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Patterns of growth and nutrient deposition in lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*) and their hybrid, F_1 splake (*Salvelinus namaycush* × *Salvelinus fontinalis*) as a function of water temperature

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Abstract

Several fish species of the genus *Salvelinus* are used for stocking freshwaters in North and South America and much of Europe but there is little information about their growth and carcass composition. Lake trout (*S. namaycush*), brook trout (*S. fontinalis*) and their hybrid F_1 splake (*S. namaycush* × *S. fontinalis*) (initial body weight ca. 2–4 g) were raised at 6.4, 10.6 and 14.9 °C to examine growth and nutrient deposition as a function of water temperature. In all species, weight gain and feed intake increased significantly with water temperature and feed efficiency was significantly lower at 6.4 than at 10.6 and 14.9 °C. In brook trout, Thermal-unit Growth Coefficient (TGC) growth rate was significantly lower at 6.4 than at 10.6 and 14.9 °C, while in F_1 splake TGC was only lower at 6.4 than 10.6 °C. Expressed in terms of relative composition a significant effect of temperature was observed. In all species, moisture content decreased while crude protein, lipid, ash and energy contents increased with increased temperature. Expressed in absolute terms, however, a significant effect of temperature was not observed. In all species carcass contents increased significantly with increased live body weight and were best described by simple linear equations. Gross energy concentration was significantly affected by both water temperature and body weight. These data indicate that the growth of these species is a function of water temperature and, in absolute terms, carcass composition is mainly a function of body weight and not water temperature. Also, such simple linear equations bode well for modification of existing feed requirement and waste outputs models; improving their applicability to these species.

KEY WORDS: carcass composition, charrs, *Salvelinus*

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Introduction

The stocking of *Salvelinus* species is practiced in many temperate waters of North and South America and much of Europe and is of particular importance in Canadian waters. Lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*) and their hybrid, F_1 splake (*Salvelinus namaycush* × *Salvelinus fontinalis*), account for approximately 80% of total fish stocked in lake rehabilitation efforts in Ontario (Kerr 2000a,b; Kerr & Lasenby 2001), but there is little information about growth and carcass composition of these species under hatchery conditions. This sort of information could be useful for the development of bioenergetics, nutrient-flow, feed requirement and waste output models (Cho & Bureau 1998). This in turn would allow fish culturists to estimate such factors as time to stocking size, feed requirement, standing biomass and waste output. There have been many attempts to mathematically describe growth of fish species using a large diversity of approaches and concepts (Brown 1946; Haskell 1959; Iwama & Tautz 1981). While most of these attempts are often made at different water temperatures, the resultant mathematical models often fail to account for the effects of water temperature. Fish are poikilotherms and as such, water temperature is a major factor regulating their metabolic rate and energy expenditure. Fish growth tends to increase as water temperature increases within an optimum range of water temperatures for growth of a given species (Sadler *et al.* 1986). Lake trout, brook trout and F_1 splake have different thermal optima for growth (Sadler *et al.* 1986), which may result in significantly different patterns of growth and nutrient deposition at different water temperatures.

The objectives of this study were to examine: (1) growth of juvenile brook trout, lake trout and F_1 splake; (2) the effect of water temperature on the growth of the three species; (3) the patterns of nutrient deposition in the three species as a function of water temperature.

Materials and methods

Fish, experimental conditions and diet

Lake trout (Killala Lake strain), brook trout (Hills Lake strain) and F_1 splake (Killala Lake × Hills Lake strain), initial body weight 2.5 ± 0.04, 3.3 ± 0.07 and 4.1 ± 0.08 g (mean ± SD), respectively, were randomly distributed, in triplicate, to three groups of nine 50 L tanks (100 fish per tank). Each group of nine tanks was maintained at one of three water temperatures, 6.4 ± 1.9, 10.6 ± 0.9 and 14.9 ± 0.6 °C (mean ± SD) over a 16-week period. Tanks were individually aerated (dissolved oxygen 9.3 ± 0.6 mg L^{-1}) and supplied with 80–90% recirculated water and 10–20% of either heated domestic water or chilled well water. Flow to each group of nine tanks, controlled by a thermoregulator (±1.0 °C) and attached solenoid valve, was 15–30 L min^{-1} (1.7–3.3 L min^{-1} per tank). Mean total ammonia, nitrate and nitrite levels were 0.2 ± 0.1, 0.8 ± 0.6 and <0.1 mg L^{-1} (mean ± SD), respectively. The fish were kept in accordance with the guidelines of the Canadian Council on Animal Care (CCAC 1984) and the University of Guelph Animal Care Committee. Fish were hand-fed three times per day to near-satiation, determined by cessation of feeding behaviour, with MNR98-HS starter diet [530 g kg^{-1} crude protein (CP), 21 MJ kg^{-1} gross energy (GE); EWOS Canada, Surrey, BC, Canada] (Tables 1 & 2).

Sampling

Water temperature was monitored daily and logged every 10 min (Optic StowAway Temp logger; Onset Computer Corporation, Bourne, MA, USA); feed intake measured weekly and weight gains (total tank weight) every 28 days. Growth rate was calculated as the Thermal-unit Growth Coefficient (TGC) [modified from Iwama & Tautz (1981) by Cho (1990)]:

$$\mathrm{TGC} = \frac{\mathrm{FBW}^{1/3} - \mathrm{IBW}^{1/3}}{\sum(T_i \times d) \times 100}; \quad i = 0$$

where FBW is the final body weight (g), IBW the initial body weight (g), T_i the average water temperature on the ith day (°C), and d is the number of days.

Whole carcass samples, 20 fish per sample, were taken from each tank at 0, 8 and 16 weeks. Carcass samples were autoclaved for 30 min at 110 °C, ground to slurry, freeze-dried, reground, sieved and stored at −20 °C until analysis.

Table 1 Diet formulation

Ingredient	g
Fish meal, 70% CP	300.0
Blood meal, animal, >85% CP, spray/ring dried	70.0
Poultry by-product meal, 65% CP	60.0
Whey, dried, 12% CP	90.0
Brewer's dried yeast, 45% CP	50.0
Corn gluten meal, 60% CP	250.0
Lysine·HCl	5.0
Vitamin premix[1]	10.0
Mineral premix[2]	5.0
Fish oil	160.0
Total	1 kg

[1] Provides per kg of premix: Vitamin A (acetate), 750 000 IU; Vitamin D_3 (cholecalcipherol), 600 000 IU; Vitamin E (DL-α-tocopheryl-acetate), 15 000 IU; Vitamin K (menadione Na-bisulphate), 0.3 g; Vitamin B_{12} (cyanocobalamin), 0.006 g; ascorbic acid (ascorbyl polyphosphate), 15.0 g; D-biotin, 0.042 g; choline (chloride), 300.0 g; folic acid, 0.3 g; niacin (nicotinic acid), 3.0 g; pantothenic acid, 6.0 g; pyridoxine, 1.5 g; riboflavin, 1.8 g; thiamin, 0.3 g (all quantities are expressed on the basis of active vitamins).

[2] Provides per kg of premix: sodium chloride (NaCl, 390 g kg^{-1} Na, 610 g kg^{-1} CL), 615.0 g; ferrous sulphate ($FeSO_4 \cdot 7H_2O$, 200 g kg^{-1} Fe), 13.0 g; copper sulphate ($CuSO_4 \cdot 5H_2O$, 250 g kg^{-1} Cu), 6.0 g; manganese sulphate ($MnSO_4$, 360 g kg^{-1} Mn), 18.0 g; potassium iodide (240 g kg^{-1} K, 760 g kg^{-1} I), 2.0 g; zinc sulphate ($ZnSO_4 \cdot 7H_2O$, 400 g kg^{-1} Zn), 30.0 g.

Table 2 Diet composition (as fed)

Composition, as is basis	MNR98-HS
Dry matter (g kg^{-1})	922.0
Crude protein (g kg^{-1})	486.0
Lipid (g kg^{-1})	186.0
Ash (g kg^{-1})	78.0
Nitrogen-free extract (g kg^{-1})	250.0
Phosphorus (g kg^{-1})	11.0
Digestible protein (DP) (g kg^{-1})	446.0
Digestible energy (DE) (MJ kg^{-1})	15.5
DP · DE (g MJ^{-1})	28.8

Digestibility trial

At the completion of the growth trial each species was distributed into two groups of three tanks (30 fish per tank). Fish were those reared at 10 °C. Each group of tanks was equipped with a faeces settling column (Guelph System) in which faeces were collected (Cho *et al.* 1982). Two fecal samples were collected per group of tanks according to the method of Bureau *et al.* (1999). Fish were hand-fed to near-satiation three times a day with the same diet (MNR98-HS) used in the growth trial (Tables 1 & 2). However, the diet was reground and mixed with Celite (10 g kg^{-1} % of diet, acid-washed diatomaceous silica, Celite AW521, Celite Corp., Lompoc, CA, USA) in a Hobart mixer (Hobart Ltd, Don Mills, ON, Canada) which acted as a digestibility marker. The diet was then pelleted with a laboratory steam pellet mill (California Pellet Mill Co., San Francisco, CA, USA), dried under forced air at room temperature for 24 h and sieved to remove fines. The apparent digestibility coefficients (ADC) for the nutrients and energy of the diet were calculated as follows (Cho *et al.* 1982):

$$\mathrm{ADC} = 1 - \left(\frac{F}{D} \times \frac{\mathrm{Di}}{\mathrm{Fi}}\right)$$

where D = % nutrient (or MJ kg^{-1} gross energy) of diet, F = % nutrient (or MJ kg^{-1} gross energy) of faeces, Di = % digestion indicator of diet, Fi = % digestion indicator of faeces.

Chemical analysis

Diet, carcass and faecal samples were analysed in duplicate for dry matter (DM) and ash according to AOAC (1995), for CP (% Nitrogen × 6.25) using a Kjeltech auto analyzer (Model # 1030; Tecator, Höganäs, Sweden), for lipid using the method of Bligh & Dyer (1959), for GE using an automatic bomb calorimeter (Parr 1271; Parr Instruments, Moline, IL, USA) and for phosphorus (P) using the method of Heinonen & Lahti (1981).

Statistical analysis

The effect of species and water temperature on live body weight, feed intake, feed efficiency and carcass composition were analysed using the SAS general linear model (GLM) procedure (SAS 1990)

$$Y_{ijk} = \mu + T_i + S_j + TS_{ij} + \varepsilon_{ijk}$$

where μ = overall mean; Y_{ijk} = the observation from the kth tank (k = 1–9) in the ith water temperature and jth species; T_i = the effect of the ith water temperature (i = 1, 2, 3); S_j = the effect of the jth species (j = 1, 2, 3); TS_{ij} = the effect of the interaction between the ith water temperature and jth species and ε_{ijk} = random error from the kth tank in the ith temperature and jth species. Tukey's honestly significant difference test (Kuehl 2000) with $P < 0.05$ was used to detect differences among means.

Statistical analysis of the ADC was performed using the SAS GLM procedure (SAS 1990)

$$\mathrm{ADC}_{ij} = \mu + S_i + \varepsilon_{ij}$$

where μ = overall mean; ADC_{ij} = the observation from the jth tank (j = 1–6) in the ith species; S_i = the effect of the ith species (i = 1, 2, 3) and ε_{ij} = the random error from the jth tank in the ith species. Tukey's honestly significant difference test (Kuehl 2000) with $P < 0.05$ was used to detect differences among means.

Linear regression analysis of proximate components was performed using the SAS GLM procedure (SAS 1990)

$$Y_i = \alpha + \beta X_i + \varepsilon_i$$

where α = intercept, Y_i = ith observation of dependent variable, β = regression coefficient of the dependent variable, X_i = ith observation of the independent variable, ε_i = random error.

Results

Growth performance and feed efficiency

Growth performance and feed efficiency (FE) data are presented in Table 3. Significant interaction effects were found between species and water temperature. For all three species, water temperature had a significant effect on weight gain, feed intake, FE and TGC. Weight gain and feed intake were significantly reduced with each decrease in rearing temperature, while FE was significantly lower at only 6.4 °C. In brook trout, TGC was significantly reduced at 6.4 °C while in F_1 splake the reduction was only significant between 6.4 and 10.6 °C.

At all water temperatures, weight gain and feed intake were significantly higher in brook trout than in F_1 splake which, in turn, were significantly higher than in lake trout. At 10.6 °C, FE was significantly higher in F_1 splake than in brook trout; while at 14.9 °C FE was significantly lower in lake trout than in both brook trout and F_1 splake. At all water temperatures TGC was significantly higher in brook trout than in both lake trout and F_1 splake while, F_1 splake exhibited a higher TGC than lake trout at 10.6 and 14.9 °C.

Table 3 Growth performance and feed efficiency (mean ± SD) of lake trout, brook trout and F_1 splake (IBW = 2.5, 3.3 and 4.1 g, respectively) at 6.4, 10.6 and 14.9 °C

Species	Water temperature (°C)	Weight gain (g per fish)	Feed intake (g per fish)	FE[1] (gain:feed)	TGC
Lake trout	6.4	3.81 ± 0.39^{az}	4.89 ± 0.06^{az}	0.74 ± 0.07^{az}	0.069 ± 0.01^{az}
	10.6	8.83 ± 0.30^{br}	8.20 ± 0.20^{br}	1.03 ± 0.02^{bpq}	0.075 ± 0.00^{ar}
	14.9	12.17 ± 0.90^{ch}	13.06 ± 1.40^{ch}	0.91 ± 0.04^{bh}	0.065 ± 0.00^{ah}
Brook trout	6.4	8.28 ± 0.17^{ax}	9.44 ± 0.41^{ax}	0.86 ± 0.03^{az}	0.108 ± 0.00^{ax}
	10.6	19.72 ± 0.63^{bp}	19.03 ± 0.87^{bp}	1.02 ± 0.02^{bp}	0.115 ± 0.00^{bp}
	14.9	38.30 ± 1.05^{cf}	36.39 ± 0.39^{cf}	1.05 ± 0.02^{bf}	0.118 ± 0.00^{bf}
F_1 splake	6.4	4.72 ± 0.39^{ay}	5.72 ± 0.05^{ay}	0.80 ± 0.05^{az}	0.066 ± 0.00^{az}
	10.6	12.67 ± 0.51^{bq}	11.31 ± 0.70^{bq}	1.09 ± 0.03^{bq}	0.081 ± 0.00^{bq}
	14.9	18.69 ± 1.88^{cg}	16.55 ± 1.56^{cg}	1.09 ± 0.03^{bf}	0.074 ± 0.01^{abg}

Means in the same column with different superscripts are significantly different ($P < 0.05$). Superscripts a, b, c represent comparisons between water temperatures within a species; x, w, z represent comparisons between species at 6.4°C; p, q, r represent comparisons between species at 10.6°C; f, g, h represent comparisons between species at 14.9 °C.

[1] FE = feed efficiency (wet weight gain, g/feed, g).

Carcass composition

Initial and final relative moisture, CP, lipid ash, P and GE contents of lake trout, brook trout and F_1 splake are presented in Table 4. Analysis revealed a significant effect of final body weight on relative carcass composition. Analysis was, accordingly, performed using final body weight as a covariate. Significant interaction effects were found between species and water temperature.

In all species, moisture concentration decreased significantly with increased water temperature. Crude protein concentration was significantly higher in lake trout reared at 14.9 than at 6.4 °C, increased significantly with increased water temperature in brook trout and was significantly higher in F_1 splake reared at 14.9 than at either 6.4 or 10.6 °C. Lipid concentration increased significantly with increased water temperature within both lake trout and F_1 splake, while being significantly higher in brook trout reared at either 10.6 or 14.9 than at 6.4 °C. No difference between water temperatures was found for ash concentration of brook trout and F_1 splake but ash concentration was significantly higher in lake trout reared at either 10.6 or

Table 4 Initial and final (mean ± SD) relative carcass concentrations of proximate components, g kg^{-1} wet weight, of lake trout, brook trout and F_1 splake reared at 6.4, 10.6 and 14.9 °C

	Body weight (g)	H_2O	CP	Lipid	Ash	*P*	GE (kJ g^{-1})
Initial							
Lake trout	2.5	803.3	142.7	36.2	20.9	4.1	4.6
Brook trout	3.3	800.5	138.0	41.9	20.9	4.0	4.7
F_1 splake	4.1	788.2	144.6	50.9	19.7	4.3	5.3
Final							
Lake trout							
6.4 °C	6.3 ± 0.4^{ax}	801.0 ± 1.2^{ax}	153.9 ± 2.4^{ax}	27.3 ± 2.1^{ax}	21.4 ± 0.2^{ax}	4.4 ± 0.1^{ax}	4.5 ± 0.1^{ax}
10.6 °C	11.4 ± 0.3^{bp}	787.1 ± 1.8^{bp}	159.0 ± 3.0^{abp}	34.2 ± 1.8^{bp}	21.4 ± 0.1^{ap}	4.4 ± 0.2^{apq}	5.0 ± 0.1^{bp}
14.9 °C	14.7 ± 0.9^{cf}	773.8 ± 1.0^{cf}	160.1 ± 0.9^{bf}	45.8 ± 0.8^{cf}	21.9 ± 0.2^{bf}	4.6 ± 0.0^{af}	5.4 ± 0.0^{cf}
Brook trout							
6.4 °C	11.6 ± 0.1^{ay}	769.7 ± 3.2^{ay}	145.3 ± 0.6^{ay}	59.0 ± 4.1^{ay}	20.4 ± 0.5^{ay}	4.7 ± 0.0^{ax}	5.8 ± 0.1^{ay}
10.6 °C	23.0 ± 0.7^{bq}	759.4 ± 1.6^{bq}	148.9 ± 0.9^{bq}	66.9 ± 1.0^{bq}	20.4 ± 0.3^{aq}	3.7 ± 0.4^{ap}	6.2 ± 0.1^{bq}
14.9 °C	41.6 ± 1.0^{cg}	749.2 ± 3.3^{cg}	153.4 ± 0.4^{cg}	74.1 ± 3.0^{bg}	20.5 ± 0.3^{af}	4.1 ± 1.7^{ag}	6.5 ± 0.1^{cg}
F_1 splake							
6.4 °C	8.7 ± 0.3^{az}	788.8 ± 1.9^{az}	152.7 ± 1.1^{ax}	37.5 ± 1.0^{az}	21.3 ± 0.1^{ax}	4.4 ± 0.0^{ax}	5.0 ± 0.1^{az}
10.6 °C	16.8 ± 0.5^{br}	775.8 ± 2.7^{br}	150.3 ± 3.1^{aq}	46.6 ± 2.7^{br}	21.2 ± 0.2^{ap}	4.5 ± 0.0^{aq}	5.4 ± 0.1^{br}
14.9 °C	22.7 ± 1.9^{ch}	765.2 ± 4.6^{cb}	162.9 ± 1.7^{bf}	55.8 ± 5.2^{cb}	21.3 ± 1.0^{af}	4.6 ± 0.1^{af}	5.8 ± 0.2^{cf}

Means in the same column with different superscripts are significantly different ($P < 0.05$). Superscripts a, b, c represent comparisons between water temperatures within a species; x, w, z represent comparisons between species at 6.4 °C; p, q, r represent comparisons between species at 10.6 °C; f, g, h represent comparisons between species at 14.9 °C.

14.9 than at 6.4 °C. No difference was found for P concentration within lake trout, brook trout or F_1 splake. Gross energy concentration of lake trout, brook trout and F_1 splake increased significantly with increased water temperature.

At all water temperatures, moisture concentration was highest in lake trout, intermediate in F_1 splake and lowest in brook trout while, lipid concentration was highest in brook trout, intermediate in F_1 splake and lowest in lake trout. Crude protein concentration was significantly higher in both lake trout and F_1 splake than in brook trout at 6.4 and 14.9 °C but was significantly higher in lake trout than in either brook trout or F_1 splake at 10.6 °C. Ash concentration was significantly higher in both lake trout and F_1 splake than in brook trout at both 6.4 and 10.6 °C. Phosphorus concentration was significantly higher in F_1 splake than in brook trout at 10.6 °C while being significantly higher in both lake trout and F_1 splake than in brook trout at 14.9 °C. Gross energy concentration was highest in brook trout, intermediate in F_1 splake and lowest in lake trout at both 6.4 and 10.6 °C. However at 14.9 °C, GE concentration was only significantly higher in brook trout than the other species. Figure 1 represents the GE concentration of lake trout, brook trout and F_1 splake at 6.4, 10.6 and 14.9 °C. Gross energy concentration of all species was found to increase with increased fish size and was described using separate power functions for each species.

Moisture, CP, lipid, ash and P contents of each species were examined on an absolute basis. Moisture content was significantly different between species; being least in brook trout, intermediate in F_1 splake and greatest in lake trout. Lipid contents were also significantly different between species but were greatest in brook trout intermediate in F_1 splake and least in lake trout. Ash contents were significantly lower ($P < 0.05$) in brook trout than in lake trout and F_1 splake while no differences in P deposits were found between species. A significant interaction was found between species and water temperature for CP contents therefore not allowing for comparison between species across water temperatures. Analysis revealed a highly linear ($R^2 > 0.94$) increase in water, CP, lipid, ash and P contents with an increase in body weight, when water temperatures were pooled, for lake trout (Fig. 2), brook trout (Fig. 3) and F_1 splake (Fig. 4); for clarity, P contents are presented in a separate figure (Fig. 5). Slopes and intercepts of the regression lines for all carcass components are presented in Table 5.

Digestibility

Apparent digestibilities of DM, ash, P and GE were significantly lower in brook trout than in lake trout and F_1 splake. Crude protein digestibility was significantly lower in brook trout than in F_1 splake while no difference was found in lipid digestibility between species (Table 6).

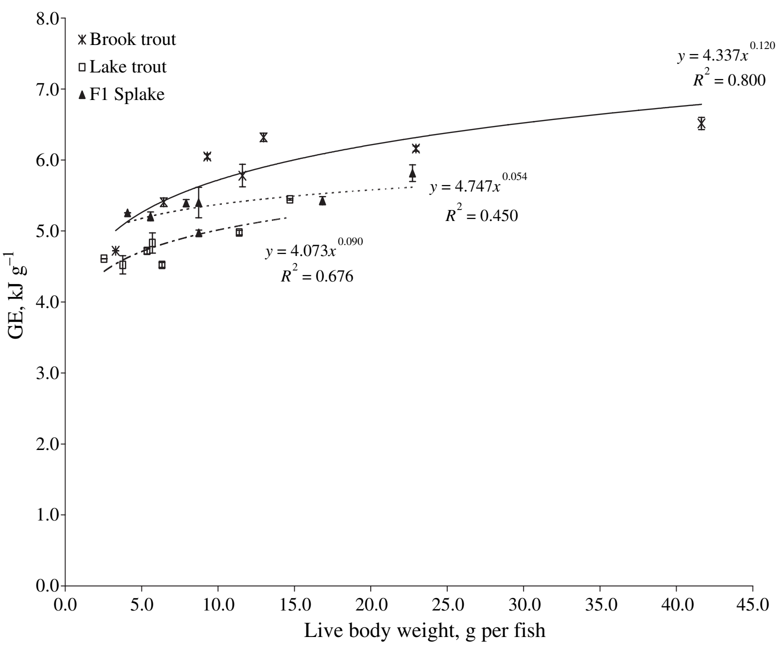

Figure 1 Gross energy concentrations of lake trout, brook trout and F_1 splake reared at 6.4, 10.6 and 14.9 °C. Each point represents the mean ± SEM.

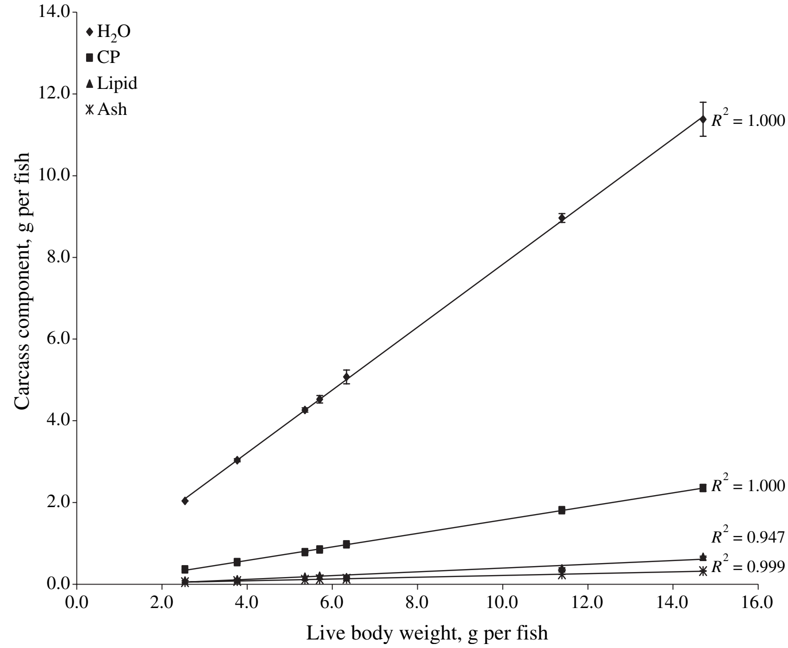

Figure 2 Absolute carcass contents of lake trout reared at 6.4, 10.6 and 14.9 °C. Each point represents the mean ± SEM.

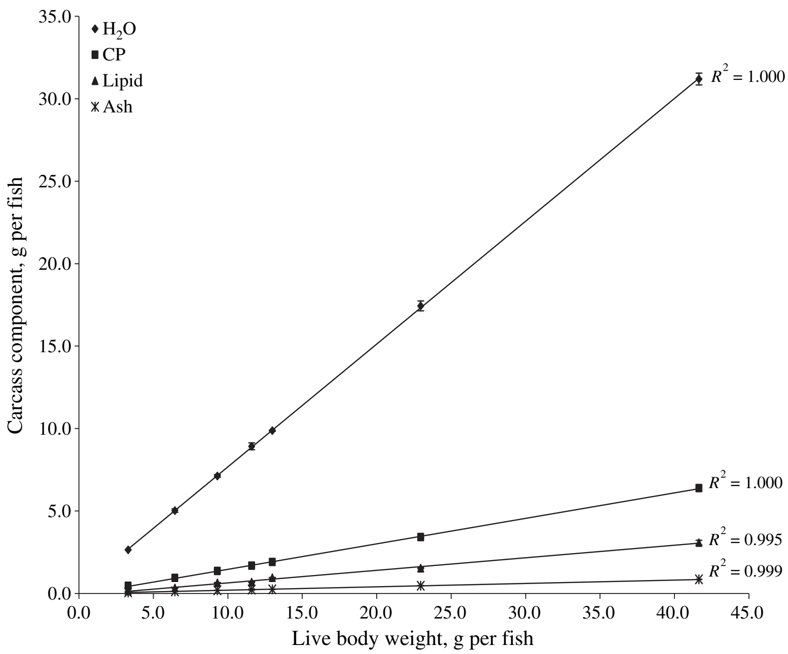

Figure 3 Absolute carcass contents of brook trout reared at 6.4, 10.6 or 14.9 °C. Each point represents the mean ± SEM.

Discussion

For each species weight gain increased with increased water temperature, in agreement with previous findings for lake trout (Dwyer *et al*. 1981; O'Connor *et al*. 1981; Sadler *et al*. 1986; Rottiers 1993; Edsall & Cleland 2000), brook trout (Baldwin 1956; Haskell *et al*. 1956; McCormick *et al*. 1972; Hokanson *et al*. 1973; Dwyer *et al*. 1983; Sadler *et al*. 1986) and F_1 splake (Sadler *et al*. 1986). Brook trout had the highest weight gain, F_1 splake had intermediate and lake trout had lower weight gain at all three temperatures. On the other hand, Sadler *et al*. (1986) found that lake trout had a higher weight gain than brook trout at 10 °C while at 16 °C brook trout had a higher weight gain than lake trout. In

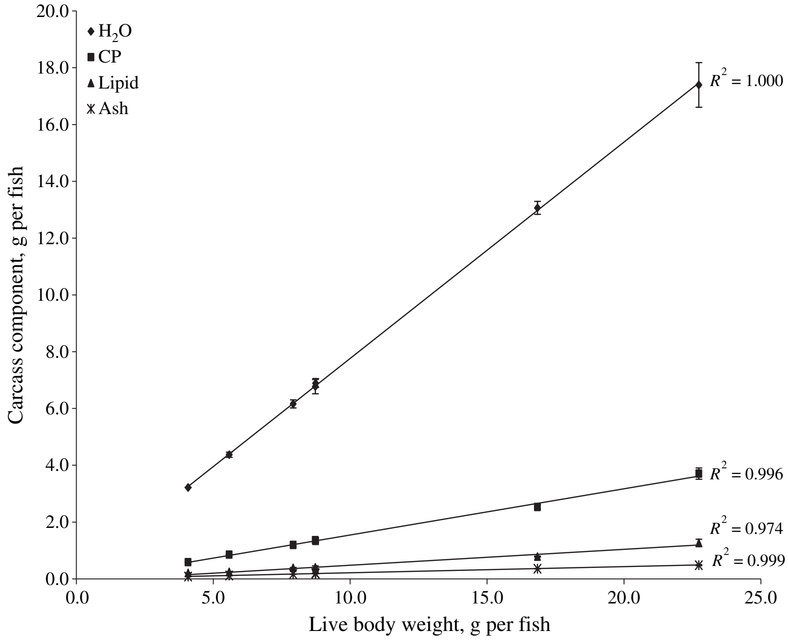

Figure 4 Absolute carcass contents of F_1 splake reared at 6.4, 10.6 or 14.9 °C. Each point represents the mean ± SEM.

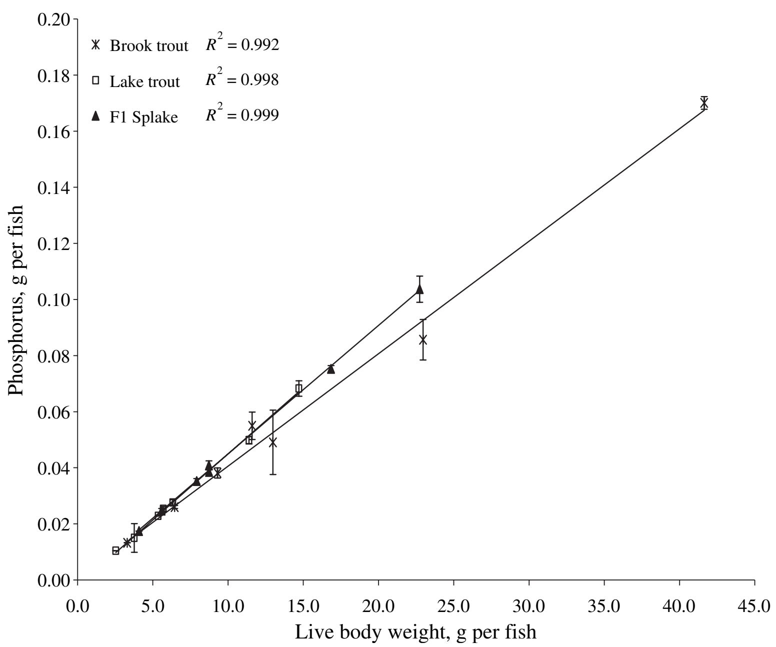

Figure 5 Absolute phosphorus contents of lake trout, brook trout and F_1 splake reared at 6.4, 10.6 or 14.9 °C. Each point represents the mean ± SEM.

agreement with the present study however, Sadler *et al.* (1986) found that the weight gain of F_1 splake was intermediate to lake trout and brook trout. Discrepancies between the present study and that of Sadler *et al.* (1986) are likely due to differences in the genetic growth potential of the particular strain of each species, but could also result from difference in nutrition, environment and husbandry (Cho 1992).

Within water temperature, TGC was highest in brook trout, intermediate in F_1 splake and lowest in lake trout. This is partially in agreement with Sadler *et al.* (1986) who found that the growth rate of F_1 splake was intermediate between lake trout and brook trout. However, Sadler *et al.* (1986) found that the growth rate of lake trout was higher than brook trout at 10 °C while being the reverse at 16 °C. Those studies that exist in the literature have utilized

Table 5 Line fitting parameters for absolute carcass contents of lake trout, brook trout and F_1 splake reared at 6.4, 10.6 or 14.9 °C

	H_2O		CP*		Lipid		Ash		*P*	
	Slope	Int	Slope	Int	Slope	Int	Slope	Int	Slope	Int
Lake trout	0.768[a]	0.146	0.165	−0.080	0.046[a]	−0.063	0.022[a]	−0.004	0.005[a]	−0.002
Brook trout	0.745[b]	0.228	0.155	−0.081	0.076[b]	−0.129	0.021[b]	−0.004	0.004[a]	−0.000
F_1 splake	0.762[c]	0.147	0.163	−0.086	0.056[c]	−0.080	0.022[a]	−0.002	0.005[a]	−0.001

Means in the same column with superscripts a, b and c are significantly different ($P < 0.05$).
*A significant interaction ($P < 0.05$) was found between water temperature and species for CP content, therefore differences between species cannot be tested across water temperatures.

Table 6 Apparent digestibility (mean ± SD) of dry matter (DM), CP, lipid, ash, P, and GE of the diet

	DM	CP	Lipid	Ash	*P*	GE
Lake trout	73.8 ± 0.6[b]	91.0 ± 0.6[ab]	77.8 ± 3.6[a]	61.8 ± 1.0[b]	61.2 ± 1.0[b]	71.5 ± 0.9[b]
Brook trout	71.0±1.4[a]	89.9 ± 0.7[a]	73.1±1.8[a]	52.5 ± 3.1[a]	50.4 ± 3.6[a]	68.3±1.9[a]
F_1 splake	74.3 ± 0.9[b]	91.7 ± 0.4[b]	77.0 ± 1.7[a]	60.1 ± 2.6[b]	60.0 ± 2.1[b]	72.0 ± 0.9[b]

Means within the same column with different superscripts are significantly different ($P < 0.05$).

instantaneous measures, such as SGR, to compare growth. As such measures do not account for water temperature, and water temperatures differed between studies, meaningful comparisons of growth rate cannot be made between those studies and the present study. However, after calculation of TGC from lake trout data (Dwyer *et al.* 1981; Edsall & Cleland 2000) and brook trout data (Hokanson *et al.* 1973; Dwyer *et al.* 1983) meaningful comparisons are possible. The growth of lake trout in the study by both Dwyer *et al.* (1981) and Edsall & Cleland (2000) was considerably higher (TGC range of 0.083–0.143) than in the present study. Brook trout growth was considerably lower (TGC range of 0.072–0.076) in the study by Hokanson *et al.* (1973) but was comparable (TGC range of 0.093–0.131) in the study by Dwyer *et al.* (1983). TGC is, however, also dependent on many factors such as species, stock, nutrition, environment and husbandry (Cho 1992). Differences in such factors between the aforementioned studies and the present study could account for the different growth coefficients observed.

A significant effect of water temperature on FE was found within species; FE being lower ($P < 0.05$) at 6.4 than at 10.6 or 14.9 °C. Although no published studies were found examining FE in lake trout, brook trout or F_1 splake, these findings are in agreement with Cho & Slinger (1980) who found that the FE of rainbow trout increased with increased water temperature but are contrary to Azevedo *et al.* (1998) that water temperature had little effect on FE. However, examination of the results of Azevedo *et al.* (1998) revealed that in rainbow trout fed to near satiation FE was significantly higher ($P < 0.05$) in rainbow trout reared at 9 than fish reared at 6 °C which is in agreement with the findings of the present study.

On a relative wet weight basis, certain general trends were observed for the changes in carcass composition with increased water temperature. Moisture, CP and lipid contents were significantly affected by water temperature; moisture content decreased while CP and lipid contents increased with increased water temperature. Ash and P contents were not affected by water temperature. Moisture, CP and lipid content were also significantly affected by species. Moisture content was highest in lake trout, intermediate in F_1 splake and lowest in brook trout. Crude protein content was generally higher in lake trout and F_1 splake than in brook trout. Lipid content was highest in brook trout, intermediate in F_1 splake and lowest in lake trout. Ash and P contents varied little between species and water temperature; remaining relatively constant over the 16-week trial.

The expression of carcass composition on an absolute basis was suggested by Shearer (1994) as a method of better examining the effect of exogenous (environmental) factors such as water temperature on carcass composition. Results of the present study have indicated that when expressed on an absolute basis, the carcass contents of each species at all temperatures increased linearly with increased fish size; indicating that water temperature had very little effect on absolute carcass composition. Such patterns were explained by Shearer (1994) who concluded that CP, ash and P contents are primarily functions of fish size and are controlled within narrow limits while lipid content is a function of fish size and of the specific energy demands of each species. As moisture content is inversely related to lipid content, moisture content is also a function of the specific energy demands of a species. Absolute carcass compositions were recalculated for the brook trout used in Phillips *et al.* (1960). These modified results were in general agreement with the results of the present study; indicating that the increase in moisture, CP, lipid and ash contents with increase in body weight was highly linear ($R^2 > 0.97$). Similar trends were also found when data from other published studies with Arctic charr (Wandsvik & Jobling 1982), rainbow trout (Papoutsoglou & Papaparaskeva-Papoutsoglou 1978; Azevedo *et al.* 1998) and sockeye salmon (Groves 1970) were recalculated on an absolute basis.

Gross energy concentration of the carcass was found to be affected by water temperature; increasing as water temperature increased for all species. An effect of species was also found for energy concentration which was generally highest in brook trout, intermediate in F_1 splake and lowest in lake trout. The GE concentration of fish depends on the chemical composition of each species (Bureau *et al.* 2002). Theoretical energy values of carbohydrate, CP and lipid are 17.2, 23.6 and 39.5 kJ g^{-1} GE, respectively. As the carbohydrate content of fish is very small (Shearer 1994) its contribution to the GE concentration of the carcass is negligible. In the present study, lipid concentration was found to differ significantly between lake trout, brook trout and F_1 splake. As lipid contributes the most amount of energy per gram to the carcass the differences between the GE concentrations of the lake trout, brook trout and F_1 splake were a function of the lipid content. Hence, brook trout which had the highest lipid concentration had the highest GE concentration; F_1 splake had intermediate amounts of lipid and subsequently contained intermediate amounts of GE, while lake trout had the lowest lipid concentration and subsequently the lowest GE concentration.

In the present study, water temperature had a positive effect on the growth of these *Salvelinus* species; weight gain and growth rate increasing at each increased water temperature. The effect of temperature on carcass composition was varied when composition of the carcass was expressed in terms of relative concentration. When expressed on in absolute terms, however, simple linear equations were used to describe the increase in carcass contents as a function of increased body weight and not temperature. These simple equations bode well for the simple modification of existing feed requirement models increasing their applicability to these *Salvelinus* species.

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