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Contents

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Abstract

We characterized the association between climate and somatic growth in 125 North American populations of smallmouth bass, *Micropterus dolomieu*. Using multivariate techniques (i.e., principal components and Procrustes analyses), we found an overall significant concordance between 8 climate variables (cloud cover, frost frequency, precipitation, mean air temperature, minimum air temperature, maximum air temperature, mean summer air temperature, and growing degree days above 10^{o}C) and 4 growth variables (body length increments for ages 1 to 4). Bivariate linear regressions revealed that there was a significant positive relationship between air temperature variables and early growth while growth at later ages was generally less influenced by climate. Given that the geographical range of smallmouth bass has been rapidly expanding over the past century, we also examined how the climate-growth relationships differed in populations that have been introduced outside the native distribution. Analysis of residuals from the Procrustes test indicated that the concordance between climate and growth was likely higher for populations within the native range and lower for introduced populations. Mechanisms that might generate this pattern include the possibility that the introduced populations have not had time to adapt to their new environments and the possibility that growth might respond atypically to the more extreme climates experienced outside the native range of the species.

Keywords: growth; climate; temperature; Procrustes; principal components analysis; invasion; species range; multivariate statistics; *Micropterus dolomieu*.

Introduction

Intra-specific variation in life history traits appears ubiquitous for many fish species (Roff 1992). Given that life history parameters such as somatic growth and maturity schedule can influence population dynamics and act as indicators of over-exploitation (Shuter et al. 1998; Trippel 1995), it is important to understand the mechanisms involved in producing life history variability. Temperature (Beamesderfer and North 1995), physical habitat characteristics (Shuter et al. 1998), and food supply (Chen and Harvey 1995) are factors identified as correlates of life history variation among fish populations, but their importance can vary depending on the spatial scale examined. For example, local differences in food availability can influence life history variation between adjacent populations (Dunlop et al. 2005a) but climate often drives life history variability among populations spread across a large geographic area (Beamesderfer and North 1995).

For the present study, we examined the influence of climate on somatic growth variability in smallmouth bass, *Micropterus dolomieu*, populations spanning a wide geographical area. Within a species' native range, somatic growth rates often vary intra-specifically along a latitudinal cline (e.g., Jensen et al. 2000; Lester et al. 2000) that is the result of an environmental response and (or) genetic adaptation to climate (Conover and Schultz 1995). As distance from the center of a species distribution increases, populations tend to experience increasingly stressful climatic conditions and as a result, populations at the range boundaries often exist at their physiological limits (Brown et al. 1996; Parmesan et al. 2000). When species are introduced outside of their native distribution, the physiological stress experienced at the range border might be further amplified and somatic growth might vary with climate in an atypical way. It might also take time for introduced populations to adapt to the climate in the new environment.

Therefore, as one moves away from the center of a species natural distribution, and from the native to the introduced range, the associations between climate and growth should weaken and perhaps change altogether.

Using the smallmouth bass as a study species, we assessed the following two hypotheses: (i) there is an association between climate and the somatic growth of populations that are distributed across a geographic area large enough to span a broad range in climate; (ii) the association between climate and somatic growth weakens at and beyond the boundaries of the species native distribution. We chose the smallmouth bass because past studies have shown a link between somatic growth and climate in this species (Beamesderfer and North 1995) and the range of the species has been expanding rapidly over the past century (Robbins and MacCrimmon 1974) and will likely continue to expand in the future with climate warming (Shuter and Post 1990). The smallmouth bass is a warm-water littoral predator native to central and eastern North America (Lee et al. 1980; Scott and Crossman 1973). Beginning primarily in the 1800s, humans started introducing smallmouth bass in waterbodies throughout North America (and eventually throughout the world) to provide angling opportunities (Robbins and MacCrimmon 1974). Introductions were made by private citizens and by government agencies; the sources of these introductions were both natural and hatchery reared populations (Kerr and Lasenby 2000; Robbins and MacCrimmon 1974). Further expansion of the smallmouth bass range has come through human activities including the release of fish from bait buckets (Litvak and Mandrak 1993) and from the construction of waterways and canals (Crossman 1991). Range expansion has also occurred by natural dispersal through the watershed both from native and introduced sources (Robbins and MacCrimmon 1974). These introductions have had large and often negative impacts on native fish communities (Jackson 2002; Vander Zanden et al. 1999).

In our analysis of the association between climate and growth in the smallmouth bass, we focused on 8 climate variables (cloud cover, frost frequency, precipitation, mean air temperature, minimum air temperature, maximum air temperature, summer air temperature, growing degree days above 10^{o}C) and 4 somatic growth variables (body length increment for ages 1 to 4). A previous study by Beamesderfer and North (1995) examined the relationship between growth and several environmental variables in 409 North American populations of smallmouth bass; in that study, age at quality length (280 mm) was used as an index of growth and was positively related to latitude and negatively related to mean air temperature and degree days above 10^{o}C (Beamesderfer and North 1995). We expand on this work by performing multivariate analyses (principal components analysis and Procrustes randomization tests) of growth and climate data, by analyzing additional climate variables (i.e., precipitation, cloud cover), and by examining differences between native and introduced populations.

Methods

We obtained data on North American populations of smallmouth bass from five sources: (i) population survey data collected by the Ontario Ministry of Natural Resources (OMNR); (ii) angler tournament data collected by the Nova Scotia Department of Agriculture and Fisheries; (iii) electrofishing data collected by the State of Connecticut Department of Environmental Protection (Jacobs and O'Donnell 1996); (iv) data published in Carlander (1977); (v) data published in the primary literature after 1975.

Body length information and calcified aging tissues were collected from smallmouth bass populations in Ontario between 1982 and 2001 by the OMNR using three types of sampling programs: the Near Shore Community Index Netting (NSCIN) program, the Fall Walleye Index

Netting (FWIN) program, and angling programs. The NSCIN program requires standardized trap nets to be placed in random locations around lakes during the late summer and early autumn (Lester et al. 1996). Angling programs typically involve a creel survey where anglers are interviewed and their fish sampled (e.g., Shuter et al. 1987); this occurs most frequently in the summer and autumn. Other samples were obtained from the FWIN program that occurs in the autumn and places bottom-set multimesh monofilament gill nets at random locations around lakes (Morgan 2002).

Body lengths were measured and scale samples collected from angler tournaments conducted on Nova Scotia populations in 1995-1998 and from electrofishing surveys conducted on Connecticut lakes, reservoirs, and streams in 1988-1995. Nova Scotia tournaments were conducted between May and October and detailed information can be found in MacMillan et al. (2002). Each location in the Connecticut electrofishing surveys was sampled one to four times using night electrofishing during April-June and October-November (Jacobs and O'Donnell 1996).

We obtained additional growth data on North American populations from Carlander's Handbook of Freshwater Fishery Biology (1977). We also searched the primary literature for smallmouth bass growth data published after 1975 (Table 1). For many populations (> 54%), sampling years were pooled to provide representative sample sizes. We also limited our analyses to populations with sample sizes greater than 30, however, 93% of populations had sample sizes greater than 50 and 70% had sample sizes greater than 100.

Back-calculations

Many sampling programs targeted adult members of the population and therefore we had to estimate lengths at younger ages from scale measurements. The OMNR and Nova Scotia scale samples were treated using a common back-calculation procedure that we were able to validate

independently. For each of our two most extensively studied populations (Provoking Lake and Opeongo Lake in Ontario, Canada), body length and scale radius measurements at capture were available for over 300 fish (N for Provoking = 315, N for Opeongo = 447) covering a broad range in body sizes (6 to 40 cm). For each population, body size and scale radius closely ($r^2 >= 0.94$) followed a single allometric relationship ($Length, L = a(scale\ radius)^b$). Despite the large differences in lifetime growth pattern between them (Dunlop et al. 2005a), both populations exhibited essentially identical body-scale relationships (Analysis of Covariance, $F_{1,623} = 0.27$, $P = 0.60$), with exponent estimates (b values) equal to 0.755 (Opeongo) and 0.744 (Provoking), and 95% confidence intervals (±0.019) that overlapped the confidence intervals for exponent estimates derived from 15 additional populations where length ranges were large enough (lengths ranged at least between 15 to 40 cm) to provide reasonable estimates of b (mean for 15 populations = 0.751, SD = 0.031). Given that 17 populations in total exhibited an exponent estimate essentially identical to the Opeongo-Provoking values (~0.75), we felt confident in using this estimate when back-calculating growth histories for our OMNR and Nova Scotia samples. We used the following equation to generate these estimates,

$L\ at\ earlier\ age = L\ at\ capture * (Scale\ radius\ at\ earlier\ age / Scale\ radius\ at\ capture)^{0.75}$ and we validated the procedure using marked and recaptured adult smallmouth bass sampled over 5 years on Provoking Lake and Opeongo Lake (sampling outlined in Dunlop et al. 2005a). For each individual, we compared back-calculated length estimates derived from scale samples taken at re-capture events with actual lengths observed at earlier capture events and found no statistical difference between estimated and actual lengths (t-value = -0.33, df = 68, $P = 0.74$). The percentage error (|estimated fork length – actual fork length|/actual fork length) of the estimates ranged from 0.03% to 24% and was below 5% for the majority (83%) of individuals. Scale ages

were also validated in the Provoking Lake and Opeongo Lake smallmouth bass populations against ages obtained from opercula.

Back-calculated lengths from scale measurements were available for all Connecticut populations (Jacobs and O'Donnell 1996). We used back-calculated lengths where available from Carlander (1977) and from other published sources. In addition, some populations were characterized using observed sizes at age. Populations that lacked data on young age classes (i.e., due to a lack of sampling or back-calculation data) were not used in our analyses. The Fraser-Lee back-calculation method (Carlander 1977; Francis 1990; Klumb et al. 1999) was used in the Connecticut study, the studies summarized in Carlander (1977), and in other published studies. To ensure that differences in back-calculation methodologies were not driving the results of our study, we repeated all of our subsequent statistical analyses using Fraser-Lee back-calculated lengths for the OMNR and Nova Scotia populations. Since the results from both sets of analyses were nearly identical, we are confident that our findings are not the product of mixing back-calculation methods. The results we will discuss in detail are those derived using our validated back-calculation method for the OMNR and Nova Scotia populations and the published estimates of size at age provided in the original literature sources.

Growth variables

Mean size (fork length) at age was estimated for each smallmouth bass population. Where necessary, we converted total length (TLEN) to fork length (FLEN) using the conversion ($FLEN = TLEN \bullet 1.04^{1}$) published in Carlander (1977). For populations where there was more than one source of data, mean size at age was averaged. Given that size at a later age is not independent of size at earlier ages (e.g., size at age 2 = size at age 1 + growth), using consecutive size at age data directly in multivariate analyses might produce spurious results (Jackson 1997). Therefore, we used body length increments as variables in our study. Length increments for ages

1 to 4 (estimated by subtracting mean size at age *a*-1 from mean size at age *a*) were used to avoid problems with missing data (some populations lacked data on ages above 5 and validity of age and back-calculation estimates likely becomes increasingly poor after age 5). We therefore had estimates of four growth variables for each smallmouth bass population: length increment from age 1 to 2, age 2 to 3, age 3 to 4, and age 4 to 5.

Climate variables

We obtained information on climate from the CRU Global Climate Dataset available through the Intergovernmental Panel on Climate Change (IPCC), Data Distribution Centre (http://www.cru.uea.ac.uk/link). These data consisted of 0.5º latitude by 0.5º longitude gridded mean monthly climatology information for the period 1961-1990. The mean monthly data were based on interpolation of data collected by surface weather stations (number of stations ranged between 3615 and 19,800 depending on the climate variable) and are considered to be of high quality (New et al. 1999). We obtained the mean monthly climate data for each smallmouth bass population using its geographical coordinates. We averaged the mean monthly data to obtain annual estimates of cloud cover, ground frost frequency, precipitation, mean air temperature, minimum air temperature, and maximum air temperature; we also estimated summer mean air temperature and annual degree days above 10^{o}C. Monthly degree days above 10^{o}C were determined by subtracting 10^{o}C from each monthly mean temperature and then by multiplying by the total number of days in each month. This was then summed for the entire year to estimate the annual degree days above 10^{o}C. We chose summer air temperature and degree days above 10 ^{o}C as additional climate variables in our study because they are related to length of the growing season for smallmouth bass and past research suggests that these variables and growing season length are important correlates of growth in this species (Beamesderfer and North 1995; Shuter and Post 1990).

Distribution map

We used the range map by Robbins and MacCrimmon (1974) to identify the native distribution of smallmouth bass in North America. The range map was digitized and the smallmouth bass populations for which we had data were placed on the map according to their coordinates. Populations that fell within the native range were classified as native and populations that fell outside of the native range were classified as introduced. Using ArcGIS (Esri Inc. 2001, version 8.0), the centre of the native distribution was identified as the geographic centroid of a polygon with the polygon representing the outline of the native distribution. The distance (in m) from the geographical center of the native distribution was estimated for each population.

Statistical analyses

We obtained estimates of the growth and climate variables for 125 smallmouth bass populations (44 were native and 81 were introduced; Figure 1). Degree days above 10^{o}C were $\log_e$ transformed for linearity in all subsequent analyses. We performed simple linear regressions between the climate and growth variables and assessed statistical significance of relationships using Analysis of Variance (ANOVA). To control for possible Type I errors with multiple tests, we adjusted significance levels using the Bonferroni correction (Quinn and Keough 2002). The adjusted significance level, $P < 0.00156$, was estimated as 0.05 (the un-corrected P-value) divided by the total number of tests (32).

Principal components analysis (PCA) was performed separately on the climate and growth data using a correlation matrix (Legendre and Legendre 1998). A Procrustes analysis (Jackson 1995; Legendre and Legendre 1998) was run with the scores (standardized to a variance of 1) of the first two principal components for both the climate and growth PCAs as inputs. We used the first two PCA components as inputs to the Procrustes analysis so that we could reduce

the multiple, often correlated variables down to two independent variables that explain most of the variation.

A Procrustes test is used to analyze the concordance between two data sets (climate and growth in this case). In a Procrustes analysis, one of the data configurations (i.e., the climate matrix) is rotated and scaled against a reference configuration (i.e., the growth matrix) until the residual sum-of-squares is minimized (Jackson 1995). To evaluate the significance of the Procrustes rotation and the concordance between the climate and growth datasets, we used the Procrustes randomization test (PROTEST) developed by Jackson (1995). The PROTEST is more powerful than the commonly used Mantel test and can assess the concordance between matrices for individual observations (Peres-Neto and Jackson 2001). In a PROTEST, the m^2 is a goodness-of-fit statistic that describes the association between data matrices; smaller values indicate a higher concordance (Jackson 1995). The steps in a PROTEST are as follows: (i) estimate the observed m^2 for two data sets (i.e., by minimizing the sum-of-square residuals); (ii) randomize the rows of one of the matrices and recalculate m^2; (iii) repeat the first two steps numerous times to give a distribution of random m^2 values (Jackson 1995). The PROTEST counts the number of random m^2 statistics that have a residual sum-of-squares smaller than or equal to the observed m^2 and a *P*-value can be generated to test the observed m^2 for significance (Jackson 1995).

We performed a PROTEST using our growth data set as the reference configuration and we repeated the randomization step 9999 times to assess the significance of the m^2 statistic (Jackson 1995). Residual distances between matrices for each observation (observations are populations in this case) were calculated in order to identify the concordance between growth and climate for individual populations; larger residuals indicate poorer concordance (Jackson 1995; Peres-Neto and Jackson 2001).

We performed two analyses of PROTEST residuals. First, to evaluate our prediction that introduced populations have lower concordance with climate, we tested for a statistical difference, using ANOVA, between introduced and native populations in the magnitude of PROTEST residuals (with residuals $\log_e$ transformed for normality). Second, we tested for a relationship between PROTEST residual and distance to the center of the native distribution (with both variables $\log_e$ transformed for normality) in order to determine if the concordance between climate and growth deteriorates as distance from the center of the native distribution increases.

Analyses of Ontario populations

We chose the Ontario populations as a focus for further study because they were represented by a relatively large sample of both native and introduced populations and because they were sampled with similar methodologies (i.e., by the OMNR sampling programs). We performed three analyses of the Ontario populations: (i) an ANOVA to compare the residuals of native and introduced populations; (ii) a regression of PROTEST residual on distance to the center of the native distribution; (iii) interpretation of Procrustes superimposition plots. The Procrustes superimposition plot (Peres-Neto and Jackson 2001), where residual vectors from the PROTEST are plotted with the growth vectors from the PCA, was used to graphically interpret the relationship between variables and the magnitude and direction of PROTEST residuals. In a Procrustes superimposition plot, the starting position of a residual vector represents the observed position of the population in the reference (i.e., growth) matrix and the arrow head (the apex of the residual vector) represents the position of the population in the rotated (i.e., climate) matrix after it has been configured; the length of each residual vector is the magnitude of the individual residual for a population (Peres-Neto and Jackson 2001). By comparing Procrustes superimposition plots, we can determine if somatic growth in native and introduced Ontario populations differ systematically in their response to climate.

To statistically compare the direction of residual vectors between native and introduced populations in Ontario, we divided populations into one of four quadrants depending on the direction of their residual vector. Quadrant A was assigned to populations with residual vectors pointing towards a positive value on the first (i.e., x) and second (i.e., y) Procrustes axis, quadrant B was assigned to those pointing to a positive value on the first axis and a negative value on the second axis, quadrant C was given to those pointing to a negative value on the first and second axis, and quadrant D was assigned to those pointing to a negative value on the first axis and a positive value on the second axis. Chi-square tests were done to determine if the direction of residual vectors among populations from native or introduced populations was different from random.

Results

There was considerable variation among populations in somatic growth (Table 1). Length increment for age 1 (i.e., growth from age 1 to 2) varied from 4.1 to 12.5 cm (mean ± SD = 6.8 ± 1.4 cm); for age 2, it varied from 2.5 to 10.0 cm (mean ± SD = 5.9 ± 1.4 cm); for age 3, it varied from 1.0 to 8.2 cm (mean ± SD = 5.0 ± 1.3 cm); and for age 4, it varied from 1.8 to 8.0 cm (mean ± SD = 4.2 ± 1.2 cm).

The bivariate regressions between climate and growth variables contained a lot of variation but some notable patterns were detected. When we adjusted *P*-values using the Bonferroni correction, there was a significant (at $P < 0.00156$) positive relationship between growth at age 2 and all temperature variables, between growth at age 1 and summer air temperature, between growth at age 3 and summer air temperature, and between growth at age 3 and growing degree days above 10^{o}C (Table 2). There was a significant (at $P < 0.00156$)

negative relationship between growth at age 2 and frost frequency (Table 2). Cloud cover and precipitation did not vary significantly with any growth variable and there were no significant relationships between any climate variable and growth at age 4.

For the PCA of climate data, the first and second axes (principal components) explained 76% and 16% of the variation respectively. The first principal component contrasted frost frequency with temperature variables and the second component differentiated precipitation and cloud cover from the other variables (Figure 2). The PCA scores of introduced populations were shifted slightly to the right of the native populations (Figure 2), indicating slightly colder temperatures in introduced populations. There was an outlier from Pine Flat Lake in California where there were low levels of cloud cover and precipitation.

The first and second components of the growth PCA explained 49% and 28% of the variation. The first principal component placed growth at all ages in the positive direction with little overall difference in magnitude and direction between variables (Figure 2). The second component separated growth at early ages (1 and 2) from growth later in life (age 3 and 4; Figure 2). Introduced and native population PCA scores were scattered and showed no distinct pattern (Figure 2).

Results of the PROTEST indicated a significant concordance between climate and growth (residual sum of squares = 1.54; $m^2 = 0.95$; $P = 0.003$). The largest residual (0.38) was for Pine Flat Lake in California (introduced) and the smallest residual (0.01) was for Skootamata Lake in Ontario (native). In our first test of PROTEST residuals, the residuals of introduced populations were significantly larger than for native populations ($F_{1,123} = 7.79$; $P = 0.006$). In our second test, we found a significant positive relationship between residual magnitude and distance to the center of the native distribution ($F_{1,123} = 4.11$; $P = 0.04$).

There was a contrast between the PROTEST residuals of introduced and native Ontario populations. Introduced Ontario populations had significantly larger residuals ($F_{1,40} = 22.91$; $P = 0.00002$) and there was a significant positive relationship between residual magnitude and distance to the center of the native distribution ($F_{1,40} = 18.12$; $P = 0.00013$; $r^2 = 0.32$; Figure 3). The positive relationship in Figure 3 is apparently being driven by the introduced populations and analysis without the native populations substantially increases the amount of variance explained ($F_{1,18} = 20.39$; $P = 0.0003$; $r^2 = 0.54$).

The Procrustes superimposition plots indicated interesting contrasts between native and introduced Ontario populations (Figure 4). The residual vectors had clumped apexes in both native and introduced populations but the clump for the native populations was located close to the origin while the clump for the introduced populations was located well above and to the left of the origin (Figure 4). This indicated a similar within category (i.e., native or introduced) climate but a different between category climate. This difference in climate between native and introduced populations was probably related to the more northern distribution of introduced relative to native populations in Ontario (Figure 1). The orientation of native Ontario residual vectors was more varied than that of the introduced populations, which were generally oriented in directions opposite to those defined by the early growth vectors (Figure 4). This indicated a varied growth response in native populations but generally faster observed growth in many of the introduced populations than was predicted by their climate characteristics. Accordingly, the direction of residual vectors did not differ from random in native Ontario populations (Figure 4c; $X^2 = 3.09$; df = 3; $P = 0.38$) but differed from random in introduced Ontario populations (Figure 4d; $X^2 = 10.68$; df = 3; $P = 0.01$).

Discussion

Climate contributed to variation in somatic growth among North American smallmouth bass populations; both the bivariate relationships between variables and the significant PROTEST supported this conclusion. Of the climate variables, those related to air temperature had the strongest relationship with growth, and in particular, growth at young ages. Warmer air temperatures result in generally higher thermal input to a waterbody and higher water temperatures (Matuszek and Shuter 1996). Warmer water temperatures and longer growing seasons positively influence smallmouth bass growth and survival (King et al. 1999; Shuter et al. 1980) which would explain the positive association between air temperature and growth we found in this study.

Smallmouth bass typically mature between ages 4 and 6 (Dunlop et al. 2005a) and thus, the influence of climate appeared stage-specific because it had a stronger relationship to growth at young, immature ages than typically mature ages. For young age classes, the positive relationship between temperature and growth means that larger body sizes can be achieved in southern, warmer climates. Larger body sizes at the end of the first growing season are associated with increased survival probabilities over the winter in smallmouth bass (Shuter et al. 1980) and in a variety of other species (Garvey et al. 1998; Hurst and Conover 1998; Schultz et al. 1998). In northern climates, temperatures are colder, growing seasons shorter, growth rates slower, and survival of young age classes limited; these relationships have likely been major drivers of the northern range limit in this species (Shuter and Post 1990). Similar to what we observed for the smallmouth bass, a positive relationship between early growth and temperature has been found in other freshwater sport fish such as walleye, *Sander vitreus* (Lester et al. 2000), and bluegill, *Lepomis macrochirus* (Tomcko and Pierce 2001). This relationship does not appear

universal, however, given that a recent study of yellow perch, *Perca flavescens*, found no association between temperature and growth in a survey of 72 Ontario populations (Purchase et al. 2005).

Whereas climate was related to early growth, biotic factors might play a large role later in life. In walleye *S. vitreus*, pre-maturation growth is influenced by air temperature (Lester et al. 2000) while asymptotic length is related to population density (Sass et al. 2004). In bluegill, *L. macrochirus*, the significant relationship between size at age and summer air temperature decreases with age whereas the relationship between size at age and lake size strengthens with age (Tomcko and Pierce 2001). In climatically similar smallmouth bass populations from Nova Scotia (MacMillan et al. 2002) and Ontario (Dunlop et al. 2005a), small adult body sizes are found in lakes that lack other predatory fish species. Another reason for more variation in the relation between climate and growth at older ages is that after maturation, energy is invested into reproduction (Lester et al. 2004). The somatic growth patterns observed in a population will be influenced by the timing of maturation and how much energy is invested in reproduction (Lester et al. 2004). As a result, the relation between climate and growth is weaker for typically mature age classes. Therefore, instead of being primarily driven by climate, adult growth might be shaped more by biotic factors such as population density, food availability, fish community structure, and reproductive investment.

Numerous studies have examined somatic growth rate variation along latitudinal clines (e.g., Beamesderfer and North 1995; Jensen et al. 2000) but none that we know of have examined how the relationship differs in introduced populations. In our study, introduced populations had higher PROTEST residuals than native populations indicating less concordance between climate and growth. Furthermore, higher residuals were observed in those populations furthest from the center of the native distribution. There are several possible reasons for the pattern of larger

residuals in non-native populations. First, some introduced populations might not have been established long enough to adapt to the climate in the new environment. A few populations in Nova Scotia, for example, were introduced as recently as 10-25 years ago (MacMillan et al. 2002). Second, the climate (and possibly other environmental conditions) in those locations outside the native distribution might be more extreme and not within the climate-growth response range typically experienced by smallmouth bass. Although there is a positive relationship between temperature and growth, for instance, there might be an upper limit to the growth, thus reducing or altering the response of growth to climate usually observed in native populations. Third, recently introduced populations might show fast somatic growth rates as their population expands into an environment with little intra-specific competition for food or other resources (e.g., Shuter and Ridgway 2002). In this third case, before population equilibrium is reached, the linkage between somatic growth and climate would be quantitatively different from the linkages characteristic of native populations at equilibrium.

The large Procrustes residuals of introduced populations were likely also the result of multiple population sources. Due to the nature and breadth of smallmouth bass introductions, we could not identify the exact source or date of origin of each introduced population. The large residuals do not imply that climate and growth are not related in introduced populations. Climate is still expected to influence growth in introduced populations but the response is just weaker, more varied, or atypical of what is normally observed within the native distribution. The multiple sources (hatcheries versus natural dispersal etc.), varied time since introduction (i.e., from 10 to 200 years ago), the vast range (i.e., from East to West and North to South) over which populations have been introduced, and varied ecological conditions (i.e., food availability) have likely all contributed to the residual variation observed in introduced populations. What our study shows is that climate-growth relationships are distinct between introduced and native

populations. Future research could aim at pinpointing the forces that have shaped the differences in these relationships.

The patterns we observed in the Ontario populations provide further evidence as to why the association between climate and growth was weakened in introduced populations. The relationship between climate and growth weakened with increasing distance from the native distribution. This might be because the climate becomes more severe in the north where the introductions have occurred and (or) because the range expansion has proceeded from south to north making those populations furthest north, the most recently introduced. From the analysis of residual vector directions, we also found evidence that growth was faster than what climate typically predicted in the introduced Ontario populations. Fast somatic growth might occur because population densities are low in recently introduced populations and not limited by resources. Another possibility is that populations have adapted to the cold temperatures or short growing seasons in Ontario (the northern limit of the species' range), by growing faster (or by increasing their capacity for growth), thus following the pattern demonstrated for Atlantic silversides, *Menidia menidia* (Yamahira and Conover 2002). In this case, the fact that introduced Ontario populations occur in more northern latitudes than the native populations, might explain why we do not see the same pattern within the native range in Ontario. Populations introduced to the south of the native range might initially show faster growth, like those introduced in northern Ontario, as they expand into their new environments. However, once stabilized, those southern introduced populations might adapt to the warmer climatic conditions in ways that vary from that observed in the north.

The bivariate relationships between climate and growth contained a large amount of unexplained variation (Table 2). The poorer concordance between climate and growth exhibited by the introduced populations no doubt produced some of the variability. Differences in the

year(s) of population sampling have likely also contributed to the variation. In our study, the climate variables represented a 30 year mean whereas the growth variables were measured along a shorter time-scale (typically over 1-4 years). However, the use of back-calculations and multi-year sampling likely reduced much of the potential sampling-year effects because the growth histories of smallmouth bass of multiple ages, sampled over multiple years, were typically used to calculate the length increments for each population. Therefore, the length increments for a population represented the growth pattern averaged over several cohorts and would be less influenced by short-term fluctuations in climate. We also acknowledge that although significant steps were taken to reduce them (i.e., through validation), errors in aging and back-calculations might have contributed to the observed variation.

Differences between the sampling years of introduced and native populations might have also contributed to the variation around bivariate relationships. If introduced populations were usually sampled more recently than native populations, discrepancies between climate and growth in introduced populations might reflect recent trends in climate. However, although introduced populations in our study were on average sampled in slightly more recent years (mean sampling year was 1987 for introduced and 1982 for native populations; but note that publication year was used for some populations for which sampling year was not available), in Ontario, residuals of introduced populations were larger than native populations even though their sampling year(s) did not differ (mean sampling year was 1995 for both introduced and native Ontario populations). Therefore, although differences in the timeframe of sampling might have contributed to the variation, they do not appear to be driving the relationships observed.

The use of air temperature rather than water temperature in our study might have also contributed to the observed variation. Waterbodies of different sizes or types might have similar climates but different water temperatures (e.g., Oswald and Rouse 2004; Shuter et al. 1983).

However, this fact is less likely to have influenced patterns among lake populations because the smallmouth bass is largely a littoral species and water temperatures in the shallow littoral areas of lakes are not as sensitive to the size of the waterbody (e.g., Dunlop et al. 2005a; Shuter et al. 1980; Shuter et al. 1983; Shuter et al. 1985). We also want to point out that our study focused on climate and how its association with growth weakens in introduced populations. We therefore did not explore many of the other variables that have likely contributed to the variation in growth. Variables found to contribute to growth variation in other freshwater species, and that might have similar effects in the smallmouth bass, include lake size (Purchase et al. 2005; Shuter et al. 1998), water clarity (Lester et al. 2000; Shuter et al. 1998; Tomcko and Pierce 2001), maximum lake depth (Tomcko and Pierce 2001), and food supply (Chen and Harvey 1995).

Past studies of environmental-growth linkages among geographically diverse smallmouth bass populations (e.g., Beamesderfer and North 1995; Putman et al. 1995), although comprehensive, have relied on traditional regression and correlation statistics. The multivariate test we used, PROTEST, was very useful in identifying patterns of concordance between climate and growth that otherwise would be difficult to detect. Whereas many of our bivariate relationships were weak, the Procrustes test was highly significant. Thus, although the relationship between individual growth and climate variables was often highly variable (with low r^2 values), there was a strong overall association between climate and growth that could only be detected through an appropriate multivariate test such as Procrustes.

In our analyses, we employed a Procrustes fit that minimized the residual sum-of-squares between the climate and growth matrices; this is the most traditional approach (Peres-Neto and Jackson 2001). However, it is possible to use other methods for minimizing differences in Procrustes analysis, for example, the repeated-medians fit, a resistant-fit approach (e.g., Olden et al. 2001). Just as is the case for non-parametric bivariate fits, resistant-fit Procrustes analysis

would be less influenced by outliers than the traditional least-squares fit (Siegel and Benson 1982) and although the least-squares approach detected meaningful patterns in our analysis, future studies might benefit from considering other, less traditional Procrustes fits.

The current study provides useful predictions of the impact of climate change on existing smallmouth bass populations and insights into the ways that newly introduced smallmouth bass populations might differ from long-established native populations. Our results suggest that climate warming will lead to faster growth rates, most notably at young ages. Juvenile growth is tightly linked to the timing of maturation (Dunlop et al. 2005b) and thus, climate change could have a significant impact on reproductive schedules through its impact on somatic growth. Furthermore, smallmouth bass introductions can have a large and negative impact on native fish communities (Jackson 2002; MacRae and Jackson 2001; Vander Zanden et al. 1999). The distribution of smallmouth bass has been expanding throughout the world as a direct result of conscious human actions (Iguchi et al. 2004; Robbins and MacCrimmon 1974). This range expansion will likely continue in the future and be facilitated by climate warming, particularly along the northern part of the range (Shuter and Post 1990) where some northerly range expansion has already been observed (Figure 1) since the Robbins and MacCrimmon (1974) map was made. Our results suggest that as these populations invade new environments, they might exhibit considerable variation in life history characteristics depending on the origin of the initial colonists, the geographical location of the introduction, and the length of time since colonization. These differences could play a significant role in determining the impact of these invasions on native fish communities, and therefore, further research on the biological factors that shape these differences would be of direct practical use and, in addition, would provide valuable insight to our understanding of the basic biology of smallmouth bass.

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Table 1. Characteristics of 125 smallmouth bass, *Micropterus dolomieu*, populations.

Waterbody	Type	Loc	Category	Source	Length increment (cm)			
					Age 1	Age 2	Age 3	Age 4
Alexander	Lake	CT	Introduced	CT Electrofishing	5.8	5.8	3.6	2.1
Aylesford	Lake	NS	Introduced	NS Tournament	6.2	4.4	4.3	4.8
Balsam	Lake	ON	Native	OMNR	6.7	5.9	5.1	4.3
Bantam	Lake	CT	Introduced	CT Electrofishing	4.1	4.9	5.9	3.8
Barkhamsted	Lake	CT	Introduced	CT Electrofishing	7.8	8.7	6.2	4.0
Bashan	Lake	CT	Introduced	CT Electrofishing	5.9	5.6	3.8	4.0
Bennett	River	MD	Introduced	Carlander (1977)	7.6	6.6	1.0	2.2
Bethany	Lake	CT	Introduced	CT Electrofishing	8.8	9.3	6.2	3.3
Big Buffalo Creek	River	MO	Native	Reed and Rabeni (1989)	5.4	4.7	4.8	4.3
Big Gull	Lake	ON	Native	OMNR	6.1	4.8	4.4	3.5
Big Lake	Lake	ME	Introduced	Carlander (1977)	6.8	6.9	5.8	4.9
Big Piney	River	MO	Native	Carlander (1977)	7.1	5.4	5.1	5.3
Black Pond	Lake	CT	Introduced	CT Electrofishing	5.8	5.4	7.4	3.8
Black	River	MO	Native	Carlander (1977)	8.6	7.6	6.3	5.9
Black River	Lake	NS	Introduced	NS Tournament	7.0	4.2	3.2	3.7
Boot	Lake	ON	Introduced	OMNR	6.7	4.5	3.6	4.3
Buckhorn	Lake	ON	Native	OMNR	6.1	5.4	4.7	5.1
Candlewood	Lake	CT	Introduced	CT Electrofishing	6.3	6.7	6.7	5.8
Catoctin	River	MD	Introduced	Carlander (1977)	9.3	5.1	5.4	5.6
Cedar	Lake	ON	Introduced	OMNR	7.1	5.2	4.1	3.3

Clarke	Lake	PA	Native	Carlander (1977)	8.8	8.3	4.6	2.7	
Clear	Lake	WI	Introduced	Marinac-Sanders and Coble (1981)	4.9	4.1	5.3	5.5	
Clearwater	River	ID	Introduced	Carlander (1977)	5.7	4.9	4.6	2.7	
Cliff	Lake	ON	Introduced	OMNR	5.5	4.4	3.5	3.4	
Connecticut, central	River	CT	Introduced	CT Electrofishing	8.8	7.7	5.9	3.8	
Connecticut, north	River	CT	Introduced	CT Electrofishing	8.3	6.7	5.5	4.1	
Conowingo Pond	River	PA	Introduced	Heisey et al. (1980)	7.8	5.2	7.7	3.8	
Couchiching	Lake	ON	Native	OMNR	6.8	6.0	6.6	5.6	
Coventry	Lake	CT	Introduced	CT Electrofishing	6.3	5.7	5.7	3.8	
Crooked Pine	Lake	ON	Introduced	OMNR	6.5	6.6	7.3	5.5	
Crotch	Lake	ON	Native	OMNR	6.6	5.9	4.9	5.9	
Crystal	Lake	CT	Introduced	CT Electrofishing	4.3	7.2	6.6	5.8	
Dashwa Crow	Lake	ON	Introduced	OMNR	8.5	6.5	4.1	3.4	
Deep Creek	Lake	MD	Introduced	Carlander (1977)	7.6	8.7	7.0	5.1	
Des Moines	River	IA	Native	Carlander (1977)	10.6	6.6	4.1	4.6	
Dickey	Lake	ON	Native	OMNR	5.9	4.6	4.1	4.0	
Drag	Lake	ON	Native	OMNR	5.3	4.7	3.3	4.0	
Easton	Lake	CT	Introduced	CT Electrofishing	8.4	8.7	7.5	3.6	
Fall Creek	Lake	NY	Introduced	Carlander (1977)	5.5	3.0	3.1	2.0	
Fort Gibson	Lake	OK	Native	Carlander (1977)	7.3	6.0	5.2	2.6	
Galena	River	WI	Native	Forbes (1989)	6.1	4.9	8.1	2.5	
Gardner	Lake	CT	Introduced	CT Electrofishing	6.7	6.6	5.9	4.9	

Gaspereau	Lake	NS	Introduced	NS Tournament	6.1	3.9	3.4	2.6	
Cayuga	Lake	NY	Introduced	Carlander (1977)	4.8	4.7	4.3	4.0	
George	Lake	NS	Introduced	NS Tournament	5.3	3.7	3.1	2.7	
Go Home	Lake	ON	Native	OMNR	6.5	5.5	5.5	4.1	
Gould	Lake	ON	Native	OMNR	8.0	10.0	7.0	4.3	
Grand	Lake	NS	Introduced	NS Tournament	5.9	4.3	3.6	3.1	
Highland	Lake	CT	Introduced	CT Electrofishing	6.6	6.0	4.9	4.2	
Housatonic	Lake	CT	Introduced	CT Electrofishing	6.5	4.3	3.9	5.7	
Idlewild	Lake	PA	Introduced	Carlander (1977)	8.7	7.6	7.3	5.4	
Jordan	River	IL	Native	Carlander (1977)	8.3	7.3	3.9	3.8	
Joseph	Lake	ON	Native	OMNR	4.5	4.6	4.4	4.7	
Kaministiquia	River	ON	Introduced	Stephenson and Momot (1991)	9.5	4.2	1.8	6.3	
Kashwakamak	Lake	ON	Native	OMNR	6.8	5.8	5.8	4.0	
Kennebec	Lake	ON	Native	OMNR	6.5	5.4	4.2	3.8	
Killams	Lake	NS	Introduced	NS Tournament	6.3	4.3	3.1	3.1	
Koshlong	Lake	ON	Native	OMNR	5.9	5.1	5.3	7.3	
Lake of the Woods	Lake	ON	Introduced	OMNR	7.8	4.9	3.9	3.7	
Lerome	Lake	ON	Introduced	OMNR	6.8	6.7	6.8	3.6	
Lillinonah	Lake	CT	Introduced	CT Electrofishing	7.3	5.8	5.4	5.6	
Little Gull	Lake	ON	Introduced	OMNR	8.0	6.6	5.9	5.0	
Little Miami	River	OH	Native	Carlander (1977)	7.3	7.1	5.3	4.3	
Little River	Lake	NS	Introduced	NS Tournament	6.2	4.4	3.7	3.8	

Little	River	OK	Native	Carlander (1977)	7.8	5.0	4.3	4.7	
Little Vermillion	Lake	ON	Introduced	OMNR	5.8	3.4	3.7	3.3	
Loch Raven	Lake	MD	Introduced	Carlander (1977)	9.7	10.0	7.8		5.8
Mansfield Hollow	Lake	CT	Introduced	CT Electrofishing	7.6	7.5	4.6	4.1	
Maquoketa	River	IA	Native	Paragamian (1984) in Weathers and Bain (1992)	5.9	6.4	5.5	6.2	
Mashapaug	Lake	CT	Introduced	CT Electrofishing	6.1	5.3	4.7	4.3	
Massie	River	OH	Native	Carlander (1977)	6.6	6.9	5.5	4.0	
Middle Bolton	Lake	CT	Introduced	CT Electrofishing	6.3	5.1	4.1	3.4	
Milo	Lake	NS	Introduced	NS Tournament	6.6	5.8	4.2	3.0	
Muddy Run Pond	River	PA	Introduced	Heisey et al. (1980)	8.5	5.5	3.5		2.4
Muscatatik	River	IN	Native	Carlander (1977)	4.1	4.9	4.1	6.2	
Nebish	Lake	WI	Native	Serns (1984)	5.8	6.2	4.9	5.4	
New River	River	VA	Introduced	Austen and Orth (1988) in Weathers and Bain (1992)	6.6	5.8	4.3	2.8	
Nishin	Lake	ON	Introduced	OMNR	5.6	4.4	3.7	2.9	
Norris	Lake	TN	Native	Carlander (1977)	12.5	8.2	4.9	3.6	
North Eels	Lake	ON	Native	OMNR	5.8	5.4	4.0	4.1	
Nym	Lake	ON	Introduced	OMNR	6.4	5.5	5.6	6.0	
Oneida	Lake	NY	Native	Carlander (1977)	6.9	6.5	5.3	3.2	
Opeongo	Lake	ON	Introduced	OMNR; Dunlop et al. 2005a	4.8	4.2	4.4		4.8
OPP	Lake	NS	Introduced	NS Tournament	8.2	5.8	4.3	4.3	
Panuke	Lake	NS	Introduced	NS Tournament	9.8	6.7	4.8	3.7	
Pats Creek	River	WI	Native	Forbes (1989)	7.8	6.8	4.9	4.1	

Pefferlaw	River	ON	Native	Robbins and MacCrimmon (1977)	6.5	6.1	5.1	4.3	
Pekagoning	Lake	ON	Introduced	OMNR	9.4	8.7	5.6	3.5	
Pickerel	Lake	ON	Introduced	OMNR	7.1	6.3	5.7	5.3	
Pine Flat	Lake	CA	Introduced	Carlander (1977)	8.1	8.7	5.3	4.6	
Pocotopaug	Lake	CT	Introduced	CT Electrofishing	5.6	7.0	7.3	5.9	
Porters	Lake	NS	Introduced	NS Tournament	7.5	5.8	4.7	3.8	
Potomac	River	MD	Introduced	Carlander (1977)	8.5	5.4	4.2	4.3	
Provoking	Lake	ON	Introduced	OMNR; Dunlop et al. 2005a	4.9	3.5	3.2	2.8	
Pseudo	Lake	ON	Introduced	OMNR	6.5	5.1	2.6	3.8	
Quabbin	Lake	MA	Introduced	Carlander (1977)	7.7	8.6	6.6	4.4	
Quinebaug	Lake	CT	Introduced	CT Electrofishing	6.8	7.5	6.0	1.8	
Rainbow	Lake	CT	Introduced	CT Electrofishing	7.3	8.8	7.3	4.0	
Red Cedar	River	WI	Native	Carlander (1977)	8.7	8.0	5.3	5.2	
Rice	Lake	ON	Native	OMNR	7.8	6.3	5.5	4.5	
Rosseau	Lake	ON	Native	OMNR	5.7	5.1	5.0	4.9	
Salmon	River	ID	Introduced	Carlander (1977)	5.3	4.1	3.9	2.7	
Salmon River	Lake	NS	Introduced	NS Tournament	9.2	6.6	4.6	2.9	
Salmon Trout	Lake	ON	Native*	OMNR	5.4	6.6	4.9	3.5	
Sandusky	River	OH	Native	Carlander (1977)	7.7	5.0	5.6	8.0	
Saugatuck	Lake	CT	Introduced	CT Electrofishing	6.3	6.7	4.5	3.8	
Shenipsit	Lake	CT	Introduced	CT Electrofishing	6.1	4.9	4.7	4.7	
Shoal	Lake	ON	Introduced	OMNR	6.8	5.0	4.8	4.2	

Shoals Reach	River	AL	Native	Slipke et al. (1998); Weathers and Bain (1992)	7.8	8.2 8.2 5.3
Simcoe	Lake	ON	Native	OMNR	5.9	5.8 5.4 5.5
Skootamata	Lake	ON	Native	OMNR	5.9	4.9 4.7 4.3
Smoke	Lake	ON	Introduced	OMNR	5.1	4.7 4.7 4.4
Snake	River	ID	Introduced	Carlander (1977)	5.9	5.9 3.4 2.5
Spectacle	Lake	NS	Introduced	NS Tournament	6.5	6.1 4.7 3.3
Stillwater	River	OH	Native	Carlander (1977)	6.1	7.8 6.8 5.9
Tadenac	Lake	ON	Native	Carlander (1977)	6.9	2.5 3.9 5.9
Terramuggus	Lake	CT	Introduced	CT Electrofishing	5.1	5.3 5.2 3.4
Turkey	River	IA	Native	Carlander (1977)	6.1	6.8 5.1 4.7
Twelve Mile	Lake	ON	Native	OMNR	7.0	7.0 4.9 5.4
Wangum	Lake	CT	Introduced	CT Electrofishing	5.8	6.3 7.0 5.3
Waramaug	Lake	CT	Introduced	CT Electrofishing	6.1	4.5 6.5 6.3
West Hill Pond	Lake	CT	Introduced	CT Electrofishing	6.9	4.9 3.5 3.1
West Thompson	Lake	CT	Introduced	CT Electrofishing	7.9	6.0 4.1 2.7
Wyassup	Lake	CT	Introduced	CT Electrofishing	8.8	7.6 6.1 5.0
Zoar	Lake	CT	Introduced	CT Electrofishing	6.1	5.7 4.7 4.9

*fell on the border of the native and introduced range and category is unsure

‘River’ includes streams and creeks and ‘Lake’ includes reservoirs and ponds; Loc = state or province abbreviation; Source = Connecticut electrofishing survey (CT Electrofishing), Nova Scotia angling tournament (NS Tournament), Ontario Ministry of Natural Resources sampling program (OMNR), or published data (showing reference).

Table 2. Statistics for bivariate linear regressions between growth and climate variables.

Dependent variable	Independent variable	r^2	*P*-value	Intercept	Slope
Age 1 growth	Cloud cover	0.02	0.17	10.12	-0.052
Age 1 growth	Frost frequency	0.08	0.00	8.56	-0.013
Age 1 growth	Precipitation	0.01	0.35	6.34	0.018
Age 1 growth	Mean temperature	0.07	0.00	6.07	0.010
Age 1 growth	Minimum temperature	0.07	0.00	6.66	0.010
Age 1 growth	Maximum temperature	0.07	0.00	5.52	0.010
Age 1 growth	Summer temperature	0.09	0.00*	4.04	0.015
Age 1 growth	Ln(Degree days 10)	0.08	0.00	-1.99	0.952
Age 2 growth	Cloud cover	0.01	0.36	8.25	-0.037
Age 2 growth	Frost frequency	0.14	0.00*	8.33	-0.018
Age 2 growth	Precipitation	0.00	0.48	5.54	0.014
Age 2 growth	Mean temperature	0.13	0.00*	4.84	0.015
Age 2 growth	Minimum temperature	0.13	0.00*	5.67	0.015
Age 2 growth	Maximum temperature	0.12	0.00*	4.10	0.014
Age 2 growth	Summer temperature	0.14	0.00*	2.21	0.020
Age 2 growth	Ln(Degree days 10)	0.14	0.00*	-6.92	1.385
Age 3 growth	Cloud cover	0.00	0.74	5.76	-0.012
Age 3 growth	Frost frequency	0.06	0.00	6.47	-0.011
Age 3 growth	Precipitation	0.00	0.52	4.66	0.012
Age 3 growth	Mean temperature	0.06	0.00	4.29	0.009
Age 3 growth	Minimum temperature	0.07	0.00	4.81	0.010
Age 3 growth	Maximum temperature	0.06	0.01	3.84	0.009

Age 3 growth	Summer temperature	0.08	0.00*	2.42	0.014
Age 3 growth	Ln(Degree days 10)	0.09	0.00*	-4.18	0.987
Age 4 growth	Cloud cover	0.01	0.34	6.17	-0.030
Age 4 growth	Frost frequency	0.00	0.92	4.29	-0.000
Age 4 growth	Precipitation	0.01	0.25	4.78	-0.019
Age 4 growth	Mean temperature	0.00	0.75	4.18	0.001
Age 4 growth	Minimum temperature	0.00	0.83	4.24	0.001
Age 4 growth	Maximum temperature	0.00	0.68	4.10	0.001
Age 4 growth	Summer temperature	0.01	0.28	3.48	0.004
Age 4 growth	Ln(Degree days 10)	0.01	0.26	1.49	0.296

*significant *P*-value with the Bonferonni correction (at $P < 0.00156$).

Figure 1. Locations of 125 sample smallmouth bass, *Micropterus dolomieu*, populations in North America. The shaded area is the native range of smallmouth bass from Robbins and MacCrimmon (1974).

Figure 2. Results of the principal components analysis (PCA) of smallmouth bass, *Micropterus dolomieu*, climate and growth data. (a) Variable scores (i.e., correlations) for the PCA of climate data. (b) Variable scores for the PCA of growth data. (c) Individual population scores for the PCA of climate data. (d) Individual population scores for the PCA of growth data. Closed circles are introduced populations and open triangles are native populations.

Figure 3. Relationship between PROTEST residuals and distance to the center of the native distribution for smallmouth bass, *Micropterus dolomieu*, populations in Ontario, Canada. Closed circles are introduced populations and open triangles are native populations.

Figure 4. PROTEST residuals of smallmouth bass, *Micropterus dolomieu*, populations in Ontario, Canada. (a) Procrustes superimposition plot for native populations. Insert shows the growth vectors from the PCA (from top to bottom of insert are growth at age 4, age 3, age 2 and age 1). (b) Procrustes superimposition plot for introduced populations. (c) Frequency distribution of PROTEST residual vector direction for native populations. Insert illustrates quadrant assignments (A, B, C, D) based on the direction of the residual vector. (d) Frequency distribution of PROTEST residual vector direction for introduced populations.

Figure 1.

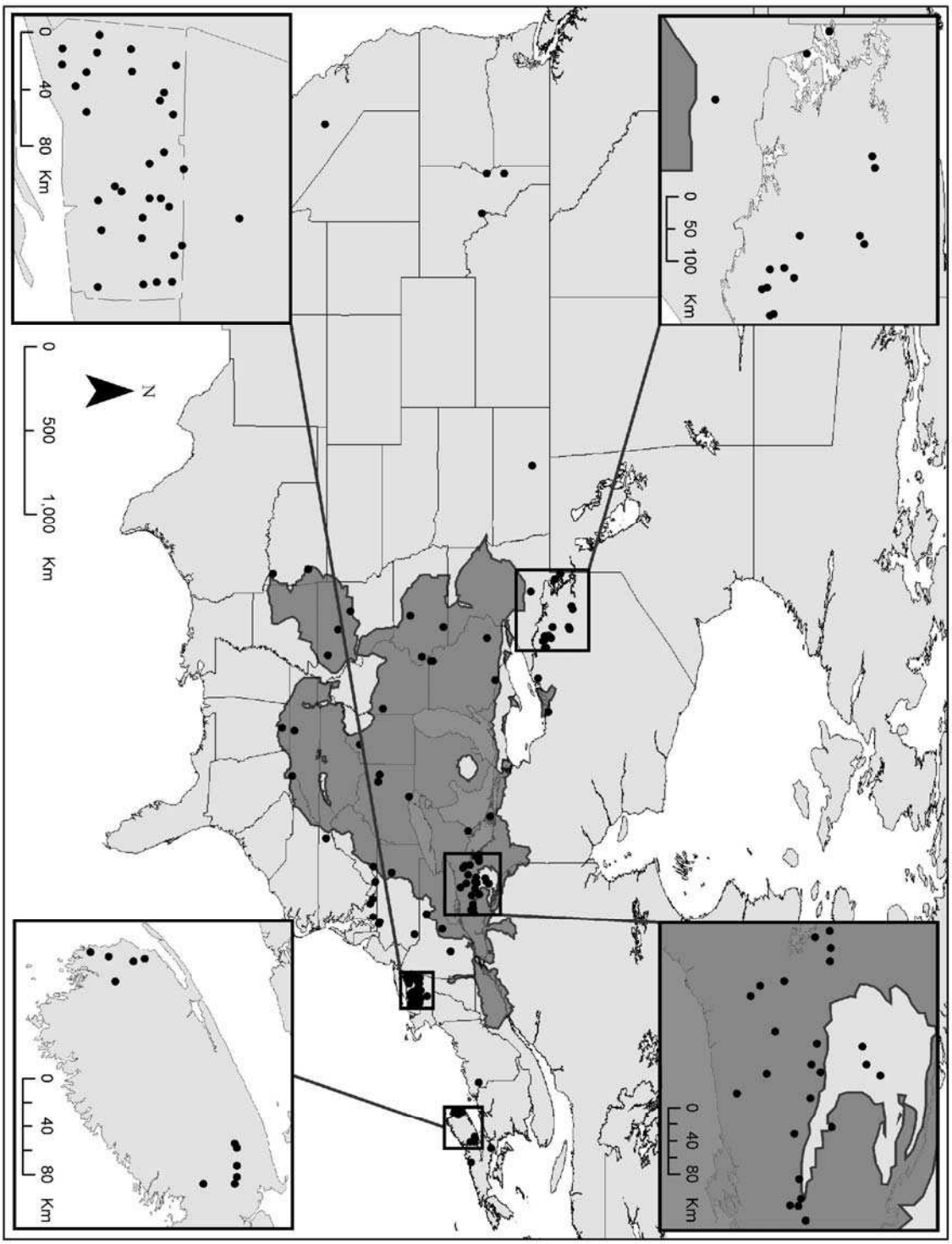


Figure 2.

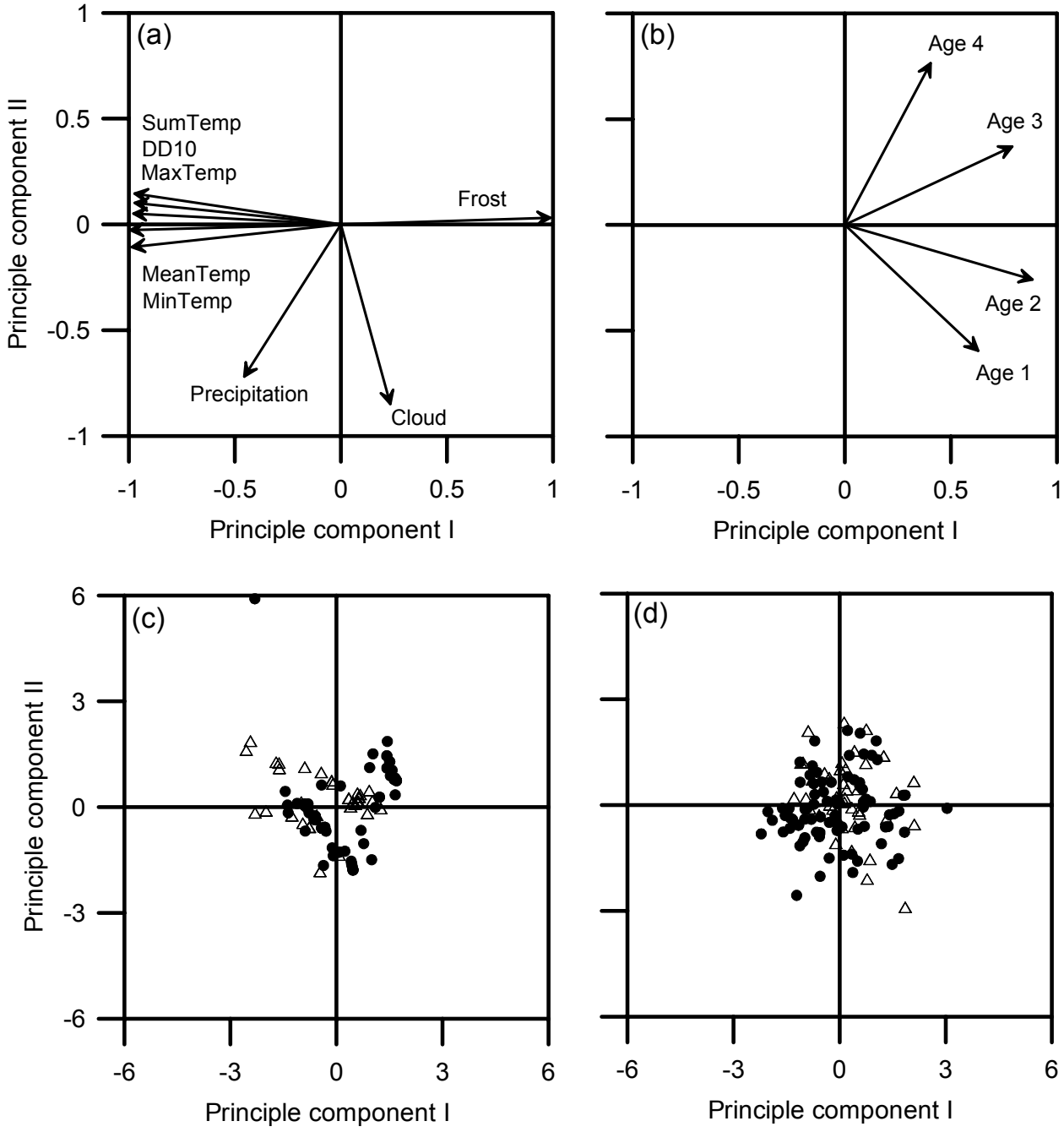

(a)
SumTemp
DD10
MaxTemp
Frost
MeanTemp
MinTemp
Precipitation
Cloud
Principle component II
Principle component I
(b)
Age 4
Age 3
Age 2
Age 1
Principle component I
(c)
Principle component II
Principle component I
(d)
Principle component I

Figure 3.

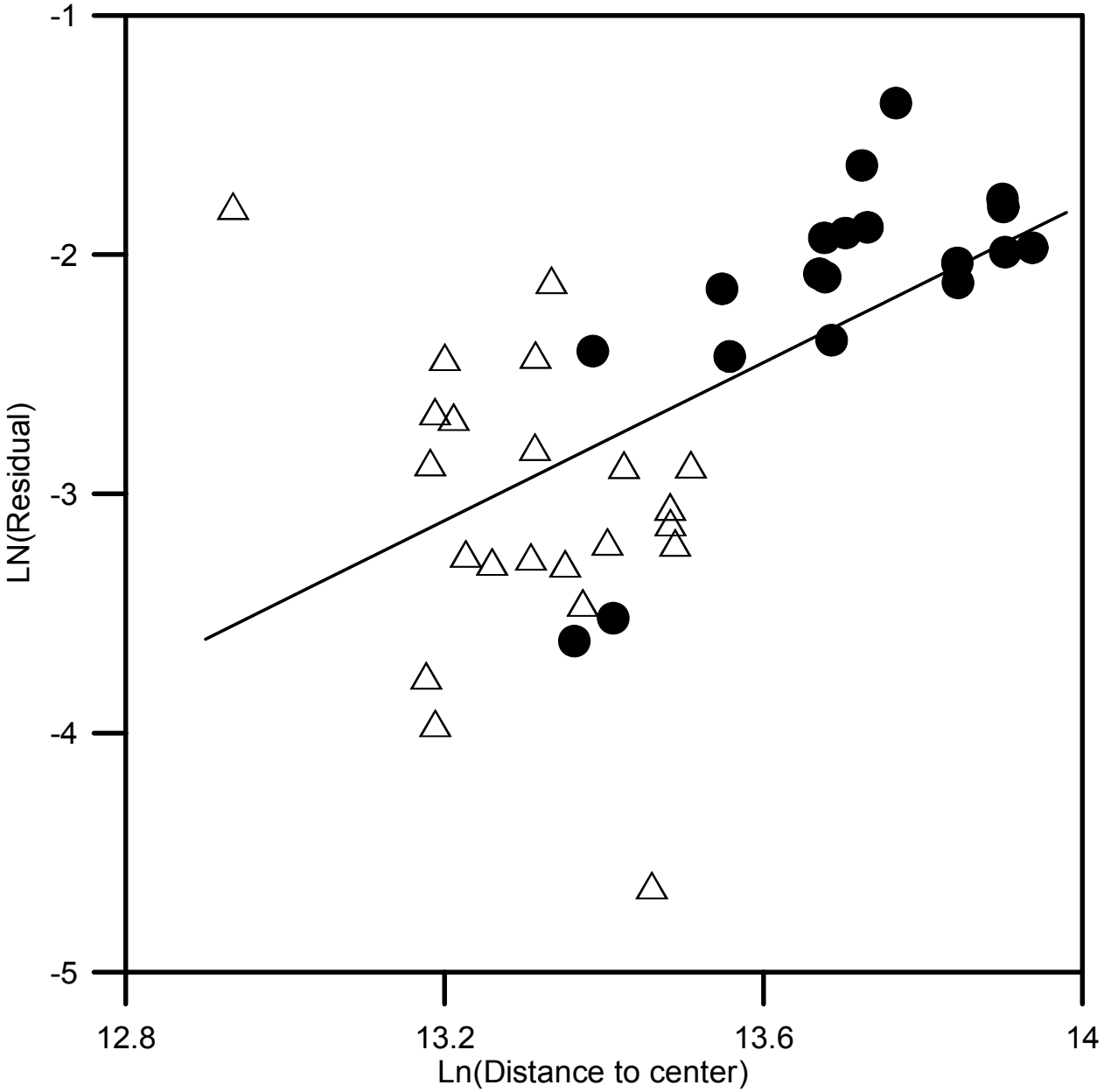
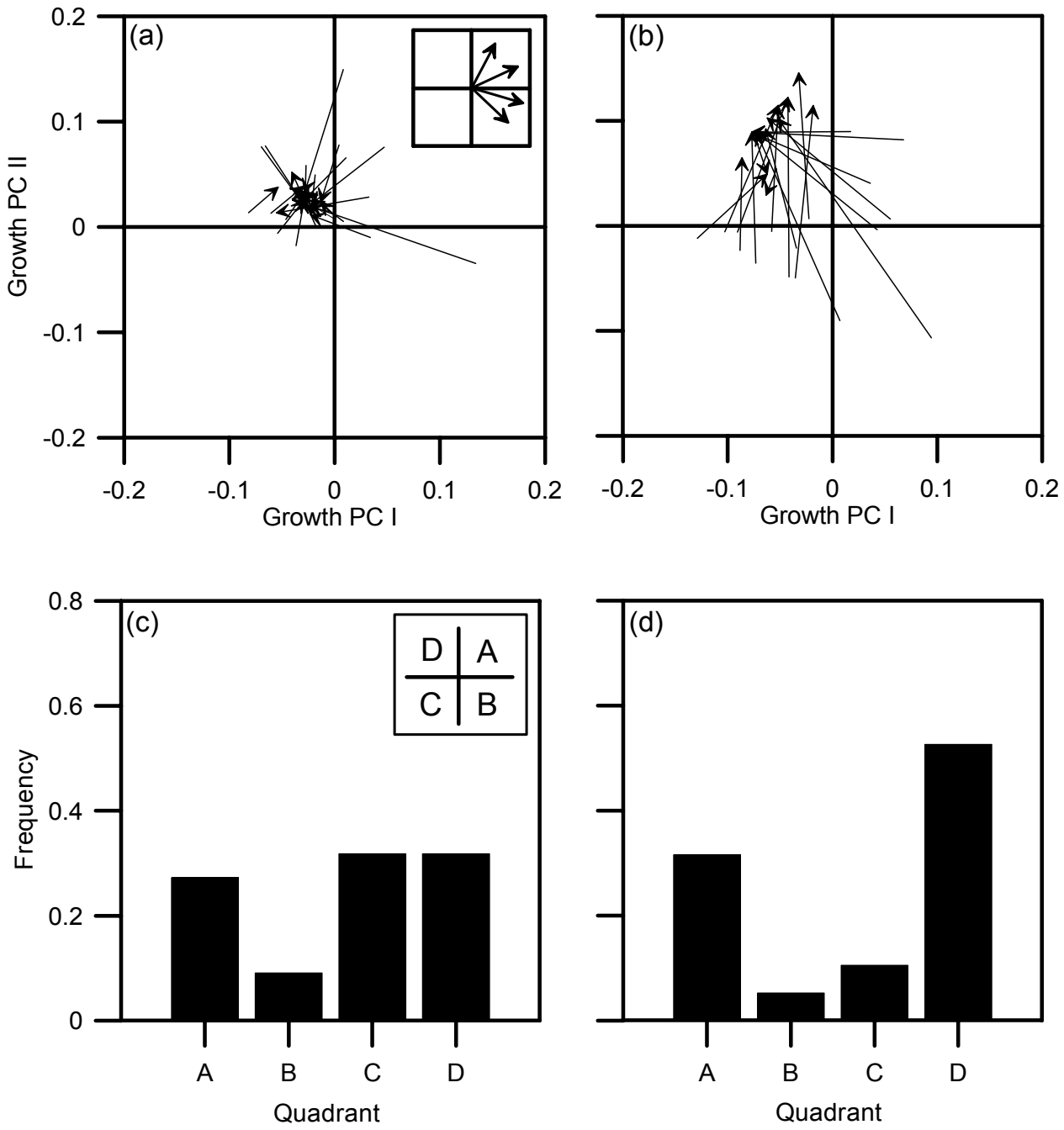


Figure 4.


(a)
(b)
(c)
(d)
Growth PC II
Growth PC I
Growth PC I
Frequency
Quadrant
Quadrant
D
A
C
B
0.2
0.1
0
-0.1
-0.2
0.8
0.6
0.4
0.2
0
A
B
C
D