

# Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*)

Ivano Pazzia, Marc Trudel, Mark Ridgway, and Joseph B. Rasmussen

**Abstract:** In this study, we compared energy budgets of lake trout (*Salvelinus namaycush*) populations in contrasting food webs. Nonpiscivorous lake trout (NPLT) reached a much smaller size and grew at a much slower rate than piscivorous lake trout (PLT) populations. Food consumption rates were, on average, 2–3 times higher in NPLT when they were expressed on a wet weight basis. However, only a slight (less than 10%) difference in their energy intake was detected once consumption rates were corrected for differences in prey caloric content. Growth efficiency was approximately two times lower in NPLT compared with PLT, while their metabolic costs were higher and their assimilation efficiency was lower. It is most likely that the increased metabolic costs were associated with higher foraging costs, since more feeding attempts must be made to acquire a given quantity of food when fish are feeding on smaller prey. Furthermore, the portion of indigestible matter is likely to be higher in the diet of NPLT than in PLT (i.e., chitin vs. bone). These results are consistent with theoretical models of fish growth that show that lake trout must have access to larger prey, even if they are rare, to reach larger body sizes.

**Résumé :** Dans cette étude, nous avons comparé le bilan énergétique des populations de touladis (*Salvelinus namaycush*) dans divers réseaux trophiques. Les populations de touladis non piscivores (TNP) ont atteint une taille beaucoup plus petite et ont grandi à un taux beaucoup plus lent que les populations de touladis piscivores (TP). Les taux de consommation de nourriture étaient, en moyenne, 2–3 fois plus élevés chez les TNP lorsqu'ils étaient exprimés sur une base de masse humide. Par contre, seulement une petite différence dans leur acquisition énergétique (moins que 10 %) a été détectée une fois que les taux de consommation ont été corrigés pour des différences dans le contenu calorique des proies. L'efficacité de croissance des TNP était deux fois plus basse par rapport à celle des TP, par contre leurs coûts métaboliques étaient plus élevés et l'efficacité d'assimilation était plus basse. Il est possible que leurs demandes métaboliques élevées étaient associées à des coûts de capture de proies plus élevés, puisque plus de tentatives doivent être faites pour acquérir une quantité donnée de nourriture quand le poisson se nourrit sur une plus petite proie. De plus, la portion de matière qui n'est pas digestible est probablement plus haute dans le régime des TNP que des TP (c.-à-d. l'os versus la chitine). Ces résultats se conforment aux modèles théoriques de croissance de poissons démontrant que les touladis doivent avoir accès à de grosses proies, même si elles sont rares, afin qu'ils puissent atteindre une grande taille.

## Introduction

Throughout their ontogeny, fish generally undergo several diet shifts by progressively consuming larger prey items that may require the use of different feeding habitats such as the pelagic and benthic environments, or as in anadromous fish, extensive migrations between fresh water and salt water (Werner and Gilliam 1984). As larvae, fish typically feed on small crustaceans such as rotifers and nauplii (Konkle and Sprules 1986). This can be followed by a transition to larger zooplankton, benthic invertebrates, and ultimately, to other

fish, depending on their size and preferred prey (Mittelbach and Persson 1998).

The ability of fish to shift to larger prey items depends mainly on prey composition and prey availability, and hence, on food web structure (Winemiller 1990; Sherwood et al. 2002a). The prey community in a given lake is determined by its postglacial zoogeographic history (Dadswell 1974), but it may be altered by anthropogenic factors such as the introduction of exotic species (Vander Zanden et al. 1999) and pollution (Sherwood et al. 2000). Thus, in some systems, some fish species may be unable to complete certain

Received 8 February 2002. Accepted 20 August 2002. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 4 October 2002.  
J16759

**I. Pazzia<sup>1,2</sup> and J.B. Rasmussen.** McGill University, Department of Biology, 1205 Dr. Penfield Avenue, Montreal, QC H3A 1B1, Canada.

**M. Trudel.** Pacific Biological Research Station, Department of Fisheries and Oceans, Nanaimo, BC V9T 6N7, Canada.

**M. Ridgway.** Aquatic Ecosystem Science Section, Ontario Ministry of Natural Resources, Third Floor North, 300 Water Street, Peterborough, ON K9J 8M5, Canada.

<sup>1</sup>Corresponding author (e-mail: [ivano.pazzia@saputo.com](mailto:ivano.pazzia@saputo.com)).

<sup>2</sup>Present address: Environmental Affairs Department, Saputo Inc., 6869 Boul. Métropolitain Est, Saint Leonard, QC H1P 1X8, Canada.

diet shifts if appropriate prey are lacking (Sherwood et al. 2002b).

A diet shift to larger sized prey is usually followed by increased growth rates (Werner and Gilliam 1984). This may result from an increase in food consumption rates, a reduction of energy expenditures, or a combination of both processes. Theoretical models of fish growth suggest that foraging costs increase when the size of a predator increases relative to its prey, since it must find and consume more prey to satisfy its energy demands (i.e., decreased growth efficiency, Kerr 1971a, 1971b). Thus, fish that are foraging on larger prey are expected to have lower energy expenditures associated with foraging than would fish feeding on smaller prey (Sherwood et al. 2002a, 2002b). In addition, foraging costs are expected to increase more quickly with body size in fish consuming smaller prey (Kerr 1971a, 1971b).

The effects of prey size on energy acquisition and energy allocation have rarely been examined in wild fish, possibly because of the difficulty of estimating energy intake of fish in situ using traditional approaches based on stomach contents. In a comparative study involving 12 populations of yellow perch (*Perca flavescens*), Boisclair and Leggett (1989a) showed that growth rate, growth efficiency, and consumption rates of yellow perch were all negatively correlated to the percent contribution of small prey in their diet. More recently, Sherwood et al. (2000, 2002a) compared the energy budget of yellow perch from metal-contaminated sites and reference sites. Yellow perch from the metal-contaminated sites consumed smaller prey and had lower growth rates and growth efficiencies, but higher foraging costs than fish from the reference sites. However, none of these studies attempted to examine how the relationships between consumption rate and fish size and between foraging cost and fish size were influenced by prey size and prey type.

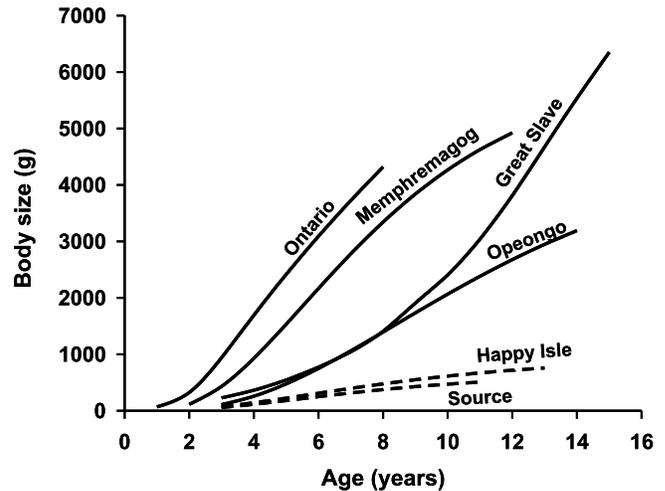
The objectives of this study were to examine the effects of food web structure and prey size on energy acquisition and energy allocation of fish. This study was conducted using lake trout (*Salvelinus namaycush*) as a model species. Lake trout populations that have suitable forage fish species available to them all year become piscivorous (hereafter referred to as PLT) and demonstrate relatively rapid growth (Martin 1966; Fig. 1). In the absence of certain prey fish species, lake trout rely on littoral minnows during the winter months, but in the summer feed primarily on zooplankton and benthic invertebrates owing to thermal restraints during lake stratification (Martin 1966; Konkle and Sprules 1986; Vander Zanden et al. 1999). These nonpiscivorous lake trout (NPLT) populations tend to grow at slower rates, mature at smaller sizes and earlier ages, and are usually found in much higher fish densities than PLT (Martin 1966; Konkle and Sprules 1986). Because of their small size (Fig. 1), NPLT are usually considered to be stunted. Hence, in this study, we tested the hypotheses that the reduced growth observed in NPLT compared with PLT is a result of (i) a decrease in consumption rates, and (or) (ii) a decrease in growth efficiency (increase in energetic costs).

## Methods

### Study sites

This study was conducted in Algonquin Park, Ontario, at the

**Fig. 1.** Growth curves of six lake trout (*Salvelinus namaycush*) populations located in Canada. Solid lines represent piscivorous populations; dashed lines represent nonpiscivorous populations.



Harkness Laboratory of Fisheries Research located on Lake Opeongo. Algonquin Provincial Park has an area of approximately 7800 km<sup>2</sup> and is situated on the Precambrian Shield (45°45'N and 78°30'W). About 150 lakes in the park contain self-sustaining lake trout populations that show varying degrees of piscivory. Two NPLT (Happy Isle Lake and Source Lake) populations and one PLT (Lake Opeongo) population were sampled in this area. Two of the three lakes sampled are easily accessible by road, but Happy Isle requires a 14-km boat ride and a 2.2-km portage. Additional PLT population data were collected from the literature for Great Slave Lake (Northwest Territories), Lake Ontario (Ontario – New York), and Lake Memphremagog (Quebec–Vermont) (Rowan and Rasmussen 1996; Trudel et al. 2000). Lake Memphremagog and Lake Ontario are stocked by governmental agencies with lake trout and other salmonids to sustain the high levels of fishing pressure from anglers. The PLT populations in this study had diets consisting almost entirely of forage fish, whereas prey fish never made up more than 11% by weight of the nonpiscivorous diet. Over 89% of the NPLT diet was zooplankton and benthic invertebrates.

### Fish collection

Fish were collected by gillnet and rod and reel from the three lakes in Algonquin Park from May until August during 1998 and 1999. Gillnets were set for approximately four hours and consisted of six panels of 50-m nets varying from 1.3 to 6.4 cm in mesh size. Lake trout heads were also obtained from anglers at the Creel Census Station on Lake Opeongo. These three lakes all support sport fisheries with angling pressure ranging from negligible to heavy depending on accessibility and quality of fishing. Total mass and fork length of each individual fish was measured to the nearest ±0.1 g and nearest millimetre, respectively.

### Age analysis

Lake trout were aged using the left sagittal otolith. Otoliths were removed and preserved in glycerol for 3 months. Otoliths were then cleaned in a 10% alcohol solution and embedded in an epoxy resin (araldite). A thin transverse sec-

tion was cut through the nucleus, at right angles to the long axis of each otolith. The section was mounted on a glass slide, buffed, and polished with lapping film. After each polished surface of the section was etched with a 2% HCl solution, acetate imprints were made (Casselman and Gunn 1992). The acetate imprints were mounted and examined with a microscope at 40× and 100× magnification.

Lake trout were assigned ages based on enumeration of annuli on their otoliths (Casselman 1983). Mounted otoliths were aged blindly, as readers were given only identification numbers to eliminate any prior bias that could have occurred while aging. An interpreter assessed the age of each otolith ( $n = 367$ ) twice; agreement of the two independent ages was within 93%. A subsample of otoliths ( $n = 125$ ) was aged by a second interpreter, and agreement with the first interpreter was 87%. Differences between the first and second interpreters were within 1–3 years. When the two interpreters could not reach a consensus, a third interpreter assessed the age until a consensus was achieved.

### Growth rates

Growth curves were fitted on mean mass-at-age using various nonlinear equations (Fig. 1; Table A1). Specific growth rates ( $G$ ,  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) were estimated as

$$(1) \quad G = \frac{1}{\Delta t} \ln \left( \frac{W_{t+\Delta t}}{W_t} \right)$$

where  $W_t$  and  $W_{t+\Delta t}$  are fish mass (g) at time  $t$  and  $t + \Delta t$ . All growth rates include both somatic and gonadal growth. To express growth on an energetic basis ( $P$ ,  $\text{kJ}\cdot\text{day}^{-1}$ ), we converted lake trout size to energy units (kJ) using the energy density–size relationship derived by Stewart et al. (1983) for Lake Michigan lake trout. The energy densities of the gonads were assumed to be 20% higher than the energy density of somatic tissue (Diana 1983). Males and females were pooled for this analysis, as the low sample size prevented us from adequately estimating energy budgets separately for each sex.

### Consumption rates

Annual consumption rates for lake trout from Lake Opeongo, Great Slave Lake, Lake Memphremagog, Happy Isle Lake, and Source Lake were estimated with the  $^{137}\text{Cs}$  radiotracer approach. The  $^{137}\text{Cs}$  approach requires determination of lake trout age, body size, growth rate,  $^{137}\text{Cs}$  concentration in fish tissue and their prey, and assimilation efficiency of  $^{137}\text{Cs}$  from food, as well as the elimination rate of  $^{137}\text{Cs}$  from fish (Rowan and Rasmussen 1996). Specific consumption rates ( $C$ ,  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) were estimated from an independently validated (Forseth et al. 1992) radiocesium mass balance model (Rowan and Rasmussen 1996) as

$$(2) \quad C = \frac{(Q_t - Q_0 e^{-(E+D)t} + Q_g)}{\alpha [^{137}\text{Cs}_p] w_0 (e^{Gt} - e^{-(E+D)t})} (G + E + D)$$

where  $Q_t$  is the  $^{137}\text{Cs}$  burden (the product of cesium concentration,  $[^{137}\text{Cs}_t]$ , and body mass,  $W_t$ ) in becquerels (Bq, 1 Bq = 0.027 Ci) at time  $t$  (days),  $Q_0$  is the initial  $^{137}\text{Cs}$  burden (Bq),  $Q_g$  is the gonadal  $^{137}\text{Cs}$  burden (Bq) released at spawning,  $G$  is the specific growth rate ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ),  $E$  is the rate of elimination  $^{137}\text{Cs}$  ( $\text{Bq}\cdot\text{Bq}^{-1}\cdot\text{day}^{-1}$ ),  $D$  is the radioactive de-

cah of  $^{137}\text{Cs}$  ( $\text{Bq}\cdot\text{Bq}^{-1}\cdot\text{day}^{-1}$ ),  $[^{137}\text{Cs}_p]$  is the concentration of  $^{137}\text{Cs}$  in the prey ( $\text{Bq}\cdot\text{kg}^{-1}$ ),  $\alpha$  is the efficiency at which  $^{137}\text{Cs}$  is assimilated from the diet, and  $w_0$  is the initial body mass (kg).  $^{137}\text{Cs}$  concentrations of lake trout and prey were determined by gamma spectroscopy with a coaxial or well germanium detector (model GCW 1521, Canberra Packard Canada, Mississauga, Ont.). To reduce the volume of the samples, lake trout were either dried at 60°C or ashed at 450°C, and subsequently homogenized with a mortar and a pestle prior to performing the  $^{137}\text{Cs}$  analyses. Ashing or drying does not alter the absolute amount of  $^{137}\text{Cs}$ , as the boiling point of Cs is 670°C.  $^{137}\text{Cs}$  concentration was individually measured for each lake trout, while prey items were pooled together according to lake and lake trout size class.  $^{137}\text{Cs}$  concentrations for lake trout were modeled as a function of age using linear and nonlinear regressions (Table A1). Annual average age-specific consumption rates were also converted to energy units ( $\text{kJ}\cdot\text{day}^{-1}$ ) using published estimates of prey energy density (Cummins and Wuycheck 1971; Rottiers and Tucker 1982; Post 1990; Mason et al. 1998).

$^{137}\text{Cs}$  concentrations of prey items consumed by lake trout were measured on undigested gut contents. Lake trout stomach contents were removed and divided into two categories, fish and invertebrates (Table 1). Each category was weighed to the nearest  $\pm 0.01$  g. Stomach contents were pooled according to site, lake trout size class, and prey type to increase the precision of  $^{137}\text{Cs}$  concentrations. Each lake trout was assigned to one of six total length classes (mm): (i) <200, (ii) 200–299, (iii) 300–399, (iv) 400–499, (v) 500–599, (vi) >600. A weighted average of  $^{137}\text{Cs}$  concentrations by volume was used to calculate overall concentration in the diet. Assimilation efficiency of  $^{137}\text{Cs}$  by lake trout from their diet was estimated using published values that were determined mainly using salmonids. We assumed that assimilation efficiency of  $^{137}\text{Cs}$  was 0.69 for fish prey (Rowan and Rasmussen 1996) and 0.234 for invertebrate prey (Forseth et al. 1992) (Table 2).

Elimination rate of  $^{137}\text{Cs}$  from fish has been shown to be species independent and can be described as a function of body size ( $W$ , g) and temperature ( $T$ , °C) as (Rowan and Rasmussen 1995)

$$(3) \quad E = e^{-6.583-0.111\cdot\ln(W)+0.098T}$$

The temperature occupied by an individual lake trout appears to be a combination of changing water temperatures, the preferred temperature, and recent temperatures experienced through vertical migration in the water column (Stewart et al. 1983). The annual water temperature cycles (epilimnion) of Lake Opeongo, Happy Isle Lake, Source Lake, Great Slave Lake, Lake Ontario, and Lake Memphremagog were modelled with a Gaussian function (Table 3). For the present study, maximum preferred temperature for lake trout was assumed to be 10°C (Stewart et al. 1983). Thus, during the summer months, lake trout were assumed to forage in deeper water where the temperature would be around 10°C, but in the winter months they were assumed to forage close to the surface (Fig. 2).

The burden of  $^{137}\text{Cs}$  lost through the gonads ( $Q_g$ ) during spawning was estimated as

$$(4) \quad Q_g = [^{137}\text{Cs}_g] \cdot \text{GSI} \cdot W_{sp}$$

**Table 1.** Lake trout diet (% volume) arranged according to lake trout (*Salvelinus namaycush*) body size (fork length, mm).

Lake	Body size (mm)					
	<200	200–299	300–399	400–499	500–599	>600
Opeongo	—	20Inv, 80C	100C	100C	100C	100C
Ontario <sup>a</sup>	50SS, 30RS, 20A	50SS, 30RS, 20A	40SS, 40RS, 20A	25SS, 50RS, 25A	10SS, 40RS, 50A	30RS, 70A
Memphremagog <sup>b</sup>	—	100RS	100RS	100RS	100RS	100RS
Great Slave <sup>c</sup>	—	100C	100C	100C	100C	100C
Happy Isle	100Inv	100Inv	89Inv, 11Y	—	—	—
Source	100Inv	100Inv	97.8Inv, 2.2Y	—	—	—

**Note:** C, cisco; RS, rainbow smelt; SS, slimy sculpin; A, alewife; Y, young-of-the-year perch; Inv, invertebrates.

<sup>a</sup>Data from Borgman and Whittle (1992).

<sup>b</sup>Data from Trudel et al. (2000).

<sup>c</sup>Data from Rowan and Rasmussen (1996).

**Table 2.** Caloric content of lake trout (*Salvelinus namaycush*) prey, Cs concentration of prey [<sup>137</sup>Cs<sub>p</sub>] (standard error in parentheses), and assimilation of <sup>137</sup>Cs from the prey (α).

Prey item	Energy density (J·g <sup>-1</sup> wet weight)	[ <sup>137</sup> Cs <sub>p</sub> ] (Bq·kg <sup>-1</sup> )	α
<b>Lake Opeongo</b>			
Cisco	10 464 <sup>a,b</sup>	4.74 (0.19)	0.69 <sup>c</sup>
Benthic invertebrates	3 210 <sup>d</sup>	2.96 (0.50)	0.234 <sup>e</sup>
<b>Great Slave Lake</b>			
Cisco	10 464 <sup>a,b</sup>	3.14 <sup>c</sup> (0.21)	0.69 <sup>c</sup>
<b>Lake Memphremagog</b>			
Rainbow smelt	6 655 <sup>a</sup>	0.70 <sup>f</sup>	0.69 <sup>c</sup>
<b>Happy Isle Lake</b>			
Young-of-the-year perch	2 511 <sup>g</sup>	4.72 (0.43)	0.69 <sup>c</sup>
Benthic invertebrates	3 210 <sup>d</sup>	2.61 (0.35)	0.234 <sup>e</sup>
<b>Source Lake</b>			
Young-of-the-year perch	2 511 <sup>g</sup>	6.68 (1.04)	0.69 <sup>c</sup>
Benthic invertebrates	3 210 <sup>d</sup>	2.43 (0.19)	0.234 <sup>e</sup>

<sup>a</sup>Data from Rottiers and Tucker (1982).

<sup>b</sup>Data from Mason et al. (1998).

<sup>c</sup>Data from Rowan and Rasmussen (1996).

<sup>d</sup>Data from Post (1990).

<sup>e</sup>Data from Cummins and Wuycheck (1971).

<sup>f</sup>Data from Forseth et al. (1992).

<sup>g</sup>Data from Trudel et al. (2000).

**Table 3.** Water temperature (*T*, °C) curves for six lake trout (*Salvelinus namaycush*) lakes in Canada.

Lake	Curve
Opeongo	$T = 3.7 + 17.7e^{-(J-204.7)^2/67^2}$
Ontario, Memphremagog <sup>a</sup>	$T = 3.8 + 14.7e^{-(J-219)^2/72^2}$
Great Slave <sup>b</sup>	$T = 3.8 + 12.0e^{-(J-220.6)^2/30^2}$
Happy Isle	$T = 2.6 + 21.0e^{-(J-200)^2/83^2}$
Source	$T = 2.6 + 21.0e^{-(J-199)^2/82^2}$

**Note:** *J*, Julian day of the year.

<sup>a</sup>Data from Trudel et al. (2000).

<sup>b</sup>Data from Rowan and Rasmussen (1996).

where [<sup>137</sup>Cs<sub>g</sub>] is the concentration of <sup>137</sup>Cs in the gonads, GSI is the gonadosomatic index (%), and *W*<sub>sp</sub> is fish weight (kg) at spawning. The GSI of lake trout was taken from Creel Census Surveys carried out in Algonquin Provincial Park; maximum GSI values were taken for both male (5%) and female (15%) lake trout and were applied to other lake trout populations.

Annual consumption rates for Lake Ontario lake trout were

estimated with a Hg mass balance model and were taken directly from Trudel et al. (2000) (Tables 4 and A2).

#### Allocation of energy to growth

The proportion of the energy budget allocated to growth was estimated as

$$(5) \quad GE = \frac{P}{DR}$$

where GE is the growth efficiency, *P* is the sum of somatic and gonad growth (kJ·day<sup>-1</sup>), and DR is the daily ration of the fish (kJ·day<sup>-1</sup>). DR was obtained by converting consumption rates from g·g<sup>-1</sup>·day<sup>-1</sup> to kJ·day<sup>-1</sup> utilizing the energy content of the different prey items in the diet of these fish (Tables A1 and A2).

#### Total metabolic rates and activity costs

The energy budget of a fish can be written as

$$(6) \quad DR = P + R_T + F + U$$

where *R*<sub>T</sub> is the total respiration or metabolic rate (kJ·day<sup>-1</sup>),

**Table 4.** Fish diet caloric content of prey, Hg concentration of prey ( $[Hg_p]$ ) according to prey size (length,  $l_p$ ), and assimilation of Hg from the prey ( $\alpha$ ) in Lake Ontario.

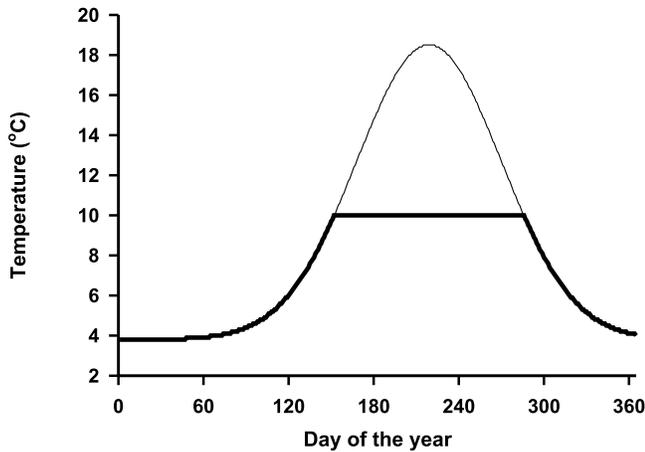
Prey item	Energy density ( $J \cdot g^{-1}$ wet weight)	$[Hg_p]$ ( $\mu g \cdot g^{-1}$ )	$\alpha$
Alewife	6822 <sup>a</sup>	$\log(Hg_p) = -5.22 + 3.22 \cdot \log(l_p)^b$	0.80 <sup>c</sup>
Rainbow smelt	6655 <sup>a</sup>	$\log(Hg_p) = -3.42 + 1.72 \cdot \log(l_p)^b$	0.80 <sup>c</sup>
Slimy sculpin	5743 <sup>a</sup>	$\log(Hg_p) = -2.28 + 0.93 \cdot \log(l_p)^b$	0.80 <sup>c</sup>

**Note:** Length of prey ( $l_p$ ) in cm.

<sup>a</sup>Data from Rottiers and Tucker (1982).

<sup>b</sup>Data from Borgman and Whittle (1992).

<sup>c</sup>Data from Trudel et al. (2000).

**Fig. 2.** Water temperature in the epilimnion of Lake Ontario (fine line). Lake trout (*Salvelinus namaycush*) were assumed to actively seek water masses that were near their thermal preferendum (thick line).

$F$  is egestion ( $\text{kJ} \cdot \text{day}^{-1}$ ), and  $U$  is excretion ( $\text{kJ} \cdot \text{day}^{-1}$ ).  $R_T$  can be estimated by difference, provided that  $DR$ ,  $P$ ,  $F$ , and  $U$  are known as

$$(7) \quad R_T = DR - (P + F + U)$$

$R_T$  can be further divided into three components

$$(8) \quad R_T = R_s + R_d + R_a$$

where  $R_s$  is the standard metabolic rate ( $\text{kJ} \cdot \text{day}^{-1}$ ),  $R_d$  is the specific dynamic action or heat increment ( $\text{kJ} \cdot \text{day}^{-1}$ ), and  $R_a$  is the cost of activity ( $\text{kJ} \cdot \text{day}^{-1}$ ).  $R_s$  is a function of body size and water temperature, while  $R_d$  is assumed to be equal to 17% of the assimilated energy (Stewart et al. 1983). Therefore,  $R_a$  can also be determined by difference if  $R_s$  and  $R_d$  are known

$$(9) \quad R_a = R_T - (R_s + R_d)$$

Trudel and Boisclair (1996) recently showed that activity costs determined using eq. (9) provided values similar (less than 8% difference) to those obtained by converting swimming speed into swimming costs. This suggests that this approach may be adequate for estimating activity costs of fish in the field. In this study,  $R_s$ ,  $R_d$ ,  $F$ , and  $U$  were determined using the parameters presented by Stewart et al. (1983) for lake trout. Fecal losses in Stewart's model (1983) are assumed to vary as a function of the proportion of indigestible matter (i.e., chitin and bone), and represent about 22 and

16% of the energy budget of lake trout feeding on invertebrates and prey fish, respectively.

### Statistical analyses

Consumption rates, growth efficiency, and activity costs of PLT and NPLT were compared using an analysis of covariance (ANCOVA; Sokal and Rohlf 1995) with body size as a covariant. We first performed the ANCOVA by including an interaction term between prey type (invertebrates vs. prey fish) and lake trout size. When it was not significant, we dropped it from the analysis, and continued the analysis by comparing the intercepts (Sokal and Rohlf 1995). Systematic differences between NPLT and PLT could not be directly assessed with the ANCOVA when the interaction term was significant. In this case, we fitted a simple linear regression of consumption rates, growth efficiency, or activity costs with size for PLT only, as this group covered the largest range of sizes. We then computed the residuals between the values observed for NPLT and the values predicted by the regression model derived for PLT, and performed a signed-ranks test on the residuals by counting the number of negative residuals (test statistics, TS). The probabilities associated with this test were computed using the binomial distribution (Sokal and Rohlf 1995). The relationship between growth rates and consumption rates of PLT and NPLT were also compared using an ANCOVA.

Standard errors for  $C$  and  $DR$  were derived by age class means from Monte Carlo simulations, which allowed us to account simultaneously for error in a number of measured parameters based on randomly generated pseudovalues (Manly 1998). One thousand estimates for  $C$  and  $DR$  were computed by solving eq. 2 with pseudovalues for their respective parameters. For  $W_t$  and  $W_{t+\Delta t}$  we used correlated pseudovalues, as fish that are larger at time  $t$  are also likely to be larger at time  $t + \Delta t$ . The correlation coefficient used for generating the correlated random numbers was set to  $r = 0.95$ . This value was derived using the back-calculated size of two consecutive age-classes of lake trout determined using otoliths (M. Trudel, Fisheries and Oceans Canada, Nanaimo, B.C., unpublished data). We used a similar procedure for  $[^{137}\text{Cs}_t]$  and  $[^{137}\text{Cs}_{t+\Delta t}]$ , as fish that have a higher  $^{137}\text{Cs}$  concentration at time  $t$  are also likely to be more contaminated with  $^{137}\text{Cs}$  at time  $t + \Delta t$ .

## Results

### Consumption rates

Food consumption rates of lake trout ranged from 1.0 to

43.9 g·day<sup>-1</sup> and were positively correlated with body size for both of PLT ( $F_{[1,38]} = 193.4$ ;  $p < 0.0001$ ) and NPLT ( $F_{[1,16]} = 302.7$ ;  $p < 0.0001$ ) (Fig. 3a). The standard error of the consumption estimates of PLT and NPLT ranged from about 13 to 22%. Food consumption rates tended to be higher for NPLT than for PLT at any given size (Fig. 3a). NPLT consumed from 1.9- to 3.3-fold more food than PLT. There was no significant interaction between body size and prey type ( $F_{[1,54]} = 2.3$ ;  $p > 0.13$ ). Only the intercepts of the relationship between consumption and body size differed ( $F_{[1,55]} = 57.7$ ;  $p < 0.0001$ ). However, when food consumption rates were converted to energy units, differences between PLT and NPLT nearly disappeared, because water content is higher and energy densities are lower in invertebrates than in prey fish (Fig. 3b) (Table 3; Table A3). The interaction between diet and lake trout body size was not significant either ( $F_{[1,54]} = 3.4$ ;  $p > 0.05$ ). However, the intercept of this relationship differed significantly between PLT and NPLT ( $F_{[1,55]} = 4.8$ ;  $p < 0.05$ ). On average, PLT consumed about 0.69 kJ·day<sup>-1</sup> more food than NPLT for any given body size. It is important to note, though, that this difference is smaller than the measurement error of these consumption rates, suggesting that the consumption rates of NPLT and PLT were not different. In addition, it may be argued that this effect is the result of a single lake, as Lake Ontario lake trout tended to consume more food than NPLT and other PLT populations (Fig. 3b). Removing Lake Ontario from the analysis resulted in a nonsignificant effect of diet ( $F_{[1,48]} = 0.2$ ;  $p > 0.6$ ).

### Energy allocated to growth

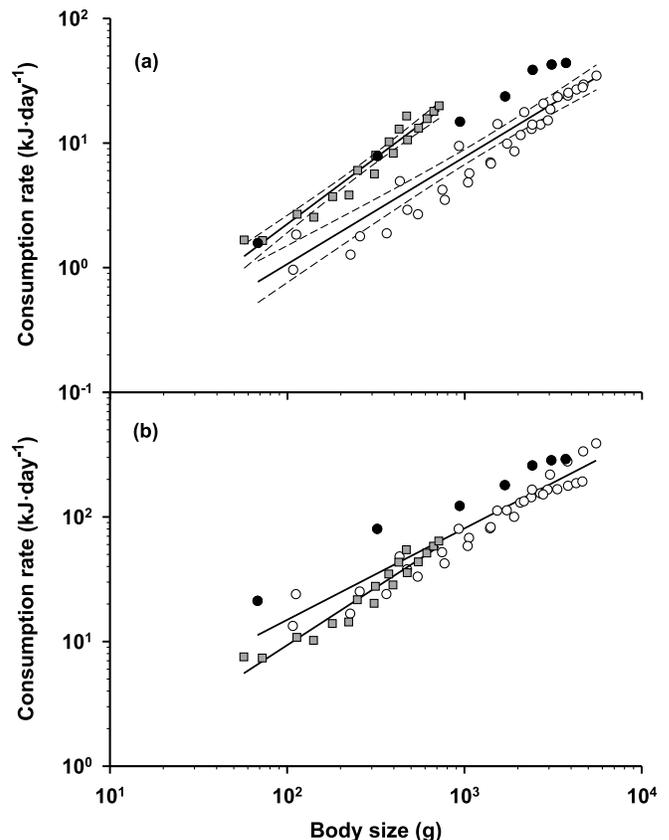
Growth rates were positively correlated to consumption rates for PLT ( $F_{[1,38]} = 728.8$ ;  $p < 0.0001$ ) and NPLT ( $F_{[1,16]} = 62.3$ ;  $p < 0.0001$ ) (Fig. 4). PLT had growth rates 1.7–3.5 times higher than NPLT at comparable consumption rates (Fig. 4). In addition, growth rates tended to increase faster with consumption rates in PLT than NPLT (Fig. 4). The interaction between growth rate and consumption rate was also significant ( $F_{[1,54]} = 42.9$ ;  $p < 0.0001$ ). Growth rates were systematically lower in NPLT than in PLT over this range of consumption rates ( $TS_{18} = 18$ ;  $p < 0.0001$ ).

Growth efficiencies of PLT and NPLT ranged from 11.0 to 24.0% and from 3.6 to 15.4%, respectively. The highest growth efficiency was observed in the PLT from Lake Memphremagog (24.0%), while the lowest value was observed in NPLT from Source Lake (3.6%). Growth efficiency tended to be higher in PLT (15.8%) than NPLT (8.3%), even when maturation status was taken into consideration. Juvenile lake trout tended to have higher growth efficiencies than adult lake trout in NPLT, but not in PLT (Fig. 5). Growth efficiency decreased significantly with body size in NPLT ( $F_{[1,16]} = 32.56$ ;  $p < 0.0001$ ), but not in PLT ( $F_{[1,38]} = 2.9$ ;  $p > 0.09$ ). In addition, growth efficiency tended to decrease much faster with body size in NPLT than PLT (Fig. 5). The interaction between prey type and body size was also significant ( $F_{[1,54]} = 42.7$ ;  $p < 0.0001$ ). Growth efficiencies were systematically lower in NPLT than in PLT over this range of size ( $TS_{18} = 18$ ;  $p < 0.0001$ ).

### Activity costs

Activity costs of PLT ranged from 2.4 to 148.1 kJ·day<sup>-1</sup>

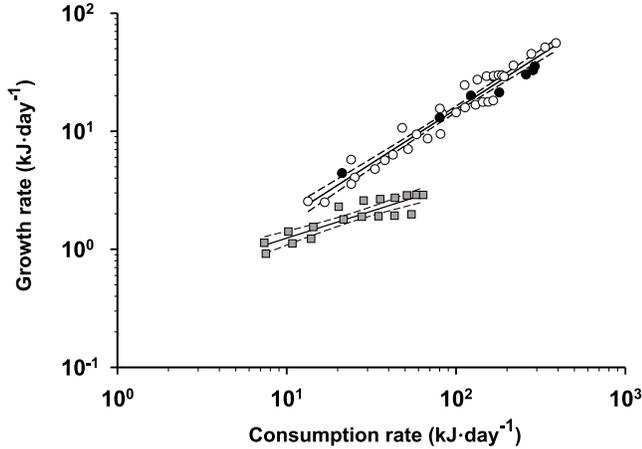
**Fig. 3.** (a) Absolute consumption rate as a function of body size. Nonpiscivorous lake trout (NPLT), *Salvelinus namaycush* (shaded squares);  $\log_{10}DR = 1.06(0.06)\log_{10}W - 1.77(0.15)$ ;  $R^2 = 0.95$ ;  $SE_{est} = 0.08$ ;  $n = 18$ ;  $p < 0.0001$ . Piscivorous lake trout (PLT, open and solid circles);  $\log_{10}DR = 0.86(0.06)\log_{10}W - 1.69(0.19)$ ;  $R^2 = 0.84$ ;  $SE_{est}$  (standard error of the estimate) = 0.19;  $n = 40$ ;  $p < 0.0001$ . (b) Absolute consumption rate corrected for differences in energy density of the two diet types as a function of body size. Lake Ontario lake trout (solid circles) were excluded from the regression analysis, as they tended to consume more food than NPLT (shaded squares) and other PLT (open circles) populations. NPLT:  $\log_{10}DR = 0.92(0.06)\log_{10}W - 0.88(0.15)$ ;  $R^2 = 0.94$ ;  $SE_{est} = 0.08$ ;  $n = 18$ ;  $p < 0.0001$ . PLT:  $\log_{10}DR = 0.73(0.05)\log_{10}W - 0.29(0.14)$ ;  $R^2 = 0.87$ ;  $SE_{est} = 0.14$ ;  $n = 40$ ;  $p < 0.0001$ .



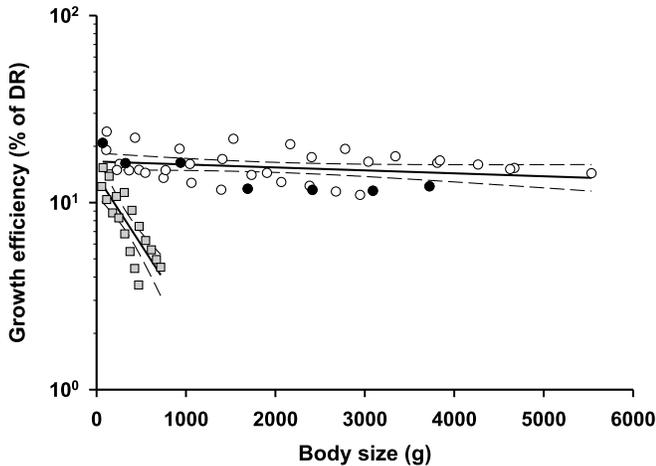
and from 0.9 to 24.2 kJ·day<sup>-1</sup> for NPLT (Figs. 6 and 7). Adult fish invested a larger proportion of their budget in activity costs than juvenile fish (Fig. 6). However, the difference in activity costs between juvenile and adult fish was higher in NPLT (18.4%) than in PLT (7.8%) (Fig. 6). Activity did not vary significantly between prey types ( $F_{[1,54]} = 3.3$ ;  $p > 0.1$ ), but it varied significantly between life stages ( $F_{[1,54]} = 3.8$ ;  $p < 0.0001$ ). The interaction between prey type and life stage was also significant ( $F_{[1,54]} = 6.2$ ;  $p < 0.05$ ).

The energy allocated to activity was positively correlated with body size in PLT ( $F_{[1,38]} = 19.5$ ;  $p < 0.0001$ ) and NPLT ( $F_{[1,16]} = 29.9$ ;  $p < 0.0001$ ) (Fig. 7). In addition, activity costs tended to increase much faster with body size in NPLT than PLT (Fig. 7). The interaction between prey type and body size was also significant ( $F_{[1,54]} = 30.5$ ;  $p < 0.0001$ ) (Fig. 7). However, activity costs were not systematically

**Fig. 4.** Relationship between growth rates and absolute consumption rates. Nonpiscivorous lake trout (NPLT), *Salvelinus namaycush* (shaded squares);  $\log_{10}P = 0.46(0.06)\log_{10}DR - 0.36(0.08)$ ;  $R^2 = 0.80$ ;  $SE_{est} = 0.07$ ;  $n = 18$ ;  $p < 0.0001$ . Piscivorous lake trout (PLT, open and solid circles);  $\log_{10}P = 0.92(0.03)\log_{10}DR - 0.65(0.07)$ ;  $R^2 = 0.95$ ;  $SE_{est} = 0.08$ ;  $n = 40$ ;  $p < 0.0001$ .



**Fig. 5.** Relationship between growth efficiency (% of DR) and body size for nonpiscivorous (NPLT, shaded squares) and piscivorous (PLT, open and closed circles) lake trout (*Salvelinus namaycush*). NPLT:  $\log_{10}GE = -7.4 \cdot 10^{-4}(0.00)W + 1.14(0.05)$ ;  $R^2 = 0.67$ ;  $SE_{est} = 0.11$ ;  $n = 18$ ;  $p < 0.0001$ . PLT:  $\log_{10}GE = -1.6 \cdot 10^{-5}(0.00)W + 1.22(0.02)$ ;  $R^2 = 0.07$ ;  $SE_{est} = 0.09$ ;  $n = 40$ ;  $p > 0.1$ .



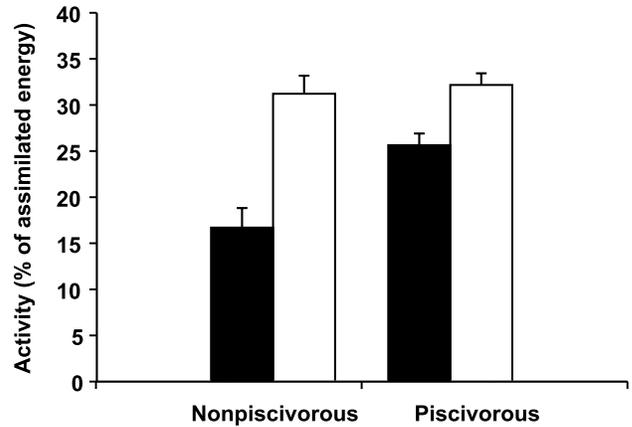
higher in NPLT than in PLT over this range of sizes ( $TS_{18} = 7$ ;  $p > 0.4$ ).

**Discussion**

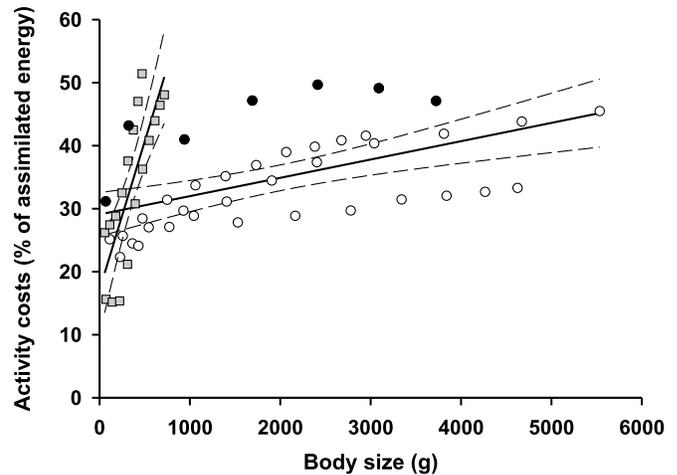
**Lake trout energetics**

Analyses performed in this study showed that food consumption rates were two to three times higher in NPLT than PLT when they were expressed on a wet weight basis. However, when differences in energy content of prey consumed by NPLT and PLT were accounted for, NPLT tended to consume slightly less food than PLT. Nevertheless, mean difference in food consumption rates was within the measurement error of these estimates, and it is thus unlikely that differences in food consumption rates contributed much to explain the substantial difference observed between the growth rates

**Fig. 6.** Proportion of the assimilated energy budget ( $DR - F$ ) allocated to activity between juvenile (solid bars) and adult (open bars) life stages of nonpiscivorous (NPLT) and piscivorous (PLT) lake trout (*Salvelinus namaycush*) (error bars represent 1 standard error).



**Fig. 7.** Relationship between activity and body size nonpiscivorous (NPLT, shaded squares) and piscivorous (PLT, open and solid circles) lake trout (*Salvelinus namaycush*). NPLT:  $R_a = 4.71 \cdot 10^{-2}(0.01)W + 17.10(3.49)$ ;  $R^2 = 0.65$ ;  $SE_{est} = 7.24$ ;  $n = 18$ ;  $p < 0.0001$ . PLT:  $R_a = 3.06 \cdot 10^{-3}(0.00)W + 28.58(1.69)$ ;  $R^2 = 0.33$ ;  $SE_{est} = 6.42$ ;  $n = 40$ ;  $p < 0.0001$ .



of PLT and NPLT. Our analysis showed that growth and growth efficiency were much lower in NPLT than PLT even when maturation status was taken into consideration, and that growth efficiency decreased much faster with body size in NPLT. Thus, our analyses suggest that lower growth and reduced growth efficiency of NPLT cannot be attributed to a lower rate of food consumption. Instead, these results imply that foraging on invertebrates incurs higher energetic costs in lake trout.

Energy losses could be higher in NPLT if they were feeding on prey that were less digestible, if they had higher metabolic rates, or if there was a combination of both factors. Stewart et al. (1983) suggested that the proportion of indigestible matter was higher in invertebrates than in prey fish (i.e., chitin vs. bone). Thus, lower growth efficiency of NPLT

observed in this study could possibly be explained by a lower assimilation efficiency of their prey. The magnitude of the difference in the assimilation efficiency assumed by Stewart et al. (1983) for NPLT and PLT (78 vs. 84%) appears to be sufficient to explain the average difference in growth efficiency observed between NPLT and PLT in this study (8.3 vs. 15.8%). However, it is important to note that assimilation efficiencies of lake trout feeding on invertebrates and on prey fish have yet to be determined. The values assumed by Stewart et al. (1983) in their bioenergetic model of lake trout were derived from experiments performed on walleye (*Stizostedion vitreum*) fed with prey fish and brown trout (*Salmo trutta*) that were fed invertebrates. Thus, these values are not necessarily valid for lake trout and could well reflect interspecific differences rather than different prey digestibility. Consequently, the hypothesis that lake trout have lower assimilation efficiency when they are consuming invertebrates remains to be tested. In addition, the interpretation that assimilation efficiency is lower in NPLT than PLT cannot explain the steeper reduction in growth efficiency of NPLT with body size observed in this study. Only the intercepts of the relationship between growth efficiency and body size are expected to differ if differences in growth efficiency were solely attributed to differences in assimilation efficiency for invertebrates and prey fish. In this study, both the slope and intercept of the relationship between growth efficiency and body size differed, indicating that there are other bioenergetic losses besides prey digestibility that may be responsible for the lower growth and growth efficiency achieved by NPLT.

When comparing individuals of the same size, foraging costs were also expected to be higher in NPLT than in PLT. First, NPLT consumed more food than PLT on a wet weight basis. Since activity costs are positively correlated with food consumption rates in actively foraging fish (Boisclair 1992), foraging costs should also be higher in NPLT than in PLT, as NPLT consumed more food on a gram per wet weight basis. Second, foraging can be divided into five components: (i) searching for prey, (ii) pursuing prey, (iii) capturing prey, (iv) handling prey, and (v) swallowing the prey. Given that lake trout tend to be much larger than their prey, the costs associated with components ii–v should be fairly small compared with searching for food. Fish like lake trout, which capture each prey item individually, must thus spend more time and more energy searching for food when they are foraging on smaller prey to obtain a given ration (Kerr 1971a, 1971b; Konkle and Sprules 1986). For instance, according to Fig. 3a, NPLT weighing 100 g (~20 cm) must consume ~225 dipteran pupae in a day (~10 mg-pupae<sup>-1</sup>) to meet its energy requirement, while a PLT of that size would need to consume only one prey fish (~1 g). Thus, NPLT must perform more work to obtain their daily ration. Finally, theoretical models of fish growth also suggest that foraging costs are higher in fish feeding on smaller prey (Kerr 1971a, 1971b). These models predict that foraging costs increase with predator-prey size ratio in gape-limited predators. As a consequence, growth efficiency is expected to (i) be negatively correlated with predator-prey size ratio, and (ii) decrease faster with body size in predators feeding on smaller prey, since predator-prey size ratio increases faster with predator size when they are feeding on smaller prey. These

predictions are consistent with the results obtained in this study, as growth efficiency decreased faster with body size in NPLT than in PLT. This is also consistent with the simulations performed by Kerr (1971a, 1971b), which showed that growth efficiency decreased faster with body size in lake trout consuming smaller prey, even if smaller prey were more abundant. Thus, the results obtained in this study suggest that foraging on invertebrates is highly costly to lake trout, as invertebrates tend to be less digestible than prey fish, and more energy must be allocated to foraging by NPLT to achieve a given growth rate.

### Genetic controls of growth

It may be argued that growth differed between NPLT and PLT simply because of genetic differences. However, this interpretation is not consistent with the results of a transplant experiment that was performed on NPLT in the 1960s in Algonquin Provincial Park (Martin 1966). In 1961 and 1962, 303 lake trout consuming primarily invertebrates were captured from Lake Louisa (Ontario), marked, and transplanted into a lake containing pelagic prey fish (Lake Opeongo, Ont.). The stomach contents of 21 out of the 57 lake trout that were recaptured were examined. Fish was the dominant prey item in the stomachs of these fish. Growth rates of these fish increased tremendously after they were transplanted into their new environment (Martin 1966). Svärdsön (1970) similarly showed that the growth of dwarf whitefish (*Coregonus* sp.) increased after they were transplanted to whitefish-free lakes. Thus, growth rates of a given species appear to be primarily a function of the environment in which they live rather than being fixed by their genetics (Werner and Gilliam 1984; Heath and Roff 1987, but see Billerbeck et al. 2000).

### Energetics of stunting in fish

Stunting represents an extreme condition in the growth of fish, and has frequently been observed in several fish families, including Salmonidae, Percidae, and Centrarchidae (Roff 1992). Stunted fish are characterized by much lower growth than normal fish, reach maturity earlier and at a smaller size, and also tend to have a shorter lifespan (Roff 1992). Stunted fish usually occur in lakes containing high densities of fish (Persson 1986; Amundsen 1989). It is commonly believed that the lower growth of stunted fish is the result of a lower rate of food consumption due to the high density of competitors. Field studies have shown that fish growth and food consumption rates increased following a large reduction in fish biomass (Persson 1986; Amundsen 1989), suggesting that stunting may be due to strong exploitative competition. However, this may represent a response to a large perturbation of the system, and may not necessarily reflect the conditions experienced by fish when the system is in equilibrium (Boisclair and Leggett 1989b). Furthermore, the lack of a reference site in these studies does not rule out the possibility that the concomitant increase of growth and feeding rates resulted from changes in local environmental conditions, such as increased prey biomass, rather than from a reduction in fish density. The importance of using a reference site to assess the effects of fish removal on fish energetics can be illustrated by the work of Hayes et al. (1992). While food consumption rates of yellow perch from Douglas Lake (Michigan) increased following the massive removal of

white sucker (*Catostomus commersoni*), it also increased in yellow perch from a nearby reference lake during the same period (Hayes et al. 1992). Thus, it is unclear if stunting occurs because food consumption rates decrease with fish density in these populations.

Stunting in fish may also occur when suitable prey are lacking or low in density (Martin 1966; Konkle and Sprules 1986). In many instances, the organisms that make up the prey base for piscivorous fish like lake trout do not always form a continuous prey-size spectrum and display gaps (i.e., significant reduction in biomass). If a gap in the prey size spectrum is large enough, the predator might be unable to achieve high growth rates and to reach a body size large enough to enable it to switch to the next size class of prey. This is usually referred to as a trophic bottleneck (Heath and Roff 1996). Other instances when bottlenecks occur are when a predator reaches its maximum size and no other available prey in that system would otherwise increase predator growth (Sherwood et al. 2002a, 2002b). This trophic bottleneck implies that there is an upper limit in body size that is obtainable for a predator feeding on a particular prey or diet in that system (Sherwood et al. 2002a, 2002b). Heath and Roff (1996), using simulation analyses, showed that trophic bottlenecks occurred as a result of low per capita consumption. In contrast to these simulations, our empirical analyses indicate that NPLT reached a trophic bottleneck owing to their high energetic costs associated with feeding on small (relative to their size) and potentially less digestible prey.

### Species invasion and fish energetics

The introduction of nonindigenous species is most often accompanied by a shift in prey communities and food web structure (Ricciardi et al. 1997; Vander Zanden et al. 1999). Thus, based on the results obtained in this study, we would expect that the efficiency at which the energy is transferred to top predators would change if the introduction of exotic species alters prey size and composition. This may explain the abrupt and drastic reduction in maximum size and in age and size at maturity of lake trout following the introduction of rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) in numerous lakes across North America (J.M. Casselman, Ontario Ministry of Natural Resources, Picton, Ont., personal communication). In lakes lacking pelagic prey fish, lake trout can consume minnows and other small fish in the littoral zone after the fall transition and during winter, as this thermal refuge does not represent a barrier for a cold-water pelagic fish like lake trout during that time of the year. The introduction of rock bass and smallmouth bass have reduced densities of littoral prey fish in these lakes to a point where lake trout now feed almost entirely on zooplankton and benthic invertebrates (Casselman and Grant 1998; Vander Zanden et al. 1999). Thus, the lower growth rate of lake trout in these lakes may be the results of a lower growth efficiency associated with feeding on smaller and less digestible prey.

The majority of species introductions that have occurred in lake trout lakes have been unintentional, mainly from bait bucket dumping, while others have clearly been deliberate attempts to enhance the growth of lake trout. Nevertheless, the consequences of altering food web structure and the intensity of the species interactions are still poorly under-

stood and warrant strict regulations and guidelines to prohibit transfer of fish from one water body to another. Therefore, fisheries management would benefit greatly from taking a multispecies point of view and should not consist only of general management policies for individual species. It should also involve looking at food web structures in individual lakes and their effects on the transfer of energy to upper trophic levels, and hence using a much broader ecosystem approach. The tracer method used in this study to estimate food consumption rates of fish may be a useful tool for understanding the impacts of exotic species on food web structure and dynamics.

### Acknowledgements

We thank Adriano Pazzia, Pierre Pannunzio, Robert Traversarie, Serge Belanger, and Sonia Di Sotto for their help in the field and laboratory. We are grateful to Adrian deBruyn, Graham Sherwood, Jake Vander Zanden, Strahan Tucker, and Mary Thiess for their helpful suggestions on earlier versions of the manuscript. Further thanks to the staff at the Harkness Laboratory of Fisheries Research, especially Gary Ridout, Doug Brown, Trevor Middel, Scot Milne, and Peggy Darraugh. A special thanks to Gary Ridout who aged all the lake trout. We thank the many fishermen who generously donated fish samples at the Creel Census Station on Lake Opeongo in Algonquin Park. Logistic support was provided through Algonquin Provincial Park and at the Harkness Laboratory of Fisheries Research. Financial support was provided by the Ontario Ministry of Natural Resources and by an operating grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to J.B. Rasmussen.

### References

- Amundsen, P.A. 1989. Effects of intensive fishing on food consumption and growth of stunted Arctic Char (*Salvelinus alpinus* L.), in Takvatn, northern Norway. *Physiology and Ecology Japan Special*, **1**: 265–278.
- Billerbeck, J.M., Schultz, E.T., and Conover, D.O. 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia*, **122**: 210–219.
- Boisclair, D. 1992. Relationship between feeding and activity rates for actively foraging juvenile brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **49**: 2566–2573.
- Boisclair, D., and Leggett, W.C. 1989a. Among population variability of fish growth: II. Influence of prey type. *Can. J. Fish. Aquat. Sci.* **46**: 468–482.
- Boisclair, D., and Leggett, W.C. 1989b. Among population variability of fish growth: III. Influence of fish community. *Can. J. Fish. Aquat. Sci.* **46**: 1539–1550.
- Borgmann, U., and Whittle, D.M. 1992. Bioenergetics and PCB, DDE, and mercury dynamics in Lake Ontario lake trout (*Salvelinus namaycush*): a model based on surveillance data. *Can. J. Fish. Aquat. Sci.* **49**: 1086–1096.
- Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures—techniques and tools. In *Proceedings of the International Workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks*, 15–18 Feb. 1983, Miami, Fla. *Edited by* E.D. Prince and L.M. Pulos. NOAA Tech. Rep. NMFS 8. pp. 1–17.

- Casselman, J.M., and Grant, R.E. 1998. Number, biomass, and distribution of fish species in the littoral zone of the Upper St. Lawrence River—quantitative electrofishing, Johnstown Bay, June to October 1995: an assessment by type habitat. Can. Manusc. Rep. Fish. Aquat. Sci. No. 2455.
- Casselman, J.M., and Gunn, J.M. 1992. Dynamics in year-class strength, growth, and calcified-structure size of native lake trout (*Salvelinus namaycush*) exposed to moderate acidification and whole-lake neutralization. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 102–113.
- Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Int. Assoc. Theor. Appl. Limnol. Proc. No. 18.
- Dadswell, M.J. 1974. Distribution, ecology, and postglacial dispersal in certain crustacean and fishes in Eastern North America. Natl. Mus. Nat. Sci. (Ott.) Publ. Zool. No. 11.
- Diana, J.S. 1983. Growth, maturation, and production of northern pike in three Michigan lakes. Trans. Am. Fish. Soc. **112**: 38–46.
- Elliott, S.E.M., Burns-Flett, C., Hesslein, R.H., Brunskill, G.J., and Lutz, A. 1981. Cesium-137, radium-226, potassium-40 and selected stable elements in fish populations from Great Slave Lake (NWT), Louisa Lake (Saskatchewan), Lake Winnipeg (Manitoba), and Experimental Lakes Area (Northwestern Ontario). Can. Data Rep. Fish. Aquat. Sci. No. 293.
- Forseth, T., Jonsson, B., Næumann, R., and Ugedal, O. 1992. Radioisotope method for estimating food consumption by brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **49**: 1328–1335.
- Hayes, D.B., Taylor, W.W., and Schneider, J.C. 1992. Response of yellow perch (*Perca flavescens*) and the benthic invertebrate community to a reduction in the abundance of white suckers (*Catostomus commersoni*). Trans. Am. Fish. Soc. **121**: 36–53.
- Heath, D., and Roff, D.A. 1987. Test of genetic differentiation in growth of stunted and nonstunted populations of yellow perch and pumpkinseed. Trans. Am. Fish. Soc. **116**: 98–102.
- Heath, D.D., and Roff, D.A. 1996. The role of trophic bottlenecks in stunting: a field test of an allocation model of growth and reproduction in yellow perch, *Perca flavescens*. Environ. Biol. Fishes, **45**: 53–63.
- Kerr S.R. 1971a. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. **28**: 809–814.
- Kerr S.R. 1971b. A simulation model of lake trout growth. J. Fish. Res. Board Can. **28**: 815–819.
- Konkle, B.R., and Sprules, W.G. 1986. Planktivory by stunted lake trout in an Ontario lake. Trans. Am. Fish. Soc. **115**: 515–521.
- Madenjian, C.P., Whittle, D.M., Elrod, J.H., O’Gorman, R.O., and Randall, W. 1995. Use of a simulation model to reconstruct PCB concentrations in prey of Lake Ontario lake trout. Environ. Sci. Technol. **29**: 2610–2615.
- Manly, B.F.J. 1998. Randomization, bootstrap, and Monte Carlo methods in biology. 2nd ed. Chapman and Hall, London.
- Martin, N.V. 1966. The significance of food habitats in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. Trans. Am. Fish. Soc. **96**: 415–422.
- Mason, D.M., Timothy, B.J., and Kitchell, J.F. 1998. Consequences of prey fish community dynamics on lake trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. Can. J. Fish. Aquat. Sci. **55**: 1273–1284.
- Mittelbach, G.G., and Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. **55**: 1454–1465.
- Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). Ecology, **67**: 355–364.
- Post, J.R. 1990. Metabolic allometry of larval juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic model. Can. J. Fish. Aquat. Sci. **47**: 554–560.
- Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1997. The role of zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can. J. Fish. Aquat. Sci. **54**: 2596–2608.
- Roff, D.A. 1992. The evolution of life histories: theory and analyses. Chapman and Hall, New York.
- Rottiers, D.V., and Tucker, R.M. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish Wildl. Serv. Tech. Pap. No. 108. pp. 1–8.
- Rowan, D.J., and Rasmussen, J.B. 1995. The elimination of radiocesium from fish. J. Appl. Ecol. **32**: 739–744.
- Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (<sup>137</sup>Cs). Can. J. Fish. Aquat. Sci. **53**: 734–745.
- Sherwood, G.D., Rasmussen, J.B., Rowan, D.J., Brodeur, J., and Hontela, A. 2000. Bioenergetic costs of heavy metal exposure in yellow perch (*Perca flavescens*): in situ estimates with a radiotracer (<sup>137</sup>Cs) technique. Can. J. Fish. Aquat. Sci. **57**: 441–450.
- Sherwood, G.D., Kovacs, J., Hontela, A., and Rasmussen, J.B. 2002a. Simplified food webs lead to energetic bottlenecks in polluted lakes. Can. J. Fish. Aquat. Sci. **59**: 1–5.
- Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., Rasmussen, J.B. 2002b. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild fish. Can. J. Fish. Aquat. Sci. **59**: 229–241.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. W.H. Freeman and Co., San Francisco.
- Stewart, D.J., Weininger, D., Rottiers, D.V., and Edsall, T.A. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. **40**: 681–698.
- Svärdson, G. 1970. Significance of introgression in coregonid evolution. In Biology of coregonid fishes. Edited by C.C. Lindsey and C.S. Woods. University of Manitoba Press, Winnipeg. pp. 35–39.
- Trudel, M., and Boisclair, D. 1996. Estimation of fish activity costs using underwater video cameras. J. Fish Biol. **48**: 40–53.
- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J.B. 2000. Estimating food consumption rates of fish using a mercury mass balance model. Can. J. Fish. Aquat. Sci. **57**: 414–428.
- Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature (London), **401**: 464–467.
- Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.
- Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. **60**: 331–367.

## Appendix A

**Table A1.** Sample size ( $n$ ), age, body size at time  $t$  ( $W_t$ ) and  $t + \Delta t$  ( $W_{t+\Delta t}$ ),  $^{137}\text{Cs}$  concentration in muscle tissue at time  $t$  ( $[^{137}\text{Cs}_t]$ ) and  $t + \Delta t$  ( $[^{137}\text{Cs}_{t+\Delta t}]$ ),  $^{137}\text{Cs}$  concentration in the prey ( $[^{137}\text{Cs}_p]$ ), pooled  $^{137}\text{Cs}$  assimilation efficiency ( $\alpha$ ), and energy density of diet for lake trout (*Salvelinus namaycush*).

$n$	Age (years)	$W_t$ (g)	$W_{t+\Delta t}$ (g)	$[^{137}\text{Cs}_t]$ (Bq·kg <sup>-1</sup> )	$[^{137}\text{Cs}_{t+\Delta t}]$ (Bq·kg <sup>-1</sup> )	$[^{137}\text{Cs}_p]$ (Bq·kg <sup>-1</sup> )	$\alpha$	Energy density of diet (J·g <sup>-1</sup> )
<b>Lake Opeongo</b>								
5	3i	108	257	4.49	5.69	4.38	0.60	9 012
15	4i	257	474	5.69	6.54	4.74	0.69	10 464
40	5i	474	748	6.54	7.17	4.74	0.69	10 464
32	6i	748	1060	7.17	7.65	4.74	0.69	10 464
29	7i	1060	1394	7.65	8.03	4.74	0.69	10 464
21	8i	1394	1733	8.03	8.33	4.74	0.69	10 464
20	9m	1733	2065	8.33	8.57	4.74	0.69	10 464
11	10m	2065	2382	8.57	8.77	4.74	0.69	10 464
8	11m	2382	2677	8.77	8.93	4.74	0.69	10 464
3	12m	2677	2947	8.93	9.07	4.74	0.69	10 464
3	13m	2947	3190	9.07	9.18	4.74	0.69	10 464
<b>Great Slave Lake<sup>a,b</sup></b>								
1	3i	227	363	4.53	4.60	3.14	0.69	10 464
1	4i	363	544*	4.60	4.69*	3.14	0.69	10 464
0	5i	544*	771	4.69*	4.81	3.14	0.69	10 464
3	6i	771	1043	4.81	4.94	3.14	0.69	10 464
6	7i	1043	1406	4.94	5.12	3.14	0.69	10 464
4	8i	1406	1905	5.12	5.37	3.14	0.69	10 464
2	9i	1905	2404	5.37	5.62	3.14	0.69	10 464
3	10m	2404	3039	5.62	5.94	3.14	0.69	10 464
7	11m	3039	3810	5.94	6.33	3.14	0.69	10 464
4	12m	3810	4672	6.33	6.76	3.14	0.69	10 464
3	13m	4672	5534	6.76	7.19	3.14	0.69	10 464
2	14m	5534	6350	7.19	7.60	3.14	0.69	10 464
<b>Lake Memphremagog<sup>c</sup></b>								
18	2i	112	430*	1.37	1.44*	0.7	0.69	6 655
0	3i	430*	928	1.44*	1.50	0.7	0.69	6 655
20	4i	928	1530	1.50	1.69	0.7	0.69	6 655
4	5m	1530	2165	1.69	1.69	0.7	0.69	6 655
13	6m	2165	2779	1.69	1.69	0.7	0.69	6 655
11	7m	2779	3342	1.69	1.69	0.7	0.69	6 655
7	8m	3342	3839	1.69	1.69	0.7	0.69	6 655
7	9m	3839	4266	1.69	1.69	0.7	0.69	6 655
8	10m	4266	4625	1.69	1.69	0.7	0.69	6 655
4	11m	4625	4923	1.69	1.69	0.7	0.69	6 655
<b>Happy Isle Lake</b>								
9	3i	72	141	4.22	4.22	2.61	0.23	3 204
19	4i	141	223	4.22	4.22	2.61	0.23	3 204
6	5i	223	309	4.22	4.22	2.61	0.23	3 204
7	6m	309	395	4.22	4.64	2.71	0.26	3 170
8	7m	395	476	4.64	5.94	2.84	0.28	3 128
12	8m	476	549	5.94	7.09	2.84	0.28	3 128
9	9m	549	613	7.09	8.12	2.84	0.28	3 128
5	10m	613	669	8.12	9.05	2.84	0.28	3 128
3	11m	669	717	9.05	9.90	2.84	0.28	3 128
3	12m	717	757	9.90	10.68	2.84	0.28	3 128
<b>Source Lake</b>								
6	3i	57	113	4.95	4.95	2.43	0.23	3 204
15	4i	113	180	4.95	5.01	2.43	0.23	3 204
35	5i	180	249	5.01	5.15	2.43	0.23	3 204
13	6m	249	315	5.15	5.51	2.53	0.24	3 189
11	7m	315	374	5.51	6.09	2.53	0.24	3 189
8	8m	374	426	6.09	6.88	2.53	0.24	3 189
1	9m	426	470	6.88	7.88	2.53	0.24	3 189
2	10m	470	507	7.88	9.09	2.53	0.24	3 189

**Note:** i, immature; m, mature.

<sup>a</sup>Data from Rowan and Rasmussen (1996).

<sup>b</sup>Data from Elliott et al. (1981).

<sup>c</sup>Data from Trudel et al. (2000).

\*Data calculated from linear and nonlinear regressions.

**Table A2.** Age, body size at time  $t$  ( $W_t$ ), and  $t + \Delta t$  ( $W_{t+\Delta t}$ ), Hg concentration lake trout (*Salvelinus namaycush*) at time  $t$  ( $[Hg_t]$ ) and  $t + \Delta t$  ( $[Hg_{t+\Delta t}]$ ), Hg concentration in the prey ( $[Hg_p]$ ), Hg assimilation efficiency ( $\alpha$ ), and energy density of diet consumed by lake trout in Lake Ontario.

Age (years)	$W_t$ (g)	$W_{t+\Delta t}$ (g)	$[Hg_t]$ ( $\mu\text{g}\cdot\text{g}^{-1}$ )	$[Hg_{t+\Delta t}]$ ( $\mu\text{g}\cdot\text{g}^{-1}$ )	$[Hg_p]$ ( $\mu\text{g}\cdot\text{g}^{-1}$ )	$\alpha$	Energy density of diet ( $\text{J}\cdot\text{g}^{-1}$ )
1i	68	322	0.03	0.06	0.021	0.80	6228
2i	322	939	0.06	0.10	0.025	0.80	6320
3i	939	1690	0.10	0.12	0.029	0.80	6467
4i	1690	2414	0.12	0.15	0.032	0.80	6647
5i	2414	3090	0.15	0.18	0.035	0.80	6772
6m	3090	3723	0.18	0.20	0.038	0.80	6772
7m	3723	4320	0.20	0.21	0.041	0.80	6772

Note: i, immature; m, mature. Data from Borgmann and Whittle (1992), Madenjian et al. (1995), and Trudel et al. (2000).

**Table A3.** Age, specific consumption rate ( $C$ ), growth rate ( $G$ ), daily ration (DR), production ( $P$ ), activity rate ( $R_a$ ), activity multiplier, standard metabolic rate ( $R_s$ ), and growth efficiency (GE) in lake trout (*Salvelinus namaycush*) (standard errors obtained from Monte Carlo simulations are in parentheses).

Age (years)	$C$ ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ )	$G$ ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ )	DR ( $\text{kJ}\cdot\text{day}^{-1}$ )	$P$ ( $\text{kJ}\cdot\text{day}^{-1}$ )	$R_a$ ( $\text{kJ}\cdot\text{day}^{-1}$ )	Activity multiplier	$R_s$ ( $\text{kJ}\cdot\text{day}^{-1}$ )	GE (%)
<b>Lake Opeongo</b>								
3i	0.0089 (0.0010)	0.0024 (0.00010)	13.3 (1.9)	2.6 (0.3)	2.4 (0.9)	1.73 (0.3)	3.3 (0.2)	19.1 (2.3)
4i	0.0070 (0.0008)	0.0017 (0.00013)	25.2 (3.8)	4.1 (0.6)	5.4 (1.8)	1.86 (0.3)	6.3 (0.5)	16.1 (2.0)
5i	0.0061 (0.0008)	0.0013 (0.00012)	37.9 (5.7)	5.7 (0.8)	9.0 (2.9)	2.00 (0.3)	9.1 (0.7)	15.0 (2.1)
6i	0.0056 (0.0008)	0.0009 (0.00012)	52.1 (9.5)	7.1 (1.4)	13.8 (4.6)	2.15 (0.4)	11.9 (0.9)	13.5 (2.0)
7i	0.0054 (0.0007)	0.0008 (0.00011)	67.9 (11.2)	8.7 (1.8)	19.2 (5.7)	2.30 (0.4)	14.8 (0.9)	12.7 (2.2)
8i	0.0050 (0.0007)	0.0006 (0.00013)	80.9 (13.3)	9.5 (2.4)	23.8 (6.5)	2.37 (0.4)	17.4 (1.2)	11.7 (2.6)
9m	0.0057 (0.0008)	0.0008 (0.00012)	113.0 (19.1)	15.9 (3.1)	34.9 (9.3)	2.74 (0.4)	20.0 (1.3)	14.1 (2.0)
10m	0.0056 (0.0009)	0.0007 (0.00013)	130.2 (24.0)	16.8 (3.6)	42.5 (12.6)	2.90 (0.5)	22.4 (1.3)	12.9 (2.6)
11m	0.0054 (0.0007)	0.0006 (0.00012)	143.7 (22.2)	17.7 (3.8)	47.9 (11.5)	3.0 (0.4)	24.5 (1.5)	12.3 (2.5)
12m	0.0053 (0.0008)	0.0005 (0.00014)	154.6 (28.8)	17.7 (5.2)	52.8 (14.5)	3.0 (0.5)	26.3 (1.9)	11.5 (2.7)
13m	0.0052 (0.0007)	0.0005 (0.00012)	165.7 (26.9)	18.2 (4.8)	57.7 (14.3)	3.1 (0.5)	28.0 (1.9)	11.0 (3.0)
<b>Great Slave Lake<sup>a,b</sup></b>								
3i	0.0056 (0.0008)	0.0013 (0.00012)	16.8 (2.7)	2.5 (0.4)	3.1 (1.4)	1.6 (0.3)	4.9 (0.4)	14.9 (2.1)
4i	0.0052 (0.0008)	0.0011 (0.00013)	24.0 (4.2)	3.6 (0.6)	4.9 (2.2)	1.8 (0.3)	6.3 (0.5)	14.9 (2.5)
5i	0.0049 (0.0008)	0.0010 (0.00012)	33.2 (6.2)	4.8 (0.9)	7.5 (3.1)	1.9 (0.3)	8.5 (0.3)	14.4 (2.3)
6i	0.0045 (0.0007)	0.0008 (0.00011)	42.4 (7.9)	6.3 (1.2)	9.6 (4.1)	1.9 (0.4)	10.6 (0.7)	14.9 (2.7)
7i	0.0046 (0.0007)	0.0008 (0.00012)	58.4 (11.1)	9.4 (1.9)	14.1 (5.8)	2.1 (0.4)	13.1 (0.9)	16.1 (3.2)
8i	0.0049 (0.0008)	0.0008 (0.00010)	82.8 (14.4)	14.1 (2.2)	21.6 (7.9)	2.3 (0.5)	16.2 (1.0)	17.1 (3.1)
9i	0.0045 (0.0008)	0.0006 (0.00011)	100.1 (19.5)	14.4 (3.1)	28.9 (10.3)	2.5 (0.5)	19.4 (1.3)	14.4 (3.0)
10m	0.0058 (0.0009)	0.0009 (0.00012)	165.3 (31.8)	28.9 (4.7)	51.7 (16.9)	3.3 (0.7)	23.0 (1.5)	17.5 (3.0)
11m	0.0061 (0.0009)	0.0009 (0.00013)	218.3 (40.6)	36.1 (6.9)	73.7 (20.6)	3.7 (0.7)	27.0 (2.04)	16.5 (2.8)
12m	0.0063 (0.0010)	0.0008 (0.00012)	278.1 (46.2)	45.3 (7.8)	97.5 (25.1)	4.1 (0.8)	31.4 (2.0)	16.3 (2.7)
13m	0.0063 (0.0009)	0.0008 (0.00014)	335.5 (57.7)	51.4 (11.1)	123.0 (30.1)	4.4 (0.8)	35.8 (2.3)	15.3 (2.9)
14m	0.0063 (0.0010)	0.0007 (0.00013)	388.9 (75.4)	55.9 (13.3)	148.1 (39.6)	4.7 (0.9)	39.8 (3.0)	14.4 (3.0)
<b>Lake Memphremagog<sup>c</sup></b>								
2i	0.0164 (0.0021)	0.0037 (0.00009)	24.0 (3.5)	5.8 (0.5)	5.0 (1.9)	2.2 (0.4)	4.2 (0.2)	24.0 (3.0)
3i	0.0115 (0.0018)	0.0021 (0.00010)	48.1 (8.2)	10.7 (1.2)	9.7 (4.5)	2.0 (0.4)	9.8 (0.5)	22.2 (3.3)
4i	0.0102 (0.0013)	0.0014 (0.00010)	80.2 (13.1)	15.6 (2.1)	19.9 (6.8)	2.4 (0.4)	14.8 (0.8)	19.4 (2.5)
5m	0.0093 (0.0015)	0.0012 (0.00009)	112.1 (18.3)	24.6 (2.6)	26.1 (10.5)	2.3 (0.5)	19.6 (1.0)	21.9 (3.0)
6m	0.0082 (0.0012)	0.0010 (0.00010)	133.5 (21.1)	27.4 (3.9)	32.2 (11.1)	2.3 (0.5)	24.0 (1.3)	20.5 (2.9)
7m	0.0075 (0.0010)	0.0008 (0.00010)	151.3 (25.9)	29.3 (5.2)	37.6 (12.8)	2.4 (0.4)	27.9 (1.7)	19.4 (3.0)
8m	0.0070 (0.0012)	0.0007 (0.00010)	166.7 (34.6)	29.5 (4.9)	43.9 (19.3)	2.4 (0.6)	31.1 (1.8)	17.7 (3.6)
9m	0.0066 (0.0011)	0.0006 (0.00010)	177.8 (32.9)	29.9 (6.0)	47.7 (17.6)	2.4 (0.5)	33.9 (2.0)	16.8 (3.2)
10m	0.0063 (0.0009)	0.0005 (0.00010)	186.4 (34.1)	29.8 (6.5)	50.9 (17.5)	2.4 (0.4)	36.1 (2.1)	16.0 (3.0)
11m	0.0061 (0.0009)	0.0005 (0.00009)	192.3 (31.6)	29.1 (6.5)	53.6 (16.1)	2.4 (0.4)	37.9 (1.9)	15.1 (2.7)
<b>Lake Ontario<sup>c</sup></b>								
1i	0.0230 (–)	0.0043 (–)	21.2 (–)	4.4 (–)	5.5 (–)	2.7 (–)	3.3 (–)	20.8 (–)
2i	0.0240 (–)	0.0029 (–)	80.1 (–)	13.0 (–)	28.9 (–)	4.6 (–)	8.0 (–)	16.2 (–)

**Table A3** (concluded).

Age (years)	<i>C</i> (g·g <sup>-1</sup> ·day <sup>-1</sup> )	<i>G</i> (g·g <sup>-1</sup> ·day <sup>-1</sup> )	<i>DR</i> (kJ·day <sup>-1</sup> )	<i>P</i> (kJ·day <sup>-1</sup> )	<i>R<sub>a</sub></i> (kJ·day <sup>-1</sup> )	Activity multiplier	<i>R<sub>s</sub></i> (kJ·day <sup>-1</sup> )	GE (%)
3i	0.0160 (-)	0.0016 (-)	122.5 (-)	20.0 (-)	42.0 (-)	3.9 (-)	14.4 (-)	16.3 (-)
4i	0.0140 (-)	0.0010 (-)	179.8 (-)	21.3 (-)	71.0 (-)	4.6 (-)	20.0 (-)	11.9 (-)
5m	0.0160 (-)	0.0007 (-)	258.7 (-)	30.2 (-)	107.6 (-)	5.5 (-)	23.7 (-)	11.7 (-)
6m	0.0140 (-)	0.0005 (-)	284.7 (-)	32.9 (-)	117.1 (-)	5.2 (-)	27.8 (-)	11.6 (-)
7m	0.0120 (-)	0.0004 (-)	291.2 (-)	35.6 (-)	114.8 (-)	4.7 (-)	31.5 (-)	12.2 (-)
<b>Happy Isle Lake</b>								
3i	0.0228 (0.0039)	0.0018 (0.00009)	7.4 (1.4)	1.1 (0.1)	0.9 (0.7)	1.4 (0.3)	2.3 (0.1)	15.4 (3.1)
4i	0.0180 (0.0033)	0.0013 (0.00009)	10.2 (2.0)	1.4 (0.2)	1.2 (1.0)	1.4 (0.3)	3.3 (0.2)	13.8 (2.8)
5i	0.0172 (0.0032)	0.0009 (0.00010)	14.3 (3.0)	1.6 (0.2)	1.7 (1.5)	1.3 (0.3)	5.1 (0.5)	10.8 (2.2)
6m	0.0183 (0.0026)	0.0009 (0.00010)	20.3 (3.3)	2.3 (0.4)	3.4 (1.7)	1.5 (0.3)	6.2 (0.4)	11.3 (1.8)
7m	0.0210 (0.0037)	0.0008 (0.00008)	28.5 (4.8)	2.6 (0.3)	6.9 (2.8)	2.0 (0.4)	7.3 (0.4)	9.1 (1.9)
8m	0.0223 (0.0036)	0.0007 (0.00010)	35.7 (6.5)	2.7 (0.4)	10.2 (3.5)	2.3 (0.4)	8.2 (0.4)	7.5 (1.5)
9m	0.0240 (0.0046)	0.0006 (0.00009)	43.6 (9.0)	2.7 (0.5)	14.0 (4.8)	2.6 (0.5)	8.9 (0.6)	6.3 (1.3)
10m	0.0256 (0.0045)	0.0005 (0.00009)	51.3 (9.7)	2.9 (0.5)	17.7 (5.3)	2.9 (0.5)	9.6 (0.5)	5.6 (1.2)
11m	0.0269 (0.0050)	0.0005 (0.00011)	58.2 (11.6)	2.9 (0.6)	21.2 (6.3)	3.1 (0.6)	10.1 (0.6)	5.0 (1.0)
12m	0.0278 (0.0051)	0.0004 (0.00010)	64.0 (13.2)	2.9 (0.7)	24.2 (7.1)	3.3 (0.6)	10.6 (0.7)	4.5 (1.1)
<b>Source Lake</b>								
3i	0.0293 (0.0049)	0.0019 (0.00013)	7.5 (1.5)	0.9 (0.1)	1.5 (0.8)	1.8 (0.4)	1.9 (0.1)	12.2 (1.8)
4i	0.0237 (0.0039)	0.0013 (0.00013)	10.8 (2.1)	1.1 (0.2)	2.3 (1.0)	1.8 (0.3)	2.9 (0.2)	10.4 (1.8)
5i	0.0207 (0.0039)	0.0009 (0.00013)	13.9 (3.0)	1.2 (0.2)	3.1 (1.5)	1.8 (0.4)	3.8 (0.5)	8.8 (1.8)
6m	0.0243 (0.0045)	0.0009 (0.00012)	21.6 (4.5)	1.8 (0.3)	5.5 (2.3)	2.0 (0.4)	5.4 (0.4)	8.3 (1.7)
7m	0.0254 (0.0050)	0.0008 (0.00011)	27.8 (6.0)	1.9 (0.4)	8.1 (3.1)	2.3 (0.5)	6.2 (0.5)	6.8 (1.3)
8m	0.0273 (0.0046)	0.0006 (0.00013)	34.8 (6.3)	1.9 (0.4)	11.6 (3.4)	2.7 (0.5)	6.9 (0.5)	5.5 (1.2)
9m	0.0303 (0.0053)	0.0006 (0.00014)	43.3 (9.5)	1.9 (0.5)	15.9 (5.0)	3.1 (0.6)	7.5 (0.6)	4.4 (1.1)
10m	0.0350 (0.0059)	0.0005 (0.00013)	54.6 (10.5)	2.0 (0.5)	21.9 (5.7)	3.7 (0.6)	8.0 (0.6)	3.6 (1.0)

**Note:** (-), standard error for weight and [Hg] not available to run a Monte Carlo simulation; i, immature; m, mature.

<sup>a</sup>Data from Rowan and Rasmussen (1996).

<sup>b</sup>Data from Elliott et al. (1981).

<sup>c</sup>Data from Trudel et al. (2000).