Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*)

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Abstract: Many salmonids, including brook trout (*Salvelinus fontinalis*), contain both anadromous (migrant) and nonanadromous (resident) forms within a population (partial migration). Although partial migration is commonly observed, the mechanisms governing the adoption of migration or residency are poorly understood. We used field estimates of fish growth coupled with in situ estimates of food consumption rates to demonstrate that a trade-off exists between the ability to efficiently exploit local environments (resident approach) and the capacity to capitalize from large-scale environmental heterogeneity (migrant approach). We demonstrate that in the year before migration, migrant brook trout have consumption rates 1.4 times higher than those of resident brook trout. However, migrants have lower growth efficiencies (ratio of growth to consumption) than residents, indicating that migrants have higher metabolic costs. Residents and migrants also differed in their stable carbon isotope signatures ($\delta^{13}C$), a time-integrated measure that has been linked to habitat use. Fish muscle $\delta^{13}C$ of migrants was depleted by 1 ± 0.1‰ compared with that of residents, and this could not be explained by any biases introduced by the time of sampling or the size of fish sampled. Our findings thus agree with the notion that a link exists between metabolic costs (efficiency) and the adopted life-history strategy.

Résumé : Plusieurs espèces de salmonidés, incluant l'ombre de fontaine (*Salvelinus fontinalis*), présentent des formes résidantes et anadromes, au sein de la même population. Ce phénomène de migration partielle est fréquemment observé mais peu de connaissances existent concernant les mécanismes déterminant l'adoption de l'anadromie ou de la résidence. Nous avons utilisé des estimés de croissance de poissons en milieu naturel couplés à des estimées de taux de consommation in situ pour démontrer qu'il y existe un compromis entre l'habilité à exploiter l'environnement local (approche des résidants) et la capacité a profiter de l'hétérogénéité environnementale à grande échelle (approche des migrants). Nous démontrons que les truites migrantes ont des taux de consommation 1,4 fois plus élevées que les truites résidantes et des efficacités de croissance (le rapport de la croissance sur la consommation) plus faibles que les résidants au cours de l'année précédant la migration. Les coûts métaboliques sont donc plus élevés chez les migrants. De plus, les valeurs d'isotopes stables ($\delta^{13}C$), une mesure intégrant le temps et reliée à l'utilisation d'habitat, diffèrent entre migrants et résidants. Dans les tissus musculaires de migrants les valeurs $\delta^{13}C$ sont inférieurs de 1 ± 0,1 ‰ comparativement à ceux des résidants. Cette différence ne peu pas être expliquée par une analyse biaisée découlant de la période d'échantillonnage ou de la taille des poissons. Nos résultats supportent donc l'idée qu'il existe un lien entre les coûts métaboliques (l'efficacité) et la stratégie de vie qui est adoptée.

Introduction

The diverse patterns of animal migration between geographically separated habitats have generated a widespread interest among biologists. In fish, migrations may occur between freshwater habitats and marine habitats or between fresh and saline waters (diadromy). Anadromy, a specialized form of diadromy, involves the migration of juveniles from freshwater into seawater and the return to freshwater as mature adults for spawning. Interestingly, a population may be composed of individuals adopting migration or residency as life-history strategies (partial migration) (Jonsson and Jonsson 1993). This is commonly observed in most salmonids including Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*), and brook trout (*Salvelinus fontinalis*).

It has been suggested that for a migratory life-history pattern to exist, the gain in fitness from moving to a new habitat minus the costs of moving must be higher than staying in only one habitat (Gross 1987). At first glance, the advantages of migration are evident; mature migrants are usually larger than mature residents and benefit from higher age-

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specific fecundity (Gross 1987). However, because only a fraction of a population migrates, the decision most likely involves a cost-benefit analysis, balancing the growth, reproductive, and mortality potential (such as predation and (or) disease) of the two habitats. Indeed, there is evidence to suggest the existence of a trade-off between the manifestation of migration and sexual maturation in fish populations exhibiting partial migration (Thorpe 1987; Hansen et al. 1989). For example, Atlantic salmon smolts do not mature sexually in the same year in which they migrate and those parr that do mature early do not smolt and migrate. However, it remains unclear as to what causes individual fish within a population to adopt one particular strategy over another (i.e., residency and early maturation versus migration and delayed maturation) (Jonsson and Jonsson 1993).

Bohlin et al. (1996) proposed that a critical threshold in body size must be reached for migration to be initiated. At this threshold, fish will either mature in their present niche or leave (delaying maturity) to seek better feeding opportunities (Jonsson and Jonsson 1993). Gross (1987) has suggested that the most important biological parameter in explaining the occurrence of diadromous migration in fish populations is the relative availability of food in freshwater versus marine habitats. Studies have shown that by changing food availability, the proportion of fish emigrating from a system can be altered (Nordeng 1983; Tipping and Byrne 1996). A lowering of food resources results in an increase in the proportion of fish adopting migration. In this situation, body size or growth is limited by food supply (Forseth et al. 1994), and the migration to areas of higher food availability could allow for a continuation of growth.

It has also been observed that within populations, fast growers often migrate at younger ages than do slow growers (Jonsson 1985; Økland et al. 1993; Forseth et al. 1999). Food supplies in the natal habitat may limit fast growers sooner than slow growers, thus switching to richer feeding habitats earlier may serve to ensure continued growth (Jonsson and Jonsson 1993). However, the opposite has also been documented. Ricker (1938) showed that faster-growing sockeye salmon (*Oncorhynchus nerka*) matured earlier and did not migrate to sea, whereas the slower-growing fish matured only after migrating to sea. A threshold size of migration or growth rate is a plausible hypothesis; however, the explanation is incomplete as most fish surpass the threshold size or achieve high growth rates and still do not migrate. Thus, simply investigating growth rates has been proved inadequate in explaining the divergence of life-history forms.

Estimating the energy intake (i.e., consumption rate) and coupling this with growth may allow for a more complete analysis of the energetic performance of fish and how this may relate to differences in life-history strategies of anadromous fish. For example, Forseth et al. (1999) investigated the partial migration pattern (stream to lake) of brown trout. In their study, brown trout began to migrate at age 2+. They found that age-2+ migrants consumed significantly more than residents; however, a larger proportion of the consumed energy was allocated towards metabolic costs, thereby leaving less energy for growth compared to age-2+ residents. The migrants were possibly leaving because of their poor energetic performance (low growth efficiency) resulting from increased metabolic costs but not necessarily low growth; age-2+ migrants grew faster because of their much higher consumption rate.

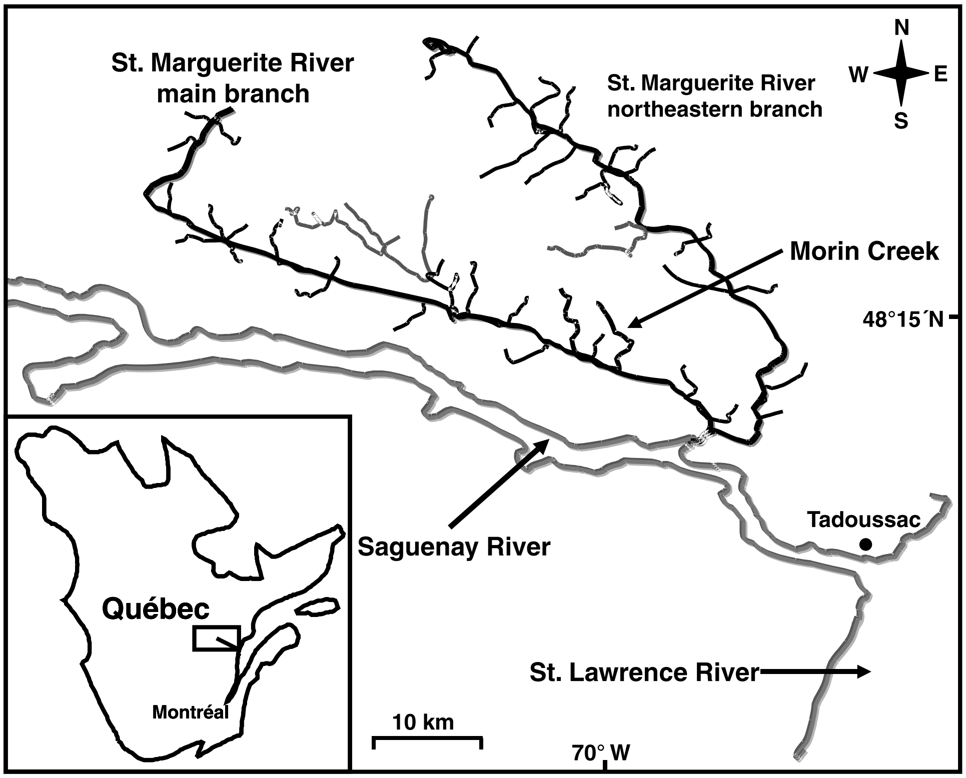
Other studies have also shown indirectly that a link may exist between metabolic costs and life-history strategies (Metcalfe and Thorpe 1992; Metcalfe et al. 1995). Increased metabolic costs could be the result of higher standard metabolic rates (SMR) and (or) activity costs. It has been shown that Atlantic salmon with higher SMR migrated sooner than those with lower SMR (Metcalfe and Thorpe 1992; Metcalfe et al. 1995). Fish residing in fluvial environments may require a higher SMR (higher aerobic scope) to feed in areas of higher food flux and may also exhibit increased activity rates if they are associated with costly habitats, such as those characterized by fast current velocity. Other fish may opt for reducing costs to a minimum when feeding by associating with energy-efficient habitats, e.g., slow currents or pools. Indeed, salmonids tend to position themselves in current velocities at which net energy benefits are maximized, balancing the trade-off between swimming costs and the delivery of drifting prey (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993), leading to a spectrum of habitat preferences. Because different species of salmonids vary in their metabolic capacity for swimming in currents and distribute themselves accordingly, it is very likely that such differences may also be found within a species exhibiting different life-history strategies. Finlay et al. (2002) showed that δ^{13}C signatures of juvenile steelhead trout, a migrant form of *Oncorhynchus mykiss* that lives and feeds predominantly in fast water, were more negative than those of rainbow trout, a resident form of the same species that obtains its food mainly from pools. It thus appears that carbon signatures may help to elucidate the links between velocity regimes, metabolic costs, and life-history variation in the field.

In this study, given a potential link between metabolic costs and life-history strategies, we propose a trade-off between the ability to efficiently exploit a local environment throughout life (resident approach) and the energetic scope required to exploit large-scale environmental heterogeneity (migrant approach). We thus expect to see migrant brook trout exhibiting higher feeding rates than resident brook trout but experiencing lower growth efficiencies, a consequence of higher metabolic costs. In addition, we expected that we might find similar differences in δ^{13}C between migrants and residents as those found in resident rainbow trout and steelhead by Finlay et al. (2002), that is, migrants will have lighter δ^{13}C signatures (indicative of feeding in faster waters) than those of residents.

Materials and methods

This study was conducted in Morin Creek, a tributary of the Ste. Marguerite River system in the Saguenay region of Quebec (Fig. 1). The Ste. Marguerite River is home to the most important anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Populations of anadromous Atlantic salmon and brook trout, as well as resident brook trout, co-occur in this region. The watershed area of Morin Creek is ~18 km^2. Habitats range from riffles to pools, to shallow, laminar flow areas. Average water velocity during the summer is ~0.30 m$\cdot$s^{-1}.

Fig. 1. The St. Marguerite River system in the Saguenay region of Quebec, Canada. Migrant and resident brook trout (*Salvelinus fontinalis*) were obtained from Morin Creek.



Fish collection

The anadromous brook trout of Morin Creek have been observed to migrate as young as age 1+ (G.R. Morinville, personal observation) to the estuarine Saguenay River. The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids (Power 1980). No obvious smoltification occurs in migrant brook trout (McCormick et al. 1985), making it very difficult to differentiate a migrant from a resident until the moment of migration. Thus, fish captured in a downstream trap were considered migrants, whereas those captured in streams following the migration period were defined as residents. Migrant brook trout were captured from mid-May to mid-June 1999. Resident brook trout were captured by electrofishing immediately following the end of migration, in late June 1999. Both fork length (FL, to the nearest millimetre) and total mass (to the nearest 0.01 g) were measured.

Age analysis and growth rates

All trout collected in the summer of 1999 were aged using sagittal otoliths, and the biological intercept method (Campana 1990) was used to back-calculate lengths (Thériault 2001). Because the trout were not captured at the same time in the spring, lengths were back-calculated to the end of the last winter for age-1+ and age-2+ trout and to one year earlier at the end of the previous winter for initial sizes of age-2+ trout. Because of size-selective mortality, the estimated back-calculated size of age-1+ trout at emergence (age 0+) corresponded to the average of the top 10% size of age-0+ brook trout captured in early June. An emergence date of 1 June was assumed. Regressions between length and weight for both migrant and resident brook trout were performed to convert back-calculated lengths to weights for subsequent growth calculations.

Specific growth rates (G; $g \cdot g^{-1} \cdot day^{-1}$ or day^{-1}) were estimated for individual 1999 trout following Ricker (1979):

$$(1) \qquad G = (1/t)\ln(w_t / w_0)$$

where w_t is the final weight (g) at time t (days) and w_0 is the back-calculated initial body weight (g).

Consumption rates

Annual consumption rates (C; $g \cdot g^{-1} \cdot day^{-1}$ or day^{-1}) of migrant and resident brook trout (summer 1999) were estimated using a ^{137}Cs mass-balance model (Rowan and Rasmussen 1996). This method of estimating consumption rates is less labour intensive, requires fewer fish sacrifices, and results in comparable feeding estimates to more traditional methods of estimating consumption rates based on gut clearance models (Gingras and Boisclair 2000). The model is defined as follows:

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

where Q_t is the total quantity of ^{137}Cs in fish, or burden (Bq), at time t (days), Q_0 is the initial ^{137}Cs burden (Bq), Q_g is the gonadal ^{137}Cs burden released at spawning (G), E is the elimination rate of ^{137}Cs ($Bq \cdot Bq^{-1} \cdot day^{-1}$or day^{-1}), D is the radioactive decay of ^{137}Cs ($Bq \cdot Bq^{-1} \cdot day^{-1}$ or day^{-1}), [$^{137}Cs_p$] is the concentration of ^{137}Cs in the diet ($Bq \cdot kg^{-1}$), α is the assimilation efficiency of ^{137}Cs from the diet (fraction), and w_0 is the initial body weight (kg).

^{137}Cs concentration in individual fish was measured by gamma spectrometry with a Coaxial Germanium Detector (Canberra Industries, Inc., Meriden, Conn.). To concentrate samples and reduce the time required to perform analyses, entire fish were ashed at 450°C for 48 h. The initial ^{137}Cs burden for age-1+ fish was assumed to be negligible (~0 Bq) at emergence, as the ^{137}Cs burden can increase several orders of magnitude in fish during their first year as a result of an increase in mass of several orders of magnitude. Initial ^{137}Cs burdens for age-1+ and age-2+ fish were back-calculated from ^{137}Cs body burden versus body weight relationships (see Tucker and Rasmussen 1999). Body burden models were determined independently for residents and migrants. The gonadal ^{137}Cs contribution was ignored because only juvenile fish were examined.

Daily water temperature (T) of Morin Tributary was modelled with a Gaussian function as

$$(3)\qquad T = -0.24 + 19\,\mathrm{e}^{\frac{-(\mathrm{JD}-209)^2}{71.95^2}}$$

where JD is the Julian day.

Elimination rates of ^{137}Cs were obtained using a species-independent model, described by a function of body size and temperature (Rowan and Rasmussen 1995). Morin Tributary specific prey ^{137}Cs concentrations (6 $\mathrm{Bq\cdot kg^{-1}}$), determined on undigested gut contents, and assimilation efficiency ($\alpha = 0.23$) were obtained from a previous study conducted in the same system (Tucker and Rasmussen 1999). The Atlantic salmon value was used because negligible differences exist between brook trout and Atlantic salmon assimilation efficiencies (Tucker and Rasmussen 1999).

Food consumption rates were estimated on a daily basis by interpolating fish size and ^{137}Cs burden between two adjacent age classes. Annual food consumption rates were then determined by summing the daily ration values obtained during these intervals.

Growth efficiency and total metabolic costs

Growth efficiency ($K1$, %) for individual resident and migrant brook trout was calculated as

$$(4)\qquad K1 = (G/C) \times 100$$

Fish with the lowest growth efficiencies will have the highest maintenance costs, defined as the amount of energy required to neither gain or lose weight (Tucker and Rasmussen 1999).

Total metabolic costs (TMC) were determined by incorporating the independently obtained estimates of growth and consumption and solving by difference the following bioenergetics model (Hewett and Johnson 1992):

$$(5)\qquad G = C - (\mathrm{TMC}) - F - U$$

where G is somatic and gonadal growth ($\mathrm{J\cdot day^{-1}}$), C is the total energy consumed ($\mathrm{J\cdot day^{-1}}$), and F (15% of C) and U (10% of C) are fecal (not assimilated) and urinary losses, respectively (Hewett and Johnson 1992). TMC incorporates specific dynamic action, the energy expenditure of digesting and processing food, standard metabolic rates (SMR), and activity costs related to swimming, foraging, and other behavioural activities (unitless). All parameters were converted to energy units with a conversion factor of 3429 $\mathrm{J\cdot g}$ wet weight^{-1} for fish tissue (Cummins and Wuycheck 1971; Hartman and Brandt 1995) and 3176 $\mathrm{J\cdot g}$ wet weight^{-1} for food items of aquatic invertebrates (Cummins and Wuycheck 1971). The relative energy allocation to the various components of the model could thus be computed.

Stable carbon signatures

Stable carbon signatures (δ^{13}C) were measured for a sample of migrant and resident brook trout. In addition, resident trout sampled later in the summer were also analysed to determine whether the signature changed throughout the summer as the fish grew larger. This would allow us to remove any biases associated with small differences in size and time of sampling between the migrants and residents at the time of capture. Samples of white muscle tissue were oven-dried at 75°C for approximately 48 h and individual samples were ground into a fine powder with mortar and pestle. The stable carbon isotope analyses were performed using a mass spectrometer (G.G. Hatch Isotope Laboratories, University of Ottawa, Ottawa, Ont.). The stable carbon isotope ratios are reported relative to a standard (Pee Dee Belemnite) and are expressed as the parts per thousand (‰) deviation from the standard.

Statistical analyses

Brook trout were divided according to trout that migrated at 1+ (1+MIG), trout that were resident at age 1+ (1+RES), trout that migrated at age 2+ (2+MIG), and trout that were resident at age 2+ (2+RES). In addition, the first year of life (age 1) of both 2+MIG and 2+RES were also considered, forming another two groups identified as 1+(2+)MIG and 1+(2+)RES, respectively.

To compare ^{137}Cs concentrations and δ^{13}C signatures of combined (all ages) migrants and residents, t tests were performed. An analysis of covariance (ANCOVA) was performed to compare the relationship of weight and ^{137}Cs body burden for combined migrants and residents. ANCOVAs were also performed to compare the relationship between δ^{13}C as a function of time and as a function of weight for both migrants and residents combined. A one-way analysis of variance (ANOVA) was conducted to compare size at age for combined migrants and residents. ANOVA were performed to compare specific growth rates, consumption rates, and growth efficiency between migrant and resident trout at age 1. Tukey's tests were also conducted for specific comparisons between groups at age 1. Comparisons between age-2+ migrants and residents were performed using t tests. Nonparametric tests were also performed and revealed the same conclusions as parametric tests, and thus the results are not presented. We also used t tests to compare δ^{13}C between migrants and residents.

Results

Specific growth rates

Migrant and resident brook trout collected from Morin Tributary followed different growth trajectories (mean size at age) over time (Fig. 2) prior to migration ($F = 11.6$, $p <$

Table 1. Mean (±1 standard error) growth rates (G), [^{137}Cs], consumption rates (C), and growth efficiency (GE) for groups of resident and migrant brook trout from Morin Tributary.

Type	Age	N	G ($\mathrm{g \cdot g^{-1} \cdot day^{-1}} \times 10^{-2}$)	[^{137}Cs] ($\mathrm{Bq \cdot kg^{-1}}$)	C ($\mathrm{g \cdot g^{-1} \cdot day^{-1}} \times 10^{-2}$)	GE (%)
Resident	1+	16	0.67±0.022	2.9±0.34	1.3±0.083	57±3.5
	1+(2+)	18	0.67±0.029	2.7±0.34	1.1±0.055	60±2.6
	2+	18	0.33±0.0079	3.1±0.42	1.2±0.062	28±1.2
Migrant	1+	38	0.66±0.014	4.3±0.24	1.8±0.081	40±2.2
	1+(2+)	14	0.44±0.023	4.8±0.24	1.9±0.12	25±2.1
	2+	14	0.30±0.012	3.9±0.31	1.7±0.11	20±1.4

Note: 1+(2+) refers to the first year of life of fish aged 2+.

Fig. 2. Mean size at age (+1 standard error) for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*). 1+(2+) refers to the first year of life of fish aged 2+. Numbers above bars represent sample size.

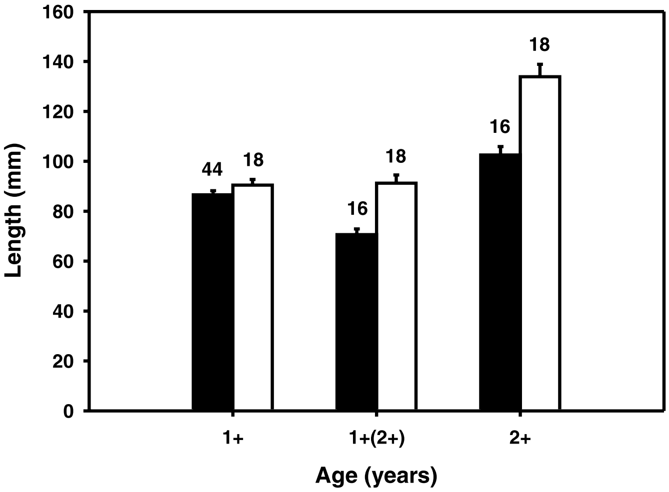
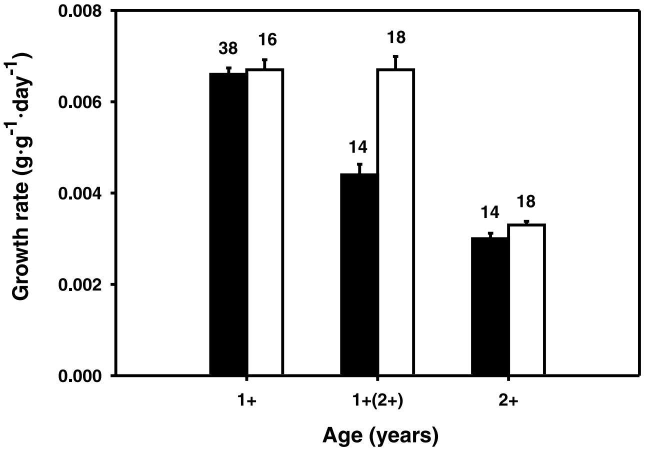


Fig. 3. Growth rates for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*). 1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.



0.001, n = 130). By age 2, residents are 1.3 times larger in size than migrants.

Growth rates for resident brook trout ranged from 0.0033 to 0.0067 $\mathrm{g \cdot g^{-1} \cdot day^{-1}}$ (Table 1; Fig. 3); growth rates for migrant brook trout ranged from 0.0030 to 0.0066 $\mathrm{g \cdot g^{-1} \cdot day^{-1}}$. There was an overall significant difference in growth between age-1 fish (Table 2). Growth rates for 1+RES were similar to those of 1+(2+)RES (p = 0.99), suggesting that growth rates for residents at age 1 did not vary between cohorts. Tukey's tests also revealed no differences between 1+MIG and 1+RES (p = 0.99) or 1+(2+)RES (p > 0.99). However, 1+(2+)MIG had significantly lower growth rates than 1+(2+)RES (p < 0.001) and 1+RES (p < 0.001). In addition, 1+(2+)MIG had lower growth rates than 1+MIG (p < 0.001). There were also no significant differences in growth between 2+MIG and 2+RES (Table 2), even though residents are larger by age 2. This indicates that 2+MIG had the lowest growth rate compared with all other groups in their first year of life and thereafter.

Fish ^{137}Cs body burden relationships

^{137}Cs concentration in resident brook trout varied from 2.7 to 3.1 $\mathrm{Bq \cdot kg^{-1}}$, whereas migrant brook trout had significantly higher ^{137}Cs concentrations, ranging from 3.9 $\mathrm{Bq \cdot kg^{-1}}$ to 4.8 $\mathrm{Bq \cdot kg^{-1}}$ (t = 3.56, df = 86, p = 0.001; Table 1). Migrants had a higher ^{137}Cs body burden as a function of weight compared with residents (F = 4.74, p = 0.032, n = 88; Fig. 4). These migrant and resident specific regressions were subsequently used to assign ^{137}Cs body burdens to individual fish for their respective back-calculated sizes.

Consumption rates

Consumption rates of migrants ranged from 0.017 to 0.019 $\mathrm{g \cdot g^{-1} \cdot day^{-1}}$, whereas residents ranged from 0.011 to 0.013 $\mathrm{g \cdot g^{-1} \cdot day^{-1}}$ (Table 1; Fig. 5). Migrants consumed more than residents at age 1, regardless of the cohort (Table 2). Specifically, 1+MIG had similar consumption rates to 1+(2+)MIG (p = 0.91) and consumed 1.4 times more than 1+RES (p = 0.011) and 1+(2+)RES (p < 0.001). 1+(2+)MIG also had consumption rates 1.4 times higher than both 1+(2+)RES (p = 0.012) and 1+RES (p = 0.001). Migrants also consumed more than residents at age 2 (Table 2). Overall, migrants consumed more than residents in the year(s) prior to migration.

Growth efficiencies and total metabolic costs

Migrants had growth efficiencies ranging from 19.9 to 40.1% (Table 1; Fig. 6). In contrast, residents had higher growth efficiencies than migrants, ranging from 27.6 to 60.2%. There was a significant difference in growth efficiencies between migrants and residents of age 1 regardless of cohort (Table 2). More specifically, 1+(2+)MIG had significantly lower growth efficiencies than 1+RES (p < 0.001) and 1+(2+)RES (p < 0.001). 1+MIG also had lower growth effi-

Table 2. Statistical comparison of the energy budget of migrants and residents using one-way analysis of variance (ANOVA; age 1) and *t* test (age 2).

	Age[a]	*F* (ANOVA)	*t* (*t* test)	df	*p*
Growth rate ($g \cdot g^{-1} \cdot day^{-1}$)	1	12.9	—	82	<0.001
	2	NA	–1.24	30	0.24
Consumption rate ($g \cdot g^{-1} \cdot day^{-1}$)	1	9.4	—	82	<0.001
	2	NA	2.66	30	0.012
Growth efficiency	1	16.6	—	82	<0.001
	2	NA	–3.2	30	0.003

Note: NA, not applicable.

[a] Age 1 includes migrants and residents captured at age 1 and the back-calculated age 1 of fish captured at age 2. Age 2 includes migrants and residents captured at age 2.

Fig. 4. Weight – ^{137}Cs body burden relationships for individual migrant ($F_{[1,52]}$ = 63.5, $p < 0.001$, r^2 = 0.55, n = 54; solid circles) and resident ($F_{[1,32]}$ = 156.3, $p < 0.001$, r^2 = 0.83, n = 34; open circles) brook trout (*Salvelinus fontinalis*) from Morin Tributary.

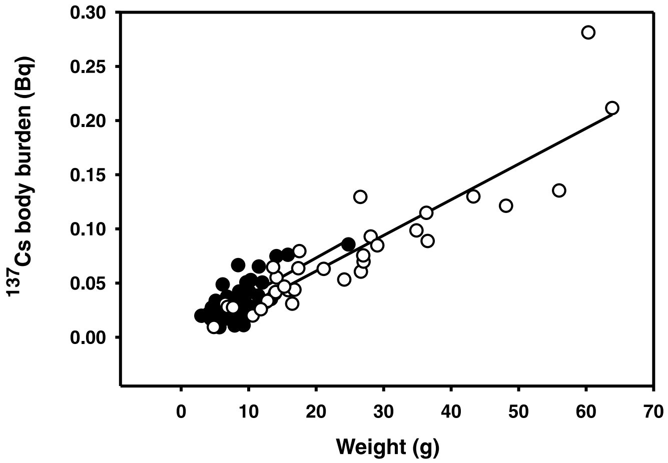
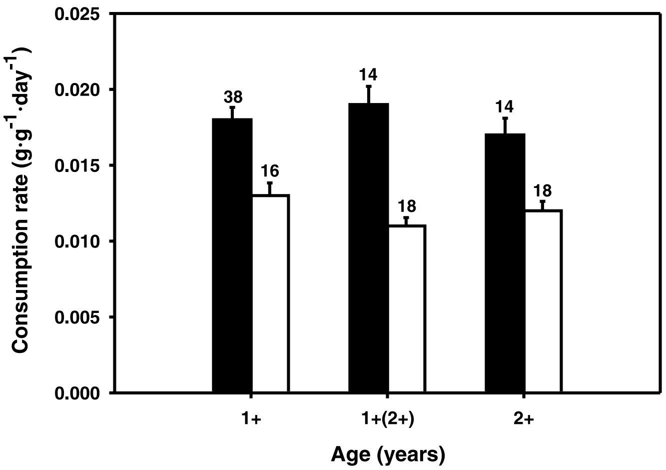


Fig. 5. Consumption rates for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*). 1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.



ciencies than both 1+RES (p = 0.004) and 1+(2+)RES ($p <$ 0.001) but had higher growth efficiencies than 1+(2+)MIG (p = 0.02). In addition, 2+MIG had significantly lower growth efficiencies than 2+RES (Table 2).

Both age-1+ (both cohorts) and age-2+ migrants allocated a higher proportion of their consumed energy to metabolism (38 and 53%, respectively) than residents (25 and 45%, respectively; Fig. 7). The proportion of energy lost to excretion and egestion was considered the same across all fish types (25% of C). Age-1+ and age-2+ residents thus allocated a higher proportion of the energy consumed to growth (62 and 30%, respectively) compared with migrants (36 and 21%, respectively).

Stable carbon signatures

There was no relationship between δ^{13}C and weight for either migrants ($F_{[1,15]}$ = 0.20, r^2 = 0.014, $p > 0.5$) or resident brook trout ($F_{[1,33]}$ = 1.9, r^2 = 0.057, p = 0.17) in the size range concerned. There was also no relationship between δ^{13}C and sampling date in our study for either migrants ($F_{[1,19]}$ = 0.18, r^2 = 0.010, $p > 0.5$) or residents ($F_{[1,41]}$ = 0.32, r^2 = 0.0080, $p > 0.5$). There were no significant differences in δ^{13}C between age-1+ and age-2+ migrants (t = 0.47, df = 18, $p > 0.5$) or between age-1+ and age-2+ residents (t = 0.48, df = 32, $p > 0.5$); therefore, age classes were pooled. As expected, δ^{13}C signatures of migrants were significantly lighter than residents by 1 ± 0.1‰ (t = –4.6, df = 52, $p < 0.001$; Fig. 8).

Discussion

Migrant and resident brook trout bioenergetic budgets

The results obtained from Morin Tributary indicate that, as predicted, migrant brook trout have noticeably different energy budgets than resident brook trout from the same system. No differences in specific growth rates were found between migrants and residents of the same age class, although age-2+ migrants had lower specific growth rates than both age-2+ residents and age-1+ migrants in their first year of life. Moreover, age-2+ migrants were smaller than both age-1+ migrants and age-2+ residents in their first year of life and were thus the smallest part of their cohort at age 1 (Thériault 2001). This contrasts the findings of Forseth et al. (1999) in which age-2+ migrant brown trout were larger (faster growing) than age-2+ resident brown trout. However, no differences in size existed between age-3+ migrant and resident brown trout.

Within migrants, our study supports previously reported findings that faster-growing individuals migrate sooner than

Fig. 6. Growth efficiency for migrant (solid bars) and resident (open bars) brook trout (*Salvelinus fontinalis*). 1+(2+) refers to the first year of life of fish aged 2+. The error bars represent +1 standard error. Numbers above bars represent sample size.

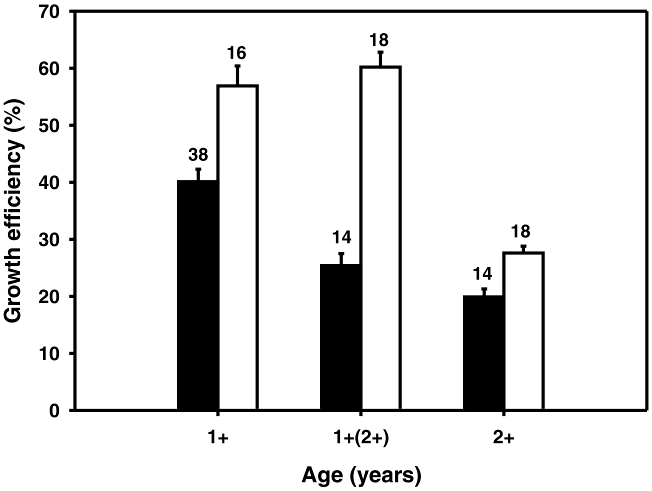
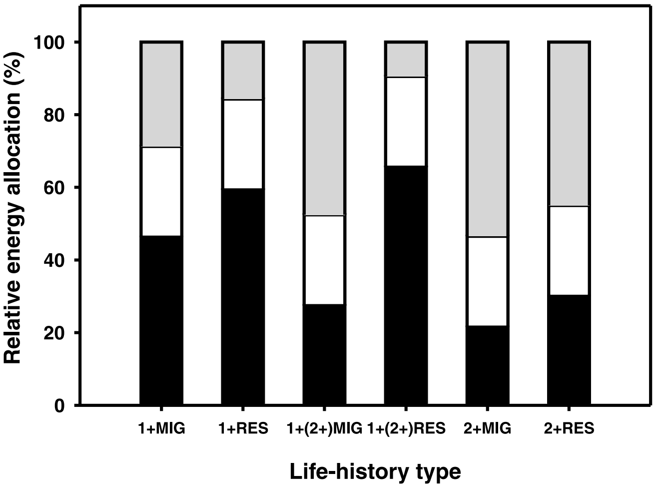


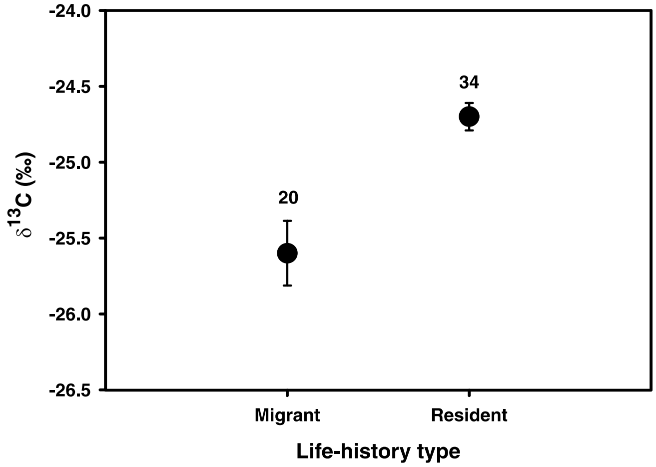
Fig. 7. Relative allocation of energy consumed to the various compartments of the bioenergetic budget of migrant (MIG) and resident (RES) brook trout (*Salvelinus fontinalis*). 1+(2+) refers to the first year of life of fish aged 2+. Solid bars refer to growth, open bars refer to fecal and urinary losses, and shaded bars refer to total metabolic costs including standard metabolic rates, activity, and specific dynamic action.



slower-growing individuals (Jonsson 1985; Forseth et al. 1999), because age-1+ migrants grew faster at age 1 than brook trout that migrated at age 2+. However, when comparing residents with migrants, no differences in growth rates were observed. In addition, the larger age-2+ trout remained residents, whereas the smaller migrated. The inconsistencies regarding size and growth may not be surprising as these are measures of excess acquired energy that ignore any underlying minimum amount of energy required to meet the physiological demands of the fish and ensure survival.

The analyses performed in this study showed that migrant brook trout consumed, on average, 1.4 times more than resident brook trout. As there were no differences in growth rates observed between migrants and residents, the results indicate that migrants require more food to grow the same amount. Migrants thus have lower growth efficiency, a consequence of higher total metabolic costs. As indicated previously, results regarding growth were not consistent between this study and that of Forseth et al. (1999). However, when consumption is included in the analysis, the results agree with those of Forseth et al. (1999) as age-2+ migrant brown trout had lower growth efficiencies than age-2+ resident brown trout. Our bioenergetic results, consistent with those observed by Forseth et al. (1999) for resident and migrant brown trout, highlight the importance of coupling growth rates with consumption rates when interpreting growth differences (or lack thereof) of fish in the wild.

Fig. 8. $\delta^{13}C$ for migrant and resident brook trout (*Salvelinus fontinalis*). Migrants have signatures reflecting use of faster current velocities than residents. The error bars represent ±1 standard error. Numbers above circles represent sample size.



According to the bioenergetic model, growth efficiency differences are the consequence of variations in energy losses related to metabolism. In salmonids, there appears to be a link between metabolic rates, behaviour, and life-history strategies. Variations in metabolic rates may be the result of differences in SMR and (or) activity. Lahti et al. (2001) recently found that migratory forms of brown trout (*Salmo trutta*) were more aggressive than resident forms. In addition, it has been found that Atlantic salmon possessing the highest SMR migrated earlier than those with low SMR (Metcalfe and Thorpe 1992; Metcalfe et al. 1995). These early migrating individuals also exhibited more aggressive and dominant behaviours. Because both Atlantic salmon and migrant brook trout adopt migration as a life-history strategy, it may be argued that there exists a strong behavioural similarity between them. It is thus possible that migrant brook trout, like early-migrating salmon, have the highest SMR compared with their nonmigrating counterparts. This is reasonable to assume because Atlantic salmon also have lower growth efficiencies and higher total metabolic costs compared with resident brook trout (Tucker and Rasmussen 1999).

In fluvial systems, fish tend to position themselves in current velocities at which net energy benefits are maximised (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Swimming in a fast current is more costly than swimming in a slow current (Beamish 1980); however, because a positive correlation exists between current velocity and drift

(Hughes and Dill 1990), a higher food flux is possible in fast current velocities. In general, stream-dwelling brook trout are usually observed in low current velocities, around 25 $cm \cdot s^{-1}$ (Griffith 1972; Fausch and White 1981), whereas Atlantic salmon inhabit faster current velocities, around 50 $cm \cdot s^{-1}$ in the wild (Heggenes 1996; Booth et al. 1997). If migrant brook trout are similar to Atlantic salmon in their behaviour and habitat use, then we might expect differences in food sources between the two life-history strategies as a result of differences in habitat use. According to Finlay et al. (1999), feeding in riffles or fast current will result in a depleted $\delta^{13}C$ signature (more negative) relative to feeding in pools or slow currents, which will result in an enriched (less negative) $\delta^{13}C$ signature. This interpretation is based on significant differences in algal $\delta^{13}C$ between riffle and pool habitats. Because there is the potential for drift-feeding fish to obtain food from a mixture of food sources as a result of the continuous downstream movement of aquatic invertebrates, detecting significant differences in stable isotopes requires low mixing of drift between pool and riffle habitats. High mixing of food sources would result in small or insignificant differences in observed signatures. In Morin Creek, $\delta^{13}C$ in migrants was depleted by 1‰ compared with residents. This difference, although small, was highly significant and could not be explained by any time or size biases. The observed difference in $\delta^{13}C$ is also consistent with expected isotopic differences between riffles and pools. Furthermore, this difference is similar in both magnitude and direction to that reported by Finlay et al. (2002) for steelhead and rainbow trout. Given the three lines of evidence (increased consumption rates, increased metabolic costs, and depleted $\delta^{13}C$), we hypothesize that migrants, like salmon, utilize faster current velocities than residents. This is a plausible explanation because similar differences in $\delta^{13}C$ are observed between Atlantic salmon and resident brook trout in Morin Creek (G.R. Morinville, unpublished data).

Bioenergetic role in partial migration: from stream to sea

This study, by focusing on the early life stages of brook trout, provides support for the idea that variations in energy allocation lead to the adoption of migration or residency as life-history strategies. Although it appears that migrants obtain more food, the fact that they migrate suggests that they do not receive enough energy to satisfy their higher metabolic demands. They most likely enter growth bottlenecks (although not necessarily apparent by simple size measurements) sooner than residents. Migrating, although potentially risky because of increases in predation threats or mortality, could serve to improve energetic performance (lowering total metabolic costs without reducing energy intake) and allow energy needs to be met. This may be similar to when fish make ontogenetic diet shifts to larger prey (Sherwood et al. 2002). This is reasonable to assume as anadromous fish grow faster in the sea than resident fish do in fresh water (Gross 1987; Rikardsen et al. 2000).

The findings suggest that migrants adopt migration most likely as a consequence of energetic limitations. It is thus reasonable to assume that residents are better adapted to living in streams than migrants as they exhibit a more energy efficient life-history strategy. Residents can be considered “winners” in streams as they perform well energetically in their immediate surroundings and are thus not required to leave their local environment. The consequence of their more efficient strategy is a lower food intake and limited growth over their life cycle. On the other hand, migrants possess the energetic scope to capitalize on better feeding opportunities and are thus better adapted to profit from large-scale heterogeneous environments. Migration can thus initially be considered a “losing” strategy as the residents manifest higher growth efficiency in freshwater but ultimately a “winning” strategy because migrants returning from sea to spawn are larger and more fecund. Nonetheless, for the two strategies to coexist, it seems unlikely that overall either strategy wins or loses. Thus the fitness benefits and costs of migration compared with those of residency should balance over the entire life cycle (Jonsson and Jonsson 1993). This most likely involves a balance between growth and predation and mortality risk in the two habitats (Gross 1987).

Interestingly, it was found that brook trout that migrated at age-2+ were the most constrained (lowest growth efficiency); however, possibly because of their small size at age 1, they delayed migration. This would support the notion that a critical threshold in body size must be reached for migration to be initiated (Bohlin et al. 1996). This delay is most likely related to the fact that smaller individuals have higher costs associated with mortality and osmoregulation in the marine environment (Svenning et al. 1992; Økland et al. 1993). However, even though most individuals surpass a critical size, not all individuals adopt migration. Thus it appears that growth efficiency and size may both play a role in determining whether a fish adopts migration over residency.

In conclusion, the present study demonstrates a link between metabolic costs and life-history strategies. In addition, the study supports the idea that a trade-off exists between the ability to efficiently exploit a local environment throughout life (resident approach) and the energetic scope required to capitalize from large-scale environmental heterogeneity across the entire life cycle (migrant approach). This trade-off is an important factor to be considered in conservation and management as a population composed of individuals able to exploit either the local environment or large-scale diverse environmental heterogeneity may be better positioned to persist through unpredictable events such as climate shifts and habitat degradation.

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References

Beamish, F.W.H. 1980. Swimming performance and oxygen consumption of the charrs. *In* Charrs: salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. W. Junik, The Hague. pp. 739–748.

Bohlin, T., Dellefors, C., and Faremo, U. 1996. Date of smolt migration depends on body size but not age in wild sea-run trout. J. Fish Biol. **49**: 157–164.

Booth, R.K., Bombardier, E.B., McKinley, R.S., Scruton, D.A., and Goosney, R.F. 1997. Swimming performance of post-spawning adult (kelts) and juvenile (smolts) Atlantic salmon, *Salmo salar.* Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2406.

Campana, S.E. 1990. How reliable are growth back-calculation based on otoliths? Can. J. Fish. Aquat. Sci. **47**: 2219–2227.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Int. Assoc. Theor. Appl. Limnol. Proc. No. 18.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

Fausch, K.D., and White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. **38**: 1220–1227.

Finlay, J.C., Power, M.E., and Cabana, G. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnol. Oceanogr. **44**: 1198–1203.

Finlay, J.C., Khandwala, S., and Power, M.E. 2002. Spatial scales of carbon flow in a river food web. Ecology, **83**: 1845–1859.

Forseth, T., Ugedal, O., and Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. J. Anim. Ecol. **63**: 116–126.

Forseth, T., Næsje, T.F., Jonsson, B., and Hårsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. J. Anim. Ecol. **68**: 783–793.

Gingras, J., and Boisclair, D. 2000. Comparison between consumption rates of yellow perch (*Perca flavescens*) estimated with a digestive tract model with a radioisotope approach. Can. J. Fish. Aquat. Sci. **57**: 2547–2557.

Griffith, J.S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Board Can. **29**: 265–273.

Gross, M.A. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. **1**: 14–25.

Hansen, L.P., Jonsson, B., Morgan, R.I.G., and Thorpe, J.E. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **46**: 410–415.

Hartman, K.J., and Brandt, S.B. 1995. Estimating energy density of fish. Trans. Am. Fish. Soc. **124**: 347–355.

Heggenes, J. 1996. Habitat selection by brown trout (*Salmo trutta*) and young Atlantic salmon (*Salmo salar*) in streams: static and dynamic hydraulic modelling. Regul. Rivers, **12**: 155–169.

Hewett, S.W., and Johnson, B.L. 1992. A generalized bioenergetics model of fish growth for microcomputer. Tech. Rep. No. WIS-SG-92-250, University of Wisconsin Sea Grant Program, Madison, Wis.

Hill, J., and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, **74**: 685–698.

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**: 2039–2048.

Jonsson, B. 1985. Life history patterns of freshwater and sea-run migrant brown trout in Norway. Trans. Am. Fish. Soc. **114**: 182–194.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Rev. Fish Biol. Fish. **3**: 348–365.

Lahti, K., Laurila, A., Enberg, K., and Piironen, J. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. Anim. Behav. **62**: 935–944.

Lesueur, C. 1993. Compte rendu des résultats obtenus lors de l'étude de l'Omble de fontaine anadrome de la rivière Ste-Marguerite (Saguenay) en 1992. Rapport réalisé dans le cadre du Programme de subvention aux projets à caractères fauniques du ministère du Loisir, de la Chasse et de la Pêche, Association de la rivière Ste-Marguerite, Canada.

McCormick, S.D., Naiman, R.J., and Montgomery, E.T. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **42**: 529–538.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. J. Fish Biol. B, **41**: 93–99.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim. Behav. **49**: 431–436.

Nordeng, H. 1983. Solution to the "char problem', based on Arctic charr (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. **40**: 1372–1387.

Økland, B., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? J. Fish Biol. **42**: 541–550.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: salmonids fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. W. Junik, The Hague. pp. 141–203.

Ricker, W.E. 1938. 'Residual' and kokanee salmon in Cultus Lake. J. Fish. Res. Board Can. **4**: 192–218.

Ricker, W.E. 1979. Growth rates and models. *In* Fish physiology. Vol III. Bioenergetics and growth. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 677–743.

Rikardsen, A.H., Amudsen, P.A., Bjorn, P.A., and Johansen, M. 2000. Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. J. Fish Biol. **57**: 1172–1188.

Rowan, D.J., and Rasmussen, J.B. 1995. The elimination of radiocesium from fish. J. Appl. Ecol. **32**: 739–744.

Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. **53**: 734–745.

Sherwood, G., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**: 229–241.

Svenning, M.-A., Smith-Nilsen, A., and Jobling, M. 1992. Sea water migration of Arctic charr (*Savelinus alpinus* L.). Correlation between freshwater growth and seaward migration based on back-calculations from otoliths. Nord. J. Freshw. Res. **67**: 18–26.

Thériault, V. 2001. Anadromie et résidense chez l'omble de fontaine (*Salvelinus fontinalis*): présence d'une stratégie conditionelle basée sur la croissance? M.Sc. thesis, Laval University, Ste-Foy, Qué.

Thorpe, J.E. 1987. Smolting versus residency: developmental conflict in salmonids. Am. Fish. Soc. Symp. **1**: 244–52.

Tipping, J.M., and Byrne, J.B. 1996. Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. Prog. Fish-Cult. **58**: 128–130.

Tucker, S., and Rasmussen, J.B. 1999. Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **56**: 875–887.