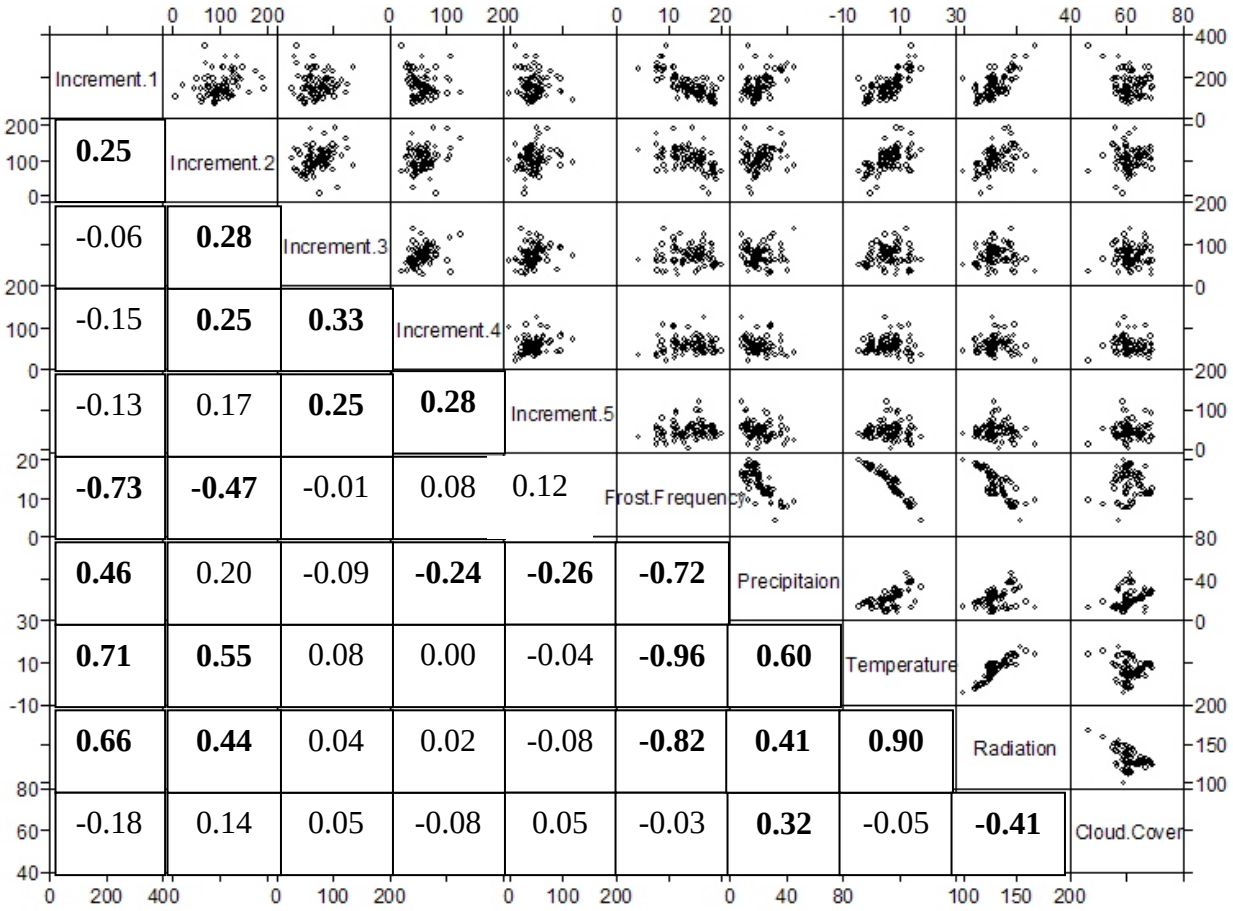
Figure 7. Superimposition plot of five growth eigenvectors (dotted lines) and residuals for five different refugia (i.e. AT, MP, MS1, MS2 and HB in the Figure 5). Note: the panel labelling "Demo" is used to explain the biological significance of the direction of residuals from PROTEST analysis (see the text for details)

Appendix I. Locations, residual groups (rank and direction) from PROTEST and walleye origin of the 89 walleye populations in North America.

ID#	Lake Name	Province	Lat	Long	Ref *	Rank **	Dir ***	Refugium ****
R1	Barton Res	GA	33.09	-81.87	1	4	2	Introduced
R2	Hiwassee Res	NC	35.11	-84.14	1	4	2	HB
R3	Apalachia Lake	NC	35.12	-84.16	1	4	2	HB
R4	Norris Res	TN	35.23	-86.57	1	4	2	HB
R5	Nantahala Res	NC	35.35	-83.57	1	3	2	HB
R6	Lake Meridith	TX	35.64	-101.66	1,2	5	3	Introduced
R7	James Res	NC	35.75	-81.92	1	3	2	HB
R8	Center Hill Res	TN	36.05	-85.76	1,2	1	1	HB
R9	Canton Res	OK	36.13	-98.61	1	4	3	Introduced
R10	Dale. H.Res	TN	36.61	-85.32	1	3	1	HB
R11	Cumberland	KY	36.96	-84.94	1	2	2	HB
R12	Claytor Res	VA	37.07	-80.6	1	4	4	Introduced
R13	Current River	MO	37.25	-91.35	2	4	2	MP
R14	Stockton Lake	MO	37.64	-93.76	1	3	3	MP
R15	Hoover Res	OH	40.17	-82.87	1	3	3	AT
R16	Utah Lake	UT	40.2	-111.79	2	4	3	Introduced
R17	Juniata River	PA	40.58	-77.59	2	3	1	Introduced
R18	Ferguson Res	OH	40.74	-84.04	1	4	1	AT
R19	Susquehanna River	PA	40.97	-76.64	2	4	1	Introduced
R20	McConaughy Res	NE	41.26	-101.84	1	3	3	Introduced
R21	Mississippi River	IA	41.29	-91.09	1	2	1	MP
R22	Lake Wallenpaupack	PA	41.41	-75.23	2	4	1	Introduced
R23	Des Moines River	IA	41.46	-92.79	1	3	2	MP
R24	BeaverCreek Res	OH	41.52	-81.22	1	1	4	AT
R25	Pymatuning Lake	PA	41.6	-80.51	2	4	1	AT
R26	Lake Erie(Western)	GL	41.75	-83	1,2	3	1	AT
R27	McBride Lake	IA	41.8	-91.56	1	2	1	MP
R28	Minature Res	NE	41.93	-103.49	1	4	4	Introduced
R29	Cedar River	IA	42.08	-91.73	1	1	3	MP
R30	Black Hawk Lake	IA	42.3	-95.05	1	3	2	MP
R31	Lake Erie(Eastern)	GL	42.5	-79.75	1	4	1	AT
R32	Whitney Res	NE	42.78	-103.31	1	3	2	Introduced
R33	Clear Lake	IA	43.13	-93.43	1,2	1	1	MP
R34	Oneida Lake	NY	43.2	-75.91	1	3	1	AT
R35	Scriba Creek	NY	43.31	-76.02	2	2	2	AT
R36	W.Okoboji Lake	IA	43.39	-95.18	1,2	1	2	MP
R37	E.Okoboji Lake	IA	43.39	-95.09	2	1	2	MP
R38	Okoboji Lake	IA	43.39	-95.16	1	1	1	MP
R39	Francis Case	SD	43.45	-99.28	1	1	3	MP
R40	Spirit Lake	IA	43.48	-95.1	2	1	1	MP
R41	Puckaway Lake	WI	43.76	-89.17	1	2	4	MP
R42	Saginaw Bay	MI	43.83	-83.67	1	1	4	MP
R43	Winnebago Lake	WI	44.04	-88.41	1	2	1	MP
R44	Lake Poygon	WI	44.15	-88.83	1	1	1	MP

R45	Sharpe	SD	44.2	-99.93	1	1	3	MS1
R46	Black Lake	NY	44.5	-75.61	1	2	2	AT
R47	Wolf River	WI	45.02	-88.65	2	3	4	MP
R48	3-mile Lake	ON	45.18	-79.46	1	3	2	AT
R49	Oahe(SD)	SD	45.2	-100.8	1	4	1	MS1
R50	Pike Lake	WI	45.32	-92.37	1	1	4	MS2
R51	John Day Res	OR	45.33	-120.54	1	4	4	Introduced
R52	N.Green Bay	GL	45.38	-87.38	1	2	1	MP
R53	Red Cedar River	WI	45.61	-91.59	1	1	3	MS2
R54	Ripley Lake	WI	45.71	-91.85	1	3	4	MS2
R55	Trout Lake	WI	46.03	-89.67	1	4	1	MS2
R56	Clear Lake	WI	46.1	-91.24	1	1	2	MS2
R57	Bass Lake	WI	46.19	-89.96	1	4	4	MS2
R58	Mile Lacs Lake	MN	46.23	-93.63	1	2	1	MS2
R59	Oahe(ND)	ND	46.29	-100.58	1	4	4	MS1
R60	Lake Gogebic	MI	46.52	-89.58	2	2	4	MS2
R61	Jamestown Res	ND	46.96	-98.62	1,2	3	4	MS1
R62	Many point Lake	MN	47.06	-95.54	2	2	1	MS2
R63	Spiritwood Lake	ND	47.07	-98.59	1,2	2	4	MS1
R64	Leech Lake	MN	47.14	-94.4	1	1	2	MS2
R65	Lake Sakakawea	ND	47.52	-101.89	1	2	4	MS1
R66	Rainbow Lake	MT	47.68	-113.95	2	4	4	Introduced
R67	Lake Vermillion	MN	47.89	-92.42	1	2	3	MS2
R68	Red Lake	MN	48.06	-94.92	1	1	1	MS2
R69	Kaministiquia R	ON	48.35	-89.45	3	2	3	MS2
R70	Nelson Res	MT	48.48	-107.57	2	3	1	Introduced
R71	Milk River	MT	48.57	-109.12	2	4	4	Introduced
R72	Lake of Woods	MN	49.07	-94.9	1,2	2	3	MS2
R73	Sandy Lake	ON	49.5	-94.53	2	1	2	MS2
R74	Savanne Lake	ON	50.5	-90.43	2	1	4	MS2
R75	Lake Manitoba	Man	50.93	-98.53	1	3	3	MS1
R76	Lake St.Joseph	ON	51.06	-90.8	2	1	2	MS2
R77	West Blue Lake	Man	51.61	-100.92	1	3	3	MS1
R78	Attawapiskat Lake	ON	52.14	-86.43	2	1	3	MS2
R79	Deer Lake	ON	52.66	-94.25	2	2	2	MS2
R80	North Caribou Lake	ON	52.82	-90.71	2	2	3	MS2
R81	Wunnummin Lake	ON	52.94	-89.18	2	1	3	MS2
R82	Petownikip Lake	ON	52.94	-92.04	2	2	4	MS2
R83	Sakwaso Lake	ON	53.02	-91.91	2	2	3	MS2
R84	Makoop Lake	ON	53.38	-90.86	2	2	3	MS2
R85	Big Trout Lake	ON	53.76	-90	2	2	3	MS2
R86	Ethel Lake	AT	54.53	-110.35	1	3	4	MS1
R87	Marie Lake	AT	54.63	-110.3	1	3	4	MS1
R88	Wolf Lake	AT	54.68	-110.97	1	3	3	MS1
R89	Wolllaston Lake	SA	58.28	-103.28	1	4	3	MS1

*1—Carlander 1997, 2—Colby et al 1979, 3—Stephenson and Momot 1991; ** 1,2,3,4,5—residual rank groups from PROTEST (Fig 2); ***1,2,3,4—four quadrants for residual direction group; **** —refugia of origin of walleye populations (Fig 4), Introduced—the introduced population close to and included in X refugium.



Appendix 2. Bi-variate plot and correlation coefficients among varibles of walleye increment-at-age and climate for 89 walleye lakes in North America.

Upper triangle—plot

Low triangle—correlations coefficient (number in BOLD type showing significant correlated between the two variables from two tail test at significant level of 0.05)

Chapter 2. Application of Bayesian MetaAnalysis to Growth of Walleye (Sander vitreus) in Different Climate Zones of North America

Abstract

Size-at-age data for walleye were assembled from 99 populations across their North American Range. They were grouped into six clusters using a Partitioning Around Medoids (PAM) algorithm based on their observed climatic conditions. A Bayesian hierarchical model was used to estimate the parameters of von Bertalanffy growth function for the 99 walleye populations. The results showed that there was a decreasing trend with an increase in latitude for walleye early growth rate and von Bertalanffy growth parameter (k). The significant differences in walleye early growth rates among six clusters suggest that walleye living in the areas with high thermal input have a high early growth rate. However, the climatic conditions showed no significant effects on the walleye asymptotic length (L_∞). A comparison study between Bayesian estimation and non-linear regression estimation carried out in the study demonstrated that Bayesian estimators are more reliable and stable. Bayesian estimation can efficiently deal with the multi-model posterior distribution and insufficient data using relatively precise prior information.

Introduction

As one of several important fish life history traits, growth is empirically and theoretically related to fish survival, reproduction and recruitment (Pauly 1980, Bayer 1989, Beverton 1992). Size-dependent growth and survival have been observed in early life stages for several fish species (Miller et al 1988, Zhao et al 2001). Fish somatic growth rate also plays an important role in determining total fishable biomass for commercial and recreational fisheries and thus is an important factor influencing the selection of appropriate fisheries management strategies.

Accurate and reliable estimation of individual growth curve is essential for the study on fish population dynamic and fisheries research. Among fish growth models, the Von Bertalanffy growth function (VBGF) is commonly used to model fish growth process by fishery researchers due to its simple mathematic form and physiological implications. Three parameters, i.e. L_∞—fish asymptotic length, k—the rate for fish to reach the asymptotic length, and t_0—the hypothetical age when fish length is zero, are involved in modeling fish length (L_t) at age (t) in the model, as follows,

$$L_t = L_\infty (1-exp (-k*(t-t_0)))$$

The biological significance of those parameters constrains the estimates of those parameter values, for example, L_∞ should be larger than a certain value (for example, the maximum observed length) for a fish species and definitely cannot be negative, and k must be in the range of 0 to 1 for most of temperate fish species. If k is equal to one or larger, the fish can grow 60% or more of its asymptotic length during the first year growth, which can be achieved by few temperate fish species.

A common method for estimating the VBGF parameters is non-linear least squares regression. However, this method can generate 'impossible' estimates and/or suffer convergence problems when faced with real data sets. It performs most reliably when both very young and very old fish are well represented in the data set. Unfortunately, this latter condition is frequently not met by many real data sets. Even though the parameters can be estimated with the non-linear least squares approach, the associated variance is usually large, which produces the high uncertainty in the parameter estimates. The other disadvantage of the non-linear least squares procedure is the high correlation (with correlation coefficients exceeding 0.8) between the estimates of L_∞ and k, and high sensitivity to the data (i.e. small changes in data can cause a significant changes in the estimates) (Gallucci and Quinn 1979). The high correlations make it difficult to draw conclusion when comparing growth patterns between two or more populations (Gallucci and Quinn 1979).

Recently, several studies have been done to improve the estimation of the VBGF parameters by using nonlinear hierarchical models, whereby the parameters were estimated either by maximum likelihood estimation (Schaajie et al 2002) or from sampling the Bayesian joint posterior distribution of the parameters (Pilling et al 2002). Like other non-linear frequentist estimation techniques (for example non-linear regression), the non-linear hierarchical models by maximum likelihood estimation can also encounter convergence difficulties (Schaajie et al 2002). In addition, the algorithm, numerical operations and estimation procedures are much more complicated than one expects (Schaajie et al 2002). By setting prior information for those parameters, however, Bayesian statistics have a great advantage in dealing with such hierarchical structure or more complicated ones, and can be

expected to efficiently deal with the problems mentioned above (Pilling et al 2002, Helser and Lai 2004).

Walleye (*Sander vitreus*) is an economically important and ecologically significant species in many of the inland waters of North America. Walleye is a cool-water species with an optimum temperature range of 18 to 22 degree Celsius and a temperature tolerance range of 0 to 30 degree Celsius (Colby et al 1979). Its zoogeographic range extends from the Arctic Ocean to the Gulf of Mexico. Using multivariate analysis approaches in the Chapter 1, I demonstrated that climatic conditions were significantly associated with walleye growth and such association, i.e. the reaction norm, varied across the walleye distribution zone. In this chapter, I explore how walleye populations grouped by climate conditions differ in their growth patterns.

The objectives of this study are (i) to investigate how growth of walleye in North American differs among different climatic zones using a Bayesian meta-analysis approach; (ii) to compare Bayesian estimates and nonlinear least squares estimates of those growth parameters; and (iii) to assess the sensitivity/reliability of the two methods when faced with incomplete data sets.

Methods

A. Data Collections and Growth Model

Walleye length at age

Walleye length-at-age data from literature sources published over the period from 1933 to 2001 were included in the data base to be analyzed. Data from 99 walleye populations in the range of latitude from 31° N to 59° N and of longitude from 75°W to 112° W were included into the database (Table 1, Fig 1). Most length-at-age data were estimated from scale back-calculation studies, and sex combined averages were used in this project to

average over the effect of sexual dimorphism. The longest series of length-at-age used for the analysis was from age 1 to age 12, and the shortest one was from age 1 to 4.

Meteorological data

The global climate variables, i.e. frost frequency, precipitation, mean air temperature, solar radiation and cloud cover for the period of 1960 to 1990, were downloaded from IPCC web site (http://ipcc-ddc.cru.uea.ac.uk/ipcc_ddc.html). The dataset consist of monthly mean values of the five variables in a resolution of 0.5° latitude by 0.5° longitude. The values for each variable were interpolated from the weather station data using thin-plate splines (New et al 1999). An annual mean for each variable for each walleye population in the walleye length-at-age database was calculated and used in the following cluster analysis.

Walleye growth model

The VBGF was used to model walleye growth. In addition to three parameters (L_∞, k, *and* t_0) in this model, the other biological parameter (ω), i.e. early growth rate, can be derived from the product of k and L_∞ (Shuter et al 1998, Quinn and Deriso 1999). This variable can provide relative stable comparisons among the populations (Gallucci and Quinn 1979) and hence was used to compare populations in different climate conditions in this study.

B. Statistical analysis of data

Cluster analysis based on five climate variables

The five climate variables were standardized to z-scores before carrying out cluster analysis in order to remove scale effects. The Partitioning Around Medoids (PAM) algorithm was used to group the 99 walleye populations into clusters based on their climate conditions, i.e. five climate variables. PAM algorithm requires users to provide the number (N) of groups at the beginning of analysis. By operating on the dissimilarity matrix of the given data set,

the algorithm computes *N* representative objects, called mediods. Each observation is then assigned to the cluster corresponding to the nearest mediod. At the end of analysis, the *N* representative objects should be selected to minimize the sum of the dissimilarities of all objects to their nearest mediod. Because the initial selection of the number (*N*) of groups is subjective, it is common practice to run PAM several times, and each time for a different *N*-value and to select the final number of clusters by comparing the resulting overall average silhouette width (OASW), an indicator of quality of clustering operation. The value of silhouette width for individual observation is between -1 (the observation is badly classified) to 1 (the observation is well classified). An observation with a silhouette width value of 0 indicates that the observation lies between two clusters. The overall average silhouette width (OASW) is the average of all the observations in the data set (Kaufman & Rousseeuw, 1990). In this study, the final number of clusters was chosen by comparing OASW among a series of cluster analysis by different cluster numbers (from 2 to 12). The other criterion for selecting the number of clusters is that, for each cluster, the sample size must be larger than 10 populations in order to make estimation of cluster means relatively stable and accurate. The clusters finally were plotted on the first two principal components from a principal component analysis (PCA).

Bayesian hierarchical structure for meta-analysis

Three levels of a hierarchical structure were set up to carry out Bayesian analysis (Fig 2). The top level is the grand means of three parameters (i.e. L_∞, t_0 and k) for all 99 populations. The parameters at each cluster level were defined as normal distributions with the means being the grand means, and the precisions defined as inverse of variances. Within each cluster, the growth parameters for individual walleye population have normal

distributions with the means being their own cluster means and the different precisions (i.e. inverse of variances). Based on fish life-history theory and walleye characteristics, the three biological parameters, L_{∞}, t_0 and k, were assigned three uniform priors as follows and the prior distribution for the precision for any normal distribution mentioned above is gamma distribution with parameters (0.01, 0.01) in order to apply relatively vague prior information:

L_{∞} ~uniform (30 cm, 130 cm)

k ~uniform (0, 2)

t_0 ~uniform (-2, 2)

The low boundary value for the uniform prior of L_{∞} (i.e. 30 cm) was selected based on the fact that none of the 99 populations has observed largest length less than 100 cm. The historical record of the largest walleye captured in North America is less than 100 cm and thus help set the upper boundary of the uniform prior of L_{∞}.

Sampling posterior distributions by MCMC and convergence assessment of MCMC chains

Markov Chain Monte Carlo simulation was used to sample the posterior distribution of parameters for each cluster and individual walleye populations. Three chains with different initial parameter sets were used in the simulation. Three sets of initial parameter values were arbitrarily picked without consideration of any prior distribution. Each chain was run 21000 iterations by sampling 30^{th} iterations only. In order to completely remove autocorrelation effects from each chain, the 2^{th} sample was further chosen to construct posterior distributions and make statistical inferences. The first 1000 iterations were discarded as the burn-in period.

Three sets of initial values of parameters were provided for starting MCMC sampling. The Gelman and Rubin (1992) convergence diagnostic approach was designed to assess the convergence of multiple MCMC chains and hence was selected as an assessment tool in this study. The approach is essentially a variance-ratio method which is based on the theories of analysis of variance and sampling from normal distribution. By comparing the variance between chains and within chains for each parameter, one can estimate the Potential Scale Reduction Factor (PSRF), a statistic used to assess the convergence of the multiple chains. As a rule of thumb, the PSRF should be approximately equal to one to conclude that the each chain is close to the target distribution (for further details refer to Cowls and Carlin 1992, Brook and Roberts 1998, and Smith 2003).

Non-linear regression to estimate the VBGF parameters

The Gauss-Newtown non-linear algorithm was used for the regression analysis; and the initial values for those parameters were randomly picked within the Bayesian prior ranges. For those populations whose growth parameters could not be estimated during the first run, at least three sets of different initial values of the parameters were provided for further efforts on estimation of those parameters.

Comparison between Bayesian and non-linear regression

I carried out two comparisons of Bayesian and non-linear regression in this study. The first method directly compares the estimators of the three parameters and the associated variations. The second one is the comparison of variability of the estimators of three parameters due to variation in the number of observed data points, i.e. length at different ages. In order to make the second comparison, I picked the populations with the longest length at age series (i.e. age 12), eliminated the length at the oldest age one at a time, and estimated the

parameters from each shortened length-at-age data series by both non-linear regression and Bayesian approach. Because non-linear regression requires at least 4 data points to estimate three parameters of VBGF, the chosen populations can only be shortened to length at age 4. The Bayesian approach, however, by taking an advantage of prior information, does not have a minimum data point requirement. Therefore, the populations chosen can be eliminated to only one point, i.e. length at age 1. In addition, the priors for the parameters of chosen populations were set as the normal distributions of means and variances of the clusters to which they belong.

Results

After a series of number of clusters (from 2 to 12) trial, eight clusters produced the largest overall average silhouette width (OASW=0.48). However, the minimum number of observations in one of the clusters was only three. Therefore, the number of cluster with the second largest OASW (0.41), i.e. six clusters, was selected from PAM analysis based on their climatic conditions with the range of sample size being from 13 to 20 (Fig. 3a). Principal component analysis (PCA) showed that the first two components explained 92.2% of the variations in climate conditions for 99 walleye populations (Table 2). The result demonstrated that the clusters were arranged mainly by thermal regime (i.e. the first component) or latitude (Fig 3b). The second principal component representing the light conditions, i.e. the contrast mainly between cloud cover or precipitation and radiation (Table 2), played a role in separating the Cluster 2 from Cluster 3 and Cluster 4 from Cluster 5 (Fig 3b). The climate for Cluster 3 and Cluster 4 are much influenced by the large water bodies, such as the Great Lakes or the Pacific Ocean, which resulted in a low light condition i.e. high cloud cover or precipitation versus solar radiation, reaching the earth surface in those areas

(Table 2, Fig 3b). Conversely, the populations in Cluster 2 and Cluster 5 located in inland areas can receive more solar radiations and produced larger second component scores compared to those in Cluster 3 and Cluster 4, respectively (Table 2, Fig 3b).

Two of three chains converged and mixed well (Fig 4a). The third chain, however, sampled the other mode and produced much larger variations among the chains. The bi-modes can also be observed by the density plots of some populations (Fig 4b). The biological significance of the three parameters implied that the third chain was not feasible for modelling walleye growth (i.e. negative estimates) and should be discarded for those populations. The remaining two chains did not show any significant autocorrelation (autocorrelation at 5^{th} lag for each parameter are substantially reduced to 0), and the convergence diagnostic results based on these two chains suggested that the chains converged well with Potential Scale Reduction Factors approximately equal 1. Therefore, posterior distribution can be well estimated from two well-mixed chains and therefore the following statistical inferences were drawn by combining only the first two chains.

The parameters of VBGF for 95 walleye populations were estimable by non-linear regression. The populations 54, 76, 78 and 79 in Table 1 cannot be fitted by VBGF due to the convergence failure of Gaussian-Newton non-linear estimation procedure. To obtain a better understanding of the reason why the parameters for some populations cannot be estimated by non-linear regression, the profile log-likelihood functions of L_∞ and k were plotted for Population 15 and Populations 76 (Table 1) which represent the populations with the parameters estimable and non-estimable, respectively (Fig 5). The two modal or multi-modal characteristics of likelihood were evident for both populations, and such complex surfaces could be one cause of the convergent difficulties for non-linear regression.

The statistics for three parameters for each individual walleye population were all in biologically reasonable ranges (Fig 6). There exists a decreasing trend with an increase in latitude for parameter *k*, but not for L_∞ and t_0 (Fig 6). The early growth rate for each cluster shaped by climate conditions showed a decreasing trend with the increase in latitude (Fig 7a). A 95% credible range for the difference between clusters showed that walleye populations located in higher latitudes grew significantly slower during their early life than their counterparts in the lower latitudes (Table 3). However, no clear trend in the asymptotic length existed among the clusters (Fig 7b).

The standard deviations of the estimates for each cluster means from Bayesian hierarchical model were much smaller than the cluster-based mean standard deviations of 95 estimable populations by non-linear regression (Table 4). The correlations between the parameters were substantially reduced by Bayesian hierarchical estimating approach compared to the non-linear regression approach (Table 5).

A total of nine populations with length at age up to 12 (the longest one in the data set) were selected for comparing the Bayesian and non-linear regression by sequentially eliminating the oldest age one at a time. The absolute changes from the original estimates, i.e. estimates from the full 12 data points, showed a general increasing trend in Bayesian and non-linear regression (Table 6), which reflects that with few data points, the less accurate estimators are obtained if one assumes the most accurate of estimators from full range of data points (i.e. 12 data points). Compared to the non-linear regression approach, the Bayesian hierarchical model produced the estimators with smallest changes. This suggests that the estimators were closer to the most accurate estimators. The standard deviations for three parameters also increased along with fewer data points (Table 7) for both Bayesian and non-

linear regression. The majority of standard deviations of the estimated parameters for non-linear regression were larger than those from Bayesian estimators. The correlations among the parameters increased along with data elimination for non linear regression. However, there was no increasing trend but a slightly decreased trend for the parameters' correlations for Bayesian estimators, especially for few data points. This suggests that the dependency of non-linear regression on parameter correlation structure to make estimations becomes stronger when data points were eliminated step by step, and the Bayesian approach can make most effective use of limited data.

Discussion

Fish early growth rate can affect the mortality and time at maturation, and thus influence fish population dynamics (Shuter et al 1998). For von Bertalanffy growth curve, the early growth rate was suggested to be a good parameter to carry out comparisons among the populations (Gallucci and Quinn 1979). The decreasing trend of early growth rate among the cluster indicates that the climatic thermal regime significantly influences the walleye early growth rate given the fact that the clusters were mainly arranged by the first principal component of climate conditions, i.e. the net thermal input. The non-existence of significant differences in the early growth rate between Cluster 2 and Cluster 3 or Cluster 4 and Cluster 5 implied that the light conditions would not affect the walleye early growth rate because both pairs of clusters were mainly divided by the second components (i.e. light conditions). The thermal effects on fish growth were also demonstrated by other researchers on walleye (Quist et al 2003) and other species, for example largemouth bass, *Micropterus salmoides* (Helser and Lai 2004). However, walleye asymptotic length was not affected by the thermal pattern. Beverton (1995) suggested that food supply may influence the fish asymptotic length.

On average, the lake productivity in the northern portion of walleye distribution range was lower than that in the south, and thus food supply to walleye would be higher in south. A common garden study by Galarowicz and Wahl (2003), however, showed that walleye from the north showed higher food conversion efficiency at a low temperature, which may compensate for the growth deficiency due to the limited food supply for northern populations. Such a compensatory growth pattern was also observed from the growth of Atlantic cod (*Gadus morhua*) larvae after their first feeding time was delayed by approximately 4 days (Zhao et al 2001). The fish age-at-maturity also affects their adult sizes as well. For example, compared to the northern populations of walleye, the early maturity for southern populations would result in a small asymptotic size due to more or earlier energy investment in the gonads instead of somatic growth (Lester et al 2004). This combined effect from the compensatory growth and age at maturity could be the cause of lack of latitudinal trend of walleye adult growth pattern (i.e. L_∞) in spite of the existence of significant latitudinal trends on walleye early growth rate.

The complexity of likelihood surface of von Bertalanffy function parameters has notoriously caused inaccuracy and difficulty in estimating the parameters using non-linear regression. Given no evidence showing that the fish growth rate (k) is correlated to the asymptotic length (L_∞) in a biological context, the high correlations among the parameters were most likely caused by the complexity of the likelihood surface. Such correlations produced inconsistent results when the comparisons among populations based on either of these parameters were made (Gallucci and Quinn 1979). By taking advantage of prior information, i.e. biological constraints of the parameters, Bayesian estimators can be more accurate, stable and reliable. Furthermore, the substantial reduction in correlations of the

parameters results in more conclusive comparisons among the populations. In addition, Bayesian approaches can be also used to take into account the correlation structures of parameters and integrate the linear or non-linear model of covariate model for any parameter to make estimations and hypothesis test (Helser and Lai 2004).

A Bayesian posterior distribution can capture the characteristics of the likelihood surface given a vague prior. Bayesian approaches can constrain the estimation by setting an appropriate prior or selecting the biologically significant estimators, as shown in my study. Instead of carrying out post-simulation selection of a significant estimator as mentioned above, one can set up a truncated distribution before the simulation to eliminate the non-meaningful estimation. For example, in this study, a normal distribution truncating negative values can be set up for L_∞, or k to remove the negative estimators for L_∞ or k.

Unlike in non-linear regression, the complexity of likelihood functions would not restrain the Bayesian estimation of the parameters although the convergence problems may occur during the posterior sampling. Particularly, when there are not enough data to carry out non-linear regression analysis and some prior information is available, one can use the Bayesian model and limited observed data to estimate growth parameters. In such case, the more accurate the priors, the more precise the estimators obtained. Compared to non-linear regression, a substantial reduction in variation of Bayesian estimators in this study may result from “borrowing strength from the neighbours’ effect” (Borgoni and Billari 2003), a feature of the Bayesian hierarchical model. In non-linear regression, the estimation of the model parameters was only made on the observation on each population itself. In the Bayesian hierarchical model, the parameter estimations for each individual population in this study involved both the observation on the population and the prior information (i.e cluster means)

that were shaped by neighbouring populations sharing the similar climatic conditions. This process can effectively reduce the variance of estimators.

In summary, the latitudinal thermal pattern shapes walleye early growth patterns. Walleye in lower latitude experience higher thermal inputs and thus exhibit a higher early growth rate. This supports the results from the last chapter: the growth increments before age 3 were more influenced by thermal conditions, but growth pattern for walleye during their late life stage (above age 3) could not be explained by simple climatic conditions. In this chapter, the analysis on walleye complete growth curves (some of them up to age 12) produced the same conclusion. Compared to the non-linear regression model, Bayesian hierarchical model can provide more reliable and accurate estimators for the von Bertalanffy growth function, and thus produce more reliable comparisons among populations. In addition if one has only limited observations, the Bayesian approach can be an ideal tool to provide the parameter estimation given that the precise prior information is known.

In addition, the Bayesian estimation procedure was shown to be robust to the absence of information on older age classes. This implies that this estimation procedure is not sensitive to the loss of precision in size-at-age estimates caused by increasing error when older fish are aged with the scale method.

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Table 1. The Locations for the 99 North American walleye populations in the study

ID	Lake Name	State	Latitude	Longitude	Reference*
1	TwinButtesRes	TX	31.36	100.54	1(1977)
2	Barton Res	GA	33.09	81.87	1(1990)
3	Hiwassee Res	NC	35.11	84.14	1(1949)
4	Apalachia Lake	NC	35.12	84.16	1(1961)
5	Norris Res	TN	35.23	86.57	1(1949,55,78)
6	Nantahala Res	NC	35.35	83.57	1(1961)
7	Santatlah Lake	NC	35.36	83.86	1(1961)
8	Lake Meridith	TX	35.64	101.66	1(1974),2(1990)
9	James Res	NC	35.75	81.92	1(1961)
10	Center Hill Res	TN	36.05	85.76	1(1966),2(1978)
11	Canton Res	OK	36.13	98.61	1(1970)
12	Dale. H.Res	TN	36.61	85.32	1(1973, 76)
13	Cumberland	KY	36.96	84.94	1(1990)
14	Claytor Res	VA	37.07	80.6	1(1951)
15	Current River	MO	37.25	91.35	2(1966)
16	Stockton Lake	MO	37.64	93.76	1(1978)
17	Gasconade River	MO	38.20	91.88	2(1958)
18	Hoover Res	OH	40.17	82.87	1(1970)
19	Utah Lake	UT	40.20	111.79	2(1960)
20	Juniata River	PA	40.58	77.59	2(1961)
21	Ferguson Res	OH	40.74	84.04	1(1981)
22	Rathbun Res	IA	40.87	93.01	1(1975)
23	Susquehanna River	PA	40.97	76.64	2(1961)
24	McConaughy Res	NE	41.26	101.84	1(1956,71)
25	Allegheny River	PA	41.27	79.80	2(1961)
26	Mississippi River	IA	41.29	91.09	1(1967)
27	Lake Wallenpaupack	PA	41.41	75.23	2(1961)
28	Des Moines River	IA	41.46	92.79	1(1959)
29	BeaverCreek Res	OH	41.52	81.22	1(1983)
30	Pymatuning Lake	PA	41.60	80.51	2(1961)
31	Lake Erie(Western)	GL	41.75	83.00	1(1993),2(1933)
32	McBride Lake	IA	41.80	91.56	1(1963,70)
33	Minature Res	NE	41.93	103.49	1(1956)
34	Cedar River	IA	42.08	91.73	1(1956)
35	Black Hawk Lake	IA	42.30	95.05	1(1982,87)
36	Box Butte Res	NE	42.46	103.10	1(1956)
37	Lake Erie(Eastern)	GL	42.5	79.75	1(1936,77)
38	Whitney Res	NE	42.78	103.31	1(1956)
39	Clear Lake	IA	43.13	93.43	1(1977),2(1949)
40	Oneida Lake	NY	43.20	75.91	1(1965)
41	Scriba Creek	NY	43.31	76.02	2(1962)
42	E.Okoboji Lake	IA	43.39	95.09	1(1982),2(1948)
43	W.Okoboji Lake	IA	43.39	95.18	2(1948)

44	Okoboji Lake	IA	43.39	95.16	1(1982,84)
45	Francis Case	SD	43.45	99.28	1(1970.77)
46	Spirit Lake	IA	43.48	95.1	2(1948,51)
47	Puckaway Lake	WI	43.76	89.17	1(1966)
48	Saginaw Bay	MI	43.83	83.67	1(1948,54)
49	Winnebago Lake	WI	44.04	88.41	1(1952,70)
50	Lake Poygon	WI	44.15	88.83	1(1952)
51	Sharpe	SD	44.20	99.93	1(1977)
52	Black Lake	NY	44.50	75.61	1(1969)
53	Wolf River	WI	45.02	88.65	2(1952)
54	3-mile Lake	ON	45.18	79.46	1(1956)
55	Oahe(SD)	SD	45.20	100.80	1(1961,77)
56	Pike Lake	WI	45.32	92.37	1(1968)
57	John Day Res	OR	45.33	120.54	1(1985)
58	N.Green Bay	GL	45.38	87.38	1(1952,59)
59	Red Cedar River	WI	45.61	91.59	1(1978)
60	Ripley Lake	WI	45.71	91.85	1(1959)
61	Trout Lake	WI	46.03	89.67	1(1942)
62	Clear Lake	WI	46.10	91.24	1(1942)
63	Bass Lake	WI	46.19	89.96	1(1942)
64	Mile Lacs Lake	MN	46.23	93.63	1(1943)
65	Oahe(ND)	ND	46.29	100.58	1(1970,76)
66	Lake Gogebic	MI	46.52	89.58	2(1950)
67	Hauser Lake	MT	46.68	111.82	2(1964)
68	Heart Butte Res	ND	46.71	101.85	1(1958)
69	Jamestown Res	ND	46.96	98.62	1,2(1972,76)
70	Many point Lake	MN	47.06	95.54	2(1958)
71	Spiritwood Lake	ND	47.07	98.59	1,2(1972,76)
72	Leech Lake	MN	47.14	94.40	1(1943)
73	Ashtabula	ND	47.16	97.99	1(1958,76)
74	Lake Sakakawea	ND	47.52	101.89	1(1969,76)
75	Rainbow Lake	MT	47.68	113.95	2(1964)
76	Lake Vermillion	MN	47.89	92.42	1(1943)
77	Red Lake	MN	48.06	94.92	1(1939,77)
78	Kaministiquia R	ON	48.35	89.45	3(1991)
79	Nelson Res	MT	48.48	107.57	2(1964)
80	Milk River	MT	48.57	109.12	2(1964)
81	Frenchman Res	MT	48.73	107.20	2(1964)
82	Lake of Woods	MN	49.07	94.90	1(1987),2(1944)
83	Sandy Lake	ON	49.50	94.53	2(1964)
84	Savanne Lake	ON	50.50	90.43	2(1967)
85	Lake Manitoba	Man	50.93	98.53	1(1930)
86	Lake St.Joseph	ON	51.06	90.80	2(1964)
87	West Blue Lake	Man	51.61	100.92	1(1957)
88	Attawapiskat Lake	ON	52.14	86.43	2(1964)
89	Deer Lake	ON	52.66	94.25	2(1961)
90	North Caribou Lake	ON	52.82	90.71	2(1961)
91	Wunnummin Lake	ON	52.94	89.18	2(1964)
92	Petownikip Lake	ON	52.94	92.04	2(1964)

93	Sakwaso Lake	ON	53.02	91.91	2(1964)
94	Makoop Lake	ON	53.38	90.86	2(1965)
95	Big Trout Lake	ON	53.76	90.00	2(1961)
96	Ethel Lake	AT	54.53	110.35	1(1986)
97	Marie Lake	AT	54.63	110.30	1(1986)
98	Wolf Lake	AT	54.68	110.97	1(1986)
99	Wollaston Lake	SA	58.28	103.28	1(1959)

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*the year in the bracket is the year when the data were published.

Table 2. Eigenvector coefficients and eigenvalues from the principal component analysis (PCA) of climate conditions for the ninety-nine walleye populations

Variables		Principle Components				
		PCA1	**PCA2**	**PCA3**	**PCA4**	**PCA5**
Eigenvector (Coefficient of)	**Frost Frequency**	0.545	0.107	-0.172	-0.706	0.404
	Precipitation	-0.377	-0.513	-0.755	-0.134	0.088
	Temperature	-0.538	0.004	0.367	-0.071	0.756
	Radiation	-0.520	0.323	0.094	-0.637	-0.470
	Cloud Cover	0.107	-0.788	0.508	-0.270	-0.192
Eigenvalues		3.137	1.427	0.329	0.047	0.010
Percentage (%)		63.37	28.84	6.64	0.95	0.20
Cumulative (%)		63.37	92.21	98.85	99.80	100.00

Table 3. Means, standard deviations (S.D) and credible interval (2.5%, 50% and 97.5% quantiles) of the differences of walleye early growth rates among 6 clusters from Bayesian hierarchical model.

clusters	means	S.D.	2.50%	50%	97.50%
1 vs 2	**4.48**	**2.14**	**0.43**	**4.43**	**8.74**
1 vs 3	2.21	2.33	-2.40	2.19	6.83
1 vs 4	**5.99**	**2.10**	**1.96**	**5.95**	**10.20**
1 vs 5	**6.23**	**2.21**	**2.02**	**6.18**	**10.70**
1 vs 6	**10.30**	**2.15**	**6.24**	**10.30**	**14.70**
2 vs 3	-2.30	2.02	-6.20	-2.30	1.70
2 vs 4	1.50	1.70	-1.90	1.53	4.83
2 vs 5	1.75	1.78	-1.70	1.72	5.28
2 vs 6	**5.83**	**1.74**	**2.43**	**5.84**	**9.28**
3 vs 4	3.78	1.98	-0.10	3.75	7.71
3 vs 5	4.02	2.07	<-0.001	4.01	8.17
3 vs 6	**8.11**	**2.03**	**4.13**	**8.08**	**12.20**
4 vs 5	0.24	1.75	-3.14	0.25	3.73
4 vs 6	**4.33**	**1.69**	**1.03**	**4.33**	**7.67**
5 vs 6	**4.09**	**1.79**	**0.57**	**4.09**	**7.57**

Note: Bold number showing the Bayesian 95% credible interval not including zero (i.e. the difference between two cluster means is significant)

Table 4. Comparisons of estimators and the associated standard deviations (SD) of the parameters of von Bertalanffy growth function between Bayesian hierarchical model and non-linear regression study.

Cluster	K				L_∞				t_0			
	Bayesian		**Non-Linear**		**Bayesian**		**Non-Linear**		**Bayesian**		**Non-Linear**	
	estimate	**SD**	**estimate**	**SD**	**estimate**	**SD**	**estimate**	**SD**	**estimate**	**SD**	**estimate**	**SD**
1	0.28	0.03	0.34	0.10	69.96	2.53	67.37	8.17	-0.73	0.12	-0.74	0.39
2	0.21	0.02	0.25	0.04	71.45	2.21	70.78	5.76	-0.23	0.08	-0.16	0.17
3	0.25	0.02	0.30	0.06	69.76	2.7	68.80	10.00	-0.39	0.10	-0.31	0.24
4	0.19	0.02	0.25	0.05	71.27	2.18	110.5	575	-0.34	0.08	-0.24	0.30
5	0.19	0.02	0.21	0.06	72.43	3.04	76.28	11.2	-0.11	0.09	-0.1	0.18
6	0.13	0.02	0.13	0.02	71.08	2.35	72.07	6.52	-0.43	0.10	-0.48	0.20

Table 5. Pearson correlation coefficients of estimators of the parameters of von Bertalanffy growth function between Bayesian hierarchical model and non-linear regression

Note: Bayesian—directly estimated from Bayesian hierarchical model
Non-linear –cluster level means of individual populations in each cluster from non linear regression

Clusters	L_∞ vs k		L_∞ vs t_0		k vs t_0	
	Bayesian	**Non-Linear**	**Bayesian**	**Non-Linear**	**Bayesian**	**Non-Linear**
1	-0.28	-0.95	-0.25	-0.82	0.58	0.93
2	-0.21	-0.97	-0.20	-0.75	0.32	0.87
3	-0.20	-0.95	-0.17	-0.76	0.40	0.89
4	-0.23	-0.96	-0.22	-0.76	0.35	0.87
5	-0.31	-0.98	-0.22	-0.79	0.30	0.87
6	-0.16	-0.99	-0.20	-0.79	0.25	0.86

Table 6. Comparisons of means of absolute changes from the full ages (i.e. 12) estimates of von Bertalanffy growth function parameters between Bayesian and Non-linear regression approaches for 9 populations (Note: the changes were calculated by subtracting original estimates (i.e. from 12 age points) from the new parameter values estimated by throwing out length at oldest age at a time and re-estimating the parameters. The means were derived from absolute values.)

		Number of Data Points (Ages)										
		11	**10**	**9**	**8**	**7**	**6**	**5**	**4**	**3**	**2**	**1**
k	**Bayesian**	0.044	0.084	0.091	0.089	0.124	0.135	0.137	0.124	0.121	0.121	0.202
	Non-Linear	0.106	0.211	0.208	0.255	0.287	0.433	0.358	0.446	-	-	-
L_∞	**Bayesian**	0.026	0.056	0.052	0.049	0.066	0.069	0.072	0.063	0.080	0.090	0.085
	Non-Linear	0.056	0.162	0.093	0.15	0.161	0.231	0.271	0.188	-	-	-
t_0	**Bayesian**	0.136	0.178	0.161	0.132	0.137	0.147	0.122	0.114	0.250	0.291	0.267
	Non-Linear	0.194	0.360	0.273	0.334	0.334	0.468	0.421	0.447	-	-	-

Table 7. Comparisons of standard deviation (SD) and correlations of estimates from the full ages (i.e. 12) structure and shortened age structure on von Bertalanffy growth function parameters between Bayesian and Non-linear regression approaches for 9 populations.

			Number of Data Points (Ages)											
			12	**11**	**10**	**9**	**8**	**7**	**6**	**5**	**4**	**3**	**2**	**1**
Standard Deviation	k	**Bayesian**	0.018	0.014	0.015	0.018	0.020	0.024	0.027	0.029	0.030	0.031	0.031	0.036
		Non-Linear	0.016	0.018	0.020	0.021	0.023	0.031	0.029	0.038	0.024	-	-	-
	L_∞	**Bayesian**	5.579	4.302	5.249	5.600	6.529	7.253	8.130	9.108	9.924	10.67	11.08	11.33
		Non-Linear	6.252	6.276	13.64	9.381	17.53	20.04	20.17	69.37	6.579	-	-	-
	t_0	**Bayesian**	0.201	0.150	0.153	0.156	0.157	0.159	0.161	0.164	0.170	0.185	0.208	0.244
		Non-Linear	0.223	0.223	0.238	0.202	0.207	0.222	0.170	0.220	0.068	-	-	-
Correlation	L_∞_k	**Bayesian**	-0.935	-0.939	-0.946	-0.946	-0.945	-0.943	-0.938	-0.930	-0.917	-0.890	-0.818	-0.537
		Non-Linear	-0.981	-0.984	-0.988	-0.988	-0.991	-0.992	-0.993	-0.995	-0.997	-	-	-
	L_∞_ t_0	**Bayesian**	-0.525	-0.628	-0.618	-0.611	-0.574	-0.538	-0.417	-0.337	-0.246	-0.103	0.037	0.206
		Non-Linear	-0.767	-0.776	-0.802	-0.804	-0.826	-0.838	-0.856	-0.885	-0.907	-	-	-
	k_ t_0	**Bayesian**	0.671	0.751	0.737	0.731	0.701	0.674	0.625	0.558	0.478	0.411	0.412	0.572
		Non-Linear	0.854	0.857	0.868	0.871	0.881	0.889	0.903	0.919	0.933	-	-	-

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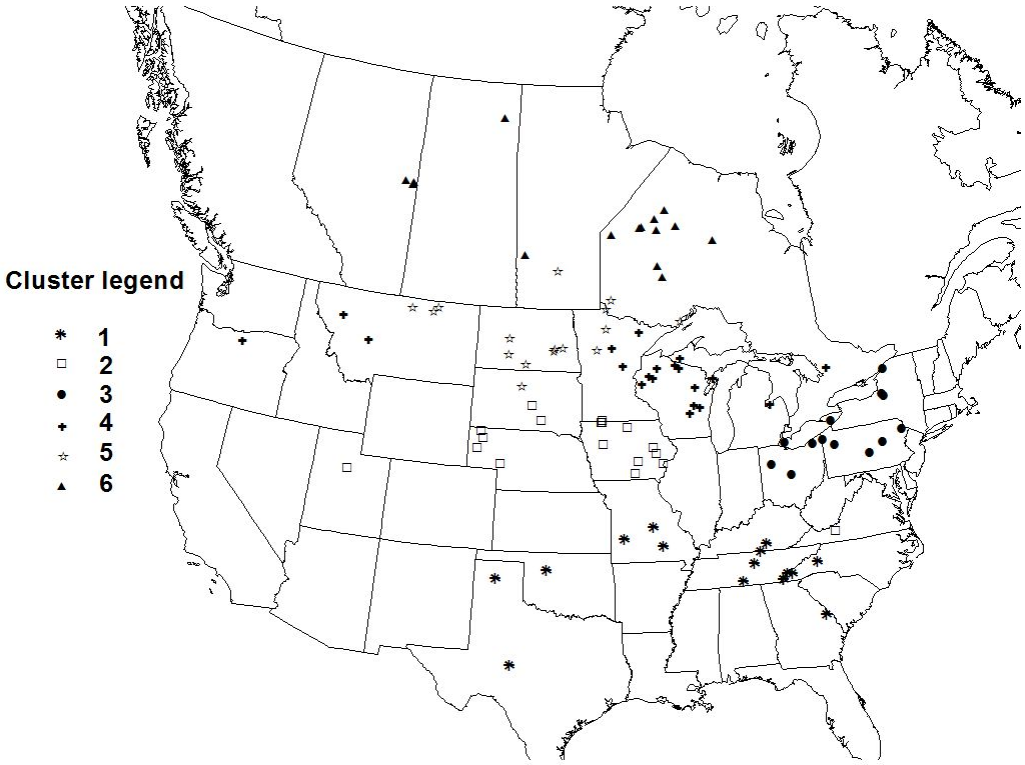

Figure 1. A map of the 99 walleye populations in North America and their six groups from cluster analysis (PAM) based on the climate conditions

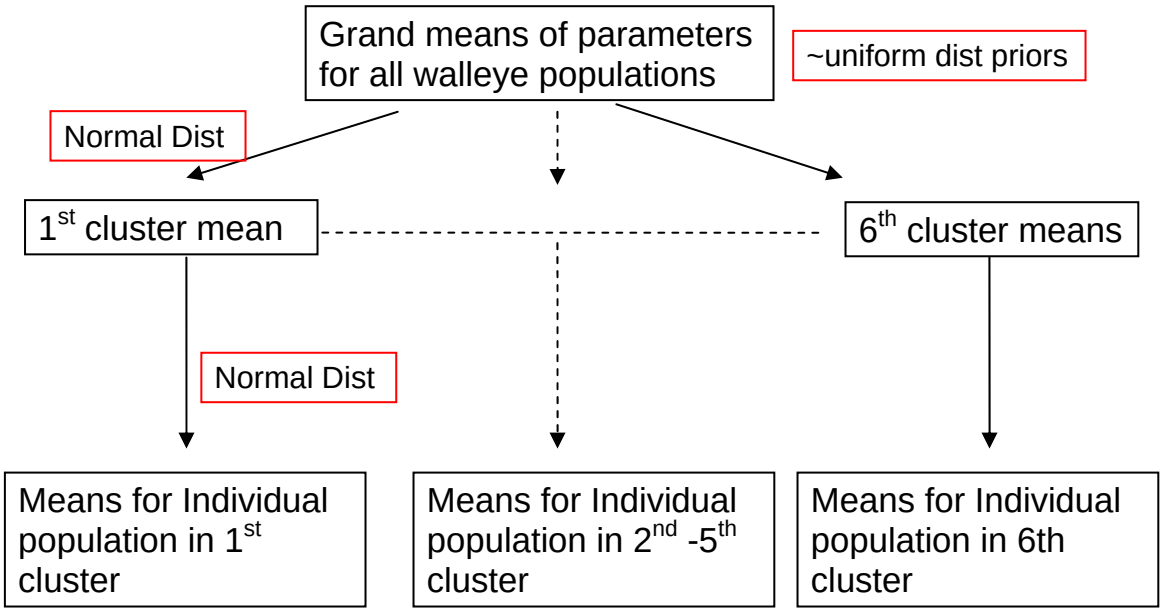

Figure 2. A hierarchical structure for Bayesian meta-analysis for 99 walleye populations in North America after clustering analysis based on their climate conditions

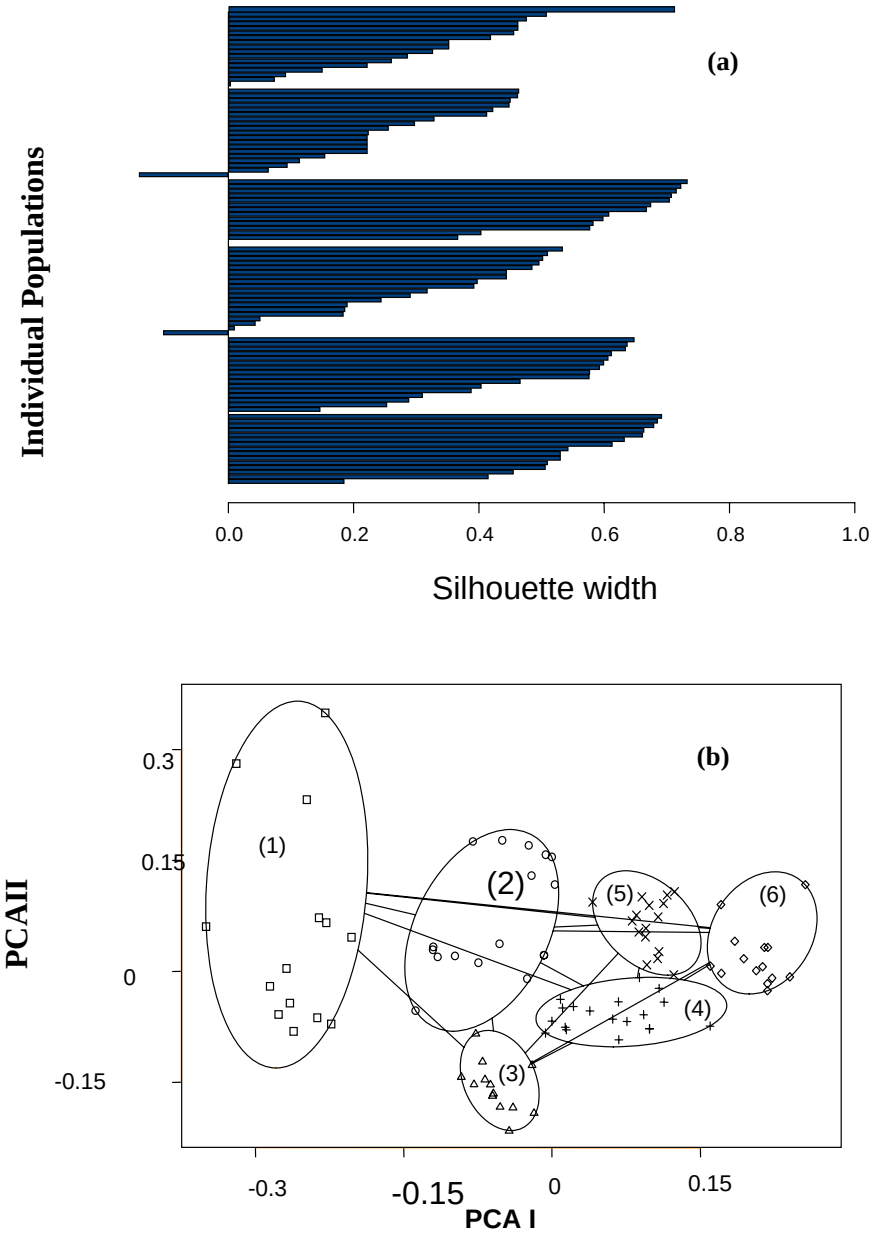

Figure 3. Silhouette (a) and Cluster (b) plots of six clusters of Partitioning Around Medoids (PAM) analysis on ninety nine walleye populations based their climate conditions.
Note: a value of -1 of silhouette width indicating the population is badly classified; a value of +1 indicating the population is well classified; a value of 0 indicating the population lies between two clusters

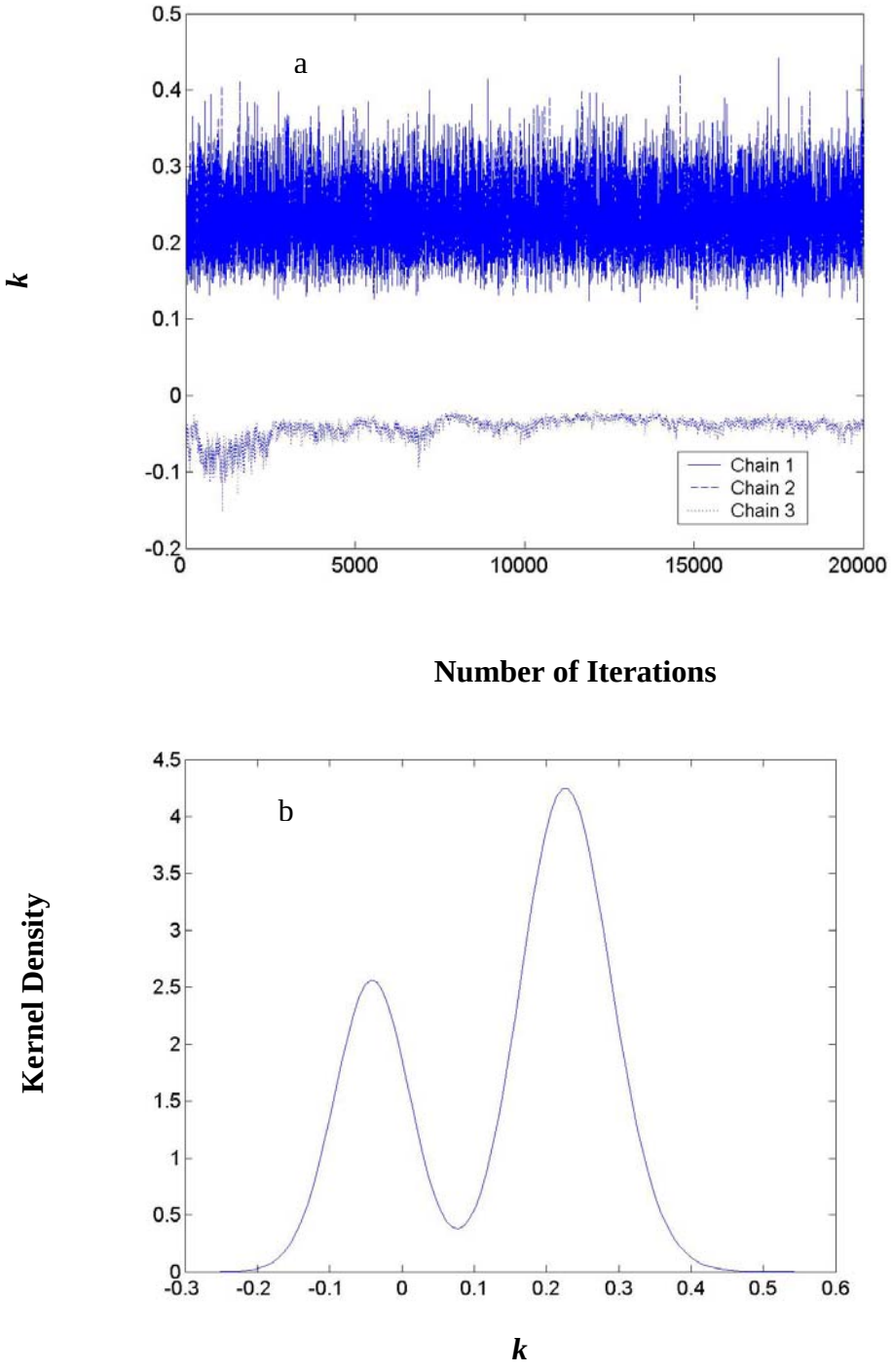

Figure 4. Trace (a) and density (b) plots the parameter *k* of von Bertalanffy growth model estimated by three parallel chains of Bayesian Hierarchical Model for the Population #67 in Table 1.
Note: parameters L_∞ and t_0 showing the same convergence properties

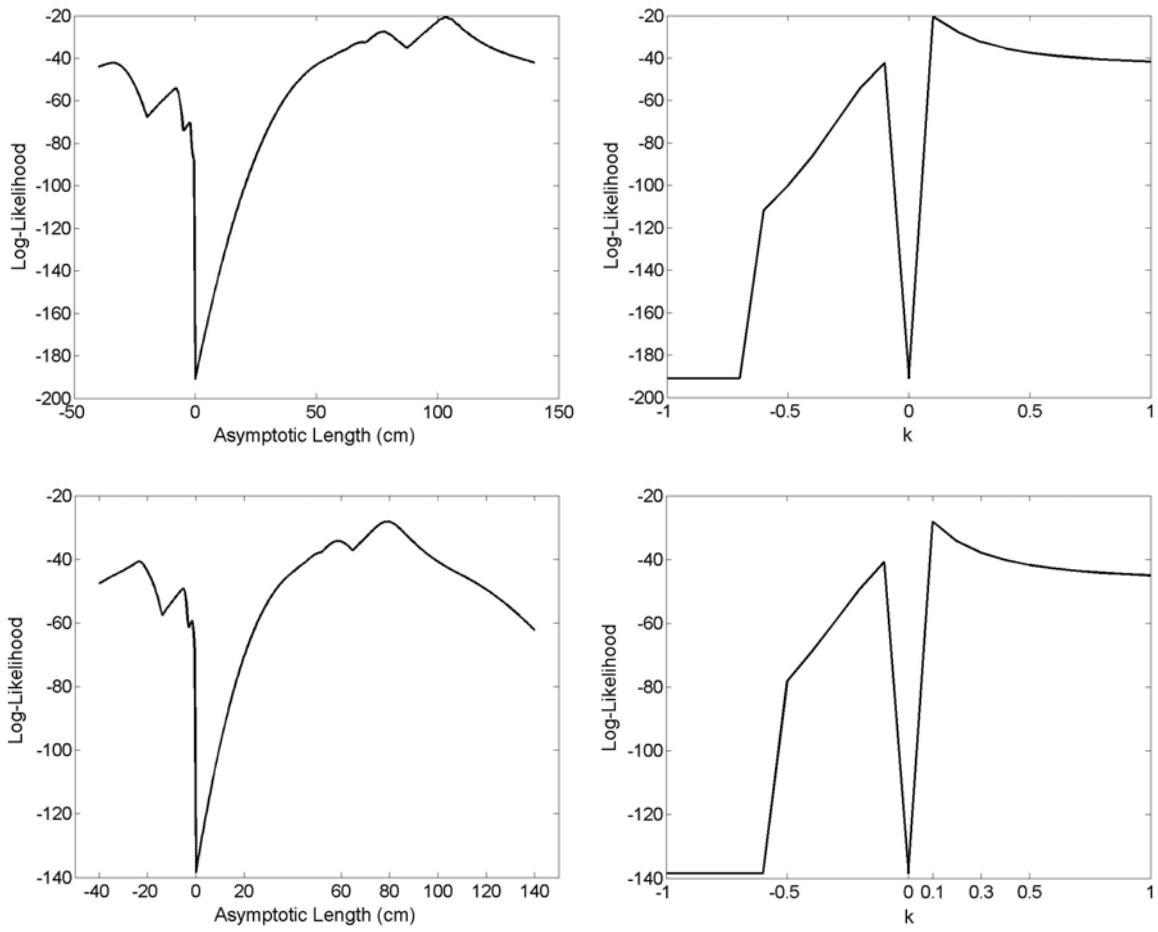

Figure 5. Profile log-likelihoods of asymptotic length (L_∞) and growth rate *k* for Population #15 (top panel) (non linear regression estimable) and Population #76 (bottom panel) (non linear regression unestimable) in Table 1

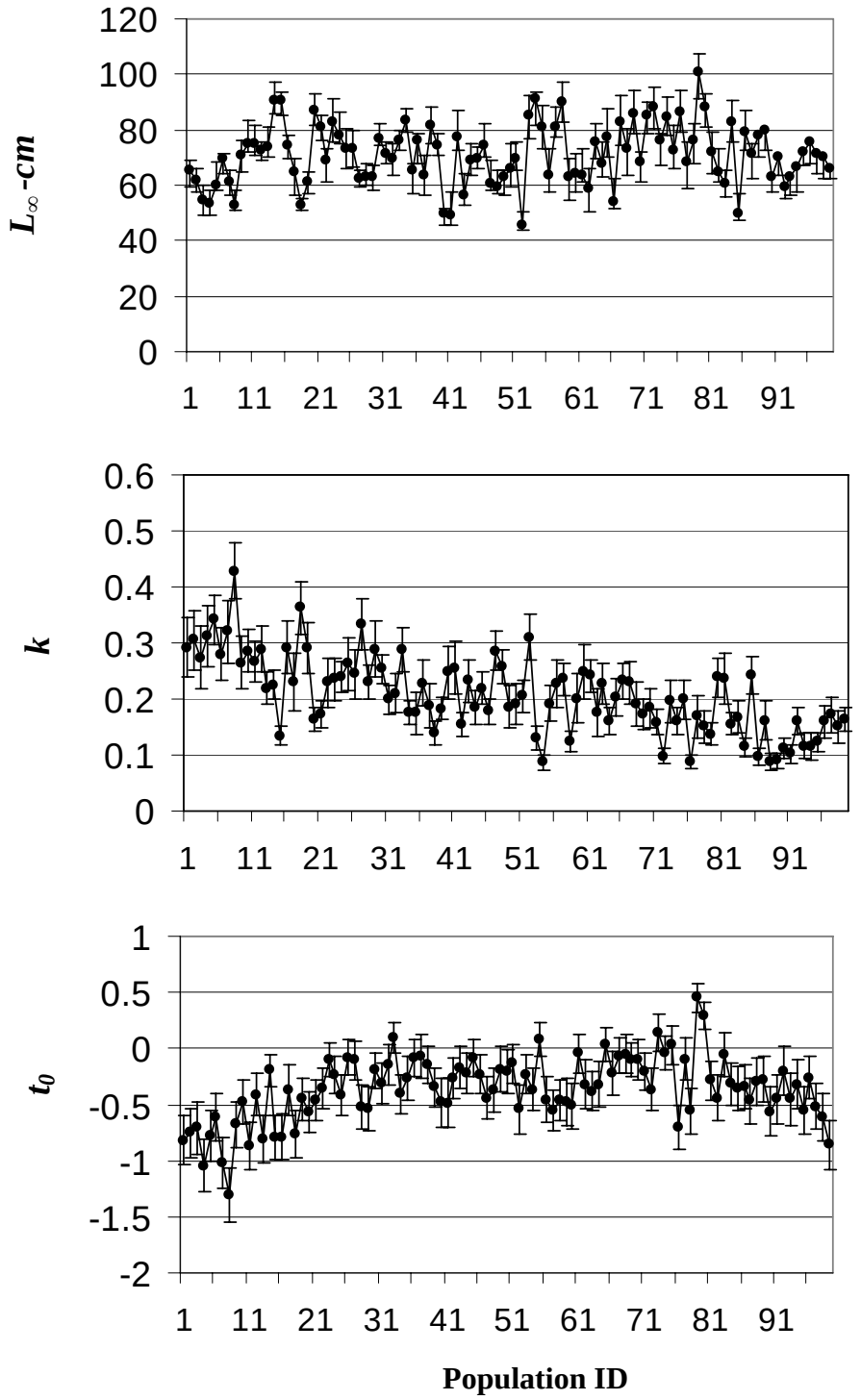

Figure 6. Means ±SD of asymptotic length (L_∞), growth rate (k) and (t_0) for ninety nine walleye populations from Bayesian hierarchical model
Note: populations ordered by the latitude from the smallest latitude value (population #1) to the largest latitude value (population #99) (see Table 1)

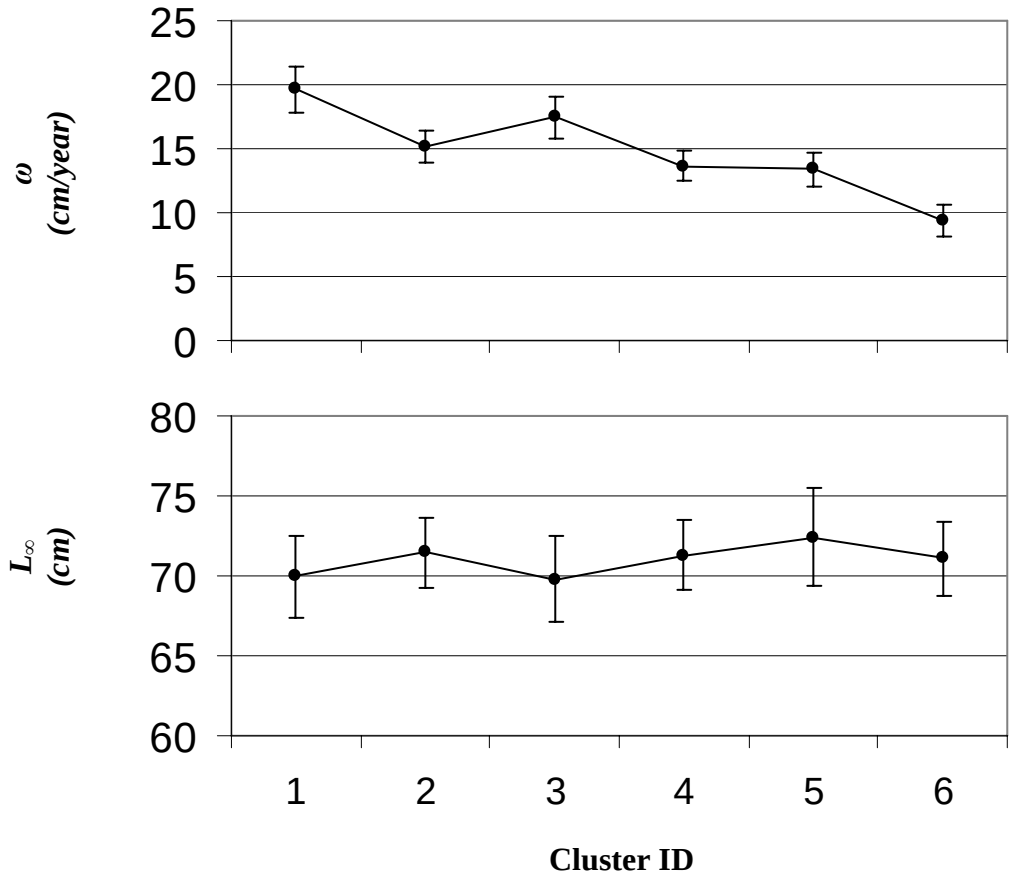

Figure 7. Mean±SD of walleye early growth rate (ω) and asymptotic length (L_∞) for six clusters

Part II. Ecology of walleye meta-population in Lake Erie

Introduction

The Great Lakes are considered the center of the distribution of walleye in North America (Regier et al 1969). Among the five Great Lakes, Lake Erie is the southernmost and shallowest one. Lake Erie consists of three distinct basins. They are the smallest and shallowest western basin, largest and flat-bottomed central basin, and the deepest eastern basin (Schertzer 1999). Lake Erie provides the largest walleye fishery (both sport and commercial) in the world. Regular commercial fishing of walleye was initiated as early as 1815 (Regier et al 1969), and walleye as a commercial fishery species became more important along with the progress of fishing activities, especially after blue pike (*Sander canadensis* formerly *Stizostedion vitreum glaucum* Hubbs), walleye's closest cousin, became extinct in the mid 1960s.

It is believed that there are several walleye sub-populations in Lake Erie, some sub-populations are lake spawners and some are river spawners. Among them, two lake spawning sub-populations and one river spawning sub-population are clearly identifiable. They inhabit different parts of the lake and the Grand River, carry different genetic information, and exhibit divergent life-history traits (Wolfert 1969, Chris Wilson pers. comms). They are the western basin sub-population, the eastern basin (Van Buren Bay) sub-population and Grand River sub-population. Walleye of the western basin sub-population spawn at the central or southern reef areas in the western basin, and the majority of fish above age 2 carry out an annual late-spring migration to the central and eastern basins (Wang 2003). The eastern basin sub-population spawns along the New York shore (mainly in Van Buren Bay, near Dunkirk,

New York) and the Grand River sub-population spawns in or near the Grand River on the northern shore of the eastern basin. In the eastern basin, the Van Buren Bay sub-population is believed to be one of dominant spawning populations (Don Einhouse, pers. comms.). The eastern basin walleye can migrate westward, but this movement is not nearly as strong as the movement from west to east (Wang 2003). This may be because the main water flow in the lake is from west to east and/or the supply of suitable habitat for walleye growth increases from late spring to fall in the central basin and the eastern basin, and decreases in the western basin.

In the central basin, the high frequency of hypoxia and anoxia in the hypolimnion of the basin during summer-fall seasons (Kling et al 2003) and its mud- and silt-dominant substrates (Minns and Bakelaar 1999) restrain the availability of spawning and nursery habitat suitable for walleye. Given no evidence of the existence of a sustainable sub-population in the central basin, it has been assumed that the summer and fall commercial and recreational catches of walleye in the central basin are a mixture of individuals migrating from the western basin and from the eastern basin, with most from the western basin. About 95% of the lakewide commercial catch of walleye is estimated to come from the western basin sub-population (MacLennan et al 2001).

The term *Metapopulation* was coined by Levins (1969, 1970) to describe ensembles of interacting populations of single species (Hanski 1991). The concept was extended to describe interacting populations composed of multiple species connected by the processes of predation and/or competition (Hanski and Taylor 1996). The concept was originally developed to model the processes of extinction and colonization of local populations. These local populations occupy spatially separated habitat areas and are connected to each other by

movements. The multiple definitions of source-sink metapopulation were made to serve different purposes and thus continue to cause confusion in the literature. For population genetics purposes, the concept describes effects of differences between emigration and immigration at equilibrium and thus emphasizes asymmetry in gene flow. For ecological purposes, the definition is based on the expected population growth rate at low density (i.e. no density-dependent effects). The sub-populations with a positive growth rate at low density are called “sources”, and the subpopulations with a negative growth rate at low density and in the absence of immigration are called “sinks”. Sinks would go extinct in the absence of immigration (Hanski and Simberloff 1997).

The above discussion of the metapopulation concept suggests that the definition of metapopulation implicitly emphasizes the importance of breeding contributions among those local populations. Here, I assume that movement of walleye between those sub-populations in Lake Erie is driven by a search for optimal growth habitat and not for reproductive habitat. Gene flow between sub-populations is assumed to be zero. In this part of my thesis, I focus on characterizing sub-populations of walleye in Lake Erie and their interactions. Two Chapters are devoted to this topic. The first chapter describes empirical studies on the demographic characteristics and habitat of the sub-populations. The second chapter describes a simulation study of some important characteristics of the Lake Erie walleye metapopulation and the potential impact of climate changes on those characteristics.

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Chapter 3. Demographic Parameters and Habitat of Walleye Sub-Populations in Lake Erie: Past, Present and Future

Abstract

In this chapter, the growth, survival and abundance for three walleye sub-populations in Lake Erie were explored and the suitable thermal and optical habitat for walleye was quantified based on observations in 1993 and 1998, and hypothetic scenarios derived from the changed climatic conditions. The growth of walleye during the first year of life was significantly different among three sub-populations, e.g. the western basin sub-population, Grand River sub-population and New York (or Van Buren Bay) sub-population. The western basin walleye had a lower first- and second-year growth rates than the eastern basin walleye. However, growth rates of the western basin walleye caught up with and overtook the New York walleye after the third growing season. Among the three sub-populations, the Grand River walleye generally grew the fastest. Sexual dimorphism was evident among the three sub-populations. Tagging studies showed that average annual survival rate of the Van Buren Bay sub-population during the period of 1990 to 2002 was about 69%, higher than the western basin walleye. The abundance of the Van Buren Bay spawning population is only about 0.1% of the abundance of the lakewide spawning population. The central basin had the most thermally-optically suitable habitat area for walleye, followed by the western basin and the eastern basin. The eastern basin had slightly more thermal-optical habitat volume than the western basin. Generally, the warmer and clearer water conditions in 1998 created more habitat for walleye in Lake Erie than in 1993. An increase in temperature and a decrease in water level from 1998 levels resulted in a decrease in thermal-optical habitat area in the

western basin but an increase in the thermal-optical habitat areas in the central and eastern basins.

Introduction

Walleye have been studied for about one and a half centuries in Lake Erie. The earliest commercial catch record can be traced back to as early as 1867 in Ontario, Canada (Baldwin et al 1979). However, data quality and quantity prevented accurate estimation of walleye abundance and mortality rates before 1970s (Regier et al 1969). Comprehensive walleye stock assessment work started in 1978 using walleye catch-at-age statistics (MacLennan et al 2001). Annual lakewide estimates of walleye abundance and mortality rate above age 2 from 1978 to 2001 are available (MacLennan et al 2001). New York researchers have sufficient data to carry out catch-at-age analysis and produced the abundance and mortality estimates for the eastern basin walleye from 1996 to 2002 (Don Einhouse, pers. comms). Recent tagging recapture studies of walleye spawning stocks in 28 sites in Lake Erie, originally designed for monitoring walleye basin-wide migration pattern, can potentially provide data to carry out abundance, recruitment and survival analysis for site specific walleye spawning populations (Wang 2003).

The earliest growth study on walleye in Lake Erie was carried out in the early 1920s, and the results were published by Adamstone (1922). This was followed by other growth and maturity studies by Deason (1933), Lawler (1948), and Wolfert (1969, 1977). By summarizing the previous studies and also combining new observations on walleye growth and maturity in Lake Erie, two papers published in the mid 1980s documented the significant density-dependent effects on walleye growth and maturity (Muth and Wolfert 1986, Hatch et al 1987). The potential effect of population density on walleye fecundity was documented by Muth and Ickes (1993).

The existence of discrete walleye sub-populations in Lake Erie was confirmed by

both tagging studies and studies on growth, maturity and fecundity done in the 1960s and 1970s (Wolfert 1963, 1969, 1977, Wolfert and Van Meter 1978). A recent tagging study showed that the main flow of migration is from the western basin to the eastern basin and that this migration starts in late spring (Wang 2003). The migratory populations are composed of walleye older than age 2 (Wang 2003). Demographic characteristics are also distinguishable between the western basin sub-population and the eastern basin sub-population from the tagging studies (Wang 2003). Microsatellite DNA analysis on the samples from nine lakewide spawning walleye sub-populations identified at least three genetically distinct groups of spawners, and they are the Grand River sub-population, New York (or Van Buren Bay) sub-population and the western basin sub-population (Chris Wilson, pers. comms..).

It is well accepted that some environmental factors, such as temperature, light condition and water currents can significantly influence walleye demographic parameters in Lake Erie (Busch et al 1975, Shuter and Koonce 1977, Madenjian 1991, Henderson and Nepszy 1994, Roseman et al 1996, Madenjian et al 1996, Kershner et al 1999). The optimal water temperature and light condition for walleye growth and survival were quantified by several researchers. Walleye older than age 1 prefer temperature from 18 degree Celsius to 22 degree Celsius (Hokanson 1977, Christie and Regier 1988) and dim light conditions (around 28 Lux) (Ryder 1977, Lester et al 2004). These factors are strongly influenced by climatic conditions. Furthermore, the impact of climate on fish species is evident at the individual level (e.g. growth and maturity), the population level (e.g. abundance) and species level (e.g. zoogeographic distributions) (Shuter and Post 1990, Minns and Moore 1992, Shuter 1990). Several researchers have applied General Circulation Models (GCMs) and

hydrodynamic models to assess the impacts of climate change on Lake Erie and concluded that the water surface temperature will increase. Annual precipitation is also expected to increase but most projections suggest that increased evaporation caused by warmer temperatures will override the increase in precipitation and cause lake levels to drop (Quinn and Croley 1999, Schertzer 1999, Lofgren et al 2002). Such changes will significantly modify walleye habitat in Lake Erie.

Minns and Bakelaar (1999) provided a detailed conceptual frame work for quantifying and mapping the suitable habitat for fish species in freshwater ecosystems. Given that the suitable walleye habitat (temperature and light conditions) can be clearly defined, it is possible to quantify availability of suitable walleye habitat based on current, observed and predicted future environmental conditions, and thus to assess the potential impacts of climate change on the supply of habitat suitable for walleye in Lake Erie.

In this chapter, I will use empirical data to examine growth in the three walleye sub-populations (i.e. New York coast, Grand River, and the western basin) and estimate abundance, survival and maturity of the New York sub-population. In addition, I will use 1993 (cool year) and 1998 (warm year, Brandt et al 2002) observed basin-specific water temperature, light condition and light-attenuation coefficients to assess the possible impacts of various climate-change scenarios on the basin-specific supply of suitable habitat for walleye in Lake Erie.

Materials and Methods

Growth Study of Walleye from the Eastern and Western Basins of Lake Erie.

Sources of Walleye Samples:

The 1264 individual walleye used in the growth study were from three locations: the

Canadian side of the western basin, Van Buren Bay of New York waters on the southern side of the eastern basin, and the lower reaches (below the Dunville dam) of the Grand River flowing into the northern side of the eastern basin. The 603 fish from the western basin were from summer or fall commercial fisheries samples; 313 walleye from New York waters were a mixture of spring samples (from a tagging study) and summer and fall survey samples; and 348 walleye from the Grand River were obtained from the spring survey sampling. Walleye samples from the western basin commercial fisheries in Canadian side were likely a mixture of river stocks and reef stocks because there is no spawning populations found in northern western basin of lake Erie in spring.

Scale collection and measurement

Walleye scales were collected by three groups of people: New York summer/fall samples were obtained from gillnet survey and spring samples from trap net or boat shockers within or adjacent to the Van Buren Bay. The scales were removed from just posterior to the pectoral fin and below the lateral line of the left side of the fish. For the Grand River samples, the scales were collected from the area below the lateral line and laterally between the insertion of pectoral fin and the leading edge of the dorsal fin on left side of the fish captured by the trammel nets or boat shockers in spring in the lower Grand River. The western basin samples were from commercial fisheries in management area of Unit 1 (OE1 in Lake Erie Fisheries Report 2001) and all the scales were from the left side of fish, below the lateral line and immediately posterior to the pectoral fin. Scales were cleaned and impressed on acetate slides. A microprojector at a magnification 40X was used to read the number of annuli (ages) and measure the distance from each annulus or edge of scale to the focus along with the anterior-posterior axis of the scale, and the results were recorded on a strip of plastic

transparency paper. These distances were then digitized using a Visual Basic program developed to drive a SummerSketch III professional digitizer. Each fish was aged by two persons (one of them are from our lab) using either otoliths (New York's summer/fall samples) or the sampled scales. Only the scales with consistent ages from all persons and relatively clear images for each annulus were used for the back-calculation study.

Establishing the walleye body scale relationship

In order to estimate the growth histories of individual fish by back-calculating body size from scale measurements, it was necessary to estimate the relationship between walleye body size and walleye scale size, based on a sample of fish that covers a wide range in body size. In this study, a sample from each of the three different locations was chosen to determine if back-calculations of growth should be carried out using sub-populations-specific body-scale relationship, or if a single relationship would suffice. A total of 235 walleye from age 0 to age 9 from the western basin, 173 walleye from age 2 to age 18 from New York waters, and 153 walleye from age 0 to age 14 from the Grand River were chosen to establish body-scale relationships. All of those fish, except for age 0 fish and some of age 1 fish, were also used in the growth back-calculation work.

The fish fork length was used to characterize growth in this study. Because only total lengths were available for the New York fish, a conversion formula (*Fork Length(mm) = 0.9552* Total length (mm) - 6.8507*, R^2=0.998, P-value<<0.001) derived from 11223 fish collected from both the western basin and the Grand River, was used to estimate their fork length. Only fork length and scale size at capture were used to estimate the body-scale relationship for each basin.

Back-calculation procedure and estimation of von Bertalanffy growth parameters

Like most fish species, walleye body growth and scale growth do not follow the geometric similarity rule (Klumb et al 1999). Hence, a logarithmic transform of body and scale size was used in the study. The scale proportional hypothesis was adopted in this study for the back calculation procedure. This hypothesis states: for each fish, the ratio of the scale radius at one age to the radius at the other age is a simple function of the lengths of the fish at these two ages. This function, either in linear or non-linear form of lengths, describes the mean relationship between fish body size and scale size (Hile and Jobes 1942, Francis 1990). Preliminary analysis of the body-scale data revealed that the logarithm of scale of Lake Erie walleye could be described by a simple second-order polynomial of logarithm of walleye fork length. The procedure that is used to back-calculate body size from scale size using this kind of relationship is outlined below:

Given the following empirical relationship between scale radius (*SL*) and for length (*FL*),

$$log(SL)=a*(log(FL))^2+b*log(FL)+c \qquad (1)$$

the following manipulations show that the scale relationship assumption holds and back-calculation procedures are justified (where *SLn*—the scale radius at annulus *n*, *FLn*—the fork length at the annulus *n*):

$$log(SL)-log(SLn) = (a*(log(FL))^2+b*log(FL)+c)-(a*(log(FLn)^2+b*log(FLn)+c) \quad (2)$$

$$log(SL/SLn)=log\{exp[a*(log(FL))^2+b*log(FL)+c]/exp[a*(log(FLn))^2+b*log(FLn)+c]\}$$

$$SL/SLn= [FL^{a*log(FL)}/ FLn^{a*log(FLn)}]*(FL/FLn)^b$$

$$SL/SLn= FL^{(a*log(FL)+b)}/ FLn^{(a*log(FLn)+b)} \qquad \text{(assuming scale relationship)}$$

From equation (2) above, the logarithm of the fork length (*FLn*) at annulus *n* was determined by solving the following quadratic equation and taking the anti-log of the positive solution,

$a*(log(FLn^2+b*log(FLn)+d = 0$,

where $d = [\log(SL)-\log(SLn)]-[a*(\log(FL))^2+b*\log(FL)]$.

After the fork length at each age for each individual walleye was estimated using this procedure, the gender identifiable samples from each sub-population were used to estimate basin- and gender-specific von Bertalanffy growth parameters. A Newton-Gaussian non-linear regression algorithm was adopted to carry out parameter estimation for the von Bertalanffy growth model.

Temperature data and the young-of-year abundance data from other studies used for analyzing walleye growth pattern

The following basin-specific water temperature data were used: daily mean drinking-water intake temperature from Leamington, Ontario for the western basin sub-population, water intake temperature in Port Dover, Ontario for the Grand River sub-population and Van Buren Bay, New York water-intake temperature for New York sub-population. Several temperature indices were calculated: mean temperature above 4 degree Celsius, degree days above 4 degree Celsius, mean temperature between 4 and 22 degree Celsius and degree days between 4 and 22 degree Celsius. Those indices were used to characterize the basin-specific thermal regimes and to examine the relationship between water temperature and growth patterns for each walleye sub-population.

Walleye young-of-year abundance indices for the western basin sub-population and New York sub-population were from the interagency trawling survey in the Ontario waters of the western basin and the New York annual autumn gill netting survey, respectively (OMNR 2001, Culligan et al 2001). The log-transformed abundance index values were used to examine density dependent effects on walleye early growth for the two sub-populations.

Statistical procedures used to process the data

The walleye lengths at the different ages were averaged by cohort for each sub-

population. A two-way ANOVA with the Tukey post-hoc pairwise comparison procedure was used to test for the existence of significant differences among sub-populations and cohorts of each sub-population. A simple linear regression approach was used to test for the presence of the relationships between growth and temperature or abundance. The statistical significance level (α) was set as 0.05.

Abundance, Survival and Maturity of Walleye in New York Waters of Lake Erie from Mark Recapture Analysis

From 1990 to 2004, 16947 walleyes were tagged with Monel butt-end jaw tags and released during spring (April to May) in 7 sites in the New York waters of Lake Erie (Table 1). During the period of 1990-1993, two different sizes of tags were applied to the different sizes of the fish. The captured walleye with total length less than 580 mm received size 10 tags (i.e. the small tags) and others received size 12 tags (i.e. the large tags). After 1993, the walleye were all tagged by size 12 tags. The relative long and continuous time series of data necessary for implementing the Cormack-Jolly-Seber (CJS) method of abundance and survival estimation were only available for two sites, Lackawanna Shoreline (site 51) and Van Buren Bay (site 53). There was no tagging study in site 51 from 1996 to 1999. No more than two years of data were available from sites other than sites 51 and 53. About 18.4 % and 68.2% of these tagged walleyes were from the site 51 and site 53, respectively. Adult male walleye comprised about 90% of the total tagged fish. Nearly all walleye tagged were mature (i.e. at least age 3, Einhouse and Haas 1995) and exceeded 328 mm in fork length. Four gear types (i.e. gill net, trap net, boat electro-fishing and Fyke net) were used in the study. About 99 percent of tagged walleye were caught either by trap net or boat electro-fishing. Gill nets were only sporadically used in Van Buren Bay in 1990 and 1991, and some Fyke nets were

used on the Lackawanna Shoreline in 1992. In Van Buren bay, about 80% of walleye were tagged and recaptured by trap net. For the Lackawanna Shoreline, however, almost all tags were placed and recovered by boat electro-fishing. A total of 1234 tagged individuals were recaptured at least once from 1990 to 2004. A total of 1451 tagged walleye were caught in the fishery, among which 400 tagged fish were killed by the fishery in the same year when they were tagged.

Based on this tag and recapture database, individual encounter histories were constructed for each recaptured and fishery encountered walleye, and the time dependent Cormack-Jolly-Seber (CJS) model was used to estimate the survival rate and recapture rate for each of the two sites, i.e. the Lackawanna Shoreline (site 51) and Van Buren's Bay (site 53). The time dependent CJS model assumes (1) every marked animal present in the population at time *i* has the same probability of recapture; (2) every marked animal in the population at time *i* has the same probability of surviving to time *i+1*; (3) marks are not lost or missed; (4) all samples are instantaneous, relative to the interval between time *i* and time *i+1*, and (5) each release is made immediately after the sample. To test if assumptions (1) and (2) are satisfied, Chi-Square Goodness of fit (Test 2 and Test 3 in the RELEASE segment of the software MARK, Cooch and White 2001) tests were carried out after estimation of parameters. Both tests are based on contingency tables that test the null hypothesis: the probability that an animal marked in a specific tagging occasion can be recaptured in a later tagging occasion and in which later tagging occasion does not depend on whether or not it is recaptured on this tagging occasion or on an earlier occasion. Therefore, both tests start from the second occasion of the mark recapture experiment (for more details refer to Cooch and White 2001).

Preliminary analysis showed that the recapture rates within each site are not significantly different. In order to reduce the number of parameters to be estimated, one recapture rate for each site was used in the CJS model. In fact, the recapture rates for two sites reflect the catchability of electro-fishing (site 51) and trap netting (site 53). The abundance and recruitment was estimated by the Jolly-Seber model (Pollock et al 1990). Because the tagged walleye were adults at the spawning grounds, the estimated recruitment is the number of the fish reaching sexual maturity (i.e. around age 3). Due to tag loss (22% Don Einhouse, pers. comms.) of small size tags (i.e. size 10 tags) during the first three years of the experiment, the survival, abundance and recruitment estimates were adjusted by the tag loss rate (Pollock et al 1990).

To illustrate the movement of walleye after being tagged in spring, the eastern basin was arbitrarily divided into four areas (Fig 1). Each fisheries recapture was located in each area and the movement pattern was identified by tracing it back to its original tagging site.

The Thermal and Optical Habitat Supplies for Juvenile and Adult Walleye Growth in three basins of Lake Erie

When walleye grow above 65 mm, they begin to exhibit two prominent characteristics of adult walleye: they prefer dim light feeding conditions and their optimum growth temperature is in the range 18 to 22 degree Celsius. These light and temperature preferences were used to quantify available habitat for walleye growth from both observed and projected environmental conditions in the three basins of Lake Erie. The habitat quantified here is suitable for walleye growth. A wider range of environmental conditions are sufficient to permit walleye survival.

Habitat Suitability Models

A habitat suitability index value, ranging from 0 to 1, was assigned to each area of the

lake, based on the thermal and optical conditions in the area. If the conditions in the area were not suitable for walleye survival and growth, then it was assigned an index value of 0; if the conditions were optimal, then a value of 1 was assigned. In the thermal habitat suitability model, the habitat suitability index is zero for temperatures below 13 degree Celsius or above 27 degree Celsius (Smith and Koenst, 1975, Colby et al 1979); and it increases linearly from 0 to 1 as temperatures increase from 13 to 18 degree Celsius; and it remains at 1 for temperatures in the range of 18 to 22 degree Celsius and then decreases linearly to zero as temperatures increases from 22 to 29 degree Celsius (Fig 2 a). The optical suitability index was defined over the range of light intensity from 0 to 200 Lux. The maximum value for the index (i.e. suitability index of 1) was assigned to the light intensity of 28 Lux , a value of 0.5 was assigned to 8 and 68 Lux, respectively and a value of 0.1 for 125 Lux (Fig 2 b). A suitability value of 0 was assigned when temperature and/or light conditions were outside of the ranges listed above (Ryder 1977; Lester et al 2004a)

Data Acquisition

Water temperature profiles and light extinction coefficients were obtained from the Lake Erie Biomonitoring (LEB) program (refer to Dahl et al 1995 for details). In the program, eight stations were sampled in 1993, among which three stations were selected as representative of the three basins for both 1993 and 1998 (Fig 3). The water temperature profiles and light extinction coefficients at these three stations were measured biweekly from early May to late October in each year. Solar radiation (PAR) measured at the Canada Centre for Inland Waters (CCIW) in Burlington in 1998 was used as surface light intensity across all three basins for the 1998 study. In 1993, solar radiation observations at the Cedar Springs Agroclimatology monitoring station (OMAF, Ridgetown) were used for the Western and

Central basins and observations at CCIW were used for the Eastern basin. Lake morphometry data were obtained from Great Lakes Environmental Research Laboratory (GLERL). The time series of light attenuation coefficients and Secchi depth were from the LEB program (Dahl et al 1995, MacDougall et al 2001).

Climate-Change Scenarios

I simulated five scenarios of climate change by (1) increasing average water temperature by 2 degrees Celsius; (2) decreasing water levels by 1 meter; (3) decreasing water levels by 2 meters; (4) combining (1) and (2); (5) combining (1) and (3). The 1998's observations were chosen as the baseline values of those scenarios. The climate-change induced effect on water temperature (i.e. an increase by 2 degree Celsius) used here simulate an extreme scenario. It is recognized that the different segments of the water column (e.g. epilimnion and hypolimnion) will differ in their responses to climate change.

Calculation of Thermal and Optical Habitat Areas or Volumes

Firstly, I represented each basin as a series of vertical layers, each 1 meter deep, based on the basin's morphometry. Secondly, for each hour of each day from May 1 to October 31, I estimated the light and temperature for each layer in each basin. Missing values were filled in using linear interpolation. Thirdly, based on the light or temperature conditions and suitability models, a suitability index was assigned to each layer for each time interval (1 hour). Finally, the area of the lake's bottom or volume was multiplied by its corresponding suitability index to obtain weighted thermal or optical suitable areas or volumes for walleye in each hour of each day from May 1 to October 31. I then summed all the weighted areas or volumes over the entire time interval (from May 1 to October 31) to obtain total basin specific thermally or optically suitable habitat areas and volumes for walleye. The product of

the two suitability indices (thermal and optical) for each layer was used to calculate the weighted thermally and optically suitable habitat area or volume for the layer. This procedure was carried out for the 1993 observed data, the 1998 observed data, and for the simulated data derived under the climate change scenarios described earlier.

Results

Differences in Growth among Eastern and Western Basin Sub-populations

A total of 1264 walleye scale samples covers 14 cohorts (from 1988-2001), 13 cohorts (from 1982-2001) and 20 cohorts (from 1982-2001) for the Grand River sub-population, the New York sub-population and the western basin sub-population, respectively (Table 2). Among them, the minimum age is one year old and maximum age is 18 years old. There are 63 (42 females and 21 males), 239 (44 females and 195 males), and 277 (150 females and 127 males) sex-identifiable samples in the samples of the western basin subpopulation, New York sub-population and Grand River subpopulation, respectively.

Body-scale relationships for the three sub-populations were derived by second-order polynomial regression and are as follows (Fig 4):

The western basin: $Y=-0.4713*X^2+6.6583*X-16.71$ $R^2=0.95$, sample size n= 199

New York: $Y=-0.4695*X^2+6.6083*X-16.973$ $R^2=0.96$, sample size n= 145

Grand River: $Y=-0.3091*X^2+4.6062*X-10.773$ $R^2=0.98$, sample size n= 242

where X is natural logarithm of fork length and Y is natural logarithm of scale radius from the focus to the edge.

ANOVA analysis showed that the source of walleye samples, i.e. sub-populations, significantly influenced walleye first-year growth ($F_{2,25}$=11.77, P_value<0.01). Tukey pairwise comparisons among the sub-populations indicated that there was no significant

difference between New York (mean=192.3mm) and Grand River (mean=192.0mm) sub-populations but they both were larger than the western basin (mean=173.5mm) sub-population in the first year length (Table 3). The Tukey pairwise comparisons of the estimates of first four years mean increment for the three sub-populations showed that the western basin sub-population had the smallest length increment during the first two growing seasons and then caught up with and overtook the New York population after the third growing season (Fig 5, Table 3). Among the three sub-populations, the Grand River sub-population generally grew the fastest after age 2.

Mean temperature and degree days above 4 degree Celsius are both highest in the western basin. The effective degree days, i.e. degree days between 4 and 22 degree Celsius, however, were substantially lower in the western basin. There were more days with temperatures greater than 22 degree Celsius (the upper limit of walleye optimum growth temperature range) in the western basin (Table 4). Within each sub-population, simple linear regression analyses showed that there was no significant effect of temperature (i.e. mean degree days between 4 and 22 degree Celsius) on the first-year growth ($F_{1,10}$ =0.85, P=0.38 for Grand River sub-population, $F_{1,18}$ =0.75, P-value=0.75 for the western basin sub-population and $F_{1,11}$=0.40, P-value=0.54 for New York sub-population) or first two years growth ($F_{1,25}$=0.19, P-value=0.67 for the western basin sub-population and $F_{1,6}$=0.05, P-value=0.83 for the New York sub-population) except for the first two years growth for Grand River sub-population ($F_{1,9}$=5.9, P-value=0.038) (Fig 6). There was no significant density dependent effect on the first-year growth on the western basin and New York sub-populations ($F_{1,13}$=0.53, P-value=0.48 for the western basin sub-population and $F_{1,11}$=0.50, P-value=0.49 for New York sub-population).

Sexual dimorphism was evident for all three sub-populations with faster growth for females after age 2 for the western basin and New York sub-populations and after age 3 for the Grand River sub-population (Fig 7). The von Bertalanffy growth parameters showed that males have a smaller asymptotic length than females. The female walleye in the western basin have a smaller asymptotic length (L_∞) but a large growth parameter (k) compared to their two eastern basin counterparts (Table 5).

Abundance and Survival of the New York Sub-population

More than 83% of walleye recaptured at each site were tagged at the same site except for site 59 (Table 6). This implies that walleye showed a strong fidelity to their spawning sites. For walleye tagged at site 56, the lower recapture rate (about 35% or 10 out of 28) in the same tagging site than that in site 53 (57% or 16 out of 28) suggests that site 56 and 53 may constitute the same spawning sites or spawners from two sites are easily exchangeable, but there is a strong tendency of flow from site 56 to 53 and hence site 53 could be the main spawning area for those walleye (Table 6).

During the fishing season, walleye tagged in southern sites tend to be recaptured in the original tagging sites or the areas northeast of the original tagging sites (Table 7). This implies that, after spawning, the main flow of male walleye migration is to the northeast. This movement may reflect drift pattern by water currents or preference for cooler environment in the north part of the lake.

For the abundance and survival analyses based on the Cormark-Jelly-Seber model, the data from Site 51 generally passed most of the contingency tests (i.e. Test 2 and Test 3 and combined test). This suggests that model assumptions that survival rate and recapture rate both are independent of the tagging occasions were satisfied (Table 8). The data from

Site 53 passed Test 2 and Test 3M but failed Test 3R. This failure was caused by tests on the last two occasions, i.e. SR13 (2002) and SR14 (2003). The latter failure was obviously due to insufficient data (Table 9). The failure of SR13 seems to be caused by data sparseness because occasion 13 is very close to the end of the experiment—a large number of newly marked animals were released on occasion 13 but there has, as yet, been little opportunity to recapture them. If the Chi-square values and degrees of freedom for SR13 and SR14 are removed from the overall test, then the test Chi-square for SR is 5.93 with df=11 and P-value=0.8779, and for combined Test 2 and Test 3, Chi-square is 87.46 with df=77 and p-value=0.1947, which passed the CJS model assumption tests. Therefore, generally, the first two important assumptions for the CJS model were supported by both sites. The results should be reliable.

Because of tag loss during the first three years (1990-1992), the survival and abundance reported here were adjusted by the tag loss rate (22%). The mean survival rate during 1990 to 2002 of male walleye spawners was 49.8% and 69.3% for site 51 (excluding 1996 to 1999) and site 53, respectively (Fig 8a b). The recapture rate in site 51 (estimated as 23.5%) was higher than that (estimated as 7.87%) in site 53, which suggests that the electro-fishing gear used in site 51 was more efficient than the trap net mostly used in the study for site 53.

Mean abundances during the period of 1991 to 2002 of male walleye spawners were 1514 for site 51 (excluding 1996 to 1999) and 10897 for site 53 (Fig 9a, b). Mean recruitments to mature male walleye populations during the period of 1992 to 2001 were 573 for site 51 and 5280 for site 53 (Fig 10 a, b). The spawning population and recruitment are both larger in site 53 than site 51.

From the length distribution of the tagging data, the minimum lengths of mature female and male walleye are 427 mm and 328 mm, respectively. Given these lengths and the age-specific growth curves derived from the back-calculation study, the age at the first maturity for New York female and male walleye were estimated at 3.49 and 2.24 years, respectively. These estimates are similar to the age at maturity at which sexual dimorphism becomes evident in the sex-specific growth curves for the New York sub-population.

Supply of Suitable Habitat for Walleye Growth in the East, Central and West Basins of Lake Erie.

The data from 1993 and 1998 both showed that there were trends toward increasing temperature and decreasing water clarity from the eastern basin to central basin to the western basin (Table 10). Each basin was warmer and clearer in 1998 than in 1993. The central basin has the most walleye adult habitat from May to November for both years. The western basin had more suitable habitat areas than the eastern basin except for optical habitat area in 1993. For thermal-optical habitat area (TOHA), the western basin had nearly 9 times as much as the eastern basin. Although the optical or thermal habitat volume in the eastern basin was much higher than that in the western basin, the thermal-optical habitat volume (TOHV) was similar for the two basins. Generally, the warmer and clearer water conditions in 1998 created more habitat for adult walleye in the three basins with the exception of optical habitat area in the eastern basin and optical habitat volume in both the eastern and western basins. This suggests that increases in water clarity in the eastern basin resulted in a decrease in the supply of optically suitable habitat. The greatest within-year variation in the hourly average suitable habitat area and volume were observed in the central basin (Fig 11, Fig 12, Fig 13). In the eastern and central basins, there was no suitable thermal habitat area for walleye until June in 1993 (Fig 11, Fig 12, Fig 13).

An increase in water temperature by 2 degree Celsius above the 1998 level resulted in greater walleye habitat in the eastern and central basins but a decrease in thermal habitat and little or no change in thermal-optical habitat in the western basin (scenario 1, Table 11). The decrease in lake water level reduced all measures of habitat supply for all three basins (Scenario 2 &3, Table 11), with the greatest effect in the western basin. Thermal habitat also decreased in the central and western basins, particularly habitat volume. Thermal habitat area, however, increased in the eastern basin, whereas the thermal-optical habitat decreased in the central and western basin, with the strongest effect on habitat volume for the western basin. Smaller changes were estimated for the eastern basin with the habitat area increasing and volume decreasing moderately. When lower water levels were combined with high temperatures (Scenario 4 and 5, Table 11), the habitat both in area and volume was substantially increased, but the western basin showed sharp declines in all metrics. For the central basin, thermal-optical habitat area increased, but volume decreased.

Discussion

Differences in Growth and Maturity among Walleye Sub-populations

The walleye growth pattern in Lake Erie is influenced by many factors, such as water temperature, prey species and abundance, and walleye density. Recent tagging and bioenergetic modeling studies on walleye growth in Lake Erie demonstrated that the migration pattern also significantly influences walleye growth (Kershner et al 1999). Walleye seem to be able to migrate across basins to locate optimum habitat (i.e preferred temperatures or forage species) and thus maximize their growth potentials.

The varieties of environmental conditions in the three basins of Lake Erie provide different habitats for different life stage of walleye. For example, the shallow and warm

western basin with its reef-like substrate provides ideal spawning habitat during spring. During summer and fall, however, the overheated western basin provides the least amount of thermally suitable habitat for walleye growth, and thus the growth of the fish that continue to live in these energy-costly conditions could be reduced. This hypothesis was supported by this study. For example, the walleye in the western basin do not initiate their basin-wide migration until the end of their second year of life (Wang 2003) perhaps because their ability to swim long distances is likely reduced at small sizes, or young walleye have evolved to reduce the predation mortality likely caused by basin-crossing migration. Thus, young western basin walleye are constrained to live in unfavourable conditions during their first two growth seasons. This is a possible explanation for the lower growth rate observed among the western basin walleye during their first two years of life, as compared to their eastern basin cousins.

As soon as the western basin walleye acquire their basin-crossing migration ability, they are able to select the warm springs of the western basin and the cooler summers and falls of the central basin and the eastern basin. In addition, some favourite walleye forage species (i.e. soft-rayed fishes such as shiners and smelt) also seek cooler water conditions and some of those species may also have eastward migration pattern (Wang 2003) and be abundant in the central and eastern basin during summer and fall. Thus, the migrating walleye may be able to find more abundant food supplies as well. These improvements in thermal conditions and foraging opportunities could explain the observed increase in the western basin walleye growth rates after age 2. Among three sub-populations, the Grand River walleye consistently had the highest growth rate from age 1 to age 4 (Fig 5, Table 3). This may result from the river-lake migration of Grand River walleye. In spring, walleye

spawn in the Grand River and the water temperature in the river increases earlier and faster than in the lake. Thus walleye in the Grand River grow in warm temperature conditions in the spring. In late spring and early summer, the Grand River walleye start to move down the river to the lake and spend the entire summer and fall in the cooler and food-abundant lake environments (Phil Ryan pers. comms.). This river-lake migration may play an important role in shaping the growth pattern of the Grand River walleye.

If the basin-specific differences in early life growth pattern observed in this study reflect basin-specific differences in the thermal environment, why was inter-annual variation in growth within a basin unrelated to inter-annual variation in thermal conditions within a basin? Within each basin, the thermal effects may be difficult to detect because of relatively narrow range in thermal conditions observed.

It is also noticed that there are discrepancies between this study and Wang (2004)'s study of differences of walleye early growth rates for different walleye sub-populations. Wang (2004) reported that walleye in the western basin have greatest growth rates at age 1-2. Several reasons could underlie this contradiction between the two studies. Wang (2004)'s measurements were obtained from the samples of the fall gillnet survey. The fish aged as one year old should be one and half year old at least (i.e. these fish had almost completed their second growing season at the time of capture). Similarly, the fish in other age classes should be at least half year older than the age assigned to them. Therefore, the growth apparently did not reflect the results from a whole growing season. The seasonal variations in walleye growth can complicate the comparison of walleye sampled during the middle of a growing season. The gillnet selectivity also has the potential to influence the growth results. In addition, the growth increments were derived from the mean size of the fish sampled in each

year, the sample sizes and year variations can distort the comparison between the sub-populations. Given all these differences between the two data sets used in these two studies, it is difficult to draw definitive conclusions from a comparison of their results.

Failure to detect density-dependent effects on walleye first-year growth in the western basin walleye could be the result of limitation inherent in the available data. The walleye young-of-year abundance index used to assess the density dependent effects on early growth of walleye of the western basin sub-population in this study were collected largely from the northern side of the western basin (OMNR 2001); however, most of walleye spawning and nursery sites are on southern coast of the western basin (Regier et al 1979, Roseman et al 1996). For the New York sub-population, the majority of cohorts used to back calculate growth are from 1982 to 1987. The lack of density dependency on the walleye first-year growth in this data set suggests that abundance of young walleye in New York during this period (i.e. the 1980s) might be well below its carrying capacity.

Sexual dimorphism in walleye growth has been observed in walleye populations in other lakes (La Rose 2004). The hypothesis that the start of bifurcation in walleye sex-specific growth pattern corresponds to sexual maturity was supported by data from the New York sub-population in this study and by data from the lakewide tagging study (Wang 2003). The low asymptotic length (L_∞) and high growth parameter (k) for female walleye in the western basin implies that the western basin walleye have a higher investment in reproduction (Lester et al 2004b) and a higher mortality rate (Pauly 1980). The study on the fecundity of walleye living in the western basin and the eastern basin confirmed the higher reproductive investment of the western basin walleye than the eastern basin walleye (Wolfert 1969). The results from lakewide tagging studies support the hypothesis that higher mortality

rate is experienced by the western basin walleye than the eastern basin walleye (Wang 2003).

Difference in Abundance and Survival among Walleye Sub-populations

There are several spawning grounds identified by Lake Erie management agencies in the eastern basin, and Van Buren Bay (site 53) is considered one of the dominant sites. Thus, the spawning activity at this location plays an important role in shaping the population dynamics of walleye in the eastern basin. Assuming a sex ratio of 1:1, the average spawning population from 1990 to 2002 in Van Buren Bay is around 22000 spawners with an increasing trend from 1998 onward in site 53 plus about 3000 from site 51. The average annual recruitment to spawning population is about 11000 for site 53 and 1200 for site 51. The tag loss rate (i.e. 22%) estimated by a double-tagging experiment significantly underestimated the true tag loss rate experienced by the walleye in the tag-recapture experiment (Don Einhouse, pers. comms.). This resulted in a biased low estimation of survival rates from 1990 to 1993 because the survival rate was adjusted by the low tagging loss rate (i.e. 22%). Generally, the walleye survival rates in the eastern basin were higher than the lakewide average annual survival rates (Fig 14). This is consistent with the observation that significantly lower harvest rates were found in the eastern basin compared to the western and central basins (MacLennan et al 2001, Wang 2003). Catch-at-age analysis on the eastern basin harvest produced abundance estimates for an unknown mixture of sub-populations from both the western basin and the eastern basin. The abundance can be regarded as total harvestable abundance of walleye in the eastern basin during the harvest seasons and was about 5% of lakewide abundance (Fig 14). My analysis of the New York tagging studies provided abundance estimates of Van Buren Bay walleye spawning population. The Van Buren Bay population was about 2% of the east basin harvestable

abundance and thus about 0.1% of lakewide adult walleye abundance. It can be concluded that a majority of walleye (above 95 percent) in Lake Erie are from the western basin.

The strong fidelity to the spawning ground discovered in this study and other studies may be one of the important factors keeping the sub-populations in Lake Erie genetically identifiable. The existence of both basin-specific, spawning site fidelity and genetic heterogeneity among sub-populations is consistent with the hypothesis that the annual eastward migration of walleye, demonstrated in the tagging studies, is not a spawning migration but rather an example of directed movement driven by some combination of avoidance of a habitat that has become too warm and selection of habitats that are thermally, and perhaps optically, more suitable for growth.

Differences in the Supply of Suitable Habitat among the three Basins of Lake Erie.

Differences in basin morphometry in Lake Erie cause basin-specific differences in the response of the aquatic habitat to changes in temperature, water level or water clarity. Generally, warmer water temperature causes an increase in the supply of thermally suitable habitat area and volume for walleye in the central and eastern basins, but, in the shallow and small western basin, any future increase in water temperature above the 1998 level will cause a substantial decrease in the supply of thermal suitable habitat area and volume. A decrease in water level reduces the supply of walleye optically suitable habitat lakewide and walleye thermally suitable habitat in the central and eastern basins, but increases the supply of walleye thermally suitable habitat areas in the eastern basin. This implied that the deepest eastern basin responds differently to the decrease in water level in the supply of walleye thermally suitable habitat areas compared to the central and western basins. Among the three basins, the western basin suffers the most when the temperature increases and water level

decreases. The central basin has the greatest supply of suitable habitat for walleye during the summer and fall because of its largest and relatively flat bottom: it takes up 72% and 77% of lakewide summer and fall hourly available suitable habitat in area and volume, respectively. The same figures for the western basin are 25% and 11%. For the eastern basin, the figures are 3% and 12%. Therefore, a majority of the supply of suitable habitat in summer and fall is located in the central basin. This immense supply of suitable habitat in summer and fall in the central basin becomes available in June (cool year-1993) or May (warm year-1998). This coincides with the beginning of the annual eastward migration of walleye from the western basin (Wang 2003). However, the summer and fall anoxia is frequent in the central basin, and this may reduce the amount of usable habitat to walleye in this basin.

Basin-specific habitat responses to climate change potentially may affect the dynamics of walleye sub-populations and their interactions. Given the fact that walleye are benthic feeders and Christie and Regier (1988) showed empirically that walleye yield was strongly linked to walleye thermal-optical habitat areas, instead of volumes, it is reasonable to consider that the amounts of thermally and/or optically suitable habitat areas serve as useful measures of basin-specific carrying capacity for walleye. A decrease in the amount of such habitats in the western basin due to climate change may intensify density-dependent effects, especially on the survival and growth of young walleye inhabiting the western basin because of their inability to migrate out of the western basin. For older walleye that are able to migrate, their annual migration circle might start earlier and the extent of their migration might increase. This could increase the intensity of density-dependent pressure on both the walleye of the eastern basin, and the migratory western basin fish as well. In next chapter, I will use a simulation study to illustrate how the changes in the habitat resulted from the

climate change can affect the dynamics of walleye sub-populations in Lake Erie.

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Table 1. Walleye mark-recapture study sites in New York waters from 1990 to 2004

Site ID	Site Name	Location	Longitude	Latitude
51	Lackawanna Shoreline	Along the Lackawanna Shoreline (Smoke's Creek)	-78.86389	42.811111
52	Cattaraugus Creek	Near Cattaraugus Creek	-79.14444	42.5625
53	Van Buren Bay	In Van Buren Bay	-79.4	42.466667
54	Shorehaven	Near Shorehaven	-79.63	42.326667
55	Evan's Bar	Southwest of Sturgeon Point.	-79.11	42.658333
56	Barcelona/Bournes	Near Barcelona Harbor	-79.60833	42.345833
59	Buffalo River	Near Eastern Lake Erie	-78.83333	42.863889

Table 2. Sample size organized by cohort from walleye scale back-calculation study for three sub-populations in Lake Eire (GR-Grand River; NY-New York; WB-the western basin)

Cohorts	GR	NY	WB	Total
1982		25	30	**55**
1983		30	30	**60**
1984		49	30	**79**
1985		30	30	**60**
1986		31	30	**61**
1987		30	30	**60**
1988	8	29	30	**67**
1989	6		29	**35**
1990	9	10	30	**49**
1991	22	9	29	**60**
1992	29		30	**59**
1993	30		30	**60**
1994	31	14	30	**75**
1995	30		30	**60**
1996	33	11	35	**79**
1997	29		30	**59**
1998	43	38	30	**111**
1999	31		30	**61**
2000	26		30	**56**
2001	21	7	30	**58**
Total	**348**	**313**	**603**	**1264**

Table 3. The results of Tukey post-hoc pairwise differences on the first four years growth from three sub-populations, i.e. the western basin (WB), New York (NY) and Grand River (GR), by Tukey method

Pairs	**1st year growth**	**2nd year growth**	**3rd year growth**	**4th year growth**
GR-NY	-0.98	7.45	15.45*	10.52*
GR-WB	19.45*	18.36*	7.85*	5.49.
NY-WB	18.47*	10.83*	-7.60*	-5.02

*-significant different at α=0.05

Table 4. Basin-specific temperature indices i.e. mean temperature (T), degree days (DD) and number of days (D) in Lake Erie from 1982 to 2001

	West Basin					New York					Grand River				
	T (>4)	DD (>4)	D (>22)	T (4-22)	DD (4-22)	T (>4)	DD (>4)	D (>22)	T (4-22)	DD (4-22)	T (>4)	DD (>4)	D (>22)	T (4-22)	DD (4-22)
1982	17.06	4385	57	14.83	2967	13.92	3493	30	12.71	2810					
1983	16.48	3956	94	11.77	1719	14.47	3718	52	12.14	2489					
1984	16.70	4008	69	13.88	2388	14.92	3565	30	13.73	2870					
1985	17.38	4223	73	14.44	2455	14.85	3684	34	13.60	2981					
1986	17.31	4103	69	14.44	2427	14.73	3668	35	13.40	2859	13.90	3448	21	13.07	2967
1987	16.58	4278	88	12.36	2102	15.03	3787	41	13.30	2813	14.01	3740	30	12.76	3024
1988	16.86	4147	73	13.08	2264	14.94	3557	46	12.80	2462	13.94	3541	33	12.52	2768
1989	16.98	4042	81	13.20	2073	13.82	3426	20	13.00	2972	14.09	3397	25	13.11	2831
1990	16.11	4254	76	12.84	2414	13.48	3827	24	12.60	3287	14.66	3650	44	12.84	2633
1991	17.41	4319	103	12.02	1743	14.19	4060	31	13.10	3348	14.65	3778	67	11.71	2236
1992	16.22	3942	62	13.86	2510	13.08	3597	0	13.10	3597	14.48	3519	4	14.35	3429
1993	16.02	3990	80	12.14	2051	15.04	3819	65	12.20	2297	14.13	3560	32	12.71	2797
1994	15.42	3949	75	11.71	2119	14.84	3903	34	13.60	3124	14.44	3639	23	13.60	3115
1995	17.15	4338	84	12.93	2186	14.43	3637	44	12.50	2599	14.76	3793	59	11.82	2340
1996	17.21	3940	80	13.20	1967	14.46	3672	40	12.90	2755	15.35	3486	46	13.24	2397
1997	15.89	3814	50	13.88	2638	13.79	3777	22	13.00	3280	13.37	3383	9	13.04	3182
1998	17.78	4943	101	13.42	2375	14.82	4608	74	12.10	2878	14.98	4088	42	13.42	3100
1999	16.62	4687	82	13.18	2635	15.20	4195	54	13.20	2923	14.54	3910	40	13.06	2990
2000	17.54	4263	89	13.71	2112	13.91	3952	35	12.70	3162					
2001	17.05	4536	89	12.72	2252	14.93	3943	44	13.30	2927					

Note: T(>4) or T(>22) indicating mean temperature above 4 or 22 degree Celsius; DD(>4) or DD(4-22) indicating the degree days above 4 degree Celsius or between 4 to 22 degree Celsius, respectively; D(>22) indicating the number of days above 22 degree Celsius.

Table 5. Basin- and sex-specific estimators and standard errors (SE) of parameters of von Bertalanffy growth model estimated by non-linear regression for the three Lake Erie sub-populations

Subpopulations	Sex	K		L∞		t0	
		Estimate	SE	Estimate	SE	Estimate	SE
Western Basin	Female	0.28	0.02	662.38	18.75	-0.07	0.08
	Male	0.36	0.01	552.06	4.64	-0.11	0.04
New York	Female	0.24	0.02	697.18	12.73	-0.45	0.14
	Male	0.38	0.03	540.78	9.16	-0.21	0.15
Grand River	Female	0.24	0.01	733.95	7.15	-0.25	0.08
	Male	0.36	0.04	601.07	14.24	-0.07	0.14

Table 6. The numbers by site of tagged and recaptured walleye spawners from walleye mark-recapture experiment from 1990-2004

Tagging Sites (T)	Number Tagged	Recapture Sites (R)								% where R=T
		51	**52**	**53**	**54**	**55**	**56**	**59**	**Sum**	
51	**3316**	337	3	15	1	0	0	0	**356**	**94.66**
52	**542**	0	32	0	0	0	0	0	**32**	**100.00**
53	**11565**	4	0	756	2	0	2	0	**764**	**98.95**
54	**432**	1	0	6	29	0	0	0	**36**	**80.56**
55	**298**	1	0	0	0	16	0	0	**17**	**94.12**
56	**983**	0	0	16	1	1	10	0	**28**	**35.71**
59*	**11**	0	0	2	0	0	0	0	**2**	**0.00**
Sum	**17147**	**343**	**35**	**795**	**33**	**17**	**12**	**0**	**1235**	
% where T=R		**98.25**	**91.43**	**95.10**	**87.88**	**94.12**	**83.33**	**0**		

* 11 tagged walleye in site 59 were transplanted from site 53 in 1994

Table 7. The number of tagged walleye removed by fisheries, by tagged sites and areas

Tagging site	Fishery Recapture (death) Areas*					
	Area 1	**Area 2**	**Area 3**	**Area 4**	**Others**	**SUM**
51	228	53	4	4	5	**294**
52	2	4	1	1	0	**8**
53	312	322	203	61	41	**939**
54	11	24	14	21	1	**71**
55	13	9	0	1	1	**24**
56	25	31	31	21	7	**115**
59	0	0	0	0	0	**0**
SUM	**591**	**443**	**253**	**109**	**55**	**1451**

* Area 1: Latitude >42.666 degree (include sites 51, 59)
Area 2: 42.5 degree <Latitude<=42.666 degree (including sites 52, 55)
Area 3: 42.33 degree<Latitude<=42.5 degree (including sites 53, 56)
Area 4: 42.166 degree<Latitude<=42.33 degree (including site 54)
Others: Latitude <= 42.166 degree

Table 8. Goodness-of-fit test results for mark-recapture analysis on walleye spawning population in Lackawanna Shoreline (i.e. site 51)

Component	Chi-square	df	P-level	Sufficient Data
3.SR2	0.7423	1	0.3889	No
3.SR3	0.7587	1	0.3837	Yes
3.SR4	0.9358	1	0.3334	Yes
3.SR5	2.6356	1	0.1045	Yes
3.SR6	0.5622	1	0.4534	Yes
3.SR7	0.0000	0	1.0000	No
3.SR8	0.0000	0	1.0000	No
3.SR9	0.0000	0	0.0000	No
3.SR10	0.0000	0	0.0000	No
3.SR11	2.2203	1	0.1362	No
3.SR12	0.2876	1	0.5917	Yes
3.SR13	1.0738	1	0.3001	No
3.SR14	0.0000	0	1.0000	No
Group 3.SR	**9.2164**	**8**	**0.3244**	
3.Sm2	0.0000	0	1.0000	No
3.Sm3	0.3106	1	0.5773	No
3.Sm4	1.0559	1	0.3041	Yes
3.Sm5	0.6420	1	0.4230	Yes
3.Sm6	1.3945	1	0.2377	Yes
3.Sm7	0.0000	0	0.0000	No
3.Sm8	0.0000	0	0.0000	No
3.Sm9	0.0000	0	0.0000	No
3.Sm10	0.0000	0	0.0000	No
3.Sm11	0.0000	0	1.0000	No
3.Sm12	0.0051	1	0.9432	No
3.Sm13	2.9167	1	0.0877	No
Group 3.Sm	**6.3248**	**6**	**0.3878**	
TEST 3	**15.5412**	**14**	**0.3422**	

Component	Chi-square	df	P-level	Sufficient Data
2.C2	1.2184	1	0.2697	No
2.C3	0.7345	2	0.6926	Yes
2.C4	0.2680	2	0.8746	Yes
2.C5	2.2570	4	0.6886	Yes
2.C6	8.5663	6	0.1995	Yes
2.C7	0.0000	0	1.0000	No
2.C8	0.0000	0	1.0000	No
2.C9	0.0000	0	1.0000	No
2.C10	0.0000	0	1.0000	No
2.C11	1.0657	1	0.3019	Yes
2.C12	0.6852	1	0.4078	Yes
2.C13	1.5179	1	0.2179	No
TEST 2	**16.313**	**18**	**0.5707**	

Goodness of Fit Results (TEST 2 + TEST 3)

Chi-square	df	P-level
31.8542	32	0.4740

Table 9. Goodness-of-fit test results for mark-recapture analysis on walleye spawning population in Van Buren Bay (i.e. site 53)

Component	Chi-square	df	P-level	Sufficient Data
3.SR2	1.0573	1	0.3038	No
3.SR3	0.7914	1	0.3737	Yes
3.SR4	0.1202	1	0.7288	Yes
3.SR5	0.3690	1	0.5435	Yes
3.SR6	0.4931	1	0.4826	Yes
3.SR7	0.0455	1	0.8311	Yes
3.SR8	2.5391	1	0.1111	Yes
3.SR9	0.0745	1	0.7848	Yes
3.SR10	0.0566	1	0.8119	Yes
3.SR11	0.0292	1	0.8644	Yes
3.SR12	0.3497	1	0.5543	Yes
3.SR13	74.7032	1	0.0000	Yes
3.SR14	41.9915	1	0.0000	No
Gooup 3.SR	**122.6203**	**13**	**0.0000**	
3.Sm2	0.0000	0	1.0000	No
3.Sm3	0.0002	1	0.9884	No
3.Sm4	0.4422	1	0.5061	No
3.Sm5	0.3245	1	0.5689	Yes
3.Sm6	0.1170	1	0.7323	Yes
3.Sm7	6.0196	1	0.0141	No
3.Sm8	0.4525	1	0.5012	Yes
3.Sm9	3.1065	1	0.0780	Yes
3.Sm10	1.2908	1	0.2559	Yes
3.Sm11	0.0146	1	0.9039	Yes
3.Sm12	3.8503	1	0.0497	No
3.Sm13	1.5658	1	0.2108	No
Group 3.Sm	**17.1839**	**11**	**0.1026**	
TEST 3	**139.8042**	**24**	**0.0000**	

Component	Chi-square	df	P-level	Sufficient Data
2.C2	0.2255	3	0.9734	Yes
2.C3	7.9964	7	0.3329	Yes
2.C4	8.6414	8	0.3734	Yes
2.C5	7.7881	8	0.4544	Yes
2.C6	7.3267	7	0.3957	Yes
2.C7	8.1677	6	0.2261	Yes
2.C8	7.5923	5	0.1802	Yes
2.C9	2.8505	4	0.5831	Yes
2.C10	3.1985	3	0.3620	Yes
2.C11	1.3528	2	0.5084	Yes
2.C12	8.5817	1	0.0034	Yes
2.C13	0.6306	1	0.4271	No
TEST 2	**64.3522**	**55**	**0.1818**	

Goodness of Fit Results (TEST 2 + TEST 3)

Chi-square	df	P-level
204.1564	79	0.0000

Table 10. Mean surface temperature (MST), seasonal-weighted means of light attenuation (SWM), and hourly average weighted habitat area (Ha per hour) and volume (hm^3 per hour) for walleye in three basins of Lake Erie from May to October in 1993 and 1998

Basins	Years	MST (°C)	SWM	Weighted Habitat Area			Weighted Habitat Volume		
				Optical Only	Thermal Only	TOHA	Optical Only	Thermal Only	TOHV
Eastern	**1998**	18.3	0.208	60,156.9	116,977.4	4,790.7	12,241.1	56,271.9	2,142.8
	1993	16.2	0.232	64,673.3	92,898.7	4,484.7	14,042.5	45,274.3	1,851.1
Central	**1998**	19.7	0.315	261,568.3	1,040,632.0	175,475.6	25,362.4	213,332.6	17,454.4
	1993	17.1	0.370	183,048.1	511,262.4	46,902.0	24,964.3	135,522.1	8,680.2
Western	**1998**	20.1	0.534	62,856.7	343,710.5	42,474.8	2,996.8	31,435.3	2,068.6
	1993	18.4	0.771	61,300.7	275,131.1	33,387.4	3,139.4	25,142.4	1,622.7

Table 11. Percentage Changes from 1998 values of hourly average weighted habitat area and volume for walleye in three basins of Lake Erie for five simulations scenarios.

Basins	Scenarios *	Weighted Habitat Area			Weighted Habitat Volume		
		Optical	Thermal	TOHA	Optical	Thermal	TOHV
Eastern	1	0	16	23	0	9	13
	2	-3	2	3	-5	-2	-2
	3	-5	5	8	-10	-4	-5
	1&2	-3	18	27	-5	7	10
	1&3	-5	22	32	-10	4	7
Central	1	0	9	14	0	1	6
	2	-4	0	-4	-10	-5	-10
	3	-9	-1	-7	-20	-10	-20
	1&2	-4	8	8	-10	-4	-6
	1&3	-9	8	3	-20	-9	-16
Western	1	0	-6	1	0	-6	0
	2	-14	-4	-14	-20	-11	-20
	3	-29	-8	-28	-38	-21	-37
	1&2	-14	-9	-12	-20	-16	-20
	1&3	-29	-13	-26	-38	-26	-38

* 1—water temperature increased 2 °C
2—water level decreased 1 meter
3—water level decreased 2 meters

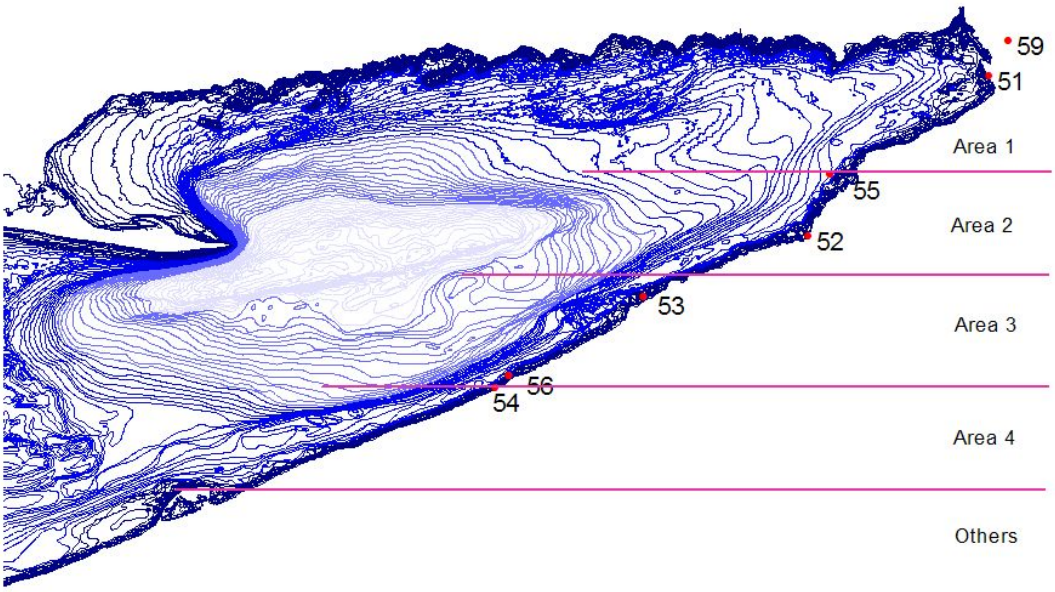

Figure 1. Locations of seven sites for mark recapture study and associated five areas defined in text and Table 1.

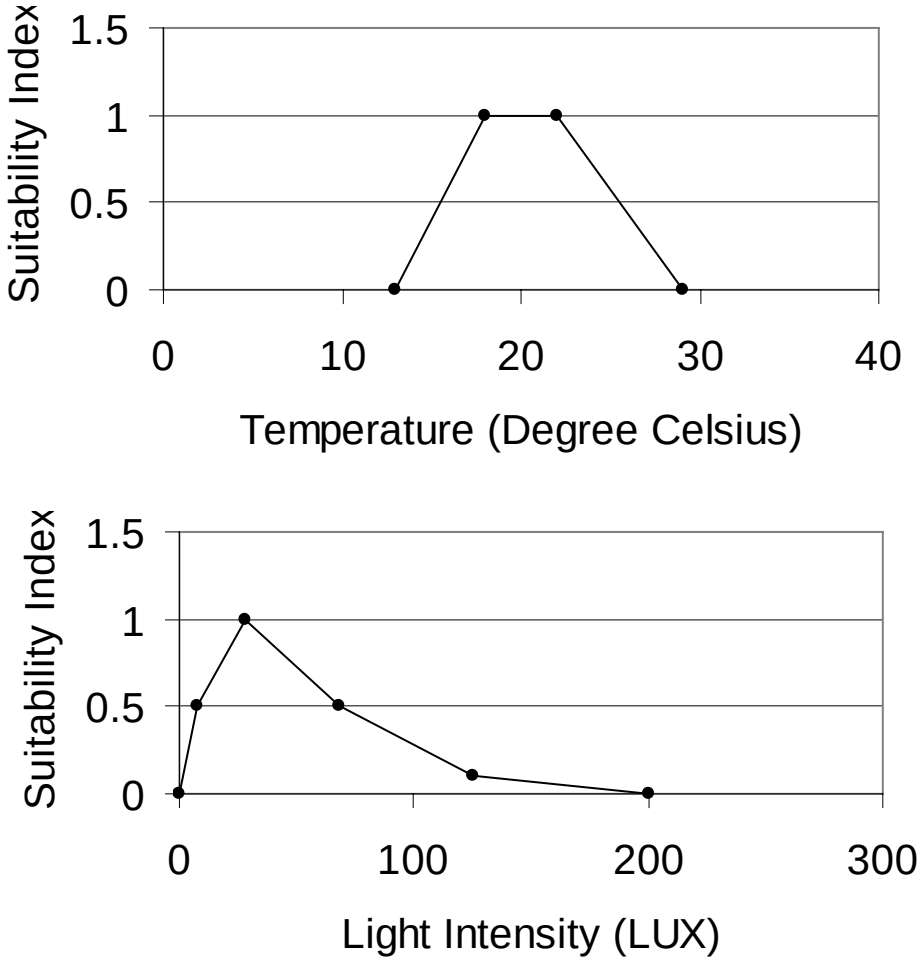

Figure 2. The thermal suitability model (top) and optical suitability model (bottom) for the juvenile and adult walleye

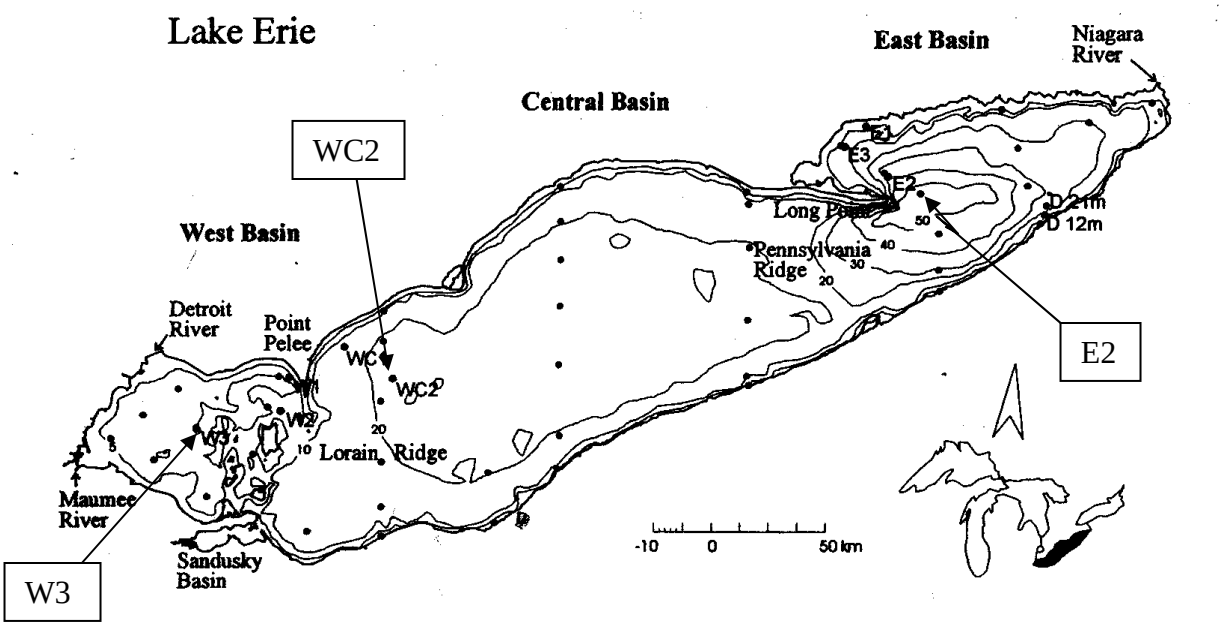

Fig. 1. **Map of Lake Erie indicating the depth contours and locations of sampling stations. The LEB and NYDEC sites are labelled.**

Figure 3. Lake Erie and three representative sampling stations: E2—the eastern basin; WC2—the central basin; W3—the western basin
From Dahl et al 1995

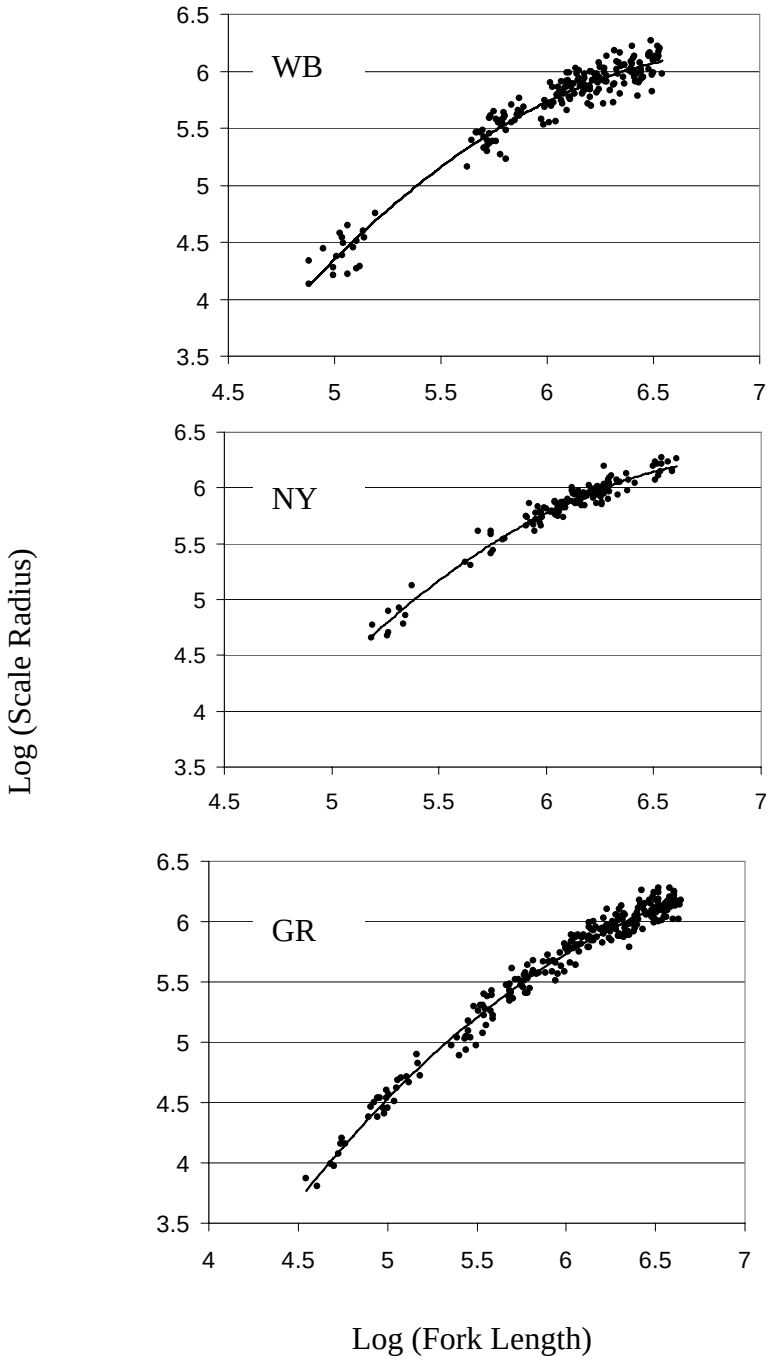

Figure 4. The body-scale relationships of walleye subpopulations in Lake Erie for back calculation study
Note: the western basin (WB); New York (NY); Grand River (GR)

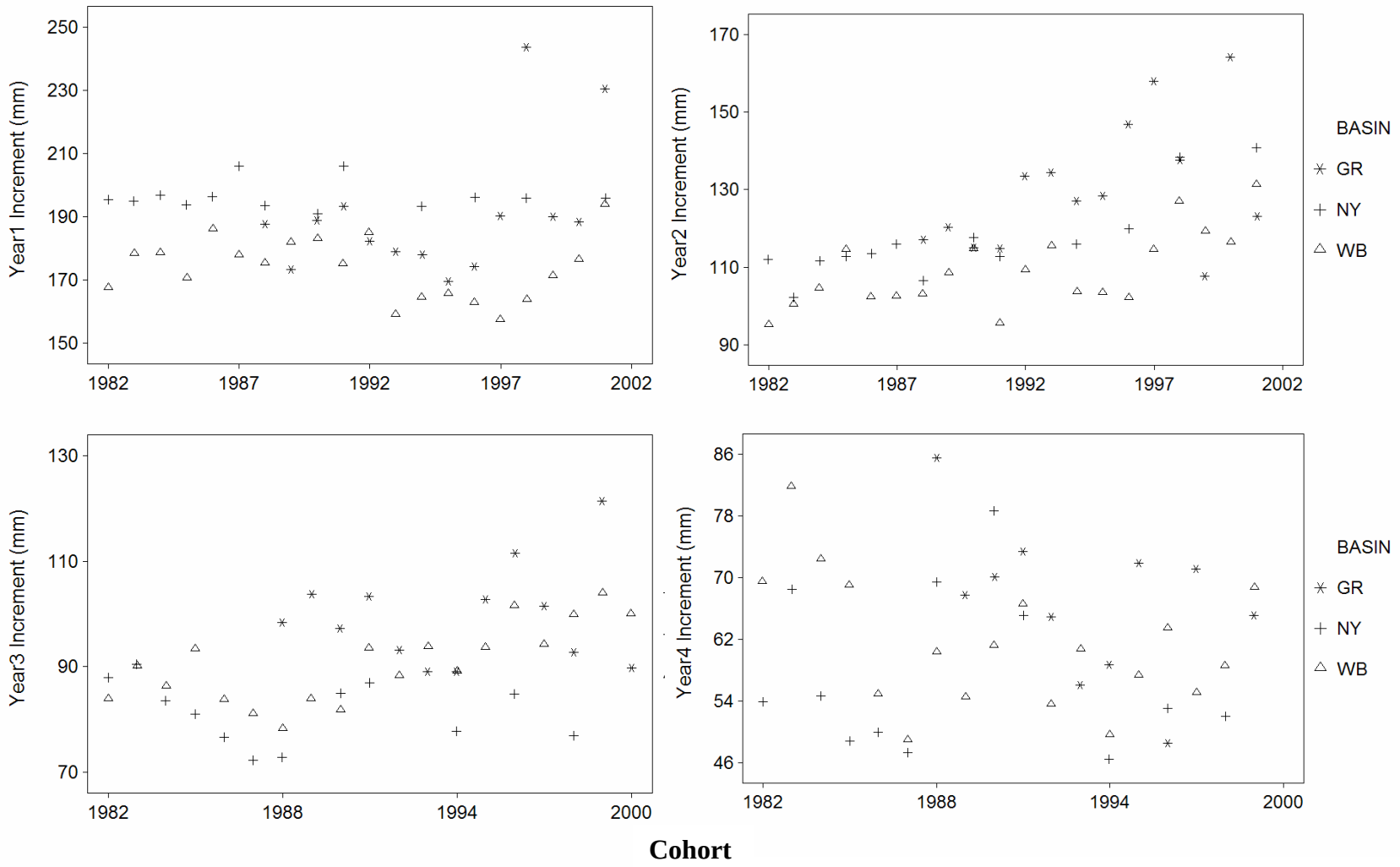

Figure 5. The mean length increments of the first four years for each cohort (from 1982 to 2002) for each sub-population Legend: GR—Grand River; WB—the western basin; NY—New York.

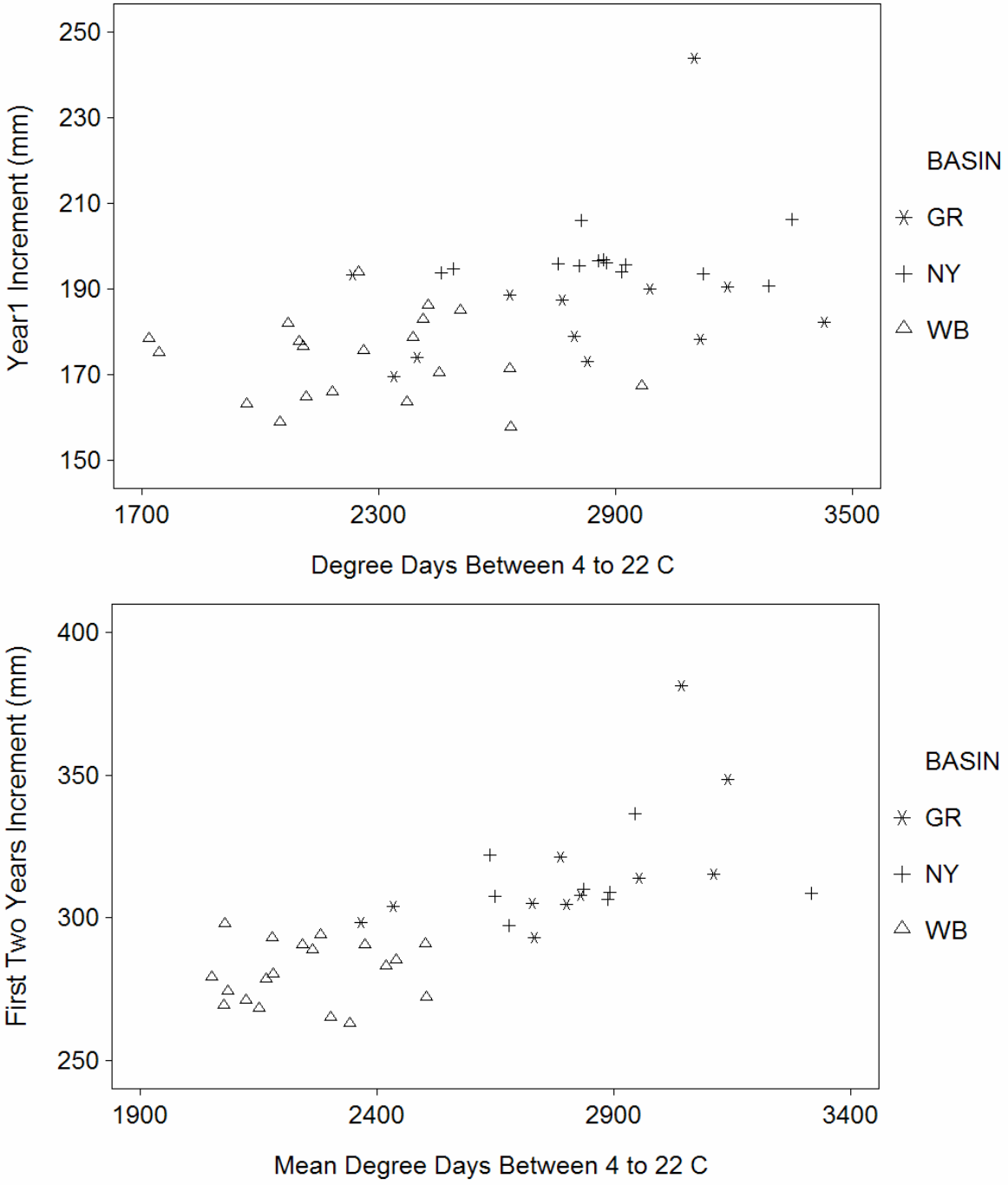

Figure 6. Plots of the first year increment (top) and the first two years increment (bottom) versus the temperature index (mean degree days between 4 C to 22 C) for three sub-populations (GR—Grand River; WB—the western basin; NY—New York)

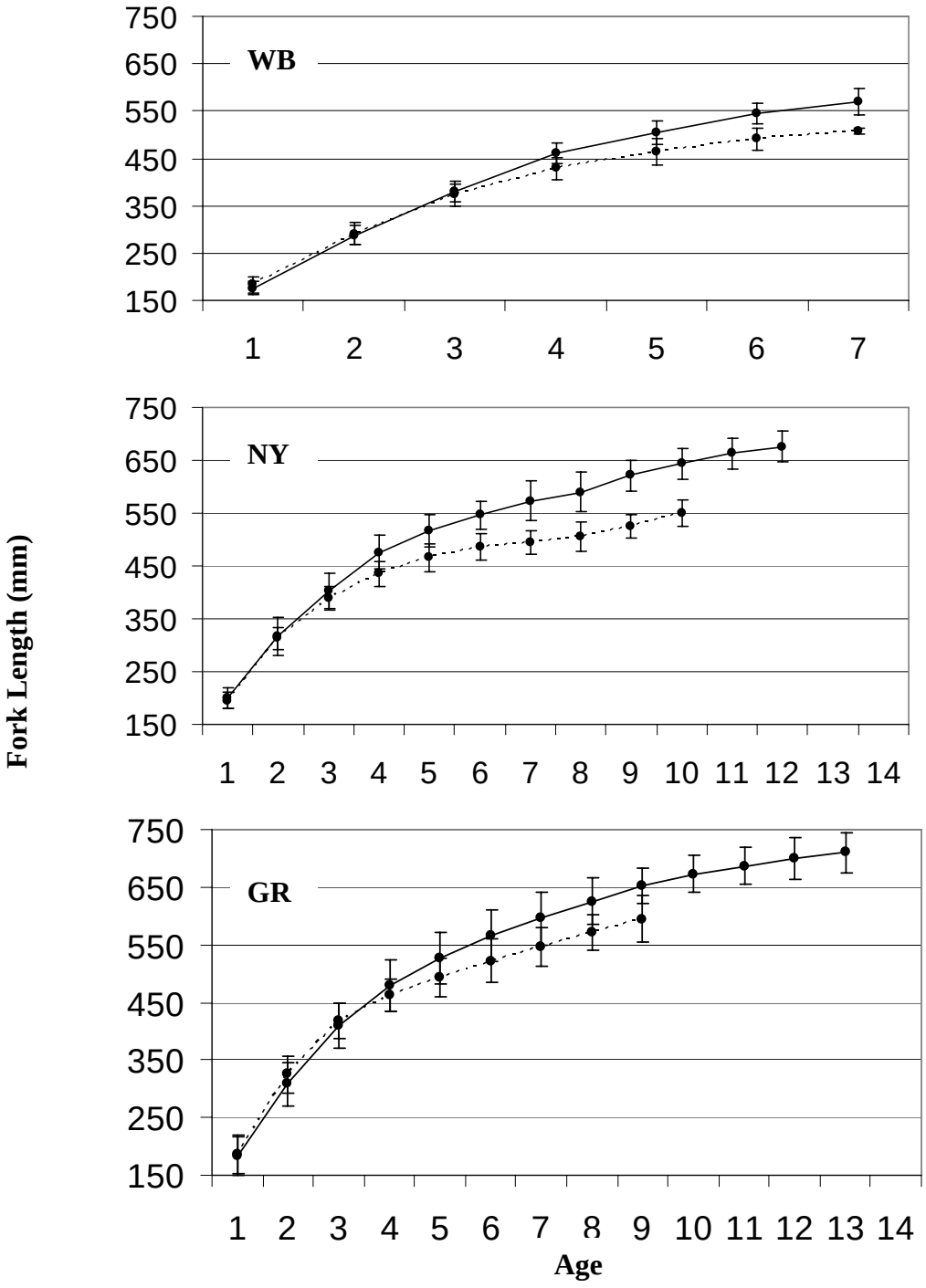

Figure 7. Sub-population-specific mean lengths at age (±SD) for male (dashed lines) and female (solid lines) walleye in Lake Eri e (WB-the western basin; NY-New York;GR-Grand River.

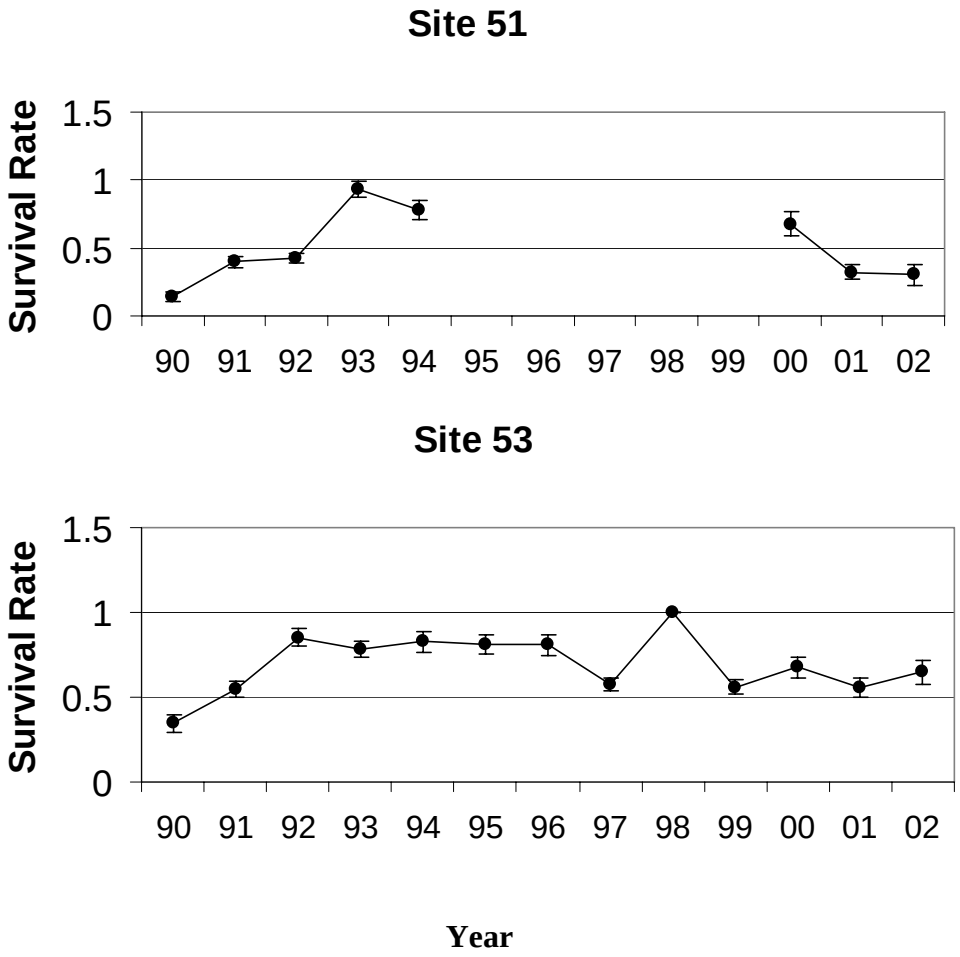

Figure 8. The estimated annual survival rates (±SD) for mature male walleye in Lackawana shoreline (site 51) and Van Buren Bay (site 53) from mark-recapture studies from 1990 to 2004

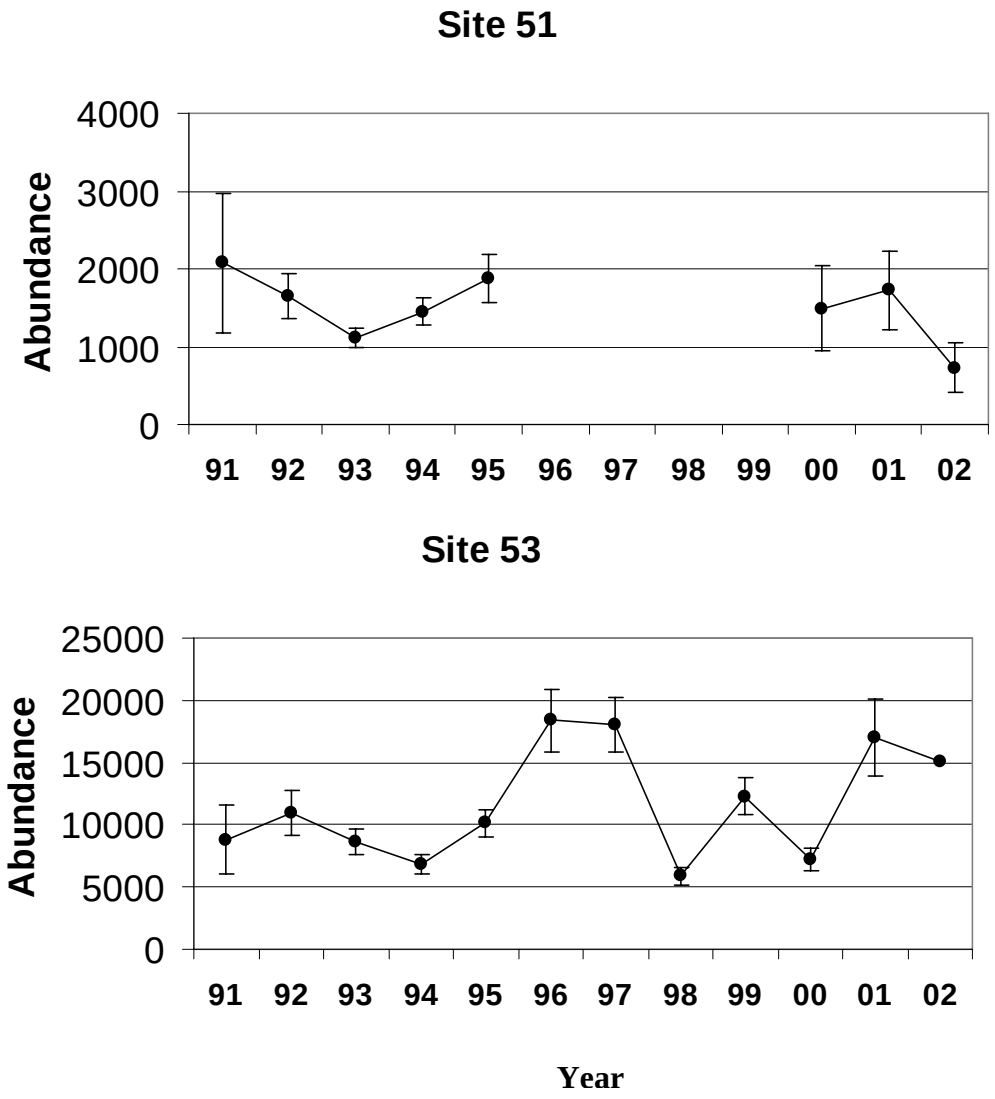

Figure 9. The estimated spawning abundances (±SD) for male mature walleye in Lackawana shoreline (site 51) and Van Buren Bay (site 53) from mark-recapture studies from 1990 to 2004

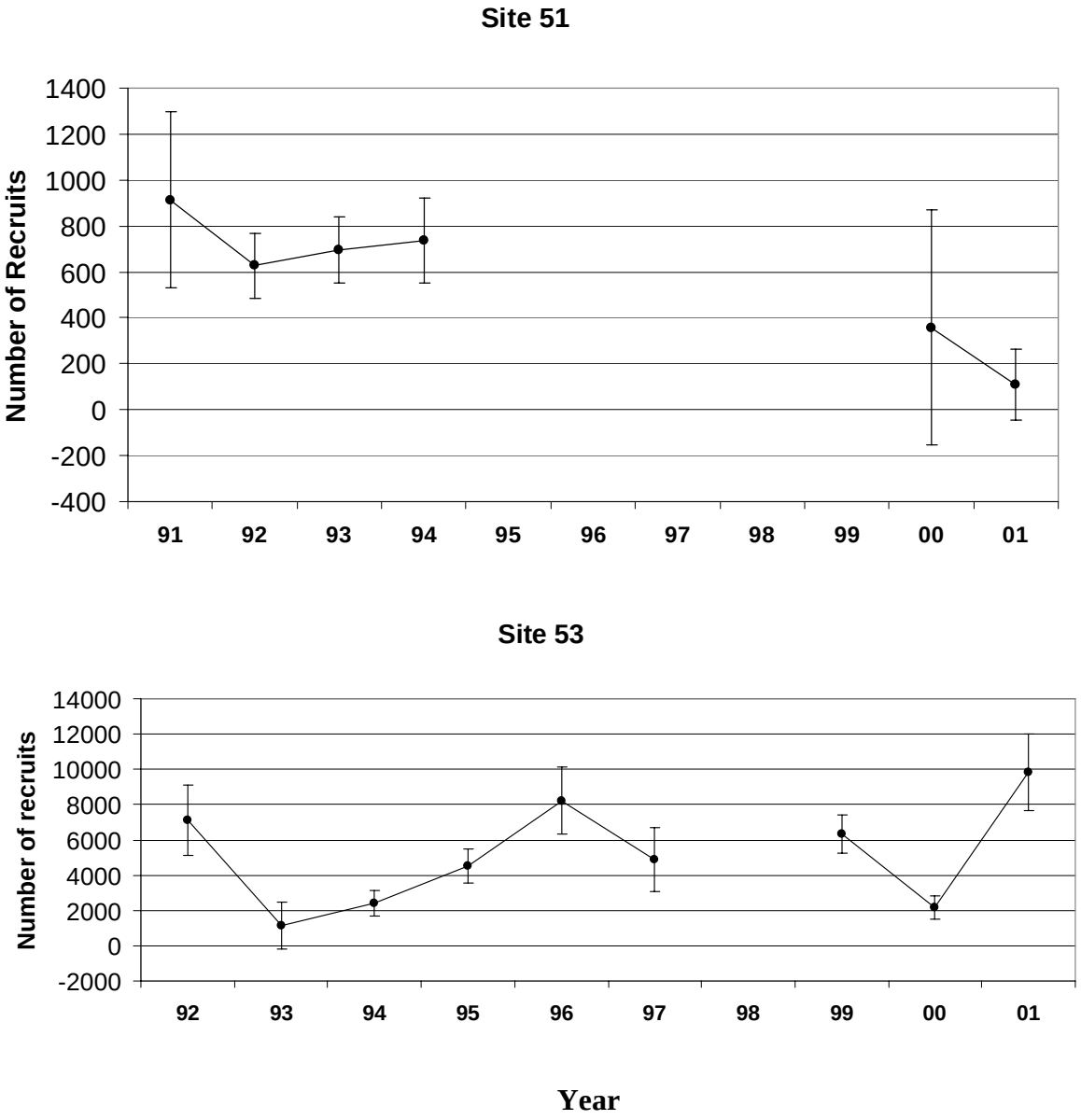

Figure 10. The estimated recruitment (±SD) for male mature walleye in Lackawana shoreline (site 51) and Van Buren Bay (site 53) from mark-recapture studies from 1990 to 2004

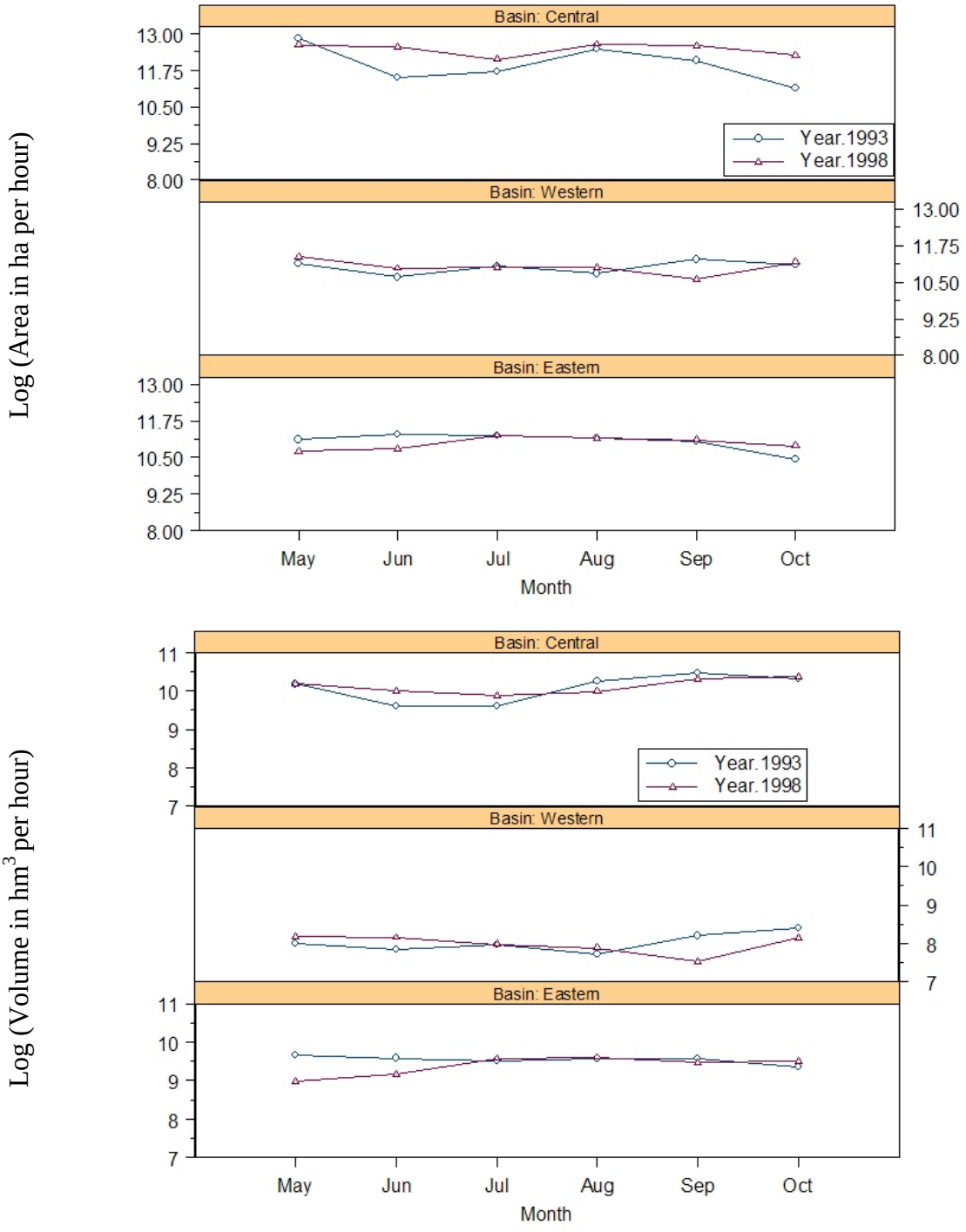

Figure 11. The hourly averages of basin-specific areas (top) and volumes (bottom) optically suitable for walleye in Lake Erie by month in 1993 and 1998

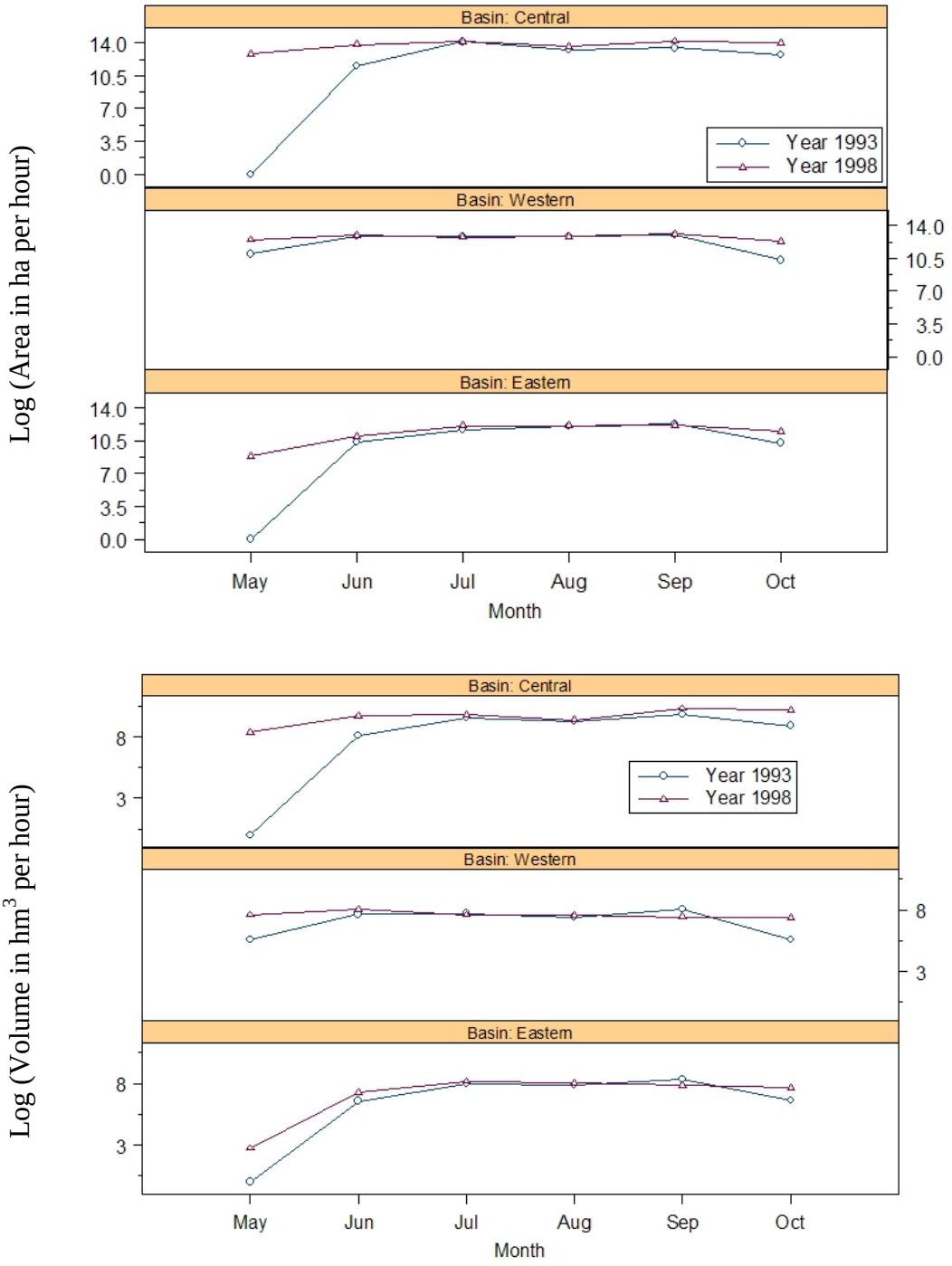

Figure 12. The hourly averages of basin-specific areas (top) and volumes (bottom) thermally suitable for walleye in Lake Erie by month in 1993 and 1998

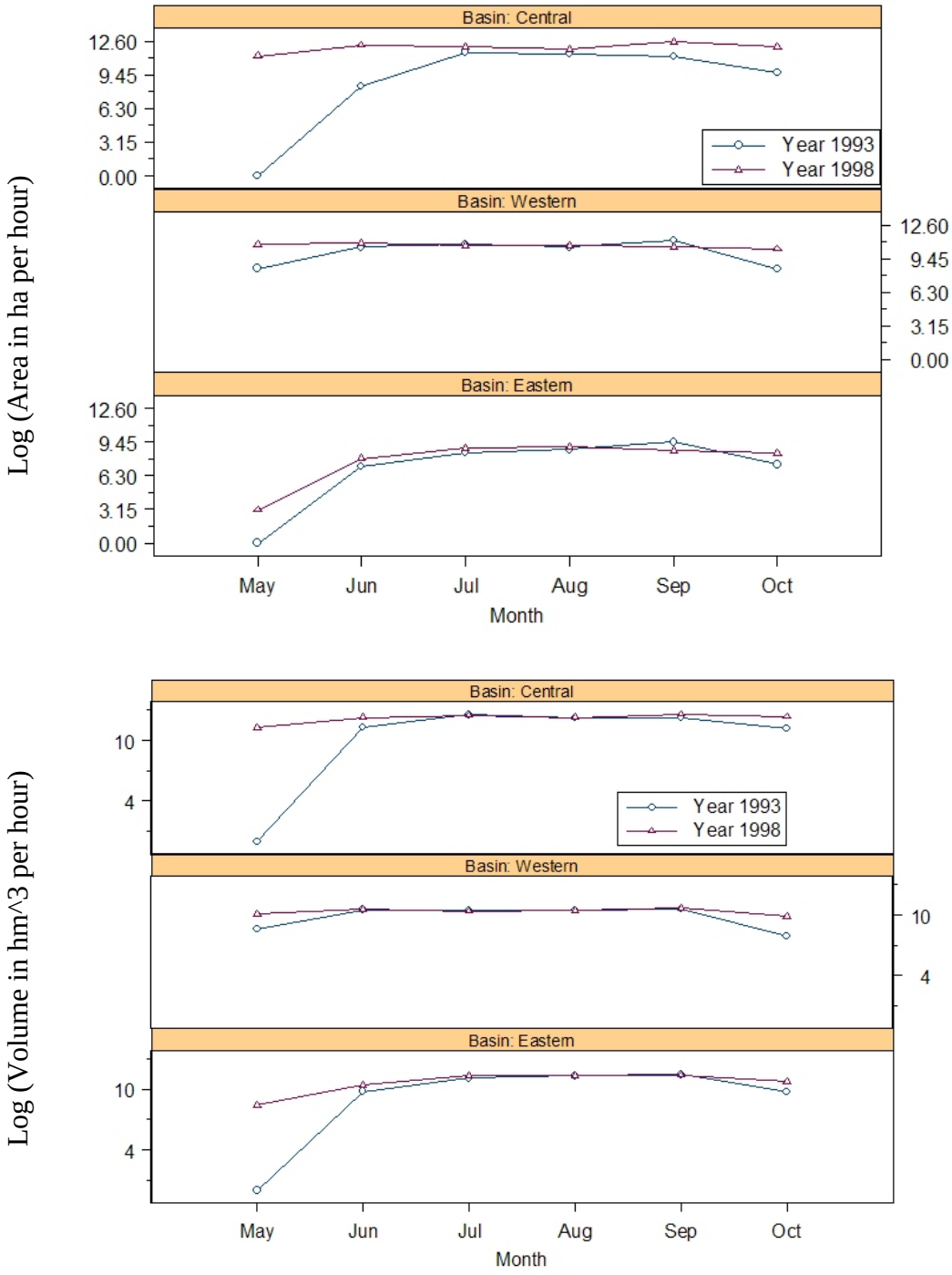

Figure 13. The hourly averages of basin-specific areas (TOHA) (top) and volumes (TOHV) (bottom) thermally and optically suitable for walleye in Lake Erie by month in 1993 and 1998

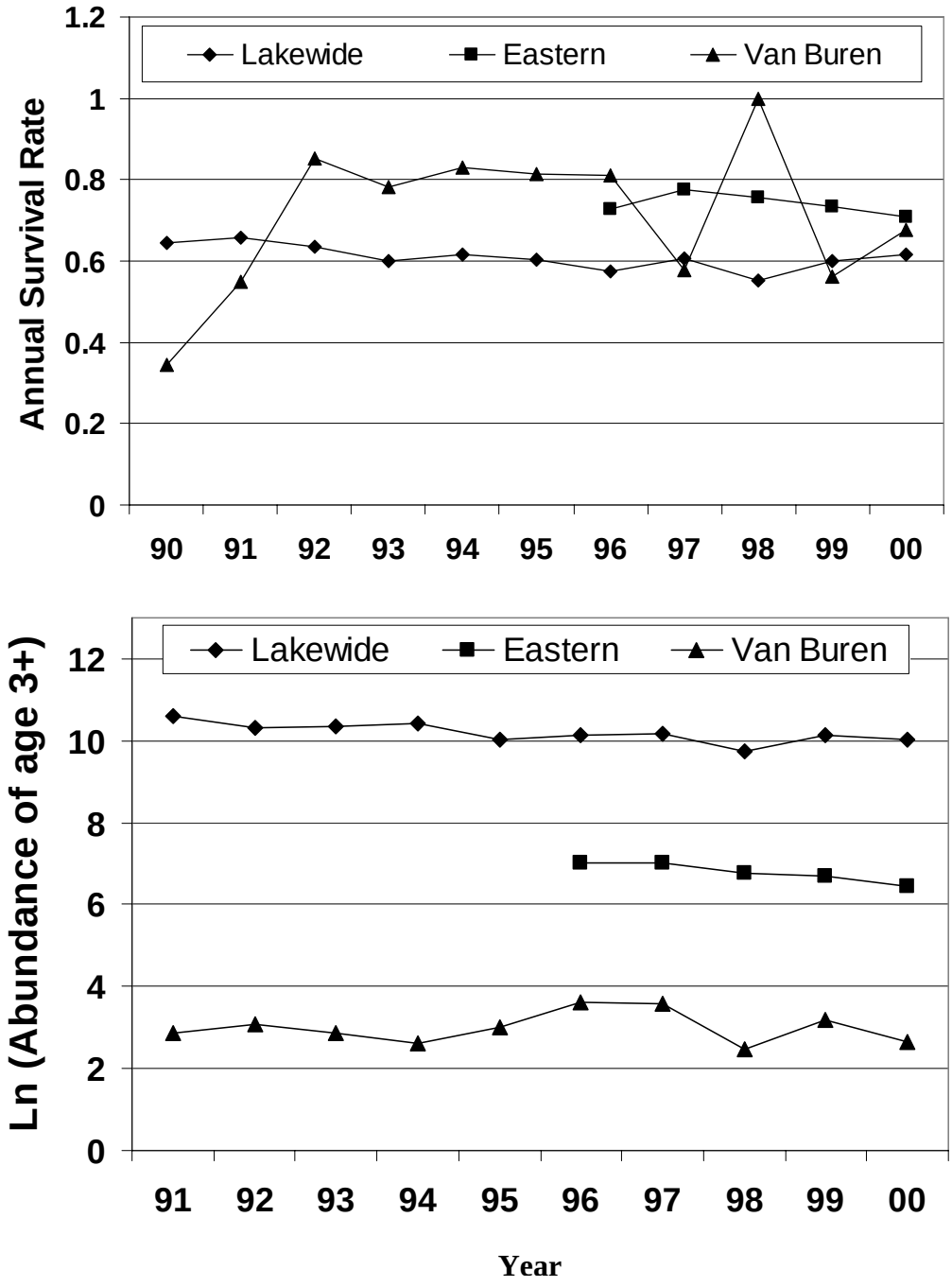

Figure 14. The time series of annual survival rate (top) and abundances of age 3 and over (bottom) estimated from catch at age (i.e. lakewide and the eastern basin) and mark recapture analyses (Van Buren Bay).

Chapter 4. A simulation study of effects of density dependent processes on walleye subpopulations in Lake Erie

Abstract

In this chapter, a Leslie matrix discrete population model was used to simulate the effect of population density-dependent early survival (i.e. recruitment) and density-dependent growth and egg production on the dynamics of walleye metapopulation in Lake Erie. A Shepherd's generalized stock-recruitment relationship derived from empirical observations for the eastern basin sub-population and the western basin sub-population was used to model density-dependent early survival. The sensitivities of population equilibrium abundance under different harvest rates and extinction harvest rate to the parameters of Shepherd stock-recruitment model and the empirical density-dependent growth model were explored extensively. The study showed that changes in density-dependent growth and egg production can modify the stock-recruitment relationship and thus population dynamics. Populations with a large lognormal standard deviation for recruitment have high extinction harvest rates. The current quota management system applied to Lake Erie walleye shelters the eastern basin walleye but exposes the western basin walleye to a higher harvest rate than expected. Shrinkage of habitat for walleye early survival in the western basin and increases of adult growth habitat in the central and eastern basin that may be caused by climate change can substantially reduce equilibrium abundance in the western basin sub-population but cause little change in the eastern basin sub-population.

Introduction

Density dependence of demographic parameters is widely accepted as an important influence on animal population dynamics (Krebs 2001). The theoretical basis for density dependence rests on the idea that an increase in the density of animals, caused either by an increase in absolute abundance within a limited habitat area or by a decrease in habitat area itself, can result in more intense competition for food and living space within the habitat. This increased competition leads to an increase in the mortality rate and/or a decrease in the birth rate. Such density-dependent effects have been observed in the Lake Erie walleye populations. The survival rate of young walleye was significantly influenced by the spawning-stock size (Shuter and Koonce 1977, Madenjian et al 1996), and individual walleye growth rates were significantly influenced by overall population abundance (Muth and Wolfert 1986, Hatch, et al 1987). Because egg production varies with body size (Wolfert 1969, Muth and Ickes 1993), the impact of density on individual growth affects overall birth rate through its influence on individual egg production.

From 1978 to 2001, a continuous time series of age specific (from age 2 to age 7+) abundance estimates is available for Lake Erie walleye from the resource management agencies responsible for fish stock assessment (MacLennan et al 2001). By combining this abundance information with age-specific fecundity estimates from two other studies (Wolfert 1969, Muth and Ickes 1993), an empirical description of the association between walleye early survival and population density can be established. Further, the length-at-age data for walleye described in Chapter 3, together with the abundance estimates, can be used to derive an empirical description of association between abundance and length-at-age of Lake Erie walleye. Therefore, the effects of density on both the survival and birth rate of Lake Erie

walleye can be empirically specified.

Substantial evidence supports the existence of sub-populations of walleye in Lake Erie (refer to Introduction of Chapter 3). At least two lake spawning sub-populations are clearly distinguishable, one with their spawning ground in the western basin and the other with their spawning ground in the eastern basin (i.e. Van Buren Bay). In Chapter 3, I quantified the supply of suitable habitat for walleye in each basin and assessed the potential impacts of climate change on habitat supply. The habitat analyses described in Chapter 3 indicate that climate change will decrease the areal supply of suitable habitat in the western basin but increase the areal supply of suitable habitat in the central basin and the eastern basin. Presumably, such changes can intensify the density-dependent effects on walleye early life survival in the western basin population because the walleye younger than age 2 may not be capable of moving out of the western basin to compensate for the effects caused by the decrease in habitat. The shrinkage of the western basin habitat would increase the intensity and hasten the onset of the eastward migration of walleye from the western basin. This could either exacerbate or ameliorate the intensity of density-dependent effects on adult walleye in the eastern basin and western basin sub-populations, depending on how the migratory western fish react to the combined effects of habitat shrinkage in the western basin and habitat expansion in the central and eastern basins.

In this chapter, I will simulate how climate change may modify density-dependent effects on walleye in Lake Erie using a discrete, age-structured Leslie matrix model (Quinn and Deriso 1999) with stochastic effects imposed on the recruitment process. I will also incorporate different harvest strategies in the simulations and examine the effects of climate change and harvest on population dynamics.

Materials and Methods

Because the metapopulation comprising the western basin and the eastern basin walleye is the subject of the model, the model structure, parameters and biological processes described below are basin or sub-population specific. I assume the only interaction between the sub-populations is the joint, density-dependence of adult growth, established by the migrations of the western basin adults into the eastern and central basin feeding grounds and the eastern basin adults into central basin feeding grounds. In my thesis, the Van Buren Bay sub-population, as one of dominant spawning populations in the eastern basin, was extensively studied and thus used as representative of the eastern basin walleye.

Leslie Survival Matrices

A Leslie matrix discrete population model with age structure was used to describe each of the two sub-populations (the western basin and the eastern basin). For each sub-population the following model structure was used:

$$\begin{pmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \\ N_{5,t+1} \\ N_{6,t+1} \\ N_{7+,t+1} \end{pmatrix} == \begin{pmatrix} R_{11} & R_{21} & R_{31} & R_{41} & R_{51} & R_{61} & R_{7+1} \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_6 & S_{7+} \end{pmatrix} \text{ X } \begin{pmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \\ N_{5,t} \\ N_{6,t} \\ N_{7+,t} \end{pmatrix}$$

where $N_{i,j}$ is the number of female walleye of age i at time j, S_i is age specific annual survival rate of age i walleye and R_{k1} (k from 1 to 7+) is the average number of Age 1 female fish which a mature female walleye at age i can produce, which reflects combined effects of density-dependent survival (from eggs to age 1) and productivity (age specific fecundity). However in this study, instead of calculating the age-specific production at age 1, I used an

empirical relationship between the number of eggs produced by each sub-population and the abundance of age 1 fish to derive total of numbers of age 1 fish for each simulation year (see the below section on density dependent processes).

Lakewide tagging studies provided the instantaneous annual natural mortality rates for the eastern basin sub-population and the western basin sub-population, 0.41 and 0.33 respectively (Wang 2003). They are equivalent to the annual survival rates of 0.66 and 0.72 for the western basin sub-population and the eastern basin sub-population, respectively. I assumed the fish at age 1 and older had the same annual survival rate in the simulation study. The fishing mortality was defined as the percentage harvested (i.e. harvest rate) by the fishing activities.

Density-dependent Processes

Density-dependent growth and fecundity

Given walleye in Lake Erie start to migrate at age 3, the whole-lake adult growth habitat would be shared by all walleye in the lake. Therefore, it is reasonable to involve whole-lake walleye abundances in the study of density-dependent effects on the growth of walleye of both sub-populations after age 2. The annual total abundances for all walleye older than age 2 from 1978 to 2000 in the lake were calculated from age specific abundance estimates in MacLennan et al (2001). The estimates of length-at-age for age groups 2 to 7+ were obtained from the back-calculation studies on the western basin walleye and New York walleye described in Chapter 3. A modified Ford growth equation was used to relate growth to the abundance (Ricker 1975). The Ford growth equation can be derived from the von Bertalanffy growth model and describes a linear relationship between length at any age (L_{t+1}) and the length at one year younger (L_t), as follows,

$L_{t+1} = L_{\infty}(1-exp(-k))+exp(-k)*L_t$----------(1)

The intercept of the equation depends on $L\infty$ (asymptotic length) and k (a curvature parameter that determines the rate at which the observed fish length approaches the estimated asymptotic length, L_{∞}). A plot of L_{t+1} versus L_t is called Walfod plot (Ricker 1975). The slope of the plot is determined solely by the value of k. The hypothesis that density-dependent effects act primarily on fish asymptotic length or adult fish growth rate was supported by tests on several fish species (e.g. plaice and haddock from Beverton and Holt 1957, Pacific Whiting from Dorn 1992, carp from Lorenzen 1996). Therefore, I modified the intercept of the Ford equation by relating it to abundance, as follows:

$L_{t+1}=a+b*Abundance+c*L_t$ ----------(2)

where L_t is length at age t (>=2), a and b are parameters for the linear relationship between L_{∞} and abundance and c is only directly related to k. The significance of an interaction term between Abundance and L_t was tested to determine if the abundance influences the k parameter.

The fecundity-length relationship was derived from the observed length specific fecundity data collected in 1969 and 1990 in the western basin (Muth and Ickes 1993). For the eastern basin sub-population, the length-specific fecundity relation was derived from the 1969 observations (Wolfert 1969, Fig 1). The age at maturity was set at age 3 for both sub-populations (Muth and Ickes 1993).

Density-dependent early survival

For the western basin sub-population, the abundances of age-specific mature female walleye (i.e. fish age 3 and over) were calculated from lakewide stock-assessment estimates

for age 2 to age 7+ from 1978 to 1999 (MacLennan et al 2003) by assuming a 1:1 sex ratio. Age-specific fecundity was obtained from Muth and Ickes (1993). Annual egg productions from 1978 to 2000 were calculated by summation of the numbers of eggs produced by each age group. The numbers of age 1 fish in each year from 1979 to 2000 were derived from number of age 2 fish by assuming the annual survival rate from age 1 to age 2 as 0.66.

For the eastern basin sub-population, the Van Buren Bay sub-population, one of the dominant spawning populations on the south shore of the eastern basin (Don Einhouse pers. comms), was assumed to be representative of the eastern basin fish generally. The abundances of mature female walleye from 1991 to 2000 were derived from the analysis of the mark-recapture study described in Chapter 3. The average fecundity of mature female walleye in the eastern basin was derived from Wolfert's (1969) study. The egg production was calculated as the product of the abundance of mature female walleye and the average fecundity. The recruitment estimates in Chapter 3 were assumed to reflect the abundance of age 3 fish. These annual recruitment values were used to estimate the abundance of each cohort at age 1 by assuming a fixed annual survival rate from age 1 to age 3 of 0.72.

The scatter plots between the number of eggs and the number of age 1 fish they produced were constructed for both sub-populations and a Shepherd's generalized stock-recruitment model (Shepherd 1982) was used to fit the data (Fig 2a, b). The Shepherd stock recruitment model is a generalization of the Beverton-Holt, Ricker, and Cushing models and it has the following form,

$$R=\alpha*E/(1+\beta*E^{\gamma}) \text{ ----------(3)}$$

where R is the number of age 1 fish, E is the number of eggs, α, β and γ are parameters. By taking different values of parameter γ, the model can exhibit the Beverton-

Holt form (γ =1), Cushing form (γ <1), and Ricker form (γ >1). Therefore, different values of the parameter (γ) reflect the different kinds of density-dependent mechanisms that can underlie the stock-recruitment relationship. Generally, parameter β defines the stock density at which the slope of the stock-recruitment curve is reduced by a significant amount and thus was used as an index parameter to simulate the density effects responding to the habitat changes in this chapter. Parameter α is the slope of the curve at origin and is directly related to the intrinsic population growth rate that is defined by juvenile survival, adult fecundity and age at maturity (Myers and Mertz 1998). The parameter α defines the extinction harvest rate (Myers and Mertz 1998). Basin-specific stock-recruitment curves were estimated from annual, basin-specific estimates of egg production and cohort abundance at age 1 using non-linear regression (Gaussian-Newton algorithm implemented in Matlab) assuming a lognormal error distribution (Hilborn and Walters 1992, Quinn and Deriso 1999). A 50:50 sex ratio was assumed for both eggs and recruits.

A preliminary study showed that the stock-recruitment data for the western basin sub-population was extensive enough to warrant fitting a Shepherd curve (Fig 2 a). However, for the eastern basin (Van Buren Bay) sub-population, lack of data at low spawning stock size and few data points created difficulties in estimating the three parameters of the Shepherd stock recruitment model. Serious overestimation of the α parameter was especially likely in this situation (Myers et al 1997). The parameter α is directly related to the population intrinsic growth rate that is defined by the fecundity, juvenile survival and age at maturity (Myers et al 1997). If the age at maturity and juvenile survival rate are assumed to be approximately the same for both sub-populations, then the average ratio of fecundity of the eastern basin sub-population versus the western basin sub-population can approximate the

ratio of parameter α between the two sub-populations. This ratio is about 0.74 (Fig 1). Using this approximation, the parameter α for the eastern basin sub-population can be derived from the well defined α value of the western basin sub-population. Given this estimate of α for the eastern basin sub-population, robust estimates for the other two parameters (β and γ) of the Shepherd stock-recruitment model for the eastern basin sub-population can be estimated from the limited data available.

Walleye Migration Patterns

The migration of walleye between two sub-populations was assumed to be driven by a search for optimal growth habitat (e.g. increased availability and preferred temperature conditions), and not for reproductive habitat. This assumption implies that, at the end of the summer-fall growing season, all migratory walleyes will return to their sub-population-specific spawning grounds. The major migration flow is from the western basin through the central basin to the eastern basin. The sub-population-specific annual migration rate was estimated from a lakewide tagging study (Wang 2003).

Harvest Strategies

During the summer harvest season, the walleye experienced the harvest strategy specific to the basin where they were resident. The harvest rate was defined as the percentage of walleye abundances caught by the walleye fishery. The quota management system was used for part of this simulation study: the annual harvest quota was derived from the desired harvest rate and the current total abundance of walleye. Basin-specific quotas were then determined by multiplying the overall quota by a fraction specific to each basin. These basin-

specific fractions were estimated from the mean observed basin-specific harvest from 1978 to 2000 (MacLennan et al 2001). The model assumes that each basin-specific quota is always taken, provided there are sufficient walleye in the basin to meet it. If the harvest allocated to any one basin exceeds the number of walleye in that basin, all of the walleye in the basin are harvested and remaining quota is evenly distributed over the other basins.

Climate Change Scenarios

The climate change scenarios were designed to mimic the results from Chapter 3. The future climate changes caused a decrease in thermally-optically suitable habitat area for walleye in the western basin but an increase in the central and east basin. Intensified migration from west to east caused by changes in the habitat quantities among the basins may change the effect of density on walleye adult growth pattern in any direction, depending on the interactions between walleye abundance and habitat in the central and eastern basins. In this chapter, I only simulated the combined effects of a decrease in juvenile habitat for the western basin sub-population and an increase in adult growth habitat for both sub-populations. This was done by increasing the β parameter of the western basin stock-recruitment relationship and decreasing the b parameter in model (2) that drives adult growth in both sub-populations.

Structure of Simulations

The processes and parameters used in the simulation study are in Table (1). Each simulation run started with an initial population of fish age 2 and over at the beginning of the first simulation year. The following processes were experienced by each sub-population in

the time sequence during each simulation year:

Egg production—Recruitment (Density-dependent)—Natural Mortality—Migration—Harvest—Growth (Density-dependent)---->next year cycle

The initial age structures for each sub-population were selected arbitrarily because the initial age structure did not influence the equilibrium population state in this study. The size structure for fish at age 2 and over was established as follows: at the beginning of each simulation year, length at age 2 for each sub-population was randomly selected from a normal distribution with mean and variation determined from basin-specific back-calculated estimates of mean cohort length at age 2 (see Chapter 3). The means of length-at-age 2 for the western basin sub-population and the eastern basin sub-population were 282 mm and 313 mm, respectively, and standard deviations were 26 mm and 21 mm, respectively. The lengths at age 3 and over for the first simulation year were sequentially calculated using density-dependent growth model based on length at age 2 of the first year and initial abundance, and age-specific egg production was calculated based on the age-specific abundance, size structure and fecundity-length relationship (see Density-dependent growth and fecundity described above for detail). For the following simulation years, the length-at-age 3 and over were calculated from the previous year's fish of one year younger and abundance of the previous year. The simulation was run for 150 years to make sure of acquisition of equilibrium for each sub-population.

A stochastic process was built into stock-recruitment models to assess the sensitivity of the extinction harvest rate (i.e. the harvest rate that is just sufficient to drive a population to extinction) of each sub-population to random variation in recruitment. In the stochastic simulation study, the number of age 1 fish in each simulation year was sampled from a log-

normal distribution with the mean calculated from *E-R* relationships and variance estimated from empirical *E-R* data (refer to the section "density dependent early survival" above). A total of 100 replicate simulations, each running for 150 years, were used in the stochastic study. The extinction probability for each sub-population was defined as the fraction of total number of replicates that exhibit extinction of that sub-population.

Result

Empirical Characterization of Effects of Density on Growth and Recruitment

Regression analysis demonstrated that population abundance significantly influences the walleye annual growth rate. The parameter *b* in the growth model (2) was significant for both sub-populations ($t_{(44)}$= -3.16,P-value=0.003 for the eastern sub-population and $t_{(64)}$= -3.01, p-value=0.004 for the western sub-population). The parameter *c* in model (2) was also significant ($t_{(44)}$= 36.26, p-value<0.001 for the eastern sub-population and $t_{(64)}$= 62.92, p-value<0.001 for the western sub-population). The fact that the interaction term, between walleye abundance and length at one year younger in model (2), was not significant ($t_{(44)}$= -1.45, P-value = 0.15. for the eastern basin sub-population and $t_{(64)}$= -0.69, p-value=0.49 for the western basin sub-population) suggests that there is a common slope for Walford's plot at different levels of walleye abundances and thus that abundance does not influence the *k* parameter in model (1). At a higher level of abundance, walleye has a lower absolute growth rate and a lower asymptotical length but the rate (*k*) of progression toward asymptotical length remains unchanged.

Generally, the Shepherd stock-recruitment model captured the main trends of walleye stock-recruitment relationships for two sub-populations. The shape parameter γ is larger than

one for both sub-populations (Table 1), indicating that walleye stock-recruitment curve in Lake Erie is similar to a Ricker curve.

Simulated Behaviours of the Meta-population Model Equilibrium Abundances

Both sub-populations increased initially from the arbitrarily selected initial levels of abundance and reached their equilibrium levels of abundance relatively quickly (Fig 3). The western basin sub-population has substantially larger equilibrium abundances than the eastern basin sub-population. For each sub-population, equilibrium abundance decreased with the increase in harvest rate, until the sub-population went extinct (Fig 4). The eastern basin sub-population had a lower extinction harvest rate than the western basin sub-population.

An increase in the parameter (α) in the Shepherd's stock-recruitment model resulted in an increase in the equilibrium abundance at each harvest levels and an increase in the extinction harvest rate (Fig 5). In contrast, an increase in parameter (β) in the Shepherd's stock-recruitment model reduced the equilibrium abundance but did not change the extinction harvest rate (Fig 6). Unlike the stock-recruitment parameters, changes in parameter *b* in the growth model (2) caused changes in both the slope and the intercept of the abundance-harvest plot (Fig 7) such that the equilibrium abundance at some harvest rates actually increased with the shrinkage in adult habitat that an increase in *b* implies.

Sensitivity of Populations Extinction Probability to Recruitment Variability

The extinction probability at low harvest rate decreased with an increase in lognormal standard deviation for both sub-populations (Fig 8), which suggests that a high variance in

recruitment helps walleye populations resist high harvest rates.

Sensitivity of Population Behaviours to Effects of Climate Changes

After imposing the basin-specific changes in juvenile and adult habitat supply expected to occur as a consequence of climate change, the equilibrium abundance for the western basin sub-population was substantially reduced. There was no effect on the extinction harvest rate levels (Fig 9) for either sub-population.

Sensitivity of Population Behaviour to Quota Management

After imposing the quota management system on the model, the dependence of both equilibrium abundance and extinction probability on harvest rates was changed for both sub-populations (Fig 10). Compared to the results from the simulation without quota system, for the eastern basin sub-population, the equilibrium abundance at all harvest rates and its extinction harvest rate increased. For the western basin sub-population, there were small decreases in both the extinction harvest rate and the equilibrium abundance at each harvest rate (Fig 10).

Discussion

Effects of Density-dependent Processes on Population Behaviour

Two density-dependent processes (i.e. recruitment and growth) controlled walleye metapopulation dynamics in this study. Although both processes modified the stock-recruitment curve to influence the population dynamics, each played an important role in a different life stage. Therefore, a better grasp of the stock-recruitment behaviour is crucial to understand those behaviours.

In Fig 11, a schematic Shepherd stock (eggs)-recruitment curve and several replacement lines with different slopes of $S(i)$ at the harvest rate i (where i =0 (harvest rate of 0), h (harvest rate of h) and e (extinction harvest rate)) were drawn. The slope $S(i)$ monotonically increases with the increase in the harvest rate i (Myers and Mertz 1998). The intercept points between replacement lines and the stock (eggs) recruitment curve defined the equilibrium level of population abundances, For example, $E(0)$ and $E(h)$ are the equilibrium levels of spawners or eggs without harvest and at harvest rate of h, respectively. A higher harvest rate resulting in a high slope $S(i)$ has a low equilibrium level of abundance, i.e. $E(h)<E(0)$. When the harvest rate is large enough to make the slope of replacement lines be equal or larger than the initial slope (i.e. $S(i)= S(e)$), the population goes to extinction.

The peak point (i.e. maximum recruitment) of the Ricker form (i.e. $\gamma >1$) of Shepherd stock-recruitment model can be found by setting the first derivative of stock recruitment equations (model 3) equal to zero and solving for stock size, the solution are:

R_p: *the maximum absolute recruitment* = $\alpha(\beta)^{(-1/\gamma)}(\gamma)^{-1}(\gamma-1)^{(\gamma-1)/\gamma}$

E_p: *the stock size (or egg production) producing* $R_P = [\beta(\gamma-1)]^{-1/\gamma}$

All three parameters in model (3) are involved in defining the peak value of recruitment. The peak point decreases with an increase in β (Fig 12) or a decrease in α (Fig 13). If the parameters in model (3) are assumed to have no impacts on fish age at maturity and survival rate after recruitment, then the replacement lines (i.e. a function of survival rate and age at maturity, Myers et al 1997) at the same harvest rate (h) remain the same. Therefore, the equilibrium level of abundance at a particular harvest rate (i.e. the point where the replacement lines and stock (or eggs)-recruitment curve intersect) decreases with an increase in β or a decrease in α (i.e. E1(h)<E2(h) in Fig 12, 13). Also, α (maximum

recruitment per spawner at low stock size) defines the extinction harvest rate: for a replacement line to specify an equilibrium abundance greater than zero, it must have a slope that is less than α (Fig 13). The smaller the α value is, the lower extinction harvest rate will be. In contrast, the parameter β affects the value and position of the maximum recruitment but it does not influence the extinction harvest rate (Fig 12).

Changes in the density-dependent process that affect growth and fecundity modify the population equilibrium abundance through a different mechanism. This mechanism produces intersecting equilibrium abundance-harvest curves, when *b* is changed (Fig 7). The mechanism that generates these intersections is described below. An increase in parameter *b* in model (2) moves the Walford plot downward (Fig 14) for the same population abundance level. This implies a decrease in adult size at the same population level and thus a decrease in the egg production due to the positive relationship between length and fecundity (Fig 1). These relations can be summarized in terms of a fixed egg-recruitment curve and a variable stock-recruitment curve, where the position of the stock-recruitment curve shifts to right as *b* is increased (Fig 15). There is an intersection point (A) where the new stock-recruitment curve (the one derived from $b^*>b$) meets the old stock-recruitment curve (the one derived from *b*). The position of A is determined by the difference between *b* and b^*, however the position of the zero harvest replacement line (S(*0*)) is unaffected by the value of *b*. If the intersection point (A) is located to the right of the replacement line S(*0*) (as shown in Fig 15), then equilibrium stock size under harvest rate of *h* will be greater for stock-recruitment curve with b^* value than the one with *b* value when S(*h*) (i.e. replacement line with a harvest rate of *h*) is located to the right of the points (A), equal when S(*h*) intersect point (A), and smaller when S(*h*) is located to the left of the replacement line S(*h*). As the difference between *b* and

*b** exceeds some threshold and the intersection point (A) is created in the right of the zero harvest rate replacement line S(*0*), we would expect that equilibrium stock size for *b** would be lower for the stock-recruitment curve with *b** than the one with *b* at all harvest rates. This provides an explanation for the behaviour of the model illustrated in Fig 7 (i.e. the curve of equilibrium abundances versus harvest rates at different values of *b* intersected each other).

Effects of Recruitment Variability and Quota Management on Population Behaviour

The lognormal distribution of recruitments used in this study has the potential to influence the population dynamics. By considering the stock-recruitment process as a series of individual life-history stages and the survival rates for each stage as independent, identically distributed random variables, the lognormal distribution of recruitment can be derived based on the Central Limit Theorem. In fisheries practice, many researchers have shown that a lognormal model provided a better fit to the observed stock-recruitment data, and thus lognormal distribution is regarded as the default distribution of recruitment (Peterman 1981, Walter and Ludwig 1981, Archibald et al 1983, Armstong and Shelton 1988, Myers et al 1997, Barrowman and Myers 1999). However, the estimates of parameters of stock recruitment models by lognormal assumption will not represent the average number of recruits for any level of spawner stock due to existence of difference between the geometric mean and the arithmetic mean (Ricker 1957). Hilborn (1985) demonstrated that the average stock-recruitment curve from lognormal model was defined by the estimated parameters modified by the lognormal standard deviation of recruitment. The modification of lognormal estimated parameters resulted in an increase initial slope (i.e. α value) of the average stock-recruitment curve with an increase in the lognormal standard deviation of recruitment. Due to

the fact that the extinction harvest rate increases with the increase in α value, the population with a large lognormal standard deviation in recruitment will be expected to have a higher extinction harvest rate (e.g. Fig 8).

The quota management system used in this study has the effect of providing a harvest shelter for the eastern basin walleye and those western basin walleye that migrate to the east. However, it also has the effect of exposing the western basin walleye to a higher harvest rate. Because of this shelter effect, the eastern basin walleye are able to sustain higher equilibrium abundance levels and a higher extinction harvest rate than they exhibit in the absence of quota management. However, this shelter effect requires the existence of the western basin sub-population. As the western basin sub-population goes to extinction, the eastern basin sub-population sharply decreases to extinction with a relatively smaller increase in the harvest rate (Fig 10). With the quota system in place, the migration pattern of walleye among the basins will significantly participate in shaping the dynamics of the populations. The basin-specific allocation of quota will interact with these migration patterns to force new dynamic behaviour on sub-populations.

Impacts of Climate Changes on Lake Erie Walleye: Preliminary Results and a Plan for Future Research

In this study, density-dependent processes are the only force driving walleye meta-population dynamics in Lake Erie. Climate changes, causing shrinkage of the western basin walleye habitat and increases in the eastern and central basin walleye habitat, were assumed to affect only the walleye early life survival rate in the western basin sub-population and adult growth rate of both sub-populations. The projections from most general circulation

models (GCMS) of the Earth's climate system, (e.g. GCMS and HadCM3), agree that future climate changes in the Great Lakes region will be characterized by increases in air temperature, precipitation, and frequency of climatic extreme events, (e.g. heavy rainstorm, tornadoes: Kling et al 2003). Lake Erie will respond to those climatic changes by an increase in evaporation, a decrease in the lake water levels and an increase in oxygen depletion in the central and eastern basins because of prolonged stratification periods in these two basins, caused by longer, warmer summers. An increase in spring warming rate can increase walleye recruitment (Busch et al 1975, Shuter et al 2002). In contrast, an increase in the frequency of storms, especially during walleye spawning season (i.e. spring season), can result in high mortality rate of walleye eggs and thus lower recruitment (Roseman et al 2001). These climate-induced effects on walleye recruitment can significantly modify walleye stock-recruitment relationships and thus change the equilibrium abundance, and extinction harvest rate of each sub-population. An increase in oxygen depletion during the summer and fall seasons in the central basin and the eastern basin can potentially increase the mortality rate and decrease the growth rate of walleye in the whole lake because the summer-fall migration pattern leads all individuals to experience this deterioration in living conditions in the central and eastern basins.

If climate change causes any changes in the parameters of the stock recruitment model (model (2)) and/or the growth model (model (1)), then the behaviours of each sub-population are predictable, as illustrated (Fig5, 6, 7) in the analysis of the sensitivity of equilibrium abundances and extinction harvest rates to changes in these parameters. In the study, age at maturity for both sub-populations was assumed to be constant (i.e. age 3). However, recent studies showed that walleye in the western basin can be mature at age 2

(Wang 2003). This earlier maturation would definitely change the empirical estimates of the stock-recruitment relationship for each sub-population by modifying its parameters (i.e. a larger number of eggs will be associated with the same level of recruitment). The sensitivity analysis provided an assessment of the sensitivity of equilibrium abundances to changes in these parameters.

The model created in this study can be used to examine the potential impacts of other changes in the environment and biology of Lake Erie walleye. For example, it is possible that the temperature increases due to global warming may increase growth, decrease age at maturity, and increase reproductive investment (i.e. relative fecundity) of walleye (Baccante and Colby 1996). Reproductive investment is directly related to the growth parameter (k) in model (1) (Lester et al 2004). In addition, walleye migration pattern may change under the influence of strong density dependent effects, when the suitable habitat shrinks in the western basin (as projected in Chapter 3). Future extensions of this model might explicitly include temperature effects on walleye early life survival and reproduction, and density-dependent migration.

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Table 1. The processes and parameters used in the simulation study

Categories	Processes or Model	Parameters	
		Western	**Eastern**
Density dependent on survival and stochasticity	$Age1=\alpha*Eggs/(1+\beta*Eggs^{\gamma})$	Age1-millions Eggs-billions α= 0.065 β= 0.2e-4 γ=1.32	Age1-thousands Eggs-billions α=50 β= 2.96 γ=1.72
	Stochastic Standard deviation	0.84	0.58
Density dependent on growth	$L_{t+1}=a+b*Abundance+c*L_t$ t: age >=2 (Length in mm)	*a*=182.9 *b*=-2.2e-4 *c*= 0.7	*a*=185.3 *b*=-3.5e-4 *c*=0.7
Length and fecundity relationship	Ln(Feundity)=A+B*Ln(Length) (Length in mm)	a= -10.39 b=3.55 In thousand: a=-17.38	a=-13.98 b=4.08
Survival rate and stochasticity	Annual survival rate above age 1	0.66	0.72
Migration rate	Basin specific	Total: 0.78 To central:0.5 To eastern:0.28	Total : 0.05 To central:0.05
Harvest rate	Lakewide average harvest rate	0-1	
	Basin specific	Quota allocation Western:0.63 Eastern:0.05 Central: 0.32	
Climate change scenarios	Habitat shrinking in western basin and increase in eastern basin	2*β *and* 0.5**b*	0.5**b*

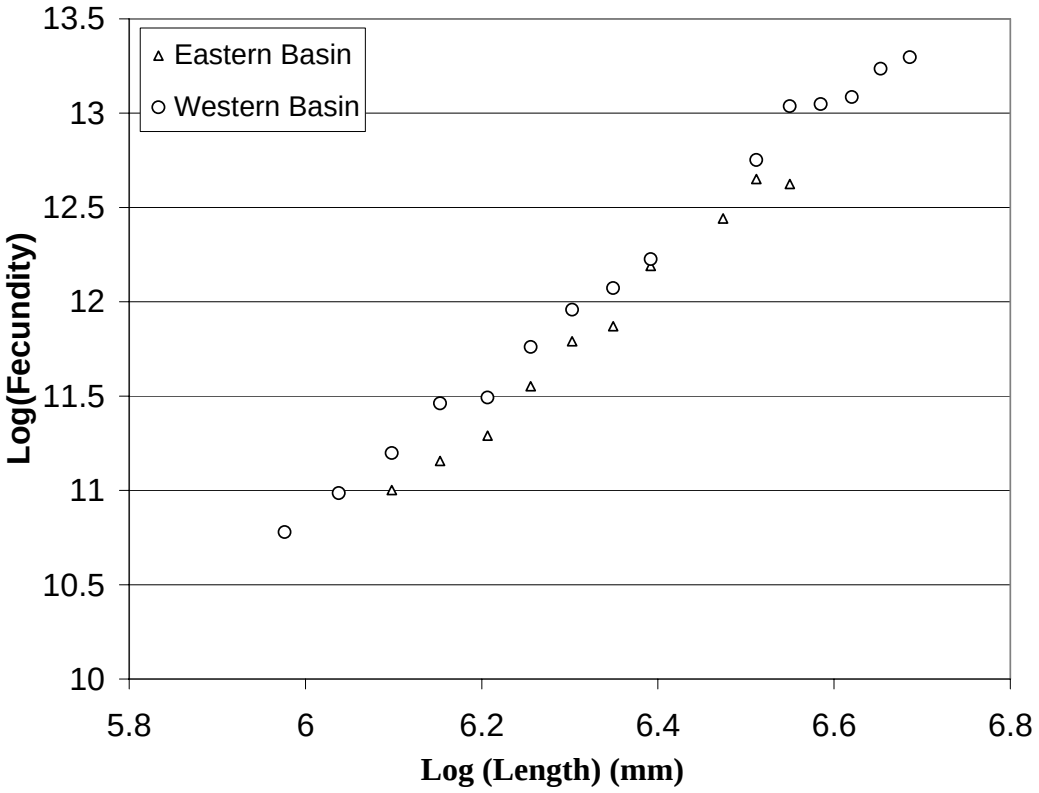

Figure 1. Relationships between fecundity and length of walleye for two subpopulations in Lake Erie.
Note: log—natural logarithmic base

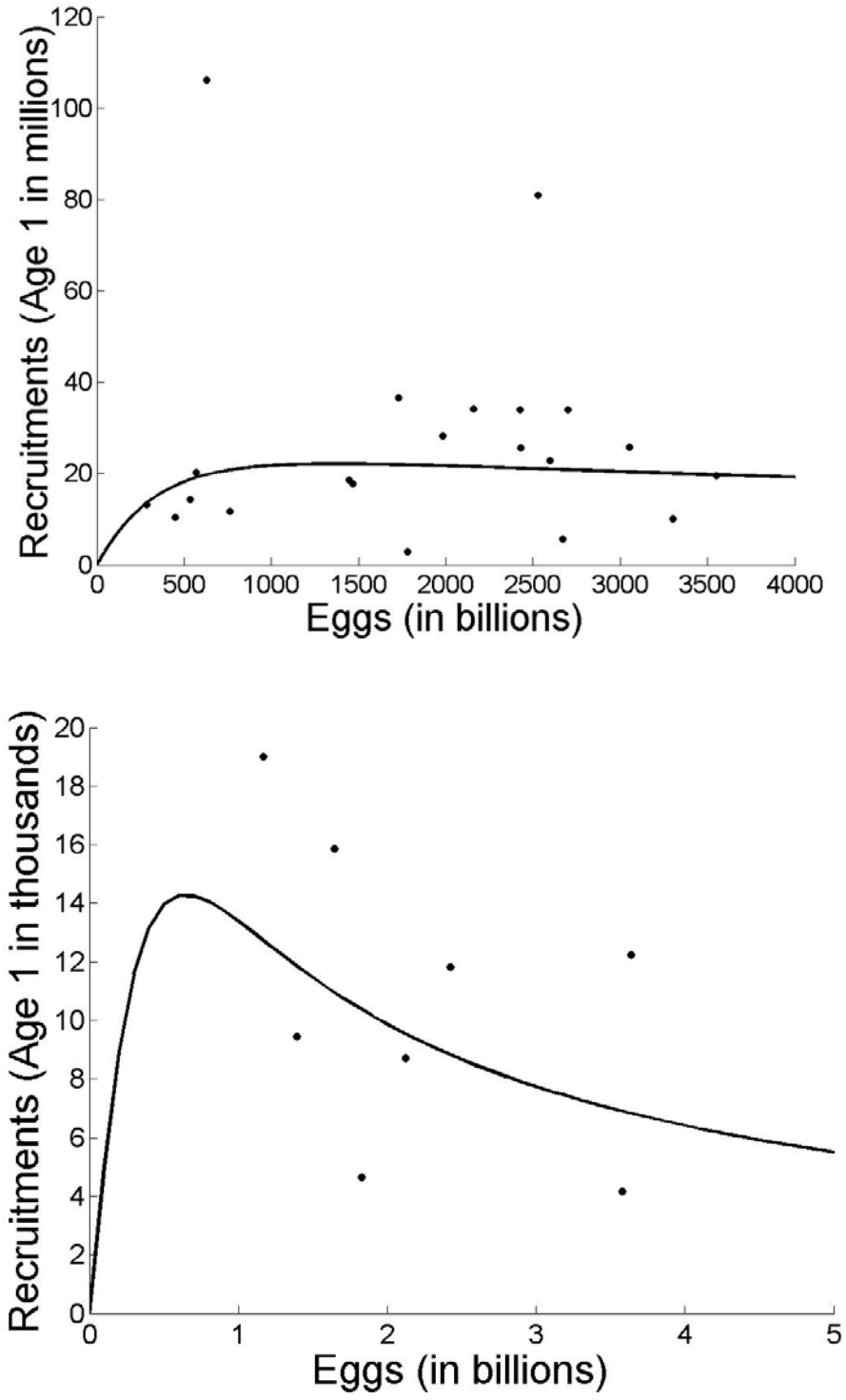

Figure 2. Relationships of number of eggs and number of age one fish for western basin (top) and eastern basin (bottom):
Dots—observed points; lines—Shepherd's stock recruitment model fitted by assuming log normal error structure

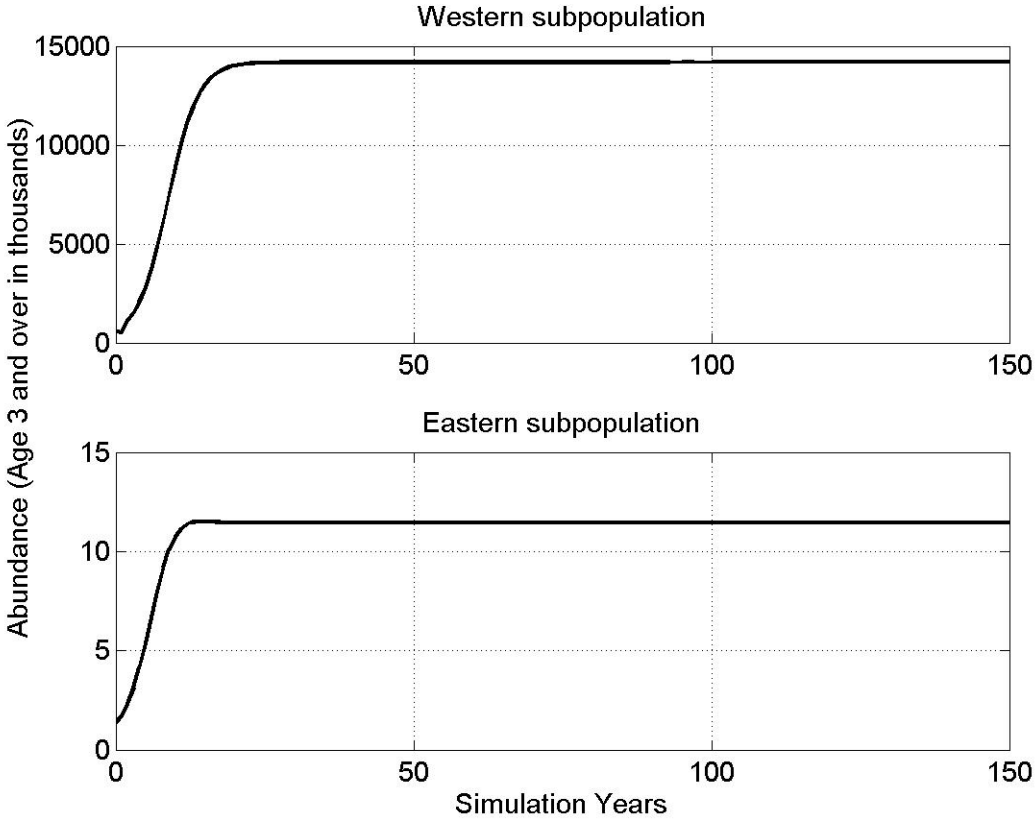

Figure 3. Population Trends of 150 simulation years for Lake Erie walleye

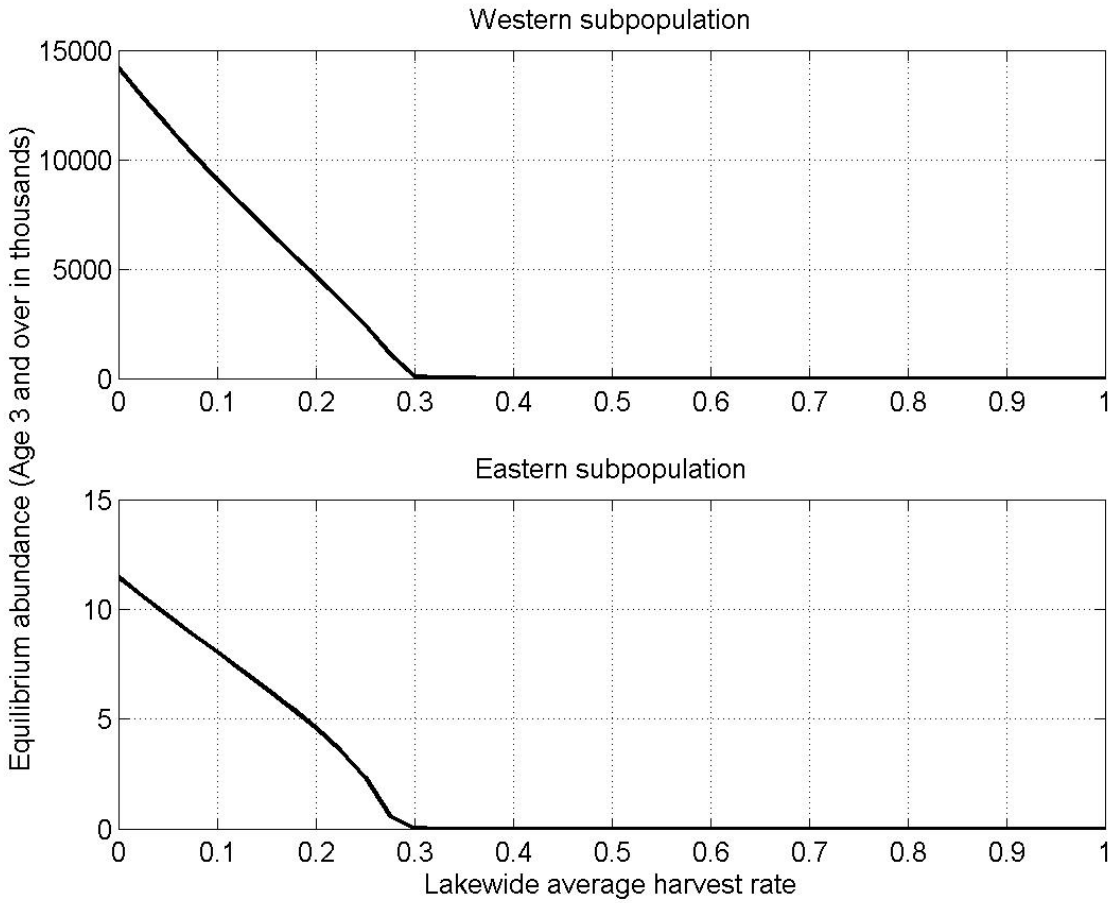

Figure 4. Relationships between equilibrium abundance and lakewide average harvest rate under deterministic conditions for Lake Erie walleye

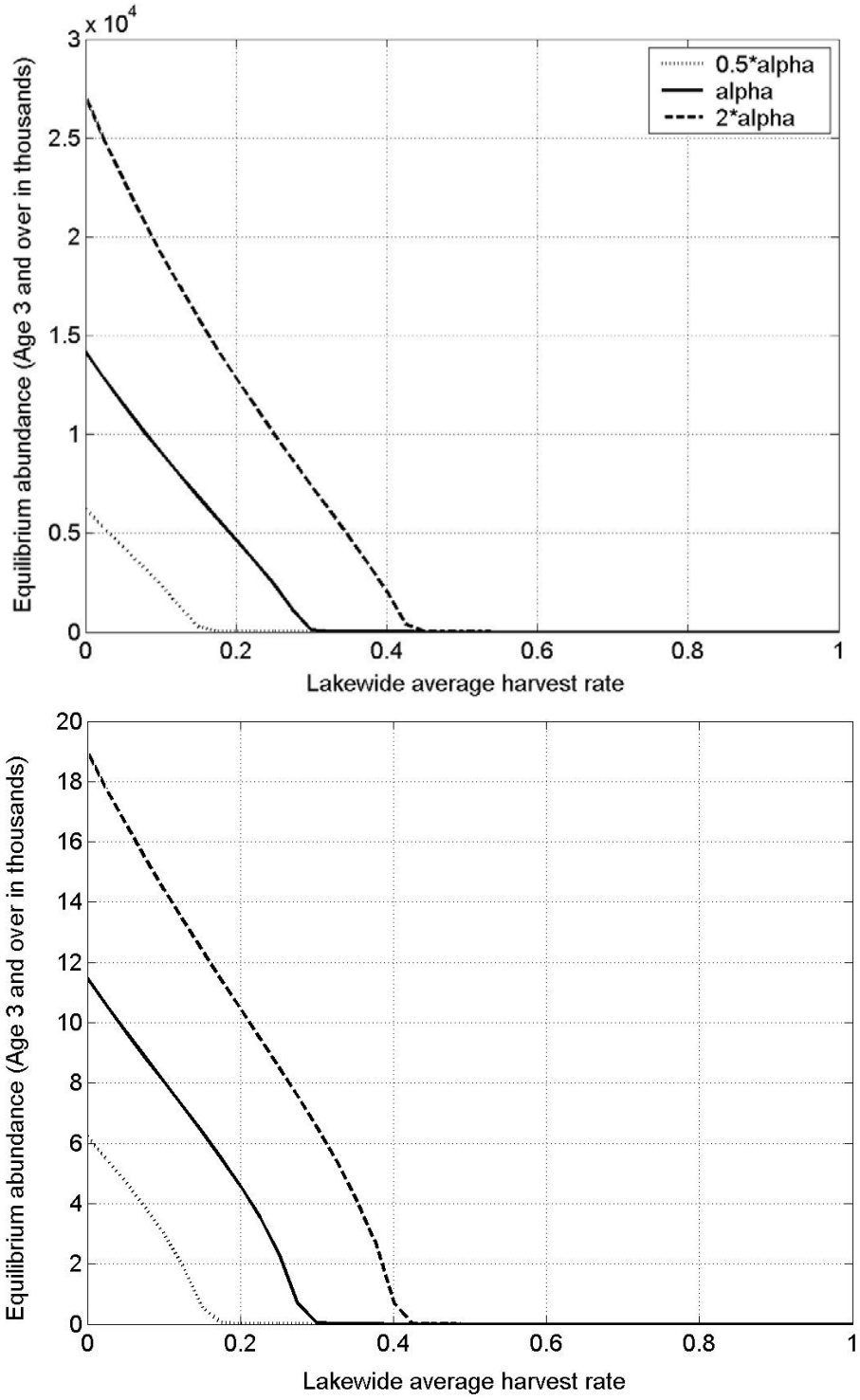

Figure 5. Changes of equilibrium abundances (top—western basin, bottom—eastern basin) vs lakewide average harvest rates at three different initial slope (α) in model (3): Alpha is the value empirically estimated from observed stock-recruitment data in Table 1.

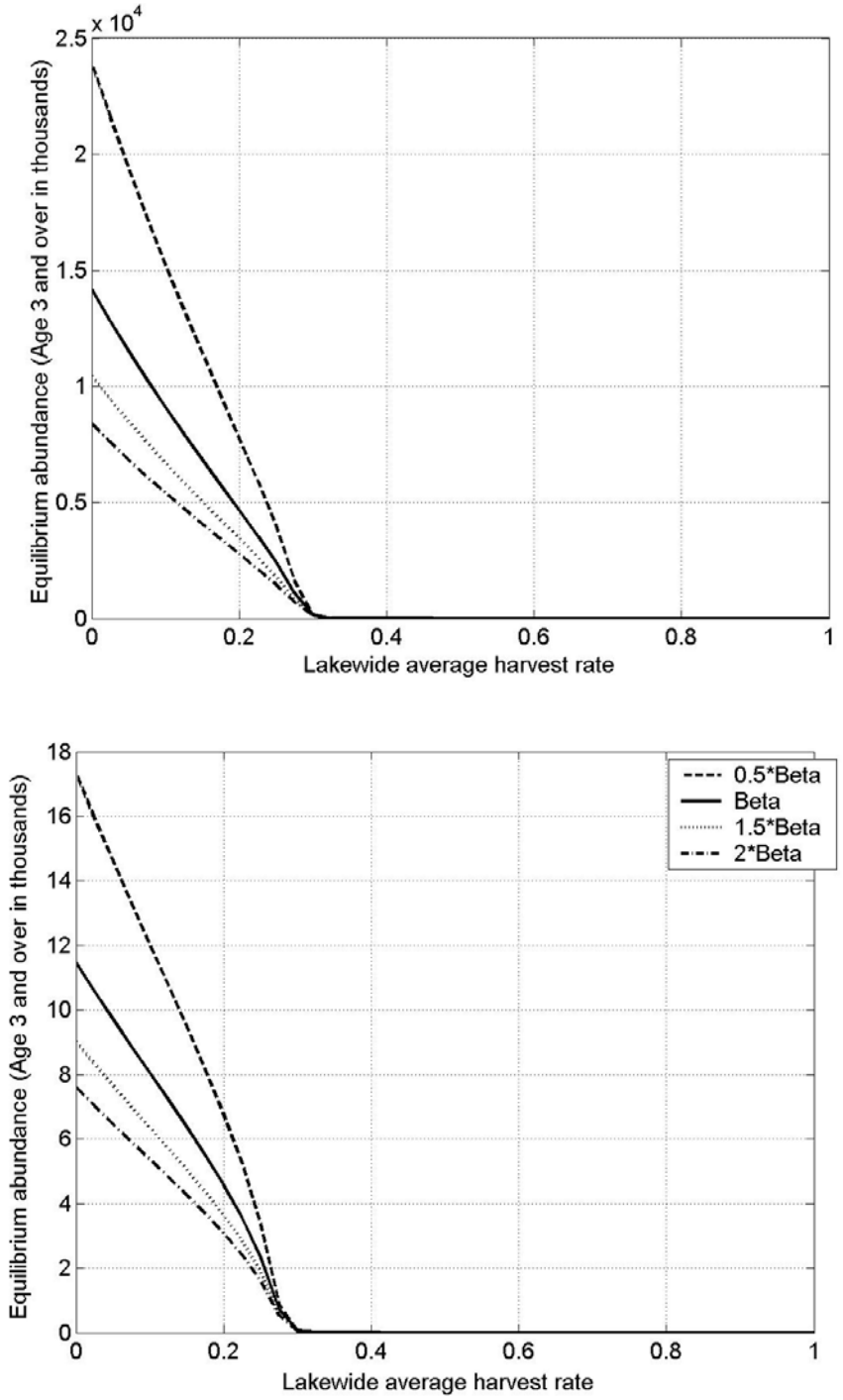

Figure 6. Changes of equilibrium abundances (top—western basin, bottom—eastern basin) vs lakewide average harvest rates at three parameters (β) in model (3): Beta (β) is the value empirically estimated from observed stock-recruitment data in Table 1.

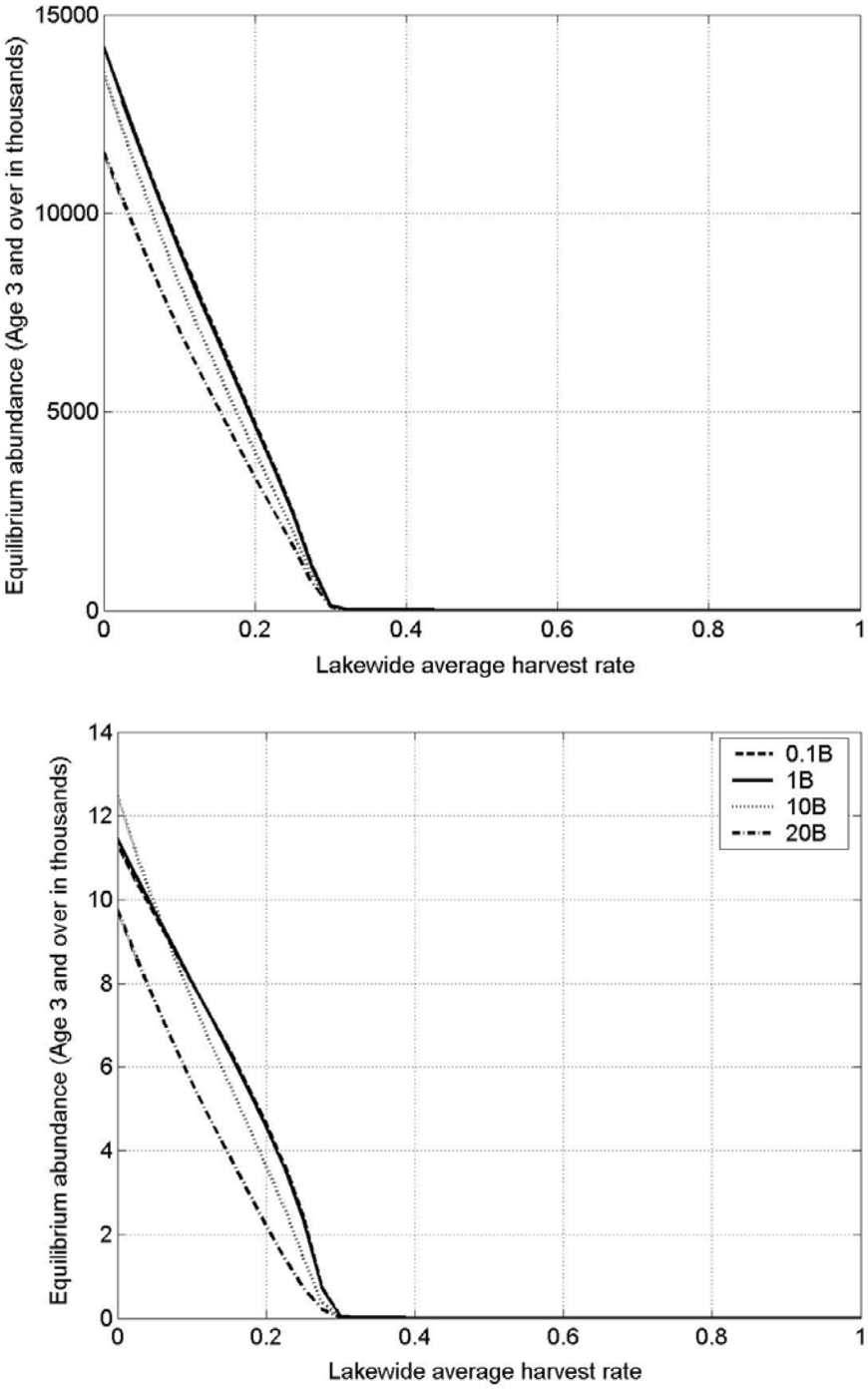

Figure 7. Changes of equilibrium abundances (top—western basin, bottom—eastern basin) vs lakewide average harvest rates at four different *b* values in model (2): B(*b*) is the value empirically estimated from observed growth data in Table 1.

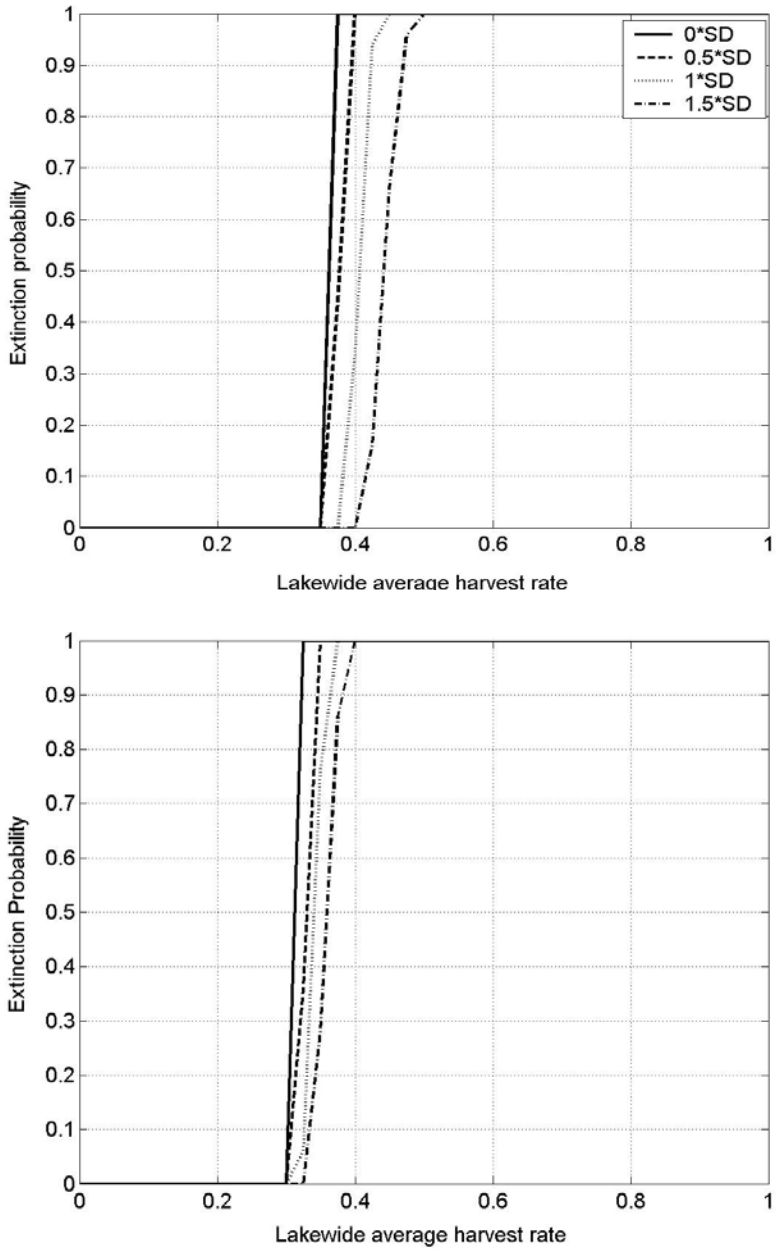

Figure 8. Sensitivities of population extinction probability to the standard deviation of log normal distribution of recruitment. SD (standard deviation) is estimated from empirical observations.
Top: the western subpopulation
Bottom: the eastern subpopulation

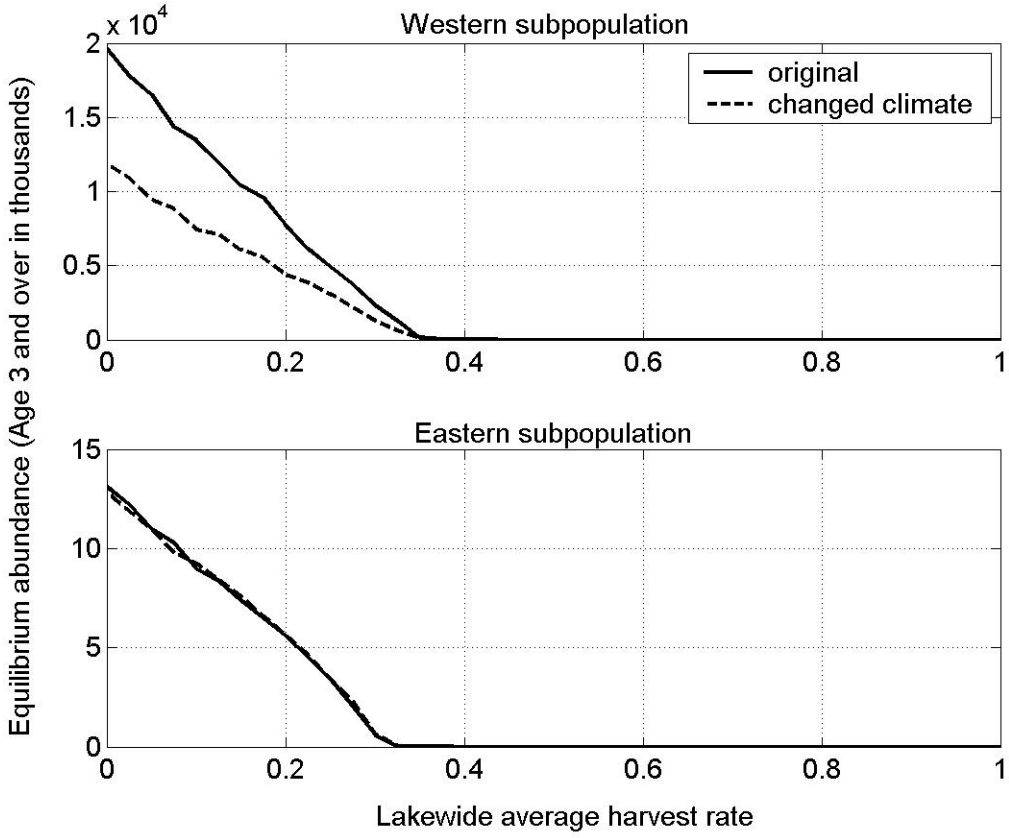

Figure 9. Comparisons of equilibrium abundance vs lakewide average harvest rate between current climate conditions (original) and changed climate conditions.
Note: one standard deviation of lognormal distribution of recruitment was used in the simulations.

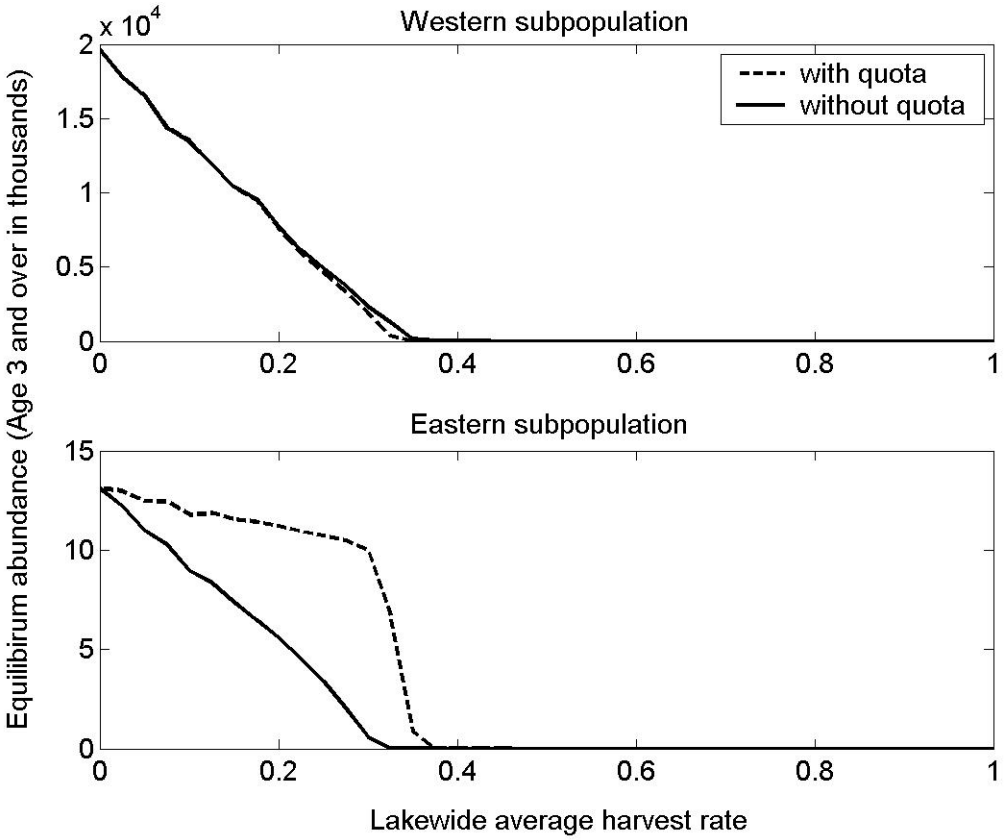

Figure 10. Comparisons of equilibrium abundances versus lakewide harvest rates between quota management and non quota management systems.
Note: one standard deviation of lognormal distribution of recuritment was used in the simulations.

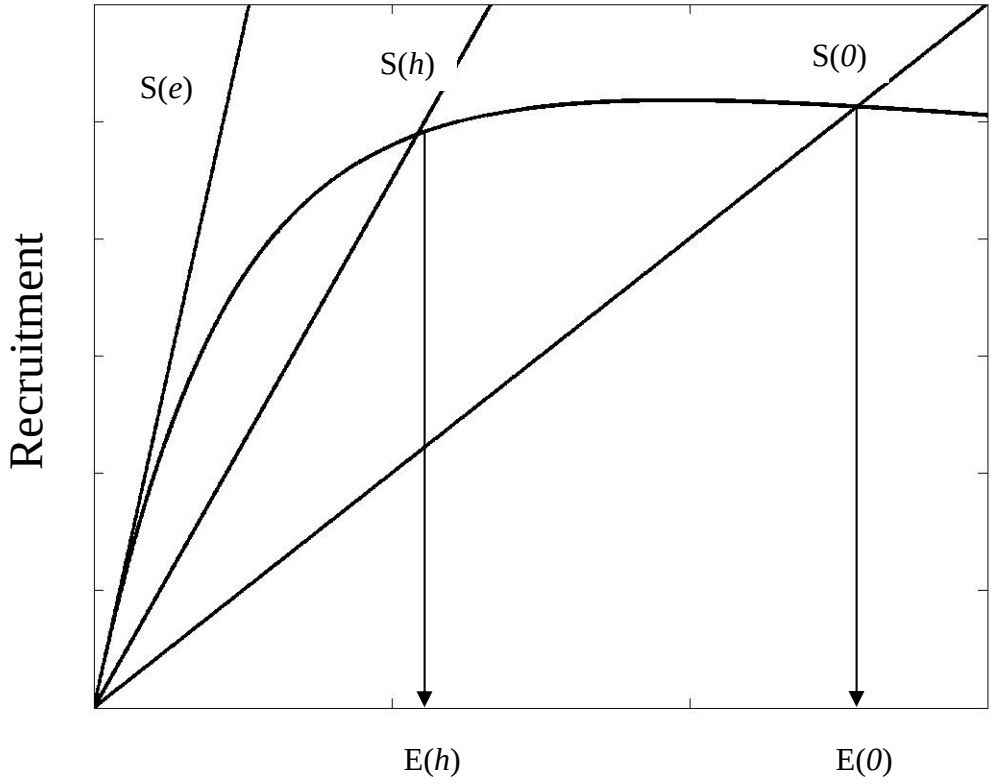

Figure 11. A schematic plot of the relationship between Shepherd stock-recruitment model and replacement lines as a function of harvest rate (fishing mortality).
Note: S(*0*)—replacement line with harvest rate of *0*; S(*h*)—replacement line with harvest rate of h; S(*e*)—replacement line with extinction harvest rate

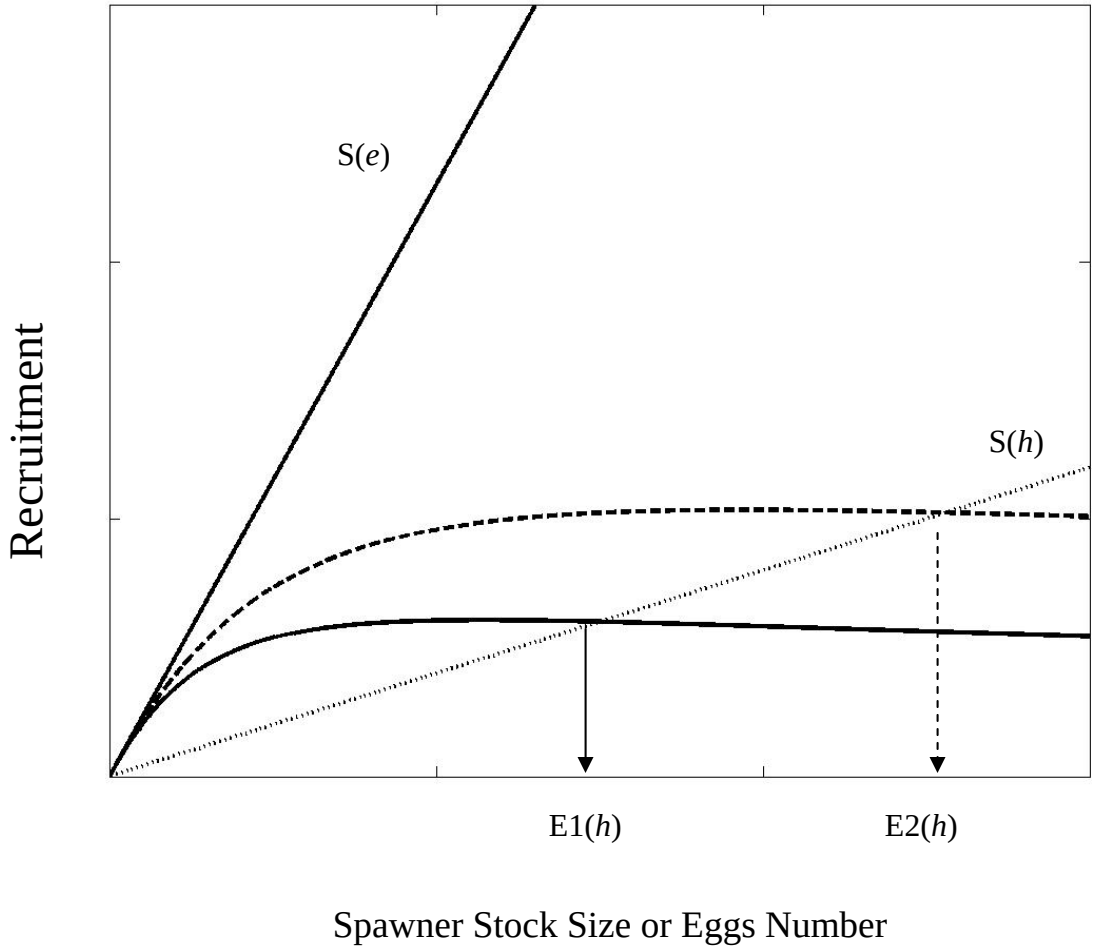

Figure 12. A schematic plot of Shepherd stock-recruitment curves with two different β values and their replacement lines under harvest rate (h) and extinction harvest rates (e). Note: Solid line and curves for small β; dashed curves for large β; dotted line: common replacement line at the harvest rate h; E1(h) and E2(h): equilibrium abundance levels from the curve with small β and large β at a same harvest rate (h); S(e) is the replacement line under the extinction harvest rates (i.e. two curves have a common extinction harvest rate and thus a common extinction replacement line)

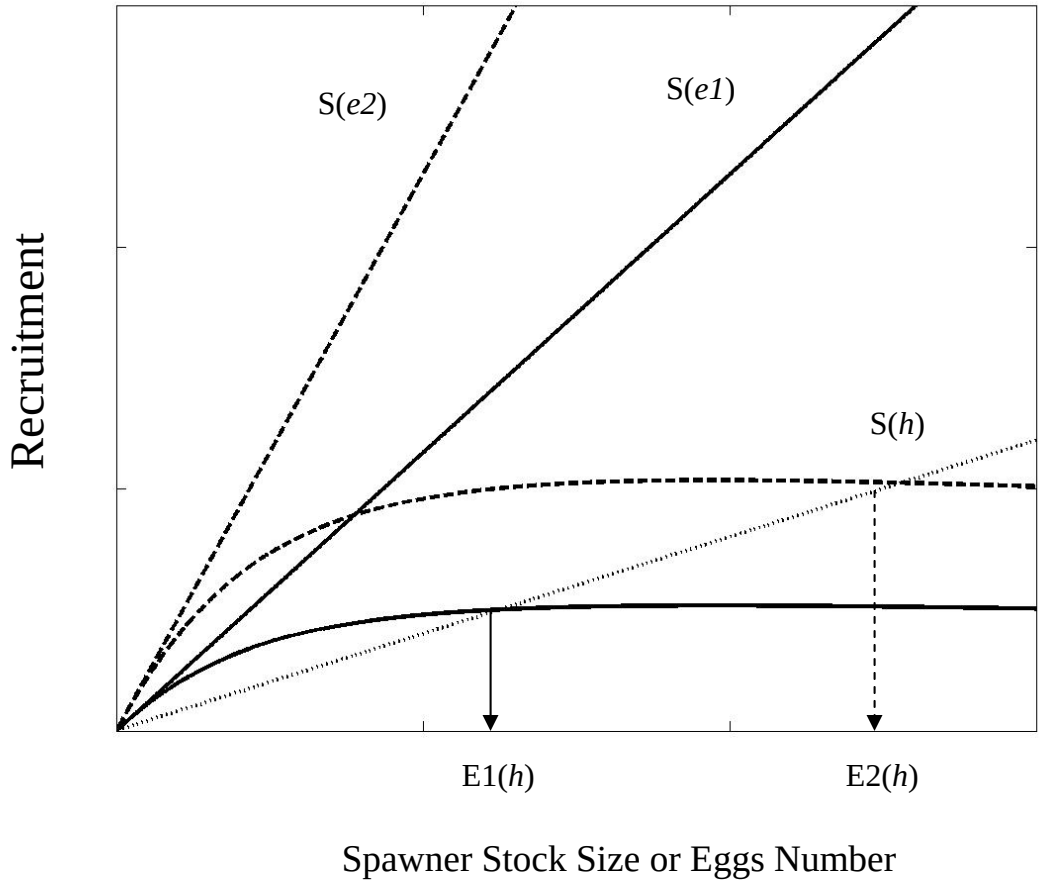

Figure 13. A schematic plot of Shepherd stock-recruitment curves with two different α values and their corresponding the replacement lines under harvest rate (h) and two extinction harvest rates (*e1*-for the large α curve and *e2* for the small α curve).
Note: Solid line and curves for the small α curve; dashed lines and curves for the large α curve; Dotted line: replacement line at the harvest rate h; E1(*h*) and E2(*h*): equilibrium abundance levels from the small α curve and the large α curves at a same harvest rate *h*, respectively.

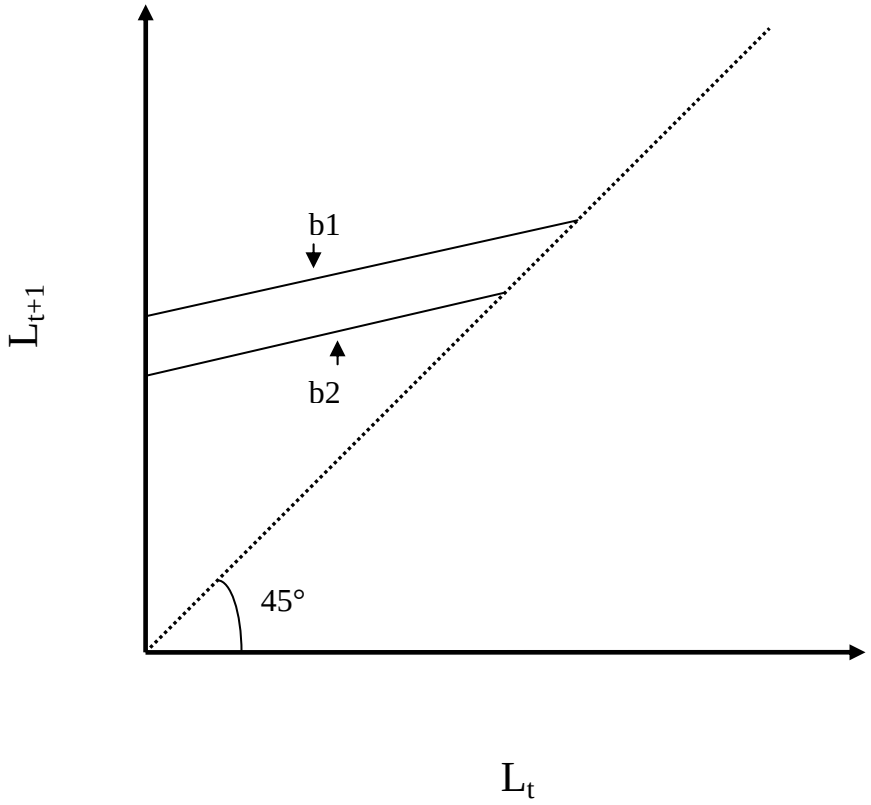

Figure 14. Two schematic Walford plots under two different b values (b1<b2) and the same abundance levels based on model (2) in the text.

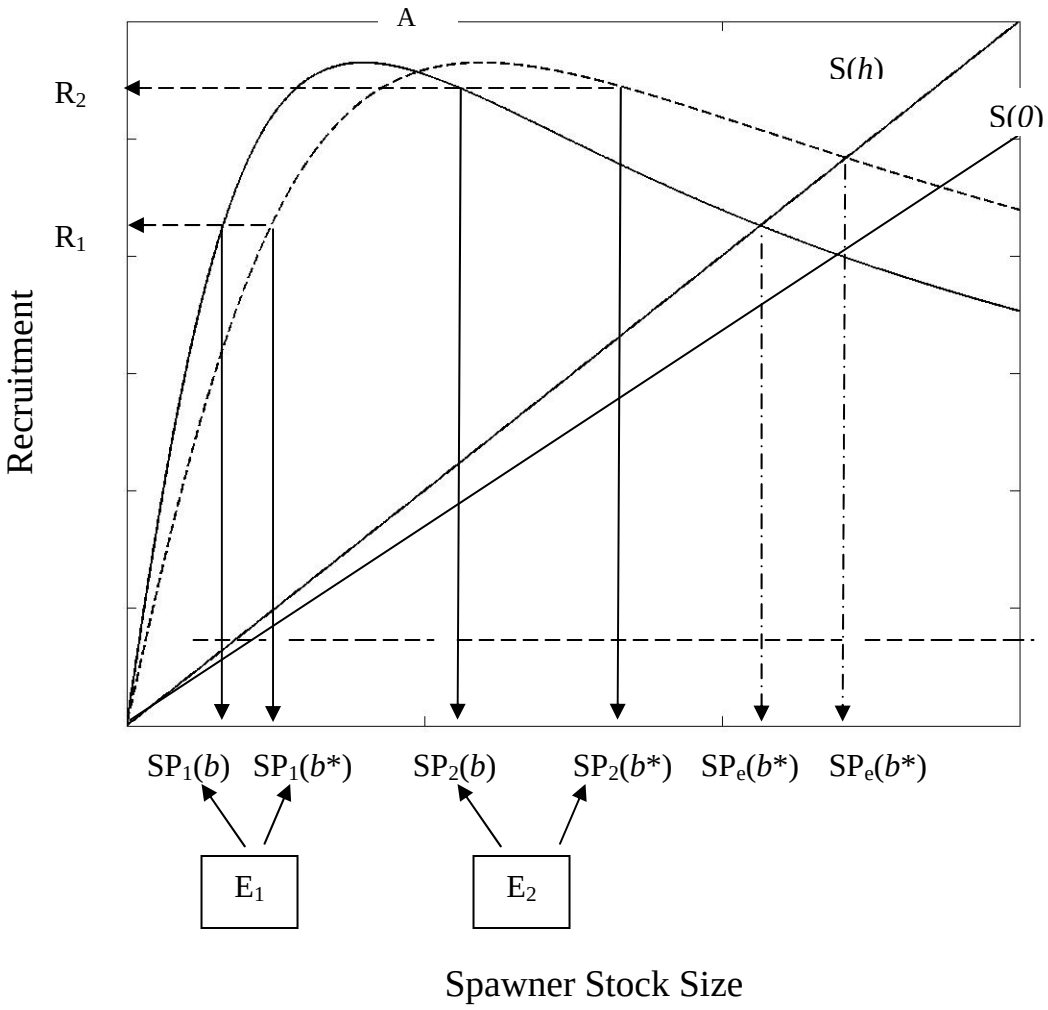

Figure 15. A schematic plot showing how the changes in parameter *b* in model (2) creates a new stock-recruitment curves and influence the equilibrium abundance. Note: solid curve—stock-recruitment curve with a value of *b*; dotted line—stock-recruitment curve with a value of $b^*>b$; A—intersection point between new (b^*)and old (b) stock-recruitment curves; S(*0*) and S(*h*)—replacement line at *0* harvest rate and *h* harvest rate, respectively; R_1 –recruitment produced by E_1 eggs; R_2—recruitment produced by E_2 eggs; $SP_1(b)$ and $SP_2(b)$—number of spawners producing E_1 and E_2 eggs under stock-recruitment curve with a value of b, respectively; $SP_1(b^*)$ and $SP_2(b^*)$—number of spawners producing E_1 and E_2 eggs under stock-recruitment curve with a value of b^*, respectively; $SP_e(b)$ and $SP_e(b^*)$—equilibrium abundance levels at *h* harvest rate under stock-recruitment curves with a values *b* and b^*, respectively; $SP_1(b)<SP_1(b^*)$; $SP_2(b)<SP_2(b^*)$; $SP_e(b)<SP_e(b^*)$ when point A is located in the left of replacement lines, and $SP_e(b)>SP_e(b^*)$ when the point A is located in the right of replacement lines.

Conclusion

In this thesis, the relationship between climate and dynamics of walleye populations were explored at both the regional scale (Chapter 1 and Chapter 2) and the local scale (Chapter 3 and Chapter 4).

In the regional scale, multivariate and meta-analytical approaches to data analysis were used to provide a general picture of how walleye populations have adapted to their regional climatic conditions. In Chapter 1, the relationship between the somatic growth of young walleye and climatic conditions was shown to differ among genetically distinct groups of walleye populations. In Chapter 2, adult somatic growth was shown to be variable, but that variation was found to be independent of climatic variation. Individual climatic variables played different roles in shaping walleye growth patterns. Walleye early growth rate was positively related to annual net thermal input, and thus it exhibited a strong latitudinal trend. However, walleye adult growth rate did not show any significant pattern along the climate gradient. This suggests that other factors, in addition to climatic conditions, affect walleye adult growth. Some environmental factors that could be important influences on adult growth include morphometry, Secchi depth, and productivity. Morphometry and Secchi depth are related to the walleye feeding conditions (i.e. optical habitat) and thus influence walleye feeding activities because walleye prefer feeding at low light condition (Lester et al 2004). Productivity indicates the food availability for walleye growth. Some biological factors that might be important include walleye population density affecting the food supply (Hatch et al 1987) and types of prey available for walleye feed on (Madenjian 1991, Kershner et al 1999).

It is well established that fish growth is significantly related to other demographic variables, such as survival (Pauly 1980), fecundity (Muth and Ickes 1993) and maturation

(Muth and Wolfert 1986). It is desirable to know how climatic conditions influence these variables and thus shape walleye population dynamics. Future studies can be aimed at setting up three multivariate data matrices: one for climatic variables, one for lake physical conditions and one for demographic variables. The multivariate statistical approaches (such as PROTEST and canonical analysis) and Bayesian meta-analysis approaches used in this thesis would be effective tools for processing these data and identifying relationships between walleye demographic variables and both the environmental and biological factors.

The local scale studies demonstrated: (i) how climatic conditions interacted with the lake morphometry to affect walleye population dynamics by shaping the amount of habitat suitable for walleye in Lake Erie (Chapter 3); and (ii) how changes in habitat, such as those expected from climate change, can affect the dynamics of the Lake Erie walleye metapopulation (Chapter 4). Three walleye sub-populations in Lake Erie showed distinct demographic characteristics. Young western basin walleye had the lowest growth rate of the three sub-populations. However, by the third growing season, they had overtaken the eastern basin walleye in the growth rate. This is consistent with the fact that summer temperatures in the western basin exceed the thermal optimum for walleye—higher than optimum temperature could result in reduced growth for young walleye that are too small to leave the basin. However, when those young walleye acquire basin-crossing migration abilities after the second growing season, they can select the warm springs of the western basin and the cooler summers and falls of the central and eastern basins to optimize their adult growth potentials. This ability to select optimal temperatures could permit them to make up their growth deficit, relative to the eastern basin walleye.

The survival of the eastern basin walleye was higher than the western basin walleye, and this may reflect the lower fishing mortality rate experienced by the eastern basin walleye (MacLennan et al 2001, Wang 2003). The abundance of walleye spawners in Van Buren Bay in New York waters (i.e. one of the dominant spawning sites in the eastern basin) was only about 0.1 % of the lakewide abundance of spawners. This suggests that the western basin produces the majority of walleye in Lake Erie. The simulation study in Chapter 4 showed that the potential bottleneck setting the overall size of the walleye population in Lake Erie could be the early survival rate (i.e. recruitment). Currently, walleye spawning and nursery habitat are located mainly in the western basin (Roseman et al 1996). The significant shrinkage of walleye suitable habitat in the western basin that could result from climate change (Chapter 3) could be of concern to scientists working on Lake Erie walleye. Because walleye suitable habitat was projected to increase in the central and eastern basins (Chapter 3), one strategy for adapting to climate change would be to create additional spawning and nursery habitat in these two basins. This could be done by building artificial reefs for spawning and by identifying suitable nursery habitat areas and protecting them during the young walleye nursery period. To implement this strategy, more studies on walleye spawning and nursery ecology in Lake Erie should be done.

The simulation study in Chapter 4 demonstrated that changes in habitat that will likely result from climate change could cause changes in walleye adult growth pattern and thus egg production. These changes could affect dynamics of the Lake Erie walleye metapopulation by modifying the stock-recruitment relationships of the individual sub-populations. The eastern basin sub-population had a lower extinction harvest rate than the western basin walleye. However, current quota management system and walleye migration

behavior can interact with each other to shelter the eastern basin walleye whilst expose the western basin walleye to a high harvest rate than expected. The results of the simulation study are obviously affected by the assumptions and quality and/or quantity of the observed data used to establish the empirical relationships in the study. Important assumptions included in the simulation study are: (i) quantity of suitable habitat is constant over time; (ii) walleye maturation schedule and reproductive investment is constant over time; (iii) annual migration rate among basin is constant over time; (iv) inter-breeding among sub-populations is non-existent. All these assumptions can be relaxed when more data are collected to establish models to characterize these processes.

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