

Body size and the adoption of a migratory tactic in brook charr

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The presence of a conditional strategy based on size attained before migration and a sex-ratio at migration biased towards females were explored in a population of brook charr *Salvelinus fontinalis* in the Sainte-Marguerite River, Quebec Province, Canada, where anadromous and resident forms live sympatrically. Seaward migration in the system occurred at 1 and 2 years old. Comparisons between backcalculated size-at-age of migrant and resident fish revealed that smaller fish at age 1 year delay migration to the following year and that bigger fish either migrated at age 1 year or remained resident for the rest of their life-cycle. Slow growth was associated with migration later in life (age 2 years) at a bigger size, which is consistent with the hypothesis of a threshold size for migration. No difference in size at age 1 year between migrant and resident fish suggests that other factors, such as growth efficiency and the presence of heritability of the tactics, are involved. Overall the sex ratio was equal for migrant and resident fish, while an age-specific bias was found: more males migrated at age 1 year and more females at age 2 years. These differences suggest that different tactics are adopted by different sexes.

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Key words: anadromy; conditional strategy; growth; life-history strategy; otolith backcalculations; *Salvelinus fontinalis*.

INTRODUCTION

Partial migration, the phenomenon in which populations are composed of migratory and resident components, is common in many salmonid species (Jonsson & Jonsson, 1993). A lower mortality rate is probably the main advantage of freshwater residency compared to anadromy in the same population. This benefit, however, is counter-balanced by a significant decrease in fecundity due to limited growth in fresh water relative to growth in the more productive marine environment (Morita & Takashima, 1998).

The theoretical context of the conditional reproductive strategy may be applicable to partial migration in salmonids (Jonsson & Jonsson, 1993). This theory implies a single genetic population in which the adoption of one tactic (in the present case, anadromy or residency) (Gross, 1996; Gross & Repka, 1998) is

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based on the individual's status, which is often associated with growth or size at a given age (Nordeng, 1983; Jonsson, 1985; Northcote, 1992; Thorpe *et al.*, 1998). Growth has an important influence on survival and fecundity at a given age, which determines the fitness attained by the individual (Roff, 1984; Hutchings, 1993, 1996). Growth is thus a component of fitness and may be a cue to individuals in the adoption of a life-history tactic to maximize their lifetime reproductive success.

Conditional strategy theory does not predict how growth influences the migratory tactic, but only that there is a switch point at which one tactic is favoured over the other beyond a critical threshold status. Two situations have been suggested in the literature. Firstly, better growth early in life, often associated with early maturation, may result in residency (Castonguay & Fitzgerald, 1982; Nordeng, 1983; Hutchings & Myers, 1994). Age-specific fecundity and the probability of reproducing are increased for fast growers relative to slow-growers (Hutchings, 1993). Migrants may thus be composed of slow-growers which gain by migrating to a new habitat where feeding opportunities are increased. On the other hand, fast growth may favour migration (Jonsson, 1985; Svenning *et al.*, 1992). Fast growers will be constrained by food limitations sooner than slow growers, and should gain fitness by exploiting richer feeding opportunities (Metcalf *et al.*, 1990; Jonsson & Jonsson, 1993). Moreover, fast growers attain the minimal size for migration [size where costs of mortality and osmoregulation are diminished (Bohlin *et al.*, 1993, Økland *et al.*, 1993)] faster than slow growers and thus migrate at a younger age.

In many partial anadromous species, females predominate among migrants (Jonsson & Jonsson, 1993). Females gain more by being larger at maturity, because of a greater fecundity (Morita & Takashima, 1998) and a competitive advantage in obtaining better spawning sites, as well as access to mates (Holtby & Healey, 1990). Another reason why females often predominate among migrants is that some males mature before migration (by adopting a sneaking reproductive tactic) and hence tend to stay in fresh water (Hutchings & Myers, 1988; Rikardsen *et al.*, 1997).

The fact that size plays a role in the determination of a migration tactic and that a sex-bias towards females is often present within the anadromous form has been documented in salmonids (Jonsson *et al.*, 1990; Svenning *et al.*, 1992; Jonsson & Jonsson, 1993; Økland *et al.*, 1993; Strand & Heggberget, 1994; Rikardsen *et al.*, 1997). Many of the studies comparing size-at-age of migrant and resident fishes, however, did so by comparing lengths of fish of the two forms captured at different times, as migrant and resident cannot be distinguished from each other in their young stages (Strand & Heggberget, 1994; Rikardsen *et al.*, 1997). Comparison of sizes backcalculated to the same time, prior to migration, have rarely been reported (Jonsson, 1985; Svenning *et al.*, 1992; Forseth *et al.*, 1999; Rikardsen & Elliott, 2000). Such backcalculations eliminate any potential misinterpretation due to sampling resident and migrating fishes at different times of the year. Few studies have followed a cohort over >1 year to evaluate how growth performance influences the decision to migrate or stay over successive years (Rikardsen & Elliott, 2000).

Brook charr *Salvelinus fontinalis* (Mitchill) were used in the present study to examine the role of size in the adoption of two alternative tactics: migrating to

sea or remaining resident in fresh water. By coupling backcalculations to sampling over successive years, it was possible to reconstruct the growth history in nature of two cohorts over 2 years and to investigate the relationship between size in years prior to migration and their life-history tactic. The first objective of this study was to examine whether fast or slow growth favours migration in the context of a conditional strategy and the second was to test the hypothesis that female brook charr are more likely to migrate than males.

MATERIALS AND METHODS

SAMPLING OF FISH

The Sainte-Marguerite River system in Quebec, Canada, sustains a large population of anadromous brook charr that migrates into Sainte-Marguerite Bay and the Saguenay Fjord (Fig. 1) before returning to fresh water to reproduce (Lesueur, 1993). Male and female resident brook charr are also present in the river and are mainly associated with tributaries. Fish were collected from one of these tributaries, Morin Creek (average 5.6 m wide, 0.3 m deep) (Fig. 1). Migrants were captured in trap nets during their downstream migration in early spring from 1998 to 2002. Traps were composed of two 5 m wings angled upstream and attached at their downstream end to a centrally-located circular trap composed of two hearts and a terminal wooden container in which trapped fish could find refuge from the current. Traps were set to cover *c.* 80–100% of the width of the stream depending on discharge. Fish caught were marked with 'T-bar' tags (Floy) and released 30 m upstream in 1999 and 2000. Twenty-five per cent (94 out of 374) of the fish

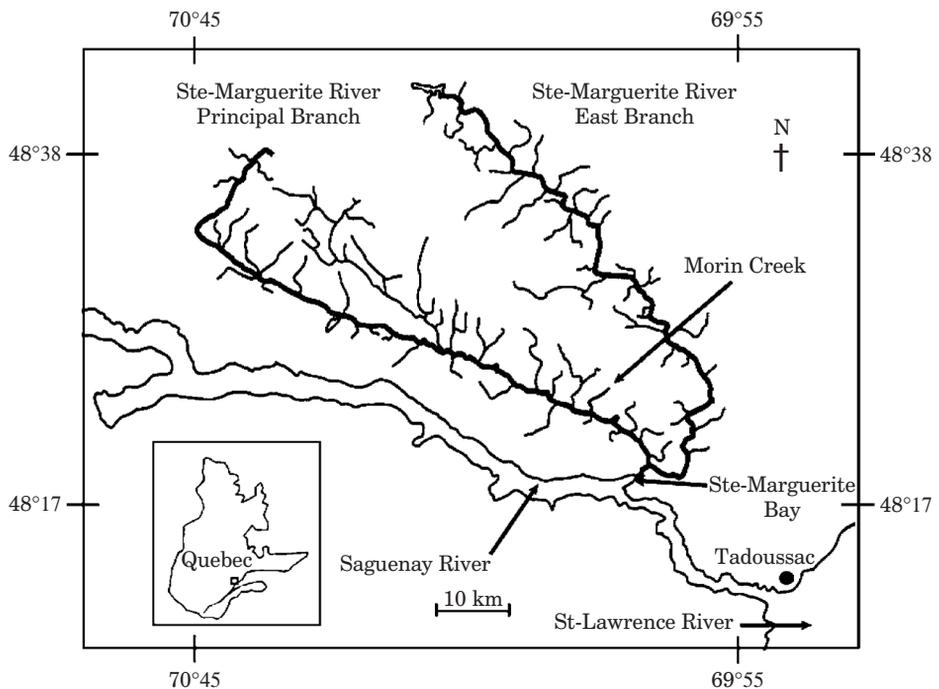


FIG. 1. Location of the study area.

marked were recaptured in the following days in 1999 and 44% (444 out of 1000) in 2000, providing an estimate of the trap's efficiency. Recaptures in other traps set downstream in the main river branch ($n=29$) as well as in the Sainte-Marguerite Bay ($n=45$) and Saguenay Fjord ($n=20$) confirmed that these fish were true migrants. Residents were captured by electrofishing in the same tributary during the summers (June to September) of 1998–2002. Sampling of residents was undertaken once the downstream migration was finished, because migrant and resident fish could not be distinguished from each other at the time of outmigration. All fish caught were measured to the nearest mm (fork length, L_F) and representative subsamples (based on Kolmogorov-Smirnoff comparisons of length distributions between all fish caught and fish sacrificed, $P > 0.15$ for all years studied) of migrant and resident fish were used for sex and age determination; otoliths were extracted from these fish for the latter.

BACKCALCULATION FROM OTOLITHS

As migrant and resident fish were not captured during the same period of time, backcalculations from otoliths were used in order to compare size at the same time for both forms. Size at a given age was used and not growth rate in the strict sense because of the variability in emergence dates present in this system. Spawning of resident fish was described by divers to occur *c.* 15 days before the spawning of anadromous fish, and emergence of resident progeny is also believed to be earlier than that of anadromous progeny. Emergence date could not be backcalculated using otoliths, as daily marks were no longer visible on otoliths of 1+ and 2+ year brook charr. Furthermore, the parental origin of the fish sampled (resident, anadromous or mixed) was not known so corrections could not be made for a potential difference in emergence date. By using size at a given age, growth rate was integrated over a year. Size at a given age is a common measure of growth in migration-decision studies in salmonids (Svenning *et al.*, 1992; Strand & Heggberget, 1994; Rikardsen *et al.*, 1997).

Sagittal otoliths were removed from sacrificed fish and subsequently ground with fine lapping film to the core of the otolith. Age was read and lengths were measured using an image analyser system (Scion/SXM) along a constant axis (from the core to the edge) on one of the pair of otoliths at the beginning of the second and third growing season (age 1 and age 2 years, respectively) [Fig. 2(a)]. The beginning of a growing season was defined by a dark annulus following a pale region on the otolith (Magnan & Fitzgerald, 1983). Length backcalculations were done using the biological intercept (BI) method (Campana, 1990): $L_{Ft} = L_{Fc} + (O_t - O_c)(L_{Fc} - L_{Fo})(O_c - O_o)^{-1}$, where L_{Ft} is the length of the fish at age t , L_{Fc} at capture and L_{Fo} at the BI and O_t is the otolith diameter at age t , O_c at capture and O_o at the BI. This method eliminates the bias caused by the growth effect (the fact that slow growers have bigger otoliths than fast growers for a given body size) by using the length of the fish and of the otolith at the biological intercept, which is empirically determined as fish length and otolith radius at hatching (Campana, 1990).

A parallel experiment was conducted in order to calculate the biological intercept. Eggs from anadromous and resident fish were reared in an *in situ* ascendant flow incubator following a natural temperature regime. Lengths of 50 fry of anadromous parents on the day of hatching were measured from digitized photographs using an image analysis system (Scion/SXM). Otolith length at hatching of these 50 fry was also measured. Five measurements were excluded due to otolith malformation or loss of otolith during removal. No L_F of resident progeny at the day of hatching could be taken as resident progeny were already hatched when the incubator was first visited in early spring. As a hatching mark is visible on the otolith, however, otolith radius at hatching could be measured on otoliths of resident progeny even if they were not directly observed at hatching [Fig. 2(b)]. Mean \pm s.d. L_F and otolith radius at the biological intercept were 14.66 ± 0.75 mm and 66.46 ± 7.1 μ m respectively. There was no significant difference between migrant and resident offspring in the otolith radius at hatching (migrant = 65.91 ± 6.78 μ m, $n=45$; resident = 70.64 ± 8.72 μ m, $n=6$; t -test, d.f. = 49, $P=0.13$). Even if fish size and otolith radius at hatching were different between the

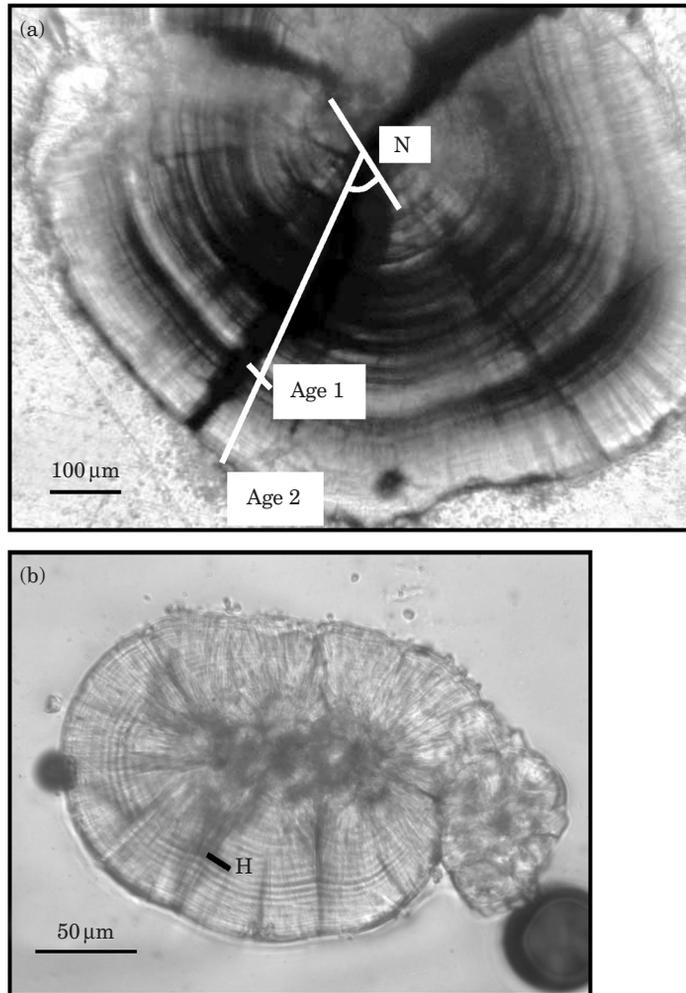


FIG. 2. (a) Sagittal otolith of aged 2 year brook charr. Lengths were measured from the nucleus along an axis forming a 45 degree angle with a line crossing the core vertically. N, nucleus; Age 1, beginning of the second growing season; Age 2, beginning of the third growing season. (b) Sagittal otolith of an 11 day old fry. H, hatch mark. Circuli are visible before hatching.

offspring of migrant and resident fish, large differences would be needed to affect the backcalculations. Because of the small values involved, backcalculation accuracy is relatively insensitive to normal variation around the biological intercept (Campana, 1990).

Two assumptions underlie the use of otoliths to backcalculate size at any given age: (1) the deposition of growth rings is periodic, and (2) proportionality exists between fish length and otolith length (Sirois *et al.*, 1998). The first assumption was confirmed by matching the number of daily increments between hatching and emergence with age (between 1 and 20 days) of the fry [Fig. 2(b)]. The second assumption was verified by regression of L_F on otolith length ($n = 377$, $r^2 = 0.8$; Fig. 3). The relationship was different between migrant and resident progeny (migrant $n = 204$, resident $n = 172$; ANCOVA, interaction term, d.f. = 3 and 369 $P < 0.001$). This difference in slope did not cause a bias

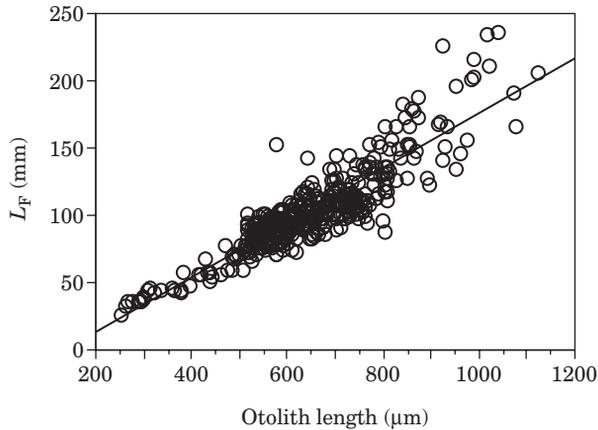


FIG. 3. Relationship between fish length and otolith length. The curve was fitted by: $y = -27.849 + 0.204x$ ($n = 377$, $r^2 = 0.802$).

in the backcalculations, however, as the same biological intercept for both forms was used.

STATISTICAL ANALYSIS

Migrant and resident fish from the 1997 and 1998 cohorts were divided into three groups: fish that migrated at the age of 1+ years (1+MIG), those that migrated at the age of 2+ years (2+MIG) and those that stayed at the age of 2+ years (2+RES). The effects of cohort, sex, groups of fish and the two-way interactions between these variables on backcalculated L_F at age 1 year ($LG1$) and age 2 years ($LG2$) were tested using a generalized linear model (GLM). The model had the following form: $LG1$, $LG2 =$ cohort + sex + groups + cohort \times sex + cohort \times groups + sex \times group. Only variables having a significant effect at a P level of 0.05 were retained in the model. *Post-hoc* tests were performed with a Bonferroni adjustment. Length distributions were also compared with a Kolmogorov-Smirnov test (KS). Results from the KS were qualitatively the same as the ones obtained with *post hoc t*-tests, so they are not presented here. Sex ratios of migrant and resident fish were compared to a 1:1 ratio with Yates corrected χ^2 . Statistical analyses were performed using SAS 8, SYSTAT 8 and STATVIEW 5 and assumptions of parametric tests were verified.

RESULTS

DOWNSTREAM MIGRATION MONITORING

Migrant brook charr left the stream during a short period of time in spring for the 5 years studied (Fig. 4). Portions of the 1998 and 2001 emigrations were missed because of a late start to trap netting. Migration in 2002 occurred later than in other years, probably because of an extremely cold spring that year. Fish left the stream at either age 1+ or 2+ years, 1+ year forming the majority in 1998, 1999 and 2000 (Yates corrected χ^2 , $P < 0.001$) and the proportion was not different from 1:1 in 2001 and 2002 (Yates corrected χ^2 , 2001, $P > 0.05$; 2002, $P > 0.1$). Size at migration was larger for fish that migrated at 2+ years than for fish that did so at 1+ years, for the four cohorts followed (Table I).

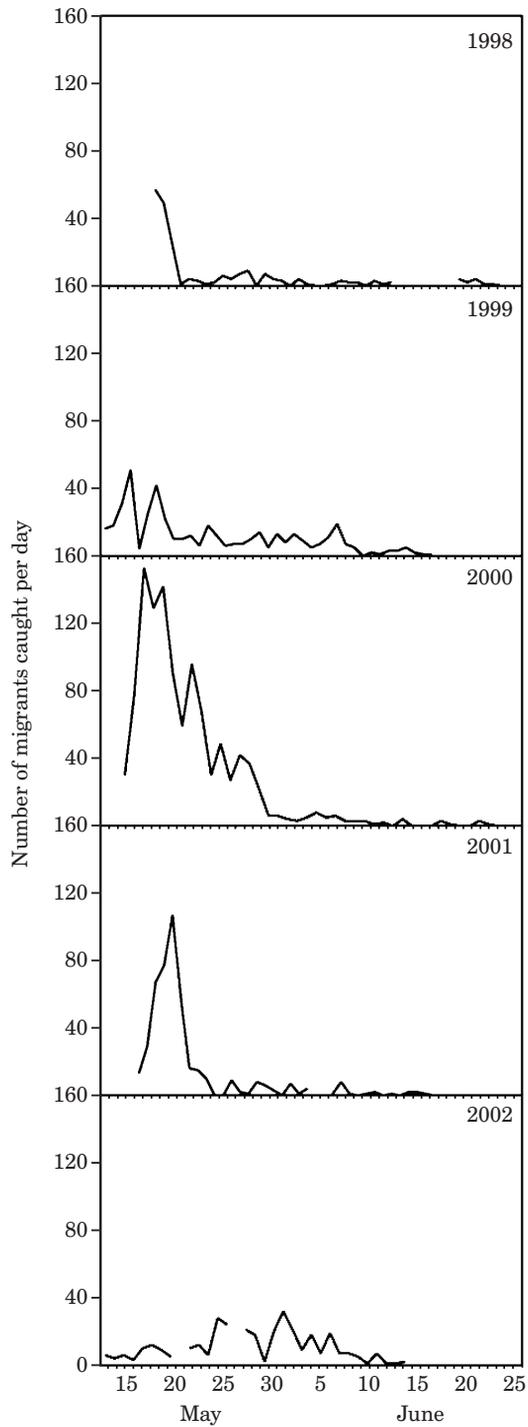


FIG. 4. Number of migrant brook charr caught per day in May and June in the trap in Morin Creek from 1998 to 2002.

TABLE I. Mean \pm S.D. fork length of age 1+ and 2+ year migrant fish captured in the downstream migration trap for each cohort. Heterogeneity among means between aged 1+ and 2+ year fish was tested by an unpaired *t*-test

Cohort	Age (years)	<i>n</i>	Mean \pm S.D. L_F (mm)	<i>P</i>
1997	1	46	91.3 \pm 9.6	0.002
	2	24	101.3 \pm 16.2	
1998	1	68	86.9 \pm 9.9	<0.0001
	2	65	107.6 \pm 16.8	
1999	1	155	82.0 \pm 14.6	<0.0001
	2	12	111.0 \pm 10.9	
2000	1	24	85.0 \pm 7.9	<0.0001
	2	43	105.7 \pm 16.0	

Date of migration was dependent on year and size (for both $P < 0.0001$), but not on age, although most variability was not explained by this model (GLM, $r^2 = 0.026$; $P < 0.0001$). There was a negative relationship between L_F and time of migration in 1999, 2000 and 2002, where L_F tended to decrease with time from the beginning of the migration, indicating that larger fish migrated first (1999, $r^2 = 0.067$, $P < 0.0001$; 2000, $r^2 = 0.036$, $P < 0.0001$; 2002, $r^2 = 0.085$, $P < 0.0001$). In 1998 and 2001, no such relationship was detected, probably because trap netting started later in these years (1998, $r^2 = 0.006$, $P = 0.26$; 2001, $r^2 = 0.001$, $P = 0.6$).

BACKCALCULATED LENGTHS OF MIGRANT AND RESIDENT FISH

The only factor significantly affecting backcalculated L_F at age 1 year was group (ANOVA, d.f. = 2 and 248 $P < 0.001$). Backcalculated L_F at age 2 years was also influenced by group (ANOVA, d.f. = 3 and 126, $P < 0.001$) and by the interaction term sex \times group (ANOVA, d.f. = 3 and 126, $P = 0.015$). The effect of sex on variation in backcalculated L_F at age 2 years differed among groups of fish. In the 1997 cohort, backcalculated L_F at age 2 years of resident and migrant males was not statistically different, whereas L_F of females was. The 1997 male comparison, however, involved small sample sizes (migrant $n = 5$, resident $n = 8$), which may explain why a difference was not detected. As this is the only case where residents were not statistically larger than migrants and is most probably related to sample size, the interaction term is probably not relevant. *Post-hoc* Bonferonni *t*-tests revealed no difference in size at age 1 year between fish that migrated out of the stream at age 1+ years and future residents (1 + MIG *v.* 2 + RES; Table II and Fig. 5). Fish that migrated out at 2+ years were part of the smallest fish at age 1 year as well as at age 2 years (2 + MIG *v.* others; Table II and Fig. 5). Age 2+ year migrants were thus slow-growers. These results indicate that larger fish at age 1 year either migrated or stayed at 1+ years while smaller fish delayed migration and migrated at age 2+ years. Larger 2+ year fish remained freshwater residents.

TABLE II. Bonferroni *t*-test results for backcalculated fork length comparisons between migrant and resident brook charr. Sample sizes are given in parentheses

Backcalculated to age 1 year	Mean \pm S.D. L_F (mm) (<i>n</i>)	<i>P</i>
1 + MIG v. 2 + RES	85.91 \pm 10.45 (109) v. 86.79 \pm 12.94 (58)	0.6271
1 + MIG v. 2 + MIG	85.91 \pm 10.45 (109) v. 72.47 \pm 10.74 (84)	<0.0001
2 + MIG v. 2 + RES	72.47 \pm 10.74 (84) v. 86.79 \pm 12.94 (58)	<0.0001
Backcalculated to age 2 years	Mean \pm S.D. L_F (mm) (<i>n</i>)	<i>P</i>
2 + MIG v. 2 + RES	104.79 \pm 15.19 (84) v. 125.33 \pm 18.31 (58)	<0.0001

SEX RATIO

Data on sex ratio were not reliable for 1998, so analyses were restricted to the years 1999–2002. Sex ratios were not different from 1 : 1 among migrants in any year or age group except in 2000 and 2002. In 2000, females were more abundant within the 2+ year age class and less abundant within the 1+ year age class and in 2002 females were also less abundant in the 1+ year age class (Fig. 6). Sex ratio was also 1 : 1 among resident fish for both years and each age class except again for 2000 where females were less abundant than males in the 2+ year age class (Fig. 6) and in 2002 where overall, males were more abundant.

DISCUSSION

By using backcalculated size-at-age to reconstruct the growth history of two cohorts over 2 years, slow growth was found to be associated with migration later in life and at a larger size, and larger individuals tended to migrate earlier during the migration season than smaller fish. Cohorts followed over successive years revealed a general pattern of migration similar to that of juveniles of brown trout *Salmo trutta* L. (Jonsson, 1985; Bohlin *et al.*, 1993, 1996), Atlantic salmon *Salmo salar* L. (Thorpe, 1987; Metcalfe *et al.*, 1989, 1990) and Arctic charr *Salvelinus alpinus* (L.) (Svenning *et al.*, 1992; Strand & Heggberget, 1994; Rikardsen & Elliot, 2000). These observations suggest that migration implies size-dependant costs, being higher for smaller individuals, and are consistent with the hypothesis of a minimal size for migration. Mortality costs associated with osmoregulation and predation are generally greater for smaller individuals (Ward *et al.*, 1989; Svenning *et al.*, 1992; Bohlin *et al.*, 1993; Økland *et al.*, 1993). Smaller 1+ year brook charr delayed migration and migrated at an older age (2+ years) and larger size, which should contribute to minimizing mortality associated with small size. Similarly, within a season, smaller fish stayed longer in the stream and migrated later, probably taking advantage of additional growth before migration. This suggests a strong selection pressure acting on size at migration. A parallel mark-recapture study conducted in the Sainte-Marguerite River revealed no size-selective mortality, as individuals recaptured that survived the first year in salt water had the same size distribution at migration as the overall population (S. Lenormand & J.J. Dodson, unpubl.

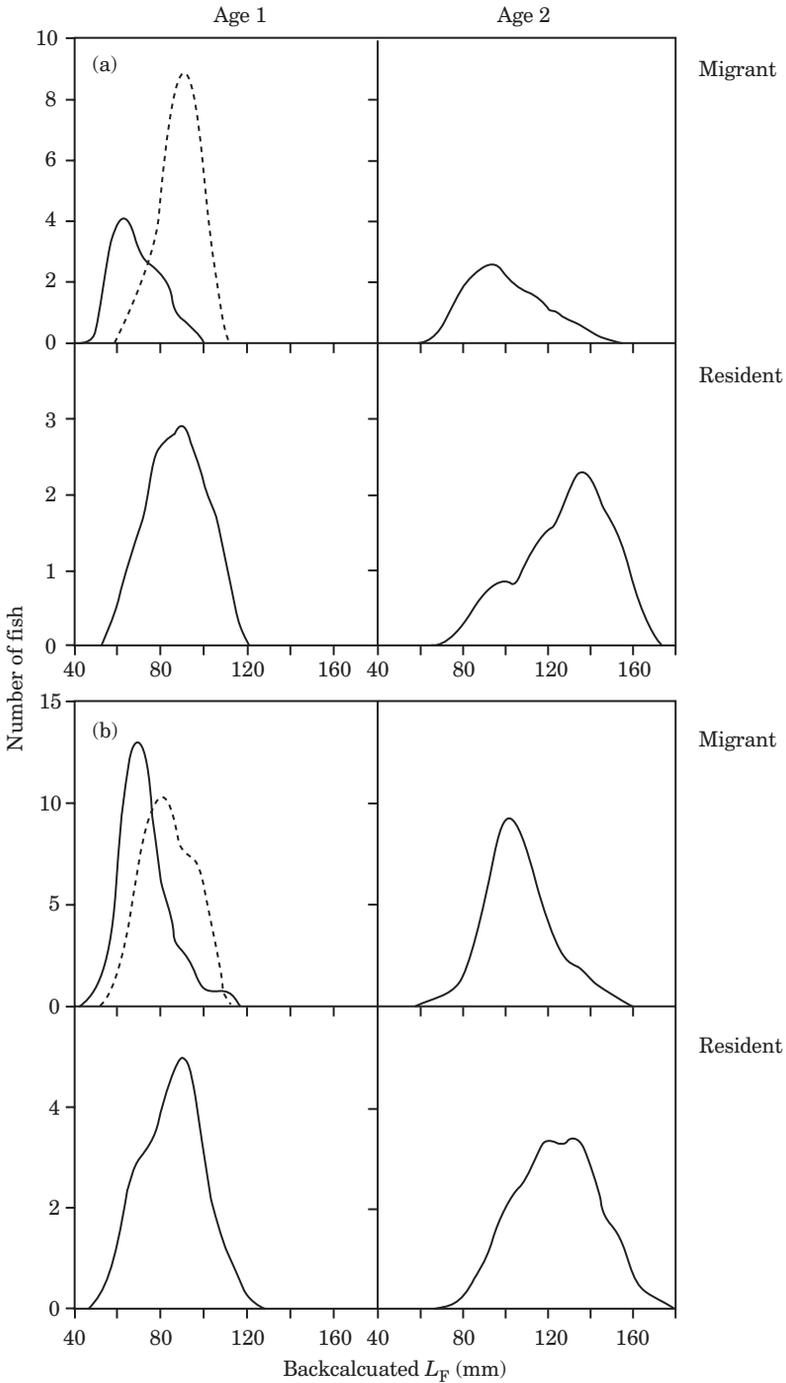


FIG. 5. Backcalculated fork length distributions at age 1 and 2 years of migrant and resident fish for (a) 1997 and (b) 1998 cohorts. Migrants were separated between fish that migrated at 1+ (1+MIG) (---) and fish that migrated at 2+ (2+MIG) (—). Residents were composed of fish that remained in fresh water at 2+ year (2+RES) (—). (See Table II for a comparison of mean sizes).

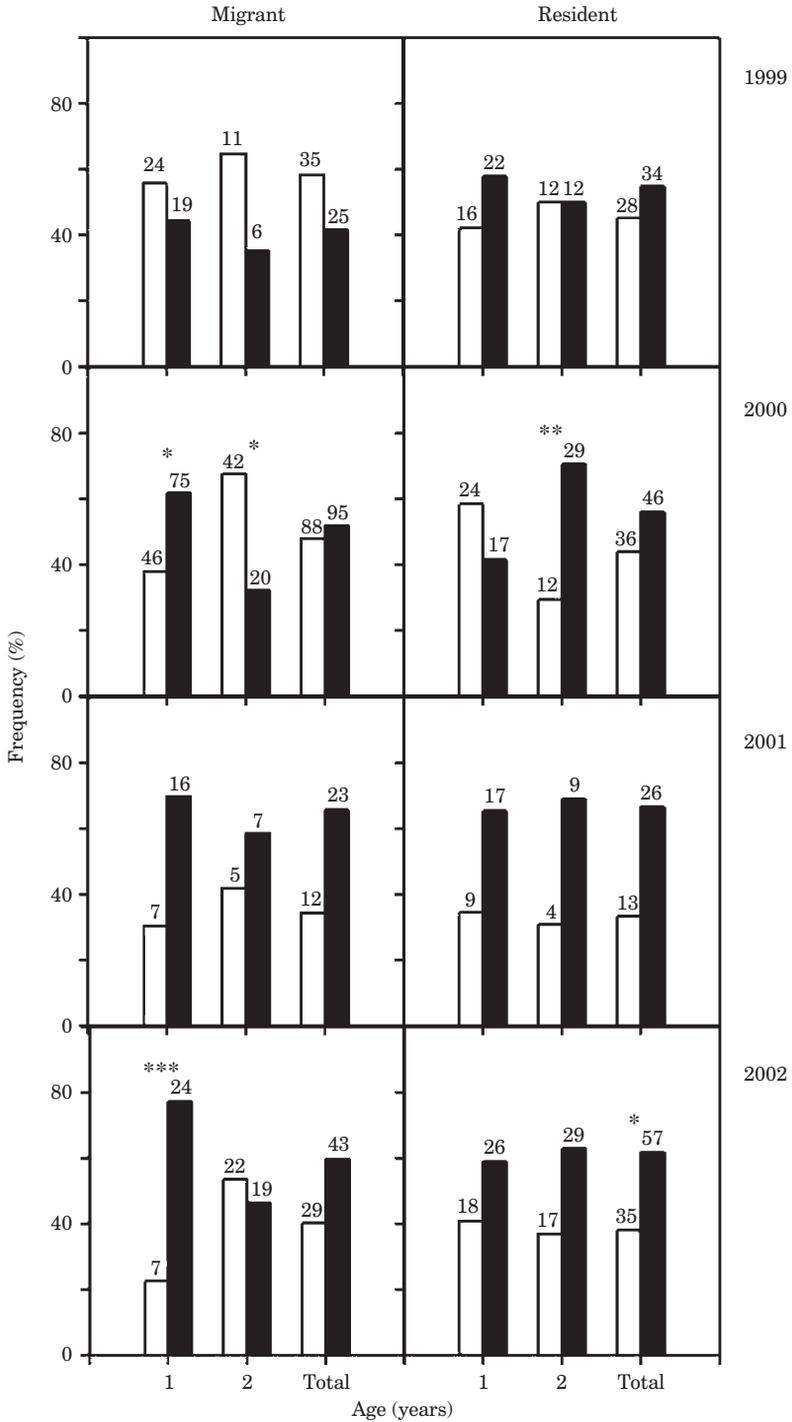


FIG. 6. Sex frequencies of age 1+ and 2+ years and both ages combined (total) for migrant and resident brook charr from 1999 to 2002. Numbers on top of bars for female (□), and male (■) fish. Comparisons with a 1 : 1 sex ratio were made by χ^2 * P < 0.025; ** P < 0.01; *** P < 0.005.

data). It appears that only individuals larger than a threshold size migrate, so mortality following migration is independent of size at migration.

Comparisons between backcalculated size-at-age revealed that smaller fish at age 1 year delay migration to the following year, when they are still the smallest fish of their cohort, and that larger fish can either migrate at age 1 year or stay resident for the rest of their life-cycle. The finding that migrant and resident exhibited no size difference at age 1 year is different from the results obtained for Arctic charr, in which younger migrants were always larger at the time of first migration compared to similar aged resident fish (Svenning *et al.*, 1992; Strand & Heggberget, 1994; Rikardsen *et al.*, 1997; Rikardsen & Elliot, 2000). It is possible that other factors, potentially related to growth rate, might affect the adoption of the tactic such as metabolic rate, lipid stores and social status (Thorpe, 1987; Thorpe *et al.*, 1998; Forseth *et al.*, 1999; Rikardsen & Elliott, 2000), and may explain why a size difference at age 1 year is not seen. A parallel study (Morinville & Rasmussen, 2003) using the same individuals captured in 1999 showed that migrants consumed, the year prior to migration, 1.4 times more food than residents, but that 1+ and 2+ year migrants allocated a higher proportion of their consumed energy to metabolism (38 and 53% respectively) than residents (25 and 45% respectively) and consequently a smaller proportion to growth. Migrants, thus, have a lower growth efficiency, a consequence of higher total metabolic costs, which could be due to differences in standard metabolic rate and activity. This difference in growth efficiency is not reflected in different sizes at age 1 year. Forseth *et al.* (1999) found similar results in studying the migration of brown trout between stream and lake habitats. Growth rate *per se* could not explain why some individuals migrated and some did not whereas their relative energy allocation to growth could. These findings suggest that size-at-age is not the only factor that contributes to status, or condition, which influences the tactic that is adopted in the context of a conditional strategy.

Heritability is also a potential reason for the adoption of a tactic. Although speculative at this time, it is possible that a threshold size is present only among that part of the population that inherited the migratory tactic. Most or all of the individuals having inherited the migrant tactic will migrate, but at different ages depending on their growth performance. Most or all individuals that inherit the residency tactic may remain in the stream regardless of their size. Heritability of reproductive tactics has been estimated on several occasions (Silverstein & Hershberger, 1992; Heath *et al.*, 1994; Wild *et al.*, 1994; Mousseau *et al.*, 1998) or has been demonstrated by crosses, in which anadromous parents produced more anadromous progeny than resident parents and *vice versa* (Nordeng, 1983). Heritability of the factors determining the status, (size, growth and developmental rates) has also been demonstrated (Thorpe, 1987; Garant *et al.*, 2002, 2003). Although inheritance could have an important influence on the tactic adopted (Gross & Repka, 1998), based on heritability estimates reported to date, it is unlikely that the expression of a threshold level to migrate would be uniquely determined by the inheritance of the migratory tactic within the theoretical context of the conditional strategy. Environmental factors influencing growth (or the underlying processes such as metabolic rate), as well as genetic factors such as a significant heritability, may act together to influence

the adoption of a migrant or resident tactic. Studies of environmental factors combined with genetic factors would be of great interest in studying partial anadromy in the context of the evolution of life-history strategies.

Strand & Heggberget (1994), Rikardsen *et al.* (1997) and Rikardsen & Elliott (2000) also found no bias in sex ratios at downstream migration for anadromous Arctic charr in Norway, nor did Spidle *et al.* (1998) for coho salmon *Oncorhynchus kisutch* (Walbaum). Populations in these systems all have a high degree of anadromy, with mature resident fish relatively rare [only 8.4% of the non-migrating fish were mature in Strand & Heggberget's (1994) study] and early-maturing males were not abundant (10–30% of the males matured before migration in Rikardsen *et al.*'s 1997 study). The relative proportion of migratory and resident fish in the Sainte-Marguerite River brook charr population is not known, but mature males do not predominate over females among the resident fish (the sex ratio is not different from 1:1 between mature males and females; unpubl. data) and early maturing males are not present. Migration occurred at 1 or 2 years of age and hence before maturation, which occurred generally at 3 years of age. The present data do not support the hypothesis that females move in a larger proportion to salt water. Two alternative hypotheses may apply: (1) the gain in fitness by migrating to salt water is the same for males and females and (2) segregation between the two forms (or a strong heritability of tactics) is present such that the sex ratio is 1:1 for both forms.

Although overall sex ratios were not statistically different from 1:1, a bias in the sex ratio by age was observed in 2000 and 2002. These data suggest that more males migrated at 1+ years, and more females at 2+ years. The fact that females migrate at an older age has also been observed in Arctic charr, where a strong predominance of downstream migrating females occurred at ages older than 6 years (Svenning *et al.*, 1992). In this case, the bias in the sex ratio may be due to the predominance of mature males over females among age groups 5 years and older (Svenning *et al.*, 1992), a predominance not observed in the present study. A parallel study done on the main branch of the Sainte-Marguerite River showed that the advantage of migrating at 2+ years in terms of fitness is related to a global improvement of survival rate from birth to maturity, as the 2+ year migrants spend an additional year in fresh water, where survival rate is better, and less time in the estuary before returning for reproduction relative to 1+ year migrants (S. Lenormand & J.J. Dodson, unpubl. data). Thus, there is a statistically significant tendency in some years for males to adopt the riskier option of migrating at 1+ years and spending two growth seasons in the estuary rather than one as in the case of female migrants. This situation is consistent with the results of Rikardsen *et al.* (1997) who also found that more males than females migrated at a younger age. In their case, females tended to dominate the returns suggesting that there was probably a relatively higher mortality among sea-run male smolts. A possible proximal explanation for this tendency among males could be that males have higher metabolic costs than females and are thus energetically constrained sooner in life. Elevated metabolic rates as well as a higher aggressiveness in male fish have been found in some species (Adams & Parsons, 1998; Johnsson & Åkerman, 1998).

The present results support the hypothesis of a minimal size that must be attained before migration, as smaller fish delay migration and migrate at an

older age and at a larger size. This hypothesis is further supported by the fact that smaller individuals migrate later during the season. Not all the fish, however, undergo migration upon achieving a size permitting it, suggesting that other factors linked to the energy budget and to the heritable component of the life-history tactic must be considered in the context of the conditional strategy. Moreover, males and females in the system adopt the migratory tactic in equal proportions. Males tend to migrate earlier in life than females, however, suggesting that the timing of migration may be associated with sex-specific reproductive strategies involving a proximal mechanism possibly related to metabolic rate differences between the sexes.

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