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Physiological correlates of seasonal growth patterns in lake trout *Salvelinus namaycush*

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Physiological correlates of seasonal growth patterns were measured in lake trout *Salvelinus namaycush* from two populations with contrasting diets (zooplankton-dominated diet in Louisa Lake; fish-dominated diet in Opeongo Lake). Fish in Opeongo Lake grew faster and were in better condition than fish in Louisa Lake. The most prominent biochemical difference between populations was higher citrate synthase (CS) and cytochrome *c* oxidase activity in the white muscle of fish from Opeongo Lake, indicating greater sustained swimming activity in this lake. In contrast, lactate dehydrogenase (LDH) activity in white muscle, an indicator of capacity for burst swimming, was similar between lakes. Nucleoside diphosphate kinase (NDPK) activity in white muscle, an indicator of protein synthesis, was higher in Opeongo Lake than in Louisa Lake but only in the autumn. In both lakes, protein concentration and therefore nutritional status increased as the growing season progressed from spring to summer to autumn. Biochemical indicators of growth and activity showed similar seasonal patterns in the two lakes with the spring characterized by high NDPK, high CS and high LDH activities (*i.e.* high levels of protein synthesis in association with high aerobic and anaerobic activities). These results suggest high foraging effort and allocation to growth early in the growing season in both lakes.

Key words: aerobic enzymes; bioenergetics; food web dynamics; glycolytic enzymes; Salmoninae.

INTRODUCTION

Enzyme activities are increasingly being used in ecological studies to evaluate hypotheses about recent growth (Sherwood *et al.*, 2002; Gauthier *et al.*, 2008). The advantages of using enzyme activity for these purposes include the ability to provide information on habitat quality and growth at a finer temporal and spatial scale (Schulte *et al.*, 2000; Gauthier *et al.*, 2008) than other methods (*e.g.* bioenergetic modelling and analysis of increment formation in calcified structures: Stewart *et al.*,

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1983; Campana & Thorrold, 2001) and elimination of the need to recapture individuals. Several studies of wild fishes using enzyme activity have tested hypotheses that account for growth differences among lakes based on broad differences in prey size distributions (Sherwood *et al*., 2002; Kaufman *et al*., 2006). Yet, for animals living in strongly seasonal environments, growth should also be sensitive to the seasonal shifts in food availability, temperature, predation risk and the demands of reproduction (Mangel & Clark, 1988; Houston & McNamara, 1999) that are characteristic of such systems.

Lake trout *Salvelinus namaycush* (Walbaum) live in seasonal environments in cool, oligotrophic lakes of North America (Power, 2002). They prefer cool temperatures (*c*. 10° C), are top predators and show tremendous trophic diversity among populations. Depending on food web structure, their diets can include zooplankton, benthic invertebrates (*e.g.* crayfish), littoral fishes and, most profitably, pelagic schooling fishes (Vander Zanden & Rasmussen, 1996; Vander Zanden *et al*., 2000). Seasonality in temperatures and type and quantity of available prey are expected to drive the broad seasonal patterns observed in *S. namaycush* growth. In winter, cold temperatures and paucity of prey are expected to generate the pattern of slow (or no) growth, typical of freshwater temperate fishes (Garvey *et al*., 2004; Byström *et al*., 2006). In spring, warmer isothermal conditions should lower foraging costs and promote extensive feeding on newly burgeoning prey to recoup winter energy losses and initiate new somatic growth (Henderson *et al*., 2000). As the growing season progresses and epilimnetic temperatures become increasingly suboptimal, *S. namaycush* are driven to occupy positions in the metalimnion at their preferred temperatures of *c*. 10° C. Feeding increasingly relies on short excursions into the epilimnion to access prey (Morbey *et al*., 2006) and thus the costs of foraging should progressively increase. Later in the growing season, energy should be diverted from growth to reproduction (*i.e.* gonads and secondary sexual traits; for mature fishes only) and storage for overwinter survival. Thus, *S. namaycush* are predicted to show a decline in growth and growth-related enzyme activity from spring to autumn.

In lakes with pelagic schooling fish prey, adult *S. namaycush* are piscivorous, grow fast and invest more in reproduction. In lakes without pelagic schooling fish prey, adults feed extensively on zooplankton (and to a lesser degree on benthic invertebrates and littoral minnows), are often designated as 'planktivorous' and typically exhibit slower growth rates and reduced reproductive effort (Pazzia *et al*., 2002). In this study, seasonal variation in the enzyme activities of white muscle in a piscivorous *S. namaycush* population was compared with seasonal variation in a planktivorous population. Biochemical markers of fast growth were predicted to be higher in the piscivorous population, while more pronounced seasonal declines in growth-related enzyme activities were predicted for the planktivorous population, under the assumption of an earlier onset of reduced prey availability.

MATERIALS AND METHODS

STUDY POPULATIONS

Salvelinus namaycush were studied in Opeongo and Louisa Lakes in Algonquin Provincial Park, Ontario (Fig. 1). These two populations have starkly contrasting life histories and diets and have been focal populations for past research on *S. namaycush* (Martin, 1951;

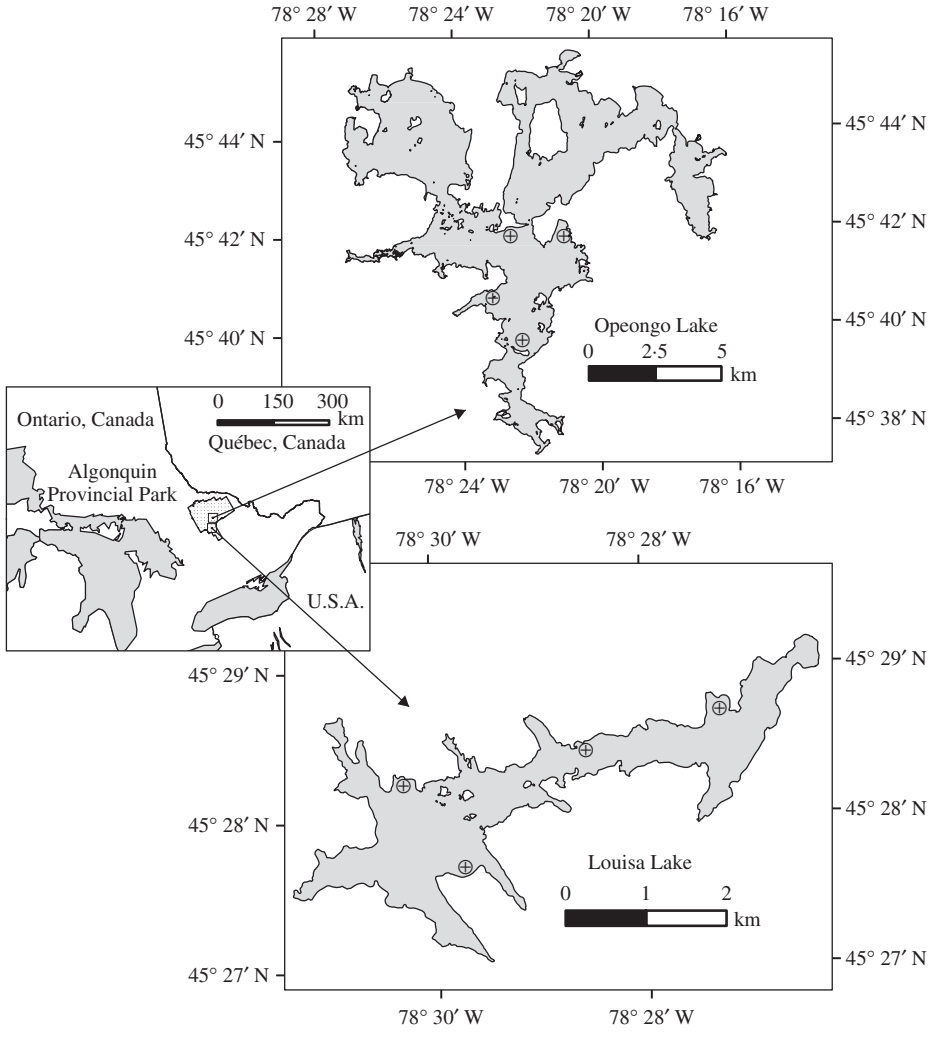

FIG. 1. Maps of Opeongo Lake, Louisa Lake and the Great Lakes region showing the location of these lakes within Algonquin Provincial Park. Netting sites within each lake are shown (⊕). Publically available layers were used to make the maps in ArcMap 9.2 (ESRI; www.esri.com). The maps are projected using the North American Albers Equal-Area Conic Projection.

McDermid *et al*., 2007). In Louisa Lake, fish undertake a gradual ontogenetic diet shift from zooplanktivory towards a mixed diet of zooplankton, benthic invertebrates and littoral fishes (Konkle & Sprules, 1986; Vander Zanden *et al*., 1999). The absence of pelagic schooling fish prey in this lake represents a trophic bottleneck that seems to constrain asymptotic size, although a few individuals overcome this bottleneck by adopting cannibalism (Vander Zanden *et al*., 2000). In Opeongo Lake, *S. namaycush* gradually shift their diet from aquatic invertebrates to littoral fishes [mostly yellow perch *Perca flavescens* (Mitchill)], to pelagic schooling fish prey (lake herring *Coregonus artedi* Lesueur). In association with this difference in food web structure, *S. namaycush* are slow-growing, early-maturing and small-bodied in Louisa Lake and fast-growing, late-maturing and large-bodied in Opeongo Lake (Shuter *et al*., 1998; McDermid *et al*., 2007).

Both lakes occur within forested watersheds with minimal foreshore development. Louisa Lake has no public road access, cottages or other buildings, whereas Opeongo Lake has access *via* one road, buildings associated with the Harkness Laboratory of Fisheries Research (Ontario Ministry of Natural Resources), a park store and dock, all located near the south end of the lake. Total mortality is somewhat higher in Louisa Lake (instantaneous mortality rate estimates: 0·4 *v*. 0·3 year^{-1} for Opeongo Lake; Quince *et al*., 2008*a*), but fishing mortality is likely to be somewhat lower since Louisa Lake can only be reached by anglers travelling on foot or by canoe. Opeongo Lake is accessible by road and very popular with anglers, recreational boaters (petrol powered) and canoeists. Both lakes are dimictic and are thermally stratified from about June to September. Gonad development begins in the spring and spawning occurs primarily in mid to late October.

TISSUE COLLECTION

Sampling of adults ($n = 107$) took place in both lakes during spring (May and June), summer (August) and autumn (October) in 2004 (Table I). Spring and summer samples were gillnetted as part of standardized assessments. Autumn samples were collected at spawning shoals by trap nets. Fish were killed by percussive stunning or clove oil anaesthesia followed by percussive stunning for the autumn samples in Opeongo Lake. The fork length (L_F, mm), mass (M, g) and sex of each fish were recorded. Neither maturity status or gonad size was recorded but both are expected to correlate positively with body size. The frequency of immature fish was probably greater in Louisa Lake than in Opeongo Lake due to gear size selectivity and the difference in age of maturity between the two lakes (Louisa Lake = 5·3 years, Opeongo Lake = 8·3 years; Shuter *et al*., 1998). Within an hour (usually 5 min), a sample of white epaxial muscle was removed midway between the dorsal fin and the lateral line and immediately stored in liquid nitrogen (−196° C). Samples were later transferred to a −80° C freezer. A *c*. 100 g cross-section of torso (excluding viscera) was taken anterior to the dorsal fin for analyses of energy content. The torso sample was homogenized with an equal part of water and a *c*. 10–25 g sub-sample of homogenate was dried and measured for per cent water and energy content (kJ g^{-1} dry mass) by isoperibol bomb calorimetry. Ageing

TABLE I. Comparison of sample sizes (with per cent female), mean ± S.E. (sample size in parentheses) von Bertalanffy growth parameters and condition indices for *Salvelinus namaycush* from Louisa and Opeongo Lakes. For K_{LC} and residual mass, $m = 3{\cdot}442$ and $\log b = -6{\cdot}123$

Variable	Louisa Lake	Opeongo Lake
Sample sizes		
Spring	13 (58%)	22 (38%)
Summer	15 (67%)	25 (50%)
Autumn	15 (33%)	17 (18%)
von Bertalanffy model		
L_∞ (mm)	410·9 ± 7·6 (43)	520·8 ± 18·0 (64)
k (year^{-1})	0·35 ± 0·04 (43)	0·31 ± 0·03 (64)
ω (mm year^{-1})	142·9	161·9
Condition indices		
K_F	99·9 ± 1·4 (43)	111·7 ± 1·8 (64)
K_{LC}	96·9 ± 1·4 (43)	103·4 ± 1·7 (64)
Residual mass (g)	0·97 ± 0·01 (43)	1·03 ± 0·02 (64)
Torso energy density (kJ g^{-1} dry tissue)	23·1 ± 0·2 (43)	26·5 ± 0·2 (58)
Torso water (%)	76·7 ± 0·3 (43)	73·0 ± 0·4 (59)
Protein concentration (mg g^{-1} wet tissue)	150·0 ± 3·3 (40)	144·9 ± 3·1 (64)

of otoliths was carried out. One exceptionally large fish ($L_F = 808$ mm from Opeongo Lake) was excluded from all analyses.

ENZYME ASSAYS

Maximal activity of four metabolic enzymes was measured in the white muscle of *S. namaycush*: lactate dehydrogenase (LDH; EC 1.1.1.27), nucleoside diphosphate kinase (NDPK; EC 2.7.4.6), citrate synthase (CS; 2.3.3.1) and cytochrome *c* oxidase (CCO; EC 1.9.3.1). Lactate dehydrogenase is a glycolytic enzyme involved in anaerobic metabolism and its up-regulation can increase metabolic rate; NDPK is an enzyme involved with protein synthesis; and CS and CCO are mitochondrial enzymes involved in aerobic metabolism required for sustained swimming. The laboratory methods used for homogenization and estimation of maximal enzyme activity and protein concentration are described in full elsewhere (Gauthier *et al*., 2008). Enzyme activity was measured at 10° C to coincide with the preferred temperature of *S. namaycush* and expressed as IU g^{-1} wet tissue or as IU mg^{-1} protein (IU = international units or μmol of substrate converted to product min^{-1}). Enzyme activity expressed on a wet mass basis reflected actual metabolic capacities per unit tissue mass, whereas expressing activity on a per protein basis allowed for the determination of enzyme up- or down-regulation relative to the total protein pool (Pelletier *et al*., 1995). Muscle total protein concentration reflects recent growth (Pelletier *et al*., 1995).

STATISTICAL ANALYSES

Growth curves were fitted for *S. namaycush* in each lake using a von Bertalanffy growth model: $L_t = L_\infty(1 - e^{-kt})$, where L_t is L_F (mm) at age t (years), L_∞ is maximum L_F (mm) and k ($year^{-1}$) is a rate constant. Pre-reproductive growth rate (ω; mm $year^{-1}$) is equivalent to kL_∞. Size at birth (*i.e.* $L_0 = 0$) was not included as a parameter in the model because there were insufficient data to estimate the shape of the curve near the origin. Fitting a simple model with few parameters was done to show gross differences in growth and body size between these lake populations in the year of study, rather than to determine the best model of fish growth which has been done elsewhere (Quince *et al*., 2008*a*). In addition, both gillnets and trap nets can overestimate length at age for the youngest age classes (Millar & Fryer, 1999), and this bias probably persists until an older age in *S. namaycush* in Opeongo Lake because of their greater L_F at age. No correction was made for this bias. Parameter estimation was done using PROC NLIN in SAS (SAS Institute, Inc.; www.sas.com).

Several condition indices based on mass (M) corrected for L_F were calculated (Rennie & Verdon, 2008). Fulton's condition index (K_F) is equal to $ML_F^{-3} \times 10^7$ (multiplication by 10^7 standardizes K_F relative to an expected value of 100). Le Cren's condition index (K_{LC}) is equal to $M(bL_F^m)^{-1} \times 100$, where b and m were estimated from $\log_{10}M = \log_{10}b + m\log_{10}L_F$ fit to the data for both lakes. K_{LC} essentially allowed the scaling coefficient (m) to differ from 3. Residual mass is the average of the residuals from $\log_{10}M = \log_{10}b + m\log_{10}L_F$. Condition indices were pooled across all ages; results did not differ substantively when considering only those ages common to both lakes (6–10 years old).

Separate general linear models were constructed for torso energy density (kJ g^{-1} dry tissue and kJ g^{-1} wet tissue), torso water (%), protein concentration (mg g^{-1} wet tissue), NDPK activity, CS activity, CCO activity and LDH activity. Enzyme activity was expressed both as IU g^{-1} wet tissue and IU mg^{-1} protein. Enzyme activity and body mass was $\log_{10}$-transformed because of expected allometric relationships. One was added to data on NDPK mg^{-1} protein, CS mg^{-1} protein and CCO mg^{-1} protein prior to $\log_{10}$-transformation to avoid negative values. These transformations only marginally improved the assumptions of normality and linearity. Torso energy density, torso water and protein concentration were all normally distributed. For each dependent variable, the best set of predictor variables was determined by backwards stepwise selection from a fully saturated model which included two factors (lake and season), body mass ($\log_{10}M$) as a covariate, all two-way interactions (lake × season, $\log_{10}M$ × lake, and $\log_{10}M$ × season) and one three-way interaction ($\log_{10}M$ × lake × season). Non-significant interactions of the highest order and with the highest P-value

were removed sequentially until only significant interactions and main effects remained. In cases of significant interactions with lake, the best model was constructed for each lake. In all models, the effect size was assessed by η^2 (SS_{effect} divided by SS_{total}) (Tabachnick & Fidell, 2007). Significant differences among seasons were assessed by least squares means *post hoc* comparison tests. Differences in torso energy density, protein concentration and enzyme activity between lakes within seasons were evaluated using one-way ANCOVAs with $\log_{10}M$ as a covariate. Differences in protein concentration between lakes within seasons were evaluated with *t*-tests.

Principal component analysis (PCA) followed by ANOVA of principal component scores was used to obtain a multivariate perspective of how the four enzymatic markers (expressed mg^{-1} protein) differed among seasons, between lakes, with $\log_{10}M$ and with other possible explanatory variables not considered in the previous analyses (K_F, K_{LC}, torso energy density, torso water and sex). The PCA was done on NDPK, CS, CCO and LDH to extract orthogonal principal components. Principal components whose eigenvalues were greater than the average eigenvalue (*i.e.* 1) were retained for further analysis by ANOVA. General linear models were simplified by backwards stepwise selection to remove any non-significant variables from the set of K_F, K_{LC}, torso energy density, torso water and sex. All statistical analyses were done using SAS version 9.1 with $\alpha = 0{\cdot}05$.

RESULTS

GROWTH AND CONDITION

Salvelinus namaycush grew faster and reached a larger asymptotic size in Opeongo Lake than in Louisa Lake (Fig. 2 and Table I). Fish in Opeongo Lake also had higher values of K_F, K_{LC}, residual mass and torso energy density and lower values of torso water compared to fish from Louisa Lake [Fig. 3(a) and Table I]. In contrast, protein concentration g^{-1} wet tissue of white muscle was similar between lakes in the spring and summer and higher in Louisa Lake in the autumn [Fig. 3(b) and Table I]. *M* was positively correlated with torso energy density in Opeongo Lake (but not in Louisa Lake) and negatively correlated to torso water in both lakes (Table II). In contrast, *M* was not related to protein concentration in either lake (Table II).

Torso energy density did not show any strong seasonal pattern in Opeongo Lake but declined slightly from summer to autumn in Louisa Lake [Fig. 3(a) and Table II]. Mirroring the pattern in torso energy density, torso water was similar in spring and summer in both lakes and increased in the autumn in Louisa Lake but not in Opeongo Lake (Table II). There was a marked seasonal variation in the protein concentration of white muscle [Fig. 3(b) and Table II]. In both lakes, protein concentration was lower among fish captured in the spring than in the summer and autumn samples, indicating low nutritional status among *S. namaycush* at the beginning of the growing season. Based on values of η^2, season accounted for 41 and 27% of the variation in protein concentration in Louisa Lake and Opeongo Lake fish, respectively.

ENZYME ACTIVITY

Untransformed mean ± S.D. values of enzyme activity expressed g^{-1} wet tissue were 40·4 ± 9·6 for NDPK, 3·9 ± 1·5 for CS, 11·6 ± 6·7 for CCO and 1102·9 ± 244·2 for LDH ($n = 104$). Untransformed mean ± S.D. values of enzyme activity expressed mg^{-1} protein were 0·28 ± 0·09 for NDPK, 0·03 ± 0·01 for CS, 0·08 ± 0·05 for CCO and 7·7 ± 2·3 for LDH ($n = 104$). The majority of the general

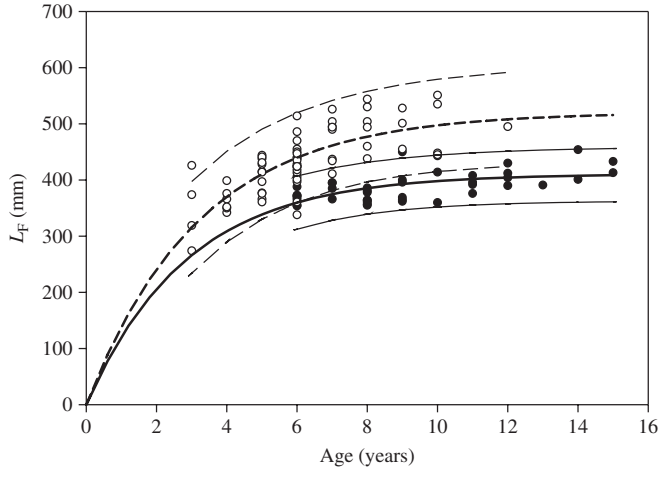

FIG. 2. Growth curves with fitted von Bertalanffy growth functions for *Salvelinus namaycush* from Louisa Lake (●) and Opeongo Lake (○). Lower and upper 95% confidence limits of predicted values of fork length (L_F), which include the variance of the parameter estimates and model error, are shown for all available ages.

linear models of $\log_{10}$-transformed enzyme activity indicated no significant scaling of NDPK, CCO, CS or LDH with body mass (Table III). The one exception was a significant positive allometry for NDPK activity g^{-1} wet tissue in Opeongo Lake fish. Based on the value of η^2, however, body mass accounted for only 6·0% of the variation in NDPK activity in this lake.

The seasonal pattern of NDPK activity differed between lakes (season × lake interaction for IU g^{-1} wet tissue: $P < 0{\cdot}01$ for IU mg^{-1} protein: $P < 0{\cdot}01$) and so the two lakes were analysed separately. In Louisa Lake, NDPK activity g^{-1} wet tissue and mg^{-1} protein showed marked seasonal declines [Table III and Fig. 4(a)]. Based on the value of η^2, season accounted for 40·2% of the variation in NDPK activity g^{-1} wet tissue. Season and a significant interaction between season and *M* accounted for 9·8 and 11·0% of the variation in NDPK activity mg^{-1} protein, respectively. In contrast, NDPK activity in Opeongo Lake showed less seasonal variation (Table III). NDPK activity g^{-1} wet tissue was similar among seasons and NDPK activity mg^{-1} protein was higher in the spring than in the autumn (*post hoc* means comparison: $P < 0{\cdot}05$). When seasons were analysed separately, NDPK (IU g^{-1} wet tissue) was higher in Opeongo Lake fish than in Louisa Lake fish in the summer (ANCOVA, $F_{1,37} = 8{\cdot}74$, $P < 0{\cdot}01$) and autumn (ANCOVA, $F_{1,26} = 6{\cdot}72$, $P < 0{\cdot}05$) but not in the spring ($P > 0{\cdot}05$). NDPK mg^{-1} protein was higher in Opeongo Lake fish than in Louisa Lake fish but only in the autumn [ANCOVA, $F_{1,26} = 13{\cdot}43$, $P = 0{\cdot}001$; Fig. 4(a)].

The seasonal pattern of CS activity differed between lakes when expressed g^{-1} wet tissue (season × lake interaction: $P < 0{\cdot}05$) but not when expressed mg^{-1} protein ($P > 0{\cdot}05$). In Louisa Lake, CS activity (g^{-1} wet tissue and mg^{-1} protein) showed a seasonal decline [Table III and Fig. 4(b)]. In Opeongo Lake, CS activity g^{-1} wet tissue was higher in the summer than in the autumn; CS activity mg^{-1} protein declined from spring to summer to autumn [Table III and Fig. 4(b)]. Thus,

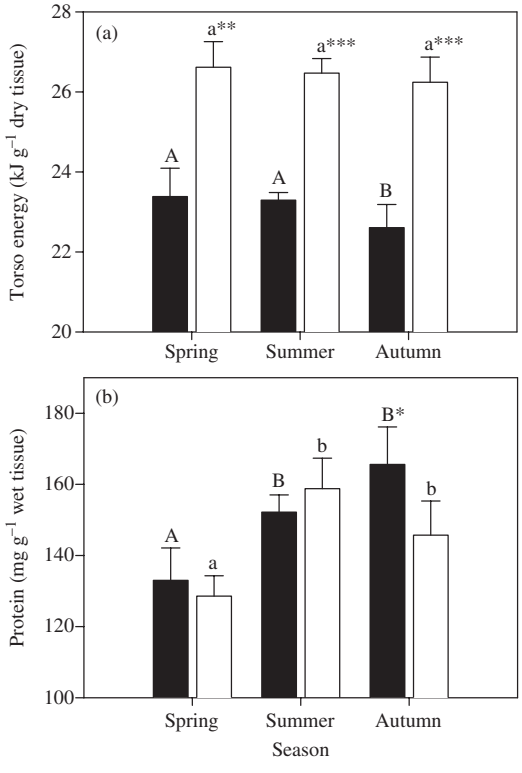

FIG. 3. (a) Torso energy density (mean with upper 95% CL) and (b) white muscle protein concentration (mean with upper 95% CL) of *Salvelinus namaycush* among seasons within Louisa Lake (■) and Opeongo Lake (□). Bars labelled with different letters within Louisa Lake (upper case) and within Opeongo Lake (lower case) indicate significant pair-wise differences between seasons based on least squares means. In each panel, asterisks (*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$) indicate the lake with the significantly higher value within a season.

expressing CS activity mg^{-1} protein exaggerated the seasonal decline in Louisa Lake and revealed a seasonal decline from spring to autumn in Opeongo Lake. Based on η^2, season accounted for 31·6 and 13·5% of the variation in CS activity g^{-1} wet tissue in Louisa Lake and Opeongo Lake, respectively, and 10·4% of the variation in CS activity mg^{-1} protein in the lakes combined. Across all seasons, CS activity was much higher in Opeongo Lake than in Louisa Lake [for IU g^{-1} wet tissue: ANCOVA, homogeneity of slopes, $P > 0{\cdot}05$, lake effect: $P < 0{\cdot}01$; for IU mg^{-1} protein: see Table III and Fig. 4(b)].

Similar to CS, CCO activity was much higher in Opeongo Lake than in Louisa Lake fish [Table III and Fig. 4(c)]. The effect of season was similar between lakes (season × lake interaction for IU g^{-1} wet tissue: $P > 0{\cdot}05$; for IU mg^{-1} protein: $P > 0{\cdot}05$). Overall, CCO g^{-1} wet tissue was higher in the summer than in the autumn, but CCO mg^{-1} protein did not differ among the three seasons [Table III and Fig. 4(c)].

Lactate dehydrogenase activity in white muscle differed among seasons but was similar between lakes [Table III and Fig. 4(d)]. Based on values of η^2, seasonality accounted for 5·7 and 7·7% of the variation in LDH activity g^{-1} wet tissue and

TABLE II. General linear models of torso energy density (kJ g^{-1} dry tissue), torso water (%) and white muscle protein concentration (mg g^{-1} wet tissue) of *Salvelinus namaycush* from Louisa and Opeongo Lakes showing the F statistics for the effects of $\log_{10}M$ (where M is body mass), season and the interaction $\log_{10}M \times$ season (if significant). The overall F statistic and r^2 value are also shown for each model

Variable		$\log_{10}M$	Season	$\log_{10}M \times$ season	Overall	r^2
Torso energy	Louisa Lake	$F_{1,37} = 0{\cdot}20$	$F_{2,37} = 5{\cdot}25^{**}$	$F_{2,37} = 5{\cdot}45^{**}$	$F_{5,37} = 3{\cdot}30^{*}$	0·31
	Opeongo Lake	$F_{1,54} = 41{\cdot}68^{***}$	$F_{2,54} = 1{\cdot}86$	—	$F_{3,54} = 14{\cdot}29^{***}$	0·44
Torso water	Louisa Lake	$F_{1,39} = 4{\cdot}78^{*}$	$F_{2,39} = 9{\cdot}73^{***}$	—	$F_{3,39} = 10{\cdot}01^{***}$	0·43
	Opeongo Lake	$F_{1,55} = 20{\cdot}83^{***}$	$F_{2,55} = 3{\cdot}10$	—	$F_{3,55} = 9{\cdot}03^{***}$	0·33
Protein	Louisa Lake	$F_{1,36} = 3{\cdot}33$	$F_{2,36} = 13{\cdot}25^{***}$	—	$F_{3,36} = 9{\cdot}80^{***}$	0·45
	Opeongo Lake	$F_{1,60} = 0{\cdot}03$	$F_{2,60} = 11{\cdot}15^{***}$	—	$F_{3,60} = 7{\cdot}55^{***}$	0·27

$^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.

TABLE III. General linear models of enzyme activities (NDPK, CS, CCO and LDH in IU g^{-1} wet tissue and IU mg^{-1} protein) in *Salvelinus namaycush* white muscle in Louisa and Opeongo Lakes. In each statistical model, F statistics are shown for the effects of $\log_{10}M$ (where M is body mass), season and the $\log_{10}M \times$ season interaction (if significant). The overall F statistic and r^2 value are also shown for each model. Models are divided into those that are lake specific and those in which lake is retained as a factor. In the latter sub-set of models, F statistics are also shown for the effect of lake

Enzyme	Lake	log$M$	Season	$\log_{10}M \times$ season	Overall	r^2
Lake-specific models						
NDPK†	Louisa	$F_{1,36} = 0{\cdot}16$	$F_{2,36} = 12{\cdot}11$***	—	$F_{3,36} = 8{\cdot}11$***	0·40
	Opeongo	$F_{1,60} = 4{\cdot}30$*	$F_{2,60} = 1{\cdot}93$	—	$F_{3,60} = 2{\cdot}41$	0·11
NDPK‡	Louisa	$F_{1,34} = 1{\cdot}30$	$F_{2,34} = 4{\cdot}64$*	$F_{2,34} = 5{\cdot}23$*	$F_{5,36} = 12{\cdot}17$***	0·64
	Opeongo	$F_{1,60} = 2{\cdot}54$	$F_{2,60} = 3{\cdot}37$*	—	$F_{3,60} = 2{\cdot}67$	0·12
CS†	Louisa	$F_{1,36} = 1{\cdot}26$	$F_{2,36} = 8{\cdot}55$***	—	$F_{3,36} = 6{\cdot}01$**	0·33
	Opeongo	$F_{1,60} = 0{\cdot}63$	$F_{2,60} = 4{\cdot}70$*	—	$F_{3,60} = 3{\cdot}19$*	0·14
Models with lake as a factor						
CS‡	$F_{1,99} = 36{\cdot}17$***	$F_{1,99} = 0{\cdot}97$	$F_{2,99} = 8{\cdot}91$***	—	$F_{4,99} = 18{\cdot}19$***	0·42
CCO†	$F_{1,99} = 63{\cdot}85$***	$F_{1,99} = 0{\cdot}11$	$F_{2,99} = 3{\cdot}21$*	—	$F_{4,99} = 21{\cdot}46$***	0·46
CCO‡	$F_{1,99} = 36{\cdot}85$***	$F_{1,99} = 0{\cdot}32$	$F_{2,99} = 2{\cdot}66$	—	$F_{4,99} = 12{\cdot}49$***	0·34
LDH†	$F_{1,99} = 0{\cdot}42$	$F_{1,99} = 3{\cdot}85$	$F_{2,99} = 3{\cdot}18$*	—	$F_{4,99} = 3{\cdot}27$*	0·12
LDH‡	$F_{1,99} = 0{\cdot}02$	$F_{1,99} = 2{\cdot}07$	$F_{2,99} = 4{\cdot}33$*	—	$F_{4,99} = 3{\cdot}20$*	0·11

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

†IU g^{-1} wet tissue.

‡IU mg^{-1} protein.

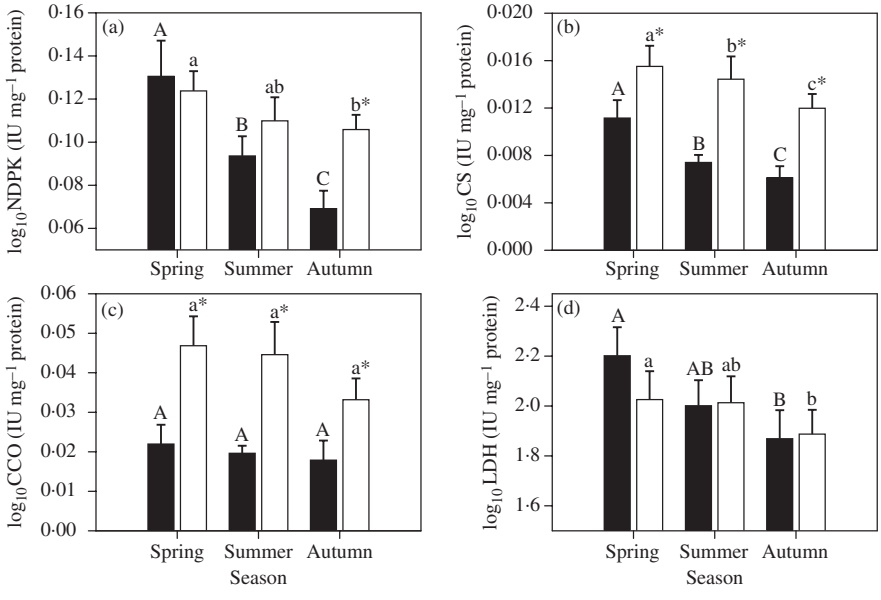

FIG. 4. Variation in enzyme activity (mean with upper 95% CL) of *Salvelinus namaycush* white muscle among seasons within Louisa Lake (■) and within Opeongo Lake (□) for (a) $\log_{10}$NDPK, (b) $\log_{10}$CS, (c) $\log_{10}$CCO and (d) $\log_{10}$LDH. Bars labelled with different letters within Louisa Lake (upper case) and Opeongo Lake (lower case) indicate significant pair-wise differences between seasons based on least squares means (Table III), and asterisks (*$P < 0{\cdot}01$) indicate the lake with the significantly higher value.

LDH activity mg^{-1} protein, respectively. The seasonal difference in LDH activity g^{-1} wet tissue was due to higher values in the summer than in the autumn (least square means, $P < 0{\cdot}05$). In contrast, the seasonal difference in LDH activity mg^{-1} protein was caused by higher values in the spring than in the autumn [least square means, $P < 0{\cdot}01$; Fig. 4(d)].

In support of the requirement that two-thirds of the variables be correlated for PCA, six of the possible seven pair-wise correlations between NDPK, CS, CCO and LDH were significant. PCA extracted two principal components accounting for a total of 84% of the variance. Principal Component 1 accounted for 57% of the variance and had positive loadings for each variable and could therefore be interpreted as an indicator of overall metabolism. Principal Component 1 was higher in Opeongo Lake than in Louisa Lake fish and showed a significant seasonal decline (based on least squares means: spring > summer > autumn; Table IV). Based on values of η^2, differences between lakes and seasons accounted for 15·1 and 16·5% of the variation in PC1, respectively. Neither $\log_{10}M$, K_F, K_{LC}, torso energy density, torso water nor sex accounted for significant variation in PC1.

Principal Component 2 accounted for 26% of the variance and had positive loadings for LDH (0·69) and NDPK (0·42) and negative loadings for CS (−0·38) and CCO (−0·45). Principal Component 2 could therefore be interpreted as investment in anaerobic capacity (LDH) and protein synthesis (NDPK) relative to aerobic capacity (CS and CCO). The pattern of seasonal variation in PC2 differed between lakes ($F_{2,97} = 3{\cdot}28$, $P < 0{\cdot}05$) and therefore lakes were analysed separately (Table IV). In Louisa Lake, a seasonal effect (based on least squares means: spring > summer =

TABLE IV. General linear models of PC1 (overall metabolism) and PC2 (relative investment in anaerobic metabolism and protein synthesis *v*. aerobic metabolism) in *Salvelinus namaycush* from Louisa and Opeongo Lakes. In each statistical model, F statistics are shown for the effects of $\log_{10}M$ (where M is body mass) and season and the F statistic and r^2 value are shown for the overall model. Models are lake specific for PC2 and retain lake as a factor for PC1. In the former model, the F statistics are shown for the effect of lake

Principal component	Lake	$\log_{10}M$	Season	Overall	r^2
PC1	$F_{1,99} = 24{\cdot}4$***	$F_{1,99} = 0{\cdot}21$	$F_{2,99} = 13{\cdot}3$***	$F_{4,99} = 15{\cdot}5$***	0·39
PC2	Louisa Lake	$F_{1,36} = 0{\cdot}14$	$F_{2,36} = 7{\cdot}57$**	$F_{3,36} = 5{\cdot}09$**	0·30
	Opeongo Lake	$F_{1,60} = 0{\cdot}50$	$F_{2,60} = 0{\cdot}06$	$F_{3,60} = 0{\cdot}20$	0·01

**$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

autumn; spring > autumn) accounted for 29·5% of the variation in PC2. In the spring, fish had high LDH and NDPK activities relative to CS and CCO activities whereas in the summer and autumn, they had low LDH and NDPK activities relative to CS and CCO activities. In Opeongo Lake, PC2 showed no seasonal variation. Neither $\log_{10}M$, K_F, K_{LC}, torso energy density, torso water nor sex accounted for significant variation in PC2 in either lake.

DISCUSSION

Salvelinus namaycush used energy differently in the two study populations. Opeongo Lake fish grew faster and were in better condition than Louisa Lake fish based on their higher values of ω, K_F, K_{LC}, residual mass and torso energy density, and lower values of torso water. In both populations, larger fish were in better condition (*i.e.* had higher torso energy density and lower torso water), but the difference in condition metrics between populations persisted even when accounting for the potentially confounding effect of body size. Given that fat has a higher caloric value than protein (Brafield & Llewellyn, 1982), the difference in torso energy density and per cent water suggests that Opeongo Lake fish stored more energy as fat rather than lean dry mass. This could account for the similar muscle protein concentration between lake populations. The large difference in growth and body size was consistent with previous research on these two populations (Martin, 1951; Shuter *et al*., 1998; McDermid *et al*., 2007).

LAKE DIFFERENCES IN ENZYME ACTIVITY

Several biochemical indicators were consistent with differences in fuel acquisition and storage between lake populations. Most notably, higher CS and CCO activities were observed in the faster growing, Opeongo Lake fish. These results are consistent with several laboratory studies showing an association between these oxidative enzymes and recent growth (Mathers *et al*., 1992; Couture *et al*., 1998; Gauthier *et al*., 2008). These results highlight the importance of aerobic activity in *S. namaycush* foraging in Opeongo Lake, which is consistent with telemetry observations of greater movement per day and larger home ranges (*i.e.* areas of

concentrated use) of fish in Opeongo Lake than in Louisa Lake (Y. E. Morbey, unpubl. data).

Differences in NDPK activity between lakes could be interpreted as differences in recent growth as found in previous laboratory and field studies (Berges & Ballantyne, 1991; Shimeno *et al*., 1997; Couture *et al*., 1998; Kaufman *et al*., 2006; Gauthier *et al*., 2008). Fish had higher NDPK activities in Opeongo Lake than in Louisa Lake but, interestingly, only for the latter part of the growing season in the summer (only when expressed g^{-1} wet tissue) and autumn. The similarity in NDPK activity between populations in the spring suggests that spring may be an equally profitable time for *S. namaycush* foraging and allocation to growth in both lakes.

Lactate dehydrogenase activity of *S. namaycush* did not differ between populations in the current study nor in an another comparison of wild fish trout between Opeongo Lake and another planktivorous population (Sherwood *et al*., 2002). Thus, LDH does not appear to be a useful index of growth rate in *S. namaycush*. In general, the complex roles of LDH can make it difficult to interpret comparative data of wild fishes. Activity of glycolytic enzymes such as LDH, pyruvate kinase and phosphofructokinase in fishes has been shown to be sensitive to a variety of factors including body size, growth rate, condition, activity (*i.e.* foraging effort), diet (*e.g.* prey size) and temperature (Pelletier *et al*., 1993*a*, *b*, 1994, 1995; Shimeno *et al*., 1997; Couture *et al*., 1998; Rennie *et al*., 2005; Kaufman *et al*., 2006; Gauthier *et al*., 2008). Enhanced glycolysis has multiple effects and, as a result, the nature of up-regulation of glycolytic enzymes in response to these factors can vary by species and ecological context. First, glycolytic enzymes enhance sprint swimming ability which is required for foraging or predator evasion (Somero & Childress, 1980; Childress & Somero, 1990; Garenc *et al*., 1999; Martinez *et al*., 2003). Second, enhanced glycolysis increases metabolic rate and therefore can be viewed as an energetic burden (Lemieux *et al*., 2003). Finally, an increase in LDH in association with lipid storage in *P. flavescens* suggests the possibility that LDH can be considered as a protein store (Gauthier *et al*., 2008).

SEASONAL DIFFERENCES IN ENZYME ACTIVITY

Spring coincided with the period of recovery from the winter low growth period and was accompanied by low muscle protein concentration. Starvation in fishes has been reported to lead to a decrease in muscle protein concentration (Yang & Somero, 1993). Mirroring the pattern in muscle protein concentration, torso water was high in the spring and then decreased in the summer as energy stores (per cent fat and lean dry mass) increased in both lakes. This gain in condition seems to have arisen from allocation to both lipids and protein because torso energy density (expressed g^{-1} dry mass) did not change from spring to summer and so did not indicate any shift in the ratio of lipid to protein.

Higher levels of enzyme activity in the spring than in the autumn were consistent with an increased effort by *S. namaycush* to forage and recoup nutritional condition at a time of high food availability. Enhanced CS activity mg^{-1} of protein in the spring compared to summer in fish from both lakes probably serves to maintain overall aerobic capacity in spite of lower protein concentration, through an up-regulation of aerobic capacity. The higher CS activities g^{-1} of muscle in Louisa Lake fish in the spring than in the summer further support spring as an important period for

foraging in this lake. Since a recent study of *P. flavescens* has also reported that muscle CS, but not CCO, shows strong seasonal variation (Couture *et al*., 2008), the mitochondrial membrane-bound electron transport chain, of which CCO is part, can be hypothesized to be more independent of nutritional status compared to matrix enzymes like CS which are part of the citric acid cycle and are directly involved in the catabolism of food-derived fuels. Interestingly, LDH activity also showed a seasonal decline in both lakes despite not differing between populations.

The data on NDPK activity suggest that *S. namaycush* in Opeongo Lake had higher foraging effort and resource allocation to growth for a greater proportion of the growing season than in Louisa Lake. One explanation for this difference between lakes could relate to lake differences in the seasonal pattern of food availability. Early in the season in Louisa Lake, zooplankton abundance is expected to be high and littoral fishes would be accessible because of isothermal conditions. As the season progresses, the abundance of zooplankton would decline and thermal stratification would make littoral areas less thermally accessible to *S. namaycush*. In Opeongo Lake, schools of *C. artedi* would be accessible throughout the period of thermal stratification. An extended availability of high quality prey in Opeongo Lake could fuel growth, gonad development and nutrient storage.

In Opeongo Lake, the maintenance of torso energy density (and torso water) into the autumn suggests that mature fish in this lake can invest in reproduction without affecting their energy stores. On the other hand, in Louisa Lake, declining NDPK activity and torso energy density from the summer to autumn (when spawning occurs) suggests reproductive consequences (Madenjian *et al*., 2000). Information on gonado-somatic index (I_G, where I_G = gonad mass $\times$ somatic mass^{-1} $\times$ 100) is consistent with this hypothesis: samples collected from a common time of year (August 2003 in Louisa Lake and August 2009 in Opeongo Lake) indicate higher reproductive investment in Opeongo Lake (I_G = 7·5, CI = 5·9–9·1) than in Louisa Lake (I_G = 3·9, CI = 3·3–4·5) (Y. E. Morbey & B. J. Shuter, unpubl. data).

OTHER FACTORS AFFECTING ENZYME ACTIVITY

The absence of positive scaling of LDH activity with body size was inconsistent with previous studies of *S. namaycush* (Pazzia *et al*., 2002; Sherwood *et al*., 2002; Kaufman *et al*., 2006). An assumption pervading these studies is that fish foraging is constrained by a fixed daily energy requirement. Foraging effort, however, is also known to be sensitive to the costs and benefits of foraging that can vary at multiple spatial and temporal scales and depend on individual state (*e.g.* size, age or energy status; Stephens & Krebs, 1986; Stephens *et al*., 2007). For example, perhaps *S. namaycush* invest in foraging effort (and therefore elevated enzyme activity) when presented with excellent foraging opportunities and store the extra incoming energy for later use to ensure overwinter survival, growth or enhanced reproduction. Such behavioural decision-making could complicate interpretation of enzyme scaling relationships.

Differences in thermal habitat use may partly account for the observed patterns in enzyme activity. *Salvelinus namaycush* are physiologically adapted to cold water, with a temperature preference considered to be *c*. 10° C (Magnuson *et al*., 1990; Dillon *et al*., 2003). They actively seek lake depths close to this value but in some lakes make short excursions into the epilimnion (Snucins & Gunn, 1995;

Morbey *et al*., 2006). Consider that *S. namaycush* in Louisa Lake have elevated body temperatures due to their frequent use of warm-water habitats (Morbey *et al*., 2006). Maintaining a constant reaction velocity requires less enzyme at warmer environmental temperatures (Hochachka & Somero, 1984; Prosser, 1986), and so Louisa Lake fish may require lower enzyme concentrations to achieve the same reaction velocity as Opeongo Lake trout. Enzyme activity measured at a constant temperature in the laboratory would then be lower for Louisa Lake fish. Body temperature alone, however, cannot fully account for the patterns observed in the current study; otherwise all the enzymes (NDPK, CS, CCO and LDH) would have shown similar differences between lake populations.

This comparative study showed that white muscle enzyme activity and condition metrics were associated with major differences in growth rate between *S. namaycush* populations. Enzyme activity also provided information about seasonal growth patterns that other physiological indices (torso energy and protein concentration) failed to provide. These seasonal growth differences between lake populations may have been driven by differences in food web structure. Further study of the mechanisms underlying seasonal variation in growth is important to predict consequences of climate change and concomitant changes in seasonality. Living in seasonal environments can impose constraints on growth patterns within a growing season and may have carry over effects on reproduction, overwinter survival and emergent patterns of life-history variation (Quince *et al*., 2008*a*, *b*).

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