



Dispersal in a stream dwelling salmonid: Inferences from tagging and microsatellite studies

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Abstract

We used both direct (mark-recapture) and indirect (microsatellite analysis) methodologies to investigate dispersal between two putative populations of brook charr (*Salvelinus fontinalis*) in Freshwater River, Cape Race, Newfoundland, Canada. Over a 5-year study period, mark-recapture data revealed some movement by fish, but the proportion of recaptured fish migrating from one population area to another was low (0–4.1%). Additionally, during sampling periods in the spawning seasons, no fish was found in the alternate population area to that of its first capture. Despite this pattern of limited movement, microsatellite analysis based on sixteen polymorphic loci provided no evidence of genetic differentiation. Indirect estimates of dispersal parameters varied greatly between different methods of analysis. While use of a coalescent-based model yielded estimated migration rates congruent with the results of the mark-recapture study, other methods resulted in much higher estimates of migration between the populations. In particular, the lack of genetic differentiation coupled with likely violations of the assumed island model prevented generation of meaningful estimates of dispersal using F_{ST} . The disparities between migration rates estimated from the mark-recapture work and from the different indirect methods highlight the difficulties of using indirect methods to estimate dispersal on an ecological timescale. However, mark-recapture methods can fail to detect historical or episodic movement that is important in an evolutionary context, and we therefore argue that a combination of direct and indirect methods can provide a more complete picture of dispersal than either approach alone.

Introduction

Understanding movement of individuals on a short-term ecological timescale is of major importance for conservation and management purposes. In particular, movement of individuals can have demographic impacts on the size and structure of local populations, affecting recruitment, persistence, and extinction rates. This movement, in the form of migration or dispersal, can be directly examined using mark-recapture methods in many taxa, including fish (e.g., Skalski and Gilliam 2000), and salmonids in particular (e.g., Bernard et al. 1995). However, such studies are typically time consuming and may be technically difficult, particularly for aquatic organisms. Additionally, mark-recapture studies within finite areas may often

be subject to systematic bias due to failure to detect long-distance dispersal (Koenig et al. 1996). These difficulties have led to alternative, indirect measures of dispersal being increasingly favored.

Since a lack of movement (and hence gene flow) between populations is expected to result in genetic differentiation, population genetic studies can be used to obtain indirect estimates of movement and dispersal patterns (e.g., Bunn and Hughes 1997; Chapman et al. 1999). In this context the number of migrants per generation ($N_e m$; where N_e is the effective population size and m is the proportion of breeding adults that are migrants) can be estimated from molecular data. Most often estimates of $N_e m$ are made from F statistics (see Cockerham and Weir (1993) and references therein), or from the frequencies of private alleles (Slatkin

1985; Barton and Slatkin 1986). Whilst the estimation of gene flow over larger geographic scales has a long history, more recent development of highly variable marker types (notably microsatellites), has facilitated the examination of population genetic structure on a finer scale. Microgeographic population genetic structure has been detected in a range of vertebrate taxa (e.g., Van Oppen et al. 1997; Prosser et al. 1999) including salmonid fishes (Angers et al. 1995; Spruell et al. 1999). Thus the use of microsatellite markers should allow indirect estimation of dispersal at a local level. These indirect measures can be used to corroborate or supplement observational work, and certainly indirect and direct methods have depicted patterns of dispersal that are at least qualitatively similar in a number of studies (e.g., Forbes and Boyd 1997; Chenuil et al. 2000; Newman and Squire 2001; Roslin 2001; Sumner et al. 2001). Genetic methods would thus seem to offer an attractive alternative to mark-recapture studies.

However, there are commonly discrepancies between direct and indirect measures of dispersal (e.g., Schilthuizen and Lombaerts 1994; Koenig et al. 1996), an important finding given that molecular techniques are increasingly being used to infer movement of individuals in the absence of direct measures. Such discrepancies may in principle be due to a failure of either method, but it is also important to note that direct and indirect approaches actually measure somewhat different quantities. Whilst the former provides an instantaneous migration rate of individuals, the latter gives an average over a time period determined by the rate of mutation or by the timescale of genetic drift (Beerli and Felsenstein 1999). However, more fundamentally, it has been argued that the theoretical basis for estimating dispersal from molecular data is weak (Rousset 2001). As a consequence it may be that molecular data cannot frequently be translated into accurate estimates of $N_e m$ (Whitlock and McCauley 1998; Bohonak 1999). Difficulties largely arise from the simplicity of the underlying models of gene flow, of which the Island model (Wright 1931) is most commonly used. Unfortunately the assumptions of the Island model are likely to be violated in most real populations (see Whitlock and McCauley 1999), and the robustness of dispersal estimates to these violations is unclear.

Furthermore, while direct approaches estimate migration rate m , genetic methods typically yield estimates of the effective number of migrants per generation ($N_e m$). Thus direct comparison of results

also requires estimation of effective population size (N_e), which is notoriously difficult to do with high precision (Waples 1991). Moreover, available methods to estimate N_e from molecular data typically assume that a population is closed with no immigration (Waples 1991; Anderson et al. 2000; Berthier et al. 2002). However, recently proposed methods using joint analysis of one- and two-locus probabilities of identity by state (Vitalis and Couvet 2001), or the coalescent (Beerli and Felsenstein 1999, 2001), simultaneously yield estimates of both effective population sizes and migration rates. This should permit more effective comparison of results to direct measures of migration, and these methods may also provide more generally realistic models of gene flow by relaxing the assumptions of constant N_e and m (among populations) that are features of the Island model. In addition to using more realistic models, improved accuracy of indirect measures of migration and dispersal may be achieved by a focus on local processes and by the use of highly informative marker systems (Rousset 2001). However there is also an urgent need to carry out more comparative studies testing indirect methods against direct estimates of dispersal (Whitlock and McCauley 1998; Rousset 2001).

In the current work we employ both direct and indirect approaches to measuring dispersal between populations of brook charr, *Salvelinus fontinalis*. Despite the obvious potential for vagility in salmonid fishes, dispersal in stream resident populations can be low (Leclerc 1979; Heggenes et al. 1991). In some cases low dispersal, rather than the availability of suitable habitat, has been postulated as a limit to in-stream distribution (e.g., Diana and Lane 1978). This pattern of movement, termed the "restricted movement paradigm" (Gerking 1959), might certainly contribute to the maintenance of genetic structure on a microgeographic scale, even maintaining differentiation between populations in the same drainage. However, more extensive movement has also been reported in stream resident salmonids (e.g., Gowan and Fausch 1996). Furthermore, the restricted movement paradigm has been criticized, since much of its support comes from mark-recapture studies that were likely subject to bias from movement of marked fish out of the study area (Gowan et al. 1994). Nevertheless, based on analysis of data from 27 populations of stream-dwelling salmonids, Rodríguez (2002) argued that limited movement is the norm. However, results from that study also indicated that populations might contain a more mobile component of

clear importance to population processes (Rodríguez 2002).

This study focuses on two putative spawning populations of brook charr (designated Lower and Upper according to their relative positions in the river), that are resident in Freshwater River, Cape Race, Newfoundland, Canada. The objectives of this work are firstly to quantify the level of migration between these populations, and secondly to examine the congruence within and between estimates of migration made using both direct and indirect approaches. We therefore use mark-recapture methods to directly examine movement of individuals between the populations, and we also conduct a microsatellite study to examine population genetic structure and generate indirect estimates of dispersal according to multiple specific methodologies. Freshwater River is one of several fluvial systems located on Cape Race, in which there are resident populations of brook charr (see Hutchings 1990), and this study system has not been subject to exploitation or other anthropogenic manipulation. A detailed description of the life history of brook charr in these systems has been reported elsewhere (Hutchings 1993, 1996). Freshwater River is isolated from other river systems, and is further closed to migration by a steep cataract at the point of entry to the ocean. Genetic differentiation between fish from different rivers has been detected previously (Ferguson et al. 1991; Wilson, unpublished data), while genetic structure within rivers has not previously been examined.

Methods

Mark-recapture study

Sampling

The mark-recapture data reported here were collected as part of a separate experiment on sex-biased dispersal (Hutchings and Gerber 2002). For the latter study, 993 individuals were captured by electrofishing and marked with PIT (Passive Integrated Transponder) tags in June 1995 ($n = 403$ fish tagged), and June 1996 ($n = 590$) in Freshwater River, Cape Race, Newfoundland. The 1.2 cm-long tags were inserted into the body cavity through a 3 mm-long incision immediately anterior to the base of the anal fins of fish anaesthetized with carbon dioxide. The adipose fin of all tagged fish was removed to permit external identification of tagged individuals upon recapture. Fish tagged

ranged from 54 to 173 mm and included both mature individuals and juveniles. To sample the river for tagged individuals, the entire length of the 2200 metre-long unobstructed section of river upstream of the mouth was electrofished twice annually in spring (late May/early June) and in autumn (late September/early October) from 1995 until 2000, when the number of recaptures was nil.

Data treatment

Three primary spawning sites exist in Freshwater River, located 240 m, 465 m, and 1865 m upstream of the river mouth (J.A. Hutchings, unpublished data). The mark-recapture data were used to quantify fish movement between the Lower (240 m and 465 m spawning sites combined) and Upper spawning areas in Freshwater River. The two sites in the Lower area were combined due to their close proximity, and due to the relatively high density of fish captured between them. In contrast the Lower and Upper areas (as defined below) are separated by a stretch of fast flowing water with low fish density (J.A. Hutchings, unpublished data).

To calculate the total number of fish marked and recaptured in the upper and lower spawning locations, and the distances moved by these individuals throughout their lives, we used two different areas of the mark and recapture locations. These areas were identified as the spawning site location (distance upstream from the river mouth) in the river plus and minus either the median or the mean distance traveled by individuals throughout their lives. Based on the recapture locations of 276 individuals, the median distance between initial tagging location and recapture location for each fish was 15 meters; the mean distance traveled was 144 meters. In the event of an individual being recaptured on multiple occasions, the distance to its most distant recapture location was used. Thus, the tagging and recapture locations were calculated as follows. Based on the median lifetime distance traveled, the Lower area was delineated by those sections of river 225 to 255 m and 450 to 480 m upstream of the mouth, while that for the Upper area was defined as 1850 to 1880 m upstream of the mouth. Based on the mean lifetime distance traveled, the Lower area extended 96 to 509 m upstream of the mouth; the Upper area extended 1721 to 1909 m upstream of the mouth. The migration rate m of individuals between the lower and upper spawning areas was estimated as the percentage of individuals recaptured in either area that were initially

Table 1. Microsatellite loci used and their species of origin

Microsatellite	Source species	Reference / Gen bank accession number
SFO 12 LAV	<i>Salvelinus fontinalis</i>	Angers et al. 1995
SFO 18 LAV	"	"
SFO C28	"	Unpublished (T. King, USGS-BRD, Leetown Science Center, West Virginia, USA)
SFO D91	"	"
SFO D100	"	"
SCO 19	<i>Salvelinus confluentus</i>	Taylor et al. 2001
SSA 20.19 NUIG	<i>Salmo salar</i>	Sanchez et al. 1996
SSA 85 DU	"	O'Reilly et al. 1996
BHMS 328	"	AF256731
BHMS 356	"	AF256751
BHMS 462	"	AF256818
BHMS 7-001	"	AF256654
BHMS 7-033	"	AF256658
STR 85 INRA	<i>Salmo trutta</i>	Presa and Guyomard 1996
OMY 38 DU	<i>Oncorhynchus mykiss</i>	Morris et al. 1996
OMY RGT46 TUF	"	Unpublished (T. Sakamoto, Tokyo University of Fisheries, Japan; pers. comm.)

tagged in the alternate area to their recapture. Population specific immigration rates m_{Lower} and m_{Upper} were also calculated as the percentage of individuals recaptured in an area that were immigrants from the alternate area. In natural populations, effective population size N_e is expected to be lower than actual population size N (Frankham 1995). Therefore the number of mature individuals in the Freshwater River population (Lower and Upper areas combined) was estimated by the Jolly-Seber mark-recapture method (Krebs 1998). Note that in comparisons between N_e and N , various different definitions of N have been used, and the estimate made here corresponds to N_A , the number of adults (Frankham 1995). Additionally, effective population size is a generational measure and hence, for strict comparison, N should be also. In this case N could only be estimated at a single point in time. Given that census sizes in the two populations are believed to be approximately equal (personal observation), the estimated number of mature fish was halved to generate an expected maximum value of N_e to allow comparison to estimates made using indirect approaches.

Microsatellite study

Sampling

Sampling was carried out from the 1st to the 3rd of October 1999. Fish of all ages were sampled by electrofishing from the spawning sites in the two areas

(Lower, $n = 398$; Upper, $n = 201$). Caudal fin clips were taken and preserved in 95% ethanol, after which fish were released. The clipped fin was used as an identification mark to prevent multiple sampling of the same individual.

DNA isolation and microsatellite analysis

DNA was isolated from caudal fin clips using a phenol-chloroform extraction protocol (Bardakci and Skibinski 1994) after an initial 24-hr soak in deionized water to remove ethanol. Sixteen microsatellite loci (isolated from a range of salmonid species) were used in the analysis (Table 1). Loci were individually amplified in the PCR using 11 μL reaction volumes containing: 5 pmol of each primer, dNTPs at 0.375 mM, 4 mM labeled TAMRA dCTP, 20 mM Tris-HCl (pH 8.4), 50 mM KCl, 1.5 mM MgCl_2 , 0.1 $\mu\text{g}\cdot\text{mL}^{-1}$ BSA, 0.25 units *Taq* DNA polymerase and 30 ng of template DNA. The thermocycling regime consisted of an initial denaturation at 95 °C for 2 min followed by 35 cycles of 1 min at the annealing temperature (which ranged from 48–60 °C), 1 min at 72 °C, and 30 s at 95 °C, then a final period of 20 min at 72 °C. Products of the PCR were separated using gel electrophoresis in a 6% polyacrylamide-7-M urea matrix. Alleles were visualized using the Hitachi FMBIOII fluorescence imaging system, and sized by comparison with 350-TAMRA lane standards loaded on each gel.

Data analysis

Allele frequencies, and the observed and expected heterozygosity, were calculated at each locus in each population using GENEPOP version 3.3 (Raymond and Rousset 2001). Weir and Cockerham's (1984) inbreeding coefficients, f (equivalent to Wright's F_{is}) were calculated, and genotypic frequencies were evaluated for departure from Hardy-Weinberg proportions with the probability test (Guo and Thompson 1992) using Bonferroni adjusted p-values (Rice 1989). Exact probability tests for detecting linkage disequilibrium were also performed with GENEPOP to determine the independence of microsatellite loci. Again Bonferroni adjusted p-values were used to determine significance. Genetic (genic) differentiation between sites was tested by generating unbiased estimates of the P -values for probability tests at each locus using GENEPOP. Results of locus specific tests were combined (Fisher's method) to give an overall test of differentiation (Raymond and Rousset 2001). Weir and Cockerham's (1984) estimators of F_{is} , F_{it} , and F_{st} , (f , F , and θ respectively) were calculated using FSTAT version 2.9.1 (Goudet 2000). Confidence intervals for multilocus estimates were obtained by bootstrapping across loci.

To estimate migration between the populations, we obtained multilocus estimates of $N_e m$, the effective number of migrants, according to the relationship $F_{st} = 1/(1 + 4N_e m)$, and using the pseudo maximum likelihood procedure in PMLE20 version 2.0 (Rannala and Hartigan 1996). A further estimate was made according to the private alleles procedure of Slatkin (1985) using GENEPOP version 3.3 (Raymond and Rousset 2001). Additionally two approaches were used to simultaneously generate population specific estimates (with confidence intervals) for N_e and m from the microsatellite data. Firstly, estimates were made using ESTIM 1.0 (Vitalis and Couvet 2001b). This uses a method-of-moments approach to generate joint estimates of N_e and m from estimates of one- and two-locus identity probabilities (F and η_s respectively; Vitalis and Couvet 2001a). Confidence intervals were computed by deriving the approximate bootstrap confidence intervals method (DiCiccio and Efron 1996) as implemented in ESTIM 1.0.

Secondly, the parameters $N_e \mu$ (where μ is mutation rate) and $N_e m$ were estimated using a coalescent-based Monte Carlo Markov chain (MCMC) method implemented in MIGRATE (Beerli and Felsenstein 1999) under an assumed infinite alleles model of microsatellite mutation. Due to the computational

requirements of this procedure, parameter estimates were generated using a randomly selected subsample of 50 individuals from each of the two populations. Estimates were generated using MCMC parameters as follows: 10 short chains with 1000 genealogies followed by 3 long chains with 10000 genealogies and a burn-in of 10000. To calculate estimates of N_e and m from these values, a constant mutation rate of 5×10^{-4} was assumed (in line with microsatellite mutation rates estimated for salmonids elsewhere; McDonald 2001; Heath et al. 2002).

Results

Mark-recapture study

Using the lower and upper areas as delineated by the median lifetime distance traveled, a total of 168 fish were initially tagged in these areas (Lower 122, Upper 46). Of these, 53 were subsequently recaptured at least once, with 45 individuals being recaptured outside of their area of initial tagging. However none of these fish had moved between the upper and lower spawning areas. Thus migration rates estimated using this delineation of the lower and upper areas equaled zero. Using the mean lifetime distance traveled to define tagging and recapture locations, a total of 678 fish were initially tagged in these areas (Lower 397, Upper 281). Subsequently, 183 individual fish were recaptured, of which 169 were in either the Lower or Upper area. Of these, 4.1% had moved between the spawning areas, six individuals moving from Lower to Upper, and one individual moving in the reciprocal direction (Figure 1). Thus population specific migration rates were calculated as $m_{Lower} = 1/94 = 1.1\%$, $m_{Upper} = 6/75 = 8.0\%$. Based on the dates of recapture for these seven fish, none were known to have been present in both the lower and upper sections during spawning. The number of mature individuals in the Freshwater River population (Lower and Upper areas combined), and associated 95% confidence intervals, was estimated to be 1460 (1097, 2337). Under the assumption of equal census sizes in the two populations, this yields a maximum value of $N_e = 730$.

Microsatellite study

The microsatellite loci varied in the degree of detectable polymorphism (Table 2). The number of alleles per locus ranged from 2 to 16 (including both popula-

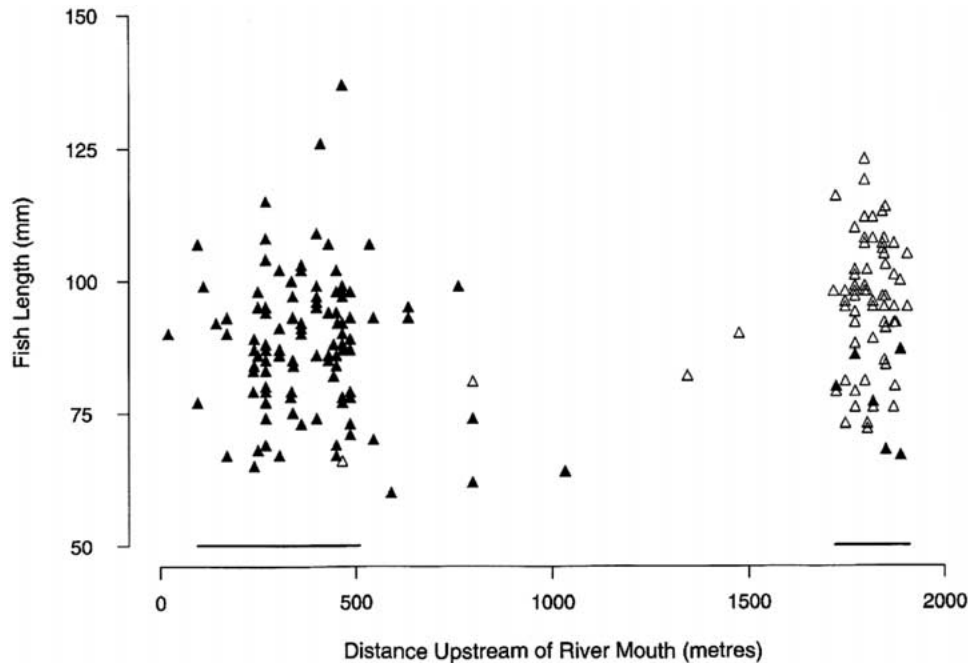


Figure 1. Recapture locations and fish lengths at initial tagging for fish first captured at Lower (solid triangle) and Upper (empty triangle) spawning sites. Horizontal lines indicate spawning areas (defined on the basis of mean lifetime distance traveled).

Table 2. Variation and differentiation at microsatellite loci showing: the number of alleles (n), observed and expected heterozygosity, p values for probability tests of Hardy-Weinberg equilibrium (Raymond and Rousset 2001), the F_{IS} estimator f (Weir and Cockerham 1984), for both populations at each locus (and over all loci where applicable), and the F_{ST} estimator θ (Weir and Cockerham 1984)

Locus	Lower					Upper					θ
	n	H_o	H_e	p	f	n	H_o	H_e	p	f	
SFO 12 LAV	2	0.550	0.497	0.03	-0.107	2	0.483	0.494	0.78	0.023	-0.001
SFO 18 LAV	4	0.394	0.392	0.31	-0.005	3	0.398	0.420	0.05	0.053	-0.001
SFO C28	4	0.621	0.613	1.00	-0.013	4	0.632	0.607	0.71	-0.041	-0.002
SFO D91	15	0.802	0.824	0.18	0.028	14	0.811	0.849	0.33	0.045	0
SFO D100	6	0.646	0.620	0.64	-0.041	6	0.670	0.617	0.16	-0.086	-0.002
SCO 19	12	0.790	0.785	0.89	-0.007	14	0.755	0.772	0.77	0.023	-0.001
SSA 20.19 NUIG	2	0.482	0.469	0.59	-0.029	2	0.478	0.458	0.64	-0.043	-0.001
SSA 85 DU	2	0.452	0.444	0.74	-0.019	2	0.448	0.407	0.17	-0.100	0.004
BHMS 328	2	0.364	0.357	0.77	-0.020	2	0.323	0.351	0.30	0.079	-0.002
BHMS 356	4	0.545	0.532	0.98	-0.024	4	0.517	0.525	0.37	0.015	-0.002
BHMS 462	2	0.292	0.288	0.86	-0.016	2	0.260	0.234	0.14	-0.111	0.004
BHMS 7-001	2	0.472	0.497	0.36	0.050	2	0.535	0.497	0.31	-0.077	-0.002
BHMS 7-033	4	0.550	0.505	0.09	-0.090	4	0.483	0.498	0.43	0.030	-0.001
STR 85 INRA	11	0.694	0.690	0.04	-0.005	11	0.701	0.722	0.20	0.029	0
OMY 38 DU	3	0.525	0.548	0.23	0.042	3	0.510	0.521	0.97	0.022	-0.001
OMY RGT46 TUF	2	0.128	0.133	0.45	0.037	2	0.101	0.096	1.00	-0.050	0.002
All loci	—	—	—	0.36	-0.014	—	—	—	0.39	-0.004	0

Table 3. Estimated migration parameters for brook charr in Freshwater River. Where available 95% confidence limits are shown in parentheses for those parameters directly estimated. Parameters inferred from estimates are indicated in italics, “—” denotes parameter could not be estimated

Method	Parameter								
	N_e	m	N_em	$N_{e(Lower)}$	$m_{(Lower)}$	$N_{em(Lower)}$	$N_{e(Upper)}$	$m_{(Upper)}$	$N_{em(Upper)}$
DIRECT (Areas defined by:)									
Median distance traveled	<730 ¹	0	0	<730 ¹	0	0	730 ¹	0	0
Mean distance traveled	<730 ¹	0.041	<29.93	<730 ¹	0.011	<8.03	730 ¹	0.080	<58.4
INDIRECT									
Fst analogue			>250						
Pseudo maximum likelihood procedure (Rannala and Hartigan 1996)				>2500					
Private alleles (Slatkin 1985)			28.9						
One- and two-locus identity probabilities (Vitalis and Couvet 2001a)				∞ (—)	—	—	22.5 (0, ∞)	0.499 (—)	11.2
Coalescent-based MCMC model (Beerli and Felsenstein 1999)				237 ²	0.006 ²	1.31 (1.13, 1.45)	167 ²	0.014 ²	2.34 (2.15, 2.52)

¹assuming equal census population sizes for Lower and Upper populations.

²calculated with an assumed mutation rate μ of 5×10^{-4} per locus per generation.

tions), with a mean of approximately 5.1 alleles. There was generally close agreement between observed and expected levels of heterozygosity in both the Lower and Upper populations, and no significant deviations from Hardy-Weinberg proportions were observed at individual loci, or over all loci, in either population. Testing over all loci and all populations (Fisher’s method; Raymond and Rousset 2001) shows no evidence for deviations from Hardy-Weinberg proportions ($p = 0.29$). No significant linkage-disequilibrium was detected between pairs of loci in either population.

Given no evidence against Hardy-Weinberg equilibrium, tests for population differentiation were performed based on allelic frequency distributions. These provided no support for the presence of genetic differentiation at individual loci (all $p > 0.05$), or over all loci ($p = 0.344$). This lack of genetic differentiation was similarly reflected by low values of θ (Table 2). As calculated over all loci θ was not significant ($\theta = 0$). Multi-locus values of Weir and Cockerham’s (1984) statistics F and f (equivalent to F_{it} and F_{is} respectively) were not significantly different from zero ($F = -0.011$ with 95% confidence intervals $-0.029, 0.005$; $f = -0.011$ with 95% confidence intervals $-0.028, 0.006$).

Estimates of migration parameters made from the microsatellite data differed greatly between the methods used (Table 3). N_{em} as estimated from θ is clearly undefined (since $\theta = 0$). However, following Roslin (2001), we used the upper 99% confidence limit of θ ($\theta = 0.001$) to give a lower bound for N_{em} of 250. The PMLE20 analysis was found to be non-informative, with the result given that under an assumed island model $4N_{em}$ is not within the interval of 0.00001 to 10,000. After correction for sample size (see Barton and Slatkin 1986), an estimate of $N_{em} = 28.9$ was obtained from private allele frequencies.

The use of one and two locus probability identities resulted in an estimated $N_{e(Lower)}$ of infinity, preventing estimation of $m_{(Lower)}$, though parameters for the Upper populations were obtained ($N_{e(Upper)} = 22.5$, $m_{(Upper)} = 0.499$). The use of the coalescent-based MCMC model yielded population specific values of N_e that were of similar magnitude to each other, though based on the confidence limits determined (Table 3), effective population size of the Lower population ($N_{e(Lower)} = 237$) was estimated to be greater than of the Upper ($N_{e(Upper)} = 167$). Using this method, estimated migration rates were low ($m_{(Lower)} = 0.006$, $m_{(Upper)} = 0.014$).

Discussion

Overall, the mark-recapture data would seem consistent with restricted levels of movement by fish in Freshwater River. Based on a five-year mark-recapture study, the migration rates between the lower and upper spawning areas of Freshwater River are estimated to range between 0 and 4.1%. Whilst direct comparison with other studies of *Salvelinus fontinalis* is difficult, Gowan and Fausch (1996) have reported values of 5–8% of fish migrating comparable distances annually. This is clearly somewhat greater than even the upper value of 4.1% reported here, since the present estimate measures the proportion of marked fish found to have moved between sites during a five-year period (as opposed to one year). Elsewhere, migration rates of the magnitude estimated here by mark-recapture have been associated with significant genetic differences among brook charr populations. For example, Adams and Hutchings (2003) documented significant genetic variation at 5 microsatellite loci among 8 lacustrine brook charr populations in the Indian Bay watershed, Newfoundland. By comparison, based on the tagging of more than 12 000 individuals over a four-year period, migration rates by charr among 11 lakes averaged only 2.4% (Adams and Hutchings 2003). Similarly, significant genetic variation distinguishes populations of Pacific salmon (*Oncorhynchus* spp.) from one another, despite straying rates in non-hatchery fish that typically range between 1 and 5% (Quinn 1993; McElhany et al. 2000).

Despite this apparent pattern of restricted movement, we found no evidence of genetic differentiation between populations in Freshwater River, and difficulties were encountered when attempting to estimate dispersal from the microsatellite data. The microsatellite study may have been inadequate to detect population structure. However this seems unlikely, as our analysis was more extensive (both in terms of the number of fish and the number of loci used) than any comparable study (e.g., Angers et al. 1995; Spruell et al. 1999). Additionally, a far less extensive analysis (based on seven microsatellite loci and two hundred individuals) was more than sufficient to detect genetic differentiation between brook charr in Freshwater River and the nearby Watern Cove River (using GENEPOP to test the null hypothesis of no genotypic differentiation over all loci, $p < 0.0001$: A.J. Wilson, unpublished data).

The observed lack of genetic differentiation between the Lower and Upper populations presents a

challenge for the indirect estimation of dispersal. This is reflected not only in the comparison of indirect to direct methods, but also in the disparity among the results of the different indirect methods. It has been argued that indirect methods might sometimes underestimate dispersal of individuals, since only migrants that successfully reproduce will affect allele frequencies in the receiving population (e.g., Tallman and Healey 1994). However, in this case, the use of genetic data might generally lead us to overestimate the level of movement by fish in the system in comparison to the mark-recapture study. For example, to reconcile even the lower bound of the θ -based $N_e m$ estimate ($N_e m = 250$) with the higher mark-recapture based estimate of m ($m = 0.041$), would require an effective population size above 6000. This is an order of magnitude larger than the adult census population size. From our data we found that the private alleles method provided a more conservative estimate of $N_e m$ that in conjunction with m of 0.041 would imply an effective population size of approximately 700. While this is less than our estimate of the adult census size, reconciling the private allele based estimate of $N_e m$ with the direct estimates of both migration and census size would suggest a ratio of N_e/N of 0.96 which is considerably higher than has been reported for salmonids elsewhere (e.g., Heath et al. 2002; Waples 2002; Ardren and Kapuskinski 2003).

Similarly, in comparing estimates of population specific parameters, the analysis of one- and two-locus identity probabilities, while uninformative for the Lower population, yielded an estimate of immigration rate to the Upper population that was much greater than that suggested by the direct study. However, much more conservative estimates of migration rates were obtained using the coalescent-based model, and values corresponded well to those obtained from the mark-recapture work. This method also yielded estimates of local N_e that were less than the expected maximum and, in conjunction with estimated census population size would imply N_e/N ratios within the range reported elsewhere (Heath et al. 2002; Ardren and Kapuskinski 2003).

Incongruent estimates of dispersal, as obtained from the mark-recapture and various genetic methods, might reflect inadequacies in one or more of the approaches. Recently mark-recapture methods for assessing movement of stream-resident salmonids have been criticized on the grounds that individuals may move completely out of the sampling area. This obviously can preclude recapture, such that the

detected level of movement is much lower than the actual level (Gowan et al. 1994; Gowan and Fausch 1996). In this case the risk of such bias is minimized by the fact that Freshwater River is a closed system, as well as by the nature of the sampling. In particular, one period of sampling in each year was just prior to the onset of the spawning season, at which times mature fish were concentrated in the vicinity of the two spawning areas. Hence we are confident in the validity of the direct migration estimates. One caveat to this is that the youngest fish in the system were too small to be PIT-tagged, and thus could not be included in the mark-recapture study. Thus, if there is extensive movement by the youngest fish, then this might explain (at least partially), the differences in dispersal rates estimated using direct and indirect methodologies. Downstream movement of young of the year brook charr has been observed previously (Hunt 1974) and may be related to territorial behavior. Additionally, as emergent brook charr are relatively weak swimmers, some degree of passive downstream dispersal would seem likely. Measurement of downstream drift has been done in this species (e.g., Randall 1982) and would seem an appropriate way to test this possibility. Inadequate targeting of young individuals by mark-recapture methods has been previously cited in relation to incongruent estimates of dispersal obtained from direct and indirect approaches (e.g., Geenen et al. 2000). In addition, we have not tested the implicit assumption that tagging of fish has no effect on either their tendency or ability to migrate between the Lower and Upper populations.

The failure of the F_{st} and pseudo maximum likelihood estimators to yield reasonable estimates of contemporary $N_e m$ is largely due to the lack of detectable genetic differentiation between the populations. It should be noted that in any case the function linking the parameters means that low values of F_{st} will necessarily yield estimates of $N_e m$ having very large confidence intervals (Whitlock and McCauley 1999; Balloux and Lugon-Moulin 2002). Additionally, it seems likely that the island model of gene flow provides an inadequate model of this system. The assumptions of the island model have been extensively discussed elsewhere (e.g., Whitlock and McCauley 1999; Rousset 2001) and will not be reviewed here. However, it is notable that both the direct approach and the use of the coalescent model are suggestive of asymmetric migration (with more movement from the Lower to the Upper population than *vice versa*),

while the latter method also indicated the presence of unequal effective population sizes. These findings thus provide a challenge to the applicability of the island model under which it is assumed that $N_e m$ remains constant through time and is equal among populations. To some degree these difficulties might be overcome by use of alternative methods such as the coalescent model (Beerli and Felsenstein 1999, 2001) as employed herein. To the extent that the mark-recapture work provided an accurate picture of movement patterns in Freshwater River, then the coalescent model yielded superior estimates of migration parameters. Unfortunately this method is characterized by very large computational requirements, and this has probably contributed to a scarcity of empirical comparisons between coalescent and F_{st} based estimates of gene flow and migration to date.

Estimating dispersal from genetic data also requires the assumption that the system has reached equilibrium between genetic drift and migration. If this assumption is not true then genetic homogeneity might persist even with restricted dispersal at present. It could be suggested that there has been insufficient passage of time since post-glacial recolonisation for genetic divergence between Lower and Upper populations to arise by drift. This argument is refuted by the detection of genetic differentiation between fish from different rivers on Cape Race (Ferguson et al. 1991; A.J. Wilson, unpublished data). Furthermore, under an assumed isolation model with $F_{st} \approx 1 - e^{-t/2N_e}$ (Nei and Chakravati 1977), an estimate of 3000 generations since the end of the Wisconsin glaciation can only be reconciled with the upper 99% confidence limit of $\theta = 0.001$ by having an effective population size of 1.5 million for each population. Additionally it has been suggested that, isolation of fish populations on Cape Race may well predate the Wisconsin glaciation, if the southeast shore of Newfoundland formed part of the proposed Acadian refuge (see Danzmann et al. 1998 and references therein). Thus the lack of genetic differentiation is itself an important finding given the low levels of dispersal indicated by the mark-recapture work.

It is important to note that while indirect approaches generally did not yield estimates of migration rates congruent with those from the mark-recapture work, only the former can provide insight into historical patterns of movement and gene flow. Thus the concurrent findings of genetic homogeneity with restricted contemporary movement could be reconciled by the recent or episodic occurrence

of movement between sites within Freshwater River. Such movement might be dependent on temporal variation in the environment, perhaps being linked to flow velocity (high velocity increasing passive downstream dispersal), or water level (high water levels allowing passage past in-stream obstacles). These possibilities cannot be evaluated at present, though they do suggest avenues of further research.

In many salmonid species demographic separation of populations is becoming increasingly prevalent due to habitat fragmentation and other anthropogenic environment modification (e.g., Neraas and Spruell 2001). In such cases the recent restriction of movement will mean that indirect approaches to estimation of contemporary dispersal will likely be unreliable. From a management perspective, Waples (1998) has pointed out that levels of migration necessary to prevent genetic differentiation at microsatellite loci may in any case be so low as to have little effect on the demographic properties of populations. Thus genetic homogeneity is not necessarily indicative of a lack of structure in the population, and treatment of genetically homogeneous source groups as single population units may not always be an appropriate basis for short-term demographic management. This is not to suggest that studies of genetic population structure have limited value for management purposes. Clearly if conservation of genetic material is a priority, genetic differentiation can be used to identify separate management units. This will help to avoid protecting small fragments of a single large stock, allowing resources to be focused on safeguarding smaller, genetically unique stocks. However, it is also important to note that the correlation between molecular and quantitative measures of genetic variability cannot be assumed (e.g., Reed and Frankham 2001), such that genetic homogeneity at microsatellite loci need not mean there is homogeneity at loci affecting fitness-related traits.

In conclusion, we find that there are severe difficulties in estimating dispersal from genetic data in this system. In particular, given a lack of significant genetic differentiation between Lower and Upper populations, it was not possible to derive meaningful estimates of migration using a traditional application of the island model. While there was agreement between the direct estimates of migration and those obtained using the coalescent-based model, other indirect methods estimated migration rates much higher than those from the mark-recapture results.

Although the private alleles method led to an estimated migration rate that was somewhat comparable to the results of the mark-recapture work, the generality of this result cannot be assumed. In fact when sufficient genetic information is available, the F_{st} and private alleles methods should yield comparable estimates over a wide range of population conditions (Slatkin and Barton 1989). Effective estimation of dispersal rates from molecular data might be aided by the further development (and testing) of alternatives to the island model (including the use of the coalescent), and by incorporation of more ecologically realistic patterns of gene flow (e.g., Berg et al. 1998). Additionally, where populations show significant genetic differentiation, allocation methods for assigning individuals to populations of origin may also be used effectively to estimate movement and dispersal rates (Hansen et al. 2001). However, we suggest that where possible ecological dispersal and migration patterns should be inferred (or at the very least corroborated), using direct studies. Certainly the use of indirect methods alone can clearly miss patterns of movement (or lack thereof), which may be vitally important in an ecological or demographic context. Nevertheless, it is also true that application of direct methods can only provide insight into contemporary patterns of movement and will likely fail to detect historical or episodic dispersal that is important in an evolutionary context. It is therefore clear that for a full understanding of dispersal and migration a combination of molecular and mark-recapture methods will provide more information than either approach can in isolation.

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Appendix 1. Allele frequencies for Lower and Upper populations of Freshwater River

Locus	Lower	Upper	Locus	Lower	Upper	Locus	Lower	Upper
SFO 12 LAV			SCO 19			BHMS 7-001		
252	0.541	0.559	144	0.275	0.286	144	0.460	0.454
276	0.459	0.441	146	0.005	0	148	0.540	0.546
SFO 18 LAV			148	0.266	0.289	BHMS 7-033		
168	0.072	0.077	150	0	0.003	106	0.010	0.005
172	0.756	0.731	152	0.048	0.046	108	0.438	0.418
182	0.171	0.192	154	0.001	0	110	0.550	0.572
186	0.001	0	182	0.004	0.003	112	0.001	0.005
SFO C28			192	0.005	0.003	STR 85 INRA		
168	0.138	0.121	194	0	0.003	138	0.020	0.013
176	0.009	0.008	196	0.147	0.126	142	0.003	0
180	0.479	0.485	198	0.003	0.008	146	0.030	0.054
184	0.373	0.387	200	0.210	0.211	150	0	0.003
SFO D91			202	0.025	0.016	152	0.012	0.023
213	0.001	0.003	204	0.010	0.008	156	0.447	0.418
217	0.048	0.041	SSA 20.19 NUIG			158	0.012	0.026
221	0.050	0.072	82	0.377	0.356	160	0.003	0.003
225	0	0.003	84	0.623	0.644	162	0.289	0.282
229	0.004	0.008	SSA 85 DU			166	0.159	0.151
233	0.052	0.077	111	0.667	0.710	170	0.025	0.026
237	0.330	0.285	115	0.333	0.290	174	0.003	0.003
241	0.007	0.018	BHMS 328			OMY 38 DU		
245	0.004	0	107	0.231	0.223	94	0.074	0.044
257	0.057	0.054	113	0.769	0.777	96	0.558	0.583
259	0.003	0	BHMS 356			98	0.368	0.374
261	0.097	0.108	126	0.521	0.528	OMYRGT46 TUF		
265	0.171	0.167	140	0.442	0.441	105	0.926	0.953
269	0.132	0.121	142	0.034	0.021	111	0.074	0.047
273	0.017	0.031	146	0.004	0.010			
277	0.030	0.015	BHMS 462					
SFO D100			115	0.171	0.139			
212	0.007	0.003	121	0.829	0.861			
216	0.481	0.482						
220	0.375	0.374						
224	0.021	0.010						
226	0.093	0.108						
230	0.025	0.023						

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