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ORIGINAL PAPER

Mating system and individual reproductive success of sympatric anadromous and resident brook charr, *Salvelinus fontinalis*, under natural conditions

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Abstract Salmonids are known for the occurrence in sympatry of two life-history forms, one that undergoes migration to sea before returning to freshwater to reproduce (anadromous) and one that inhabits freshwater without a migration phase (resident). Whereas one breeding population is often suggested by population genetic studies, mating patterns have rarely been directly assessed, especially when both sexes are found within each life-history form. By using highly polymorphic microsatellite loci and parentage analysis in a natural population of sympatric anadromous and resident brook charr (*Salvelinus fontinalis*), we found that gene flow occurred between the two forms and was mediated by resident males mating with both resident and anadromous females. Determinants of reproductive success, estimated by the number of surviving juveniles (ages 1 and 2 years), differed between the sexes. No strong evidence of the influence of size on individual reproductive success was found for males, whereas larger females (and hence most likely to be anadromous) were more successful. The higher individual reproductive success of anadromous fish compared to residents was mainly explained by this higher reproductive success of anadromous females. We suggest that resident males adopt a "sneaking" reproductive tactic as a way of increasing their reproductive success by mating with females of all sizes in all habitats. The persistence of the resident tactic among females may be linked to their advantage in accessing spatially constrained spawning areas in small tributary streams unavailable to larger females.

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Introduction

The study of mating systems provides insights into the reproductive strategies adopted by both sexes to maximize reproductive success and contributes to our understanding of selection and local adaptation (Reynolds 1996). The use of highly polymorphic genetic markers along with parentage assignment analyses has made major contributions to the field, namely, by revealing important discrepancies between behavioral- and genetic-based definitions of mating systems. Early genetic work on birds and mammals showed that many species were far more polygamous than previously thought (Westneat 1987; Hughes 1998; Coltman et al. 1999). More recent work on fishes, known for their great diversity of mating systems and reproductive tactics, has also provided a more complete picture of mating patterns than that previously described based on behavioral observations alone (DeWoody and Avise 2001; Avise et al. 2002). In addition to the discovery of unsuspected elevated levels of polygamy in both sexes (Garant et al. 2001; Feldheim et al. 2004), field studies have provided genetic evidence for cuckoldry, extra-pair paternity, nest-takeover events, and egg thievery in nest-tending species (Conrad et al. 2001; DeWoody and Avise 2001; Blomqvist et al. 2002) and have provided more direct measures of individual reproductive success (Garant et al. 2001, 2005; Neff 2001; Blanchfield et al. 2003). This body of work has emphasized the existence of alternative mating tactics in many taxa and species as a way of achieving substantial mating success (Scott and Williams 1993; Jones et al. 1998; Coltman et al. 1999; Kempenaers et al. 2001).

Salmonid mating systems have been the focus of many studies (Fleming 1998; Blanchfield et al. 2003; Dickerson et al. 2004; Seamons et al. 2004b), especially that of Atlantic salmon (*Salmo salar*) that involves alternative mating tactics among males (Thomaz et al. 1997; Garant et al. 2001, 2003; Garcia-Vazquez et al. 2001; Jones and Hutchings 2002). In this species, a proportion of male parr (a term referring to the juvenile freshwater stages of salmon) mature in freshwater at younger ages and smaller sizes than anadromous males that migrate to sea before returning to spawn. Whereas anadromous males fight among themselves to control access to female salmon, mature parr sneak into females' nests to gain access to mating. However, in many other species of salmonids, both males and females may adopt residency (maturation without going to sea) and are often found in sympatry with the anadromous form. Population genetic analyses have generally failed to demonstrate significant genetic differentiation between sympatric forms (but see Foote et al. 1989; Wood and Foote 1990, 1996). Most studies have revealed greater genetic differentiation between geographical localities than between coexisting life-history forms within any one locality [brown trout *Salmo trutta* (Hindar et al. 1991; Schreiber and Diefenbach 2005), brook charr *Salvelinus fontinalis* (Jones et al. 1997; Boula et al. 2002; Castric and Bernatchez 2003), rainbow trout *Oncorhynchus mykiss* (Docker and Heath 2003; Narum et al. 2004)]. Moreover, experimental crosses and transplant studies have shown that parr from "pure" anadromous or resident crosses can either become one form or the other and that transplanted resident fish have given rise to anadromous stock or vice versa (Nordeng 1983; Morita et al. 2000; Olsson and Greenberg 2004; Schreiber and Diefenbach 2005). Behavioral observations also provided evidence for reproduction between anadromous and resident fish (Jonsson 1985; Schreiber and Diefenbach 2005). Altogether, these studies strongly suggest that in most circumstances, sympatric resident and anadromous forms of salmonids belong to a single gene pool. Yet, population genetic analyses and behavioral observations provide little insight into mating patterns: The actual reproduction is not seen and, even if it was, would not reveal which fish were successful in reproducing. No studies have yet documented the mating system and associated reproductive success of sympatric forms of anadromous and resident salmonids, other than Atlantic salmon, either in controlled or natural environments.

Adult size in salmonids has often been identified as an important determinant of reproductive success (Fleming 1996). Size certainly represents a major discrepancy between anadromous and resident forms. Anadromous individuals benefit from higher growth rates at sea (Gross 1987; Morita and Takashima 1998), and a bigger size confers a fecundity advantage to females (Fleming 1996) and a dominance advantage in males (Blanchfield et al. 2003). Furthermore, because males are able to achieve substantial reproductive success by adopting alternative reproductive tactics (Hutchings and Myers 1988), females often predominate within the anadromous part of the population (Kristoffersen et al. 1994; Rikardsen et al. 1997; Doucett et al. 1999) and, in some instances, only males adopt the resident tactic (Bohlin et al. 1994). Reproductive success and its correlation with size have never been compared between sympatric anadromous and resident individuals where females, and not just males, are adopting both life-history forms.

The brook charr is native of northeast North America and commonly occurs as landlocked, freshwater–river resident and anadromous forms. Colonization of northeast North America is believed to have taken place from south to north after the retreat of glaciers 10,000 years ago. Founders of extant populations are thus considered to have been anadromous (Castric and Bernatchez 2003) and now coexist with resident individuals in many populations occupying tributaries of the Gulf of St. Lawrence and the St. Lawrence River Little is known about the life history of sympatric anadromous and resident brook charr. However, it has been shown that growth rate and growth efficiency differ between future migrants and future residents and are proximate factors linked to the form adopted (Morinville and Rasmussen 2003; Thériault and Dodson 2003). This suggests that anadromy and residency in this species may be under a conditional mode of regulation, where a threshold exists that must be exceeded to adopt one form or the other (Hazel et al. 1990; Roff 1996).

The objective of this study was to use highly polymorphic microsatellite loci and parentage analysis to document the mating systems of sympatric resident and anadromous brook charr in a tributary of the Sainte-Marguerite River, Québec, Canada, under natural conditions. By means of parentage analysis, we first determined if reproduction occurs between the two forms and, if so, if it is mediated by resident males only. We then estimated individual reproductive success and its variance for both resident and anadromous fish based on the number of surviving young (ages 1 and 2 years). We further investigated the mating system by documenting and comparing the relationship between reproductive success, size, and number of mates for both sexes and forms.

Materials and methods

Study site and brook charr reproductive behavior

The Sainte-Marguerite River system in Quebec, Canada, sustains a large population of anadromous brook charr that

migrates into the Sainte-Marguerite Bay and the Saguenay River before returning to the freshwater to reproduce (Fig. 1). They migrate at 1 or 2+ years of age and to a lesser extant at age 3+, and sex ratio is 1:1 at both downstream and upstream migration (Lenormand 2003; Thériault and Dodson 2003). Male and female resident brook charr also occur in the river and are mainly found in tributaries of the main river branch. Sampling as well as underwater observations at different sites of the river showed that anadromous charr use tributaries for reproduction, and thus that both forms are present on the same spawning grounds (Thériault, personal observation). Reproductive behavior of brook charr is typical of other river salmonids: Females excavate their nests in gravel substrates during the fall where they deposit their eggs. Males compete for access to females and hence for opportunities to fertilize the eggs. Sneaking and satellite behavior by small males has previously been observed in lacustrine populations of this species (Blanchfield et al. 2003).

Sampling

The study was performed on a small tributary of the Sainte-Marguerite River, Morin Creek (average 5.6 m wide, 0.3 m deep, Fig. 1). An impassable waterfall (75 m high) is located 4 km upstream from the mouth of the tributary. The study was conducted in a 2.5-km section below this waterfall, accessible to anadromous fish.

An upstream migration trap was installed at 1 km from the mouth of the stream and was operated from the end of June to the end of October in 2000 and 2001 for intercepting upstream-migrating anadromous spawners (Fig. 1). The trap covered the entire width of the stream except for some periods of high flood where fish could pass either over or under it (see "Results" section). Traps were visited twice daily, fish were measured (fork length) and marked individually with a T-bar Floy Tag, the adipose fins were taken and preserved in 95% ethanol, and subsequently, fish were released 200 m upstream. Fish caught in the upstream migration trap were differentiated into anadromous or resident forms based on length, morphological identification, maturation stage (when available), and/or recapture information (Thériault and Dodson 2003; Lenormand et al. 2004). Thus, fish bigger than 250 mm were always classified as anadromous as this length approaches the maximum size of residents observed in this stream. Only three resident fish recorded during 7 years of survey of this stream exceeded 250 mm (253, 256, and 258 mm fork lengths) (Thériault, unpublished data). Fish between 170 and 250 mm were either mature resident when signs of maturation were present (coloration, body shape, sperm release, oviposition pore visible) or immature anadromous when no such signs were detected. Although some mature resident fish were caught in the upstream migration trap, most were captured with electrofishing gear from June to September 2000 and 2001 in three distinct areas along the 2.5-km section (Fig. 1). All

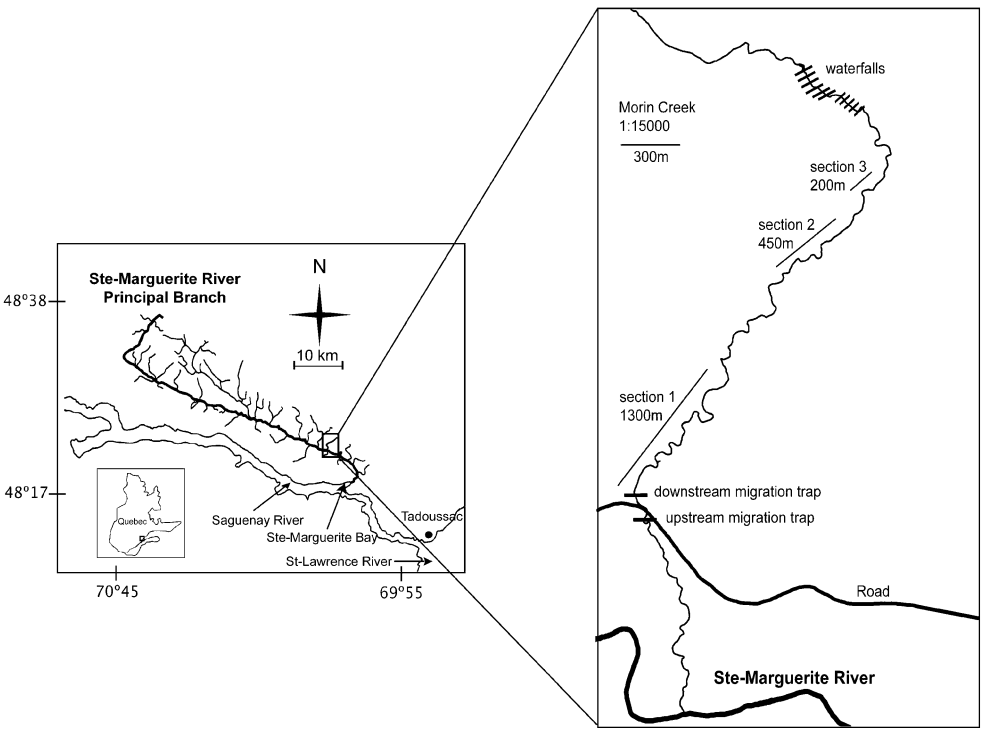

Fig. 1 Location of study area, sampling traps, and electrofishing sites

fish greater than 120 mm were considered as potential resident spawners as this was approximately the minimum observed length at sexual maturity in this stream (114 mm, Lenormand 2003). Fish were measured (with their adipose fins sampled) and then released not more than 50 m from their capture site. Sex was noted when external signs of maturation were present.

In 2002, 2003, and 2004, 1+ and 2+ juvenile fish (progeny from the 2000 and 2001 spawners sampled) were collected either by means of a downstream migration trap intercepting first time migrants in May and June or by electrofishing from June to October in the same 2.5-km section as for resident spawners (Fig. 1). Fish were classified as either 1+ or 2+ based on length distribution, previously validated with age determination based on otoliths from the same system (Thériault and Dodson 2003). All fish were measured (with their adipose fins sampled) and subsequently released near their site of capture.

Microsatellite polymorphism analyses

Total DNA was extracted from the adipose fin tissue using Qiagen® DNeasy™ extraction kit. Microsatellite polymorphism was analyzed at 13 loci using fluorescent-labeled primers (*SfoB52*, *SfoC113*, *SfoC129*, *SfoC28*, *SfoC88*, *SfoC115*, *SfoD100*, and *SfoD75*, T. L. King, US Geological Survey, unpublished; *SCO204*, *SCO216*, and *SCO218*, DeHaan and Ardren 2005; *Sfo262Lav* and *Sfo266Lav*, Perry et al. 2005). Five polymerase chain reactions (PCR) were carried out using either a Perkin–Elmer 9600 thermocycler v.2.01 or a Biometra® T1 thermocycler (Table 1). PCR products 1 and 2 (Table 1) were purified with a PCR_{96} Cleanup Plate Manu30 from Millipore and were subsequently separated electrophoretically using a BaseStation™ DNA Fragment Analyzer (MJ Research) (gel 1: quintuplex; gel 2: triplex). Allelic sizes were scored against the size standard GENESCAN ROX-500 (Applied Biosystems) using CARTOGRAPHER™ analysis software v.1.2.0. PCR products 3, 4, and 5 (Table 1) were pooled and run together on an ABI™ 3100 automated capillary sequencer (Applied Biosystems). Allelic sizes were scored against the size standard GENESCAN ROX-500 (Applied Biosystems) using GENESCAN™ analysis v.3.7 and GENOTYPER™ v.3.7 NT software. Allelic sizes for each locus were standardized with the software ALLELOGRAM v.1.

Statistical analyses

Standard genetic statistics

Genetic diversity in the adult population was quantified by the number of alleles per locus and by observed and expected heterozygosities. Hardy–Weinberg equilibrium (HWE) was tested separately for each year and form (anadromous and resident), using the score test (*U* test), implemented in GENEPOP v.3.4 (Raymond and Rousset 1995). Significance level was adjusted to account for multiple testing using Bonferroni correction procedure (k=52 for single-locus comparisons, $\propto=0.05/k=0.00096$). As we subsequently used a parentage allocation procedure (see below), several features were investigated that could affect our analysis, namely, the presence of null alleles, linkage disequilibrium, and pairwise relatedness in the adult population (Pemberton et al. 1995; Dakin and Avise 2004). The potential occurrence of null alleles was tested by estimating their frequency using the Brookfield (1996) null allele estimator implemented in MICRO-CHECKER (Van Oosterhout et al. 2004). Linkage disequilibrium among loci

Table 1 PCR conditions for the 13 loci amplified

PCR	Loci	Amplification state	Rx volume (μl)	Rx buffer[a] (μl)	dNTPs[b] (μl)	*Taq* (U)	DNA (ng)	Cycle (temperature in °C)
1	*SfoC113/SfoC28/ SfoB52/SfoC129*	Quintuplex	20	2	0.8	0.3	8	5 min at 95, 35×(45 s at 95, 45 s at 56, 45 s at 72), 10 min at 72
2	*SfoC115/SfoD100/ SfoD75*	Triplex	20	2	0.8	0.3	8	5 min at 95, 35×(45 s at 95, 45 s at 58, 45 s at 72), 10 min at 72
3	*SCO204/SCO216/ SCO218*	Simplex	15	1.5	0.3	0.2	8	3 min at 94, 38×(30 s at 94, 30 s at 60, 30 s at 72), 7 min at 72
4	*Sfo262Lav*	Simplex	10	1	0.3	0.2	8	3 min at 94, 35×(30 s at 94, 30 s at 60, 45 s at 72), 7 min at 72
5	*Sfo266Lav*	Simplex	10	1	0.3	0.2	8	3 min at 94, 35×(30 s at 94, 30 s at 52, 45 s at 72), 7 min at 72

[a] Comprise 10 mM Tris–HCl [pH 9.0], 1.5 mM MgCl2, 0.1% Triton X-100, 50 mM KCl
[b] 10 mM each dNTP

was examined using the genotypic linkage disequilibrium option implemented in GENPEOP v.3.4 (Raymond and Rousset 1995). Finally, pairwise relatedness in the adult population was estimated using the identity index implemented in IDENTIX (Belkhir et al. 2002) and was compared to its random expectation under the hypothesis of a panmictic association after 1,000 permutations.

Population genetic structure

The hypothesis of genic (allelic frequency) differentiation between anadromous and resident spawners for each year of sampling was tested using a Fisher exact test at individual loci as well as over multiple loci using GENEPOP v.3.4 (Raymond and Rousset 1995). The extent of genetic differentiation was quantified by F_{ST} estimated by θ (Weir and Cockerham 1984) using GENETIX v.4.02 (Belkhir et al. 2000). Significance level for single as well as multilocus F_{ST} was tested by 2,000 permutations and was adjusted to account for multiple testing using Bonferroni correction procedure (k=13 for single-locus comparisons, $\propto$=0.05/13=0.0038; k=4 for multilocus comparisons, $\propto$=0.05/4=0.0125).

Parentage analysis

Parental allocation was performed using PASOS 1.0, a software package allowing the allocation of progeny to either one or two parents in an open system, where parents are potentially missing (Duchesne et al. 2005). Allocation can be performed whether the sex of putative parents is known. Using a sequential allocation and simulation procedure, PASOS provides an estimate of the overall allocation correctness rate as well as an estimate of the proportion of parents that contributed to reproduction but were not collected. Briefly, to allocate an offspring, PASOS first searches for the most likely pairs among all potential pairs of collected parents. The likelihoods are computed according to a fixed error model, wherein the transmission probability from allele X to X equals 0.98 and the remaining 0.02 is evenly distributed over all remaining offspring alleles for any given locus. At least one most likely pair is always obtained this way. False parents are filtered out by building the most likely transmission scenario and by subsequently computing the distances between each transmitted parental allele and its presumed offspring counterpart. If the transmission distance for one putative parent is not within the maximum offset tolerance (MOT—see below) determined a priori, this parent is rejected (only a single mismatch—one locus—is needed for rejection). The MOT is a user-defined parameter (set to either 0, 1, or 2) and refers to the maximum number of offsets between a parental and an offspring allele that PASOS accepts as possibly due to a scoring error. For example, 254 and 258 are two offsets apart within a dinucleotide locus, or one offset apart within a tetranucleotide locus.

Allocation with PASOS was performed following two steps. We first allocated the offspring using the sequence allocation option, starting with the most informative loci, with MOT set to 0. Adults sampled in 2000 and 2001 were treated as potential parents for all juveniles, allowing for repeat spawning and incomplete adult sampling. The resulting curve provided an estimate of the percentage of parents collected among the pool of spawners needed to produce the juveniles analyzed, which typically corresponds to the point where the curve reaches a plateau (Fig. 2). The second step consists of performing simulations with this estimate to produce a simulated curve that fits the true allocation curve. This provides an estimate of the overall correctness rate (confidence). Simulated offspring were created from the true parental file with a 2% error model and an offset of 2, the transmission probability being 0.98 for the focal allele, 0.008 at one offset, and 0.002 at two offsets. The simulated allocation was performed at MOT 0 to better reflect the true allocation. True and simulated allocations were also performed at MOT 1 and 2, but we opted for a conservative approach by keeping MOT at 0, as this was the value that provided the maximal confidence, albeit at the cost of lowering allocation rate (see "Results" and "Discussion" sections).

For each allocated offspring, we thus obtained the identity of either one or both parents as well as the number of offspring assigned to each parental pair and, hence, to each individual. When a single parent fathered or mothered

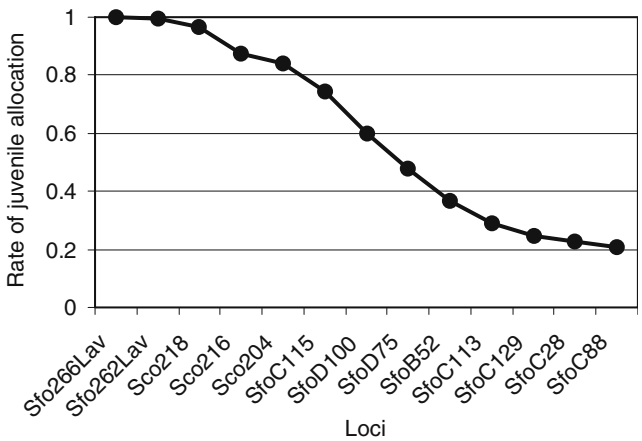

Fig. 2 Rate of juvenile allocation obtained with PASOS as a function of cumulative number of loci and using a maximum offset tolerance set to zero (MOT 0—see text). A plateau is starting to appear at the end of the cumulative curve, and the 20% rate attained at *SfoC88* was used as a first estimate of the proportion of sampled spawners

two juveniles or more, those offspring were further partitioned into full-sib families using COLONY v.1.2 (Wang 2004). COLONY uses a maximum likelihood method to assign individuals sampled into full-sib families nested within half-sib families based on offspring genotype, allowing for typing errors. Thus, even if the identity of the mating partners was not known (i.e., in the cases where only one parent was found), this exercise provided an estimation of the number of mates involved in a particular mating event.

Analyses from the parental allocation results

We first used the results of the allocation procedure to assess if reproduction occurred between anadromous and resident life-history forms. We then performed an analysis of variance (ANOVA) to detect any significant difference in individual reproductive success (mean number of juveniles produced per individual) as well as number of mates between forms. This analysis was performed by considering both each sex separately and both sexes combined. We used linear regression analysis and ANCOVA to assess the relationship between reproductive success, length, and form, as well as between number of mates (estimated from COLONY), size, and form for each sex separately. Those tests were done using JMP v.5.0.1a (SAS Institute Software).

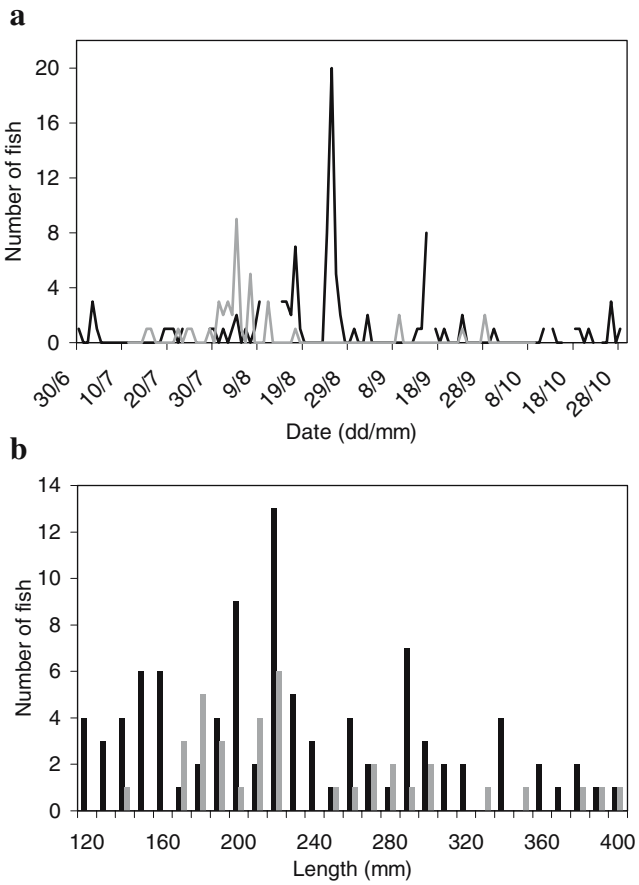

Fig. 3 **a** Number of fish caught in the upstream migration trap in 2000 (*black*) and 2001 (*gray*) and **b** corresponding length distribution

Results

Characteristics of fish sampled

Upstream migration of spawners occurred principally in August and to a lesser extent in September (Fig. 3a). Four heavy floods in 2000 interrupted the monitoring of upstream-migrating fish and probably resulted in the undersampling of the spawning run. In 2000, 55 fish were classified as anadromous, either mature (N=31, 255 to 398 mm fork length, mean=312.16 mm) or immature (N= 24, 177 to 244 mm fork length, mean=207.92 mm) (Fig. 3b). In 2001, 30 were anadromous, with 15 being mature (254 to 394 mm fork length, mean=310.71) and 15 immature (range 179 to 241 mm fork length, mean= 201.73 mm) (Fig. 3b). A total of 153 and 334 potential resident spawners were caught in 2000 and 2001, respectively, mainly by electrofishing but also in the upstream or downstream traps (2000, 120 to 258 mm fork length, mean= 155.53 mm; 2001, 120 to 256 mm fork length, mean= 154.94 mm). The significantly higher number of captures in 2001 reflects an increased electrofishing sampling effort in that year. A total of 981 juveniles were sampled from 2002 to 2004, with 828 aged 1+ (56 to 115 mm fork length, mean=84.41 mm) and 153 aged 2+ (80 to 140 mm fork length, mean=121.54 mm).

Standard genetic statistics

The 13 loci used showed moderate to high degrees of polymorphism in the adult population, with 6 to 30 alleles observed per locus and H_E ranging from 0.30 (*SfoC28*) to 0.89 (*SCO216*) for an overall expected heterozygosity level of 0.76 (Table 2). One temporal sample (RES 2001) displayed significant departures from HWE with a heterozygote deficiency observed at five loci (Table 2). Three of these, *SfoC115*, *SfoD100*, and *SfoD75*, showed evidence of null alleles with estimated frequencies of 0.045, 0.052, and 0.061, respectively (see parentage analysis results to see how they were dealt with for parental allocation). Furthermore, the magnitude of the difference between observed and expected heterozygosities for those five loci was small, suggesting that nonconformation to HW equilibrium was not of main concern in this sample. Exact test of genotypic linkage disequilibrium revealed a higher proportion of

Table 2 Numbers of samples (*N*), number of alleles (*A*), F_{IS}, observed (H_O) and expected (H_E) heterozygosities, and probabilities of conforming to Hardy–Weinberg equilibrium [*P*(HW), score *U* test] for each locus and each temporal sample (*RES* resident, *ANA* anadromous) separately

Locus	*A*		2000		2001	
			ANA	RES	ANA	RES
SfoB52	12	*N*	32	95	15	323
		A	7	9	7	12
		F_{IS}	−0.054	0.160	0.048	0.044
		H_O	0.81	0.65	0.80	0.77
		H_E	0.76	0.77	0.81	0.81
		P(HW)	0.8465	0.0191	0.4848	**0.0066**
SfoC113	9	*N*	32	95	15	323
		A	6	7	6	9
		F_{IS}	−0.093	0.013	−0.043	0.005
		H_O	0.84	0.73	0.80	0.74
		H_E	0.76	0.73	0.74	0.75
		P(HW)	0.7546	0.2372	0.5893	**0.0008**
SfoC129	7	*N*	32	95	15	322
		A	5	6	5	7
		F_{IS}	−0.021	0.128	0.000	0.019
		H_O	0.75	0.62	0.73	0.73
		H_E	0.72	0.71	0.71	0.74
		P(HW)	0.2523	0.0120	0.1192	0.0890
SfoC28	9	*N*	32	95	15	323
		A	6	8	5	8
		F_{IS}	−0.108	0.020	0.138	0.079
		H_O	0.59	0.54	0.27	0.51
		H_E	0.53	0.54	0.30	0.56
		P(HW)	0.7300	0.4056	0.3206	0.0918
SfoC88	6	*N*	32	95	15	322
		A	5	6	4	6
		F_{IS}	0.026	−0.097	−0.213	0.024
		H_O	0.63	0.68	0.73	0.64
		H_E	0.63	0.62	0.59	0.66
		P(HW)	0.3889	0.7596	0.9427	0.0230
SfoC115	16	*N*	32	94	15	322
		A	7	12	5	15
		F_{IS}	0.146	0.063	−0.212	0.115
		H_O	0.47	0.44	0.60	0.59
		H_E	0.54	0.46	0.48	0.67
		P(HW)	0.2163	0.4483	1.0000	**0.0003**
SfoD100	10	*N*	32	93	15	322
		A	8	10	6	10
		F_{IS}	0.206	0.078	−0.183	0.118
		H_O	0.59	0.75	0.80	0.72
		H_E	0.73	0.81	0.66	0.81
		P(HW)	0.0791	0.1036	0.9509	**<0.001**
SfoD75	13	*N*	32	94	15	321
		A	10	11	8	13
		F_{IS}	0.090	0.080	0.058	0.136
		H_O	0.75	0.79	0.73	0.71
		H_E	0.81	0.85	0.75	0.83
		P(HW)	0.1699	0.0249	0.1482	**<0.001**
SCO204	15	*N*	32	90	15	322
		A	7	9	6	15
		F_{IS}	0.113	0.062	−0.197	0.002
		H_O	0.69	0.74	0.87	0.81
		H_E	l0.76	0.79	0.70	0.81

Table 2 (continued)

Locus	*A*		2000		2001	
			ANA	RES	ANA	RES
		P(HW)	0.2271	0.2531	0.9715	0.2030
SCO216	18	*N*	32	92	15	322
		A	15	13	9	18
		F_{IS}	0.091	0.069	−0.057	0.042
		H_O	0.81	0.82	0.93	0.86
		H_E	0.89	0.87	0.86	0.89
		P(HW)	0.1305	0.0954	0.6490	0.0264
SCO218	14	*N*	32	90	15	322
		A	7	9	6	14
		F_{IS}	−0.007	0.007	−0.170	−0.023
		H_O	0.81	0.79	0.87	0.82
		H_E	0.79	0.79	0.72	0.80
		P(HW)	0.6297	0.7035	0.9580	0.3894
Sfo262Lav	19	*N*	31	87	15	319
		A	12	13	7	19
		F_{IS}	−0.033	−0.074	0.115	0.008
		H_O	0.87	0.91	0.73	0.84
		H_E	0.83	0.84	0.80	0.84
		P(HW)	0.6626	0.9460	0.2865	0.5147
Sfo266Lav	30	*N*	32	92	15	322
		A	13	21	7	29
		F_{IS}	0.002	−0.008	0.239	0.048
		H_O	0.88	0.86	0.60	0.83
		H_E	0.86	0.85	0.76	0.87
		P(HW)	0.0688	0.1244	0.0611	**<0.001**
Global		*N*	31–32	87–95	15	319–323
		A moy	8.3	10.3	6.3	13.5
		A tot	108	134	81	175
		H_O	0.73	0.72	0.73	0.73
		H_E	0.74	0.74	0.68	0.77
		P(HW)	0.0709	0.0052	0.6102	**<0.001**

Bold values are significant at $\propto$=0.0096 following Bonferroni corrections.

significant *P* values than expected by chance (17 out of 78 observed, 3.9 out of 78 expected by chance at $\propto$=0.05), again for the temporal sample RES 2001 only. The mean observed pairwise identity coefficient did not depart significantly from its expected distribution under the hypothesis of a random association for any of the temporal samples (ANA 2000, *P*=0.117; RES 2000, *P*=0.06; ANA 2001, *P*=0.998; RES 2001, *P*=0.136). Adults were thus not composed of individuals more related than expected by chance.

Population genetic structure

Significant temporal variation in allele frequency was detected among years within the adult resident sample (exact test of genic differentiation, *P*<0.001), although this variation was mainly due to the effect of two loci out of 13 (*SfoC28* and *SfoC115*). Population differentiation between anadromous and resident samples was estimated separately for each year. No evidence for differentiation was found in 2000, with none of the 13 loci showing significant allele frequency differences among forms (Table 3). In 2001, the differentiation between anadromous and resident samples was significant (F_{ST}=0.012, *P*=0.003). However, F_{ST} values differed greatly among loci (four loci had negative values, Table 3), and the significance of the differentiation was entirely due to a single locus (*SfoD100*). Estimating F_{ST} and correcting for the presence of null alleles using FreeNA (Chapuis and Estoup 2007) did not change any of our results (not shown). Overall, these analyses do not refute the null hypothesis that anadromous and resident adult fish are part of the same breeding population.

Parentage analysis

A total of 494 potential spawners (85 anadromous and 409 resident) and 974 juveniles (1+ and 2+) were used for

Table 3 Genetic differentiation between anadromous and resident brook charr estimated by θ_{ST} for each locus

Locus	θ_{ST} 2000	θ_{ST} 2001
SfoB52	−0.0035	−0.0057
SfoC113	0.0071	−0.0098
SfoC129	−0.0046	0.0146
SfoC28	−0.0007	0.0284
SfoC88	−0.0023	−0.0067
SfoC115	−0.0005	0.0176
SfoD100	0.0006	0.0573*
SfoD75	0.0027	0.0097
SCO204	−0.0062	0.0227
SCO216	0.0027	0.0116
SCO218	−0.0035	0.0126
Sfo262Lav	0.0147	−0.0105
Sfo266Lav	−0.0010	0.0172
Multilocus	0.0007	0.0124*

N=32 anadromous and 98 resident fish in 2000; N=15 anadromous and 323 resident fish in 2001

*P<0.001 after 2,000 permutations with alpha adjusted for multiple testing using Bonferroni correction ($\propto$=0.0038 for single-locus comparisons and $\propto$=0.0125 for multilocus comparisons)

parentage allocation. A total of 315 juveniles were assigned to a single parent, whereas 42 were assigned to both parents, leading to a total allocation rate of 21%. These 42 juveniles were either half-sibs or unrelated, suggesting that they were offspring of 42 different couples. That is, no more than one offspring was assigned to the same couple. The sequential allocation curve did not reach a true plateau but decreased more slowly toward the end of the sequence (Fig. 2). The allocation rate estimated from the last loci added was used to estimate the fraction of sampled spawners (20%, see Fig. 2) even though the plateau was not attained because simulation suggested a stabilization of the curve in adding one or two more loci (data not shown). However, parental allocation was complicated by the occurrence of null alleles, which may cause the false exclusion of a true parent. Any such bias would be conservative (i.e., excluding true parents rather than including false parents, Marshall et al. 1998; Dakin and Avise 2004). On the other hand, this can have an impact on the estimation of the proportion of sampled/missed spawners and, consequently, on the estimated confidence in our allocations. PASOS is not designed to account for null alleles as the error model used in the simulation procedure allows error at a maximum of two offsets apart from the focal allele, whereas the error associated with null alleles is not necessarily restricted to alleles close to the focal allele. Because removal of loci with null alleles from our parentage analysis decreased confidence significantly (results not shown), we chose to retain them in the analysis, making an upward correction to the estimated proportion of sampled spawners as follows. We estimated the probability of a false exclusion given by the three loci showing null alleles to be 12% (see formula developed by Dakin and Avise 2004). This 12% was added to the 20% of sampled parents (estimated by the allocation curve given by PASOS). We thus concluded that a maximum of 32% of the parents were sampled, and therefore that 68% of the spawners were missing. This estimate was subsequently used in the simulation procedure, which yielded an allocation correctness rate of 87%. A total of 72 spawners had two or more offspring (maximum of 19), and their progeny was divided into full-sib families with COLONY. Family sizes were small, ranging from one to four individuals (mean=1.37). That is, no more than four individuals shared the same unsampled parent. Analysis with COLONY allowed us to find full-sib individuals in our sample, which could not have been detected with PASOS because of the high proportion of unsampled spawners.

Mating patterns

Out of the 42 couples reconstructed from the parentage allocation analysis, half (21) involved an anadromous and a resident spawner, clearly showing reproduction and viability of offspring between the life-history forms. The sex of the adults was known for 13 of those 21 interform crosses, and in every case, the male was the resident fish. The remaining crosses were anadromous–anadromous, produc-

Table 4 Number of samples (N), mean, variance, and range of individual reproductive success (*RS* number of offspring assigned to individuals) for males and females together (overall) and separately according to life-history form

	RS overall				RS females				RS males			
	N	Mean	Variance	Range	N	Mean	Variance	Range	N	Mean	Variance	Range
Anadromous	31	4.48	18.52	1–19	9	8.22	35.94	2–19	4	3.25	4.25	1–5
Resident	138	1.88	2.15	1–10	17	2.18	3.9	1–9	28	2.39	3.73	1–10
F value		33.62	39.97			14.75	17.96			0.68	0.37	
df		1, 167	1, 167			1, 24	1, 24			1, 30	1, 30	
P-Value		<0.0001	<0.0001			0.0166	0.0003			0.4161	0.5466	

Means and variances of life-history forms are compared with ANOVA and Levene's test, respectively.

ing five offspring, and resident–resident, producing 16 offspring. The mean number of partners estimated with COLONY did not differ between life-history form and sex (ANOVA, $F_{1,\ 26}$=0.995, P=0.33 for form; $F_{1,\ 26}$=0.024, P=0.88 for sex) and ranged from one to eight (mean=3.25) for anadromous and one to seven (mean=2.52) for resident fish. When anadromous females were found mating with multiple partners, males were either all resident or they were composed of a single anadromous fish and many resident fish (three resident males in one mating event, four in the other). No more than one anadromous male was found mating with the same female. However, the number of partners must be viewed as conservative as it is limited by the total number of offspring assigned to each individual.

Individual reproductive success

Globally, individual reproductive success of anadromous (total number of offspring assigned to each spawner, 1+ and 2+ combined) was significantly higher than reproductive success of resident fish (ratio anadromous/resident=2.9), and the same was true for variance in individual reproductive success (Table 4). This difference was due to anadromous females having a higher reproductive success than resident females. No difference was observed among males (only four anadromous males were available for this analysis, Table 4).

Female determinants of reproductive success

Reproductive success was positively related to length for females and explained 46% of the variation (linear regression, F=20.75, P=0.0001, R^2=0.46, Fig. 4a). This relationship seems to be driven by a few anadromous females that dominated spawning, but a quadratic regression did not fit the data better than the linear one (F test, F=2.19, P=0.15). An analysis of covariance revealed that the effect of the life-history form on reproductive success was not significant when length was included ($F_{1,\ 22}$=4.28, P=0.05 for length; $F_{1,\ 22}$=0.07, P=0.79 for form). The interaction term was not significant, and thus the effect of length on reproductive success was the same within each form (length by form, $F_{1,\ 12}$=1.19, P=0.25). The number of mates was not related to length in either form (ANCOVA, $F_{1,\ 12}$=0.13, P=0.73 for length; $F_{1,\ 12}$=0.02, P=0.90 for form; $F_{1,\ 12}$=0.09, P=0.77 for the interaction term; Fig. 4b).

Male determinants of reproductive success

For males, neither length nor life-history form had a significant effect on reproductive success (ANCOVA, $F_{1,\ 28}$=1.61, P=0.21 for length; $F_{1,\ 28}$=1.35, P=0.26 for form; $F_{1,\ 28}$=1.47, P=0.24 for the interaction term; Fig. 5). However, the low number of anadromous males (four) in this analysis limits our conclusion. Analyses involving numbers of mates were omitted because mate numbers for anadromous males were available for two individuals only.

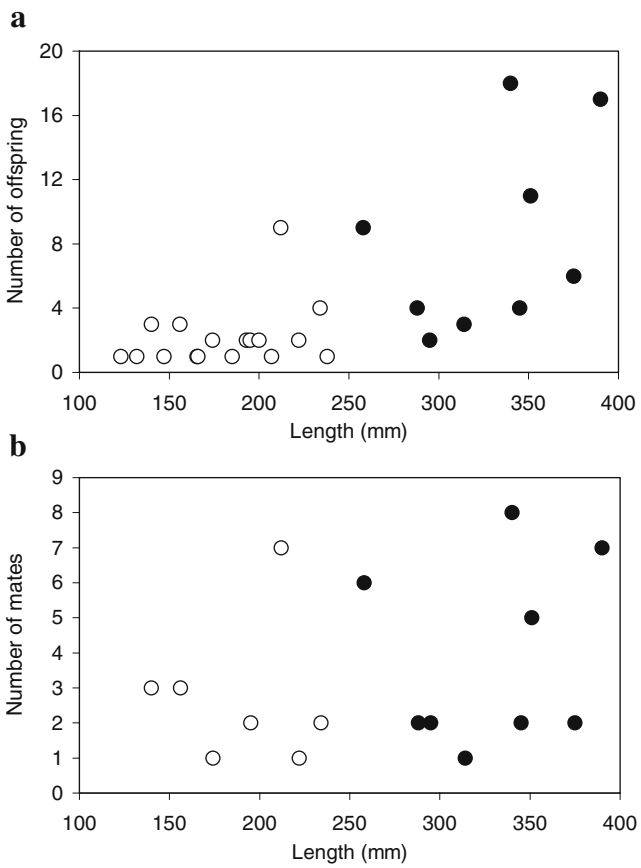

Fig. 4 Reproductive success (number of offspring assigned per individual) (**a**) and number of mates (**b**) as a function of body size for female spawners. *Open circles* are resident life-history fish, while *closed circles* are anadromous life-history fish

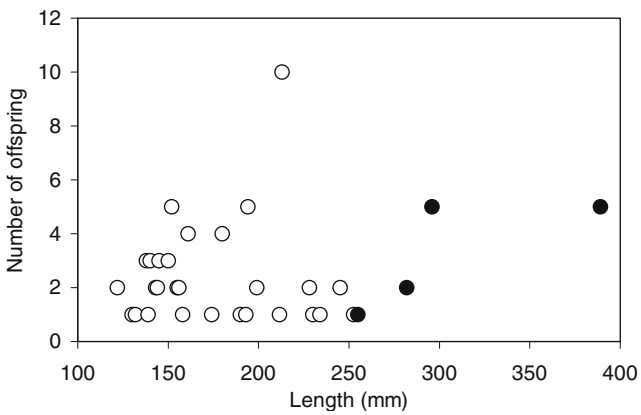

Fig. 5 Reproductive success (number of offspring assigned per individual) as a function of body size for male spawners. *Open circles* are resident life-history fish, while *closed circles* are anadromous life-history fish

Discussion

Gene flow and mating patterns

Our results showed that anadromous and resident brook charr in this system most likely belonged to the same breeding population based on both F_{ST} and parentage analysis. Reproduction between the forms occurred principally through anadromous females and resident males and confirmed previous behavioral observations in this system and in other species (Wood and Foote 1996; Schreiber and Diefenbach 2005). For instance, Wood and Foote (1996), despite extensive observations, never observed male sockeye (anadromous, *Oncorhynchus nerka*) orienting to female kokanee (resident), but male kokanees were frequently observed as sneak males to sockeye females either in the absence or presence of a sockeye male. Schreiber and Diefenbach (2005) observed anadromous female brown trout and resident males over the same spawning grounds, and the unequal sex ratio found in favor of females led them to suggest a frequent interbreeding of anadromous females with resident males.

Although anadromous males did not appear to mate with resident females in this study, reproduction between bigger males (normal phenotype) and smaller females (dwarf phenotype) was suggested in a lacustrine Arctic charr population where normal males appear to fertilize eggs of normal females first, then those of dwarf females, whose spawning period was delayed (Jonsson and Hindar 1982). In our study system, the resident females spawn first—about 2 weeks before anadromous females—and it is the resident males that take part in both reproductive events, exhibiting an extended spawning window overlapping the two spawning periods. It is possible that the predominance of the pairing of anadromous females with resident males, as well as the few offspring assigned to anadromous–anadromous mating (only five), can be explained in part by the apparent rarity of males within the anadromous run. Biased sex ratio in favor of anadromous females is commonly seen among salmonids, notably in Arctic charr and brown trout (Kristoffersen et al. 1994; Rikardsen et al. 1997; Doucett et al. 1999; Schreiber and Diefenbach 2005). Sex was known for 13 anadromous fish, of which only four were males. Indeed, the fact that sex was most of the time undetermined could argue in favor of a bias in sex ratio favoring females. Most anadromous males are usually already differentiated in August, having a more laterally compressed reddish belly and a small kype. Most anadromous fish caught in the upstream trap exhibited few morphological signs, enabling us to clearly identify the sex. We believe that these fish were most likely females. Moreover, sizes of reproducing anadromous fish entering the Morin Creek (from 254 to 398 mm fork length) were at the low end and almost outside the size range of anadromous charr in the Sainte-Marguerite River system (measuring from 312 to 561 mm fork length, data not shown). Females in this system are typically smaller than males (females, mean=421.46 mm fork length; males, mean=448.42 mm fork length, t test, $t_{97}=-2.5$, $P=0.01$). It is noteworthy that such a possible biased sex ratio toward females occurs in Morin Creek as we know that sex ratio at downstream migration is 1:1 in this stream (Thériault and Dodson 2003) and that the sex ratio is also 1:1 during both the downstream and the upstream migration in the main stem of the river (Lenormand 2003). We hypothesize that availability of adequate spawning grounds or resting pools is size-limiting for anadromous charr in small tributary creeks, selecting for smaller anadromous fish and, consequently, mostly females.

Reproductive success

Anadromous fish had a higher individual reproductive success than residents, and this was due to the fact that anadromous females were bigger, thus producing more juveniles than resident fish. Size in salmonid females has often been reported as an important determinant of reproductive success (Fleming and Gross 1994; Fleming et al. 1997), accounting for up to 80% of the variability in the reproductive success of Atlantic salmon (Fleming 1996). This positive relationship is often related to higher fecundity and larger eggs among bigger females (Morita and Takashima 1998; Hendry et al. 2001), to better access to preferential breeding sites (Foote 1990), and to the digging of deeper nests, providing increased protection against scouring (Steen and Quinn 1999). A greater number of mates has also been proposed as a determinant of higher reproductive success for females through genetic and ecological benefits in unstable environments (see the paper of Garant et al. 2001 for discussion about Atlantic salmon). In our study, females were found to have multiple partners (one to eight, mean 3.38), regardless of size and form, and this range must be viewed as conservative because the number of partners was limited by the number of offspring assigned to each parent. Analyses linking the number of mates and reproductive success were omitted due to the probable artifact related to the very small numbers of offspring sampled for the majority of individuals, inevitably resulting in a positive relationship.

Anadromous and resident males were found having similar reproductive success, but this result must be considered with caution as only four anadromous males were available for this analysis. However, none of the four anadromous males, although bigger, produced a number of offspring outside the resident male's range. Therefore, no association of size with reproductive success was found. Size is expected to be a determinant of reproductive success in males due to

its relation to dominance: Dominant males usually win in intrasexual competition for access to females (Quinn and Foote 1994; Fleming 1998; Blanchfield et al. 2003; Dickerson et al. 2005). However, in many salmonid studies, little or no relationship has been found between male size and reproductive success (Garant et al. 2001; Jones and Hutchings 2002; Blanchfield et al. 2003; Seamons et al. 2004a; Dickerson et al. 2005). Other factors such as arrival timing, ripeness of available females, numbers of mates, or operational sex ratio, allowing even small males to mate in years where more females are available, may influence reproductive success (Seamons et al. 2004a; Dickerson et al. 2005). In our study system, it is likely that resident males use alternative tactics to increase their reproductive success, being less selective or more opportunistic, as illustrated by individual males fertilizing eggs of both resident and anadromous females. This suggests that they might adopt an alternative behavior (for example, sneaking instead of fighting) in the presence of bigger anadromous males to gain access to mating.

Where have all the parents gone?

Parentage allocation in an entirely wild, open system without partial complementary behavioral information on mating events has rarely been attempted (but see the studies of Seamons et al. 2004a, b; Dickerson et al. 2005). The parentage allocation procedure used in PASOS, combined with a correction owing to null alleles, allowed us to estimate that approximately 68% of the spawners needed to have produced the pool of juveniles analyzed were missing from the pool of putative parents. This high proportion of missing spawners limits our allocation success by forcing us to perform conservative allocations (MOT set to 0 and hence no mismatch tolerated) to achieve an acceptable correctness rate (87%). First, we may have missed anadromous spawners because of flooding events that were seen in both years, principally in 2000. Those events probably allowed anadromous spawners to pass by without being intercepted at the trap, as seen in a similar study with steelhead trout (Seamons et al. 2004b). Second, resident spawners were probably missed because we electrofished in a single pass in open sections, which is certainly not the most efficient electrofishing method (Rosenberger and Dunham 2005). Moreover, the deepest sections had to be omitted. Spawners breeding outside the study stream where their progeny may have immigrated into the stream during their first year of life could also explain in part the high proportion of missing spawners. However, the observation that most of the juveniles successfully allocated were done so to only one parent suggests that the missing parent must have been reproducing somewhere in the stream, and thus it is not consistent with the hypothesis of juvenile immigration from outside the study system.

Although an allocation success rate of 21% seems small, the allocated juveniles are nevertheless representative of the reproductive outcome in the creek. We sampled a large proportion of the stream (49% by stream length), and the sections omitted were not preferential habitat of juvenile brook charr. Moreover, half-sib offspring were not clustered in one or adjacent sampling sections. Qualitative analysis of our data showed that only members of five half-sib families out of 44 were sampled in the same 300-m sampling section. All other juveniles sharing one parent were found all along the stream, from several hundred meters to 3 km apart, suggesting considerable dispersal during the first and/or second year of life or, at least in some cases, by movement between spawning events by the shared parent. We thus concluded that we had equal chances of sampling members of different families.

Conclusion

This study directly assessed for the first time the genetic mating system and individual reproductive success of a population of salmonids composed of both anadromous and resident forms, under natural conditions, where males and females may adopt either tactic. Gene flow occurred between the two forms and was mediated by resident males mating with both resident and anadromous females. Reproduction between anadromous males and resident females was not seen in this study. Discrepancies were found between the sexes in terms of determinants of reproductive success. Size in males did not have any influence on individual reproductive success, whereas larger females (and hence most likely to be anadromous) were more successful. This finding corroborates other studies suggesting that anadromy would be more beneficial to females than males (Jonsson and Jonsson 1993; Fleming 1998) and provides evolutionary explanations of why residency is not observed among females in some populations or species (especially Atlantic salmon, Hutchings and Jones 1998; and Pacific salmon species as chinook salmon, Unwin et al. 1999; and masu salmon, Tsiger et al. 1994). However, for females to persist in some populations as residents, benefits must be provided. One such benefit is the higher survival rate associated with residency, which can be as low as 10% in saltwater in the first year following migration and as high as 50% in freshwater for the same cohort that remains in freshwater (Dodson and Lenormand, unpublished data). However, such an advantage would apply equally to both sexes. Whereas resident males, by adopting a “sneaking” reproductive tactic, increased their reproductive success by mating with females of all sizes in all habitats, females may also adopt different tactics in selecting spawning sites (Holtby and Healey 1986; Seamons et al. 2004a). We suggest that resident females would enjoy

an advantage in accessing spatially constrained spawning areas in small tributary streams unavailable to larger females. Structural complexity has recently been shown to influence the competitive ability of males pursuing alternative reproductive tactics in mites, and thus it is likely to influence the tactic frequency in different species or populations (Lukasik et al. 2006). Spatial complexity associated with small and higher-order tributaries could explain why residency is virtually absent within the main stem of the river and why only small anadromous fish composed the Morin anadromous run. Larger anadromous females would probably outcompete and exclude smaller females from larger spawning areas, typically associated with larger rivers. However, large females would be at a disadvantage in the more restricted spawning habitats associated with tributaries. Small tributary streams may thus be viewed as a refuge for residency or, at least, a way of ensuring that the resident tactic persists within females.

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