Life history variation parallels phylogeographical patterns in North American walleye (*Sander vitreus*) populations

Yingming Zhao, Brian J. Shuter, and Donald A. Jackson

Abstract: Walleye (*Sander vitreus*) is a native fish species in North America, and its zoogeographic range covers several climatic zones. Using multivariate statistical approaches and published growth data, we explored the association between climatic conditions (frost frequency, precipitation, air temperature, solar radiation, and cloud cover) and growth of walleye from 89 populations in North America. We found significant concordance between climatic conditions and walleye growth; however, the pattern of concordance differed among populations that originated from geographical regions that were colonized from different glacial refugia. This suggests that contemporary differences in walleye growth patterns related to local climatic conditions may have been shaped by evolutionary divergence that occurred among refugia during the last glaciation. We suggest that caution should be taken when assessing possible effects of climate variation and climate change on the life history traits of different walleye and other fish populations, especially when such assessments potentially include several genetically distinct groups. Procrustes analysis was shown to be an effective tool for characterizing how a multivariate set of response variables change in response to generalized changes in a multivariate set of independent variables.

Résumé : Le doré (*Sander vitreus*) est un poisson indigène d'Amérique du Nord dont la répartition géographique couvre plusieurs zones climatiques. Des méthodologies statistiques multidimensionnelles et des données de croissance tirées de la littérature nous ont servi à explorer l'association entre les conditions climatiques (fréquence des gels, précipitations, température de l'air, radiation solaire et nébulosité) et la croissance des dorés de 89 populations nord-américaines. Il existe une concordance significative entre les conditions climatiques et la croissance des dorés; cependant, les patrons de concordance diffèrent entre les populations qui proviennent de régions géographiques colonisées à partir de refuges glaciaires différents. Cela laisse croire que les différences actuelles dans les patrons de croissance des dorés reliées aux conditions climatiques locales ont pu être façonnées par la divergence évolutive qui s'est développée entre les refuges durant la dernière glaciation. Nous croyons qu'il faut être prudent lorsqu'on évalue les effets possibles de la variation climatique et du changement climatique sur les caractéristiques démographiques des différentes populations de dorés ou d'autres poissons, particulièrement si de telles évaluations incluent potentiellement plusieurs groupes qui sont génétiquement distincts. L'analyse Procuste s'est avérée être un outil efficace pour caractériser la manière dont un ensemble multidimensionnel de variables de réponse change en réaction à des changements généralisés dans un ensemble multidimensionnel de variables indépendantes.

[Traduit par la Rédaction]

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, studies of fish growth require an explicit consideration of the environmental variables that characterize the ecosystem where the fish lives. Climatic conditions are a major component of these environmental variables.

Walleye (*Sander vitreus*) is a cool-water species (Hokanson 1977) and one of the most economically important fish species in the north-temperate fresh waters of North America. The optimal temperature range for walleye growth is 18–22 °C (Christie and Regier 1988). Because walleye

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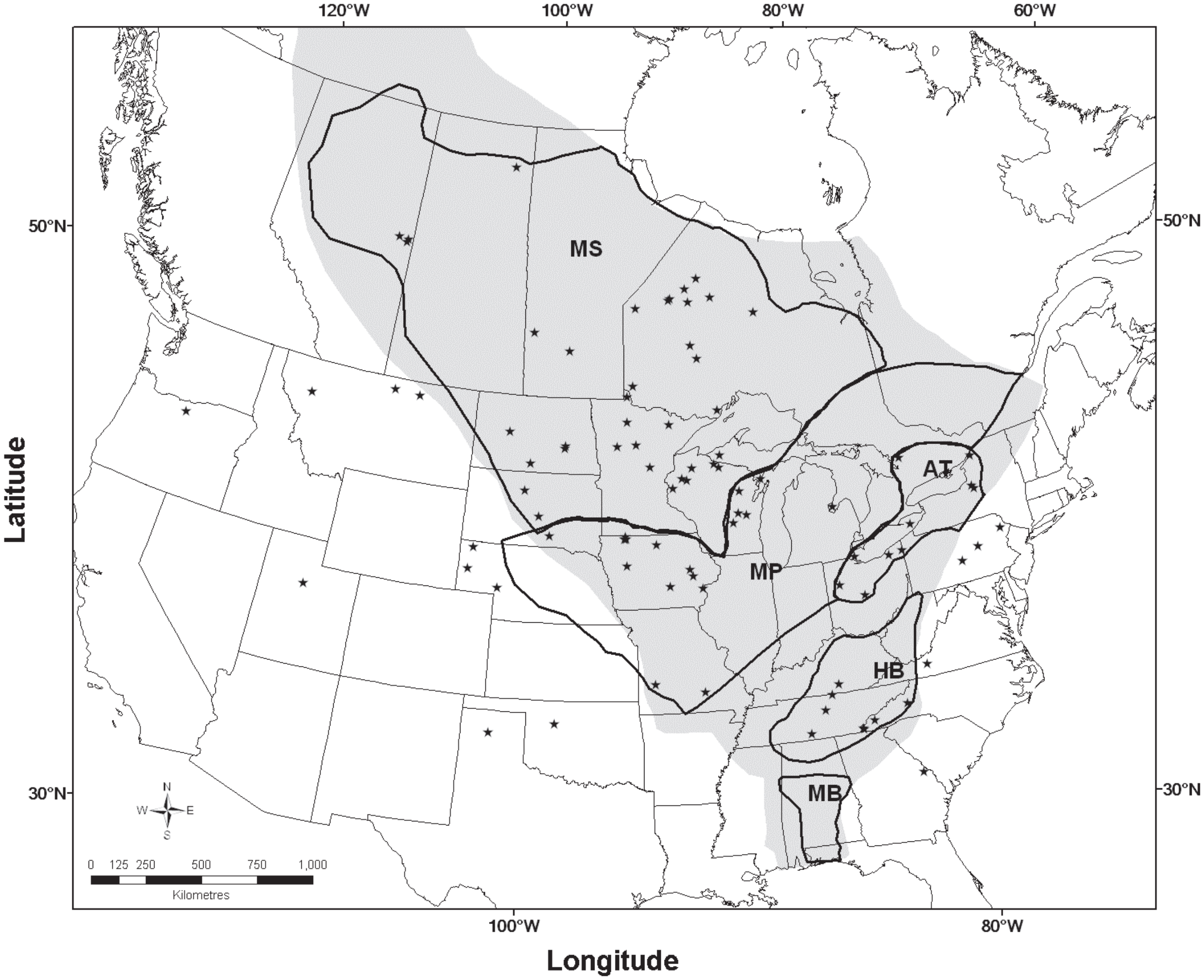
Fig. 1. A map of 89 walleye (*Sander vitreus*) populations collected in this study: the native distribution (shaded area) of walleye populations in North America (redrawn from Colby et al. 1979) and five genetically distinct groups (polygons enclosed by thick lines — redrawn from Billington 1996). AT, Atlantic refugium; MS, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.



change their retinal response from positive phototaxis to negative phototaxis during their first year of life, adult walleye prefer feeding in a low-light environment (Ryder 1977). Therefore, both light and thermal conditions 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). Owing to its economic importance as a primary sport and commercial fish species, the walleye has been widely introduced outside of its native range, particularly in western reservoirs (Goodson 1966), along the Atlantic seaboard, and elsewhere 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 significant associations between growth differences and climatic differences (i.e., air temperature) have been discovered (Colby et al. 1979; Colby and Nepszy 1981).

Colby and Nepszy (1981) found that variation in growing degree-days above 5 °C (GDD5) explained 72% of the variation in body length of first-year walleye in 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.

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, which 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 Basin (MB) drainage, Billington and Strange (1995) and Billington (1996) provided evidence for the existence of five genetically and geographically distinct groups of walleye populations in North America. In addition to the three groups from the refugia described above, a fourth walleye group (located in the southeastern states of Tennessee and Kentucky) was identified as a mixture of stocked fish from the AT and MP refugia (HB in Fig. 1). Gulf Coast walleye were found to be genetically distinct from other groups and were classified as a fifth group, the MB drainage group (Fig. 1) (Billington 1996). The inclusion of walleye populations into western Ontario and Minnesota in the MS refugium (Billington 1996) is debatable, however, because few populations (about three in the southern part of western Ontario) from western Ontario were characterized genetically and because both haplotypes 4 and 10 (the genotypes of populations from the MP and MS refugia, respectively) appeared in the Minnesota populations that were characterized (Billington et al. 1992). Genetic distinguishability among the groups implies that the walleye from different origins (i.e., different glacial refugia) experienced evolutionary divergence during the period of their geographic isolation from each other (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 range can be further subdivided into five genetically distinct groups. However, no study has been done to test if there are differences among these groups in the response of their life history traits (e.g., growth) to variation in climatic conditions. In addition, the previous studies characterizing the variations in walleye life history traits (e.g., growth, fecundity, and maturation) over a large segment of its zoogeographic range have focused mainly on the effect of air temperature (Colby and Nepszy 1981; Baccante and Colby 1996). However, other climatic variables such as solar radiation and cloud cover should affect optical habitat of walleye and may lead to differences in walleye growth pattern.

In this study, we use published size-at-age data for walleye in North America to (*i*) assess the association between somatic growth and climatic conditions; (*ii*) explore spatial patterns in the concordance between somatic growth and climatic conditions; and (*iii*) investigate whether such concordance patterns between life history traits and environmental factors reflect the genetic divergence associated with ancestral linkage to different glacial refugia.

Materials and methods

Data collection

Data on walleye length-at-age were derived from two syntheses (Colby et al. 1979; Carlander 1997) of growth information for walleye in North America and from Stephenson and Momot (1991). The prior two syntheses were obtained by compiling data from more than 300 studies published in the scientific literature over the period from 1933 to 1993. A total of 89 walleye populations were included in the final growth database, with over 80% of these data collected over the period 1950–1990. These populations covered a latitudinal range from about 33°N to 59°N and a longitudinal range from about 75°W to 121°W (Fig. 1, Appendix A) and included both native and introduced populations. For the native group, we were unable to obtain data for populations located in the MB refugium region. 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 ages 1 to 14, and the shortest series was from ages 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 (Craig 2000; Munger 2002). The accuracy of scale ages also tends to decline with older fish. Therefore, we chose to work only on the first 5 years growth to minimize estimation problems associated with missing data, sexual dimorphism, and aging errors. Because size at older age is not independent of size at younger age (i.e., size at age (i) = size at (i – 1) + growth increment over ith year of life, where i = 1, 2, 3, 4, and 5), we only used age-specific estimates of annual incremental growth in our analyses. Thus, the growth data for each population reflect the influence of five consecutive annual sets of climatic conditions.

We chose to use the Intergovernmental Panel on Climate Changes (IPCC) 1961–1990 climatic normals (available from the IPCC climate data distribution centre website: www.ipcc-data.org/obs/get_30yr_means.html), specific to the location for each population, to characterize the climatic conditions associated with the growth increments exhibited by each population. The following climate variables were used: ground frost frequency (days), precipitation ($\text{cm}\cdot\text{day}^{-1}$), mean air temperature (°C), cloud cover (%), and solar radiation ($\text{W}\cdot\text{m}^{-2}$). The IPCC 1960–1990 normal data sets consist of monthly mean values for the five variables at a resolution of 0.5° latitude by 0.5° longitude. The values for each variable were interpolated from weather station data using thin-plate splines (New et al. 1999). For each population location in the walleye database, an annual mean for each variable was calculated, and this location-specific set of five mean values was used to represent the climatic conditions experienced by that population over the period when the observed growth increments were generated.

We believe that these well-validated and readily available climatic data are sufficient for our purpose because almost all of the growth data sets in our database were collected prior to the onset of the warming trends that are ubiquitous in recent North American air temperature time series. Retrospectively, such trends typically begin in the late 1960s to early 1970s; however, they do not escape the historical range of variation set by the 1900–1970 period until at least the mid-1980s (e.g., Stott et al. 2000; Jones et al. 2006). Hence, we felt that the 1961–1990 normal values would reflect the spatial differences in climate that would largely be responsible for driving any systematic, climate-based differences in the growth patterns exhibited by the populations in our data set. We carried out the following tests of this assumption. First, we selected 8 locations, each representative of a geographically distinct group of populations in our growth database (one location for each of the glacial refugia AT, MP and HB; one location for the western half of MS; one location for the eastern half of MS; one location for each of the three regionally distinct groups of introduced populations). Second, for each population, we used the IPCC location-specific, historical air temperature time series database derived using the same methodology as was used to derive the 1961–1990 normal values (Mitchell et al. 2004) to estimate the annual air temperature at the reference location closest to the population for the decade immediately prior to the year when the growth data for the populations was reported. Third, we generated six group means from these decade-specific values by averaging across populations within each of the five refugium groups and by averaging across all of the introduced populations. Finally, we compared the decade-specific, reference site air temperatures with the 1961–1990 normal air temperatures for each group. We found that within each group, the spatial variation in air temperature between populations over a fixed time period (as measured by the standard deviation of the original 1961–1990 normal temperatures for the populations in the group) was typically two or three times greater than the temporal variation in air temperature associated with different growth time periods at the reference site for each group. This confirms our expectation that any associations between growth and climate in our data would be largely driven by the spatial variation in climate, captured in the 1961–1990 normal data. In addition, the within-group differences between these two temperature indices were small (<0.2 °C for the introduced populations and for three of the five refugia, including the east half of MS; about 0.6 °C for the west half of MS; and about 1.0 for HB); the two indices were highly correlated ($r^2 > 0.99$, $p < 0.001$) and followed a linear, 1:1 relationship (i.e., the slope was not significantly different from 1; $p > 0.1$); and the intercept was not significantly different from zero ($p > 0.1$). This is consistent with our hypothesis that at the regional level, the mean climate evident over the period of data collection was essentially identical with the mean climate characterized by the 1961–1990 climate normals.

Statistical analysis of data

Incremental growth-at-age and climate data sets were standardized to *z* scores before carrying out any further analysis 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 growth and climate. A Procrustean randomization test (PROTEST: Jackson and Harvey 1993; Jackson 1995) was applied to the first two principal components from each data set. 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 and then generates a standardized residual for each individual observation. It then tests whether this match is significantly different from random using a randomization test and then generates a standardized residual for each individual observation. The standardized residuals are used to rank each observation in terms of its fidelity to the overall pattern of association that PROTEST has identified between the two data sets (Jackson 1995; Olden et al. 2001).

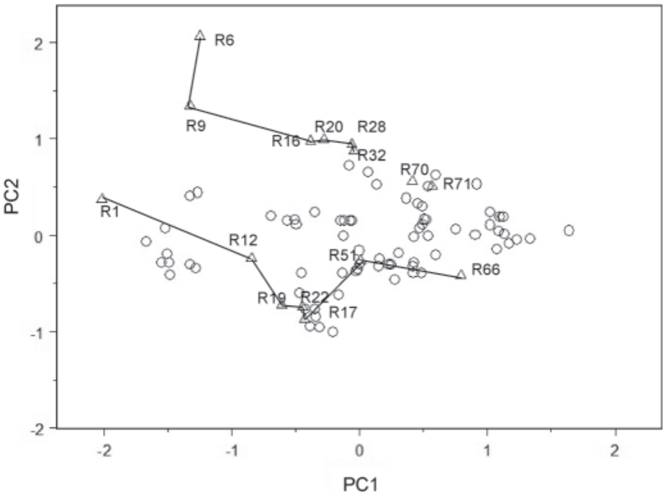
Comparison of the direction and magnitude of the residual vectors from the Procrustes analysis can determine whether groups of observations exhibit similar deviations from the best matching pattern generated by the analysis. In this study, each residual vector was produced by subtracting the observed growth vector for each population (in the growth space determined by the first two principal component axes) from the corresponding growth vector predicted from the climatic conditions for that population. The predicted growth vector is just the climate vector mapped into growth PCA space by the Procrustes fit (i.e., a set of rescaling, rotating, and reflecting operations that maximize the concordance between the climate and growth data matrices). The four quadrants of the two-dimensional ordination plot, based on the first two principal component axes derived from the growth data, were used to classify each individual observation into one of four groups depending on the quadrant where the residual vector for the observation was located. The quadrant classification was assigned in a counterclockwise manner. For example, a population with its residual vector in quadrant 1 would have two positive components and a population with two negative components to its residual vector would be in quadrant 3. The assignment of individual residuals to four different quadrants can characterize the residual patterns among populations located in different refugium regions and help us understand the relationship between climate-based predicted values and observed values. A two-tailed *t* test was used to compare the magnitude of residual vectors between different population groupings: (*i*) populations located outside the native range (subsequently referred to as introduced populations) versus populations located within the native range (subsequently referred to as native populations); and (*ii*) among native populations, grouping based on the glacial refugium associated with the location of the populations. A χ^2 test was applied to each group to test for a nonrandom distribution of residual vectors among the four 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 criterion, which is adversely affected by atypical observations (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).

Table 1. The eigenvector coefficients and eigenvalues for the first two principal components (PCs) from principal component analysis (PCA) of walleye (*Sander vitreus*) incremental growth data.

Variable	PC1	PC2
Growth		
Increment at age 1	0.082	0.792
Increment at age 2	–0.437	0.549
Increment at age 3	–0.536	0.016
Increment at age 4	–0.545	–0.152
Increment at age 5	–0.466	–0.216
Eigenvalue	1.789	1.243
Percentage (%)	35.79	24.86
Climate		
Frost frequency	0.543	0.080
Precipitation	–0.406	–0.439
Temperature	–0.541	0.033
Radiation	–0.496	0.352
Cloud cover	0.036	–0.822
Eigenvalue	3.251	1.355
Percentage (%)	65.02	27.11

Fig. 2. Biplot of the first two principal component (PC) scores for climate conditions showing difference of climate conditions for the introduced populations (triangles) and the native populations (circles). The labels in the figure are the population ID numbers provided in Appendix A.



Results

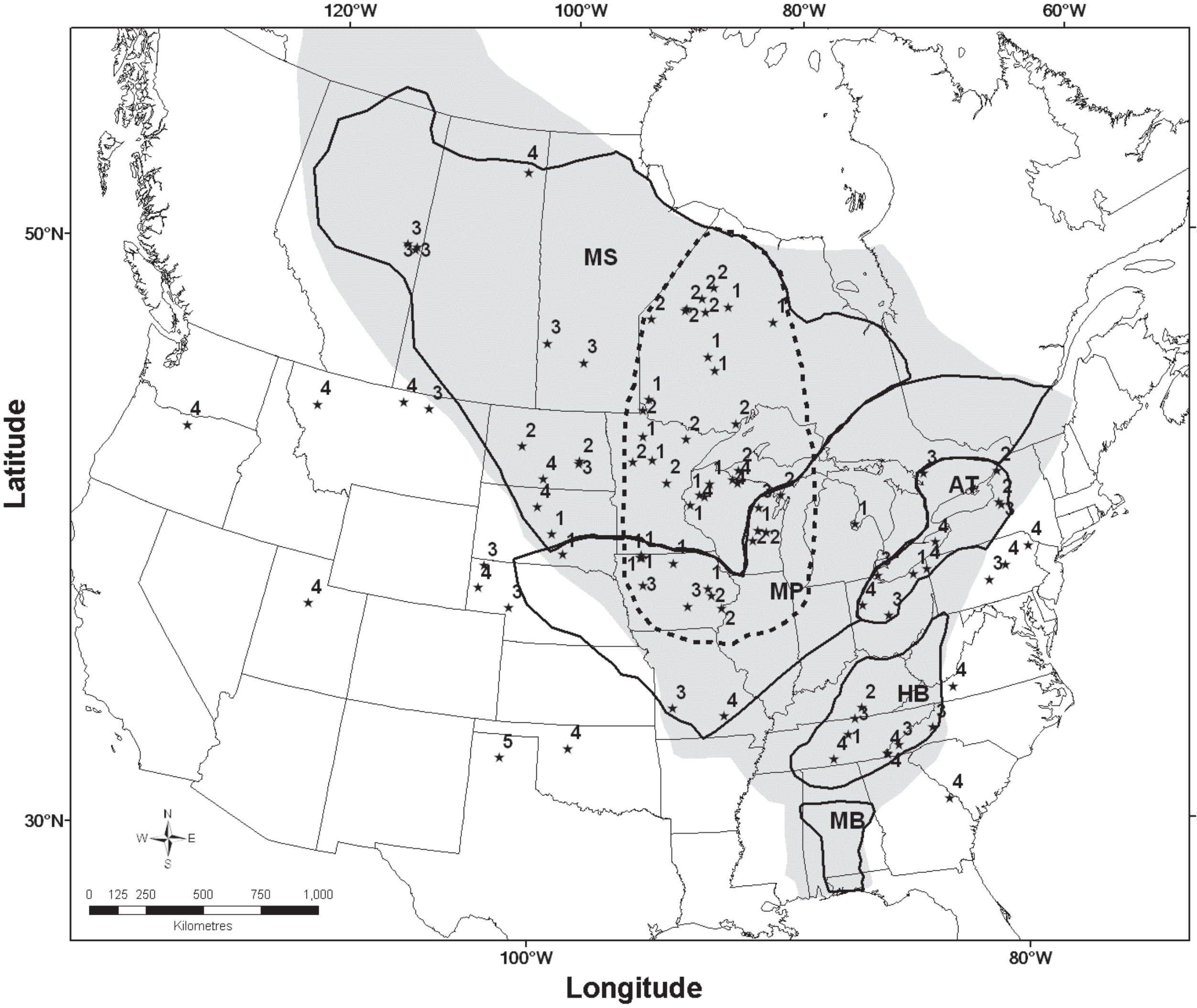
For the growth data set, the first principal component represents walleye average growth rate after age 1, because the PCA coefficients of standardized increment-at-age variables for ages 2–5 are similar to one another in sign and magnitude (Table 1). Age 1 growth was generally unrelated to this first component given its small PCA coefficient (0.082). However, for the second principal component, the absolute values of the coefficients for increment at age 1 (0.792) and increment at age 2 (0.549) were more than twice as large as the ones for the increments at older ages. This indicates that the second principal component was most influenced by the early growth rate. The PCA analysis showed that walleye early growth rate and average young adult growth rate, as summarized by the second and first PCA components, composed 60.65% (24.86% and 35.79%, respectively) of the 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 influence on this component, given the low value (0.036) for its coefficient in the component (Table 1). The second principal component contrasted solar radiation with both precipitation and cloud cover. The first two components accounted for about 92.13% of the total variation in the climate data (65.02% and 27.11%, respectively). 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 that 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 (i.e., Lake Meridith, Texas, in Appendix A) exhibited growth and climatic characteristics that were least consistent with the overall association between growth and climate, whereas the population with the smallest residual (i.e., Attawapiskat Lake, Ontario, in Appendix A) exhibited the growth and climatic characteristics that were most consistent with the overall association. The residual obtained for Lake Meridith was so different (i.e., twice as much as the second largest residuals and six times as much as the average residual values of the remaining 88 populations) from all others that it is considered independently of the others. The remaining 88 populations were divided into four groups with an equal number of 22 populations in each group, based on their rank-ordered residuals (Appendix B, Fig. B1). Groups 3 and 4 were the populations with the poorest match, whereas groups 1 and 2 had the best match. The Lake Meridith population was placed alone in group 5 (Appendix B, Fig. B1). Most populations that exhibit a good match between growth and climate are located in the central region of North America: western South Dakota, Iowa, Minnesota, and northwestern Ontario. Regions surrounding this well-matched group exhibited a relatively poor match between walleye growth pattern and climatic conditions (Fig. 3). Residual magnitudes for introduced populations were significantly larger than those for the populations in the native range (t test, $t_{15} = -3.96$, $p = 0.001$). This finding suggests that the overall association between climatic conditions and growth pattern is shaped largely by populations within the native range for walleye and that it does not hold for introduced populations outside the native range.

Comparing populations within the native range, nearly half the populations exhibiting a close growth–climate rela-

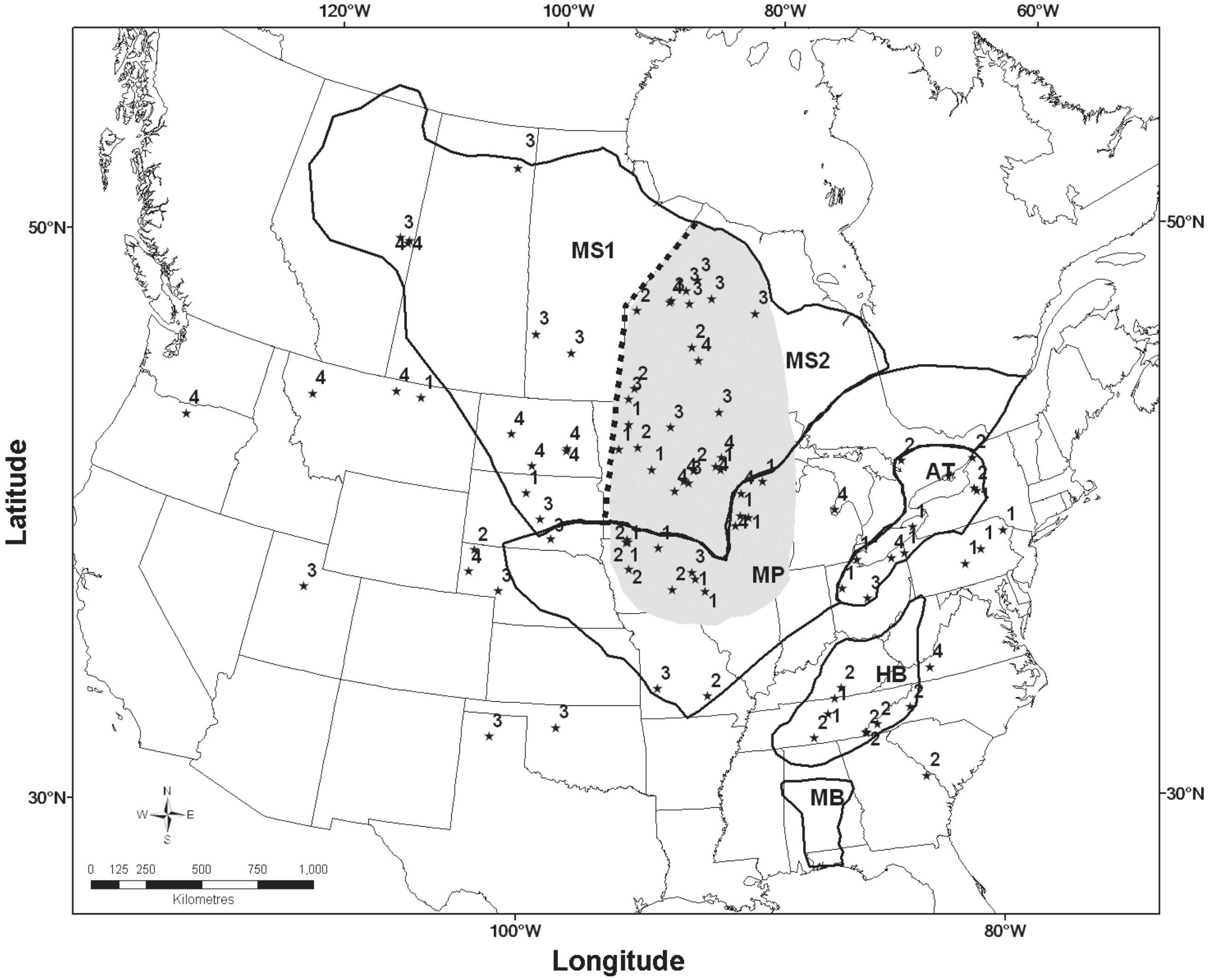
Fig. 3. A map of rank groups of residuals of individual walleye (*Sander vitreus*) populations from Procrustes analysis. Numbers designate the rank groups in Appendix B, Fig. B1. The lower the number for the rank group (e.g., 1 vs. 2), the better the concordance between climate conditions and walleye growth. The shaded area shows walleye native distribution (redrawn from Colby et al. 1979); populations enclosed by the thick, broken line compose the majority of the population with high concordance. AT, Atlantic refugium; MS, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.



tionship (i.e., those from residual groups 1 and 2) are located in the region colonized from the MP refugium (Fig. 3), whereas the remaining half are located in Minnesota and north-western Ontario (Fig. 3 and region MS2 in Fig. 4). Billington (1996) suggested that this latter region (MS2 in Fig. 4) was colonized from the MS refugium; however, this classification is questionable because (*i*) the Minnesota populations exhibit allele frequencies that are similar to populations attributed to the MP refugium; and (*ii*) the sample size from northwestern Ontario is small ($N < 5$) (Billington et al. 1992). A majority of populations from the AT refugium region (Fig. 3), the remainder from the MS refugium region (MS1 in Fig. 4), and the populations from the hybrid region (HB in Fig. 3) did not follow the same walleye climate–growth relations shaped by the MP and MS2 regions and therefore exhibited large residuals (in groups 3 and 4) from the general relationship. The residuals for the populations from the MP and MS2 regions were significantly smaller than the residuals for the populations from the AT, MS1, and HB regions (*t* test, $t_{48} = -4.96$, $p < 0.001$).

The dominant direction of the residuals also differed among populations from regions with different genetic histories (Fig. 4). The null hypothesis of a uniform distribution of residual directions among the four quadrants was rejected for populations from the MS1 ($\chi^2_3 = 8.67$, $p = 0.03$) and HB ($\chi^2_3 = 9.57$, $p = 0.02$) regions; residuals from the MS1 region tended to lie in the third and fourth quadrants, while residuals from the HB region tended to lie in the second quadrant (Fig. 4, Appendix Fig. B2). The distribution of residual directions for population from the AT region was skewed to the first quadrant (Fig. 4, Appendix Fig. B2), but was not significantly different from uniform ($\chi^2_3 = 4.4$, $p = 0.22$). However, the power of this particular test was low because the sample size was small (total 10 populations). With a sample size of 10, the power to detect a 20% departure from the null hypothesis is only 0.075 (i.e., with a sample of size

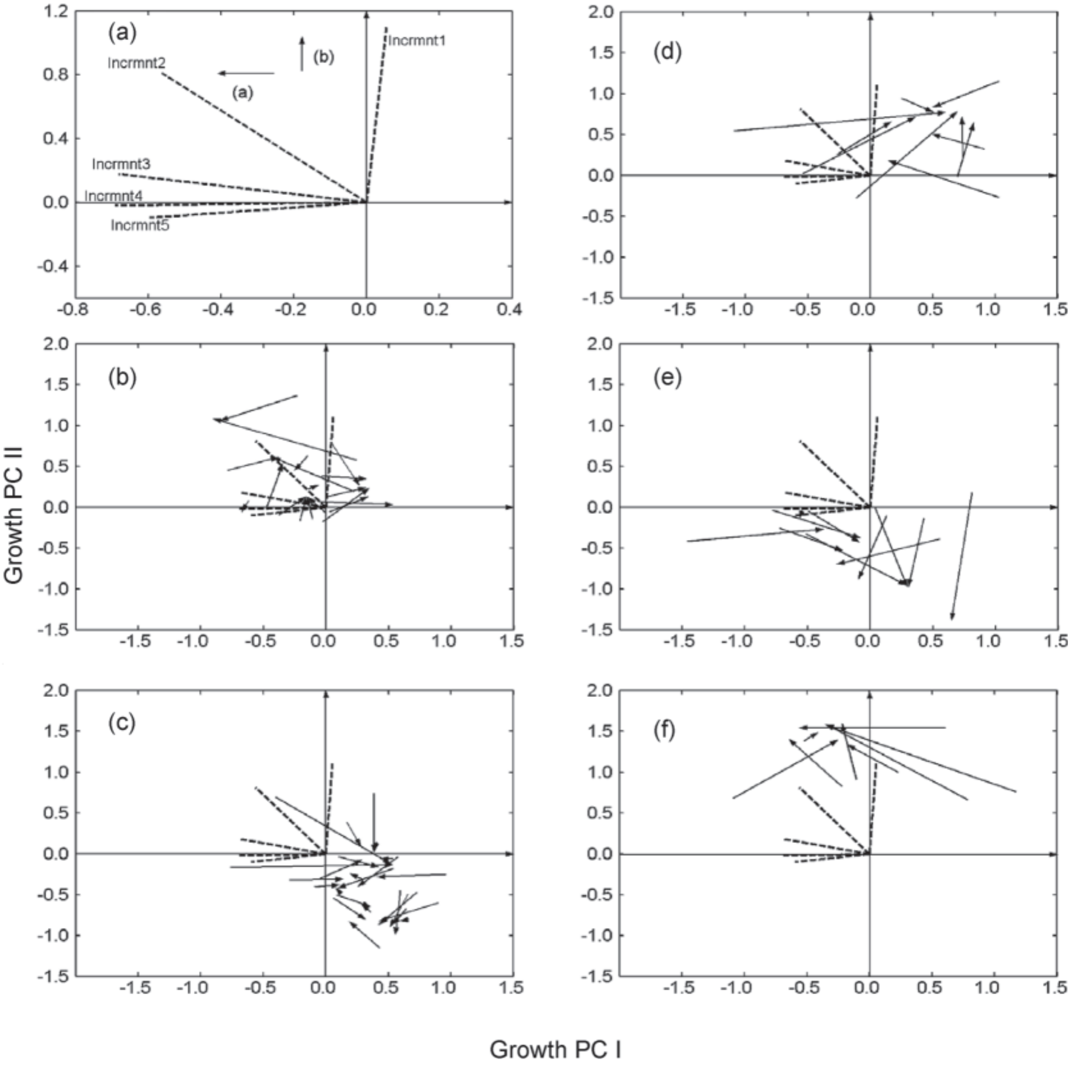
Fig. 4. A map of directions of residuals of individual walleye (*Sander vitreus*) populations from Procrustes analysis and five genetically distinct groups. Numbers (1, 2, 3, 4) show quadrants where the residuals are located, quadrant 1 being the top-right quadrant and progressing counterclockwise. Polygons with thick lines show groups of genetically distinct populations; the broken line is a proposed separating line of Missouri refugium (MS) based on this study. The shaded area is same as the circled area in the broken line in Fig. 3. AT, Atlantic refugium; MS1 and MS2, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.



of 10 and at the 5% significance level, there is only a 7.5% probability of detecting at least a 20% shift from the uniform distribution). The distribution of residual directions was not significantly different from uniform for populations from the MP region ($\chi^2_3 = 3.53$, $p = 0.32$) and for populations from the MS2 region ($\chi^2_3 = 2.91$, $p = 0.41$). Therefore, both the residual direction pattern (i.e., uniform distribution among the four quadrants) and residual magnitude (low rank) for populations from the MP and MS2 regions were similar. A uniform distribution of residual directions was also evident for populations located outside the native range of the species ($\chi^2_3 = 1.27$, $p = 0.73$) (Appendix Fig. B2).

The superimposition plots (Fig. 5) demonstrate how observed growth differs from expected or predicted growth, given the observed climatic conditions. For example, a population with the residual vector (***a***) in Fig. 5*a* exhibits a lower observed adult growth rate than was predicted by the climatic conditions experienced by the population because the vector (***a***) is largely parallel to the eigenvectors for young adult growth (primarily increments 3, 4, and 5) that make up the first principal component (PC 1), and it points from an observed position of lower adult growth on PC 1 to a predicted position of higher adult growth on PC 1. Similarly, the population with residual vector (***b***) in Fig. 5*a* exhibits a lower observed early growth than predicted from the climatic conditions it experienced, because vector (***b***) is almost parallel to the eigenvectors for early life growth (primarily ages 1 and 2) that largely make up PC 2, and it points from an observed position of lower early growth to a predicted position of higher early growth. The residual vectors for populations from the regions MP and MS2 were relatively small in magnitude and did not exhibit a dominant direction (Fig. 5*b* and Fig. 5*c*). However, populations from the regions associated with the other three refugia produced larger residuals that exhibited dominant directions: (*i*) among populations from the MS refugium region (Fig. 5*e*), early growth rate

Fig. 5. Superimposition plot of five growth eigenvectors (broken lines) and residuals for the populations located in different refugium regions: (*a*) example; (*b*) MP (Mississippi refugium); (*c*) MS2 (Missouri refugium 2); (*d*) AT (Atlantic refugium); (*e*) MS1 (Missouri refugium 1); (*f*) HB (hybrids from MS and MP). Refer to the text for more detail. In the Example panel, the direction of residual (***a***) is parallel to the principle component that characterizes young adult (ages 3, 4, and 5) growth, thus indicating that the populations with this residual exhibited a smaller observed young adult growth rate than expected given its climatic conditions; a similar explanation applies to residual (***b***) in the example and to all the residuals in the other five panels.



tended to be higher than expected; (*ii*) among populations from the HB region (Fig. 5*f*), both early and later growth rates were lower than expected; and (*iii*) among populations from the AT refugium region (Fig. 5*d*), early growth rate tended to be lower than expected, while growth in later life tended to be higher than expected.

Discussion

Significant relationships between life history traits and environmental factors are caused by phenotypic plasticity responding to environmental gradients and (or) by natural selection (Pigliucci 2001). A relationship based solely on phenotypic plasticity should apply consistently across the geographic distribution of a species, as long as the values for the environmental factors that drive the relationship remain within the range over which well-defined phenotypic responses have developed. The current patchy geographic distribution of walleye genotypes is the outcome of postglacial colonization from multiple refugia coupled with continuing spatial isolation of the different refugial groupings (Billington 1996). Therefore, we expect that walleye populations from the same genetic region will carry similar refuge-specific genotypes, whereas walleye populations from different genetic regions will carry the different genotypes associated with those regions. It is expected that such genetic variation may account for at least some of the phenotype variation.

The lack of concordance between observed and expected somatic growth for introduced populations, given their climatic conditions, suggests that either the introduced populations have not been established long enough to adapt to the environmental conditions in their new locations, or the extreme environmental conditions in those locations are outside the range over which a well-defined plastic response has developed. The latter possibility is consistent with the fact that most introduced populations lie at or outside the boundaries of the climate space defined by the native distribution of the species, and it is the climate space of the native populations that would most likely have set the boundaries over which a well-defined phenotypic response could develop (Dunlop and Shuter 2006). In addition, given that the introduced populations likely derive from a variety of sources, a random distribution for the direction of their residual vectors is expected and was observed. The vector direction for each introduced population tends to match the dominant direction found among the residual vectors in its neighbouring refugial group. This suggests that introductions largely derive from nearby native stocks.

In evolutionary ecology and genetics, the terms norm of reaction or reaction norm are used to describe how a genotype is expressed by different phenotypes across a range of environmental conditions (Pigliucci 2001). The decreasing concordance between climate and walleye growth, from the centre of the native distribution to the edges of the current distribution, may indicate that walleye climate–growth reaction norms vary across the current geographic range of the species. Genotypic variation among walleye populations in the native range could be the cause of variation in the walleye climate–growth reaction norm. In our study, the concordance between walleye growth and climate identified by the PROTEST analysis is shaped primarily by populations located in the region colonized from the MP refugium and from the populations located in western Ontario and Minnesota populations (i.e., MP–MS2). It is possible that this climate–growth linkage reflects a single reaction norm, common to this genetically similar group of populations. Populations located in the three other geographic regions (i.e., AT, MS1, and HB) that were identified as genetically distinct from each other and from the MP–MS2 region by Billington et al. (1992), Billington and Strange (1995), and Billington (1996) also exhibited large deviations from the MP–MS2 climate–growth reaction norm. In addition, the directions of the vector residuals from the populations within each of these regions (i.e., AT, MS1, and HB) exhibited a common direction, and that common direction differed among regions. These findings are consistent with the hypothesis that the walleye climate–growth reaction norm differs systematically among populations with different postglacial colonization histories.

Other fish species have been shown to exhibit genetic-based differences in the reaction norm linking the response of life history traits to changes in environmental factors. Yamahira and Conover (2003) compared the effect of water temperature on growth rate in northern and southern populations of Atlantic silverside (*Menidia menidia*). They found a significant difference in the temperature–growth reaction norm between northern and southern populations, and they also found that this difference had a strong genetic basis. In young-of-the-year walleye, common garden experiments (Galarowicz and Wahl 2003) point to the presence of a strong genetic component in the significant differences in metabolic rate, food consumption, food conversion efficiency, and growth observed among stocks from different geographic regions that cross the boundaries of several glacial refugia, likely across two or more regions that were genetically distinguishable.

Because this study and other studies mentioned above suggest that genetic variation is a likely cause of variation in fish growth – environment reaction norms, our finding that populations from region MP and MS2 exhibit similar vector residuals (both in direction and magnitude) suggests that populations from the MS2 region could be more closely linked to the MP refugium populations rather than to the MS refugium populations as suggested by Billington (1996). Resolution of this issue would require more intense genetic work on populations in the MS2 region. Similarly, our hypothesis that different walleye phylogeographic lineages exhibit different growth–environment reaction norms requires further testing, ideally through a program of common garden studies.

In conclusion, climatic conditions significantly influence walleye growth patterns across their geographic range; however, the response of walleye growth to climate differs among groups of populations that exhibit evidence of genetic divergence. For most fish species, somatic growth is significantly related to other life history traits, such as fecundity and maturation. Those traits, therefore, would also be expected to show similar divergent patterns among those groups. These considerations suggest that caution should be taken when assessing possible effects of climate variation and climate change on the life history traits of different walleye populations (e.g., Shuter et al. 1998), especially when such assessments include several genetically distinct groups of walleye. Similar concerns would likely apply to other fish species that exhibit substantial genetic diversity within their zoogeographic ranges.

Our analysis demonstrates the effectiveness of the Procrustes approach to characterize and test how a multivariate set of response variables changes in response to generalized changes in a multivariate set of independent variables. While King and Jackson (1999) showed the use of PCA and Procrustes analysis in relating climate data to aquatic systems, we have extended its use in examining life history relationships. The Procrustes framework imposes relatively few restrictions on the shape of the response relationship and naturally accommodates a multivariate characterization of both response variables and independent variables — it integrates the individual response of each dependent variable into a comprehensive picture of an overall pattern of response to extensive changes in a set of independent variables. In our analysis, the resistant-fit Procrustes characterization of the concordance between a multivariate set of biological response variables (e.g., fish growth increment) and a multivariate set of environmental independent variables (e.g., climatic conditions) permitted us to identify groups of populations that exhibited not only a common response to environmental variation within each group, but also significant differences among groups in the common response specific to each group. Thus, the resistant-fit version of Procrustes can be effective in identifying heterogeneity in the response pattern among different subsets of the data, as well as in identifying an overall pattern of response.

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Appendices A and B appear on the following pages.

Appendix A

Table A1. Locations, residual groups (rank and direction) from PROTEST and walleye origin of the lakes in North America.

ID No.	Lake name	State or province[*]	Latitude (°N)	Longitude (°W)	Reference[†]	Rank[‡]	Direction[§]	Refugium[¶]
R1	Barton Reservoir	GA	33.09	81.87	1	4	2	Introduced
R2	Hiwassee Reservoir	NC	35.11	84.14	1	4	2	HB
R3	Apalachia Lake	NC	35.12	84.16	1	4	2	HB
R4	Norris Reservoir	TN	35.23	86.57	1	4	2	HB
R5	Nantahala Reservoir	NC	35.35	83.57	1	3	2	HB
R6	Lake Meridith	TX	35.64	101.66	1,2	5	3	Introduced
R7	James Reservoir	NC	35.75	81.92	1	3	2	HB
R8	Center Hill Reservoir	TN	36.05	85.76	1,2	1	1	HB
R9	Canton Reservoir	OK	36.13	98.61	1	4	3	Introduced
R10	Dale H. Reservoir	TN	36.61	85.32	1	3	1	HB
R11	Cumberland	KY	36.96	84.94	1	2	2	HB
R12	Claytor Reservoir	VA	37.07	80.60	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 Reservoir	OH	40.17	82.87	1	3	3	AT
R16	Utah Lake	UT	40.20	111.79	2	4	3	Introduced
R17	Juniata River	PA	40.58	77.59	2	3	1	Introduced
R18	Ferguson Reservoir	OH	40.74	84.04	1	4	1	AT
R19	Susquehanna River	PA	40.97	76.64	2	4	1	Introduced
R20	McConaughy Reservoir	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 Reservoir	OH	41.52	81.22	1	1	4	AT
R25	Pymatuning Lake	PA	41.60	80.51	2	4	1	AT
R26	Lake Erie (western)	GL	41.75	83.00	1,2	3	1	AT
R27	McBride Lake	IA	41.80	91.56	1	2	1	MP
R28	Minature Reservoir	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	42.30	95.05	1	3	2	MP
R31	Lake Erie (eastern)	GL	42.50	79.75	1	4	1	AT
R32	Whitney Reservoir	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	43.20	75.91	1	3	1	AT
R35	Scriba Creek	NY	43.31	76.02	2	2	2	AT
R36	West Okoboji Lake	IA	43.39	95.18	1,2	1	2	MP
R37	East 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	95.10	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	44.20	99.93	1	1	3	MS1
R46	Black Lake	NY	44.50	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	45.20	100.80	1	4	1	MS1
R50	Pike Lake	WI	45.32	92.37	1	1	4	MS2
R51	John Day Reservoir	OR	45.33	120.54	1	4	4	Introduced
R52	North 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	46.10	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

Table A1 (*concluded*).

ID No.	Lake name	State or province*	Latitude (°N)	Longitude (°W)	Reference[†]	Rank[‡]	Direction[§]	Refugium[¶]
R60	Lake Gogebic	MI	46.52	89.58	2	2	4	MS2
R61	Jamestown Reservoir	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	94.40	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 River	ON	48.35	89.45	3	2	3	MS2
R70	Nelson Reservior	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	94.90	1,2	2	3	MS2
R73	Sandy Lake	ON	49.50	94.53	2	1	2	MS2
R74	Savanne Lake	ON	50.50	90.43	2	1	4	MS2
R75	Lake Manitoba	MB	50.93	98.53	1	3	3	MS1
R76	Lake St. Joseph	ON	51.06	90.80	2	1	2	MS2
R77	West Blue Lake	MB	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	90.00	2	2	3	MS2
R86	Ethel Lake	AB	54.53	110.35	1	3	4	MS1
R87	Marie Lake	AB	54.63	110.30	1	3	4	MS1
R88	Wolf Lake	AB	54.68	110.97	1	3	3	MS1
R89	Wolllaston Lake	SA	58.28	103.28	1	4	3	MS1

*State or province abbreviations follow postal abbreviations.

[†] 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 populations.

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Appendix B

Fig. B1. Magnitude of standardized vector residuals from PROTEST analysis and the groups assigned based on their rank orders. The number beside the bar indicates the populations ID number in Appendix A. Low ranks indicate the better match between climate conditions and walleye (*Sander vitreus*) growth.

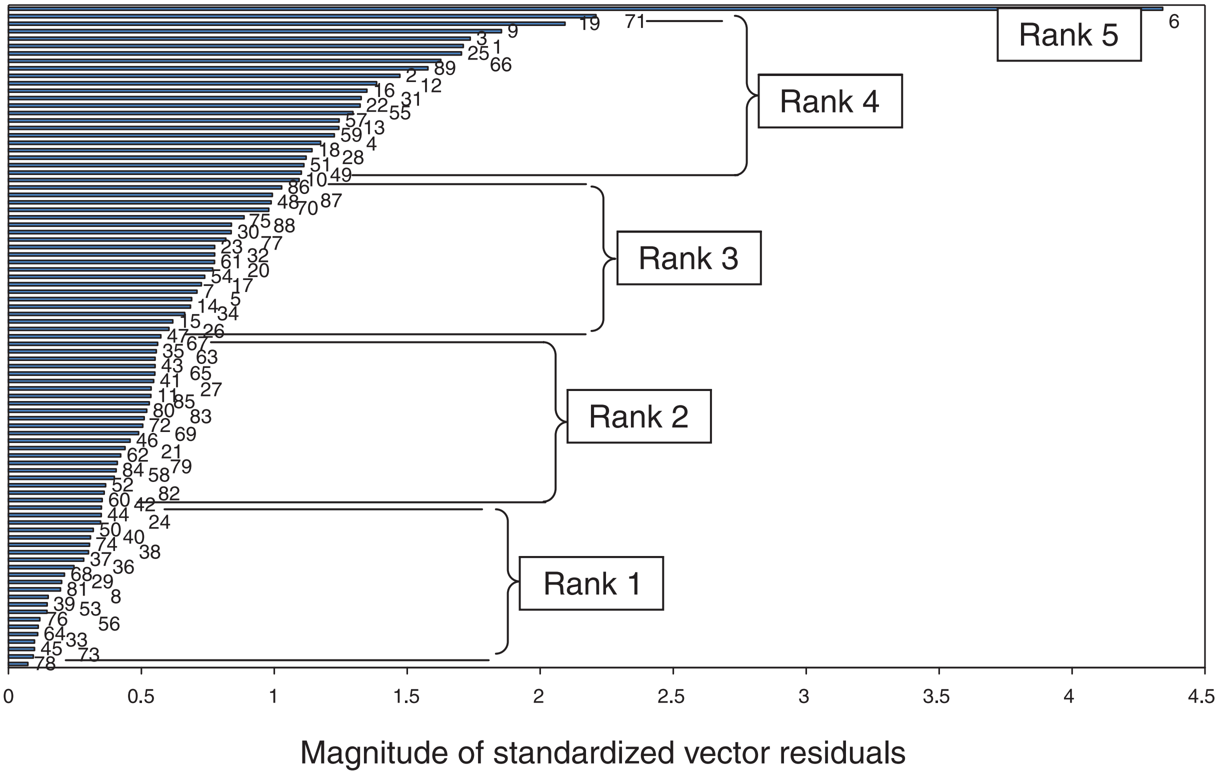

Fig. B2. The frequency of directions of vector residuals from PROTEST analysis from each genetically distinct group (*a–f*) showing distinct characteristics of the vector directions within each group. (*a*) AT (Atlantic refugium); (*b*) MP (Mississippi refugium); (*c*) MS1 (Missouri refugium 1); (*d*) MS2 (Missouri refugium 2); (*e*) HB (hybrids from MS and MP); (*f*) combined introduced populations.