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Using Radiocesium (¹³⁷Cs) to Measure and Compare the Bioenergetic Budgets of Juvenile Atlantic Salmon (*Salmo salar*) and Brook Trout (*Salvelinus fontinalis*) in the Field

Strahan Tucker

Department of Biology, McGill University, Montreal

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of Masters of Science

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Preface

Thesis specifications stipulate that the following five paragraphs appear at the beginning of all manuscript-base theses:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

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The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". **The thesis must include:** a Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and the originality of the research reported in the thesis.

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This thesis is based on two manuscripts. Chapter 1 will be submitted to the journal Canadian Journal of Fisheries and Aquatic Sciences. Dr. Joe Rasmussen, my supervisor, will be co-author. I performed all the sampling, analyses, and wrote the paper. Chapter 2 will be submitted to the journal Limnology and Oceanography. Benthic invertebrate densities and current velocities were generously provided by Zhongyan Weng and Nandita Mookerji. I carried out fish density sampling under the supervision of Dr. Joe Rasmussen, Dr. Mazumder and Dr. Rodriguez as part of a stream inventory analysis through the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA). I carried out all analyses and wrote the paper. J. Rasmussen and A. Mazumder will be included as co-authors on the paper. Dr. J. Rasmussen provided insight and suggestions, as well as improvements to both manuscripts.

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Finally...to the salmon- a remarkable species of wilderness, mystery and exceptional drive.

In loving memory of Florence, George, Bill and Mike.

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Abstract

Through the ¹³⁷Cs mass balance method, annual consumption rates were estimated for juvenile Atlantic salmon parr and precocious males, as well as brook trout from 4 sites within the Ste Marguerite river system, Quebec. With explicit age analysis, feeding 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. The individual fish approach provided a range of data for a single site, as opposed to a single estimate per age class, allowing for an evaluation of the relationship between consumption and growth for each species or life-history variant. Subsequently, the concept of field maintenance ration was introduced as the intercept of consumption over growth.

There was a strong positive relationship between individual annual consumption and growth rates for salmon and trout at all sites. Feeding rates for salmon parr ranged between 0.015 and 0.048 $g \cdot g^{-1} \cdot d^{-1}$ and varied among sites. Precocious males had consumption rates 1.5 times greater than non-maturing parr. As well, salmon parr had consumption rates approximately 2.7 times greater than trout. Salmon parr had maintenance rations between 0.010 $g \cdot g^{-1} \cdot d^{-1}$ and 0.016 $g \cdot g^{-1} \cdot d^{-1}$ across sites. Trout had a maintenance ration approximately half that of salmon at 0.0059 $g \cdot g^{-1} \cdot d^{-1}$. Growth efficiencies for salmon parr ranged between 9.1% and 16.8% and varied significantly amongst sites. In addition precocious males had growth efficiencies approximately half those of non-maturing parr despite higher feeding and growth rates. Trout growth efficiencies ranged between 12.3% and 14.4%. The lower growth efficiencies observed for salmon were probably due to increased metabolic costs associated with higher activity costs. On average, salmon parr spent 2.4-fold more energy in activity than trout. Salmon precocious males spent 1.7 times more in activity than parr. Activity was probably related to swimming costs associated with the high feeding rate of salmon.

Salmonid feeding rates were coupled with density estimates to derive total fish exploitation rates for two streams. Independent estimates of benthic invertebrate standing stocks showed that fish were consuming between 18% and 67% of invertebrate production or two-thirds of the invertebrate P/B. The application of age- and site- specific feeding rates derived from the ¹³⁷Cs mass balance method, solved a long standing paradox in stream ecology as all previously inferred salmonid exploitation rates have been in excess of prey turnover.

Résumé

Au moyen de la méthode du bilan bioénergétique par le ¹³⁷Cs, les taux annuels de consommation des tacons Atlantiques juvéniles et des saumons mâles précoces ont été estimés, de plus que ceux de la truite mouchetée, à 4 sites du système riverain de la Ste.-Marguerite (Qué.). A partir d'une analyse d'age explicite, les taux d'alimentation et de croissance des poissons ont été déterminés sur une base individuelle et par classe d'age. L'estimation des bilans individuels à procuré une portée de données pour chaque site, contrairement à une seule estimation par classe d'age, permettant ainsi d'établir le rapport entre la consommation et la croissance de chaque espèce ou de chaque variante de cycle de vie. Nous présentons ici le concept de la ration de maintien qui correspond à l'intercepte de la relation entre la croissance et la consommation.

Nous avons observé une relation positive entre les taux annuels de consommation et les taux de croissance chez le saumon et la truite. Les taux de consommation des tacons échelonnaient entre 0.015 et 0.048 g·g⁻¹·d⁻¹ et variaient parmi différents sites. Ils étaient 2.7 fois plus élevés que ceux des truites, tandis que les saumons mâles précoces manifestaient des taux de consommation 1.5 fois plus élevés que les saumons immature. Les rations de maintien des tacons se tenaient entre 0.010 g·g⁻¹·d⁻¹ et 0.016 g·g⁻¹·d⁻¹, alors que celles des truites étaient moins élevées de moitié, près de 0.0059 g·g⁻¹·d⁻¹. L'efficacité de croissance des saumons se trouvait entre 9.1 et 16.8% et variait parmi différents sites. Celle des mâles précoces étaient inférieure, n'équivalant qu'à la moitié de celle des tacons immatures, ceci malgré les taux de consommation et de croissance plus élevés des mâles précoces. Les truites, elles, manifestaient une efficacité de croissance entre 12.3 et 14.4%. La valeur moindre de l'efficacité de croissance observée chez les

saumons était probablement associée à un plus grand coût d'activité. En moyenne, les tacons dépensaient 2.4 fois plus d'énergie en activité que les truites, et les saumons mâles précoces 1.7 fois plus que les tacons. L'excès en coûts d'activité chez les saumons étaient probablement relié à la nage requise pour maintenir des taux d'alimentation élevés.

Les taux de consommation des salmonidés ont été jumelés avec des estimations de densité pour en dériver les taux totals d'exploitation des poissons dans deux ruisseaux. Des évaluations indépendantes de la biomasse invertébrée ont démontré que les poissons consommaient entre 18% et 67% de la production d'invertébrés, soit 2/3 du P/B des invertébrés. L'application de taux de consommation spécifiques à l'age et au site, au moyen de la méthode du ¹³⁷Cs, résout un paradoxe de longue date en écologie en milieu lotique, comme tout le taux d'exploitation des salmonidés déterminé précédemment excédaient le renouvellement des proies.

Background

There is mounting concern over the general and continual decline of Atlantic salmon over its range (Mills 1989). The decline of stocks has worsened despite moratoriums on commercial harvests, reductions in catch by recreational fisheries and attempts to mitigate human impact on river spawning sites and juvenile nursery habitat. Naturally, much of the management of stocks has focused on the river-phase portion of the life history given the perceived amenability of direct actions on the river environment. Managers have pursued stocking programs, habitat restoration and considered river fertilization (Mills 1989) with mixed success with the objective of increased smolt outmigration. However, to date there is still little concrete knowledge of the actual complex nature and dynamics of the lotic system and the subsequent factors controlling juvenile Atlantic salmon production (Power 1993; Richardson 1993; Waters 1993).

Most research on juvenile Atlantic salmon has been narrowly directed towards some very practical factors affecting growth, for the expressed purposes of exploitation and aquaculture. The focus has been concerned with optimizing nutritional status and food intake, defining factors influencing or controlling maturity, and examining underlying genetics (Power 1993). Natural populations have received far less attention. Thus, little is known about how these factors interact in the wild to influence production of juvenile Atlantic salmon stocks (Power 1993). Furthermore, field studies have focused solely on salmon, and have largely ignored broader questions of ecosystem and community processes, which may act to alter overall smolt production.

The growth and production dynamics of lotic salmonids are complex (Richardson, 1993). Factors to be considered include potential inter and intra-specific competition, alternate life-history strategies, and the productivity of the food base. Research has documented habitat preferences and provided general descriptions of diets of Atlantic salmon in nature (e.g. Egglishaw 1967; Gibson and Cunjak 1986). Very few studies have actually measured juvenile salmon production (e.g. Egglishaw and Shackley 1977; Randall and Paim 1982; Randall and Chadwick 1986). There is evidence that growth rates and densities of salmonids are positively related to food supply (Richardson 1993) as a number of whole-stream fertilization studies have shown a positive relationship between benthic invertebrate production and an increase in salmonid size and/or densities (Huntsman 1948; Warren et al. 1964; Hyatt and Stockner 1985; Johnston et al. 1990). The specific details of these food web processes and transfers of nutrients and energy are poorly understood due to the inconsistency of results from these fertilization studies. Moreover, it has been difficult to estimate the production of the lotic food base with traditional techniques given the complex dynamics of invertebrate drift and inputs of allochtonous food sources (Waters 1977; 1988). Therefore, the link between stream productivity and salmonid productivity has never been clearly established. In fact, within the realm of stream biology, the "Allen paradox" has persisted for over 40 years. This paradox stems from the repeated observation that salmonid food exploitation rates exceed benthic invertebrate turnover rates (Allen 1951; Horton 1961; Allan 1983; Huryn 1996). In part, the paradox is due to the fact that fish consumption rates have always been inferred and never measured in conjunction with invertebrate production (Boisclair and Leggett 1985). Daily rations have not been estimated for wild populations of juvenile

Atlantic salmon and very few exist for other lotic salmonids (Power 1993). Feeding is a starting point in understanding the dynamic factors regulating the productivity of the species as the addition of biomass depends on the ability of fish to acquire food and convert it into somatic or reproductive tissue (Soofiani and Hawkins1985). Controlled feeding experiments point to food availability or the rate of food acquisition as fundamental in determining overall growth and also in influencing alternate life-history decisions related to the rate of maturity (Rowe and Thorpe 1990; Fleming 1996).

Alternate life-history strategies in salmonids relate to the size and age of maturation. In Atlantic salmon, age of maturity is highly variable both within and among systems (Scott and Crossman 1973; Fleming 1996). Typically, salmon parr in Eastern Canada spend 2-4 years in freshwater then smolt and go to sea (Bielak and Power 1986). However, juvenile males can mature and spawn while still in the freshwater part stage and are commonly known as precocious males (pm). Size and age of maturity is variable for brook trout as well, particularly when anadromy is an option for a given system. The relative importance of genetic and environmental factors influencing the variation of maturation rates noted for populations of Atlantic salmon is still in question (Fleming 1996). It has been observed in nature that there are large variations in the incidence of precocious males between years and stretches of a river (Thorpe 1975; Glebe et al. 1978; Bailey et al. 1980; Saunders et al. 1982) and that high frequencies are associated with so called favourable growing conditions such as abundant food, high temperatures and suitable habitat (Bailey et al. 1980; Bagliniere and Maisse 1985). This is in contrast with the observation that favourable conditions enhance smoltification (Thorpe 1986; Metcalfe et al. 1986). To date, it is unclear what causes individual salmon within a population

exposed to similar conditions to adopt a particular life history strategy (anadromy and delayed maturity vs. maturity). It seems however to be related to some aspect of food supply or acquisition. Thorpe (1986), coupled environmental and genetic factors and proposed that maturation would proceed if the rate of accumulation of surplus energy exceeded a genetically determined threshold. Indeed, in laboratory feeding studies, the incidence of male parr maturation has been shown to be contingent on surplus food acquisition in spring months that replenish fat stores required to fuel gonadal development (Rowe and Thorpe 1990; Rowe et al. 1991; Simpson 1992).

In North America, Atlantic salmon are often found with stocks of brook trout. In general, trout are considered inhabitants of pools or stream margins and salmon are considered as riffle or fast water dwellers, although a wide range of stream habitats can be used by both salmonids (Gibson et al. 1993). However, Atlantic salmon are known to aggressively defend a territory. Since food and feeding behaviour are so similar, it is felt that the observed differences in habitats occupied are a result of competitive segregation (Gibson and Cunjak 1986; Hearn 1987). However, the mechanism of potential competition is unknown as total inputs and outputs to the energy budget have never been assessed.

This thesis is concerned with addressing some fundamental questions about the biology of juvenile Atlantic salmon in the wild as well as brook trout from an energy perspective. Energy is the fundamental currency of biological and ecosystem processes (Lindeman 1942). As there is considerable variation in incidences of various life history strategies and overall densities of salmonids amongst systems (Thorpe 1986; Kennedy 1988), I have taken a comparative approach. These questions involve estimating basic consumption rates of salmon parr and precocious males, evaluating variation in feeding rates amongst various sites, as well as determining any difference in feeding rates for sympatric brook trout leading to speculation about the influence on salmon energy budgets. These questions have remained unanswered due to the constraints and destructive nature of standard techniques to estimate feeding rates. These techniques are labour intensive and require the sacrifice of too many fish to be acceptable or viable for these stocks. Basic inputs to energy budgets and the efficiency of energy use and partitioning are addressed in Chapter 1 through the application of the ¹³⁷Cs mass balance technique for estimating consumption (Forseth et al. 1992; Rowan and Rasmussen 1996). This method is integrative and requires the sampling of far less fish to determine annual or seasonal consumption estimates. The chapter focuses on addressing the basic hypothesis that juvenile Atlantic salmon, maturing parr, and brook trout have different rates of energy intake and allocation.

In Chapter 2, I examine energy flow at the population level by assessing community food exploitation rates. This was accomplished by integrating age-specific consumption rates defined in Chapter 1, with density estimates, to derive a total fish consumption rate for two streams that differ greatly in their hydrodynamic regimes. These fish exploitation rates were subsequently compared to independent estimates of invertebrate production to examine the relationship between food use and food availability and the potential link between the food base, habitat and densities of the two species and life history variants.

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Chapter One

Estimating bioenergetic budgets of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) in the field

Introduction

Feeding rates have never been measured for juvenile Atlantic salmon in the wild (Power 1993) and very few estimates 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 input to the energy budget is essential for an evaluation of the efficiency of energy use leading to growth (Soofiani and Hawkins1985). From a community perspective, estimating consumption allows for an assessment of the demands fish make on their food resources, and how these in turn, might limit production (Soofiani and Hawkins 1985).

Throughout its range in North America, Atlantic salmon is often found with brook trout. 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 an aggressively defended territory (Gibson et al. 1993): areas where there is likely to be a steady supply or concentration of food (Everest and Chapman 1972; Hill and Grossman 1993). Brook trout, also drift feeders, occupy stream margins or relatively slower water habitat, particularly in the presence of salmon and are generally thought of as being less aggressive and less territorial (Gibson et al. 1993). Within small streams however, it is felt that food and feeding behaviour are similar enough giving way to interspecific competition particularly when resources are limited (Gibson and Dickson 1984; Thonney and Gibson, 1989). In addition, studies have suggested that trout can have a negative effect on growth of large salmon in pool-type habitats (Gibson and Dickson 1984) or have shown an inverse correlation between brook trout and salmon densities (Ryan 1993) in lakes. Competition in streams is inferred from subsequent habitat segregation (Chapman 1966). However, habitat suitability has never been evaluated in conjunction with explicit energy demands of individual fish. Given that food intake has never been measured, let alone in conjunction with density estimates, it is left unclear whether the observed habitat segregation or inferred competition actually represents an impediment to food acquisition and energy allocation for one of the two salmonids.

Odum and Pinkerton (1955), speculated that different species within an environment might be selected for either maximum efficiency of energy use or maximum output in the form of growth, reproduction and maintenance. Alternatively, the two salmonids might have different energy requirements and strategies of energy allocation reflected by their different feeding strategies; a more aggressive and active strategy of territorial and resource acquisition and a less active, sedentary, opportunistic feeding behaviour. Different energy strategies might involve trade-offs in balancing inputs and outputs to the energy budget.

Apart from 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 (pm). The proportion of maturing parr varies among stocks, years, and environmental conditions

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(Thorpe 1975; Glebe et al. 1978; Bailey et al. 1980; Saunders et al. 1982). It appears that maturation is affected by a genetically determined threshold related to growth rate or to the rate of acquisition of energetic reserves (Thorpe 1986) rather than a specific body size or level of energy reserves. Rowe and Thorpe (1990) found that spring growth opportunity was important for maturation to proceed. However, no relationship between monthly specific growth rates and maturation has been found although precocious males tend to be larger individuals (Fleming 1996) and increases in condition factors have been observed (Simpson 1992). Alternatively, maturation appears to be 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). Fat stores are required to fuel gonadal development. The differences in fat content and storage suggest differences in energy partitioning amongst maturing and non-maturing part. 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). In some respect, precocious maturation appears to be related to an aspect of food supply or acquisition.

Measurements of *in situ* consumption rates by conventional techniques require estimates of gut fullness and laboratory derived gut clearance rates over numerous sampling dates to simply derive a mean annual estimate (Eggers 1977; Elliott and Persson 1979; Trudel and Boisclair 1993). This entails the sacrifice of many fish and is extremely labour-intensive. To avoid these problems we employ the ¹³⁷Cs mass balance technique to yield

consumption rates for wild fish populations (Forseth et al. 1992; Rowan and Rasmussen 1996). Because the ¹³⁷Cs 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. Radiocesium is a globally dispersed isotope due to fallout from nuclear weapons testing and accidents and can easily be detected at low levels with modern gamma spectrometry (Rowan and Rasmussen 1996).¹³⁷Cs is a non-essential element however it is useful as a tracer of food web dynamics as organisms take up and accumulate ¹³⁷Cs through their food. The ¹³⁷Cs method requires the determination of ¹³⁷Cs in fish and their prey, ¹³⁷Cs elimination from fish, and ¹³⁷Cs assimilation efficiency from food. Its elimination from fish has been modeled as a simple function of body size and temperature and shown to be species independent (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). The method has recently been tested and corroborated on two salmonid species by Forseth et al. (1992,1994) with independent estimates of consumption obtained with stomach contents.

Thus, the objectives of this study were to estimate and compare consumption and growth rates for juvenile Atlantic salmon parr and precocious males, and, brook trout. More specifically, we tested the hypothesis that Atlantic salmon and brook trout have different energy requirements. Namely, salmon have greater consumption rates given associated costs of their more aggressive feeding strategy (territoriality) while trout have lower consumption rates, yet greater growth efficiencies given lower costs associated with their feeding strategy (non- territoriality). In addition, we tested the hypothesis that maturing

male parr in the wild have differences in energy partitioning and/or increased rates of energy accumulation relative to non-maturing salmon parr.

Here we define the concept of a field maintenance ration as the intercept of consumption over growth. 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. This concept is fundamental to evaluating throughputs and efficiencies of energy budgets and identifying different energy strategies.

Methods

Fish collection and ¹³⁷Cs analysis

This study was conducted in the Ste-Marguerite River system in the Saguenay region of Quebec (Figure 1) which supports both the juvenile stages of anadromous Atlantic salmon and brook trout and resident populations of brook trout. In the river system, salmon smolt between 3-4 years of age after which they will spend from 1-2 years at sea (Bielak and Power 1986). Like many other 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 its extent in this system, poorly quantified. However residents will remain to mature and spawn between 3-5+ years old (unpublished observation).

Fish were collected from several sites and tributaries of the Ste-Marguerite River system during the summers of 1996 and 1997 by electrofishing. These sites included three

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second order tributaries, Allaire, Morin, Xavier, as well as a section along the main branch of the river. Approximately 40 juvenile salmon and 40 trout (if present) were collected at each site, each at the beginning of June (1997) and the end of August (1996,1997). Fork length was measured to the nearest 0.1 cm and total mass was measured to 0.01 g. Temperature profiles for streams and the river were constructed by daily measurements with a thermometer.



Figure 1: Sampling sites (*) in the Ste-Marguerite River system.

Age Analysis and Growth rates

Salmon were aged using scales taken from below the dorsal fin near the lateral line. Length at the formation of the annulus was back-calculated by the Fraser-Lee method (Carlander 1981; Busacker 1990; 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 (Appendices 4 and 5).

Trout were aged using opercular and subopercular bones. A subsample of trout otoliths were mounted, cross sectioned and analyzed, and subsequently compared blindly to test the validity and accuracy of age determination by use of the opercular bones. Size at age was back-calculated with the Fraser-Lee method. All age estimates and measurements were done double blindly with less than 5% inter-observer error.

Growth back-calculations from age structures assume that the relationship between fish length and age structure radius is constant through time (Campana 1990). However, studies have demonstrated that 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 salmon and trout, multiple regression analysis was performed with categorical variables for season, site, age and life history pattern (or sex). Specific growth rates (G; $g \cdot g^{-1} \cdot d^{-1}$) were estimated for individual fish and age classes following Ricker (1979);

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

where W_f is the final weight (g) at time t (d) and W_i is the initial weight (g).

Consumption Rates

Annual consumption rates for juvenile Atlantic salmon (age 0-2+) and brook trout (age 0-4) from the Ste-Marguerite River system were estimated with a ¹³⁷Cs radiotracer approach on an age-class and individual basis. Specific consumption rate (C; $g \cdot g^{-1} \cdot d^{-1}$) is estimated from a radiocesium mass-balance model (Rowan and Rasmussen 1996);

(2)
$$C = \frac{(Q_t - Q_o e^{-(E+D)\cdot t} + Q_g) \cdot (G + E + D)}{\alpha \cdot [^{137} Cs_f] \cdot w_o \cdot (e^{-G \cdot t} - e^{-(E+D)\cdot t})}$$

where Q_t is the ¹³⁷Cs burden (Bq) at time t (days),Q₀ is the initial ¹³⁷Cs burden (Bq), Q_g is the gonadal ¹³⁷Cs burden released at spawning, G is the specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$), E is the elimination rate of ¹³⁷Cs (Bq·Bq⁻¹·d⁻¹), D is the radioactive decay of ¹³⁷Cs (Bq·Bq⁻¹·d⁻¹), [¹³⁷Cs_f] is the concentration of ¹³⁷Cs in the diet (Bq·kg⁻¹), α is the assimilation efficiency of ¹³⁷Cs from the diet(fraction), and w_o is the initial body mass (kg). The elimination rate of ¹³⁷Cs 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).

This model 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 salmon and trout were determined by comparing August 1996 with August 1997 fish. Alternatively, if there are strong and consistent ¹³⁷Cs body burden relationships with size or age within a system, consumption rates can be estimated for individual fish by back-calculating size at annulus formation and then determining ¹³⁷Cs burden with regression models of ¹³⁷Cs burden vs. size (Appendix 3). In this manner, individual consumption rates were determined from observed body burdens of the June and the August 1997 fish with modeled burdens from the previous fall. The ¹³⁷Cs 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). 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 ageclass mean basis.

Whole fish were dried, ashed at 450 °C for 48 hours, and whole body ¹³⁷Cs was measured by gamma spectrometry with a Coaxial Well Germanium Detector (Canberra Industries Inc.). ¹³⁷Cs 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 ¹³⁷Cs Assimilation Efficiency

Fish diets were determined by examining gut contents. Prey ¹³⁷Cs concentrations were determined on undigested gut contents. Gut contents were pooled by fish species and site for each sampling period to increase the precision of ¹³⁷Cs determination. Pooling is assumed to integrate diet variability over time and among individuals.

Typically, ¹³⁷Cs 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 efficiency of ¹³⁷Cs from food may vary among prey type and in relation to the clay content of the prey (Kolehmainen 1972; 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: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 ¹³⁷Cs uptake and subsequently underestimate consumption rates.

¹³⁷Cs assimilation efficiency (α ; %) 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 fore to hindgut to which assimilated material can be compared. The amount of ¹³⁷Cs taken up by fish is determined by baseline correction (Jobling 1994):

(3)
$$\alpha = 100 \cdot \left(1 - \frac{\left[AIA_{fg}\right]}{\left[AIA_{hg}\right]} \cdot \frac{\left[{}^{137}Cs_{hg}\right]}{\left[{}^{137}Cs_{fg}\right]} \right)$$

where AIA_{fg} and AIA_{hg} are the concentrations of acid insoluble ash in the foregut and hindgut (g·g⁻¹wet weight) respectively and ¹³⁷Cs_{hg} and ¹³⁷Cs_{fg} are the ¹³⁷Cs concentrations of in the hindgut and foregut (Bq·kg⁻¹) 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 pooled samples integrate the assimilation efficiency of a complex natural diet and variation in diets. Samples were washed in 1molar HCl acid for 10 minutes 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 cesium-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):

$$(4) \qquad G = C + A*SMR + SDA + F + U$$

where G is specific growth rate; C is the specific consumption rate; SMR is the standard metabolic rate; SDA is specific dynamic action (approximately 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 the standard metabolic rate. Activity includes such extraneous costs as swimming, foraging and other behavioural activities. 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 $J \cdot g^{-1}_{wet weight}$ for fish tissue (Cummins and Wuycheck 1971; Hartman and Brandt 1995) and 3176 $J \cdot g^{-1}_{wet weight}$ 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. Relative growth rates were plotted against relative consumption rates to examine the intercept of consumption or maintenance ration. All salmon and trout were within the same size range such that differences remain significant on an absolute basis ($F_{1,77}$ =22.38; p<0.0001; regression with categorical variable for species and life history). One-way ANOVA (Sokal and Rohlf 1981) was used to check for significant differences in growth rates, consumption rates, growth efficiencies (% consumption allocated to growth), total metabolic costs and activity multipliers amongst salmon parr, precocious males or brook trout between sites. Significant differences in these parameters in single pair comparisons between salmon parr and precocious males, or salmon parr and brook trout within sites were checked 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

¹³⁷Cs Assimilation efficiencies and diets

Trout had a greater component of terrestrial invertebrates in their diet than salmon (21% vs. 9-15%), however ¹³⁷Cs assimilation efficiencies in Allaire were similar for both salmon and trout (40%) (Table 1). Despite almost identical diets in salmon from Morin, the ¹³⁷Cs assimilation efficiency was half that for 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:dry ratio of foregut contents. Salmon from the main river had the highest ¹³⁷Cs assimilation efficiency (73%). This is most probably due to a large component of zooplankton in their diet (40%), as the laboratory derived ¹³⁷Cs assimilation efficiency for zooplankton is 81.6%.

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 ($F_{3,239} = 1.457$;
Section	species	diet (Aquatic (A), Terrestrial (T) inverts)	ash:dry	[acid-insol ash] foregut (g ^{·g⁻¹wet)}	[acid-insol ash] hindgut (g ⁻¹ wet)	¹³⁷ Cs foregut (Bq kg ⁻¹)	¹³⁷ Cs hindgut (Bq kg ⁻¹)	α (%)
Allaire	salmon trout	88% A. & 12% T. 79 % A & 21% T	0.39 0.28	0.074 0.025	0.109 0.038	4.5 5.3	4 4.9	39 42
Morin	salmon	85% A & 15% T	0.49	0.050	0.100	2.7	4.1	23
Xavier	salmon	91% A & 9% T	0.20	0.027	0.062	4	5.3	43
Main	salmon	50% A+ 40% zooplankton +10% T	0.09	0.007	0.011	2.3	1	73

Table 1: Fish diet, acid insoluble ash concentrations and ¹³⁷Cs concentrations from foregut and hindgut, and, assimilation efficiency (α) of ¹³⁷Cs from diet. Aquatic invertebrates in fish diets include in order or prevalence: ephemeroptera > tricoptera > plecoptera > diptera > coleoptera. Terrestrial invertebrates include diptera > homoptera > lepidoptera.

p=0.227) or season ($F_{2,239}$ =0.323; p=0.570) on the scale radius-body length relationship for salmon (entire model: adj. r²=0.89, p<0.0001, n=239; Appendix 6). In addition, all interaction terms were non-significant. Similarly, the opercular radius-body length relationship (entire model: adj. r²=0.90, p<0.0001, n=97; Appendix 7) did not vary for 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 intercept of 3.01 cm for salmon closely matched the "biological intercept" (Campana 1990) of size-atemergence observed for these populations (unpublished observation). Correcting the trout intercept of -0.506 cm with a biological 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;).

Growth rates

At all sites and for both species, younger smaller fish had greater specific growth rates than older fish (Table 2). As well, 1⁺ and 2⁺ precocious males had greater growth rates than respective non-maturing parr. Growth rates for salmon ranged between 0.0015 and 0.0046 g·g·d⁻¹, and varied significantly amongst sites ($F_{3,83}$ =20.29; p<0.000), with the lowest rates for all age classes observed in the Main River and the highest in Morin. Salmon parr were able to maintain higher growth rates than trout for all age classes (t=5.752; p<0.0001), which resulted in a greater size at age (Figure 2). There was good corroboration between individual growth estimates and those derived by comparing age class means (Table 2). However, standard errors were smaller in the individual estimates providing a more precise estimate of growth.

Species	Section	age	G Individual mean	G Age class mean (%d ⁻¹)	C Individual mean (%d ⁻¹)	C Age class mean (%d ⁻¹)
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
		l⁺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	ı+	0.30 + 0.07	039+011	23+01	25+05
		· · ·	0.37 ± 0.03	0.37 ± 0.11	2.5 ± 0.1	2.5 ± 0.3
		1 mm	0.34 ± 0.04 0.47 ± 0.03	0.28 ± 0.15	2.4 ± 0.1	37+06
		2*nm	0.47 ± 0.02	0.45 ± 0.10	38 + 01	3.2 ± 0.0
	ļ	- p	0.40 ± 0.03	0.30 ± 0.14	J.8 ± 0.1	3.4 ± 0.8
	Xavier	1.	0.33 ± 0.07	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
		l*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		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	1.0 ± 0.1	2.6 ± 0.5
		2 pm	0.21 ± 0.06	0.25 ± 0.13	2.4 ± 0.3	2.2 ± 0.6
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
	Yavier	1.	ND	016+014		11+01
	Advict	2*		0.13 10.14		1.1 ± 0.3
	L		ND	0.30 ± 0.13		1.3 ± 0.3

Table2: Mean growth and consumption rates for salmon and trout from different sites from age class comparisons and individual calculations. Errors for age class means were estimated from a Monte Carlo simulation. Note: $\% d^{-1}=100*g \cdot g^{-1} \cdot d^{-1}$



Figure 2: Mean size at age for Atlantic salmon parr and brook trout sampled in August 1997. Error bars represent standard errors.

Annual Consumption rates

In general, younger fish had greater relative consumption rates than larger older fish. Feeding rates for salmon ranged between 0.015 and 0.048 g·g⁻¹·d⁻¹ and varied significantly among 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 (1.5x) than non-maturing 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), salmon parr had consumption rates approximately 2.7 times greater than trout. Feeding rates for trout ranged between 0.011 and 0.017 g·g⁻¹·d⁻¹.

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

Maintenance rations

There was a strong positive relationship between individual annual consumption and growth rates for salmon and trout at all sites (Figure 3). Salmon had maintenance rations between 0.010 $g \cdot g^{-1} \cdot d^{-1}$ and 0.016 $g \cdot g^{-1} \cdot d^{-1}$ across sites. There were significant differences between intercepts amongst streams (F_{3,50}= 22.21; p<0.0001). Xavier had a greater intercept (0.016 $g \cdot g^{-1} \cdot d^{-1}$) than the rest of the streams and Allaire (0.0125 $g \cdot g^{-1} \cdot d^{-1}$) was



Figure 3: Growth and consumption rates for individual salmon parr (O), precocious males (•) and brook trout () from various sites in the Ste Marguerite river system. a) Allaire: the regression for salmon parr: C=5.34 G + 0.0125 (r^2 =.53; p=0.001); brook trout: C=3.25 G + 0.0059 (r^2 =.77; p=0.001). b) Xavier: salmon parr: C=5.74 G + 0.0164 (r^2 =.77; p=0.000); brook trout: C=2.84 G + 0.0059 (r^2 =.76; p=0.024). c) Morin: salmon parr C=3.33 G + 0.0103 (r^2 =.53; p=0.001). d) Main River: salmon parr: C=2.85 G + 0.010 (r^2 =.34; p=0.029).

marginally greater than the Main River (0.010 $g \cdot g^{-1} \cdot d^{-1}$). However, all slopes were similar (F_{3,50}=0.897; p=0.348). Trout had a subsistence ration approximately half that of salmon at 0.0059 $g \cdot g^{-1} \cdot d^{-1}$ in both Allaire and Xavier.

Age class means are plotted in Figure 4, with 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⁻¹·d⁻¹ for salmon and 0.0069 g·g⁻¹·d⁻¹ for trout, which mirrors the general trend for each stream when rations are calculated on an individual basis.

Growth efficiencies

Growth efficiencies for salmon parr ranged between 9.1% and 16.8% and varied significantly amongst sites ($F_{3,50}=27.32$; 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 non-maturing parr within a stream despite higher feeding and growth rates (Table 2). Trout growth efficiencies ranged between 12.3 % and 14.4% with significant differences between streams (t=2.872; p=0.004). Trout had significantly greater growth efficiencies than salmon within a particular stream (Table 3). That is, salmon had to feed more to sustain a given growth rate.



Figure 4: Annual growth and consumption rates for Atlantic salmon parr (O), precocious males (•) and Brook trout (\Box) derived from age class means for various sections in the Ste Marguerite River system. Regression for salmon parr is C=3.39·G + 0.014 (r²=.33; p=0.000); regression for brook trout is C=2.11·G + 0.0069 (r² =.91; p=0.000). Errors and 95% confidence intervals were determined by Monte Carlo simulation.

Metabolic costs and Activity multipliers

Total metabolic costs for salmon parr ranged between 0.7 and 2.8 $\times 10^{-2}$ J·d⁻¹ with significant differences amongst all sites (F_{3,50}=74.19; p<0.0001) with the highest costs in Allaire and the lowest in the Main River (Table 3). In addition, salmon had 5 times greater total metabolic costs than trout. Accounting for the SMR, these translate into activity multipliers 2.4 fold greater for salmon parr (2.4) than trout (1.0) within Allaire and in Xavier (t=8.911; p<0.0001). Activity costs for salmon varied significantly amongst sites (F_{3,50}=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 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% however remained significantly greater such that higher metabolic rates could not account for the greater activity costs observed in precocious males.

Over-winter Consumption rates

Over-winter rations, integrating springtime feeding, were estimated from the June sampling period (Figure 5). This was the first point when it was possible to sample by electrofishing. Given the small sample size, data were pooled by site after factoring out Table 3: Growth efficiencies, metabolic costs and activity multipliers for salmon and trout. Activity multipliers were modified for precocious males by assuming a higher SMR. Mean growth efficiencies, total metabolic costs and activity costs were compared between salmon parr and precocious males, and, between salmon parr and trout within a stream by T-test, where: * = 0.05 ; <math>** = p < 0.01. There were no significant differences between immature and mature trout within a stream.

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Species	Section		Growth efficiency (%)	total metabolic costs (x 10^{-2} J [·] d ⁻¹)	Activity multiplier	Modified Activity multiplier
Salmon	Allaire	parr	11.2 +/- 0.6	2.8 +/- 0.2	2.4 +/- 0.2	
		pm	6.9 +/- 0.8 **	4.5 +/- 0.3 **	4.1 +/- 0.1 **	2.9 +/- 0.3 *
	Morin	parr	16.8 +/- 1	1.0 +/- 0.1	1.4 +/- 0.1	
		pm	13.4 +/- 0.5 **	1.6 +/- 0.1 **	2.4 +/- 0.1 **	1.7 +/- 0.1 *
	Xavier	parr	9.1 +/- 0.3	1.8 +/- 0.1	2.4 +/- 0.1	
		pm	10.4 +/-0.6 *	1.6 +/- 0.1	2.5 +/- 0.1	1.8 +/- 0.2 **
	Main River	parr	12.5 +/- 0.6	0.7 +/- 0.03	1.2 +/- 0.1	
		pm	8.4 +/- 0.12 **	1.2 +/- 0.1 **	2.2+/- 0.1 **	1.6 +/- 0.2 **
Trout	Allaire	imm	14.2 +/-1.4 **	0.5 +/-0.04 **	0.97 +/- 0.1 **	
		mat	14.4 +/- 2.1 **	0.6 +/-0.07 **	1.3+/- 0.3 **	
	Xavier	imm	12.3 +/- 2 **	0.6 +/-0.04 **	0.97 +/- 0.1 **	

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 subsistence 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 portion 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 (Figure 6).



Figure 5: Overwinter growth and consumption rates above maintenance ration for Atlantic salmon parr from the Ste Marguerite River system. Closed circles (•) are female parr; open circles (0) are male parr. Regression line and prediction interval is for female parr.



Figure 6: The incidence of male parr feeding above maintenance ration (mr) in spring and the incidence of precocious males (% male parr) observed at the end of the summer in individual streams.

Discussion

Through the ¹³⁷Cs mass balance method, combined with age analysis, we have estimated consumption rates and growth rates of individual salmon parr, precocious males, and brook trout in the field. This method is contingent on the validity of the back-calculation of size from age structure analysis as well as modeling the initial ¹³⁷Cs body burden. 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 salmon or trout, and since the statistical intercept for salmon matched the biological intercept of size at emergence, or the intercept-correction suggested by Campana (1990) had no significant effect for trout, it was felt that the application of the Fraser-Lee method for back-calculating sizes was valid. The ¹³⁷Cs 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 effect the final consumption estimate (Rowan and Rasmussen 1996). For example, the ratio of change in parameter to the change in the consumption estimate is 0.5 for w_0 and 0.15 for Q_0 , whereas it is 1 for the assimilation efficiency, 1 for O_t and 0.5 for W_f (Rowan and Rasmussen 1996; Appendix 8). In addition, the individual approach was corroborated by estimating consumption and growth rates with age class means. Given the smaller standard errors, individual growth rates and consumption rates were more precise than age class means. Back-calculating size at age for individual fish allows for a more accurate measurement of growth, as opposed to using the relative change in weight for a population, given the

problems associated with size selective mortality (Chapman 1978) and the high variation of size at age for salmon, particular in tributaries (Mills 1989).

These are the first field estimates of consumption rates for juvenile Atlantic salmon. Moreover, we have examined growth efficiencies in a comparative manner amongst streams for different life-history strategies of salmon and in the presence of sympatric populations of brook trout. In this study, precocious males were found to have a greater total energy budget than non-maturing parr. In addition, salmon parr had twofold greater consumption rates than sympatric trout as well as greater metabolic costs of activity related to their feeding strategy. However, the two species differed with respect to their field maintenance ration reflecting two different strategies of energy acquisition and allocation.

Precocious maturation and energy budgets

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) in a series of laboratory experiments of restricted rations demonstrated 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 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 noting that an early onset of feeding was required for replenishment of stores following winter. Silverstein et al (1997), working on amago salmon support the hypothesis of a size/energy threshold hypothesis for maturation and suspect that the decision to mature is made very early in development, and relate this to potential differences in size of the energy store defended by these fish. They speculate that these differences could be accounted for by differences in metabolic rates and/or food consumption.

The results presented here support the hypothesis that maturing salmon parr in the wild have increased rates of energy accumulation as well as an early onset of spring feeding. Precocious males had a greater total energy budget than non-maturing parr. It would appear that they require a consumption rate of greater than 2.5-3% of body mass in their year of maturation; approximately 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 non-maturing parr. This would then suggest that precocious males have a different set point with respect to basic energy requirements analogous to the 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 2 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.

An analysis of back-calculated size at age through scale analysis shows an early divergence, or bimodality between 2⁺ parr and 2⁺ precocious males (Figure 7). 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^+ part however there was a similar divergence between 1^+ parr and 1^+ precocious males. 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 (Thorpe 1977; Thorpe et al. 1980; Bailey et al. 1980; Saunders et al. 1982, 1989; Metcalfe et al. 1988; Stefansson et al. 1989). Typically, salmon parr in the upper mode mature. However, it has been more difficult to observe a clear divergence in wild populations of young salmon given the large variations in growth rates and sizes amongst life-history variants (Nicieza et al. 1991). 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 which might reflect their earlier feeding activity compared



Figure 7: Backcalculated size at age for 2⁺ precocious males and nonmaturing parr. Error bars are standard error.

with females. The results of over-winter feeding rates, which integrate spring time feeding, demonstrate that there is a sub-population of male part at each site with an early onset of feeding or which maintained higher feeding rates over the winter. A similar scenario has been observed in laboratory populations over winter, where there is a suppression of appetite to a maintenance ration for part 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.

Atlantic salmon and Brook trout energy budgets

In general, salmon had consumption rates 2 times greater than brook trout. This difference was manifested at a fundamental level as trout had a field maintenance ration half that of salmon parr. This difference is further exacerbated when considering salmon precocious male salmon.

The lower growth efficiencies observed for salmon are probably due to increased metabolic costs associated with higher activity costs. On average, salmon parr spent 2.4-fold more energy in activity than trout. Salmon precocious males spent 1.7 times more in activity than non-mature parr. Activity is probably related to swimming costs associated with the high feeding rate of salmon. 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. Trout, with activity multipliers of 1 virtually had no extraneous activity costs associated with their stream margin, opportunistic feeding strategy. However, the feeding strategy of salmon allows them to maintain growth rates that are 2-fold greater than trout on average, despite higher overall costs and activity.

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 1949). Odum and Pinkerton (1955), considering energy flow through organisms, speculated 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. In addition, it was outlined that low efficiency is necessary for maximum output. Thus, maximum output entails high throughput with low efficiency of energy use. Subsequently, it was argued that we might expect to see a range of species or spectrum of energy strategies within a given system depending upon the rate of supply of limiting raw materials.

In this study, we have outlined three energy budgets that are fundamentally different with respect to maintenance ration and subsequently energy strategies. On one extreme, the brook trout has a low maintenance ration, lower consumption rates, higher growth efficiency and lower costs associated with its strategy. Atlantic salmon parr have a high maintenance ration, higher consumption rates, lower growth efficiencies and subsequently high activity costs. However, the salmon is able to maintain higher growth rates on average. Behaviourally, this is accomplished by a defended ration through the establishment and maintenance of territories. On the other extreme, precocious males have even greater consumption rates, lower growth efficiencies and higher activity costs than salmon parr.

Thus, we have a spectrum of energy budgets 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 trout, or throughput and outputs are maximized with a sacrifice to efficiency, as in the case of precocious males. Non-maturing salmon part are intermediate between the two. Activity can be perceived as an investment to secure a high input of energy resources. Trout minimize costs in general by assuming a more sedentary, opportunistic existence within the stream margins or lower flow areas. Their strategy is clearly efficient as activity multipliers are at the minimum. The activity multipliers for trout are some of the lowest observed for both endothermic and ectothermic organisms (Hammond and Diamond 1997). Salmon activity multipliers are within the high range observed for fish (Rowan and Rasmussen 1996; Hammond and Diamond 1997). Thus in a general sense, it appears that fish with low maintenance rations are set for high efficiencies while those with high maintenance rations are set for high outputs. The maintenance ration can be perceived as an integrative, set point energy requirement of a particular species or life history variant displaying a particular feeding strategy and living within a particular system. It is fundamental to the subsequent allocation of energy to other components of the budget and reflects different energy

strategies. Furthermore, it has implications for the competitive allocation of food resources within a stream.

Habitat use has been used almost exclusively as an indicator of competitive dominance between sympatric populations of juvenile lotic salmonids (Hearn 1987). This is based on Chapman's (1966) hypothesis that food limitation is mediated through space limitation or territoriality. That is, competition for space substitutes for direct competition for food, cover and other resources. Habitat segregation and overlap has since been assessed for nearly all combinations of stream salmonids (e.g. Gibson 1978, 1981; Kennedy and Strange 1982; Cunjak and Green 1983). In these studies, one of the paired salmonids is declared competitively superior based on its dominance of a "preferred" habitat based on its value as a food acquisition site, cover, or access to cover. The greatest potential net energy gain is thought to be obtained by maintaining positions in minimal currents adjacent to swift flows (Fausch 1984; Puckett and Dill 1985). Such positions are postulated to require minimal energy expenditure to maintain and have the highest drift concentrations. Furthermore, Puckett and Dill (1985) calculated that territorial fish had a net energy intake advantage over other fish because of reduced costs associated with search and pursuit of prey.

In these studies however, little or no consideration is given to actually defining the energy demand, capacity or strategy of these salmonids. Total inputs and outputs to energy budget are not measured with the implicit assumption that that they have similar energy demands. The results presented here suggest that territoriality and the feeding

strategy of salmon are more costly than previously thought as they are exploiting a high energy regime. Furthermore, territorial fish were shown to have a higher maintenance ration. As such, they would be perceived of as having a net energy intake advantage over non-territorial fish when in fact both types of fish are balancing their respective budgets. Territoriality might be a necessity to secure and protect a food source in order to meet high intrinsic food demand. In addition, results suggest that habitat segregation is a result of energy segregation or species specific differences in energy requirements and use. The choice of habitat could be contingent on its yield of required food supply balanced with the associated costs of occupying that habitat. Studies have suggested that there is a negative correlation between the observed presence of trout and growth of large salmon in pool-type habitats (Gibson and Dickson 1984) or have shown an inverse correlation between brook trout and salmon densities (Ryan 1993) in lakes although the mechanism of potential competition is unknown. The difference in intrinsic maintenance rations presented here, coupled with the link between habitat and rates of food delivery provides a framework for considering density dependent, territorial and competitive interactions amongst these fish. High densities of trout might be able to meet their food demands in large pools. Large salmon might not be able to balance their high-energy requirements with foraging costs in these environments as there are more diffuse prey sources or lower rates of food delivery. This problem would be compounded by the presence of trout.

Each of these energy strategies could be advantageous under different circumstances. Whether the coexistence of salmon and trout is stable or unstable is unclear, however these alternate strategies might allow for a complementary division of resources, as either salmonid could exploit an unusable portion of the resource; either fast-flow water or low food concentration areas. Indeed, total salmonid biomass is often highest in the presence of two paired salmonids (Kennedy and Strange 1980; Gibson and Haedrich 1988; Gibson et al 1993). In this context, competitive superiority is questionable and could depend on various circumstances such as the productive capacity of the system, existing densities and extraneous conditions and events.

Differences in energy budgets amongst sites

There were significant differences in total energy budgets of salmon amongst sites. Salmon parr and precocious males in Allaire and Xavier, despite the highest feeding rates, had the lowest growth efficiencies as costs associated with activity were highest in these streams. Maintenance rations in these streams were also highest. Since it is unlikely that basal metabolic rates are fundamentally different amongst salmon of a similar life history strategy, the differences in maintenance rations likely integrate differences in activity costs associated with living in particular streams. There were no differences in energy budgets amongst parr and precocious males in Xavier. However virtually all parr were female as the incidence of precocious maturation in this stream was approximately 90%. Thus, it appears parr will feed at high levels if given the opportunity or requirement to do so.

The observed site-specific differences in growth efficiencies for salmon and trout within the Ste-Marguerite River system suggest potential differences in stream productivity, habitat suitability, or a link between habitat and food availability (Chapter 2). No one has yet been able to adequately quantify or relate stream invertebrate production to lotic fish production given the problems associated with quantifying benthic invertebrate standing stocks and drift dynamics (Waters 1988; Power 1993), yet it is likely that differences in growth efficiencies reflect differences in energy regimes mediated through density dependent factors, stream conditions, habitat suitability and overall growth opportunity.

Applications of the ¹³⁷Cs mass balance technique

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 trout-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. This type of approach, relating growth and life history strategies to the energy budget, was successful in describing and modeling niche shift and sexual maturity of Arctic char (Forseth et al. 1994). This was possible in their study and in ours through the application of the ¹³⁷Cs mass balance technique, which allows for broad comparative work.

We have presented two refinements to the ¹³⁷Cs method. First, we have estimated consumption rates for individual fish by combining the mass balance method with explicit age analysis. 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-dependent mortality. This approach is preferable when dealing with scarce or endangered stocks.

Second, we have presented a simple method to estimate ¹³⁷Cs assimilation efficiency for fish populations in the field. Aquatic invertebrates were the dominant prey items in both the diets of salmon and 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 ¹³⁷Cs assimilation efficiencies by tracking the passage of a nonassimilated marker through the gut represents a considerable refinement to the method as the assimilation of ¹³⁷Cs can contribute most to the uncertainty of consumption rates. 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 ¹³⁷Cs uptake by fish.

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 salmon parr 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 an evaluation of the integrated factors controlling Atlantic salmon and sympatric salmonid production.

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Chapter Two

Food exploitation rates by stream salmonids - a reappraisal of the Allen paradox

Introduction

Growth of juvenile salmonids is variable in the field (e.g. Bley and Moring 1988; Bjornn and Reiser 1991; Chapter 1). It has been suggested that this variation is caused by differences in invertebrate production, biomass or drift rate (Bjornn and Chapman 1968; Cada et al. 1987; Richardson 1993; Filbert and Hawkins 1995). However, a direct link between secondary production and fish production, although generally acknowledged to exist, has never been established for streams (Waters 1988; Power 1993). Analyses of production budgets of salmonid streams have generally shown that benthic invertebrate production is insufficient to support salmonid exploitation rates and production. This phenomenon is termed the "Allen paradox" and stems from the finding that the calculated trout consumption was 40-150 times the standing stock of invertebrates in the Horokiwi stream, New Zealand (Allen 1951). Estimates of invertebrate turnover rates indicate that such exploitation rates are unfeasible (Waters 1988). Downward revisions in both the estimated trout production (Chapman 1967; Le Cren 1969) and consumption rates (Gerking 1962) have been suggested. However, the discrepancy remains large despite these corrections. Community feeding rates have never been derived for Atlantic salmon. Moreover, no estimates of benthic production or of other food sources have been made for Atlantic salmon streams in North America (Waters 1993).
There have been few attempts since Allen (1951) to estimate total predation by fish in streams yet all subsequent fish consumption rates have been found to be in excess of invertebrate production. Horton (1961) estimated fish exploitation to be 9-26 times the mean standing stock of benthic invertebrates. Allan (1983) considered both invertebrate and brook trout predation in order to account for all invertebrate production. He obtained closer agreement between food availability and food use, however the discrepancy still existed. Fish exploitation rates ranged between 8-25 and still exceeded invertebrate turnover rates. Waters (1988) concluded in a review of stream fish and benthos production that, of 12 trout streams for which there were data on invertebrate production. More recently, Huryn (1996) found no surplus production by benthic invertebrates in a New Zealand trout stream. A balanced budget could only be obtained if all other food sources were considered and if trout were consuming more than 80% of benthic production.

Clearly, the paradox is only apparent, as fish populations are obviously obtaining sufficient food. Several reasons have been proposed to account for the discrepancy in invertebrate and fish production related to methodology and the complex dynamics of lotic systems. The first has to do with problems associated with accurate, quantitative sampling of stream benthos, and subsequently estimating invertebrate production (Power 1993; Waters 1993, 1988). Most estimates of benthic standing stocks have probably been underestimated to some degree (Kroger 1972; Waters 1988). However, totally accurate measurements of the benthos will not resolve the discrepancy entirely (Waters 1993).

The second main problem revolves around defining the food requirements and use of fish. In attempting to estimate fish community exploitation rates in streams, all previous studies have relied on inferring consumption rates from growth data using physiological, bioenergetic models, or food conversion efficiencies. These approaches can result in large errors in consumption (Gerking 1962; Rowan and Rasmussen 1996). Gerking (1962) argued that Allen's initial consumption estimates were at least 2-3 times too high as he applied adult growth efficiencies to the whole population. For similar reasons, it has been suggested that Horton (1961) overestimated trout feeding rates by at least a factor of two (Allan 1983). Allan (1983) estimated consumption rates for brook trout (Salvelinus fontinalis) using Ellliot's (1975) equations of maximum daily ration for brown trout (Salmo trutta) and acknowledged his estimates might be too high. Huryn (1996) based estimates of trout feeding rates on literature derived growth efficiencies as well. It is likely that these general corrections have not been sufficient to resolve the deficit, as consumption rates and growth efficiencies for salmonids and fish in general can vary significantly amongst sites (e.g. Rowan and Rasmussen 1996; Chapter 1). Apart from failing to estimate food use by fish directly, researchers have often neglected to consider other food sources in the diet apart from the traditional benthos (Waters 1988). This can include to a large degree terrestrial insects and other invertebrates (Mills 1989; Power 1993).

The potential influence of food availability on consumption rates and the interaction between food and other habitat attributes in determining overall habitat quality has subsequently been poorly defined. For example, current velocity affects potential prey encounter rates (Bjornn and Chapman 1968; Smith and Li 1983; Hill and Grossman 1993) for juvenile salmonids as well as abilities to detect and capture prey (Hughes and Dill 1990; Hill and Grossman 1993). Physical habitat features have been the focus of most studies of habitat suitability in salmonid streams and have neglected the potential link to food availability (Nislow et al. 1998).

The objective of this study was to compare fish food use in two streams, with explicit site- and age-specific consumption estimates, to food availability with independent estimates of invertebrate production. Measuring fish consumption directly is more precise and integrates all food sources in the diet, potentially alleviating problems associated with the Allen paradox. The two streams differed greatly in their hydrodynamic regimes and fish community structures. Food use at the system level was then related to individual fish energy demands (Chapter 1), observed population structures and habitat differences amongst the two streams.

Site description

The watershed area of Allaire is approximately 15 km². The stream has a dense cover of riparian vegetation throughout its reach. Allaire runs over a bed of large boulders of 0.5m to 1m in diameter, particularly in the upper reaches, mixed with large cobble, rubble and coarse gravel. The gradient of the stream is fairly constant at 8.5%. Habitats are typically rapids and riffles interspersed with pools, and vertical drops can often exceed 0.5m at summer water levels. Pools range in size and depth with depths of 1m in some pools in

the upper reach. On average, water velocities are $0.68 \text{ m} \cdot \text{s}^{-1}$, with a range of $0.58-0.86 \text{ m} \cdot \text{s}^{-1}$ during summer months, although there are marked variations amongst rapids and pools. The only fish species found in this stream are juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). Typically, trout are found within the larger pools and salmon in the rapids, riffles and adjoining small pools. The highest incidences of precocious males are found in the upper reaches where there are the greatest constrictions of flow amongst the large boulders (unpublished observations 1996 and 1997).

The watershed area of Morin is approximately 18 km^2 . The substrate of the stream ranges from coarse cobble and small boulders in the upper reaches, to gravel, to fine gravel and pebbles, and finally to sand in the lower 250m. Habitats range from riffles, very few pools, to smooth, shallow, laminar flow areas. Average water velocity during summer is 0.48 m·s⁻¹, with a range of 0.38-0.62 m·s⁻¹. Again, cover of riparian vegetation is relatively dense, although it thins in the lower reaches. Atlantic salmon, brook trout and longnose dace (*Rhinichthys cataractae*) are present in Morin. The distribution of salmonids shows a general size and age gradient paralleling the substrate and habitat gradient of the stream, with the youngest fish found in the lowest reaches. The stream gradient is 6.8% in the upper reaches and levels off to 1.7% in the lower 500m. Nests and newly emerged salmon have been found in the spring in the lower gravel sections. Longnose dace are also found only in this lower section of the stream.

Methods

Fish Densities

Densities of fish were estimated by the removal method (Zippin 1956, 1958) for four sites at 500-m intervals (beginning at 250m from the mouth of the stream) in both Allaire and Morin at the end of June, July and August during the summer 1997. Sites were approximately 30m in length with an area of 100m⁻². Block nets were placed at both upstream and downstream ends and electrofishing was carried out in an upstream sweep with a minimum of 3 passes covering the entire section. Mean summer densities were determined on an age specific basis. Age was determined for salmonids from stream specific size-at age distributions developed from explicit age analysis in the previous chapter. Densities of precocious males were determined through observed incidences from independent samples in each stream (Chapter 1).

Fish Consumption Rates

Annual age-specific consumption estimates were measured for juvenile Atlantic salmon, including precocious male parr, and brook trout using a ¹³⁷Cs mass balance method as outlined in Chapter 1. Total fish consumption per site (C_s ; $g \cdot d^{-1} \cdot m^{-2}$) was calculated by integrating age-specific biomass for salmon and trout multiplied by mean age-specific consumption rates analogous to Boisclair and Leggett (1985):

$$C_s = \sum \overline{D}_a \cdot \overline{C}_a \cdot \overline{w}_a$$

where D_a is mean age-specific density (#·m⁻²), C_a is mean annual age-specific consumption rate (g·g⁻¹·d⁻¹) and w_a is mean age-specific weight (g). The proportion of terrestrial invertebrates in the diet (Allaire: 12% for salmon, 22% for trout; Morin: 15% for salmon, 22% for trout) was subsequently factored out of fish consumption rates.

Given the low densities of resident trout in Morin, it was difficult to justify sacrificing them in sufficient numbers to estimate consumption without *a priori* knowledge that the individual approach would work (Chapter 1). Since brook trout had similar consumption rates and growth efficiencies across age classes in two different streams (Chapter 1), we assumed they would be the same for trout in Morin. Given the low densities of individual age classes of trout, age 0 and 1, 2 and 3 and 4⁺ trout were grouped together. In addition, we assumed that longnose dace (*Rhinichthys cataractae*) had consumption rates of 0.031 g·g⁻¹·d⁻¹ (Trudel and Boisclair 1993; Rowan and Rasmussen 1996).

Benthic Invertebrate Production

Mean annual benthic invertebrate production (P; $g_{dry mass} m^{-2} year^{-1}$) was estimated for each stream using the model of Morin and Bourassa (1992);

$$P = 0.18 \cdot B^{1.01} \cdot M^{-0.34} \cdot 10^{0.037 \cdot T} \quad (r^2 = 0.87, SE_{est} = 0.117, n = 291, P < 0.0001)$$

where B is biomass ($g_{dry mass} \cdot m^{-2}$), M is mean individual mass ($g_{dry mass}$) and T is the mean annual water temperature (°C). Sampling of invertebrates by Surber and kick nets

was caried out at 4 sites, adjacent to fish density sites, at the beginning of June, July and August as well as the end of August 1997. Mean biomass was obtained from estimates of mean benthic invertebrate densities and mean weight. Mean standing stock for Allaire and Morin were 1500 $\# \cdot m^{-2}$ and 2150 $\# \cdot m^{-2}$ respectively; mean invertebrate weight for both streams was 0.002 g_{wet}. Wet weights were converted to dry weights using a wet:dry ratio of 0.14 obtained from benthic invertebrate samples .

Results

Invertebrate production estimates

Mean invertebrate biomass for Allaire and Morin were 0.42 $g_{dry} \cdot m^{-2}$ and 0.60 $g_{dry} \cdot m^{-2}$ respectively. Invertebrate production was estimated to be 2.8 g $_{dry} \cdot m^{-2} \cdot year^{-1}$ for Allaire and 4.1 g $_{dry} \cdot m^{-2} \cdot year^{-1}$ Morin. Turnover rates or the P/B ratios were subsequently 6.7 yr⁻¹.

Fish densities and size distribution

Total salmonid densities in Morin ranged from 9.7 to 35.5 fish 100m⁻² amongst sites. Morin also had a large population of longnose dace, 57 fish 100m⁻², found only below the 500m point in the stream. Total salmonid densities in Allaire ranged from 11.5 to 15.9 fish 100m⁻² amongst sites. There were significant differences in age specific densities among the two streams (Figure 1). As well, size at age was significantly greater in Allaire (Table 1). Allaire was dominated by older age classes of salmon parr and brook trout (Table 2) as well as a high incidence of salmon precocious males (60 % of males). Morin was dominated by younger age classes and lower incidences of precocious males (40 % of males) as well as lower densities of brook trout.

Total Fish Consumption and Exploitation Rates

Age-specific consumption rates for Atlantic salmon parr, precocious males and brook trout are summarized in Table 1. Total fish consumption for Allaire was 1.89 ± 0.29 $g_{dry} \cdot m^{-2} \cdot year^{-1}$ (Figure 2). Total salmonid consumption for Morin was 0.71 ± 0.13 $g_{dry} \cdot m^{-2} \cdot year^{-1}$ (Figure 2). Longnose dace consumption in Morin was 1.95 $g_{dry} \cdot m^{-2} \cdot year^{-1}$, bringing total fish consumption to 2.66 $g_{dry} \cdot m^{-2} \cdot year^{-1}$ for that stream.

The ecotrophic coefficient for Allaire, or the amount of food consumed to food production, was 67%. The ecotrophic coefficient for salmonids in Morin was 18%. However, when considering longnose dace, the other consumer fish species, the total ecotrophic coefficient rises to 65%. Total exploitation rates, or the proportion of benthic invertebrate biomass consumed by fish ($C_{fish}:B_{invert}$), were subsequently 4.5 year⁻¹ for Allaire and 4.4 year⁻¹ for Morin.



Figure 1: Mean densities of age classes (0-4) of Atlantic salmon parr (S), precocious males (PM) and Brook trout (T) from Morin and Allaire. Error bars represent standard errors.

Stream	Age class	Mean Weight	C ± se
		± se (g)	(g'g ^{-l.} d ^{-l})
Morin	S 0	11+02	0.024 ± 0.001
	S1	3.2 ± 0.2	0.024 ± 0.001 0.023 ± 0.001
	S2	3.2 ± 0.3 8.0 ± 0.8	0.023 ± 0.001 0.024 ± 0.001
	DM1	5.0 ± 0.0	0.024 ± 0.001
	DM2	3.4 ± 1.4	0.034 ± 0.001
		11.2 ± 1.1	0.038 ± 0.001
		1.8 ± 0.2	0.017 ± 0.001
	12	8.8 ± 2.5	0.014 ± 0.001
	T4	19.9 ± 2.4	0.012 ± 0.002
	Rhca	4.3 ± 0.5	0.032 ± 0.01
Allaire	S 0	1.5 ± 0.3	0.034 ± 0.004
	S1	6.3 ± 1.1	0.034 ± 0.004
	S2	14.2 ± 1.3	0.030 ± 0.003
	PM1	7.8 ± 2.0	0.037 ± 0.005
	PM2	184 ± 17	0.048 ± 0.003
	TO	23+02	0.017 ± 0.001
	T2	86+25	0.014 ± 0.001
	τ <i>ι</i>	0.0 ± 2.0	0.017 ± 0.001
	14	39.0 ± 3.0	0.012 ± 0.002

Table 1: Mean annual size and consumption rates (C) for age classes of salmon parr (S), precocious males (PM), brook trout (T) and longnose dace (Rhca) from Morin and Allaire

Stream	Section	Age class	Density (#100m ⁻²)	Stream	Section	Age class	Density (#100m ⁻²)
Morin	250m	narr ()	26.1	Allaire	250	narr ()	16
	230111	parr 1	62			parr 1	27
		pan i	1.6			parr 2	2.1 A 5
		+2	1.0			pan 2	4.5
		rhea	57.0			pm 2	0.5
		mua	57.0				1.4
	750	norr 1	6.2			10	3.7
	/ 50m	parr 1	0.2			12	1.7
		parr z	2.3		760		2.0
		pm 1	1.7		/ 50	parr 1	2.0
		pm 2	2.3			parr 2	4.7
		tÜ	3.5			pm 1	0.2
		ť2	0.7			pm 2	1.5
						tO	1.5
	1250m	parr 1	2.8			12	2.8
		parr 2	3.4			t4	3.2
		pm 1	1.4				
		tO	6.6		1250	parr 1	1.6
		t2	1.7			parr 2	0.3
						pm 1	0.5
	1600m	parr 1	2.7			pm 2	2.5
		parr 2	2.6			tO	1.5
		pm 1	1.4			ť2	4.0
		t0	0.9			t4	1.1
		t2	1.5				
		t4	0.6		1750	parr 1	0.8
						parr 2	0.3
						om 1	0.3
						pm 2	2.0
						t0	31
						12	44
						12 14	7.7 2 A
							4 .7

Table 2: Density of fish (#100m⁻²) by site for Morin and Allaire.



Figure 2: Mean total food consumed by age class for salmon parr (S), precocious males (PM) and brook trout (T) for Morin and Allaire. Error bars represent standard errors.

Discussion

Invertebrate production and fish exploitation rates

This is the first study in which community exploitation rates have been estimated explicitly for salmonids feeding in streams. Only the study of Boisclair and Leggett (1985) estimated fish community consumption rates directly through an analysis of feeding rates and biomass for individual species and age groups. However, this was for fish in the littoral zone of lakes. All previous studies, including studies on salmonid streams, have inferred fish consumption rates from growth data using physiologically based models. This approach in part, has lead to Allen paradox. Several authors have speculated that for systems in equilibrium, predator consumption should approximate production of food (Slobodkin 1960; Sheldon et al. 1977). That is, fish community exploitation rates should approximate the turnover or P/B ratio of the benthic prey assemblage. However, it is unlikely that fish would consume the entire benthos production as there is, for example, emergence of adult insects from streams many of whom are consumed by terrestrial predators. Consequently, production in excess of fish consumption must be postulated (Waters 1988). The results here, unlike all previous studies, bear out this assertion, as in both streams total fish exploitation was less than the invertebrate P/B ratio. Fish in Allaire consumed annually 67% of the available benthic invertebrate production. Exploitation rates were subsequently 4.5 year⁻¹. Invertebrate production (2.8 $g_{drv} \cdot m^{-2} \cdot year^{-1}$) was thus in excess of fish consumption (1.89 $g_{drv} \cdot m^{-1}$) ²·vear⁻¹). Salmonids in Morin consumed only 18% of the available production. However, when dace were considered, 65% of the food production was consumed by fish. The exploitation rate of 4.4 year⁻¹ was subsequently less than the invertebrate P/B of 6.7 year⁻¹. The values of standing crop invertebrate biomass reported here of 0.60 g_{dry} ·m⁻² for Morin and 0.42 g_{dry} ·m⁻² for Allaire are low compared to other estimates from temperate and northern streams, e.g., Horton, (1961) reported values of 1.5-3.5 g_{dry} ·m⁻² in the Walla Brook, UK; MacKay and Kalff (1969), 2.2 g_{dry} ·m⁻² in West Creek, Quebec and Coffman et al. (1971), 4.8 g_{dry} ·m⁻² in Linesville Creek, Pennsylvania. In a review of published estimates of invertebrate production and turnover ratios Waters (1977) concluded that P/B values between 4-7year⁻¹ were typical for most univoltine and bivoltine species and values of 1-3 were usual for longer-lived species. Allan (1983) estimated P/B ratios ranging between 3-8 for invertebrates in a cold, high mountain stream. Higher annual turnover rates have been documented however these have been in warm-water streams (Waters 1977; Neves 1979; Hall et al. 1980). Thus, it is likely that the P/B value of 6.7 year⁻¹ presented here for both Allaire and Morin is reasonably representative of invertebrate communities in streams of this latitude.

Fish densities between 0.3-26 fish·100m⁻² reported here, are typical of the range observed in other salmonid streams (Kennedy 1988; Mills 1989). For example, Gibson et al. (1993) reported densities of Atlantic salmon to range between 0.5-55 fish·100m⁻² and densities of brook trout to range between 1-25 fish·100m⁻² in both riffle and flat habitats of 3 Newfoundland rivers. Atlantic salmon densities ranging between 2 and 25 fish·100m⁻² were recorded in the Tweed River system, Great Britain (Mills and Tomison 1985) and Allan (1983) reported brook trout densities between 0.8-5.7 fish·100m⁻² in a Colorado stream. However, like the invertebrate production estimates for the two streams in this study, the mean salmonid density of 14.2 fish $100m^{-2}$ for Allaire and Morin is thought to be low as well. In general, juvenile salmon densities of < 15 fish $100m^{-2}$ are considered marginal to poor (Gibson et al. 1993).

The exploitation rates presented here fall well below the range reported by other authors. Horton (1961) estimated the exploitation rate of brown trout to range between 8.7-26 times the annual mean biomass. A revision of Allen's estimates for brown trout, placed exploitation rates between 13-75 (Gerking 1962). The high range in exploitation rates is thought to reflect problems in quantifying invertebrate biomass and errors associated with inferred fish consumption rates (Boisclair and Leggett 1985). For example, Allan used Elliott's equation of maximum daily ration for brown trout to derive consumption estimates for brook trout (5.29 g_{drv}·m⁻²·year⁻¹). Allan also considered invertebrate predators in deriving community consumption rates. The total exploitation rate (8.7 year ¹) was subsequently in excess of invertebrate turnover although the magnitude of discrepancy was less than previously reported. A revision of feeding rates (3.44 gdry m⁻ 2 yr⁻¹) using the daily rations for brook trout presented here, places the community exploitation rate (7.4 year⁻¹) and fish exploitation (4.2 year⁻¹) within the range of invertebrate P/B. It is likely that invertebrate predator consumption estimates are too high as well (Allan 1983) which would further reduce the exploitation rate. Conversely, substituting consumption rates in this study with estimates derived from Elliott's (1975) equation of maximum daily ration for brown trout, overestimates total salmonid consumption in Morin by a factor of 3.9 and by 2.8 in Allaire. Subsequently, total fish exploitation rates rise 1.8 fold in Morin to 7.9 year⁻¹, and 2.8 fold in Allaire to 12.6 year⁻¹.

These exploitation rates are above the range of the invertebrate P/B and their use would imply that fish are consuming food well in excess of invertebrate production. The application of Elliott's (1975) consumption estimates to this study, as opposed to the explicit estimates derived for these populations, would thus have confirmed the Allen Paradox.

Uncertainty in fish consumption rates will contribute directly to 1:1 ratio of uncertainty in community exploitation rates. This point emphasizes the necessity of age- and site-specific consumption estimates when attempting to derive fish community exploitation rates. All things being equal with respect to the error associated with estimating benthic invertebrate production, the fish exploitation rates presented here are more reasonable and presumably more precise. We therefore suggest that more careful consideration of fish feeding rates by fisheries and stream biologists can lead to a resolution of the Allen paradox.

Habitat differences and food availability

Previously, we demonstrated that juvenile Atlantic salmon of varying life history strategies as well as brook trout have different energy budgets (Chapter 1). There is a range in energy requirements and allocation. Brook trout were found to have low food intake, lower growth rates and low costs. Atlantic salmon parr were found to have a much higher (2-fold) maintenance ration with high costs associated with their more active and territorial feeding strategy. In addition, precocious males were found to have even a greater energy budget. In this two-stream comparison, differences were noted with respect to individual fish consumption and growth rates as well as differences in population structure and densities. Total densities and food consumption of salmon parr were similar in both Allaire and Morin; what varied was the age distribution and the numbers of precocious males and trout.

Total salmonid consumption was higher in Allaire as there were a greater number of older salmon and trout, as well as a greater incidence of precocious males. Morin was characterized by higher densities of smaller, younger fish, fewer trout and a lower incidence of precocious males. In Allaire, fish were also larger for a given age. On an absolute basis, large fish consume more food than small fish. In addition, relative salmon consumption rates were greater in Allaire for any age class (Chapter 1). As well, precocious males have a consumption rate 1.5 times more than salmon parr. It is likely that high food demanding fish require higher rates of food delivery. It is noteworthy that although both streams have fish community consumption rates on the order of two-thirds the invertebrate production, the salmonid contribution to community consumption appears highly variable, ranging from 27% of the total in Morin to 100% in Allaire. The lower salmonid density and food exploitation in Morin, despite slightly higher food resources, points to physical habitat criteria and the link to food availability as determinant in production. This parallels the issue raised by Boisclair and Leggett (1985) of *potential* vs. *real* food availability in the littoral zone of lakes.

Studies on habitat occupancy for salmon in streams demonstrate that selection revolves around balancing food acquisition with cover from predation. Water velocity is the prime consideration in food availability (DeGraaf and Bain 1986; Morantz et al. 1987) as there is a positive correlation with increasing velocity and the amount of drift (Everest and Chapman 1972). Water velocity selection is subsequently modified by risk of predation and competition (Morantz et al.1987). Typical salmon habitat is described as relatively shallow, moderately fast-flowing riffle sections over coarse substrate such as cobble or rubble (Keenleyside 1962). However there are age and size related differences with respect to habitat preferences, most probably linked to rates of food delivery. Young of the year are typically found in shallow pebbly areas with adequate food supply but subsequently not occupied by competing older juvenile salmon (Symons and Heland 1978). As salmon grow, there is an increasing preference for deeper and swifter parts of riffles (Keenleyside 1962).

Allaire is characterized by higher water velocities, deep pools, intermediate rapid and riffle sections, boulder size substrate, drops, and steeper gradients of approximately 8.5% throughout its reach. Subsequently there are more areas of constricted and high velocity flow; these factors are greater in the upper reaches where one finds the largest trout and highest incidence of precocious males. As salmon nests have never been observed in Allaire, it seems likely that most fish move into the stream to feed. Morin is characterized by lower water velocity, shallow depth and small gravel size substrate particularly in the lower reaches, below 500m were the stream gradient is 1.7%. Fish in the lower section are predominantly young of the year (YOY) and small 1⁺. Most of the larger salmonids are found between 500m and 1250m where the stream gradient becomes considerably steeper at 6.8% and where there are more areas of suitable and typical habitat. Based on

descriptions of habitat preferences, the lower reaches represent ideal nursery habitat for YOY fish (Symons and Heland 1978), yet poor habitat for older fish. Dace, which are benthic feeders are likely profiting from the absence of salmon and the lower stream gradient. It is probable that the greater velocities and constriction of flow in Allaire and the upper reaches of Morin allow for a higher funneling of food and therefore more efficient feeding on drifting insects. Given their respective habitat attributes, Allaire is able to support larger, more energy demanding fish while Morin can best support smaller younger fish.

Differences in salmon consumption, growth, size and incidences of precocious males (Chapter 1) are reflected in differences in habitat amongst other sites as well. The site sampled in the Main River, like Morin, had the smallest fish and lowest incidences of precocious males. Habitat was characterized by cobble riffle sections yet greater depths (0.5m) and higher volumes of water as well as low riparian cover. It is likely that drift is more diffuse at these sites. Xavier, with high salmon consumption, growth and incidence of precocious males had densities approximately 3-fold those of Allaire (unpublished observation). The stream is characterized by a cobble substrate, with a continuum of riffles and small, shallow pools (unpublished observation).

Previous studies have not been able to adequately relate differences in food abundance to differences in food use in streams (Nislow et al. 1998). Consequently, the potential importance of food availability on consumption rates and the interaction between food and other habitat attributes in determining overall habitat quality has been poorly defined.

The energy approach in defining food requirements, coupled to habitat influences on food availability provides insight, albeit descriptive at this point, into the interplay between food delivery and intrinsic energy requirements, and the subsequent structure of overall salmonid populations.

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Summary

This thesis represents a first foray into an explicit examination of field-energy requirements of juvenile Atlantic salmon and brook trout. Conventional methods of estimating food intake through gut content analysis require too much sampling effort and too many fish to justify a broad comparative approach amongst these relatively small stream populations. In general, salmon biologists are interested in a comparative approach, as there are large variations in salmonid growth rates, densities and incidences of life-history strategies within and among systems. Quantifying feeding rates was possible through the application of the ¹³⁷Cs mass balance method. In addition, ¹³⁷Cs assimilation efficiencies were determined by tracking the passage of a non-assimilated marker through the gut. This represents a considerable refinement to the model as most of the error associated with consumption estimates is related to uncertainty in the assimilation efficiency.

Consumption and growth rates for Atlantic salmon parr, precocious males and brook trout were determined for age-classes and individual fish. The latter estimate had the advantage of providing a range of data for a single site, as opposed to a single estimate per age class. This allowed for an evaluation of the relationship between consumption and growth for each species or life-history variant. I subsequently introduced the concept of field maintenance ration as the intercept of consumption over growth. This was reasoned to be analogous to the scenario of zero growth, where fish are merely balancing food input with metabolic costs. In this study, precocious males were found to have a greater total energy budget than non-maturing parr. In addition, salmon parr had twofold greater consumption rates than brook trout as well as lower growth efficiencies and higher metabolic costs of activity related to their feeding strategy. However, the two species differed with respect to their field maintenance ration reflecting two different strategies of energy acquisition and allocation. Defining energy strategies on an individual basis, particularly with respect to the concept of maintenance ration, allows for a more inclusive analysis of competition, territoriality and life-history strategies. These life-history strategies have always been perceived of as involving a decision. However, the difference in maintenance rations outlined in this thesis for salmon parr and precocious males, suggests potential differences in metabolic rates or set-point energy requirements.

The daily consumption rates and energy requirements defined in Chapter 1 provide a definitive first step in examining energy flow at the community level. This was done in Chapter 2 by integrating age-specific rations with density estimates for two streams. In this study, it was found that invertebrate production was in excess of fish consumption. All previous work has outlined the paradox of fish consumption exceeding prey production. There have been few attempts to derive production budgets for salmonid streams, most probably in light of the paradox, and stream biologists have focused on the problems of accurately quantifying benthic invertebrate production. In general, salmon biologists have not focused on measuring energy requirements of stream fish in the field nor have they widely contributed to a systems approach in the lotic environment. Thus, fish consumption rates have always been assumed. This has subsequently lead to

overestimates of exploitation. The results presented here suggest that advances in estimating fish consumption rates can lead to greater resolution in the area of stream ecology where the Allen paradox has persisted for over 40 years. Appendix 1: Data used to calculate growth and consumption rates for individual Atlantic salmon and brook trout from the August 1997 sampling period.

Site	Length (cm)	Weight (g)	Sex	Age	Scale radius (mm)	Annulus radius (mm)	¹³⁷ Cs burden (Bq)
Allaire	9.2	9.5	parr	1	0.463	0.176	120.4
	9.6	9.4	parr	1	0.477	0.161	116.8
	9.6	11.4	parr	1	0.621	0.210	140.3
	10.5	12.3	parr	1	0.562	0.214	69.8
	11	14.4	parr	1	0.611	0.210	165.4
	11.1	19.1	parr	1	0.627	0.300	157.5
	8.5	7.6	parr	1	0.476	0.164	97.5
	8.5	7.1	parr	1	0.535	0.195	85.3
	8.8	8.3	parr	1	0.514	0.149	116.0
	9	9.6	parr	1	0.442	0.151	122.7
	11.1	15.4	parr	1	0.721	0.429	95.4
	10.1	13.5	parr	2	0.600	0.407	84.4
	10.5	13.2	parr	2	0.755	0.411	79.9
	10.7	14.4	parr	2	0.591	0.463	95.1
	11	14.4	parr	2	0.671	0.476	95.6
	11.5	17.1	parr	2	0.665	0.379	126.7
	11.6	18.1	parr	2	0.650	0.289	141.1
	11.6	20.6	parr	2	0.709	0.394	184.5
	11.9	25.3	parr	2	0.709	0.312	278.1
	12	17.7	parr	2	0.702	0.388	135.2
	13.4	29.2	parr	2	0.976	0.614	318.1
	10.1	11.4	parr	2	0.530	0.356	49 .1
	10.9	16.3	рагт	2	0.709	0.390	1 07.2
	11.4	17.2	part	2	0.744	0.440	118.3
	12.4	20.4	parr	2	0.721	0.361	222.0
	8.8	8.4	pm	1	0.537	0.145	104.3
	9.7	14.0	pm	1	0.715	0.231	171.5
	9.7	13.7	pm	2	0.650	0.356	112.7
	10.4	17.4	pm	2	0.665	0.346	175.8
	11. 6	28.1	pm	2	0.807	0.493	275.1
	11.8	26.6	pm	2	0.855	0.629	342.2
	11 .9	27.9	pm	2	0.860	0.589	376.5
	12	21.9	pm	2	0.767	0.535	393.3
	12.3	28.8	pm	2	0.818	0.413	265.7

Atlantic salmon

	12.6	28.7	pm	2	0.868	0.614	368.9
	12.7	27.7	pm	2	0.746	0.627	343.6
	13.1	31.5	pm	2	0.71 9	0.553	456.2
	13.2	28.9	pm	2	0.675	0.426	392.7
Xavier	6.7	3.7	parr	1	0.405	0.243	33.3
	6.7	4.2	parr	1	0.382	0.184	45.0
	7.1	4.4	рагт	1	0.365	0.147	27.2
	7.84	4.7	parr	1	0.375	0.184	38.4
	7.1	5.1	parr	I	0.423	0.210	33.3
	5.8	2.7	parr	1	0.310	0.159	22.1
	6.4	3.2	parr	1	0.306	0.147	17.0
	6.7	3.8	parr	1	0.352	0.134	48.1
	6.8	3.9	parr	1	0.291	0.147	48.3
	7.1	4.9	parr	1	0.405	0.166	56.5
	10.5	13.9	parr	2	0.600	0.382	131.7
	10.5	13.9	parr	2	0.780	0.512	126.7
	7.1	5.4	pm	1	0.413	0.231	33.8
	7.4	5.6	pm	1	0.455	0.247	25.3
	7.7	5.9	pm	1	0.491	0.260	26.0
	7.6	7.1	pm	1	0.426	0.176	43.7
	9.5	12.2	pm	1	0.535	0.224	107.4
	9.6	12.7	pm	1	0.491	0.216	98.7
	10	12.8	pm	2	0.646	0.470	115.2
	9.4	12.9	pm	2	0.574	0.382	116.5
	10. 6	15.1	pm	2	0.662	0.444	138.9
	10.7	17.6	pm	2	0. 776	0.491	163.2
	12.3	26	pm	2	0.618	0.405	263 .1
Morin	8.6	8.04	parr	I	0.434	0.216	34.2
	8.5	7.32	parr	1	0.491	0.170	28.4
	7.3	4.77	parr	1	0.388	0.197	21.1
	6.5	3.78	parr	1	0.317	0.142	16.8
	8.5	7.55	parr	1	0.426	0.147	39.8
	8.4	8.03	parr	1	0.436	0.159	39.6
	8.0	6.58	parr	1	0.583	0.256	26.6
	8.6	7.22	parr	1	0.507	0.241	32.0
	9.2	9.49	parr	2	0.524	0.273	53.0
	9.9	10.72	parr	2	0.498	0.367	61.7
	9.3	10.13	parr	2	0.579	0.231	57.5
	8.9	9.00	parr	2	0.461	0.241	42.9
	9.1	9.64	parr	2	0.476	0.203	54.1
	8.6	8.62	pm	1	0.499	0.231	47.0
	8.9	8.88	pm	1	0.556	0.205	48.8

	9.0	9.74	pm	1	0.543	0.219	49.4
	8.8	10.50	pm	1	0.451	0.226	60.2
	8.7	10.30	pm	1	0.545	0.203	58.7
	8.9	11.20	pm	1	0.608	0.335	73.1
	10.3	14.75	pm	2	0.666	14.8	96.4
Main	6	2.5	parr	1	0.310	0.138	24.2
	6.2	2.8	parr	1	0.323	0.124	11.3
	6.4	3.4	parr	1	0.432	0.201	7.0
	6.5	3.5	parr	1	0.300	0.151	47.9
	6.4	3.5	parr	I	0.403	0.155	29.4
	7.3	5.2	parr	1	0.493	0.231	45.0
	6.1	2.6	рагт	1	0.231	0.092	31.8
	6.4	3.2	parr	1	0.396	0.145	21.3
	6.4	3.4	parr	1	0.273	0.130	30.5
	7.4	4.9	parr	1	0.417	0.168	47.4
	8.7	8.6	parr	2	0.472	0.201	54.1
	9.4	10.4	parr	2	0.541	0.314	65.3
	10.1	12.2	parr	2	0.612	0.434	82.7
	9.2	11.1	parr	2	0.738	0.507	73.8
	8	6.4	parr	2	0.484	0.377	46.1
	8.2	7	pm	1	0.501	0.384	73.3
	6.2	7.8	pm	1	0.252	0.159	40.9
	9	9.5	pm	2	0.480	0.358	65.2
	9	10.5	pm	2	0.639	0.514	79.3

Brook trout

Site	Length (cm)	Weight (g)	Age	Sex m_=mature	Opercular radius (mm)	Annulus radius (mm)	¹³⁷ Cs burden (Bq)
Allaire	6.3	2.8	1		3.6	4.4	1 6 .1
	6.2	2.8	1		3.6	4.2	21.3
	11.4	16.4	2	f	6.4	5.3	108.5
	11.2	16.4	2	f	6.7	5.4	109.2
	10.6	12.6	2	f	6.1	5.6	79.0
	9.9	12.8	2	m	6.5	5.4	80.3
	13.3	29.3	2	m	6.8	5.7	191.2
	10.6	15.8	2	f	6.7	6.5	100.2
	1 6 .1	41.7	3	mm	8.5	7.2	414.6

	14.2	36.3	3	m	8.5	8.1	249.4
	13.1	28.0	3	mf	8.6	7.8	182.4
	13.9	30.9	3	mf	7.8	6.8	202.2
	13.4	28.8	3	f	7.8	7.0	187.8
	1 2.6	24.8	3	f	7.9	7.0	160.6
	11.2	19.5	3	f	7.3	6.4	124.9
	16.1	49.0	3	mf	9.4	7.6	327.7
	11 .9	22.1	3	f	9.6	6.8	142.3
	19	72.5	4	mf	9.2	8.3	539.4
	17.5	74.1	4	mf	9.7	8.6	445.0
	16.7	54.3	4	mm	9.4	8.8	387.7
	16.7	71.9	4	mm	9.9	8.0	345.1
Xavier	12	21.6	3	f	7.0	6.3	127.8
	8.6	6.8	2	m	5.0	4.0	38.3
	8.9	8.1	2	m	5.7	4.9	45.9
	10. 9	14.4	3	f	6.5	5.7	83.7
	10.8	15.3	3	f	6.6	5.8	89.2
	9.3	9.5	3	m	6.0	5.5	54.2

Appendix 2: Data for age-class means of salmon and trout used to calculate growth and consumption rates; initial(W_o) and final (W_f) weights, initial (137 Cs Burden_o) and final (137 Cs Burden_f) 137 Cs body burdens and (137 Csp) 137 Cs concentration in food.

Site	Sex	Age	Wo	Wr	¹³⁷ Cs Burden _o	¹³⁷ Cs Burden _f	¹³⁷ Csp
			(g)	(g)	<u>(Bq)</u>	(Bq)	(Bq/Kg)
Allaire	parr	1	2.3 ± 0.2	10.9 ± 0.9	21.4 ± 1.9	108.8 ± 14.0	4.5
	parr	2	7.0 ± 0.9	17.4 ± 1.0	64.6 ± 9.1	139 ± 12.0	4.5
	pm	1	2.3 ± 0.2	12.2 ± 1.0	21.4 ± 1.9	114 ± 11.3	4.5
	pm	2	7.0 ± 0.9	23.6 ± 1.5	64.6 ± 9.1	318.2 ± 24.1	4.5
Morin	parr	1	2.3 ± 0.1	8.5 ± 0.6	10.9 ± 1.2	34.2 ± 5.1	6.0
	parr	2	5.3 ± 0.8	13.7 ± 1.7	19 ± 4.1	78.9 ± 12.5	6.0
	pm	1	2.3 ± 0.1	9.7 ± 0.4	10.9 ± 1.2	54.7 ± 5.6	6.0
	pm	2	5.3 ± 0.8	17.8 ± 3.3	19 ± 4.1	117.1 ± 23.5	6.0
Xavier	parr	1	1.9 ± 0.2	4.2 ± 0.3	32.5 ± 3.7	30.1 ± 3.2	5.0
	parr	2	5.3 ± 0.1	13.9 ± 1.1	66.7 ± 2.9	122.7 ± 12.3	5.0
	pm	1	1.9 ± 0.2	7.34 ± 1.4	32.5 ± 3.7	69.3 ± 13.5	5.0
	pm	2	5.3 ± 0.1	20.1 ± 3.3	66.7 ± 2.9	154 ± 27.2	5.0
Main	parr	1	2.0 ± 0.1	3.9 ± 0.4	16.3 ± 1.0	21.4 ± 3.1	2.3
	parr	2	3.5 ± 0.3	10.6 ± 1.1	28.1 ± 2.7	64.8 ± 8.8	2.3
	pm	2	3.5 ± 0.3	8.1 ± 0.8	28.1 ± 2.7	65.2 ± 7.8	2.3

Atlantic salmon

Brook trout

Site	Age	W _a (g)	W _f (g)	¹³⁷ Cs Burden _o (Bq)	¹³⁷ Cs Burden ₍ (Bq)	¹³⁷ Csp (Bq/Kg)
Allaire	1	1.9 ± 0.1	3.4 ± 0.5	10.8 ± 1.1	18.5 ± 3.2	4.5
	2	5.3 ± 1.3	12.4 ± 2.4	29.5 ± 7.6	72.2 ± 15.3	4.5
	3	10.6 ± 0.9	20.9 ± 4.0	57.2 ± 7.2	124 ± 26.0	4.5
	4	20.9 ± 1.2	36.6 ± 6.4	110.3 ± 12.1	222.2 ± 43.2	4.5
Xavier	I	2.1 ± 0.2	4.2 ± 0.3	10.7 ± 1.5	23.8 ± 2.9	5.0
	2	5.1 ± 0.2	13.9 ± 1.1	30 ± 2.6	79.1 ± 9.7	5.0

Appendix 3: Weight-¹³⁷Cs body burden relationships for individual and pooled samples of salmon and trout from the Ste-Marguerite river system. Entire model for all brook trout adj. $r^2=0.92$, p<0.0001, n=82; Allaire salmon adj. $r^2=0.92$, p<0.0001, n=65; Main River salmon adj. $r^2=0.92$, p<0.0001, n=48; Xavier salmon adj. $r^2=0.92$, p<0.0001, n=48; Xavier salmon adj. $r^2=0.92$, p<0.0001, n=49.









Appendix 4: Length-weight relationship for all salmon parr and precocious males. Model for salmon parr: $W=0.011L^{3.07}$ (r²=0.98).


Appendix 5: Length weight relationship for all brook trout. Model: W=0.014 $L^{2.94}$ (r²=0.99)



Appendix 6: Salmon scale-length relationship, adj. $r^2=0.84$, p<0.0001, n=243.



Appendix 7: Trout opercular-length relationship, adj. r²=0.93. p<0.0001, n=97



Appendix 8: Sensitivity of consumption estimates to a 10% change in the parameters of the ¹³⁷Cs mass balance model (equation 2).