Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*)

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Abstract: Migration patterns of brook charr (*Salvelinus fontinalis*) from the Sainte-Marguerite River, Québec, Canada, were investigated to explore the hypothesis that migratory behaviour changes according to size during the critical period of first downstream migration, when survival is likely to be related to size, and during subsequent seasonal movements. We hypothesized that as fish grow, they should adopt more conservative behaviours to protect the reproductive assets that they have accumulated. First downstream migration occurred over a month in spring. Larger juvenile charr migrated early, whereas smaller charr seemed to delay offshore migration. As predicted, migratory patterns of charr changed through ontogeny. Sea age 0 juveniles stayed in estuarine areas until October and overwintered outside their natal river. Sea age 1 juveniles returned to their natal river earlier in the fall and some of them overwintered there. Adults (some sea age 1 migrants and older migrants) undertook their upstream migration to spawning areas from July to September, larger ones migrating earlier than smaller ones. Postspawners migrated downstream after reproduction or overwintered in the river. Environmental differences related to geographical location may be responsible for the variation of migration patterns and other life-history traits observed among brook charr populations, emphasizing the coevolution of anadromy and life history.

Résumé : Les patrons de migration de l'omble de fontaine (*Salvelinus fontinalis*) de la rivière Sainte-Marguerite, Québec, Canada, ont été étudiés dans le but d'explorer l'hypothèse selon laquelle le comportement migrateur change en fonction de la taille lors de la période critique de la première dévalaison, où la survie est susceptible de dépendre de la taille, mais aussi lors des mouvements saisonniers ultérieurs car, au fur et à mesure que les poissons grandissent, ils devraient adopter des comportements de plus en plus prudents pour protéger les atouts reproductifs qu'ils ont accumulés. La première dévalaison se déroulait sur un mois, au printemps, mais les migrants les plus grands descendaient la rivière en premier tandis que les plus petits semblaient retarder leur migration vers le large. Tel que prédit, les patrons de migration des ombles changeaient au cours de leur ontogénie. Les juvéniles d'âge en mer 0 restaient en estuaire jusqu'en octobre et passaient l'hiver hors de leur rivière natale. Les juvéniles d'âge en mer 1 regagnaient leur rivière natale plus tôt à l'automne et une partie d'entre eux passaient l'hiver là. Les adultes (une partie des migrants d'âge en mer 1 et les migrants d'âge en mer supérieur) entreprenaient leur migration vers les sites de fraie de juillet à septembre, les plus grands plus tôt que les plus petits. Les géniteurs dévalaient à nouveau après la reproduction ou passaient l'hiver en rivière. Les différences environnementales associées à la situation géographique peuvent expliquer les variations des patrons de migrations et du cycle vital qui sont observées entre les populations d'ombles de fontaine, mettant en évidence l'évolution conjointe du comportement anadrome et du cycle vital.

Introduction

Migration involves specialized behaviours that have arisen through natural selection (Dingle 1980). Therefore, migrants are expected to maximize their inclusive fitness by changing habitats when appropriate (Krebs and Davis 1993). From this evolutionary perspective, Gross (1987) developed a model for understanding diadromy: fish would migrate if "the growth and survivorship advantages of utilizing a second habitat, plus the cost of moving between habitats … exceed the advantages of staying in only one habitat for the same period of time". Concerning anadromy in salmonids, though moving to salt water involves energetic costs, osmotic stress, and a higher predation risk than in fresh water, the fitness payoff of migration to sea results from an enhanced growth rate in a richer feeding area (Jonsson and Jonsson 1993).

Salmons (*Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. masou*, *O. nerka*, *O. tshawytscha*, and *Salmo salar*) undertake only two transitions between fresh and salt water before reproduction: one at smolting and the other when mature individuals return to reproduce. However, in many charr

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(*Salvelinus*) and trout (e.g., *Oncorhynchus clarki*, *Salmo trutta*) populations, fish move back and forth between their natal rivers and estuarine areas at the juvenile and adult stages (Randall et al. 1987). As in salmon, some of their movements are clearly ontogenetic in nature. There is first a downstream migration, the timing of which depends on size and growth rate (e.g., Økland et al. 1993; Rikardsen et al. 1997; Thériault and Dodson 2003), and then an upstream migration to spawning areas. Other movements are related to seasonal changes affecting the habitats exploited. Juveniles and adults tend notably to overwinter in fresh water (Randall et al. 1987). According to the model of Gross (1987), such observations imply that the growth–mortality trade-off constraining anadromy varies among seasons.

The immediate advantages and costs of staying in a given habitat may vary with the individual's body size (Werner and Gilliam 1984). In salmonids, where osmotic stress is lower for larger migrants (McCormick and Saunders 1987) and vulnerability to predation and disease may also decrease with greater size (Marschall et al. 1998), a common example of size-dependent costs of migration to sea is size-selective mortality during or shortly after migration to sea (references in Bohlin et al. 1996). Moreover, even in the absence of size-dependent effects on growth or mortality, dynamic models suggest that lifetime fitness benefits of any behavioural act may depend on the individual's age, size, or physiological state at the time that the act is performed (McNamara and Houston 1986; Ludwig and Rowe 1990; Clark 1994). Individuals with greater reproductive value (e.g., juveniles close to size at maturity, adults with a large size and in good condition) should be more averse to risk predation because they would gain less from a given absolute increase in reproductive assets relative to what they would lose if caught by a predator (Clark 1994). Therefore, we would expect that the migratory behaviour of salmonids carrying out seasonal movements would change according to the individual's age (or age since migration, if size depends more on sea age than on total age), maturity stage, size, and condition.

Although this issue has never been studied as such, there is some evidence that seasonal migrations differ according to the individual's size in several charr and trout populations. For instance, larger individuals return to fresh water sooner than smaller ones (e.g., Castonguay et al. 1982; Dempson and Green 1985; Jonsson 1985). Castonguay et al. (1982) also suggested that smaller brook charr (*Salvelinus fontinalis*), corresponding to migrants-of-the-year, do not return to the Saint-Jean River, Québec, at the end of the summer growing season. If such size- or age-dependent patterns exist, their study is of major importance for the protection and enhancement of salmonid populations. First, the identification of how different life stages may be exposed to different rates of exploitation in time and space is an obvious prerequisite to the establishment of successful local management plans. Moreover, the effectiveness of conservation policies relies on a good understanding of the evolution of salmonid life history, which is intimately connected with anadromy. Migratory behaviour and other life-history traits should co-evolve to form adaptive strategies that convey selective advantages in specific environmental settings (Hutchings and Morris 1985). Ontogenetic patterns in the migration of salmonid populations would represent optimal behavioural paths towards the maximization of inclusive fitness and may provide interesting insights into the evolution of anadromy.

The brook charr is native to eastern North America, where it is one of the most popular game fishes. Like many salmonids, it may exist as migratory and freshwater resident forms that differ in life-history patterns (Power 1980). Marine movements of anadromous brook charr are of short duration (2–4 months) and seem to be limited to estuarine and coastal regions near their natal river (e.g., Castonguay et al. 1982; O'Connell 1982; Montgomery et al. 1990). Reproduction takes place in the fall, but adults start their upstream migration during the summer. Anadromous brook charr usually mature during their second or third growing season in salt water and multiple spawning is common (Power 1980). There are, however, significant differences between populations. Ages at first downstream migration range from 1 to 7 years (Randall et al. 1987). Although exploitation of estuarine areas usually takes place during the summer, a variety of seasonal movements has been described throughout the *S. fontinalis* distributional range (reviewed by O'Connell 1982; LeJeune 1987). The extensive life-history and behavioural differences observed in brook charr makes this species a particularly interesting model in which to explore the relationship between anadromous behaviour and the evolution of life history (see Dodson 1997).

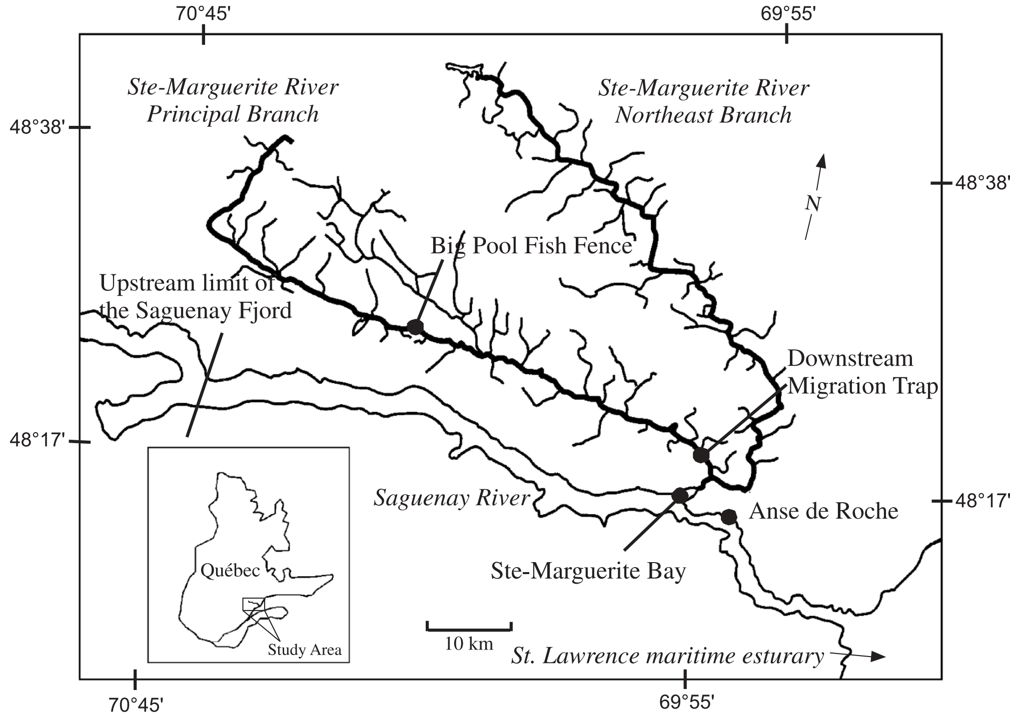
In the present study, we explored the hypothesis that migratory behaviour of anadromous brook charr changes according to their size during the critical period of first downstream migration (when survival is likely to be related to size) but also during subsequent seasonal movements, as larger fish should be more averse to risk to protect the reproductive assets that they have accumulated. Migratory patterns were investigated combining a monitoring of first downstream migration, direct sampling in estuarine areas, creel census, and a mark–recapture experiment, in collaboration with anglers. Seasonal movements were analyzed according to sea age, maturity stage, and size of individuals. We predicted that as fish grow, they should opt for more conservative migratory behaviours.

Materials and methods

Study area

The Sainte-Marguerite River (48°27′N, 69°95′W; Fig. 1) empties into the Saguenay Fjord, 25 km upstream from its confluence with the St. Lawrence maritime estuary (Québec, Canada). It is divided in two main branches: the Principal Branch and the Northeast Branch, each of which is 100 km long and around 25 m wide and drains an area of 1000 km^2. Daily flows range between 10 $m^3{\cdot}s^{-1}$ (February) and 430 $m^3{\cdot}s^{-1}$ (May). The river is ice-covered from December to April. Maximum observed water temperature during the study was 25 °C (July). In addition to brook charr, the river also contains Atlantic salmon (*Salmo salar*) and, to a lesser extent, longnose and white sucker (*Catastomus catastomus* and *C. commersoni*), longnose dace (*Rhinichthys cataractae*), fallfish (*Semolitus corporalis*), and American eel (*Anguilla rostrata*). Predators of anadromous charr present in the river are merganser (*Mergus merganser*), mink (*Mustela vison*), osprey (*Pandion haliaetius*), and river otter (*Lutra canadiensis*).

Fig. 1. Location of the Sainte-Marguerite River – Saguenay River system and sampling sites in the province of Québec, Canada.



Anadromous charr migrate to the Sainte-Marguerite River estuary, which forms a large shallow bay, the Sainte Marguerite Bay. From there, they have access to the Saguenay River (Fig. 1). The 100-km downstream part of the Saguenay River (the Saguenay Fjord), under tidal influence, is a mixing zone between fresh water coming from upstream and salt water coming from the St. Lawrence maritime estuary. In a subarctic fjord such as the Saguenay, freshwater inputs are considerable and show important fluctuations. From May to October, strong thermohaline stratification is observed. The water column is divided into a thin mixed layer (5–10 m) of warm (5–15 °C), brackish (0–18‰) water and a thick (up to 275 m), underlying layer of cold and saline water (<0.5 °C, >26‰ at 15 m). In the fall, as surface temperature decreases, exchanges between the two layers increase and salinity at the surface rises to 22‰ in November. During the ice-covered period (December to April), surface temperature stays around 0 °C and surface salinity stabilizes at low values (less than 7‰ vs. 20‰ at 10 m). From mid-March to the beginning of May (ice-melt period), the increase of freshwater inputs and surface water temperature gradually restores the summertime thermohaline stratification (Chassé and Côté (1991) and references therein).

The Saguenay River is characterized by a low primary production but high densities of zooplankton. At least 410 species of marine benthic invertebrates are present in the fjord (ZIP Saguenay 1998). Among them, amphipods (Gammaridae), mysids, and polychaetes may constitute major prey items for juvenile anadromous brook charr, as observed in other estuaries (White 1940; Gaudreault et al. 1982). Fish populations are also relatively diverse, with 76 species recorded to date. Common prey of large (more than 25 cm) anadromous charr are present: smelt (*Osmerus mordax*), sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), and sand lance (*Ammodytes* spp.). High productivity and abundance of large prey (large invertebrates and fish) are two factors that may explain the fast growth of salmonids in the sea vs. in river systems (Keeley and Grant 2001). Thus, as in many estuaries, the Saguenay River should constitute a better feeding habitat than charrs' natal river, especially in winter when prey are still abundant in the former area. However, predation risk is also likely to be higher in the Saguenay River. Potential predators of anadromous charr in that area are cormorant (*Phalacrocorax auritus*), heron (*Ardea herodias*), loon (*Gavia immer*), merganser (*Mergus merganser*), osprey (*Pandion haliaetius*), harbor seal (*Phoca vitulina*), and Greenland shark (*Somniosus microcephalus*).

Sampling and mark–recapture experiment

Anadromous brook trout were sampled and tagged at different life stages during 4 years (1998–2001). In 1999 and 2000, descending charr were caught by an Alaskan trap (1-cm mesh) set 7 km from the river's mouth on the Principal Branch of the Sainte-Marguerite River (Fig. 1). Monitoring started just after the ice breakup period, when discharge was beginning to decrease, and ended when catches had been minor for 10 consecutive days. The trap covered one-third of the river and caught at least 1000 charr every year. Fish were measured (fork length (FL), to the nearest mm). Twelve percent of total catches in 1999 and 10% in 2000 were sacrificed for laboratory analyses (see below). The rest of the fish were marked with clear, individually labelled T-bar anchor tags (Floy FF-94), provided that their fork length was greater than 75 mm. Tag retention was tested in an aquarium with 20 fish ranging in size from 75 to 132 mm FL. No tag loss, mortality, or serious injury was observed after 3 months.

In the Sainte-Marguerite Bay, sampling and tagging of anadromous juveniles was carried out by approximately weekly hauls of a 40-m beach seine (0.5-cm mesh, 1.5 m deep) in September and October 1998, from the beginning of May until mid-October in 1999 and 2000, and in May 2001. All fish caught by seining were measured; recaptures were recorded and untagged fish were marked with T-bar tags (Floy FF-94). In July 1999, we made two additional seine samplings in a deeper, colder, and more saline area of the Saguenay Fjord, Anse de Roche (Fig. 1), where several migrants-of-the-year had been recaptured by anglers. Every year, anadromous spawners were sampled during their upstream migration by inserting a trap into the Big Pool (Fig. 1) fish fence (wire covered by a net, 4-cm mesh). The fence only operates in July and serves to delay the upstream migration of Atlantic salmon for conservation purposes. An additional seine haul (5-cm mesh) was made at the same location at the end of August to complete the sampling. All fish were measured and those that were not recaptures were tagged with T-bar tags (Floy FD-94).

Fishing for anadromous charr is permitted in the Saguenay River (including Sainte-Marguerite Bay) all year long and in the Sainte-Marguerite River from 15 June to 31 October. Tag returns from the sportfishery were encouraged with a $5 cash reward and the opportunity to participate in an annual draw for prizes. In 1998, 1999, and 2000, we completed the mark–recapture experiment by a creel census in the Sainte-Marguerite River and the Sainte-Marguerite Bay. Two registration stations were operated, at 30 km upstream on the river and at the river's mouth. Catches were measured and weighed. In the fall, future spawners or postspawners were identified according to external signs of maturation (hooknose, orange to black belly, and sperm outflow by abdominal stripping in males; dilation of urogenital papilla and egg outflow by abdominal stripping in females). Subsamples of fish were dissected for more detailed analysis (see below) on a regular basis.

In winter, as angling is forbidden in the Sainte-Marguerite River, we made two additional samplings under ice cover, using four rods baited with worms and corn: in the downstream pools of the Sainte-Marguerite on 20 February 2000 and 31 January 2001 and at the river mouth on 1 and 16 February 2001. All fish caught were sacrificed for laboratory analysis.

Charr that had been sacrificed or sampled from anglers (tagged fish and subsamples of untagged fish) were measured, weighed, and classified with respect to sex and stage of maturity (Nikolskii 1963). Stomach contents were analysed for a related study (conducted by Geneviève Morinville and Joe Rasmussen, Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada). Sagittal otoliths were removed, cleaned, and fastened to glass slides with a clear mounting adhesive at its melting point (50 °C). After hardening of the adhesive, total age and age at downstream migration were read under a binocular microscope using reflected light. Age at downstream migration was determined at the first major increase of annulus width (Fig. 2). This method was tested using fish that had been tagged during their downstream migration (i.e., fish for which sea age was already known) and were subsequently recaptured after several years in salt water. The sea age of 95% of 545 tagged fish (528) was correctly identified based on otolith microstructure. As a result, total age and age at sea of all sacrificed fish were identified using otoliths.

Data analysis

First downstream migration was characterized according to age and body size of migrating charr. Seasonal migratory patterns were analyzed according to sea age, maturity stage, and body size of migrants. Differences in length between two groups were tested by two-tailed Student's *t* test when data met the required assumptions and by Mann–Whitney *U* test otherwise. Total length distributions (all charr caught) were right-skewed in both years and differed significantly from normal distributions. However, for a given age class, lengths were normally distributed and samples met the required assumptions to be compared by Student's *t* tests. Proportions were compared by χ^2 test (using Yates' correction for continuity when some expected frequencies became less than 10). Statistical analyses were performed using Statistica 5.5.

Results

First downstream migration

The monitoring of downstream migration in 1999 and 2000 resulted in the capture of 1483 and 1019 migrants-of-the-year, respectively. Subsamples of 178 fish in 1999 and 92 in 2000 were used for age determination. According to the temporal distributions of catches in the trap (Fig. 3), we probably missed the onset of downstream migration in 1999. However, the first significant catches of first-time migrants in Sainte-Marguerite Bay (SMB) started 4 days after the trap was installed in the river and included recaptures of fish tagged in the trap. Therefore, the migration peak that we observed on the first day of monitoring was most likely the first one. In both years, the outmigration of brook charr occurred over a period of approximately 1 month (Fig. 3). Migration time (days after first day of monitoring) decreased with length of migrating charr (1999, slope = –0.116, R^2 = 0.07, $p < 0.0001$; 2000, slope = –0.083, R^2 = 0.05, $p < 0.0001$). Although significant, the relationships are weak as the migration of smaller fish was distributed throughout the period of outmigration, whereas larger fish were observed mostly at the beginning of the outmigration (in 1999, 50% of fish of FL < 120 mm had not migrated before day 10, whereas 70% of fish of FL ≥ 120 mm had migrated by day 9, and in 2000, 50% of fish of FL < 120 mm had not migrated before day 15, whereas 72% of fish of FL ≥ 120 mm had migrated by day 14).

There was no significant difference in the length of emigrating charr between 1999 and 2000 samplings (Fig. 4): 1999, mean FL = 111.8 mm; 2000, mean FL = 112.4 mm; Mann–Whitney *U* test, $z = -1.19$, $p = 0.23$. Charr belonged to three age classes: 1+ (29% of migrants in 1999 and 26% in 2000), 2+ (68% of migrants in 1999 and 69% in 2000), and exceptionally 3+. Fish migrating at age 2 were significantly bigger than fish migrating at age 1 (1999, 2+ FL ± standard deviation (SD) = 118.4 ± 14.7 mm and 1+ FL = 89.0 ± 9.8 mm, $t = -14.8$, $p < 0.001$; 2000, 2+ FL = 114.5 ± 16.2 mm and 1+ FL = 91.0 ± 10.8 mm, $t = -7{,}33$, $p < 0.0001$). None of the sampled fish showed any signs of a previous reproduction.

When they entered the SMB, migrants-of-the-year (sea age 0 migrants) were easily distinguished from migrants of greater sea age because of almost no overlap between length

Fig. 2. Left sagittal otolith of age-3 brook charr (*Salvelinus fontinalis*) caught in the Sainte-Marguerite River (Big Pool, July 2000) with different migratory patterns: (*a*) charr having migrated at age 1, (*b*) charr having migrated at age 2, and (*c*) freshwater resident charr. Downstream migration is characterized by a major increase of annulus width. Numbers in italics indicate beginning of year *n*. Otoliths in (*b*) and (*c*) were enlarged relative to otolith in (*a*) to enhance comparisons.

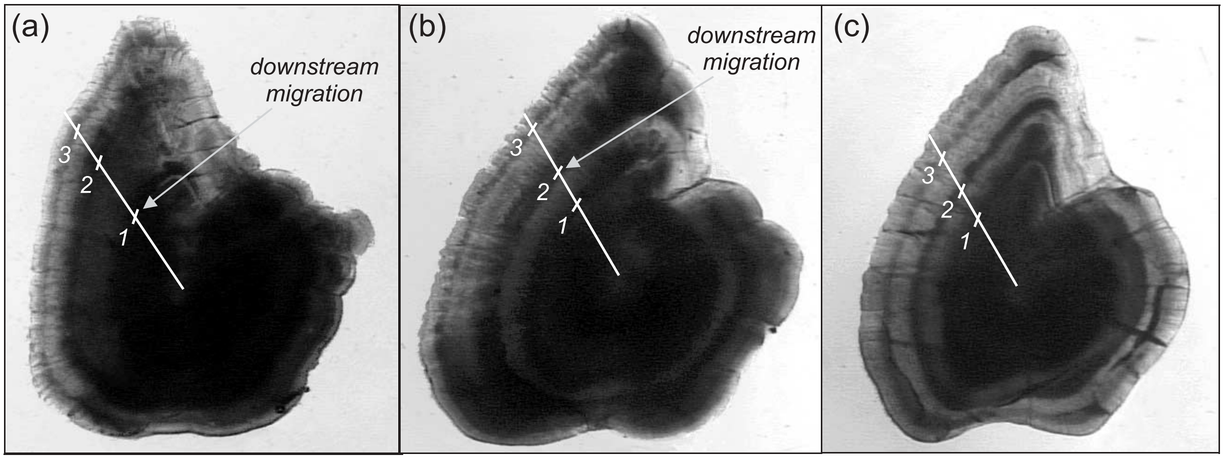


Fig. 3. Number of emigrating brook charr (*Salvelinus fontinalis*) caught per day in the Principal Branch trap in 1999 (solid line) and 2000 (broken line).

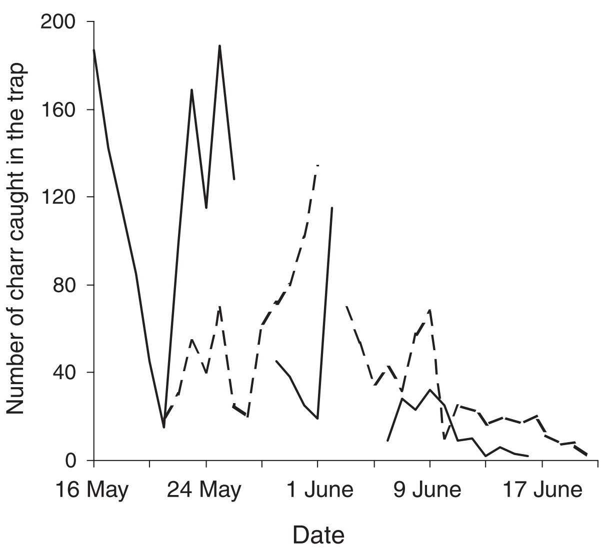
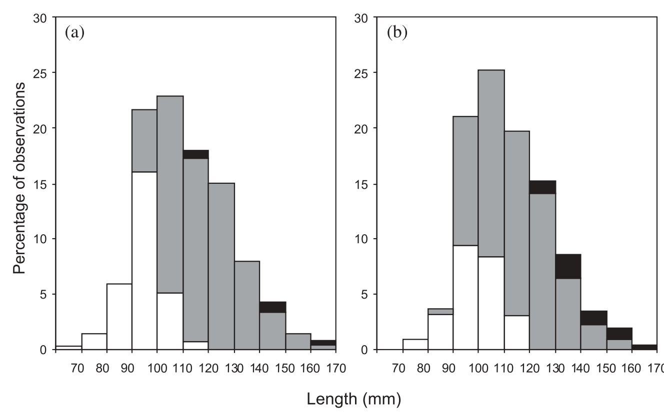


Fig. 4. Length frequencies of all emigrating brook charr (*Salvelinus fontinalis*) caught in the Principal Branch trap from mid-May to mid-June in (*a*) 1999, n = 1483, and (*b*) 2000, n = 1019, and distribution of ages (1+, open bars; 2+, shaded bars; 3+, solid bars) in length classes according to laboratory analysis (1999, n = 178, and 2000, n = 92).



distributions of sea age 0 and sea age 1 charr: by the third week of May 1999 and 2000, more than 97% of sea age 1 charr (charr having migrated in the spring of 1998 and 1999, respectively) had a fork length greater than 155 mm (seine sampling: 1999, n = 43; 2000, n = 49), whereas more than 99% of new migrants had a fork length smaller than 155 mm.

The tagging program

A total of 8412 charr were marked with T-bar tags from September 1998 until August 2001. We recaptured 1262 (15.0%) of these fish during subsequent samplings. Anglers from the Sainte-Marguerite River (SMR) and the Saguenay River sportfishing before December 2001 reported 1402 tagged fish (16.7%). Only three charr were recaptured in estuarine areas out of the Saguenay Fjord. These fish were caught in the St. Lawrence River less than 20 km from the Saguenay River mouth. We did not observe any effect of tagging on growth: length distributions of fish tagged at migration and recaptured 1 year later did not differ significantly from length distribution of untagged fish of the same sea age (May 2000, untagged charr, n = 29, length ± SD = 230.7 ± 42.4, and tagged charr, n = 39, length = 235.6 ± 30.6, t = 0.56, p = 0.58; May 2001, untagged charr, n = 29, length = 220.7 ± 36.3, and tagged charr, n = 49, length = 225.5 ± 22.6, t = –0.73, p = 0.47).

No size-specific mortality following downstream migration was detected. Length distributions at the time of downstream migration of fish tagged during migration and recaptured 1 year later did not differ significantly from length distributions revealed by downstream migration monitoring (Mann–Whitney U test, 1999 downstream migration, 54 recaptures in 2000, p = 0.87, and 2000 downstream migration, 34 recaptures in 2001, p = 0.54). The latter observation also shows the absence of size-specific mortality resulting from tagging.

Temporal evolution of catches and recaptures of tagged fish according to sea age, maturity stage, and body size

Spring

Temporal patterns of beach seine catches in SMB were similar in 1998, 1999, 2000, and 2001 as far as presence or absence and size of migrants were concerned. Analysis of the evolution of the length of anadromous charr caught in the bay, on a weekly basis, from May to October 1999 and 2000 (the two years in which sampling was the most extensive) revealed that the largest fish were found at the end of April – beginning of May, just after the ice melt (Fig. 5). Sampling of anglers' captures at this time (n = 14, length ± SD = 386.1 ± 64.2 mm; Fig. 6) and analysis of recaptures (Table 1) showed that these charr were mainly sea age 2 migrants and older (representing more than 90% of sampled fish and tag returns in early spring 1999 and 2000). Most of these fish were caught directly at the river mouth and all had the characteristics of kelts that had overwintered in the river after spawning (dark colour, low condition factor, frailty, white flesh, empty and contracted stomachs). All sea age 3 migrants but only 5 of 12 sea age 2 migrants were identified as spawners from the previous year (hook nose in males, well-developed but flabby gonads, presence of a few remaining ovulated eggs in females), and recaptures included fish tagged on the spawning grounds. At the same period, charr of sea age 2 and older were also recaptured in the upstream part of the Saguenay River (essentially in fresh water; Table 1) but were more silvery in colour and in better condition.

From mid-May to the beginning of June 1999 and mid-May to mid-June 2000, we observed a progressive decrease in the length of charr present in the SMB (Fig. 5). This change in length structure corresponded to successive shifts in sea age structure. Firstly, the decrease of maximum observed length in seine hauls (Fig. 5) was associated with a progressive disappearance of the oldest migrants in anglers' captures (Fig. 6) and recaptures (Table 1). Secondly, this period included peak catches of sea age 1 and sea age 2 charr in the SMB (Fig. 6; Table 1). Before the third week of May, sea age 1 migrants were almost exclusively recaptured in the Saguenay River, upstream from the SMB (Table 1). Anglers from the SMB call charr that arrive by mid-May "blue trout" because of their silver-blue colour. They are also characterized by their orange flesh, originating from intensive feeding on marine crustaceans (Geneviève Morinville, Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada, personal communication). Lastly, by the third week of May, migrants-of-the-year entered the bay, which induced a decrease in the mean length of charr caught by seining.

Summer

Significant numbers of migrants-of-the-year were caught by seining in the SMB every week from the third week of May until the last week of July (Fig. 5). On the other hand, some sea age 0 charr left the SMB as soon as the first week of June, migrating to upstream or downstream areas of the Saguenay Fjord, as shown by tag returns (Table 1). Migrants-of-the-year sampled at Anse de Roche (Fig. 1) on 1 and 2 July 1999 were significantly larger than migrants-of-the-year sampled in the SMB on 4 July 1999 (Anse de Roche, n = 83, mean length = 143.2, and SMB, n = 96, mean length = 132.0, Mann–Whitney U test, z = 3.27, p = 0.001). As smaller migrants were not large enough to be targeted by anglers in June and July, we could not use recaptures from the sportfishery to compare the length at tagging of charr that migrated first to deeper, colder, and more saline areas of the Saguenay Fjord with the length of charr that stayed longer in the SMB.

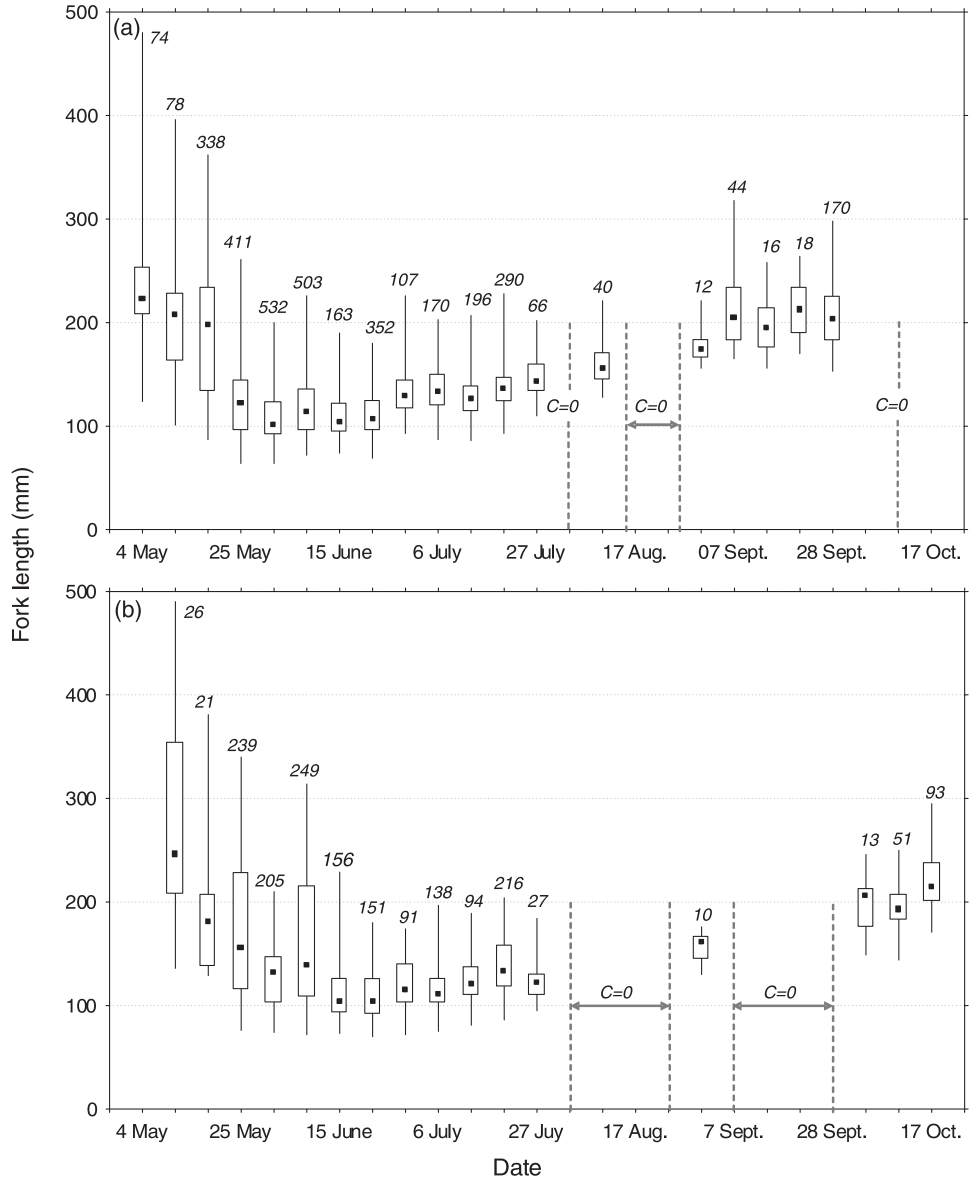
In June and July, we observed a general dispersal of migrants in the Saguenay River (Table 1). However, by mid-July, large charr (FL > 300 mm) started to be caught at Big Pool, in the upstream part of the SMR (Fig. 1). In July and August, all but one charr sampled from anglers' captures in the river had spent at least two growing seasons in the Saguenay River (n = 258, 1998–2001 pooled data). Sea age 2 (and older) migrants were all spawners (n = 153), but only 81% of sea age 1 migrants were sexually mature (n = 104). In August, older migrants (sea age = 2) disappeared from recaptures in the Saguenay River, suggesting that most of them had started their upstream migration to spawning areas by that time of the year. From mid-July until the beginning of September, no tagged fish was caught in the freshwater part of the Saguenay River.

Fall and winter

In September, recaptures of sea age 0 and sea age 1 migrants decreased in areas downstream from the SMB (Table 1). Sea age 1 migrants disappeared totally from recaptures in the Saguenay River and were only observed in the SMB and in the downstream part of the SMR. Captures of sea age 1 charr in these two areas included a few mature individuals (less than 10% every year). These late upstream migrants were significantly smaller than sea age 1 spawners already present in the river during the summer (Table 2). In the same period, sea age 0 juveniles were also observed in the SMB and the SMR. However, tag returns in the upstream part of the Saguenay River indicated that part of the migrants-of-the-year had moved into this freshwater area (Table 1).

The return of some of the juveniles towards the SMR in the fall was associated with an increase of the sportfishery in both the SMB and the SMR. Catches of juveniles were almost completely made up of sea age 0 and sea age 1 migrants (only five catches of immature sea age 2 migrants were recorded in 4 years out of 1546 juveniles sampled in the fall). There were significant differences in length and sea age structures of captures between the SMR and the SMB. Every year and for every sampling period, the length of charr caught in the downstream part of the SMR was significantly greater than the length of charr caught in the SMB (Table 3). The greater body size of charr caught in the river was associated with a higher proportion of recaptures of sea age 1 charr (Table 1), which were larger than migrants-of-the-year in every sampling area (see mean lengths of recaptures in Table 1, $p < 0.01$ in all cases). Sea age 1 charr made up 34% of nontagged juveniles sampled from anglers in the river in 1998 (n = 438), 60% in 1999 (n = 255), and 69% in 2000 (n = 74). In contrast, they constituted only occasional catches in the SMB (Fig. 6). The length of charr caught in the SMB and in the SMR tended to decrease from mid-September until the end of October (Table 3). The parallel

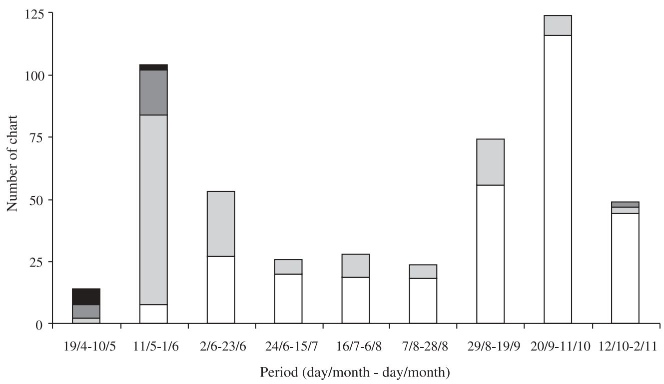
Fig. 5. Temporal evolution of length (median, 25–75% range, total range) of brook charr (*Salvelinus fontinalis*) caught by seining in the Sainte-Marguerite Bay in (*a*) 1999 and (*b*) 2000, on a weekly basis. Numbers in italics are the numbers of charr caught per week (fishing effort was increased when catches were low). "*C* = 0" indicates that no fish could be caught, although fishing effort was maximal.



increase of sea age 0 juveniles in recaptures from the SMR (Table 1) suggests that part of the migrants-of-the-year were leaving the SMB to enter the river. At the end of October, catches of juveniles in the SMB were dominated by small migrants-of-the-year. Stomachs continued to contain prey in almost all charr collected in the SMB in October 1998, 1999, and 2000, whereas at the same periods, less than 52% of the charr collected in the river had stomach contents (Table 4). The end of October was also characterized by a downstream migration of part of the adults after reproduction, as shown by tag returns of postspawners in the downstream part of the SMR and in the SMB (Table 1). Catches of brook charr always decreased in the SMB at the end of October, followed by a usual cessation of the sportfishery.

During winter, we recorded significant tag returns in the freshwater part of the Saguenay River but none in the Saguenay Fjord (Table 1). These recaptures included juveniles (sea age 0 and sea age 1 migrants) and postspawners. Angling was forbidden in the SMR and unusual in the SMB at this time. Sampling in the downstream part of the SMR on 20 February 2000 revealed only the presence of sea age 1 and sea age 2 migrants. Sea age 2 migrants (n = 2) were postspawners but sea age 1 migrants included juveniles (seven out of nine). In 2001, we did not catch any charr in the downstream pools of the SMR. These pools contained large amounts of frazil ice and flow was constrained to narrow high-velocity channels. Two half-day samplings at the river mouth led to the eventual catch of 10 postspawners and four sea age 1 juveniles. The significant number of adults tagged before reproduction in 1999 (n = 463) enabled a comparison between fish that migrated downstream just after reproduction and fish that migrated downstream the following spring. Postspawners recaptured when leaving the SMR in early spring were part of the largest spawners

Fig. 6. Number of brook charr (*Salvelinus fontinalis*) subsampled for laboratory analysis while monitoring sportfishery in the Sainte-Marguerite Bay, according to date and sea age (1998–2000, pooled data). Numbers of sampled fish per period were approximately proportional to catches. Percentages of each sea age class for a given period did not differ between years (χ^2, $p > 0.2$ in all cases): 0+, open bars; 1+, lightly shaded bars; 2+, darker shaded bars; 3+, solid bars.



tagged during the previous year and were significantly larger at the time of tagging than postspawners recaptured in the Saguenay River during winter (Fig. 7). Survival from reproduction to the following summer was higher in large than in small spawners tagged in 1999, but we did not observe any size-selective mortality in spawners tagged in 2000 (comparison of the length distributions, at tagging, of all fish tagged and of fish tagged and recaptured the following year: 1999, 463 spawners tagged and 67 recaptures, Mann–Whitney U test, $p < 0.03$, and 2000, 171 spawners tagged and 46 recaptures, Mann–Whitney U test, $p = 0.51$).

As anticipated by the differences in abundance and size of prey in winter between the SMR and the Saguenay River, most of the stomachs collected in the SMR area were empty, whereas 84% of the stomachs collected in the Saguenay River during the same period contained prey (Table 4).

Discussion

The migration patterns of anadromous brook charr from the SMR inferred by the study are presented in Fig. 8. We observed an emigration of migrants-of-the-year in spring during a short period of time. That size of descending charr did not differ between 1999 and 2000 samplings, length distributions were right-skewed in both years, larger charr migrated first, and no size-selective mortality following migration was observed all suggest that there has been selection for a threshold size at first migration. As in other salmonids demonstrating a size-dependent salinity tolerance (and associated survival) (McCormick and Naiman 1984), the growth–mortality trade-off associated with migration to estuarine areas may be negative before charr reach a critical body size. Part of the migrants-of-the-year stayed in the SMB at least until the beginning of August. Others left the bay as soon as early June and dispersed in the Saguenay Fjord. Sea age 0 migrants caught in the fjord in July were significantly larger than sea age 0 migrants caught in the SMB at the same period. Thus, larger migrants left the SMB earlier and (or) growth is enhanced when fish leave the SMB. The study of Montgomery et al. (1990) suggested that larger sea age 0 brook charr moved to deeper and more saline water more readily than did smaller ones. A regular departure of the largest migrants-of-the-year from the SMB would explain why we did not observe any significant increase in the length of fish present in that area in July. Laboratory studies on brook charr have shown that exposure to intermediate salinities before exposure to seawater had a positive effect on survival (McCormick and Naiman 1982) and that salinity tolerance of juveniles increased with body size (Sutterlin et al. 1976; McCormick and Naiman 1984). The prolonged residence of smaller migrants-of-the-year in the SMB (where salinity does not exceed 14‰) may constitute a necessary period of acclimation and growth before entering salt water, as suggested by Montgomery et al. (1990). The major decrease of seine catches in August indicated that most fish had left for the fjord by this time of the summer.

During the fall, migrants-of-the-year moved back towards fresh water. This observation is in accordance with many studies on charr and trout (see Randall et al. 1987) showing a return to the natal river at the end of the summer. However, in our study case, migrants-of-the-year had access to fresh water either in the natal river or in the upstream part of the Saguenay and used both areas. Thus, the tendency of juveniles to return to fresh water in the fall does not appear to involve homing behaviour. As suggested by Dutil and Power (1980), it is more likely that brook charr "sheltered" from the decrease in temperature in the salt water, which can create a severe osmotic stress in this species (Saunders et al. 1975). This hypothesis is particularly relevant in the Saguenay Fjord, where the decrease of temperature in the fall induces a major increase of surface water salinity (up to 22‰). During winter, migrants-of-the-year were still observed in the upstream part of the Saguenay River. As angling stopped in the SMR at the end of October, we only have indirect information about the fate of migrants that moved back to their natal river in the fall. We did not observe any sea age 0 juveniles while sampling in the river or at the river mouth during winter, nor did we observe any significant emigration of sea age 1 charr from the SMR the following spring. Knowing that during the ice-covered period of the Saguenay Fjord, surface temperature stays around 0 °C and surface salinity stabilizes at low values (<7‰), it is possible that after the unfavourable fall period, juveniles descended the river a second time to reach the freshwater part of the Saguenay River. We know that such movements occurred as four juveniles tagged in the SMR in October were caught during the following winter in the upstream part of the Saguenay River. Downstream movements of anadromous brook charr at the end of fall have been observed in other studies (e.g., Smith and Saunders 1958; Castonguay et al. 1982).

Sea age 1 migrants reappeared in the SMB the following spring during a 15-day period starting around May 15. Their good condition and their dark orange flesh suggested that they were already feeding intensively on crustaceans in the fjord when they arrived, in accordance with their probable arrival from upstream areas of the Saguenay River. Sea age 1 migrants left the bay more readily than migrants-of-the-year and occupied all areas of the Saguenay Fjord (including the more saline areas downstream of the SMB) by the beginning

Table 1. Number and mean length (± standard deviation, mm) of tagged brook charr (*Salvelinus fontinalis*), reported by anglers, according

		Area					
		Saguenay freshwater		Fjord, upstream of SMB		Ste-Marguerite Bay (SMB)	
Date	Sea age	Number	Mean length	Number	Mean length	Number	Mean length
19 Apr. – 10 May	0+	0		0		0	
	1+	4 (0 P-S)	254.3±9.0	4 (0 P-S)	251.0±21.2	1 (0 P-S)	293
	2+	6 (3 P-S)	363.0±47.8	3 (3 P-S)	328.3±36.2	5 (2 P-S)	370.5±20.8
	≥3+	6 (6 P-S)	456.0±72.2	1 (1 P-S)	430	16 (16 P-S)	466.7±49.0
11 May – 1 June	0+	0		0		3 (0 P-S)	154.7±26.9
	1+	4 (0 P-S)	226.4 (1 measured)	2 (0 P-S)	250 (1 measured)	64 (2 P-S)	230.6±29.6
	2+	7 (4 P-S)	355.2±45.7	2 (1 P-S)	355.5±50.2	28 (7 P-S)	341.6±37.8
	≥3+	8 (8 P-S)	446.3±46.0	3 (3 P-S)	469.0±32.6	4 (4 P-S)	435.0±24.3
2 June – 23 June	0+	0		1	153	34	159.4±15.8
	1+	2	266 (1 measured)	8	265.0±42.4	41	231.4±29.7
	≥2+	2	455.5±62.9	2	Not measured	0	
24 June – 15 July	0+	0		5	154.3±27.7	20	159.3±32.0
	1+	1	Not measured	4	270.5±17.8	22	241.7±24.7
	≥2+	2	427.5±50.7	3	382.0±37.0	1	339
16 July – 6 Aug.	0+	0		1 (0 S)	Not measured	25 (0 S)	180.1±26.7
	1+	0		6 (3 S)	298±16.1	21 (1 S)	249.7±23.7
	≥2+	0		0		2 (2 S)	320.5±30.4
7 Aug. – 28 Aug.	0+	0		4 (0 S)	197.5±22.8	29 (0 S)	189.8±24.7
	1+	0		0		7 (0 S)	266.5±17.2
	≥2+	0		0		0	
29 Aug. – 19 Sept.	0+	2 (0 S)	234 (1 measured)	4 (0 S)	238.3±23.2	73 (2 S)	213.5±32.5
	1+	0		0		14 (1 S)	285.4±23.4
	≥2+	0		0		1 (0 S)	340
20 Sept. – 11 Oct.	0+	9 (0 S)	229.7±30.6	3 (0 S)	191.0±3.6	96 (0 S)	229.9±26.7
	1+	0		0		21 (0 S)	294.8±31.7
	≥2+	0		0		0	
12 Oct. – 1 Nov.	0+	18 (0 P-S)	224.2±35.1	0		33 (0 P-S)	224.4±24.1
	1+	0		0		8 (4 P-S)	283.4±33.4
	≥2+	0		0		2 (2 P-S)	472.5±60.1
2 Nov. – 18 Apr.	0+	44 (0 P-S)	246.4±30.6	1 (0 P-S)	Not measured		
	1+	30 (17 P-S)	354.8±27.6	0		No angling	
	≥2+	10 (10 P-S)	428.8±50.3	0			

Note: Data were pooled over the 1999–2001 experimental period. Tag return rates at a given sea age were similar every year. Fish recaptured less than sea age classes, but comparisons may be made between cells, except those including sea age 0 charr in May–July, because their size is too small for the

of June. Some of the sea age 1 charr were mature and migrated to spawning areas from mid-July to September, larger ones returning to the river earlier in the summer. However, even immature sea age 1 migrants moved back to the river at the end of the summer. They dominated captures of juveniles in the SMR in the fall of 1999 and 2000 and were never observed in the upstream part of the Saguenay River during that period, unlike migrants-of-the-year. We also had evidence that part of them actually overwintered in the SMR and waited until the following spring to move back to the Saguenay Fjord. These observations are in accordance with the study of Castonguay et al. (1982), which suggested that migration patterns of sea age 0 and sea age 1 juvenile brook charr are different in some populations.

The analysis of stomach contents confirmed that food was still abundant in the Saguenay River in winter and that fish present in the Saguenay during that period fed more than fish present in the SMR. Whether or not smaller migrants may face starvation if staying in the SMR in winter is not known. Starvation risk may oblige migrants-of-the year to overwinter in the Saguenay, where the increased costs associated with variable abiotic conditions and higher predation risk would be compensated by greater growth opportunities. The fact that sea age 0 charr overwinter in the Saguenay may also reflect a more risky behaviour of these fish to maximize growth during their first year in salt water to increase the probability of reproducing the next fall. It could be the case of an environment selecting for early maturation (for instance, where adult survival is low relative to juvenile survival (see Stearns 1992)). In contrast, sea age 1 juveniles adopted a more conservative behaviour: they returned to the SMR earlier in the fall and a significant portion of them stayed there until the following spring. This observation is in accordance with our prediction, coming from Clark's (1994) asset-protection principle: at the end of their second growing season in estuarine areas, charr give priority to increasing survival by sheltering instead of increasing growth in a riskier environment. In the fall, sea age 1 charr are larger than migrants-of-the-year. Size is intimately connected with reproductive success in salmonids as fecundity of fish generto date, sea age, and fishing area.

Fjord, downstream of SMB		Ste-Marguerite River downstream		Ste-Marguerite River upstream	
Number	Mean length	Number	Mean length	Number	Mean length
0					
1 (0 P-S)	240				
0		No angling		No angling	
0					
0					
10 (0 P-S)	216.5±27.2				
3 (0 P-S)	359.7±48.6	No angling		No angling	
2 (2 P-S)	481.5±0.7				
6	166.7±14.6	0		0	
27	246.5±23.7	0		0	
18	422.9±48.3	0		0	
12	172.7±28.7	0		0	
31	273.6±32.4	0		0	
7	408.8±48.3	0		1 (1 S)	466.6
12 (0 S)	188.2±15.2	0		0	
20 (3 S)	283.4±19.8	0		9 (8 S)	353.1±22.7
2 (2 S)	338 (1 measured)	0		9 (9 S)	445.0±61.4
17 (2 S)	205.8±28.7	0		1 (1 S)	209
6 (4 S)	304.8±22.0	0		11 (7 S)	349.0±16.1
0		0		23 (23 S)	434.5±60.8
12 (0 S)	208.0±23.1	1 (0 S)	220	0	
4 (0 S)	261.7±12.6	21 (4 S)	302.1±33.9	13 (12 S)	330.4±46.1
0		0		25 (25 S)	426.2±45.3
0		38 (0 S)	240.6±18.9		
0		63 (4 S)	306.5±31.5	No angling	
0		0			
0		48 (0 P-S)	251.5±26.2		
0		35 (10 P-S)	321.3±34.3	No angling	
0		22 (22 P-S)	434.4±45.9		
0					
0		No angling		No angling	
0					

2 weeks after tagging were omitted. Proportions of recaptures according to sea age do not represent absolute proportions of sportfishery. SMB, Ste-Marguerite Bay; S, spawners; P-S, postspawners.

Table 2. Length (mean ± standard deviation, mm) of sea age 1 brook charr (*Salvelinus fontinalis*) spawners sampled while monitoring sportfishery in the upstream part of the Sainte-Marguerite River (SMR upstream) during the summer and in the Sainte-Marguerite Bay (SMB) and the downstream part of the Sainte-Marguerite River (SMR downstream) in the fall in 1998, 1999, and 2000.

Year	SMR upstream, summer	SMB and SMR downstream, fall	Student's t test results
1998	326.9±31.0 (n = 14)	303.1±18.6 (n = 12)	$p < 0.03$
1999	343.6±26.3 (n = 17)	314.5±28.0 (n = 15)	$p < 0.05$
2000	345.5±28.1 (n = 19)	284.9±28.6 (n = 13)	$p < 0.0001$

ally increases with body size and because a larger size may constitute an advantage in territorial competitions at the time of reproduction (Dodson 1997). Thus, without considering age at maturity, sea age 1 migrants have greater reproductive assets to protect than migrants-of-the-year. In addition, sea age 1 charr (having reached size at maturity) will reproduce the following fall, which is not the case of many migrants-of-the-year. Therefore, in terms of time to elapse before reproduction, sea age 1 charr have greater reproductive prospects to protect than migrants-of-the-year. The more conservative behaviour of older juveniles may be limited by energy constraints, as suggested by the arrival of some sea age 1 juveniles in the Saguenay River during winter. A portion of sea age 1 juveniles may not have had sufficient energy reserves to spend winter without feeding and (or) to reproduce the following year.

Charr having spent more than two growing seasons in the Saguenay River showed migration patterns very similar to

Table 3. Length (mean ± standard deviation, mm) of juvenile brook charr (*Salvelinus fontinalis*) measured while monitoring sportfishery in the fall in 1998, 1999, and 2000, according to area and period.

		Area	
Year	Period	Ste-Marguerite Bay	Ste-Marguerite River
1998	29 Aug. – 19 Sept.	241.7±48.8a (n = 36)	286.3±36.9b (n = 188)
	20 Sept. – 11 Oct.	235.3±28.7a (n = 109)	270.4±39.8c (n = 415)
	12 Oct. – 2 Nov.	228.6±20.3a (n = 19)	265.6±33.6d (n = 515)
1999	29 Aug. – 19 Sept.	238.3±32.7a (n = 39)	295.4±41.8c1(n = 139)
	20 Sept. – 11 Oct.	238.6±34.9a (n = 220)	299.9±43.8c2 (n = 441)
	12 Oct. – 2 Nov.	226.3±22.9b (n = 59)	292.8±52.7c1, d2 (n = 285)
2000	29 Aug. – 19 Sept.	259.1±36.8a (n = 28)	301.2±37.4c (n = 39)
	20 Sept. – 11 Oct.	272.0±39.8a (n = 42)	297.7±46.1c (n = 324)
	12 Oct. – 2 Nov.	220.5±27.6b (n = 18)	290.6±53.3c (n = 55)

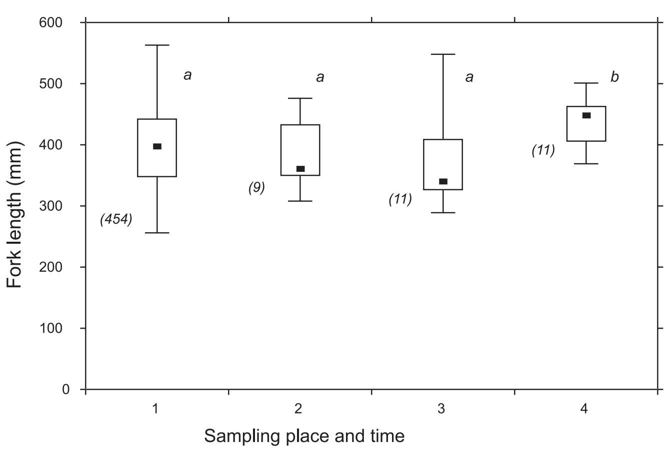
Note: For a given year, different letters (associated with a given number if need be) indicate significant difference at p = 0.05 (Student's t test).

Table 4. Percentage of stomachs with contents in brook charr (*Salvelinus fontinalis*) sampled in the fall and winter, according to area.

Season	Sampling site	Period	N	Percentage of stomachs with contents
Fall		Oct. 1998	48	93.8
	SMB	Oct. 1999	42	92.9
		Oct. 2000	14	100
		Oct. 1998	238	43.3
	SMR	Oct. 1999	168	48.8
		Oct. 2000	47	51.1
Winter	Saguenay	Jan.–Feb. 2000	11	62.5
	Saguenay	Jan.–Feb. 2001	11	100
	SMR	Feb. 2000	11	0.9
	SMR (mouth)	Feb. 2001	12	33.3

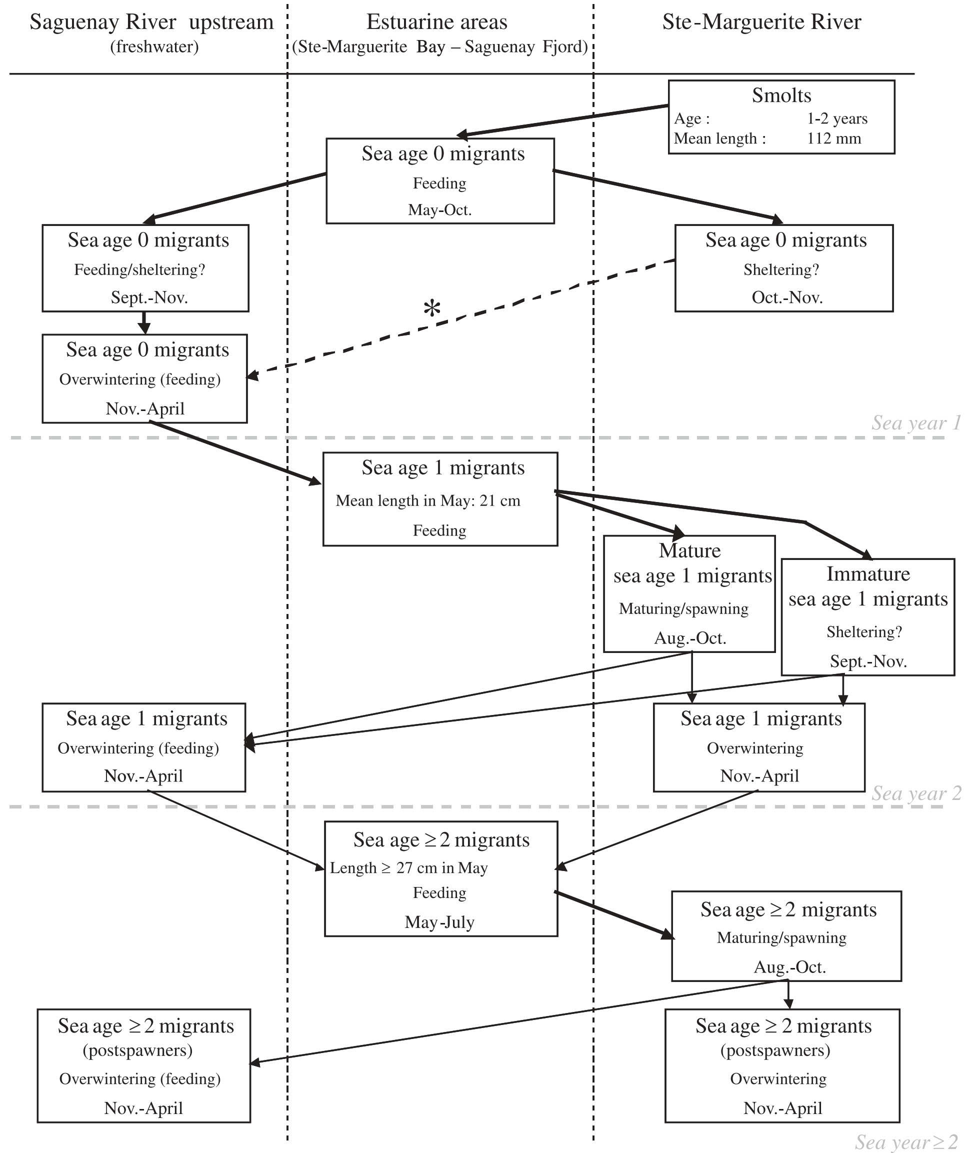
Note: SMB, Sainte-Marguerite Bay; SMR, Sainte-Marguerite River (Geneviève Morinville and Joe Rasmussen, Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada, unpublished data).

Fig. 7. Length at tagging (median, 25%–75% range, total range) of (1) all brook charr (*Salvelinus fontinalis*) spawners tagged at the Big Pool during summer 1999 and (2–4) spawners tagged at the Big Pool in 1999 and recaptured migrating downstream the Sainte-Marguerite River in October (2), recaptured while overwintering in the Saguenay River (3), and recaptured in the Sainte-Marguerite Bay in spring 2000 (4). Samples sizes are given in brackets. Different letters indicate significant difference at p = 0.05 (Mann–Whitney U test).



sea age 1 charr, except that they were almost all mature and undertook their upstream migration to spawning areas early in the summer. After reproduction, some left the SMR to overwinter in the upstream part of the Saguenay River, whereas some overwintered in the SMR. The mark–recapture experiment carried out on adults present on spawning grounds (including some of sea age 1 migrants) showed that postspawners leaving the SMR in early spring were part of the largest spawners tagged during the previous year and were significantly larger, at the time of tagging, than postspawners recaptured in the Saguenay River during winter. This observation was associated with a higher mortality in smaller adults. Therefore, the larger size of fish leaving the SMR in early spring may be the result of two phenomena that are not mutually exclusive: smaller postspawners exhibit a greater probability of mortality if they remain within the SMR and smaller postspawners exhibit a greater probability of outmigration from the SMR to exploit the richer feeding areas of the Saguenay River in winter. Both scenarios suggest that smaller adults face higher energy constraints following reproduction. As such, larger adults may be behaving conservatively by remaining sheltered in the river during the winter following reproduction, whereas smaller adults are obliged to feed in the Saguenay immediately after reproduction.

Fig. 8. Schematic model for the migratory patterns of anadromous brook charr (*Salvelinus fontinalis*) from the Sainte-Marguerite River, Saguenay, Québec, Canada, according to sea age and maturity stage. *, inferred.



Finally, we had evidence that abiotic factors may affect the seasonal behaviours of anadromous brook charr. The presence of large amounts of frazil ice during winter 2001 seemed to have driven fish towards the river mouth. A telemetry study on winter movements of cutthroat trout showed that fish moved downstream when their habitat was affected by frazil and anchor ice (Brown 1999). In Ellerslie Brook (Prince Edward Island), major outward movements of brook charr at 0 °C may be associated with the formation of frazil ice (Smith and Saunders 1958). Frazil ice represents a major danger for fish (which may be affected by ice crystals in their mouth and gills), limits available habitat, and constrains flow to channels where velocity may be too high for fish to maintain position (see references in Brown 1999). The fact that 2000 spawners overwintering in the river had to leave it may explain why we did not observe any size-specific mortality in tagged fish, as mortality risk was high for both small and large postspawners.

Growth rate and mortality risk in fresh water and estuarine areas will change according to specific environmental settings. Migratory behaviour of brook charr populations should reflect local opportunities and constraints. For instance, age at first downstream migration tends to increase with latitude (Castonguay et al. 1982). This latitudinal cline could result from slower growth in northern rivers (e.g., Dutil and Power 1980), where charr need a longer stay in fresh water to reach the size at first migration observed in southern rivers (e.g., White 1940). However, brook charr from the SMR migrate earlier and at smaller size than brook charr from the Moser River, Nova Scotia (ages 2 and 3, modal sizes 170–200 mm; White 1940), located south of the SMR, or than brook charr from the Saint-Jean River, Québec (ages 2 to 4, 100–200 mm; Castonguay et al. 1982), located at a similar latitude. If the existence of a threshold size at first migration is associated with the size-dependent salinity tolerance of brook charr, a smaller size at downstream migration in the SMR may be explained by the low salinity of the SMB (<5.5‰ in spring). Comparable sizes of smolts, associated with low salinity conditions, were also observed in the Moisie River estuary (Montgomery et al. 1990). Similarly, the thermohaline stratification of the Saguenay River may promote the long distance movements (as far as 100 km) of juveniles and adults rarely observed in other populations (see Power 1980). This could be especially true in winter; in populations of brook charr observed overwintering outside their natal river, those fish caught were only a short distance from the river mouth (e.g., Smith and Saunders 1958; Castonguay et al. 1982). A low age at downstream migration and an intense exploitation of estuarine areas in brook charr from the SMR is associated with fast growth and a low age at maturity (3+) relative to other populations from Québec and the Maritimes (see Power 1980; Castonguay et al. 1982), emphasizing the link between migratory behaviour and other life-history traits.

In summary, our results showed that if anadromous behaviour depends on a growth–mortality trade-off, it is dynamic in nature. Migratory patterns of brook charr from the Sainte-Marguerite River imply that fitness payoffs in river and estuary may vary according to time of year, growth, maturity stage, and condition of individuals. As predicted by behavioural models, migratory patterns of charr changed throughout their ontogeny, and as fish grew and accumulated fitness assets, they tended to adopt a more conservative behaviour. Factors affecting migration may have an effect on other life-history traits and vice versa. Environmental differences related to geographical location can be responsible for the variation of migration patterns and life histories that we commonly observe within salmonid species or between closely related ones. Accurate knowledge of the influence of environmental factors on growth and mortality of salmonids is necessary to fully understand the link between migratory behaviour and the life history of anadromous species.

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