

Life history differences parallel environmental differences among North American lake trout (*Salvelinus namaycush*) populations

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Abstract: Lake trout (*Salvelinus namaycush*) exhibit substantial life history variation range-wide and at a local scale. This study addresses two hypotheses that have been proposed to account for this: (i) over the zoogeographic range, climatic conditions are associated with life history differences; and (ii) within smaller geographic regions, physical lake attributes are associated with life history differences. Multivariate statistics (Procrustean analysis and canonical correlation analysis) identified a strong, range-wide association between climate and life history variables. Colder climates were associated with slower pre-maturation growth, older age at maturity, and increased longevity. Winter conditions were also important; longer, warmer winters were associated with slower pre-maturation growth, smaller maximum sizes, and increased weight at a standard length of 425 mm. In southern populations, these general trends were further modified by physical lake attributes. High productivity lakes had lake trout with faster pre-maturation growth and larger maximum sizes; deeper lakes were associated with larger maximum sizes and later ages at maturity; and larger lakes were associated with slower pre-maturation growth, greater longevity, and larger maximum sizes. This study identifies abiotic variables that should be incorporated into existing lake trout management models, thus extending their applicability range-wide and permitting them to deal with possible impacts of climate change.

Résumé : Le touladi (*Salvelinus namaycush*) connaît une importante variation de son cycle biologique à l'échelle de son aire de répartition et au niveau local. Nos examens deux hypothèses proposées pour expliquer le phénomène, soit (i) qu'à l'échelle zoogéographique, ce sont les conditions climatiques qui sont associées avec les différences de cycle biologique et (ii) que dans les régions géographiques plus restreintes, ce sont les caractéristiques physiques des lacs qui expliquent les différences de cycle. Des analyses statistiques multidimensionnelles (analyse Procruste et analyse des corrélations canoniques) révèlent une forte association, à l'échelle de l'aire de répartition, entre le climat et les variables du cycle biologique. Les climats plus froids sont associés à une croissance plus lente avant la maturation, un âge plus avancé à la maturation et une longévité accrue. Les conditions hivernales sont aussi importantes: les hivers plus longs et plus chauds sont associés à une croissance plus lente avant la maturation, des tailles maximales inférieures et une masse plus élevée à la taille standard de 425 mm. Dans les populations plus au sud, ces tendances générales sont modifiées en plus par les caractéristiques physiques des lacs. Les touladis des lacs de forte productivité ont une croissance plus rapide avant la maturation et des tailles maximales plus fortes; les lacs plus profonds sont associés à des tailles maximales plus élevées et une maturité à un âge plus avancé, alors que les lacs de plus grande taille le sont à une croissance plus lente avant la maturation, une longévité plus grande et des tailles maximales plus importantes. Notre étude identifie les variables abiotiques qui devraient être incorporées dans les modèles existants de gestion du touladi, pour étendre ainsi leur applicabilité à toute l'aire de répartition et leur permettre de traiter des impacts possibles du changement climatique.

[Traduit par la Rédaction]

Introduction

Intraspecific life history variation at the population level is common among fish species (Roff 1992) and has been associated with differences in both abiotic and biotic factors. Temperature (e.g., Haugen and Vøllestad 2000), physical habitat (e.g., Shuter et al. 1998), food availability (e.g., Ridgway and Chapleau 1994), predation rate (e.g., Reznick

et al. 1997), and fishing pressure (e.g., Conover and Munch 2002) have all been associated with among-population differences in those life history traits (e.g., growth rate, maturity schedule, reproductive investment) that play a critical role in shaping population dynamics (Roff 1992). Recent research has shown that interpopulation differences in lifetime somatic growth patterns parallel differences in climate at zoogeographic (range-wide) scales in smallmouth bass

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(*Micropterus dolomieu*), a warm-water species (Dunlop and Shuter 2006), and walleye (*Sander vitreus*), a cool-water species (Zhao et al. 2008). The objective of this paper is to extend the approach introduced by Dunlop and Shuter (2006) and Zhao et al. (2008) to provide a comprehensive assessment of associations linking variation in climate and other habitat variables to life history variation in lake trout (*Salvelinus namaycush*), a cold-water species common to freshwater lakes in Canada.

Lake trout was chosen as our study species for several reasons: (i) the broad zoogeographic range of lake trout (i.e., from the Arctic Ocean in the north to parts of the northern United States in the south; Scott and Crossman 1973) covers a wide range in climatic conditions; (ii) large interpopulation differences in life history traits such as somatic growth rate, age and size at maturity, fecundity, spawning time, and spawning frequency have been documented for lake trout in previous studies (reviewed in Martin and Olver 1980); (iii) qualitative associations linking differences in lake trout life history traits with differences in temperature have been mentioned by many authors (e.g., somatic growth rate (Martin 1952; Martin and Olver 1980), maximum adult size (Healey 1978; Burr 1997), longevity (Martin and Olver 1980), age at maturity (Healey 1978), and spawning frequency (Kennedy 1954; Healey 1978)); (iv) studies have found that the diet of adult lake trout has a strong influence on both somatic growth pattern and age and size at maturity (Martin 1952; McDermid et al. 2007); and (v) given similar climatic conditions, differences in physical lake attributes (i.e., lake size, concentration of total dissolved solids) have been shown (Shuter et al. 1998) to parallel differences in a suite of lake trout life history characteristics.

Lake trout populations also support economically significant commercial and sport fisheries throughout central and northern Canada. Accordingly, clarification of the role that climate plays in shaping population-level life history differences should be useful to managers responsible for developing conservation and management strategies for this species and for assessing future impacts of climate change on those strategies.

Our analysis applies the same multivariate approach used in analyzing growth variation in smallmouth bass (Dunlop and Shuter 2006) and walleye (Zhao et al. 2008) to a comprehensive lake trout life history database derived from 130 distinct populations spread across much of the North American range of the species. Our objective was to assess the degree to which climatic differences parallel life history differences in lake trout across its zoogeographic range. This range-wide comparison was supplemented by a further analysis of the life history variation evident among a large subsample of populations from Ontario and Quebec existing under relatively similar climatic conditions. The objective of this second analysis was to assess the role of habitat variables in accounting for the residual variation in life history traits that persists in the absence of differences in climate.

As lake trout have a complex phylogeographic history (Wilson and Hebert 1998), we also investigated the extent to which observed variation in life history traits parallels population ancestry or phylogeographic origins.

This study represents a first step towards resolving the relative contributions of ancestry and environment to the production of life history variation in lake trout. The results add to our understanding of basic lake trout biology and ecology and provide a more complete picture of the degree of life history variation expressed by the species across its zoogeographic range.

Materials and methods

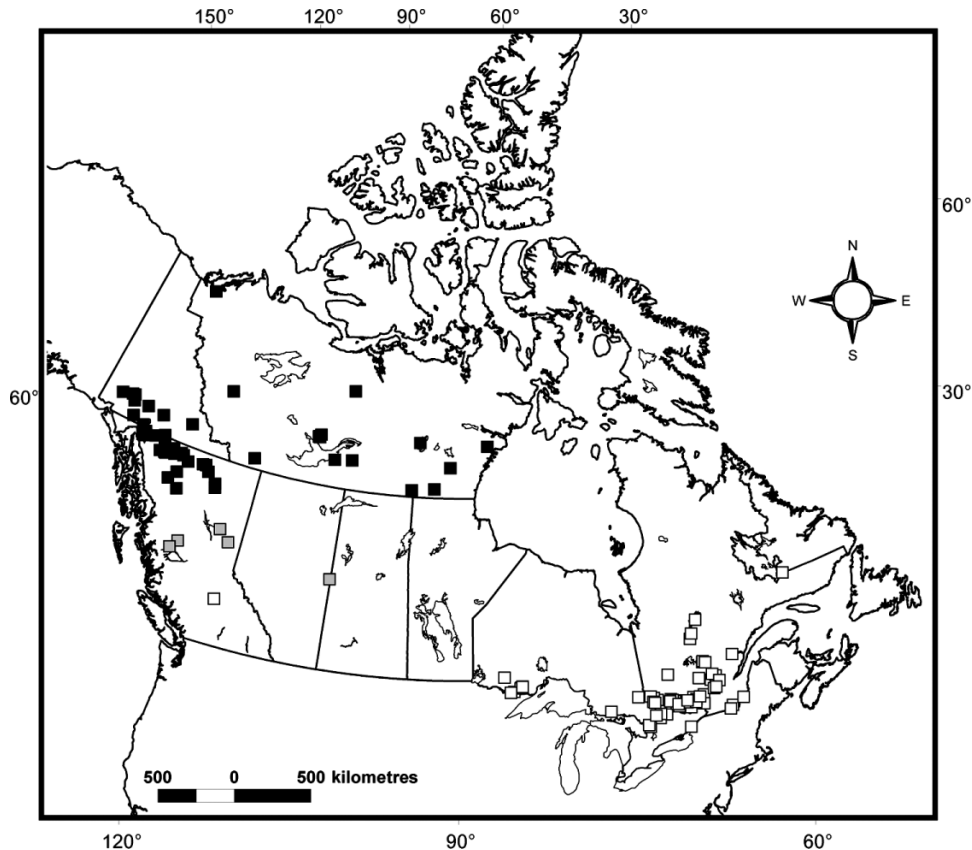
Data collection

Resource management agencies were asked to contribute lake trout data from across the range of lake trout in Canada. Data from 240 lakes were submitted and assembled in a database that included sampling year, sampling method, lake morphology, water quality, and individual fish data (i.e., fork length (“length” henceforth), age, sex, and maturity). This study is based on 130 lakes for which life history data were available (Fig. 1). Populations from the northwestern and Laurentian great lakes were not considered in this study because (i) they do not exhibit a single, characteristic life history, but rather support a variety of sympatric ecomorphs (Blackie et al. 2003; Eshenroder 2008; Zimmerman et al. 2009) with different life histories, and (ii) they live in multiple habitats in which both abiotic and biotic factors vary widely, and hence, a single set of climate and lake attribute variables could not be used to accurately characterize their habitat. Most populations were surveyed using multi-mesh gill-netting methods (see Supplemental Table S1, available online from the NRC Data Depository²). In five cases, lakes were sampled by angling alone, and in five others, the gill-net data were supplemented by angling data. Gill nets used by the different agencies were designed to capture the full size range of fish; nonetheless, differences in mesh size composition may have led to some differences in gear selectivity.

Each population was scanned for outliers by plotting (i) age versus length and (ii) weight versus length (see example in Appendix A, Fig. A1). In many cases, these outliers were obvious errors and were removed. Additionally, these plots identified that in some lakes, a few individuals were substantially larger than the general population for a given age. Because these individuals most likely represent a cannibalistic ecomorph (Brian Monroe, Ontario Ministry of Natural Resources, Algonquin Fisheries Assessment Unit, Algonquin Park, East Gate, Highway 60, Whitney, ON K0J 2M0, personal communication) whose growth and maturation pattern is not representative of the general population (Appendix A), they were removed from the population sample prior to analysis. Generally, if multiple ecomorphs were strongly represented in a population sample (as other investigators (Zimmerman et al. 2007; Eshenroder 2008) have reported in earlier studies of lake trout

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5322. For more information on obtaining material, refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

Fig. 1. Locations of 130 sample lake trout populations in Canada: southern populations (<52° latitude), open symbols; northern populations (>56° latitude), solid symbols; central populations, shaded symbols.



populations), that population was excluded from our analyses. The number of fish sampled from each population ranged from 14 to several thousand, with 78% of populations having sample sizes greater than 50 fish (see Supplemental Table S1²). For populations in which the sample size was very large (i.e., $A > 1000$), we based our analysis on a random sample of 1000 fish.

The large range in sample size was partly due to variation in lake size (i.e., 30 to 383 000 ha; Table 1). Areal density of adult lake trout typically ranges from approximately 1–11 fish·ha⁻¹ (Healey 1978; Matuszek et al. 1990; Mills et al. 2002). Consequently, in some small lakes, there may be as few as 200 adults in the population (e.g., Mills et al. 2002), and extensive sampling was not feasible without impacting the population. We recognized that a small sample size may bias measurement of some life history traits, and where possible, we used corrections based on sample size. In addition, we repeated analyses without data from poorly sampled lakes to determine if our results were distorted by their inclusion. We also repeated analyses without data from lakes sampled by angling to determine if our results were sensitive to differences in selectivity related to angling and multimesh gill-netting. We found that our results were robust to the inclusion or exclusion of lakes with small sample sizes and lakes that were sampled by angling (see Supplemental Table S3²).

Life history traits

Life history was described using indices that character-

ized each population at several different stages in its life cycle. These traits included prematuration growth rate (h , mm·year⁻¹), age and length at 50% maturity (t_m (years) and L_m (mm), respectively), maximum length (L_{max} , mm), longevity or maximum age (t_{max} , years), exponent of the weight–length relationship (b), and weight at 425 mm (w_{425} , g). Calculation methods are described below, and the values obtained for each population (including sample size and coefficient of variation) are provided in Supplemental Table S2².

Prematuration growth (h)

An index of prematuration growth rate (h) was calculated as the mean of length divided by age for immature fish that were within three years of the age at 50% maturity (i.e., $t = t_m - 1$, $t_m - 2$, or $t_m - 3$). This method supplies a growth index that is relatively insensitive to potential biases that may result from including very young fish. Because only the larger members of a young age class may be vulnerable to fishing by gill nets and (or) angling, the mean size of young age groups may be overestimated. For this reason, we used only fish that are close to maturation to measure prematuration growth rate. Our method assumes that growth is linear just prior to spawning, an assumption supported by recent empirical studies (Lester et al. 2004; Shuter et al. 2005; Quince et al. 2008) and also by our data. Plots of length versus age indicated that prematuration growth was approximately linear for most of our populations (see example in Appendix A).

Table 1. Summary statistics of climate and lake attribute variables for lakes across the Canadian geographic range of *S. namaycush*, showing mean, coefficient of variation (CV), and range for each variable.

	<i>N</i>	Mean	CV	Range
Climate variables				
Minimum temperature (°C)	130	-23.65	-0.23	-35.9 to -12.83
Mean temperature (°C)	130	-1.11	-4.09	-11.9 to 6.06
Frost frequency (days)	130	19.49	0.15	13.88 to 24.05
Precipitation (mm)	130	1.81	0.45	0.49 to 3.18
Lake attribute variables				
Lake area (ha)	114	14 809.5	3.0	30 to 383 320
Mean depth (m)	89	20.3	0.8	2.9 to 87.5
Maximum depth (m)	89	62.5	0.8	13.8 to 283.5
Secchi depth (m)	78	7.3	0.5	3.0 to 19.5
TDS (mg·L ⁻¹)	83	44.8	0.9	1.97 to 266

Note: Values of lake attribute variables are for all lakes where data were available, not just for those included in the southern population analysis. TDS, total dissolved solids.

Age (t_m) and length (L_m) at 50% maturity

Age and length at 50% maturity were assessed using the logit-based estimator, as well as a method developed by Chen and Paloheimo (1994). The two methods produced nearly identical results ($r^2 = 0.89$ and $r^2 = 0.95$, respectively). We used results from the Chen and Paloheimo (1994) method, as it provided a convenient method for estimating coefficient of variation and evaluating precision. Accordingly, estimates of age at 50% maturity (t_m) were obtained as follows:

$$\text{ASR}(P_t) = \frac{\pi/2}{1 + e^{-c(t-t_m)}}$$

where t is a given age; $\text{ASR}(P_t)$ is the arcsin-transformed square root of the proportion of fish that are mature at age t ; and parameters c and t_m are the parameters to be estimated, c is the parameter representing the instantaneous rate of fish maturation, and t_m is age at 50% maturity. For a small number of cases (see Supplemental Table S2²), the instantaneous rate of fish maturation was knife-edged (i.e., no intermediate maturity values: maturity = 0% or 100%); we therefore used a c value of 10 to force a knife-edged model. The same methods were used to estimate length at 50% maturity; however, proportion mature at length was calculated using length classes of 50 mm. For knife-edged models for L_m , we used a c value of 0.5.

Maximum length (L_{max})

Maximum length was estimated as the mean length of the top 10% of fish sampled (minimum of five fish to maximum of 10 fish).

Maximum age (t_{max})

Maximum age was estimated as the oldest fish sampled in each population. This estimate was adjusted for small sample sizes: although overall there was no significant relationship between sample size and maximum age ($r^2 = 0.0074$, $p = 0.33$), when we examined populations with only a small number of individuals aged ($n < 50$), there was a significant, positive correlation ($r^2 = 0.168$, $p = 0.002$). Consequently, for populations with fewer than 50 individuals aged, maximum age was adjusted to determine the estimated maximum

age if 50 individuals had been aged. The adjustment was derived from the formula for instantaneous mortality (Z) provided in Hoenig (1983) that links maximum age to sample size and population mortality rate. Estimated maximum age for 50 individuals ($E(t_{max(50)})$) was calculated as follows:

$$E(t_{max(50)}) = \left([E(t_{max}) - t_c] \cdot \frac{\ln(2(50) + 1)}{\ln(2n + 1)} \right) + t_{c(50)}$$

where t_c is the youngest age fully represented in the catch, $E(t_{max})$ is the estimated maximum age, and n is the sample size.

Weight-length relationship (b) and weight at 425 mm (w_{425})

The weight and length of a fish is linked through the following formula: $w = a \cdot L^b$, where w is weight and L is length. In the fisheries literature (Anderson and Gutreuter 1983), b is often assumed to have a value of 3, and the value of a ($= w/L^3$; Fulton's K), the condition factor of the population, is estimated and then interpreted as a measure of health. However, in the morphometric literature (Anderson and Gutreuter 1983), the value of b itself is of interest. Deviations from 3 are often interpreted as demonstrating systematic shifts in the design of the animal, for example, a value less than 3 indicates a shift to a more streamlined form as body size increases.

In this study, systematic shifts in lake trout body form were assessed through least squares estimates of b obtained by regressing \log_e weight against \log_e length for each population. As expected, the parameters a (intercept) and b (slope) were tightly correlated ($r^2 = 0.99$). In addition, the average condition of lake trout within a lake was estimated as the weight at 425 mm (w_{425}) from the population-specific weight-length equation. The standard length of 425 mm was chosen from the centre of the length range that was present in the data from all populations.

Sexual dimorphism

The life history traits described above were obtained by pooling data across gender. Combining data from both sexes was necessary because in many cases, sex-specific data were

not available. To check that this procedure would not seriously bias our results, we examined sexual dimorphism using 27 populations with large sample sizes of both males and females (minimum $n = 50$ of each sex). The following traits were examined: h , t_m , L_m , and L_{max} . Two-way analysis of variance on each variable indicated that all varied significantly among lakes ($p < 0.0001$ for all), whereas only t_m and L_m differed significantly between sexes ($p = 0.14$ for h ; $p = 0.003$ for t_m ; $p < 0.0001$ for L_m ; $p = 0.36$ for L_{max}). On average, females matured 0.75 years later and 37 mm larger than males. In contrast, the variation among lakes is 3.74 years for t_m and 4438.5 mm for L_m . Clearly, the degree of sexual dimorphism in these traits is small (5% of observed variation) relative to the among-population variation (76% of observed variation). Thus, life history traits obtained by pooling data across sexes will not seriously affect our ability to distinguish interpopulation differences.

Climate variables

For each population location, we estimated values for the following climate variables from the Intergovernmental Panel on Climate Change database (IPCC 2005) for the period of 1961 to 1990: mean annual ground frost frequency (days), mean annual precipitation (mm), mean annual air temperature (degrees Celsius, °C), mean for the annual minimum air temperature (°C). Climate data for this period of time were considered to be representative of average climate condition during the life span of the lake trout in our database (see Supplemental Table S1² for years fish sampled) and of sufficient duration to encompass a typical range of climate variation (Canadian Institute for Climate Studies 2005). The IPCC data set itself provides mean monthly values for each variable on a latitude–longitude grid, scaled in 0.5° increments. Values at this spatial scale were interpolated from weather station data using thin-plate splines (New et al. 1999).

Statistical analyses

Statistical analysis of life history and climate data followed the procedures described in Dunlop and Shuter (2006) and Zhao et al. (2008). To begin, life history and climate variables were centered and standardized to z scores to account for differences in measurement units among variables. Principal components analysis (PCA) was performed separately on the climate and life history data. One advantage to PCA is that it is robust to variations in the precision of the data (Legendre and Legendre 1998). This was important for our analyses as the biological data were compiled from different researchers and agencies that likely had somewhat different standards for data collection.

A Procrustean randomization test (PROTEST; Jackson and Harvey 1993; Jackson 1995; Peres-Neto and Jackson 2001) was performed on the first two PCA axes from the climate and life history data sets to assess the degree of concordance or similarity between the climate and life history data sets (see Dunlop and Shuter (2006) and Zhao et al. (2008) for a detailed description of the use of this technique on climate and life history data). The PROTEST was performed using the climate axes as the reference configuration and the life history axes as the target configuration to pro-

vide an m^2 statistic of goodness-of-fit. Data were then randomized and the PROTEST was repeated. This was done 9999 times, and the resultant distribution of m^2 values was used to assess the significance of the observed value for the m^2 statistic (Jackson 1995). The PROTEST produces residual distances between matrices for each population. These values can be used to identify the concordance between life history and climate data — smaller residuals indicate better concordance (Jackson 1995; Peres-Neto and Jackson 2001). An analysis of variance (ANOVA) was conducted on the PROTEST residuals among provinces to investigate regional differences in fit.

Lake trout have a complex zoogeographic history, with four glacial lineages that overlap in distribution throughout a large portion of the range (Wilson and Hebert 1998); however, there are geographic regions represented primarily by one lake trout glacial lineage: British Columbia (Nahanni refuge), Northwest Territories – Nunavut – Yukon (Berin-gian refuge), and Quebec (Atlantic refuge) (Wilson and Hebert 1998). We used an ANOVA on the PROTEST residuals from these regions to identify whether lake trout from different glacial lineages differed in their degree of concordance between life history and climate variables.

A canonical correlation analysis (CCoA) was performed on the standardized life history and climate data sets to assess the association between specific lake trout life history variables and climate variables. Bartlett's test of sphericity (Bartlett 1947) was applied to determine the significance of the canonical variate pairs. Canonical correlation analysis was developed to measure the correlation between the two multidimensional data sets (Legendre and Legendre 1998). This technique identifies pairs of linear combinations of the original variables, one combination from each data set. The members of each pair are chosen to maximize the correlation between them and are ordered from the pair with the highest correlation to the pair with the lowest correlation (Manly 1986; Legendre and Legendre 1998). Unlike PCA, which attempts to explain the total variance in a data set, canonical correlation analysis tries to maximize the covariance between two groups of variables (Legendre and Legendre 1998).

Analyses on southern populations

The analysis of Canada-wide life history variation was supplemented with a regional analysis that capitalized on the large sample sizes from Ontario and Quebec populations. Climatic variation among these populations is small relative to climatic variation nationally, but variation in physical lake attributes (particularly area, mean depth, and maximum depth) is large. The above set of analyses (i.e., PCA, PROTEST, CCoA) was repeated to assess associations between life history variation among these populations and variation in physical lake attributes (lake area, mean depth, and maximum depth, secchi depth, and total dissolved solids (TDS); $n = 45$ populations; see Supplemental Table S1²). Similar analyses were not done for northern populations because the number of populations sampled was relatively small, within-population sample size could be small, and variation in physical lake attributes among populations was limited.

Results

Climate and life history

There was considerable variation in life history variables among populations ranging from the northern to the southern portions of the range (Table 2). Between the north and south, lake trout differed in rate traits (i.e., prematuration growth rate, age at 50% maturity, and maximum age), but not in size traits (i.e., length at maturity and maximum length). Body shape traits (i.e., w_{425} and b) also differed between northern and southern lake trout populations. Climatic variables for the surveyed lakes also varied substantially (Table 1).

The first two principal component axes of the climate variables explained 96% of the observed variation. The first PCA axis (PCA 1 = 85.8%) contrasted minimum temperature, mean temperature, and precipitation with frost frequency (Fig. 2), thus capturing the difference between warmer, wetter, annual climatic patterns (high annual net thermal input) and colder, drier, annual climatic patterns (low annual net thermal input). The second PCA axis (PCA 2 = 10.2%) represented both minimum temperature and frost frequency (Fig. 2). As both frost frequency and minimum temperature increase together, this axis captures the difference between colder, shorter winters (low minimum temperature, low frost frequency) and warmer, longer winters (warmer minimum temperatures, high frost frequency). Lakes within provinces were strongly associated with one another. The first PCA axis separated lakes in the Northwest Territories (NT), Nunavut (NU), and Yukon (YT) (colder net thermal input) from those in Ontario (ON) and Quebec (QC) (warmer net thermal input) (Fig. 2). The second PCA axis primarily separated the BC and YT lakes with warmer, but longer winters from all other regions (Fig. 2).

The first three principal component axes of the life history variables explained 77% of the variation. The first PCA axis (PCA 1 = 34.2%) contrasted larger maximum sizes and older, larger sizes at maturity (positive t_m , L_m , and L_∞) with high prematuration growth rates (Fig. 3). The second PCA axis (PCA 2 = 27.2%) contrasted high prematuration growth rates and a more rotund body form with development (positive h and b) with greater longevity and w_{425} (negative t_{max} and w_{425} ; Fig. 3). Lakes within provinces were loosely associated with one another (Fig. 3).

PROTEST results showed concordance between climate variables and lake trout life history variables ($m^2 = 0.657$, $p = 0.0001$). The population with the smallest residual value, South Henik Lake, NU (0.0031), showed the closest match between data sets, whereas the largest residual, Tagetochlain Lake, BC (0.27), showed the weakest association between data sets (see Supplemental Table S1²). The magnitude of residuals varied significantly among provinces (excluding Alberta; $F_{5,123} = 4.53$, $p = 0.007$) and appeared to be driven by geographic extremes (BC (mean residual of 0.085) differed at $p < 0.05$ from QC (mean residual of 0.050) and Nunavut (mean residual of 0.034)). Because of the lack of differences between all other pairs of provinces, it appears that all provinces contain a mixture of populations with good and poor matches between life history and climate data.

Table 2. Summary statistics of life history variables for southern populations ($n = 63$; southern British Columbia, Ontario, and Quebec) and northern populations ($n = 62$; northern British Columbia, Northwest Territories, Nunavut, and Yukon).

Variables	Southern		Northern	
	Mean	CV	Mean	CV
h (mm·year ⁻¹)	64	0.25	45	0.28
t_m (years)	7.3	0.28	10.4	0.34
L_m (mm)	454	0.18	439	0.17
L_{max} (mm)	647	0.19	647	0.25
T_{max} (years)	23.8	0.30	34.3	0.27
w_{425} (g)	716	0.17	853	0.08
b	3.18	0.06	3.03	0.07

Note: CV, coefficient of variation; h , prematuration growth rate; t_m and L_m , age and length at 50% maturity, respectively; L_{max} , maximum length; T_{max} , maximum age; w_{425} , weight at 425 mm; b , weight-length relationship.

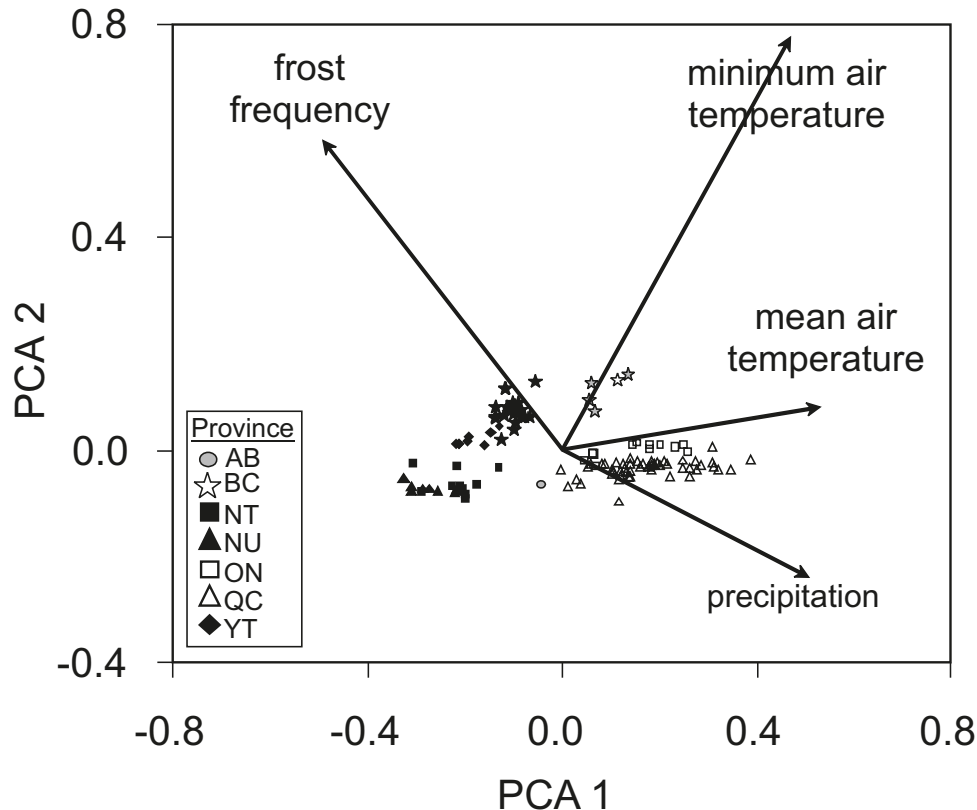
We found no clear association between glacial lineage and PROTEST residuals. The regions represented by a single glacial lineage (British Columbia (Nahanni refuge), Northwest Territories – Nunavut – Yukon (Beringian refuge), and Quebec (Atlantic refuge)) exhibited similar degrees of concordance between life history and climate variables with the exception of Quebec, which differed somewhat from British Columbia.

Canonical correlation analysis produced four pairs of canonical variates; however, only the first three pairs were significant at $p < 0.05$ (Table 3). The first canonical variate (V1) linked colder net thermal input and lower precipitation ($|r| > 0.80$: climate C1 in Table 3) to slower growth prematuration (h), greater longevity (t_{max}), and greater w_{425} ($|r| > 0.50$: life history LH1 in Table 3). These results indicate that lake trout in the north generally tend to grow slower prior to maturity, live longer, and weigh more at 425 mm. Similar to the climate PCA axis 2, the second and third canonical climate variates (C2 and C3) described winter conditions and were negatively correlated with minimum temperature (i.e., colder winters) and frost frequency (i.e., shorter winters), respectively ($|r| > 0.40$; Table 3). The second canonical life history variate (LH2) was positively correlated with L_{max} and negatively correlated with w_{425} (Table 3). The third canonical life history variate (LH3) was positively correlated with h , L_{max} , and b (Table 3). Accordingly, lake trout in the regions with warmer, longer winters (BC and YT) generally tended to show slower prematuration growth and attain smaller maximum sizes but weighed more at 425 mm than in regions with colder, shorter winters (NT, NU, ON, and QC).

Analyses on southern populations

Southern populations from Ontario and Quebec showed strong concordance between physical lake attributes and lake trout life history traits (PROTEST: $m^2 = 0.804$, $p = 0.0002$). Canonical correlation analysis produced three significant canonical variates ($p < 0.05$; Table 4). The first canonical lake variate (A1) was positively correlated with TDS and negatively correlated with secchi depth, and the first canonical life history variate (LH1) was positively correlated

Fig. 2. Biplot of the first two principal component axes for climate variables illustrating climate differences among provinces: southern populations, open symbols; northern populations, solid symbols; central populations, shaded symbols. Each symbol represents a province (see legend). Principal components analysis (PCA) loadings for minimum temperature, mean temperature, frost frequency, and precipitation are 0.47, 0.53, -0.49, and 0.51, respectively, for PCA 1, and 0.78, 0.08, 0.58, and -0.24, respectively, for PCA 2.



with h and L_{\max} and negatively correlated with t_m (Table 4). In southern lakes, TDS and Secchi depth are correlated; high TDS and low Secchi tend to describe lakes with high productivity (Trippel and Beamish 1993; Shuter et al. 1998). Thus, these results suggest that higher productivity lakes tend to have lake trout that exhibit faster pre-maturation growth, mature earlier, and are capable of achieving larger maximum sizes. The second canonical lake attribute variate (A2) was positively correlated with mean depth and maximum depth, and the second canonical life history variate (LH2) was positively correlated with L_m and t_m (Table 4). Lake trout in deep lakes therefore tend to mature at larger sizes, later in life. The third canonical lake attribute variate (A3) was positively correlated with lake area, and the third canonical life history variate (LH3) was positively correlated with L_{\max} and t_{\max} and negatively correlated with h (Table 4). Therefore, in large lakes, lake trout appear to grow more slowly prior to maturity but attain larger maximum sizes and live longer.

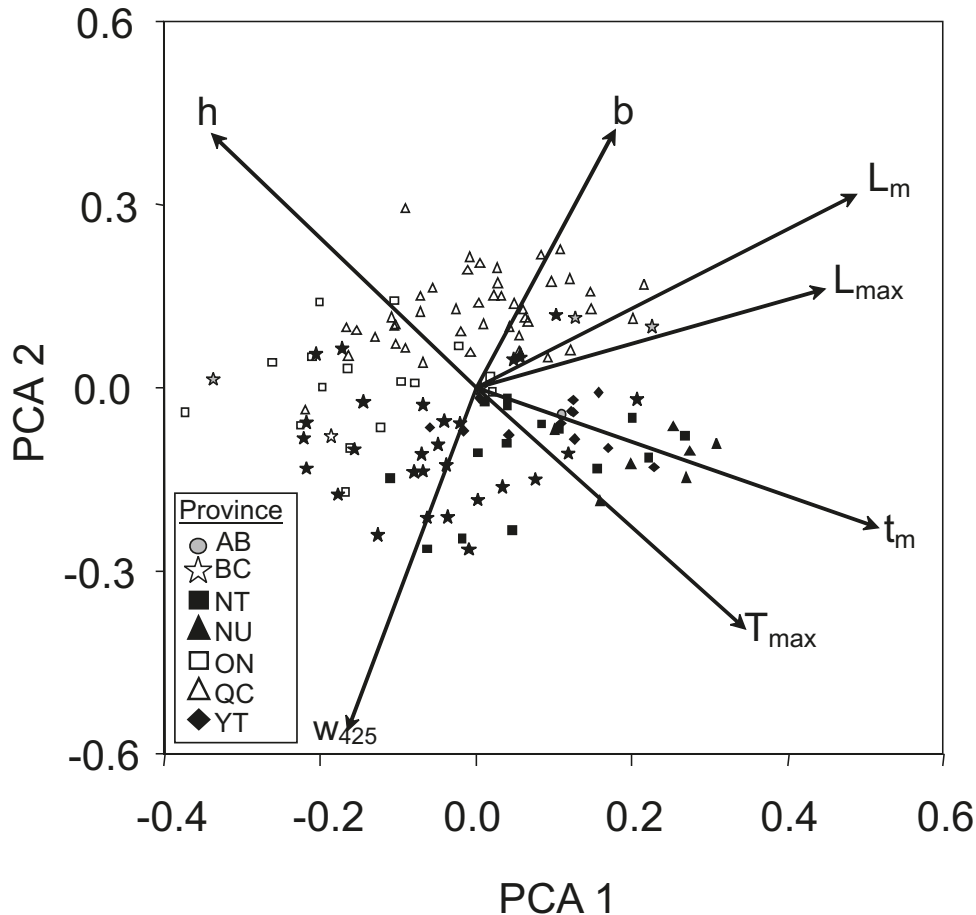
Discussion

Extensive life history variation was observed among lake trout populations across most of their North American range. The multivariate statistical approach employed here demonstrated significant associations among life history variables and abiotic factors such as climate and physical lake attributes (Jackson 1995; Olden et al. 2001; Peres-Neto and Jackson 2001). The results of this study can be summarized in

three main findings. (i) Colder net thermal inputs were associated with lake trout populations that exhibited slower pre-maturation growth, increased age at maturity and longevity, and increased weight at 425 mm. These findings are consistent with statements in earlier studies regarding differences between northern and southern populations in growth rate (Martin 1952; Martin and Olver 1980), age at maturity (Healey 1978), and longevity (Martin and Olver 1980). (ii) Regions with longer, warmer winter conditions were associated with lake trout populations that exhibited slower pre-maturation growth, smaller maximum sizes, and increased weight at 425 mm when contrasted with regions with colder, shorter winters. This association between life history characters and both the duration and intensity of winter has not been noted in previous studies. (iii) Within the southern climate zone, lakes with high productivity (higher TDS, smaller Secchi depth) were associated with lake trout populations that exhibited faster growth prior to maturity and larger maximum sizes. Deeper lakes were associated with populations that exhibited larger sizes at maturity and later ages at maturity, whereas larger lakes were associated with populations that grow more slowly prior to maturity and exhibit greater longevity and greater maximum sizes. These results are consistent with the earlier findings of Shuter et al. (1998) and extend our understanding of this relationship across a larger area.

Life history traits in lake trout have a strong association with climate across their zoogeographic range. Climate is

Fig. 3. Biplot of the first two principal component axes for life history variables (h , prematuration growth rate; t_m and L_m , age and length at 50% maturity, respectively; L_{max} , maximum length; t_{max} , maximum age; w_{425} , weight at 425 mm; b , weight–length relationship) with lake trout populations by provinces: southern populations, open symbols; northern populations, solid symbols; central populations, shaded symbols. Each symbol represents a province (see legend). Principal components analysis (PCA) loadings for h , t_m , L_m , L_{max} , t_{max} , w_{425} , and b are -0.34 , 0.52 , 0.49 , 0.44 , 0.35 , -0.17 , and 0.18 , respectively, for PCA 1, and 0.41 , -0.23 , 0.32 , 0.16 , -0.39 , -0.56 , and 0.42 , respectively, for PCA 2.



closely associated with rate traits (i.e., prematuration growth, age at maturity, and maximum age) but not with size traits (i.e., length at maturity and maximum size). The bioecological mechanisms for the patterns observed in this study are not certain. As fish are ectothermic, temperature plays a crucial role in physiological processes that determine growth rates (Fry 1947, 1957). Consequently, lakes that experience colder net annual thermal inputs would tend to support lake trout with slower prematuration growth rates, and given a relatively common length at maturity, this would lead to later ages at maturity. If we assume that most populations are close to demographic equilibrium, then lifetime reproductive investment should be the same for all populations (i.e., net reproductive rate should be close to 1). Given later maturation and the potential of not spawning every year (Kennedy 1954; Healey 1978; Martin and Olver 1980), lake trout in colder regions would need to live longer to achieve similar reproductive investment to those in the southern portion of the range (Roff 1992).

The duration and intensity of the winter was also associated with prematuration growth and maximum size. Lakes that experience winters that are warmer but longer had lake trout with slower growth both prematuration (slow prematu-

ration) and postmaturation (smaller maximum sizes). If winters are sufficiently longer in certain regions, even if they are warmer, this would shorten the feeding and growing season. Lake trout would be less able to feed both pre- and post-maturation, thus retarding their growth rate and possibly reducing the maximum sizes attained (Roff 1992).

As an obligate cold-water species, effects of climate change on thermal habitat may be expected to impact life history traits in lake trout. The associations found in this study between climate variables and life history traits identify the potential impacts that climate change may have on lake trout life history traits. With higher net thermal inputs, we may expect lake trout to show faster prematuration growth, earlier age at maturity, and decreased longevity. Additional changes may occur depending on how winter conditions are affected by climate change.

At the local or regional scale, life history traits varied with lake attributes in southern populations: higher productivity lakes supported populations with faster growth prior to maturity and larger maximum sizes. Deeper lakes supported populations with larger sizes at maturity and later ages at maturity, whereas larger lakes supported populations with greater longevity and greater maximum sizes. Although

Table 3. Pearson correlations (r) linking each life history and climate variable with its respective canonical correlation variate for the complete data set.

(a) Canonical correlation life history variates.			
Life history variables	V1: LH1	V2: LH2	V3: LH3
h	-0.548	-0.074	0.110
t_m	0.491	0.154	-0.059
L_m	-0.058	0.291	0.044
L_{max}	0.087	0.361	0.250
t_{max}	0.628	0.256	0.05
w_{425}	0.578	-0.328	0.096
b	-0.310	-0.020	0.109
(b) Canonical correlation climate variates.			
Climate variables	V1: C1	V2: C2	V3: C3
Minimum temperature	-0.819	-0.524	-0.087
Mean temperature	-0.948	-0.250	0.179
Frost frequency	0.895	-0.141	-0.421
Precipitation	-0.983	0.147	-0.103
Eigenvalues	2.455	0.415	0.139
Percent variance explained	80.2	13.5	4.5

Note: Only significant ($p < 0.05$) canonical correlation variates (V) for life history (LH1, LH2, and LH3) and climate (C1, C2, and C3) data sets are reported, and they are ordered by their explanatory power, as indicated by eigenvalues and percent variance explained. For each canonical variate (V), influential life history and climate variables are identified by high correlation values. The life history variables considered were h (pre-maturation growth rate), t_m and L_m (age and length at 50% maturity, respectively), L_{max} (maximum length), t_{max} (maximum age), w_{425} (weight at 425 mm), and b (weight-length relationship).

the life history size variables did not tend to vary with climate, these variables were important at the local scale (southern portion of the range), as were rate variables. Shuter et al. (1998) also observed greater growth prior to maturation in higher TDS Ontario lakes. High TDS is associated with higher zooplankton productivity and zooplankton is the primary food for juvenile lake trout. Shuter et al. (1998) also observed that the twofold variation in asymptotic length among Ontario lake trout populations was associated with differences in lake area and suggested that this association likely reflected differences in the biota found in small and large lakes. Lake area is positively related to species richness, resulting in greater community complexity including a generally more abundant prey community (Barbour and Brown 1974). The availability of suitable prey is known to be important in determining body size of fish (Pazzia et al. 2002; Sherwood et al. 2002). Lake trout in small lakes are less piscivorous and attain smaller body sizes than those in larger lakes (Pazzia et al. 2002), and this difference in asymptotic length has been attributed to food availability (Martin 1952; McDermid et al. 2007). Matuszek et al. (1990) found that when a large prey item such as cisco (*Coregonus artedii*) was added to a system previously lacking a large pelagic prey resource, lake trout responded by maturing at a larger size and attaining larger asymptotic lengths. Thus the associations between body size and lake size-depth identified in this study may be related to availability of suitably sized prey. The situation may be more prevalent in the southern extent of the lake trout range because cold-water forage may not be available. Nevertheless,

Table 4. Pearson correlations (r) linking each life history and lake attribute variable with its respective canonical correlation variate for southern populations from Ontario and Quebec.

(a) Canonical correlation life history variates.			
Life history variables	V1: LH1	V2: LH2	V3: LH3
h	0.444	-0.083	-0.224
t_m	-0.323	0.360	0.172
L_m	0.074	0.401	0.135
L_{max}	0.381	0.242	0.255
t_{max}	0.043	-0.106	0.266
w_{425}	0.137	-0.319	-0.007
b	0.018	0.238	0.037
(b) Canonical correlation lake attribute variates.			
Lake attributes variables	V1: A1	V2: A2	V3: A3
Lake area	0.396	0.148	0.842
Mean depth	-0.217	0.891	0.076
Maximum depth	0.213	0.901	0.375
Secchi depth	-0.604	0.513	0.149
TDS	0.653	0.512	-0.411
Eigenvalues	0.654	0.309	0.212
Percent variance explained	50.2	23.7	16.2

Note: Only significant ($p < 0.05$) canonical correlation variates (V) for life history (LH1, LH2, and LH3) and lake attribute (A1, A2, and A3) data sets for southern lake trout populations are reported, and they are ordered by their explanatory power, as indicated by eigenvalues and percent variance explained. For each canonical variate (V), influential life history and lake attribute variables are identified by high correlation values. The life history variables considered were h (pre-maturation growth rate), t_m and L_m (age and length at 50% maturity, respectively), L_{max} (maximum length), t_{max} (maximum age), w_{425} (weight at 425 mm), and b (weight-length relationship).

McDermid (2007) found that larger, deeper lakes in the northern portion of the range had lake trout that had increased longevity and asymptotic size. To resolve this issue, there is a real need for biological community data to be collected and included in future analyses of life history variation.

No consistent spatial patterns were detected among the PROTEST residuals, and hence our analysis suggests that a common quantitative association between climate and life history holds across the zoogeographic range of this species. This contrasts with the findings of Zhao et al. (2008) and Dunlop and Shuter (2006) who, in similar studies of walleye and smallmouth bass, respectively, found a strong positive association between the distance of a population from the centre of its zoogeographic distribution and the magnitude of its PROTEST residual. This may simply be an artifact of the geographic distribution of samples in our analysis: the edges of the zoogeographic distribution of lake trout are more strongly represented in our sample than is the core of the distribution. This seems an unlikely explanation with respect to associations between climate and life history, however, as our samples are relatively evenly distributed over the range of climates represented across the zoogeographic range. A more likely explanation is that virtually all of the populations in this study are native populations that have occupied their present locations for thousands of years. In both the walleye and smallmouth bass studies, populations distant from the centre of the range were largely newly introduced

populations experiencing climates at the boundaries of the climatic range typical of the native zoogeographic distribution. Thus, although life history evolution can occur rapidly when a fish species is introduced to a novel environment (e.g., Kinnison et al. 1998; Hendry et al. 2000; Haugen and Vøllestad 2001), the time frame associated with bass and walleye introductions (<100 years) still may be too short for these populations to have completely adapted to their new environments.

Zhao et al. (2008) also found geographic patterning in the PROTEST residuals that matched the regional distribution of different glacial lineages of walleye. In our analysis of lake trout, we found no association between glacial lineage (Wilson and Hebert 1998) and PROTEST residuals. Glacial lineages are more numerous and more geographically distinct across the zoogeographic range for walleye than for lake trout. Nevertheless, the lack of association between the geographic distributions of haplotypes and PROTEST residuals suggests that the current variation in life history characteristics observed among regions is not due to local adaptation that occurred among refuge populations during their isolation in separate glacial refugia.

The apparent difference in the degree of local adaptation among glacial lineages of walleye and lake trout may be partly due to their differing thermal physiologies. The optimal temperature range for walleye is quite high (20–25 °C), and they spend much of their lives in shallow aquatic environments (e.g., lake surface waters, rivers) where the thermal environment is directly influenced in many ways by the local climate. In contrast, the optimal temperature range for lake trout is much lower (8–12 °C). In cold climates, these animals occupy surface waters, but in warmer climates, they insulate themselves from local atmospheric conditions by occupying the cold, hypolimnetic waters of stratified lakes. This capacity to adapt behaviorally to differences in the range of aquatic environments available in a particular refuge would tend to narrow differences in the range of aquatic environments actually experienced in different glacial refuges and hence limit the scope for differences in local adaptation among those refuges.

These findings suggest that as the glaciers receded and lake trout dispersed across North America, there were no refugium-based genetic drivers of life history variation among colonizing populations, and thus, at least initially, phenotypic plasticity must have played a large role in generating life history variation. This expectation is consistent with the recent work of Braaten and Guy (2002), who demonstrated significant phenotypic-driven covariation between climate and life history traits in several species of fish. They found that longevity increased from south to north along a latitudinal gradient of the Missouri River for emerald shiner, sicklefin chub, river carpsuckers, and sauger, whereas early growth rate increased for river carpsuckers and saugers from north to south along this gradient.

In our regional analysis of Ontario and Quebec populations, considerable variation in life histories remained after accounting for variation in our short list of lake characteristics. Extending this type of comparative analysis to a larger data set, including more populations and additional important environmental variables (e.g., pH, biotic community, prey type, exploitation), should provide important insights

into which additional influences are actually shaping life history variation in lake trout in this geographic region. However, such studies would need to be supplemented with common garden experiments (e.g., McDermid et al. 2007) to sort out the relative contributions of phenotypic plasticity and local genetic adaptation to any observed associations between life history traits and environmental variables.

As this study is correlational in nature, the results cannot be used to revise existing management models but they do suggest that climatic characteristics should be incorporated into future models if they are to apply across the zoogeographic range for lake trout. Our results also demonstrate the importance of considering not only net thermal input, but also specific winter conditions, when modeling the effects of climate on lake trout habitat and life history traits. In addition, this study identifies possible impacts of climate change on lake trout life history traits, thus providing useful information for prioritizing future research in this area.

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Appendix A

Fig. A1. Example of lake trout data from Alexie Lake, Northwest Territories. (a) Plot of fork length vs. age for immature (□) and mature (■) fish. Life history traits include prereproductive growth (h ; thick, solid line), age and length at 50% maturity (t_m and L_m , respectively; broken lines), maximum age (t_{max} , dotted line), and maximum length (L_{max} , mean of 10 largest fish (encircled); dotted line). Data points indicated by \times represent those that were removed as outliers. (b) Plots of the natural log of weight versus fork length were used to determine both the slope of the weight-length relationship (b ; solid line) and weight at 425 mm (w_{425} ; broken line).

