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Spatial structuring of length-at-age of the benthivorous white sucker (*Catostomus commersoni*) in relation to environmental variables

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Abstract — Great variations were observed in length-at-age among populations of white sucker, *Catostomus commersoni*, in 32 Ontario lakes. The spatial structuring of these data was examined using the Mantel test with respect to the corresponding spatial structuring for various environmental variables which might affect growth of the white sucker. These environmental variables include lake geographic location, lake morphometry, water chemistry, food supply, presence/absence of major predator species, and population density and length at sexual maturity of the white sucker. Geographic distances among lakes and among-lake differences in water chemistry were significantly related to among-population differences in length-at-age. Among-lake differences in lake morphometric variables, benthos densities, presence/absence of predator species, and length at maturity and population density of the white sucker were not significantly related to among-population differences in length-at-age. No sex-specific differences in the effects of environmental variables on length-at-age were observed. This study suggests that the among-lake differences in water chemistry (thus, physiological stresses) and isolation-by-distance (thus, genetic forces) are the two most important factors in patterning the large variations in length-at-age among white sucker populations. However, discerning the separate effect of each of these two factors is not possible because the spatial patterns of these two factors are related. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Freshwater fish / length-at-age / environmental variables / spatial structuring / Mantel test / distance matrix / *Catostomus commersoni* / Ontario lakes / Canada

Résumé — Structure spatiale des tailles par âge du poisson benthivore, *Catostomus commersoni*, en relation avec des variables environnementales. Des variations importantes ont été observées dans les tailles par âge chez *Catostomus commersoni,* dans 32 lacs de l'Ontario (Canada). La structure spatiale de ces données a été étudiée au moyen du test de Mantel, en considérant celle de diverses variables environnementales correspondantes susceptibles d'affecter la croissance de ce poisson. Ces variables environnementales incluent la situation géographique et la morphologie des lacs, les caractéristiques chimiques de l'eau, la présence de nourriture, la présence/absence des principales espèces de prédateurs, la densité de population et la taille à la maturité sexuelle. Les distances géographiques entre lacs et les différences de caractéristiques chimiques de l'eau sont liées de façon significative aux différences de tailles par âge entre les populations. En revanche, ne sont pas significativement liées aux tailles par âge : les différences entre les variables de morphologie des lacs, de densité du benthos, de la présence/absence de prédateurs. Aucune différence liée au sexe n'est observée entre les tailles par âge et les variables environnementales. Cette étude indique que les deux facteurs les plus importants dans la détermination des grandes variations en tailles par âge sont les différences de caractéristiques chimiques de l'eau entre les lacs (c'est-à-dire le stress physiologique), et l'isolement lié aux distances (c'est-à-dire l'aspect génétique). Cependant, il n'est pas possible de distinguer séparément l'effet de ces deux facteurs car ils sont liés. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Poisson d'eau douce / taille par âge / variables environnementales / structures spatiales / test de Mantel / matrice des distances / *Catostomus commersoni* / lacs de l'Ontario / Canada

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1. INTRODUCTION

The white sucker, *Catostomus commersoni*, is a widely distributed, frequently occurring, and often very abundant species that may comprise half of the total fish biomass in some Ontario lakes [23, 28, 29, 59, 66, 67]. This fish itself is of little sport or commercial importance, but is often described as an important bait fish [59], a potential competitor for food with commercially and recreationally important fishes [1, 34, 35, 46], and an indicator species of the health of aquatic ecosystems [9, 10, 33, 51].

Great variation has been observed in length-at-age among different populations of white suckers [7, 17, 24, 66, 67]. This suggests white suckers in different lakes may have different rates of growth in length. Such differences may result from biotic and abiotic variables that differ among lakes [7, 64–66]. Many environmental variables have been identified as factors that may increase or reduce the rate of fish growth [52]. In general, for ecology studies involving lakes, the variables that may affect the rate of fish growth in length include density-independent and density-dependent factors [12, 15, 56]. The former often includes spatial segregation among lakes, lake morphometry and water chemistry [7, 18, 60]. The latter often includes prey density, predator density and fish population density [17, 66, 67]. These environmental variables affect fish growth through different mechanisms [52, 56, 66]. Differences in biotic and abiotic variables among lakes should contribute to differences in growth among populations of white sucker.

The purpose of this study is to test a series of hypotheses that relate the differences in length-at-age among populations of the white sucker to the differences in biotic and abiotic variables among lakes. More specifically, we evaluated the observed among-lake spatial structuring in length-at-age among populations of the white sucker in relation to isolation-by-distance and among-lake differences in: 1) lake morphometry; 2) water chemistry; 3) densities of the principle food organisms; 4) presence or absence of significant fish predators; 5) population densities; and 6) length at first maturation. Distance matrices [57] were computed among lakes for biotic and abiotic variables and among populations for length-at-age. Pair-wise analyses were then performed using the Mantel test [49] to evaluate whether the spatial structuring of length-at-age among populations of the white sucker was related to the corresponding spatial structuring in these environmental variables among lakes.

It should be noted that a correlation between two distance matrices is not equivalent to a correlation between the two variables behind these distance matrices or to the canonical correlation between two data sets. A correlation of the original variables or canonical correlation analysis measures the association between the variables or between two data sets, whereas a correlation of two distance matrices measures the extent to which the variations in the distances of one of two matrices correspond to the variations in the other matrix. In our study, comparisons between the distance matrix of white sucker length-at-age and the distance matrix of environmental variables reveal whether among-population differences in length-at-age are related to among-lake differences in environmental variables. Although such an analysis is not sufficient to establish a cause–effect relationship between among-lake spatial structuring of size data and environmental variables, it can identify environmental factors that may be important in forming the spatial patterns of length-at-age for white suckers.

2. MATERIALS AND METHODS

2.1. Collection of fish data

A total of 2 223 white suckers was collected from 32 Ontario lakes between 1978 and 1990 (*table I*). Fish fork length was measured to the nearest 0.1 cm. The first pectoral finray was clipped from one fin of each fish for the purpose of age determination and back-calculation of growth [8]. Fish scales located above the lateral line and just posterior to the origin of the dorsal fin were taken for verification of the first annulus. Validation of annuli was based on recapture of tagged fish. Sex determination was based on macroscopic inspection of the gonads or on a feature of mature males: the long anal fin ray bearing horny tubercles and pelvic ray seven being longer in males versus ray three in females [7, 65]. Stages of sexual maturation were assigned based on the criteria of Trippel [65]. The procedure of back-calculation of length-at-age was described by Chen [16]. Lengths at ages 2, 3 and 4 were chosen for the analysis owing to the relatively large sample sizes compared with older and younger age groups for all populations (*figure 1*). Sample sizes ranged from seven white suckers for Harp lake to 199 white suckers for Dickie lake. Although sample sizes were small for several lakes (*table I*), the back-calculation approach we used made the estimation of length-at-age possible for populations with small sample sizes [16]. Variation in length-at-age is much smaller within a population than among populations [7, 16]. Thus, even though the length-at-age data for some populations were derived from small samples, they still should represent the length-at-age of the sampled populations in this study which is focused on the among-population variability in length-at-age. Inclusion of the populations with small sample sizes is not likely to affect the outcome of our study substantially.

For each population where maturity information was collected, the percentage of mature fish was calculated with respect to fork length. The percentages were arcsine-transformed, and regressed on fork length using a simple linear model. Significant regression equations were solved to estimate the length at which 50 % of the fish (L50) were mature for each sex

Table I. Sample size of white suckers and geographic locations and four morphometric variables of the 32 study lakes.

Lake	Code	Sample size	Location		H	S	V	LP
			N. Lat.	W. Long.				
Barry	1	74	48.21	84.20	13	17	43.7	4.1
Bentshoe	2	126	45.02	78.56	9	6.9	16.8	2.6
Bigwind	3	65	45.03	79.03	32	118	111	8.2
Blue Chalk	4	71	45.12	78.56	23	46.4	49.4	4.6
Buck	5	67	45.23	79.00	30	37.9	40.3	3.6
Chub	6	93	45.13	78.59	27	28.7	32.2	3.9
Cinder	7	63	45.04	78.56	37	63.9	77.0	8.2
Crosson	8	108	45.05	79.02	25	47.7	56.8	3.9
Dan	9	16	45.09	78.52	17	9.9	16.8	2.1
Dickie	10	199	45.09	79.05	12	46.6	93.2	7.8
Fawn	11	103	45.10	79.15	8	29.4	86.6	4.1
Fletcher	12	100	45.21	78.47	23	202	256	19.8
George	13	49	46.02	81.24	37	275	147	13.0
Glen	14	69	45.13	78.50	15	11.7	16.3	1.8
Gullfeather	15	77	45.06	79.01	13	31.6	65.9	5.3
Harp	16	7	45.23	79.07	40	82.3	66.9	4.6
Harvey	17	56	45.17	78.50	14	24.4	55.5	4.8
Heeney	18	21	45.08	79.06	6	6.2	21.5	2.4
Herb	19	97	45.14	78.48	16	24.3	57.8	7.4
Jill	20	37	45.09	78.57	4	2.4	11.1	2.1
Kakakise	21	18	46.04	81.20	35	145	118	7.9
Leech	22	23	45.03	79.06	15	55.8	82	5.6
Little Clear	23	12	45.25	78.18	25	8.8	10.9	1.5
Little Wren	24	31	45.11	78.51	12	6.6	15.8	3.1
McQuaby	25	107	46.02	79.34	14	224.2	NA	NA
Poorhouse	26	47	45.22	78.45	13	12.4	30.2	3.1
Red Chalk	27	139	45.11	78.57	38	62.0	56.9	4.8
Solitaire	28	118	45.23	79.00	31	133	124	6.0
Teapot	29	42	45.08	78.59	11	13.4	33.5	4.5
Troutspawn	30	54	45.24	78.45	14	51.5	99.1	6.9
Wolf	31	27	45.26	78.42	23	56.5	92.7	9.0
Secord Pond	32	150	45.58	79.16	6	1.5	NA	NA

H, lake maximum depth (m); S, lake surface area (ha); V, lake volume (m^3); LP, lake perimeter (km). NA, not available.

of the population [17, 69]. This length was used to represent the length at maturation [69].

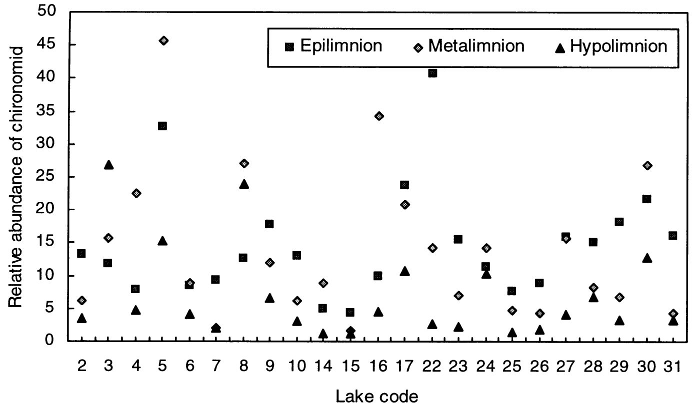
Population sizes of white sucker were estimated for 16 of the 32 study lakes. Only white suckers with fork length longer than 10 cm were included in population estimations. For five populations, estimates and their associated confidence intervals were determined by the Petersen mark–recapture method [55]. Sizes of the other 11 populations were estimated in Trippel [65].

Whereas fish density is often expressed as population size divided by lake surface area, the use of this index in subsequent analyses may lead to spurious correlations [39]. To avoid this problem, a least-square regression analysis was performed between log population size of white sucker and log lake area to remove lake-area effect from the population size. This lake-area-removed population size was then used as a measure of white sucker population density as proposed by Johnson [40].

2.2. Selection of environmental variables

Environmental variables were grouped as lake morphometry, water chemistry, density of benthic organisms and fish predators. Selection of variables for analysis was dependent upon their potential ecological importance, descriptive ability, overall representation and conformity with previously published analyses.

In general, the white sucker is considered a secondary consumer that feeds on benthic invertebrates and microcrustaceans [1, 2, 6, 43]. While most major zooplankton groups present in lakes were found in the gut contents of white suckers, chironomid larvae and ephemeropterans have been identified as the largest components [14, 19, 64] and have been related to the growth of white suckers in some populations [65, 66]. Thus, subsequent analysis was limited to the abundance of chironomid and ephemeropteran larvae. Benthos sampling and processing in the field and laboratory were based on the methods of Allison and



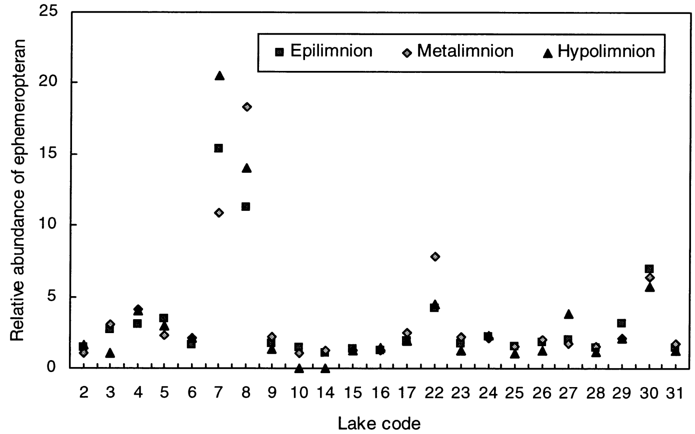


Figure 1. Relative abundance of chironomids and ephemeropterans. The numbers are the average numbers of chironomids and ephemeropterans per sampling tube cross-sectional area (19.6 cm^2) calculated from 60 cores for each lake in the three thermal zones. Data are only available for 22 lakes.

Harvey [3]. Benthic cores, 60 per lake, were taken from the sediment in the epilimnion (i.e. from water surface to 1 m above the thermocline), metalimnion (i.e. from 1 m above to 1 m below the thermocline), and hypolimnion (i.e. from 1 m below the thermocline to the lake maximum depth), respectively. To avoid problems of spurious interpretation in analysis [39], the average number of the benthic organisms per sampling tube (cross-sectional area = 19.6 cm^2) was used to represent relative abundance of benthos (*figure 1*).

Reduction of redundancy and maximization of data diversity and ecological importance were considered in selection of lake morphometric variables. Whereas compound variables derived from two or more simple variables (e.g. mean depth) may have more descriptive power, they tend to increase redundancy and complicate interpretation when added to a list of morphometric measurements. Also, the use of compound or ratio variables in statistical analysis has been criticized as leading to spurious correlations [4, 39]. Therefore, no compound morphometric variables were used. Lake area and volume were selected as they represent a surrogate measure of environmental heterogeneity and are of importance in determining fish community composition [37, 66]. Maximum depth may identify cold-water habitat (hypolimnion) associated with thermal stratification, and thus may be most important in determining the three-dimensional complexity of lakes [47]. White suckers have been reported to undergo daily inshore–offshore migrations during summer [63, 64, 66], being inactive in deeper water during daylight, moving inshore and feeding at night [22]. The energy-conserving behaviour of fishes described by Biette and Geen [13] could be hypothesized for white sucker: feeding in warm littoral waters and digesting in colder water at depth, but the analysis of stomach contents did not support this hypothesis [45]. Much of a lake's primary and secondary production occurs in the littoral zone [72] and may be especially important for white sucker feeding, and length of lake shoreline was included in the analysis.

Based on a literature search of chemical variables important to fishes in low-ionic waters, lake pH, conductivity, alkalinity, calcium, magnesium, sodium and potassium were selected for assessment of their potential roles in length-at-age of white sucker (*table II*). In numerous studies, these variables have been

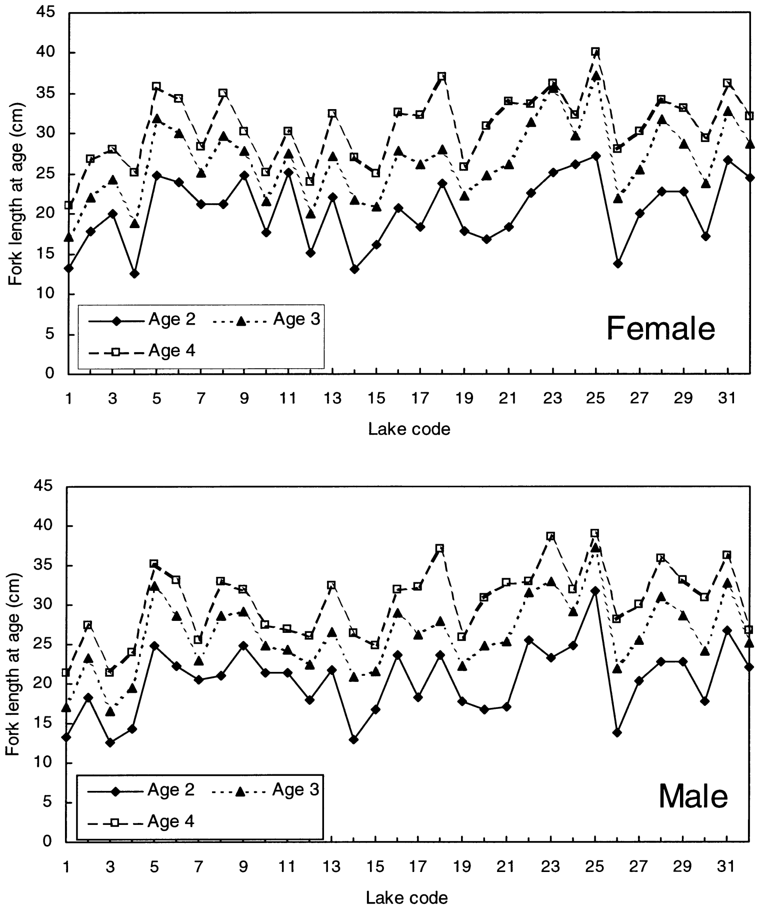


Figure 2. Variations in fork length for white suckers aged 2, 3 and 4 years among 32 populations.

shown to be important in: 1) iono-regulation or other physiological performance [31]; 2) the composition of fish species in lakes [29, 58, 62]; 3) benthic composition and abundance [27, 32, 58]; and 4) lake primary production [21].

Fish species presence and relative abundance were determined by extensive sampling. Four fish species were identified as the major predators of white sucker in the study lakes (Harvey, unpubl. data): northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), smallmouth bass (*Micropterus dolomieui*) and largemouth bass (*Micropterus salmoides*). Another three fish species, yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*) and pumpkinseed (*Lepomis gibbosus*), are also good candidates as predators of very young white suckers, but no data are available. Lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) are known predators on white suckers [59], but occurred in few lakes [37]. Because the effects on white suckers may differ greatly with respect to predator species, three situations were identified: 1) only considering the presence/absence of the four major predator species; 2) considering the presence/absence of the first seven predator species; and 3) considering the presence/absence of all nine potential predator species.

2.3. Statistical analysis

A commonly used statistical method for examining the association between two distance matrices is the Mantel test [36, 38, 49, 57, 61]. This method yields a standardized Mantel statistic, Z, which has values ranging between –1 and 1, and is equivalent to a Pearson product-moment correlation coefficient. However, because of the dependencies among values in a distance matrix, unlike the traditional correlation coefficient, the Mantel statistic Z cannot be tested for significance with the traditional method. An approximate randomization test is usually used to examine the significance of the calculated Z [20, 38, 57]. Thus, Z is tested against a distribution of values obtained by randomly permuting the rows and columns of one of the distance matrices and recomputing the Z, each case corresponding to one of the possible realizations of the null hypothesis [49, 57].

Table II. Water chemistry variables selected for this study.

Lake	pH	Ca ($mg \cdot L^{-1}$)	Alkal. ($\mu g \cdot L^{-1}$)	Conduc. ($\mu S \cdot cm^{-2}$)	Na ($mg \cdot L^{-1}$)	K ($mg \cdot L^{-1}$)	Mg ($mg \cdot L^{-1}$)
Barry	7.80	16.00	58.2	101.0	1.00	0.55	2.81
Bentshoe	5.59	2.46	14.0	32.5	1.67	0.29	0.68
Bigwind	6.62	4.20	6.0	31.0	0.70	0.40	0.70
Blue Chalk	6.50	2.68	55.0	28.0	0.71	0.36	0.65
Buck	6.68	3.20	6.0	32.0	0.60	0.55	0.80
Chub	5.56	5.50	9.2	28.0	0.50	0.40	0.60
Cinder	5.35	2.16	9.0	24.0	0.47	0.33	0.75
Crosson	5.91	2.05	10.0	23.7	0.52	0.28	0.55
Dan	5.89	2.40	24.0	25.5	0.56	0.43	0.65
Dickie	5.73	2.50	9.6	28.0	0.70	0.40	0.60
Fawn	5.47	2.40	3.7	30.0	0.80	0.55	0.60
Fletcher	6.70	2.73	67.0	32.5	0.85	0.48	1.08
George	5.00	2.70	–3.2	39.0	0.80	0.45	0.92
Glen	7.85	19.20	52.0	154.0	0.80	1.40	5.05
Gullfeather	5.51	2.21	18.0	24.5	0.50	0.30	0.65
Harp	6.57	3.20	6.0	36.0	0.90	0.50	0.85
Harvey	6.39	2.85	41.0	30.0	0.84	0.35	0.84
Heeney	5.98	2.40	2.0	27.0	0.60	0.45	0.55
Herb	5.12	2.16	4.0	22.0	0.45	0.25	0.49
Jill	6.20	3.41	63.0	31.0	0.93	0.54	0.83
Kakakise	5.90	8.00	15.0	40.0	1.10	0.48	1.10
Leech	6.08	3.00	10.0	31.0	0.70	0.45	0.65
Little Clear	6.91	3.00	4.0	34.0	0.90	0.65	0.80
Little Wren	5.80	2.72	20.0	30.0	1.23	0.34	0.66
McQuaby	5.90	2.20	1.2	30.3	1.00	0.51	0.62
Poorhouse	6.90	3.10	122.0	42.0	0.94	0.60	1.97
Red Chalk	6.43	2.57	38.1	30.5	0.66	0.37	0.70
Solitaire	6.33	3.20	4.0	32.0	0.80	0.55	0.70
Teapot	6.00	2.90	54.0	30.0	0.75	0.44	0.84
Troutspawn	6.31	2.83	23.0	30.0	0.82	0.45	0.77
Wolf	6.50	2.40	23.0	26.5	0.68	0.41	0.66
Secord Pond	8.01	NA	8512	832	NA	NA	NA

NA, not available.

The association between distance matrices of length-at-age and environmental variables was tested using the standardized Mantel statistic, Z [45, 57]. The following computation procedure was used: 1) all variables (excluding pH) were log-transformed (i.e. log (X), or log (X + 1)) if data have an observation with 0 value; log-transformation for variable alkalinity was performed using log (X + 4.2) because alkalinity value for George lake was –3.2) to normalize the data [41, 42]; 2) each character was standardized using a linear transformation $X'_i = \frac{X_i - \bar{X}}{Std}$ to reduce the effects of different scales of measurement among the variables, where $\bar{X}$ is the mean of the variable, and Std is its associated standard deviation [44, 57]; 3) the Euclidian distance matrices were computed separately for length-at-age and L50 of the white sucker, lake geographical location, lake morphometric and chemical variables, benthos density, predator presence/absence, and population density [25, 26, 44, 57]; 4) the distance matrices of fish length-at-age and L50 versus lake geographical location, lake morphometry plus water chemistry, lake benthos abundance, predator presence/absence and population density of white sucker were compared; 5) significance levels (P[random$|Z|$ > observed $|Z|$]) of the observed Z-value (Mantel's normalized correlation statistic) were estimated by comparing the observed Z with its permutational distribution created by carrying out 10 000 permutations [38]. A one-tailed test was used since a significant unidirectional (e.g. positive) deviation was logically predicted when fish length-at-age was tested against distance matrices of environmental variables. All computations were performed using NTSYS-PC [57]. Two distance matrices having a Mantel Z with *P* value smaller than 0.05 was interpreted as significantly correlated.

Environmental variables of some study lakes had missing values (*tables I, II*) and (*figure 1*). Half of the study populations had no estimates of fish length at first maturation and population size. In a specific statistical analysis, lakes or populations with missing values were excluded from the analysis.

Table III. Summary of the Mantel test between environmental variables. Numbers in the lower triangle are the Mantel normalized Z. Numbers in the upper triangle are the probability that the observed Z is smaller than the random Z from 10 000 permutations. The number of lakes used in a specific Mantel test is included in the brackets.

Variable	Geography	Morphometrics	Chemistry	Benthos
Geography	–	0.388 (30)	0.003 (31)	0.401 (22)
Morphometrics	0.01	–	0.332 (30)	0.422 (22)
Chemistry	0.42	0.03	–	0.462 (22)
Benthos	0.03	0.03	0.02	–

3. RESULTS

Large variations were observed in lake morphometry and water chemistry among the lakes: maximum depth varied from 4 to 40 m, lake surface area varied from 1.5 to 275 ha and lake pH ranged from 5.0 to 8.01 (*tables I, II*).

Variability among lakes in average number of chironomid larvae per sampling tube (cross-sectional area = 19.635 cm^2) was: epilimnion, 11.7X; metalimnion, 29.2X; hypolimnion, 21.9X between extremes (*figure 1*). Variation among lakes in the average number of ephemeropterans per sampling tube was 14.1- and 17.4-fold for epilimnion and metalimnion, respectively. No ephemeropterans were observed in the hypolimnion for two lakes (*figure 1*).

No significant association was found between the distance matrices of lake morphometry and water chemistry in the Mantel test (*table III*). Observed among-lake differences in both morphometric variables and benthos densities did not show a significant dependency on geographic distances among lakes. However, observed among-lake differences in water chemistry variables were significantly and positively related to the geographic distances among lakes. Among-lake differences in benthos densities were not significantly related to the differences in water chemistry and lake morphometry among lakes.

Lengths of female white suckers in the lakes varied from 12.6 to 27.2 cm for age 2, from 17.2 to 31.7 cm for age 3 and from 21.0 to 40.0 cm for age 4 (*figure 2*). Large variations in length-at-age were also observed for male white suckers among populations: 12.6–31.7 cm for age 2, 16.5–37.2 cm for age 3 and 21.4–38.9 cm for age 4 (*figure 2*). The among-population differences in length-at-age were highly correlated between females and males (Z = 0.757; P[random Z > observed Z] = 0.0001). For females, the observed differences in length-at-age among populations were related significantly to the geographic distances among lakes (*table IV*). However, this spatial dependency of length-at-age differed among age groups: it was not significant for age 2, but was significant for ages 3 and 4. Similar patterns could be observed for males; however, the attained significance level (0.062) was greater than the significance level of 0.05.

Associations between distance matrices of length-at-age and lake morphometric variables were not significant for both females (Z = –0.04 and P[random Z > observed Z] = 0.331) and males (Z = –0.07 and P[random Z > observed Z] = 0.205). However, the observed differences in length-at-age of both sexes among populations were associated significantly with the among-lake differences in water chemistry (*table V*). For both females and males, the Mantel tests showed that the distance matrix of length-at-age was not significantly related to the distance matrices of K and Na, but was associated significantly with the distance matrices of the other five variables (conductivity, alkalinity, pH, Ca and Mg). Both males and females showed these significant associations, but males had less extreme *P* values than females (*table V*).

The association between distance matrices of length-at-age and benthos densities was not significant for both females (Z = –0.05 and P[random Z > observed Z] = 0.363) and males (Z = –0.01 and P[random Z > observed Z] = 0.502). Similarly, the

Table IV. Summary of Mantel test between lake geographic distance and differences in length-at-age among populations of white sucker.

Length at age	Female (N = 32)		Male (N = 32)	
	Z	Prob.	Z	Prob.
Overall	0.28	0.028	0.26	0.049
Age 2	0.17	0.113	0.20	0.120
Age 3	0.29	0.028	0.28	0.049
Age 4	0.37	0.021	0.25	0.050

The number of lakes/populations is 32.
Prob.: probability that the observed Z is smaller than the random Z from 10 000 permutations.

Table V. Summary of Mantel test between distance matrices of water chemistry and length-at-age of white suckers. Due to missing data in water chemistry variables for one lake, 31 of the 32 study lakes were included in the Mantel test.

Water chemistry	Female		Male	
	Z	Prob.	Z	Prob.
Overall	0.32	0.012	0.28	0.019
Conductivity	0.32	0.008	0.31	0.014
Alkalinity	0.25	0.004	0.16	0.033
pH	0.20	0.017	0.21	0.022
Ca	0.28	0.026	0.32	0.018
K	0.11	0.118	0.10	0.152
Na	–0.04	0.641	–0.10	0.877
Mg	0.35	0.004	0.31	0.014

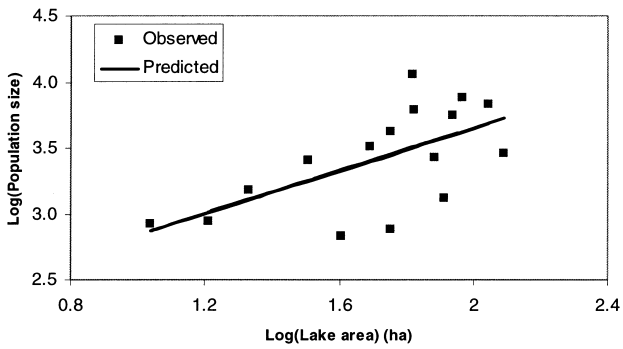


Figure 3. The least-square regression analysis of logarithm population sizes (PS) of the white sucker versus logarithm lake areas.

among-lake differences in the number of predator species present were not correlated with differences in length-at-age among populations of white sucker (Z = –0.02 and P[random Z > observed Z] = 0.618 for females; Z = –0.01 and P[random Z > observed Z] = 0.467 for males).

Population sizes of white sucker estimated for 16 lakes ranged from 676 to 11 329 and the regression analysis between log lake area and log population size was conducted (*figure 3*). No significant Mantel Zs were observed between distance matrices of lake-size-removed white sucker population size and length-at-age for both females (Z = –0.10 and P[random Z > observed Z] = 0.206) and males (Z = –0.11 and P[random Z > observed Z] = 0.176).

Size at first maturation for white suckers represented by length at which 50 % of fishes were mature (i.e. L50) differed greatly among populations, ranging from 16.7 to 30.9 cm for males and from 20.3 to 36.3 cm for females. The correlation of inter-population differences in L50s of females and males was significant (Z = 0.815; P = 0.0001). There were no significant associations of among-population differences in L50 and in length-at-age of white suckers (Mantel Z = –0.067 for females and –0.185 for males; P = 0.408 for females and 0.162 for males).

4. DISCUSSION

The significant and positive association observed between the distance matrix of length-at-age of the white sucker and geographic distances among lakes suggests that differences in length-at-age tend to be smaller for white suckers from two lakes close to each other compared with those from two lakes far away from each other. This result implies that some spatial-segregation factors such as genetic factors may contribute to the among-population differences in length-at-age [37]. However, no conclusive results can be reached without a detailed genetic study of white suckers from each lake [7].

Correlations were not significant between spatial structuring of the lake morphometry and spatial structuring of length-at-age. This implies that the differences in physical characteristics among lakes were not important in explaining the differences in length-at-age among the white sucker populations. McLaren [50] suggested that the reduced metabolic rate that occurred in poikilotherms which descended to colder hypolimnetic water during non-feeding periods would result in a larger amount of energy available for growth. This growth-enhancing behaviour was supported by observations on young sockeye salmon (*Oncorhynchus nerka*) [13] and largemouth bass [54]. White suckers were reported to feed in shallow water at night but stay in deeper and colder water during the day [22]. This is only possible if a lake thermally stratifies in summer and does not become anaerobic at those depths. Cold hypolimnetic water (about 4–6 °C) typically occurs during the summer in temperate lakes deeper than 12 m at maximum depth, depending on factors such as fetch, rate of warming, wind velocity, etc. [72], whereas shallow, polymictic lakes warm to about 24 °C in north-temperate latitudes, and do not stratify thermally [30]. Most of the lakes in this study had depth maxima greater than 12 m. For these populations it would be possible to maximize their growth if they made use of such an energy-saving feeding strategy. Logan et al. [45] recently found that white suckers were feeding in the main where they were captured; thus, their results did not support the energy-saving hypothesis. Because most of the lakes in this study stratified thermally, among-lake differences in the maximum lake depth were not important to among-population differences in length-at-age. The inclusion of more lakes with maximum depths less than 12 m (i.e. lakes uniformly warm in summer) may be needed to test the hypothesis that the availability of hypolimnetic water has a significant effect on white sucker growth. The greater magnitudes of the other selected lake-size-related morphometric variables (i.e. lake area, lake perimeter and lake volume) would be expected to result in fishes of larger lengths [52]. However, no such effects were apparent in this study: among-lake differences in each of the three variables were not significantly correlated with the among-population differences in length-at-age. We concluded that the spatial structuring of lake physical attributes was not related to the spatial structuring of length-at-age of the white sucker.

Among-population differences in length-at-age of both female and male white suckers were related significantly to the among-lake differences in water chemistry (*table V*). As described earlier, water chemistry may affect fish growth in four main ways. The last three (see the section on Selection of environmental variables) were directly or indirectly related to invertebrate abundance. However, the among-lake differences in densities of two main invertebrate organisms were found to have no significant contribution in explaining the among-population differences in length-at-age of the white sucker. The among-population differences in physiological stresses due to water chemistry might be significant in explaining the differences in length-at-age among populations. However, the distance matrix of length-at-age was significantly related to the lake geographic distances, which was in turn related to the distance matrix of water chemistry variables. Therefore, the significant association of inter-lake differences in water chemistry and observed among-population differences in length-at-age might result from their common correlation with geographic distances among lakes. As a result, no firm conclusion could be given as to which factor, water chemistry or geographic distance, was more important in explaining the among-population differences in length-at-age of the white sucker, based on this study alone.

The absence of a significant association of the among-lake differences in length-at-age and the abundance of chironomids and ephemeropterans was somewhat surprising. White sucker population density is related to benthos abundance [66]. Chironomid density typically is one or two orders of magnitude greater than that of other mesobenthos [32]. Dense white sucker populations with sparser than average chironomid populations showed much reduced reproductive success [68]. However, a quantitative analysis of sucker gut contents is usually difficult, owing in part to the absence of a stomach. White suckers may be highly selective feeders, e.g. on *Pisidium* (Harvey, unpubl. data) or euryphagic [1]. In one lake, *Hyalella* was more common in sucker gut contents than in benthic samples, whereas in a second lake chironomids dominated benthos and were most abundant in gut contents [45]. This population-specific use of food organisms may result in different food compositions among populations, and is perhaps one of the reasons that the correlation is not significant between differences in the abundance of chironomids and ephemeropterans among lakes and differences in length-at-age among populations of the white sucker. However, the conclusive explanation will not be available until we understand the trophic structure of each lake. Up till now, our understanding of trophic structure in these lakes is limited. However, we do know that the trophic structure differs considerably among these lakes owing to the large differences in fish communities and the presence and absence of crayfish, clams and snails [29, 37]. More studies on the lake trophic structure are needed to help us understand the role of food supply in patterning the spatial variations in size-at-age of the white sucker.

The Mantel test shows that among-lake differences in the number of the predator species present is not a significant factor in explaining the among-population differences in length-at-age of the white sucker. However, this test involves two assumptions: 1) the effects of different predator species in a lake on growth of white sucker are the same; and 2) the contribution of the same predator species to growth of white sucker are the same among lakes. In practice, however, these assumptions may not be realistic. Biomass of predator species might be a better indicator than presence/absence. However, the lack of such information for these lakes prevents us from using this more accurate index in this study.

In general, growth of young fishes is density dependent [52]. The inverse relationship among population densities and growth rates of fishes has been observed in many studies. This relationship between growth and population density is so important that Backiel and Le Cren [5] concluded that studies of environmental influences on fish growth are of little relevance without data on population density. Based on the Mantel test, the correlation between distance matrices of population density and length-at-age of the white sucker was not significant. This implies that among-lake differences in population density are not significant in shaping among-population differences in length-at-age of the white sucker.

Maturation in fishes may divert energy that could otherwise be used for growth [11, 18, 53, 60]. This certainly affects the lengths of fishes at ages close to or older than age at sexual maturity. Thus, a white sucker which matures earlier tends to have a smaller length-at-age. However, among-population differences in length-at-maturity did not show significant association with among-population differences in length-at-age in this study. This result was somewhat surprising. Lengths-at-maturity in four populations (Bentshoe, Blue Chalk, Gullfeather and Red Chalk) were greater than their lengths at age 4. Thus, the ages at 50 % maturity for these four white sucker populations were all greater than 4, the oldest age group large enough to be included in the overall analysis. This might affect the results of the Mantel test as the lengths of immature fishes are unaffected by maturation.

Significant correlations were found for inter-population differences in length-at-age and L50 between female and male white suckers. This implies that length-at-age and L50 were consistent between females and males in the study populations, and the contribution of among-lake differences in the environmental variables to among-population differences in length-at-age is similar for female and male white suckers.

Recent studies of landscape ecology [70] suggest that landscape positions of lakes, defined as the lake's explicit locations related to the type and strength of connections between the lakes and a drainage network [48], can have great impacts on the coherent dynamics of the lakes and influence the dynamic response of lakes to climatic variability [48, 71]. Such impacts tend to differ for different biotic and abiotic variables of the lakes [48]. As pointed out by an anonymous reviewer, this may explain the lack of significant relationships between the among-population spatial structuring of length-at-age of white suckers and among-lake spatial structuring of some biotic and abiotic variables in our study. The significant relationships among distance matrices of water chemistry, especially non-nutrients such as Ca, alkalinity and conductivity, lake locations, and length-at-age of white suckers seem to be consistent with other new ideas that are developing regarding the role of landscape position on the status and coherent dynamics of lakes [48]. A detailed analysis of impacts of lake landscape positions on the coherence of biotic and abiotic variables of the lakes may be needed to help us understand the underlying causes of the observed relationships. This cannot be achieved with the information currently available, and a time series of data such as those described by Magnuson and Kratz [48] needs to be collected.

In conclusion this study shows that among-lake differences in water chemistry and isolation-by-distance may be more important than those in lake morphology, food supply, predation, population density or fish length at maturity in explaining the spatial structuring of length-at-age observed in the white sucker populations included in this study. However, more information is needed to identify the mechanisms involved in the relationships discovered in this study.

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