Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in the field

S. Tucker and J.B. Rasmussen

Abstract: Through the ^{137}Cs mass balance method, annual consumption rates were estimated for juvenile Atlantic salmon (*Salmo salar*) parr and precocious males as well as for brook trout (*Salvelinus fontinalis*) at four sites in the Ste-Marguerite River system, Québec. With explicit age analysis, consumption rates and growth rates were derived on an individual fish and age-class basis. These represent the first consumption estimates for Atlantic salmon in the wild. Precocious males had consumption rates 1.5 times greater than nonmaturing parr, while Atlantic salmon parr consumption rates were 2.7 times greater than brook trout. There was a strong positive relationship between individual annual consumption and growth rates for Atlantic salmon and brook trout at all sites. Subsequently the concept of field maintenance ration was introduced as the intercept of consumption over growth. Maintenance rations for Atlantic salmon parr ranged from 0.010 to 0.016 g·g^{-1}·day^{-1} between sites. Brook trout had maintenance rations approximately half those of Atlantic salmon at 0.0059 g·g^{-1}·day^{-1}. Precocious male growth efficiencies were half those of nonmaturing parr despite higher feeding and growth rates. Brook trout growth efficiencies were significantly greater than those of Atlantic salmon parr. The lower growth efficiencies observed for Atlantic salmon are likely due to increased metabolic costs associated with higher activity. On average, Atlantic salmon parr spent 2.4-fold more energy in activity than brook trout. Atlantic salmon precocious males spent 1.7 times more energy in activity than parr.

Résumé : Au moyen de la méthode du bilan massique du ^{137}C, on a estimé les taux de consommation annuelle de mâles précoces et de tacons juvéniles de saumon atlantique (*Salmo salar*), ainsi que d'ombles de fontaine (*Salvelinus fontinalis*) à quatre sites dans le bassin de la rivière Ste-Marguerite, au Québec. Après analyse explicite des âges, on a établi les taux de consommation et de croissance par poisson et par classe d'âge. On a ainsi obtenu les premières estimations de la consommation chez le saumon atlantique dans son milieu naturel. Les taux de consommation des mâles précoces étaient 1,5 fois supérieurs à ceux des tacons immatures, tandis que ceux des tacons de saumon étaient 2,7 fois supérieurs à ceux des ombles de fontaine. On a observé une forte corrélation positive entre la consommation annuelle individuelle et les taux de croissance chez les saumons atlantiques et les ombles de fontaine à tous les sites. On a par la suite établi le concept de ration d'entretien dans le milieu naturel, fournie par la relation mathématique entre la consommation et la croissance. Les rations d'entretien pour les tacons de saumon variaient de 0,010 et 0,016 g·g^{-1}·jour^{-1} selon les sites. Les rations d'entretien des ombles de fontaine (0,0059 g·g^{-1}·jour^{-1}) correspondaient à environ la moitié de celles des saumons atlantiques. L'efficacité de la croissance des mâles précoces correspondait à environ la moitié de celle des tacons immatures, malgré le fait que les taux d'alimentation et de croissance des premiers étaient supérieurs. L'efficacité de la croissance des ombles de fontaine était significativement plus grande que celle des tacons de saumon. L'efficacité inférieure de la croissance des saumons atlantiques est probablement due aux coûts métaboliques élevés liés à la plus grande activité de ces derniers. En moyenne, les tacons de saumon dépensent 2,4 fois plus d'énergie par leur activité que les ombles de fontaine. Les saumons atlantiques mâles précoces dépensent 1,7 fois plus d'énergie par leur activité que les tacons.

[Traduit par la Rédaction]

Introduction

Feeding rates have never been measured for juvenile Atlantic salmon (*Salmo salar*) in the wild (Power 1993) and very few measurements exist for other lotic salmonids (Walsh et al. 1988; Angradi and Griffith 1990). Wild stocks are considered a valued resource, making it difficult, even unacceptable, to sacrifice them in sufficient numbers to estimate daily rations by conventional gut analysis (Power 1993). However, measuring inputs to fish energy budgets is

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essential for an evaluation of the efficiency of energy use leading to growth (Soofiani and Hawkins 1985). From a community perspective, estimating consumption rates allows for an assessment of the demands that fish make on their food resources and how these in turn might limit production (Soofiani and Hawkins 1985).

Throughout their range in North America, juvenile Atlantic salmon are often found with brook trout (*Salvelinus fontinalis*). These two salmonids differ with respect to feeding strategies. Atlantic salmon feed on invertebrate drift in relatively fast-flowing water by maintaining a stationary position within a defended territory (Gibson et al. 1993); this occurs in areas where there is likely to be a steady supply or concentration of food (Everest and Chapman 1972). Brook trout are also drift feeders, but occupy stream margins or relatively slower water habitat, particularly in the presence of Atlantic salmon, and thay are generally thought of as being less aggressive and less territorial than Atlantic salmon (Gibson et al. 1993). Within an ecosystem, however, it is unclear whether closely related species of fish have similar or different energy requirements or strategies of energy allocation and whether this might be reflected by feeding behaviour (Odum and Pinkerton 1955).

A positive relationship between growth rate and maturation rate in Atlantic salmon and other salmonids is well established (Thorpe 1986). Therefore, the rate of maturation is hypothesized to be correlated with the rate of acquisition of surplus energy. In contrast with the typical parr–smolt life history of juvenile Atlantic salmon, male parr often mature at a small size in freshwater and are known as precocious males. In some respect, precocious maturation in nature appears to be related to an aspect of food supply or acquisition. In laboratory feeding experiments, maturation has been linked to the replenishment of fat stores through surplus food acquisition in spring, accomplished by an early onset of feeding (Rowe and Thorpe 1990; Rowe et al. 1991; Simpson 1992). The differences in fat content and storage suggest differences in energy partitioning among maturing and nonmaturing parr. It has been hypothesized that differences in metabolic rates and other physiological parameters or even consumption rates could account for observed differences in fat storage (Rowe and Thorpe 1990; Hutchings and Myers 1994; Silverstein et al. 1997).

The objectives of this study were to estimate and compare consumption and growth rates between Atlantic salmon and brook trout and between maturing and nonmaturing Atlantic salmon parr. More specifically, we tested the hypothesis that Atlantic salmon and brook trout have different energy requirements and strategies as reflected by their different feeding behaviours. In addition, we tested the hypothesis that maturing male parr in the wild have increased rates of energy accumulation relative to nonmaturing Atlantic salmon parr.

To measure consumption rates of wild fish populations, we employ the ^{137}Cs mass balance technique (Forseth et al. 1992, 1994; Rowan and Rasmussen 1996). Because the ^{137}Cs burden is integrative, this method requires the sacrifice of relatively few fish and allows for easy and simultaneous sampling of many sites for comparative work. In this study, we present two refinements to the method. First, we have estimated consumption rates for individual fish. Second, we

have derived a simple method to estimate ^{137}Cs assimilation efficiency for fish populations in the field.

Methods

Fish collection

This study was conducted in the Ste-Marguerite River system in the Saguenay region of Québec (Fig. 1), which supports both anadromous Atlantic salmon and brook trout and resident populations of brook trout. In this river system, Atlantic salmon smolt between 3 and 4 years of age after which they spend 1–2 years at sea (Bielak and Power 1986). Like many other Atlantic salmon rivers (Thorpe 1986), the incidence of precocious males varies spatially and temporally (unpublished observation). Factors controlling anadromy in brook trout are poorly understood, and in this system, its extent is poorly quantified. However, residents remain to mature and spawn between 3 and 5 years old (unpublished observation).

Fish were collected from four sites in the Ste-Marguerite River system during the summers of 1996 and 1997 by electrofishing. These sites included three second-order tributaries, Allaire, Morin, and Xavier, as well as two sections in the main branch of the river (Fig. 1). Approximately 40 juvenile Atlantic salmon and 40 brook trout (if present) were collected at two locations within each stream site both at the beginning of June (1997) and at the end of August (1996, 1997). Fork length was measured to the nearest 1 mm and total mass was measured to the nearest 0.01 g.

Age analysis and growth rates

Atlantic salmon were aged using scales taken from below the dorsal fin near the lateral line (Anonymous 1984). Brook trout were aged using opercular and subopercular bones (Sharp and Bernard 1988). A subsample of brook trout otoliths ($n = 15$) were compared blindly to verify the accuracy (95%) of age determination by use of opercular bones (Sharp and Bernard 1988). Annuli were measured to the nearest 0.01 mm under a stereomicroscope. All age estimates and measurements were double blind, with less than 5% interobserver error. Length at the formation of the annulus was back-calculated by the Fraser–Lee method (Francis 1990). This method assumes that any deviation of an individual fish from the fish–scale regression will be maintained proportionally at back-calculated lengths. Weights were estimated by length–weight relationships specific for the populations.

Back-calculations of body size from age structures assume that the relationship between fish length and age structure radius is constant through time (Campana 1990). However, the proportionality between fish length and age structure radius is not always constant and can vary with growth rate (Campana 1990; Francis 1990). This results in errors in back-calculated lengths, particularly when considering older age-classes of fish. In order to evaluate any potential growth effect on the age structure to body size relationship for both Atlantic salmon and brook trout, multiple regression analysis was performed with categorical variables for season, site, age, and life history pattern (or sex).

Specific growth rates (G, grams per gram per day) were estimated for individual fish and age-classes following Ricker (1979):

$$(1) \qquad G = \ln(W_f/W_i)/t$$

where W_f is the final weight (grams) at time t (days) and W_i is the initial weight (grams).

Consumption rates

Annual consumption rates for juvenile Atlantic salmon (ages 0–2^+) and brook trout (ages 0–4^+) from the Ste-Marguerite River system were estimated with a ^{137}Cs radiotracer approach on an age-class and individual basis. Radiocesium is a globally dispersed isotope due to fallout from nuclear weapons testing and accidents and

Fig. 1. Sampling sites in the Ste-Marguerite River system, Québec. These include three second-order tributaries, Allaire, Morin, and Xavier, as well as the Principal Branch. Atlantic salmon and brook trout were caught by electrofishing at two locations within each site at the end of August (1996 and 1997) and the beginning of June 1997.
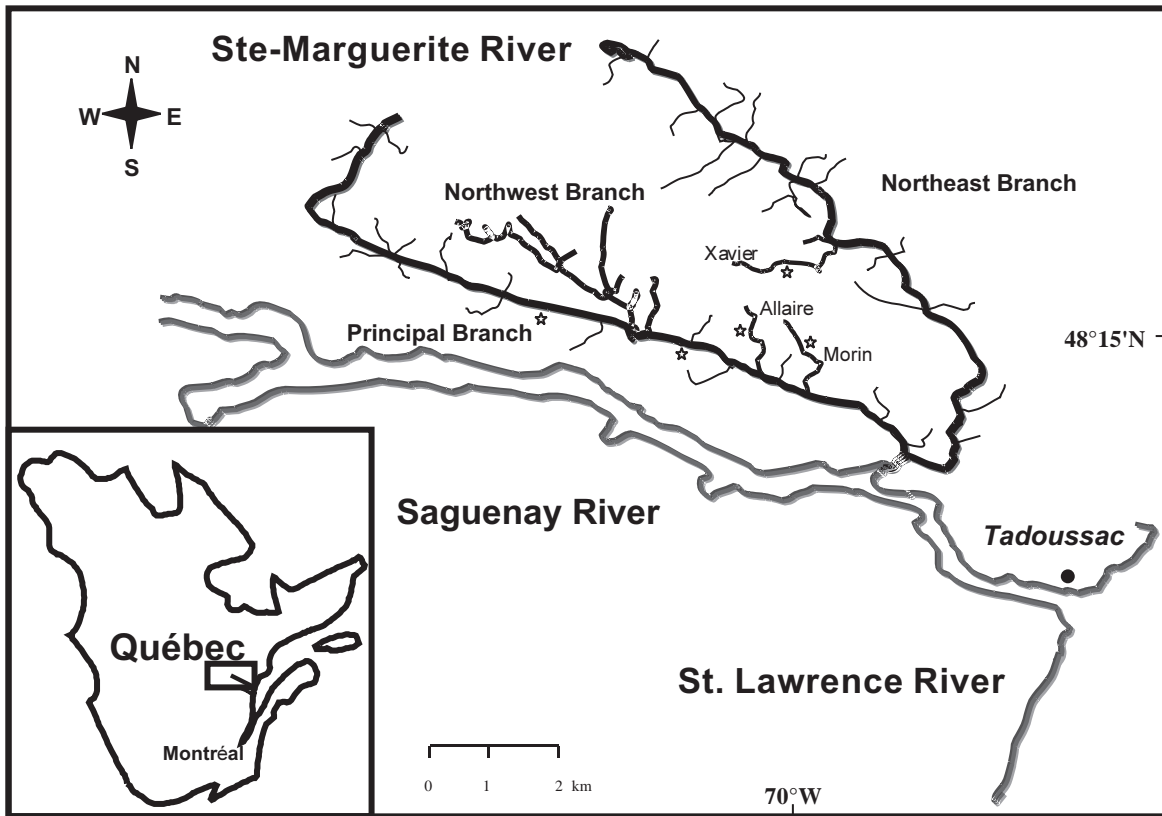
can easily be detected at low levels with modern gamma spectrometry (Rowan and Rasmussen 1996). The ^{137}Cs method requires the determination of ^{137}Cs in fish and their prey, ^{137}Cs elimination from fish, and ^{137}Cs assimilation efficiency from food. The elimination rate of ^{137}Cs from fish has been shown to be species independent and can be described by a simple function of body size and temperature (Rowan and Rasmussen 1995). The assimilation efficiency of ^{137}Cs has been determined for a few fish species and may vary with prey type (Forseth et al. 1992). Specific consumption rate (C, grams per gram per day) was estimated from a radiocesium mass balance model (Rowan and Rasmussen 1996):

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

where Q_t is the ^{137}Cs burden (becquerels) at time t (days), Q_0 is the initial ^{137}Cs burden (becquerels), Q_g is the gonadal ^{137}Cs burden (becquerels) released at spawning, G is the specific growth rate (grams per gram per day), E is the elimination rate of ^{137}Cs (becquerels per becquerel per day), D is the radioactive decay of ^{137}Cs (becquerels per becquerel per day), $[^{137}\text{Cs}_f]$ is the concentration of ^{137}Cs in the diet (becquerels per kilogram), α is the assimilation efficiency of ^{137}Cs from the diet (fraction), and w_0 is the initial body mass (kilograms).

Equation 2 can be solved from a single sampling by comparing adjacent age-classes or, similarly, with two sampling periods by comparing age-class means. Annual consumption rates for all age-classes of Atlantic salmon and brook trout were determined by comparing August 1996 fish with August 1997 fish. Alternatively, if there are strong and consistent ^{137}Cs body burden relationships with size or age within a system, consumption rates can be esti-

mated for individual fish by back-calculating size at annulus formation and assigning an initial ^{137}Cs burden from those site-specific regression models. In this manner, individual consumption rates were determined from observed body burdens of the June and August 1997 fish with modeled burdens from the previous fall. Consumption rates were measured on an individual basis for half of the fish in an age-class for each stream. All of the fish in an age-class were combined within a stream to measure consumption rates on an age-class mean basis.

Whole fish were dried and ashed at 450°C and whole-body ^{137}Cs was measured by gamma spectrometry with a coaxial or well germanium detector (Canberra Industries Inc.). ^{137}Cs was measured individually for half of the fish per site; the remaining fish were pooled within a site according to species, size, and developmental stage and then measured.

Fish diets and ^{137}Cs assimilation efficiency

Prey ^{137}Cs concentrations of fish were determined on undigested gut contents. While prey or prey size may vary with body size in Atlantic salmon (Keeley and Grant 1997), independent sampling of invertebrates from this system has shown that ^{137}Cs concentrations do not vary significantly among functional groups or by size within groups of invertebrates (unpublished data). Subsequently, gut contents were pooled by species and site for each sampling period to increase the precision of ^{137}Cs determination. Pooling is assumed to integrate diet variability over time and among individuals.

Typically, ^{137}Cs assimilation efficiencies for fish are calculated by weighting proportions of food items in gut contents with laboratory-derived assimilation efficiencies for food items (Forseth et al. 1992, 1994; Rowan and Rasmussen 1996). The assimilation effi-

Table 1. Fish diet (% occurrence of aquatic (A) and terrestrial (T) invertebrates), ash to dry ratio of the foregut, and assimilation efficiency (α) of ^{137}Cs from the diet for Atlantic salmon and brook trout from sites in the Ste-Margureite River system.

Site	Species	Diet	Ash:dry	α (%)
Allaire	Atlantic salmon	88% A, 12% T	0.39	39
	Brook trout	79% A, 21% T	0.28	42
Morin	Atlantic salmon	85% A, 15% T	0.49	23
Xavier	Atlantic salmon	91% A, 9% T	0.20	43
Main	Atlantic salmon	50% A, 10%T, 40% zooplankton	0.09	73

Note: Aquatic invertebrates in fish diets include in order of prevalence Ephemeroptera > Tricoptera > Plecoptera > Diptera > Coleoptera; terrestrial invertebrates include Diptera > Homoptera > Lepidoptera.

ciency of ^{137}Cs from food may vary among prey type and in relation to the clay content of the prey (Eyman and Kitchings 1975; Rowan and Rasmussen 1994). This was thought to be of particular relevance in the Ste-Marguerite given the observation of clay in gut contents denoted by different ash to dry ratios of similar diets of fish from different sites (Table 1). Thus the direct application of laboratory-derived assimilation efficiencies was thought to be questionable, since these would overestimate ^{137}Cs uptake and subsequently underestimate consumption rates.

^{137}Cs assimilation efficiency (α, percent) was determined by tracking the concentration of an unassimilated marker through the digestive tract, namely acid-insoluble ash. This unassimilated marker provides a baseline estimate of the changes in concentration of materials from foregut to hindgut with which assimilated material can be compared. The amount of ^{137}Cs taken up by fish is determined by baseline correction (Jobling 1994):

$$(3) \qquad \alpha = 100\left(1 - \frac{[A_{\text{fg}}][^{137}CS_{\text{hg}}]}{[A_{\text{hg}}][^{137}CS_{\text{fg}}]}\right)$$

where $[A_{\text{fg}}]$ and $[A_{\text{hg}}]$ are the concentrations of acid-insoluble ash in the foregut and hindgut (grams per gram wet weight), respectively, and $[^{137}Cs_{\text{hg}}]$ and $[^{137}Cs_{\text{fg}}]$ are the ^{137}Cs concentrations of in the hindgut and foregut (becquerels per kilogram), respectively.

Foregut and hindgut samples were pooled by species and site over sampling dates due to the small size of individual stomach contents. It is assumed that pooled samples integrate the assimilation efficiency of a complex natural diet and variation in diets. Samples were washed in 1 M HCl for 10 min at room temperature, filtered, and reweighed to determine the concentration of unassimilated ash in foreguts and hindguts, respectively.

Metabolic costs and activity multipliers

By inserting growth and Cs-based consumption estimates into a standard bioenergetics equation (Hewett and Johnson 1992), we can solve for total metabolic costs or activity by using laboratory-derived metabolic and excretion parameters (Hewett and Johnson 1992):

$$(4) \qquad C = G + A\cdot\text{SMR} + \text{SDA} + F + U$$

where G is specific growth rate, C is the specific consumption rate, SMR is the standard metabolic rate, SDA is specific dynamic action (about 15% of C), F is egestion (15% of C), and U is excretion (10% of C). Activity, A, is defined as an integer multiplier of SMR. Activity includes such extraneous costs as swimming, foraging, and other behavioural activities. Total metabolic costs are defined as the difference between consumption, growth, SDA, egestion, and excretion. Job's (1955) SMR model was used for brook trout and Higgins' (1985) model was used for Atlantic salmon. Activity multipliers for precocious males were recalculated with a higher SMR based on the maximum observed deviation from Metcalfe et al. (1995). All parameters were converted to

energy units with a conversion factor of 3429 J·g wet weight^{-1} for fish tissue (Cummins and Wuycheck 1971; Hartman and Brandt 1995) and 3176 J·g wet weight^{-1} for food items of aquatic invertebrates (Cummins and Wuycheck 1971).

## Maintenance rations and statistical analysis

Estimating consumption and growth rates by considering age-class means provides only one estimate per site for each age-class. However, estimating growth and consumption rates for individual fish provides us with a range of data for a particular species, age-class, or life history strategy at one site. Specific growth rates of individual fish were plotted against specific consumption rates. Here, we define the concept of field maintenance ration as the intercept from the regression of growth rate on consumption rate. This is thought to be analogous to a steady-state scenario, where the fish is not growing but balancing food intake with catabolism and other internal maintenance costs (i.e., consumption rate required to maintain body size). This concept is fundamental to evaluating throughputs and efficiencies of energy budgets and identifying different energy strategies. Differences in intercepts between Atlantic salmon parr and brook trout among sites were tested by ANCOVA (Sokal and Rohlf 1981) after verifying that slopes were not significantly different. One-way ANOVA (Sokal and Rohlf 1981) was used to check for significant differences in mean growth rates, consumption rates, growth efficiencies (GE, where GE = $(G/C) \times 100$), total metabolic costs, and activity multipliers among Atlantic salmon parr, precocious males, or brook trout between sites. Significant differences in these parameters in single pair comparisons between Atlantic salmon parr and precocious males or Atlantic salmon parr and brook trout within sites were determined by Student's t test (Sokal and Rohlf 1981). Effects of site and age on the growth–consumption relationship derived for age-class means were analyzed by multiple regression analysis with categorical variables for site and age. Standard errors for growth and consumption rates derived by age-class means were determined from Monte Carlo simulations (Efron and Tibshirani 1986).

Results

^{137}Cs assimilation efficiencies and diets

Brook trout had a greater component of terrestrial invertebrates in their diet than Atlantic salmon (21 versus 9–15%); however, ^{137}Cs assimilation efficiencies in Allaire were similar for both Atlantic salmon and brook trout (40%) (Table 1). Despite almost identical diets in Atlantic salmon from Morin, the ^{137}Cs assimilation efficiency was half that for Atlantic salmon in Allaire and Xavier. This was thought to be due to greater levels of sedimentary clay minerals in the guts of invertebrate prey, denoted by a higher ash to dry ratio of foregut contents. Atlantic salmon from the main

Fig. 2. Weight – ^{137}Cs body burden relationships for individual and pooled samples of (*a*) brook trout from the Ste-Marguerite River system (entire model for all brook trout: adjusted $r^2 = 0.92$, $p < 0.0001$, $n = 82$) and Atlantic salmon from the (*b*) Allaire (adjusted $r^2 = 0.92$, $p < 0.0001$, $n = 65$), (*c*) Main River (adjusted $r^2 = 0.92$, $p = 0.0001$, $n = 48$), (*d*) Xavier (adjusted $r^2 = 0.92$, $p < 0.0001$, $n = 26$), and (*e*) Morin (adjusted $r^2 = 0.84$, $p < 0.0001$, $n = 48$) sites of the Ste-Marguerite River. Lines represent least squares regression and 95% confidence intervals.
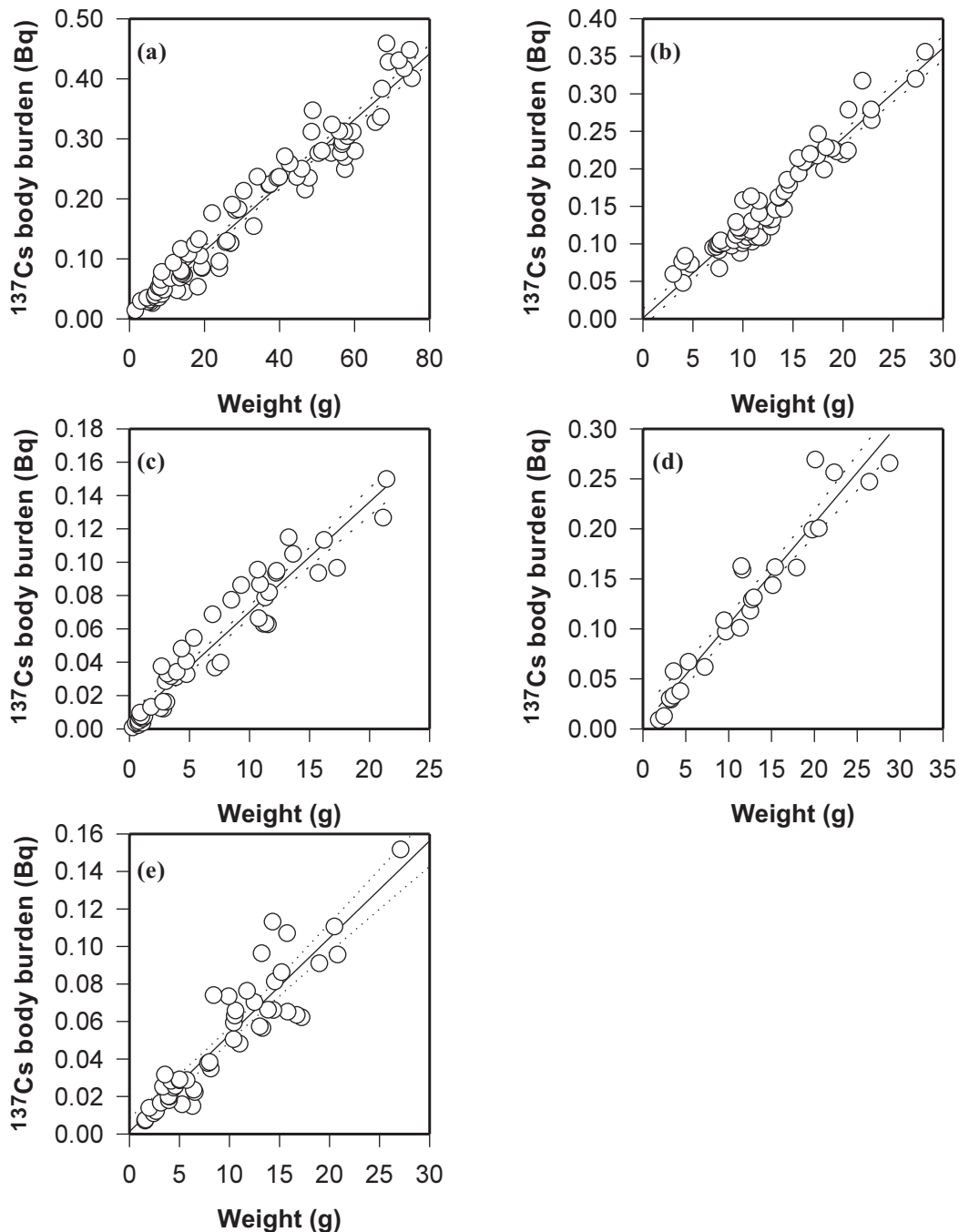
river had the highest ^{137}Cs assimilation efficiency (73%). This is most probably due to a large component of zooplankton in their diet (40%), as the laboratory-derived ^{137}Cs assimilation efficiency for zooplankton is 81.6%.

Fish ^{137}Cs body burden relationships

There was a strong positive relationship between ^{137}Cs body burden and weight for Atlantic salmon and brook trout at all sites (Fig. 2). Site-specific regressions were subse-

quently used to assign ^{137}Cs body burdens to individual fish for back-calculated weights.

**Age analysis**

Stepwise multiple regression analysis revealed no significant effects of life history pattern ($F_{2,239} = 0.851$, $p = 0.428$), age ($F_{2,239} = 1.437$, $p = 0.240$), site ($F_{3,239} = 1.457$, $p = 0.227$), or season ($F_{2,239} = 0.323$, $p = 0.570$) on the scale radius – body length relationship for Atlantic salmon (entire

Table 2. Mean (±SE) growth rates (G) and consumption rates (C) for age-classes of Atlantic salmon parr, precocious males (pm), and brook trout from different sites estimated from age-class comparisons and individual fish calculations.

Species	Site	Age	G, individual mean (g·g^{-1}·day^{-1} × 10^{-2})	G, age-class mean (g·g^{-1}·day^{-1} × 10^{-2})	C, individual mean (g·g^{-1}·day^{-1} × 10^{-2})	C, age-class mean (g·g^{-1}·day^{-1} × 10^{-2})
Atlantic salmon	Allaire	1+	0.46±0.05	0.45±0.12	3.4±0.4	3.4±0.6
		2+	0.30±0.03	0.27±0.12	3.0±0.3	2.4±0.6
		1$^+$ pm	nd	0.48±0.12	nd	3.7±0.5
		2$^+$ pm	0.33±0.04	0.36±0.12	4.8±0.3	4.0±0.7
	Morin	2+	0.34±0.04	0.28±0.13	2.4±0.1	2.7±0.7
		1$^+$ pm	0.47±0.02	0.43±0.10	3.4±0.1	3.2±0.6
		2$^+$ pm	0.46±0.03	0.36±0.14	3.8±0.1	3.4±0.8
	Xavier	1+	0.33±0.02	0.24±0.12	3.6±0.1	2.5±0.5
		2+	0.25±0.01	0.28±0.11	3.0±0.1	2.4±0.6
		1$^+$ pm	0.41±0.04	0.40±0.13	3.5±0.3	3.2±0.7
		2$^+$ pm	0.27±0.03	0.39±0.13	3.1±0.1	3.2±0.6
	Main River	1+	0.20±0.01	0.20±0.12	1.5±0.1	2.4±0.6
		2+	0.15±0.02	0.33±0.12	1.6±0.1	2.6±0.5
		2$^+$ pm	0.21±0.06	0.25±0.13	2.4±0.3	2.2±0.6
Brook trout	Allaire	1+	0.38±0.04	0.17±0.13	1.7±0.1	1.0±0.3
		2+	0.24±0.03	0.25±0.16	1.4±0.1	1.3±0.4
		3+	0.19±0.03	0.20±0.14	1.2±0.1	1.2±0.3
		4+	0.17±0.03	0.16±0.13	1.1±0.2	1.1±0.3
	Xavier	1+	nd	0.15±0.14	nd	1.1±0.3
		2+	nd	0.30±0.13	nd	1.3±0.3

Note: Errors for age-class means were derived from a Monte Carlo simulation. nd, not determined due to small sample size.

Fig. 3. Mean size at age (±SE) for Atlantic salmon parr (solid bars) and brook trout (open bars) from Allaire sampled in August 1997.
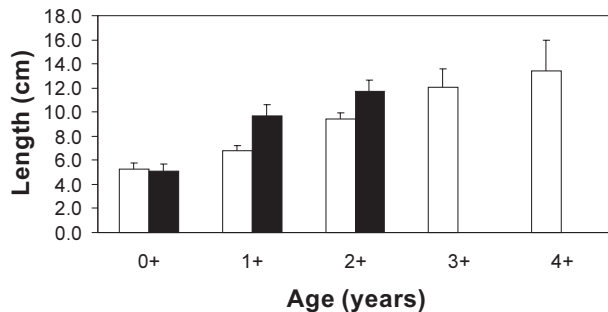
model: adjusted $r^2 = 0.89$, $p < 0.0001$, $n = 239$). In addition, all interaction terms were nonsignificant. Similarly, the opercular radius – body length relationship (entire model: adjusted $r^2 = 0.90$, $p < 0.0001$, $n = 97$) did not vary for brook trout from different sites ($F_{3,97} = 0.390$, $p = 0.761$), sex ($F_{2,97} = 1.242$, $p = 0.294$), age ($F_{2,97} = 0.532$, $p = 0.751$), or season ($F_{2,97} = 0.237$, $p = 0.628$). Moreover the statistical intercepts of 3.01 cm for Atlantic salmon closely matched the "biological intercept" (Campana 1990) of size at emergence observed for these populations (personal observation). Correcting the brook trout intercept of –0.506 cm with a bio-

logical intercept of size at emergence, as suggested by Campana (1990), did not result in significant changes in back-calculated sizes ($F_{1,27} = 0.009$, $p = 0.926$). The assumption of the Fraser–Lee method is that the scale – fish length relationship is constant and does not vary in a systemic fashion with growth rate (Campana 1990). Since there was no apparent growth effect on the relationship between body size and age structure for either Atlantic salmon or brook trout, it was felt that the application of the Fraser–Lee method for back-calculating sizes was valid.
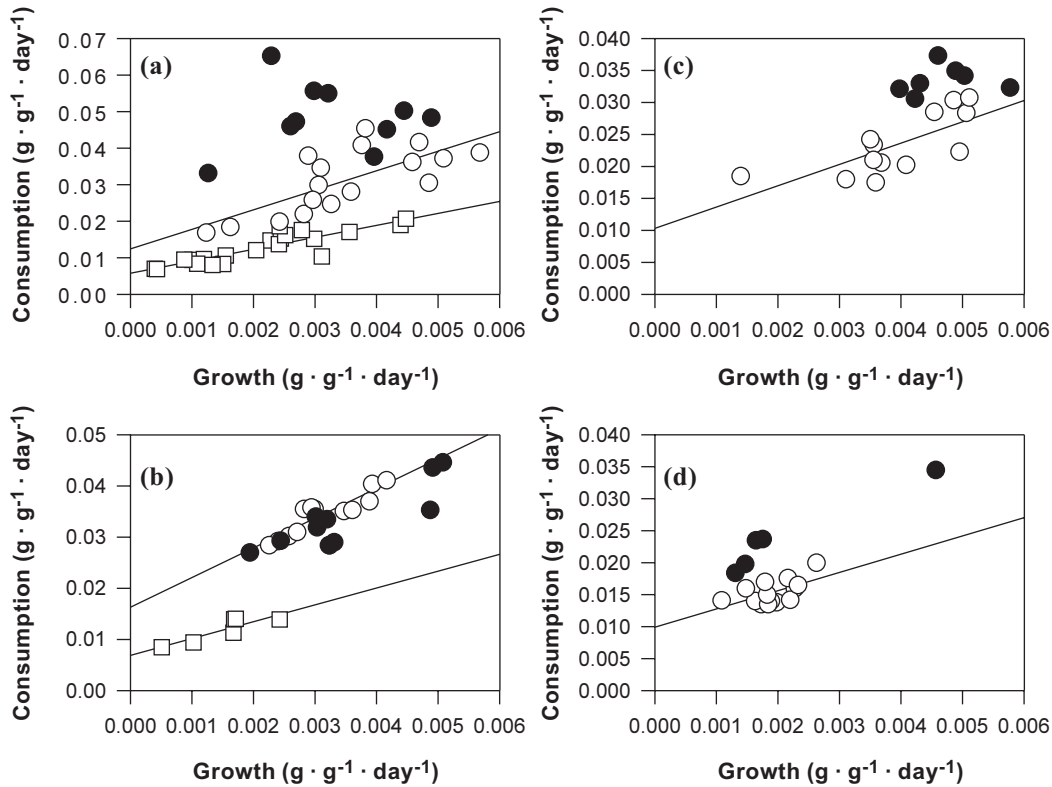
Growth rates

Growth rates for Atlantic salmon ranged between 0.0015 and 0.0046 g·g·day^{-1} (Table 2) and varied significantly among sites ($F_{3,83} = 20.29$, $p < 0.0001$), with the lowest rates for all age-classes observed in the Main River and the highest in Morin. As well, 1$^+$ and 2$^+$ precocious males had greater growth rates than respective nonmaturing parr. Atlantic salmon parr were able to maintain higher growth rates than brook trout for all age-classes ($t = 5.752$, $p < 0.0001$), which resulted in a greater size at age (Fig. 3). There is good corroboration between individual growth estimates and those derived by comparing age-class means (Table 2). However, standard errors are smaller in the individual estimates, providing a more precise estimate of growth.
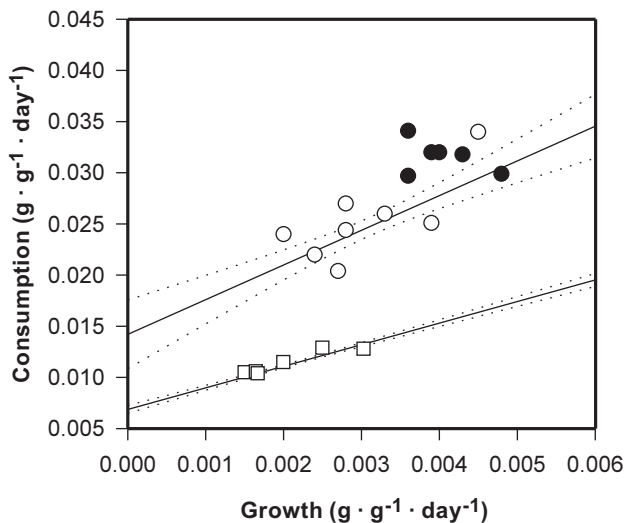
Annual consumption rates

Consumption rates for Atlantic salmon ranged between 0.015 and 0.048 g·g^{-1}·day^{-1} and varied significantly among

Fig. 4. Growth and consumption rates for individual Atlantic salmon parr (open circles), precocious males (solid circles), and brook trout (open squares) from sites in the Ste-Marguerite River system. (*a*) Allaire: Atlantic salmon parr, $C = 5.34G + 0.0125$ ($r^2 = 0.53$, $p = 0.001$); brook trout, $C = 3.25G + 0.0059$ ($r^2 = 0.77$, $p = 0.001$). (*b*) Xavier: Atlantic salmon parr, $C = 5.74G + 0.0164$ ($r^2 = 0.77$, $p < 0.0001$); brook trout, $C = 2.84G + 0.0059$ ($r^2 = 0.76$, $p = 0.024$). (*c*) Morin: Atlantic salmon parr, $C = 3.33G + 0.0103$ ($r^2 = 0.53$, $p = 0.001$). (*d*) Main River: Atlantic salmon parr, $C = 2.85G + 0.010$ ($r^2 = 0.34$, $p = 0.029$). Lines are least squares regressions.

Fig. 5. Annual growth and consumption rates for Atlantic salmon parr (open circles), precocious males (solid circles), and brook trout (open squares) derived from age-class means for sites in the Ste-Marguerite River system. Lines represent least squares regression and 95% confidence intervals. Errors were determined by Monte Carlo simulation. Atlantic salmon parr, $C = 3.39G + 0.014$ ($r^2 = 0.33$, $p < 0.001$); brook trout, $C = 2.11G + 0.0069$ ($r^2 = 0.91$, $p < 0.001$).

sites ($F_{3,52} = 43.33$, $p < 0.0001$) (Table 2). Consumption rates were highest in Allaire and Xavier and lowest in the Main River. Furthermore, precocious males had significantly greater consumption rates (1.5 times) than nonmaturing parr except in Xavier where feeding rates were similar. As well, in Allaire ($t = 8.385$, $p < 0.0001$) and Xavier ($t = 12.35$, $p < 0.0001$), Atlantic salmon parr had consumption rates about 2.7 times greater than brook trout. Feeding rates for brook trout ranged between 0.011 and 0.017 g·g^{-1}·day^{-1}.

With the exception of the Main River, there was good correspondence between consumption rates derived both by age-class means and on an individual basis. The deviation in the Main River was due to an overestimation of growth rates by comparing age-classes, which could be due to size-selective mortality or simply a chance effect associated with small sample size.

Maintenance rations

There was a significant positive relationship between individual annual specific consumption and growth rates for Atlantic salmon and brook trout at all sites (Fig. 4). Atlantic salmon had maintenance rations between 0.010 and 0.016 g·g·day^{-1} across sites. There were significant differences between intercepts among streams ($F_{3,56} = 22.21$, $p < 0.0001$). Xavier had a greater intercept (0.016 g·g·day^{-1}) than the rest of the streams, and Allaire's (0.0125 g·g·day^{-1}) was marginally greater than the Main River's (0.010 g·g·day^{-1}). However, all slopes were similar ($F_{3,56} = 0.897$, $p = 0.348$).

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Table 3. Mean (±SE) growth efficiencies, total metabolic costs, and activity multipliers for Atlantic salmon and brook trout.

Species		Site	Growth efficiency (%)	Total metabolic costs (J·day^{-1} ×10^{-2})	Activity multiplier	Modified activity multiplier
Atlantic salmon	Parr	Allaire	11.2±0.6	2.8±0.2	3.2±0.2	
	pm		6.9±0.8**	4.5±0.3**	5.5±0.1**	3.9±0.3*
	Parr	Morin	16.8±	1.0±0.1	1.9±0.1	
	pm		13.4±0.5**	1.6±0.1**	3.2±0.1**	2.3±0.1*
	Parr	Xavier	9.1±0.3	1.8±0.1	3.2±0.1	
	pm		10.4±0.6*	1.6±0.1	3.3±0.1	2.4±0.2**
	Parr	Main River	12.5±0.6	0.7±0.03	1.6±0.1	
	pm		8.4±0.12**	1.2±0.1**	2.9±0.1**	2.1±0.2**
Brook trout	imm	Allaire	14.2±1.4**	0.5±0.04**	1.3±0.1**	
	mat		14.4±2.1	0.6±0.07	1.7±0.3	
	imm	Xavier	12.3±2**	0.6±0.04**	1.3±0.1**	

Note: Activity multipliers were modified for precocious males (pm) by assuming a higher SMR. Growth efficiencies, total metabolic costs, and activity costs were compared in single pair comparisons between Atlantic salmon parr and precocious males and between Atlantic salmon parr and brook trout within a site by *t* test: *0.05 < *p* < 0.01; **p* < 0.01. There were no significant differences between immature (imm) and mature (mat) brook trout within a stream.

Brook trout had a maintenance ration about half that of Atlantic salmon at 0.0059 g·g·day^{-1} in both Allaire and Xavier. All Atlantic salmon and brook trout were within the same size range such that differences in specific growth and consumption rates among Atlantic salmon parr, precocious males, and brook trout remain significant on an absolute basis ($F_{1,115} = 22.38$, $p < 0.0001$; regression with categorical variable for species and life history).

Age-class means (Fig. 5) showed no significant effect of site ($F_{2,85} = 0.553$, $p = 0.459$) or age-class ($F_{2,85} = 0.652$, $p = 0.422$) on the relationship between consumption and growth. The intercept of consumption is 0.014 g·g·day^{-1} for Atlantic salmon and 0.0069 g·g·day^{-1} for brook trout, which is similar to the general trend for each stream when rations are calculated on an individual basis.

Growth efficiencies

Growth efficiencies for Atlantic salmon parr ranged between 9.1 and 16.8% and varied significantly among sites ($F_{3,56} = 27.32$, $p < 0.0001$). The highest efficiencies were observed in Morin (16.8%) and the Main River (16.6%) (Table 3). The lowest growth efficiencies were observed in Xavier (9.1%) and Allaire (11.2%). In addition, with the exception of Xavier, precocious males had significantly lower growth efficiencies than nonmaturing parr within a stream despite higher feeding and growth rates (Table 3). Brook trout growth efficiencies ranged between 12.3 and 14.4%, with significant differences between streams ($t = 2.872$, $p = 0.004$). Brook trout had significantly greater growth efficiencies than Atlantic salmon within a particular stream (Table 3), i.e., Atlantic salmon had to feed more to sustain a given growth rate.

Metabolic costs and activity multipliers

Total metabolic costs for Atlantic salmon parr ranged between $0.7 × 10^{-2}$ and $2.8 × 10^{-2}$ J·day^{-1}, with significant differences among all sites ($F_{3,56} = 74.19$, $p < 0.0001$); the highest costs were in Allaire and the lowest in the Main River (Table 3). In addition, Atlantic salmon had five times greater total metabolic costs than brook trout. Accounting for the SMR, these translate into activity multipliers 2.4-fold greater for Atlantic salmon parr (2.4) than for brook trout

(1.0) in Allaire and in Xavier ($t = 8.911$, $p < 0.0001$). Activity costs for Atlantic salmon varied significantly among sites ($F_{3,56} = 22.48$, $p < 0.0001$) with similar high multipliers observed in Allaire (2.4) and Xavier (2.4) and similar low multipliers in Morin (1.4) and the Main River (1.2).

Precocious males had activity costs 1.7 times greater than Atlantic salmon parr (Table 3). The exception to this was Xavier, where parr and precocious males had similar high feeding rates, growth rates, and growth efficiencies. Activity multipliers for precocious males were recalculated with a higher SMR based on the maximum observed deviation from Metcalfe et al. (1995). Activity multipliers subsequently decreased by 30% but remained significantly greater such that higher metabolic rates could not account for the greater activity costs observed in precocious males.

Overwinter consumption rates

Overwinter rations, integrating springtime feeding, were estimated from the June sampling period (Fig. 6). Given the small sample size, data were pooled by site after factoring out maintenance rations for respective streams. The sex ratio was 3:1, skewed towards males at all sites (as opposed to a 1:1 ratio in midsummer), with 58% of those male parr feeding above the maintenance ration derived for each stream. Feeding rates were not related to condition factors ($p = 0.24$ for female parr, $p = 0.79$ for male parr). The proportion of male parr feeding above maintenance in June is seemingly related to the average incidence of precocious males observed for the system at the end of August (57% of male parr). Furthermore, the proportion of high-feeding male parr in June is related to the incidence of precocious males in August within each stream (Fig. 7).
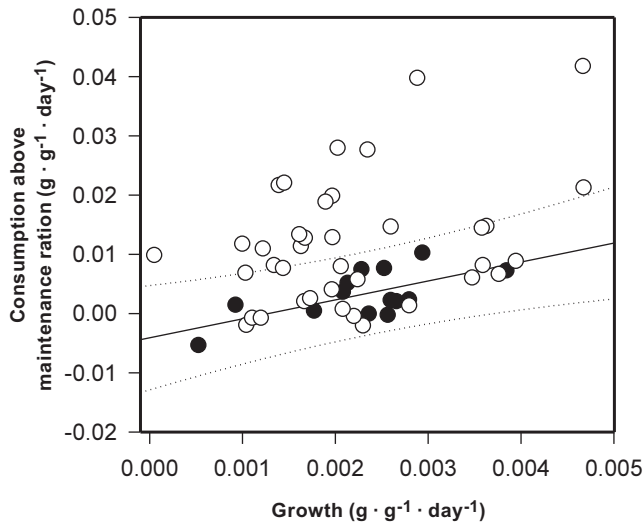
Discussion

Atlantic salmon and brook trout energy budgets

Through the ^{137}Cs mass balance method, we have estimated consumption rates of juvenile Atlantic salmon and brook trout in the field. These are the first estimates for juvenile Atlantic salmon. Moreover, we have examined growth efficiencies in a comparative manner among streams

Fig. 6. Overwinter growth and consumption rates above maintenance ration for Atlantic salmon female parr (solid circles) and male parr (open circles) from the Ste-Marguerite River system. Given the small sample size, data were pooled by site after factoring out maintenance rations for respective streams. The sex ratio was 3:1, skewed towards males at all sites (as opposed to a 1:1 ratio in midsummer), with 58% of those male parr feeding above the maintenance ration derived for each stream. The least squares regression line and confidence intervals are for female parr.

Fig. 7. Incidence of male parr feeding above the maintenance ration (MR) in June and the incidence of precocious males (percentage of male parr) observed in samples from August 1997 from sites in the Ste-Marguerite River system. The 1:1 line is shown.
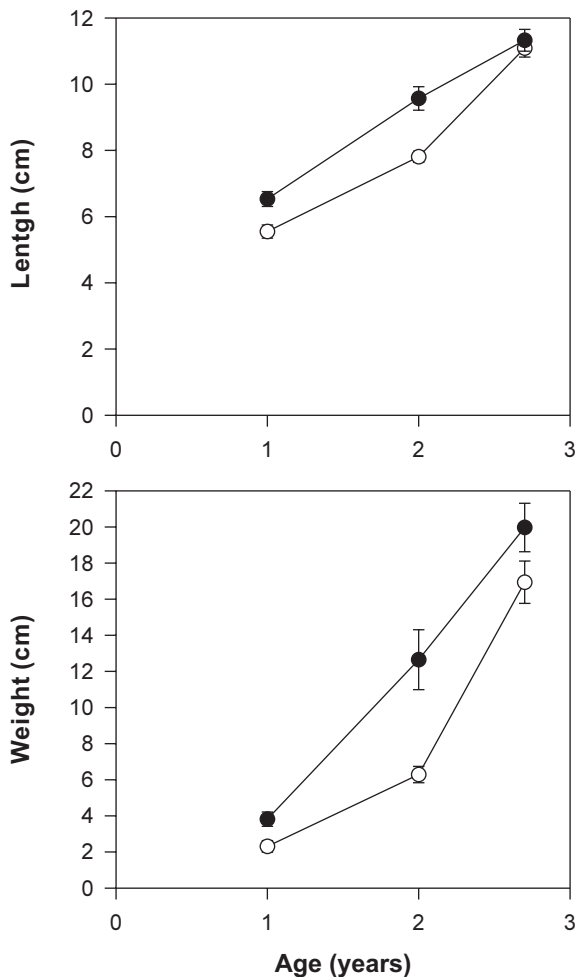

for different life history strategies of Atlantic salmon and in the presence of sympatric populations of brook trout.

Energy is the fundamental currency of ecosystem processes, and the efficiency of trophic transfer and allocation of energy determines growth rates of individuals and the overall production of the system (Lindeman 1942). Odum and Pinkerton (1955), considering energy flow through organisms, hypothesized that different species might be selected for either maximum efficiency of energy use or maximum output in the form of growth, reproduction, and energy dissipated through maintenance and activity. Consequently, it was argued that we might expect to see a range of species or spectrum of energy strategies within a given system depending on the rate of supply of limiting raw materials. In addition, it was outlined that maximum output entails high throughput with low efficiency of energy use. It is unclear, however, whether closely related species will have similar strategies of energy use or if the energy strategy is related to the behaviour of the fish.

In this study, Atlantic salmon parr had consumption rates two times greater than brook trout. This difference was manifested at a fundamental level, as brook trout had a field maintenance ration half that of Atlantic salmon. However, brook trout growth efficiencies were 1.3 times higher than those of Atlantic salmon parr. These differences are further exacerbated when considering Atlantic salmon precocious males, which had consumption rates 1.5 times greater than those of nonmaturing parr. Growth efficiencies for precocious males were half those of non-maturing parr despite higher feeding and growth rates.
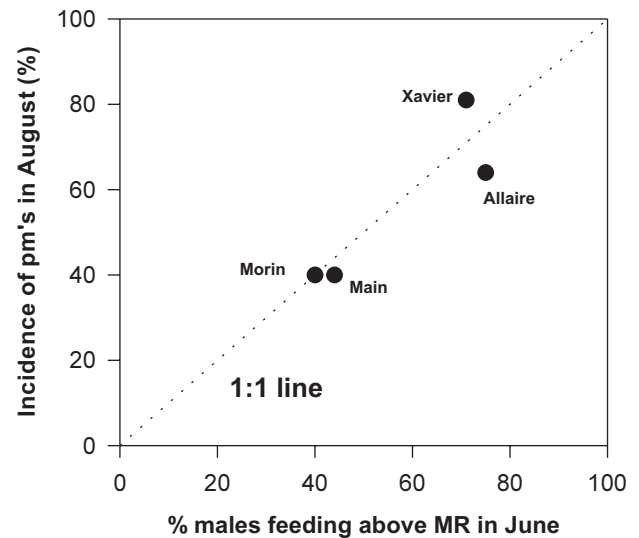
The lower growth efficiencies observed for Atlantic salmon are likely due to increased metabolic costs associ-

ated with higher activity. On average, energetic modeling indicated that Atlantic salmon parr spent 2.4-fold more energy in activity than brook trout. Atlantic salmon precocious males spent 1.7 times more energy in activity than parr. Activity is likely related to swimming costs associated with the high feeding rate of Atlantic salmon. Atlantic salmon typically accelerate to intercept prey items from their holding position above a rock at burst speeds requiring a relatively large expenditure of energy (Godin and Rangeley 1989). In addition, activity would integrate costs associated with territorial defense. It seems that brook trout had virtually no extraneous activity costs associated with their stream margin, opportunistic feeding strategy. The activity multipliers for brook trout are some of the lowest observed for both endothermic and ectothermic organisms (Hammond and Diamond 1997), whereas Atlantic salmon activity multipliers are within the high range observed for fish (Rowan and Rasmussen 1996; Hammond and Diamond 1997). However, it appears that the feeding strategy of Atlantic salmon allows them to maintain growth rates that are twofold greater than those of brook trout on average, despite higher overall costs and activity.

We have outlined three energy budgets that are fundamentally different with respect to maintenance ration and subsequently energy strategies. There is a spectrum of energy strategies resulting from a trade-off between efficiency and throughput. Either efficiency is maximized as both inputs and outputs are minimized, as in the case of brook trout, or throughput and outputs are maximized at great cost to efficiency, as is the case for precocious males. Atlantic salmon parr are intermediate between the two. Activity can be perceived as an investment to secure a high input of energy resources, as suggested by Odum and Pinkerton (1955). Brook trout minimize costs in general by assuming a more opportunistic existence within the stream margins or lower flow areas. Their strategy is clearly efficient, from the standpoint of

Fig. 8. Mean backcalculated (*a*) length and *b*) weight at age for 2+ precocious males (solid circles) and nonmaturing Atlantic salmon parr (open circles) sampled in August 1997. Error bars represent SE's.

Precocious maturation and energy budgets

In the wild, the proportion of maturing parr varies among stocks, years, and environmental conditions (Thorpe 1975; Bailey et al. 1980; Saunders et al. 1982). Thorpe (1986), coupling environmental and genetic factors, proposed that precocious maturation would proceed if the rate of accumulation of surplus energy exceeded a genetically determined threshold in early spring. Subsequently, Rowe and Thorpe (1990) demonstrated in a series of laboratory experiments of restricted rations that the rate or incidence of maturation increased with feeding and growth opportunities. Rates of maturation were highest at optimal feeding rates in early spring. Spring values of condition factor, not specific growth rates, were positively correlated with incidence of maturation. Maturation is thus linked to the accumulation of fat reserves in springtime, as there is a strong correlation between fat content and condition factor in salmonids (Rowe and Thorpe 1990). Rowe et al. (1991) elaborated further on the role of fat stores in Atlantic salmon parr, notably mesenteric fat, in fueling gonadal development. They found that an early onset of feeding is required for replenishment of stores following winter. Silverstein et al. (1997), working on amago salmon (*Oncorhynchus masu ishikawai*), supported the hypothesis of a size/energy threshold hypothesis for maturation and suspected that the decision to mature is made very early in development. They related this to potential differences in size of the energy store defended by these fish and speculated that these differences could be accounted for by differences in metabolic rates and (or) food consumption.

The results presented here support the hypotheses that maturing Atlantic salmon parr in the wild have increased rates of food consumption as well as an early onset of spring feeding. It would appear that precocious males require a consumption rate of >2.5–3% in their year of maturation, about twofold greater than the maintenance ration of parr. However, there was not a concomitant increase in growth rates, as growth efficiencies were significantly less than those of parr. This would suggest that precocious males have a different set point with respect to basic energy requirements analogous to the Atlantic salmon parr – brook trout comparison. Any subsequent environmental influence on the decision to mature or the incidence of maturation within a stream might be mediated through this high food requirement. Precocious males had metabolic costs two times greater than parr in their year of maturation. This might in part reflect higher basal metabolic rates. Higher feeding rates in Atlantic salmon parr are associated with dominance in social structures that has been linked to higher basal metabolic rates (Metcalfe et al. 1995). Thus, activity multipliers for precocious males were recalculated with a higher SMR based on the maximum observed deviation from Metcalfe et al. (1995). However, this was not sufficient to account for differences in activity, as activity costs were still significantly greater. Thus, it is likely that greater activity costs are related to higher feeding rates and (or) potentially reflect costs associated with gonadal development.

The development of bimodal size–frequency distributions during the first growing season is a commonly observed phenomenon in hatchery-reared populations of Atlantic salmon and has been linked to precocious maturation (Bailey et al. 1980; Saunders et al. 1982; Metcalfe et al.

growth, since activity multipliers are at the minimum. The maintenance ration can be perceived as an integrative, set-point energy requirement of a particular species displaying a particular feeding strategy and living within a particular system. Maintenance rations were significantly higher for Atlantic salmon in streams where consumption rates were highest and growth efficiencies were lowest. Since it is unlikely that basal metabolic rates are fundamentally different among Atlantic salmon of a similar life history strategy, the differences in maintenance rations likely integrate differences in activity costs associated with living in particular streams. The maintenance ration is fundamental to the subsequent allocation of energy to other components of the budget and reflects different energy strategies. Furthermore, it may have implications for the competitive allocation of food resources within a stream. The outcome of competitive interactions might be related to both total exploitation and efficiency of resource use. The difference in intrinsic maintenance rations presented here, coupled with a link between habitat and rates of food delivery, may provide a more comprehensive framework for considering density-dependent territorial and competitive interactions among these fish.

1988). Typically, Atlantic salmon parr in the upper mode mature. However, it has been more difficult to observe a clear divergence in wild populations of young Atlantic salmon given the large variations in growth rates and sizes among life history variants (Nicieza et al. 1991). An analysis of back-calculated size at age through scale analysis shows an early divergence, or bimodality, between 2^+ parr and 2^+ precocious males (Fig. 8). The point at which this divergence occurred is unknown, yet was established by age 1. It was not possible to observe this clear bimodality when examining the size distribution of 1^+ parr; however, there was a similar divergence between 1^+ parr and 1^+ precocious males. In this study, there were no differences in growth rates, as increments are similar between 1 and 2 years old. However, a spring growth spurt in the scale was observed in precocious males in the year of maturation (personal observation). Moreover, sampling in June showed a skewed sex ratio in favour of males. The results of overwinter feeding rates, which integrate springtime feeding, demonstrate that there is a subpopulation of male parr at each site with an early onset of feeding or that maintained higher feeding rates over the winter. A similar scenario has been observed in laboratory populations over the winter, where there is a suppression of appetite to a maintenance ration for parr in the lower modal group, while fish in the upper mode maintain feeding motivation (Metcalfe and Huntingford 1986; Simpson et al. 1996). Moreover, there were a greater number of males feeding above the maintenance ration in streams with a higher incidence of precocious males at the end of the summer. This would then suggest and indirectly corroborate the experimental observations that the rate of food acquisition in spring is related to the incidence of maturation within a population.

Applications of the ^{137}Cs method

We have presented two refinements to the ^{137}Cs method. First, we have estimated consumption rates for individual fish by combining the mass balance method with age analysis. The individual approach was corroborated by estimating consumption and growth rates with age-class means. This method has the advantage of simultaneously increasing the sample size of a particular system and providing a more accurate measurement of growth, free from potential confounding effects of size-selective mortality (Chapman 1978) and the high variation of size at age for Atlantic salmon in tributaries (Mills 1989). This approach is preferable when dealing with scarce or endangered stocks. The method is contingent on the validity of the back-calculation of size from age structure analysis as well as modeling the initial ^{137}Cs body burden. The ^{137}Cs mass balance model is least sensitive to the initial input terms of burden and weight such that any error associated with these modeled terms would not greatly affect the final consumption estimate (Rowan and Rasmussen 1996).

Second, we have presented a simple method to estimate ^{137}Cs assimilation efficiency for fish populations in the field. Aquatic invertebrates were the dominant prey items in the diets of both Atlantic salmon and brook trout. Laboratory assimilation efficiencies for aquatic invertebrates, namely chironomids and ephemeroptera larvae, are 54 and 23%, respectively (Forseth et al. 1992), with an average of 40%.

Thus, the results presented here denote an integrated average assimilation of two of the main prey components of the diet. Determining ^{137}Cs assimilation efficiencies by tracking the passage of a nonassimilated marker through the gut represents a considerable refinement to the method, as the assimilation of ^{137}Cs can contribute most to the uncertainty of consumption rates (Rowan and Rasmussen 1996). The uncertainty in assimilation can lead to a 1:1 ratio of uncertainty for the consumption estimate. It is assumed that the method integrates the assimilation of complex natural diets under variable conditions, which might affect total ^{137}Cs uptake by fish.

We propose a new context for examining productivity, competitive ability, territoriality, and life history strategies of lotic salmonids through a bioenergetics approach in defining and comparing field consumption rates, growth efficiencies, and maintenance rations. The energy budgets described here are not necessarily absolute or fixed. Indeed, we might expect additional energy budgets within a spectrum if we considered different systems, different species, or additional life history strategies. For example, if migration is a response to food demand, then we would hypothesize that anadromous brook trout would have greater energy demands than resident brook trout of the same age. Similarly, the brook trout – Atlantic salmon difference might exist for other pairs of sympatric salmonids, and the observed energy spectrum and differentiation might be further expanded in the case of three or more salmonids within a system.

The application of the refined ^{137}Cs method has allowed us to discriminate differences in energy budgets within and among salmonid species in the wild. We have answered the call of Power (1993) in his review of Atlantic salmon production to use new approaches to evaluate the ecology and energy requirements of juvenile Atlantic salmon in their natural habitat. However, rather than an approach based on extrapolation of laboratory-derived physiological parameters, ours is field based, estimating energy flux in situ allowing for a more comprehensive evaluation of the integrated factors controlling Atlantic salmon and sympatric salmonid production.

Acknowledgements

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