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Temporally stable genetic structure and low migration in an Atlantic salmon population complex: implications for conservation and management

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Abstract

The evolutionary potential of a population is closely related to two key population genetic parameters, namely the effective population size (N_e) and migration rate (m). Furthermore, knowledge of these parameters is required in order to assess potential constraints on local adaptation and for the development of biologically sound management strategies. We addressed these key issues by investigating the temporal and spatial genetic structure of over 2000 adult Atlantic salmon (*Salmo salar*) collected from 17 sites in the Teno and Näätämö rivers in northernmost Europe with up to five time points spanning temporal intervals up to 24 years (~4 generations). In all cases except one, local populations were found to be temporally stable within the river system. Estimates of N_e were generally a magnitude larger for the mainstem and headwater populations (MS+HW, N_e ~340–1200) than for the tributary populations (N_e~35–160), thus explaining the higher genetic diversity and lower divergence of the MS+HW populations compared to tributaries. The overall migration rates to tributaries were low, and in some cases, low enough for local adaptations to potentially evolve, despite their lower N_e. Signs of a population bottleneck and natural recruitment from nearby populations were detected in one local population. This highlights a fact which is relevant for the conservation and management of highly substructured population systems in general: that even when the overall census size is large, local populations can be vulnerable to perturbations. To preserve the current and to regain the historical distribution of salmon within the river system, we propose that the status of the total population complex should be evaluated at the local population level rather than from descriptive statistics at the system level.

Introduction

Although extrinsic forces such as destruction of natural habitats or over-exploitation are regarded as primary concern in conservation of endangered species (Lande 1988), it is clear that with increasing anthropogenic habitat modification the need for predicting the viability of populations, rather than simply explaining their demise, is increasingly important (Schwartz et al. 2007). The evolutionary potential of a population is closely related to two key parameters, namely the effective population size (N_e) and migration (Frankham et al. 2002). While N_e defines the rate at which genetic variation is lost and at which inbreeding increases in a population, migration acts as a homogenizing force limiting the divergence of natural populations. Low level of migration may also have great fitness benefits to small populations vulnerable to inbreeding (Tallmon et al. 2004). Knowledge of these parameters, as well as their relative roles in driving population structure is required in order to assess potential constraints on local adaptation (Adkison 1995; Hansen et al. 2002; Hendry et al. 2002; Hendry and Taylor 2004).

This knowledge is important for the development of biologically sound management strategies.

The relationship between census size and the effective size of a population is complex (Wright 1938; Hill 1972; Nunney 1991), but the two major factors affecting N_e are fluctuations in population size and variance in reproductive success among individuals (see Leberg 2005; Wang 2005 for reviews). In extreme cases, these may result in 'cryptic bottlenecks', especially in species with high reproductive output, such as fish, and be detectable only by applying genetic methods (Luikart et al. 1998; e.g. Shrimpton and Heath 2003). There are several ways for estimating N_e using genetic approaches, but temporal genetic change in allele frequencies across generations has been shown to be the most satisfactory (Waples 2005; Fraser et al. 2007a; Waples and Yokota 2007), while analyses made from single time point samples may fail to detect even demographically explicit population bottlenecks (Spong and Hellborg 2002; Busch et al. 2007). However, if a population is divided into demes, neglecting migration may result in distorted results on estimates of N_e (Wang and Whitlock 2003; Fraser et al. 2007a).

The effect of migration on the estimate of N_e of small populations is pivotal: in the short term, migration will increase change in allele frequencies, while in long term it may render genetic diversity from being lost or frequencies changed (Wang and Whitlock 2003). The effect of migration may also depend on whether immigration occurs from a source with a correlated or diverged distribution of allele frequencies (Fraser et al. 2007a). Thus, in subdivided populations with high potential for migration between demes, the temporal stability of genetic structure is an especially important issue for understanding the relative roles of contemporary evolutionary forces. However, the availability of temporal samples over generations is often the limiting resource. In this respect, systematically collected and archived fish scales, which are available for a number of commercially important fish species are a treasure trove (e.g. Nielsen et al. 1997; Tessier and Bernatchez 1999; Spidle 2001; Gatt et al. 2002; Hauser et al. 2002).

Due to its recreational and economical value, Atlantic salmon (*Salmo salar*) is one of the most studied fish species with many stocks having a long history of systematic monitoring programs and scale archives. Consequently, these archives have been utilized to span the temporal component of the population genetic studies of Atlantic salmon beyond 70 years (Nielsen et al. 1999a,b). However, the majority of studies where effective population sizes have been deduced have been carried out assuming one river – one population (but see Fraser et al. 2007a). Several studies have, however illustrated significant genetic differences among samples collected from multiple distinct sites within a single river (Elo et al. 1994; Garant et al. 2000, Landry and Bernatchez 2001; Spidle 2001; Primmer et al. 2006). Indeed, a large river system may actually be comprised of several genetically diverged populations constituting a population complex with deep population structure (Vähä et al. 2007). The effect of population structure within the system on the estimation of total N_e may be substantial, but the direction of the effect depends on the particular metapopulation dynamics (Nei and Takahata 1993; Whitlock and Barton 1997). For this reason and from a conservation and management perspective it is the estimate of contemporary, local N_e that is the most pertinent (Leberg 2005). Furthermore, focusing only on broader scale demographic effects can result in negative changes in local populations being missed. This is because while overall dynamics may be relatively stable, local populations may be influenced by drastic stochastic events such as over-exploitation or natural perturbations (e.g. Heath et al. 2002).

In a previous study of Atlantic salmon within the large Teno river system in northernmost Europe, we investigated the spatial genetic population structure with single time point samples (Vähä et al. 2007). We found remarkably high levels of differentiation between tributary populations and between tributary and the mainstem populations. We also found that the mainstem populations were less differentiated and possessed greater allelic diversity, and the level of genetic diversity in a population could be well predicted by the proportion of multi-sea-winter females in the population as well as the habitat size. It remained unclear however, whether the divergence of the tributary populations was primarily the result of genetic drift, possibly due to unstable populations or whether these differences could be driven by selection and local adaptation. Understanding the relative importance of these contemporary evolutionary forces would greatly enhance the refinement of management strategies such as delineating the appropriate geographical scale for defining management units.

By taking advantage of systematically collected and archived fish scales from adult salmon collected from 17 sites in the Teno River with up to five time points spanning temporal intervals up to 24 years (~4 generations), we investigated the temporal component of variation in the genetic structure of Atlantic salmon populations within a single river system. This was then put in to a larger context by juxtaposing with the results obtained for the nearby Näätämö River. Using this information, we address the following questions: (i) how large are the differences in the temporal stability and effective population sizes between populations, especially between the

mainstem and the tributaries? (ii) are these patterns compatible with the potential for the evolution of local adaptations? Knowledge of the level of independence/dependence of tributary populations from the presumably larger mainstem populations, in terms of demography and gene flow, and the scale of potential for the evolution of local adaptations are essential for defining the appropriate geographical scale of managing these exploited fish stocks, and can provide general guidelines for other large river systems.

Material and methods

Study area

Rivers Teno (catchment area 16 386 km^2) and Näätämö (catchment area 2962 km^2) are located in northernmost Europe (68–70′N, 25–29′E) with estuaries *c.* 250 km apart (Fig. 1). Both rivers support naturally reproducing stocks of salmon managed based solely on fishery regulation; release of reared fish and eggs is strictly forbidden and salmon production is entirely dependent on natural reproduction. The mean salmon catch in the River Teno is 135 t (range 70–250t in 1972–2006), accounting for up to 20% of the annual riverine salmon harvest in Europe (ICES 2007). The mean annual catch of Näätämö salmon is 8.5 t (range 3–16t in 1972–2006). The total length of the river Teno is 351 km with more than 1200 km of waterway passable by adult salmon. There are 20–30 tributaries in the river system, where salmon reproduce, but the sizes of the tributaries and of the spawning stocks vary considerably, from several hundred to several thousands spawners. The River Näätämöjoki system includes *c.* 110 km of passable waterway for adult salmon along the main stem and one main tributary, Silisjoki.

Specimen and sampling sites

Samples of adult salmon from the River Näätämöjoki (n = 102) and 17 distinct sites throughout the River Teno system (n = 1952) were obtained from scale archives of Finnish Game and Fisheries Institute. Out of 2054 salmon included in this study 792 were obtained from the study of Vähä et al. (2007) (Fig. 1). Scale analyzis had been carried out to determine the age of each fish by detecting the differences in the growth patterns both in freshwater zone and at sea. To minimize the likelihood of sampling transient individuals i.e. to maximize the chance of sampling members of the local breeding population, only mainstem samples which had been collected between August 15–31 were included in the data set. This period is approximately 1 month after most individuals have entered the river (Niemelä et al. 2006b), but 4–6 weeks prior to spawning. Samples of individuals from the tributaries had been collected during July and August. Subscripts are used throughout the text to denote the sampling site: MS – mainstem (LM – lower mainstem, UM – upper mainstem), HW – headwater and T – tributary.

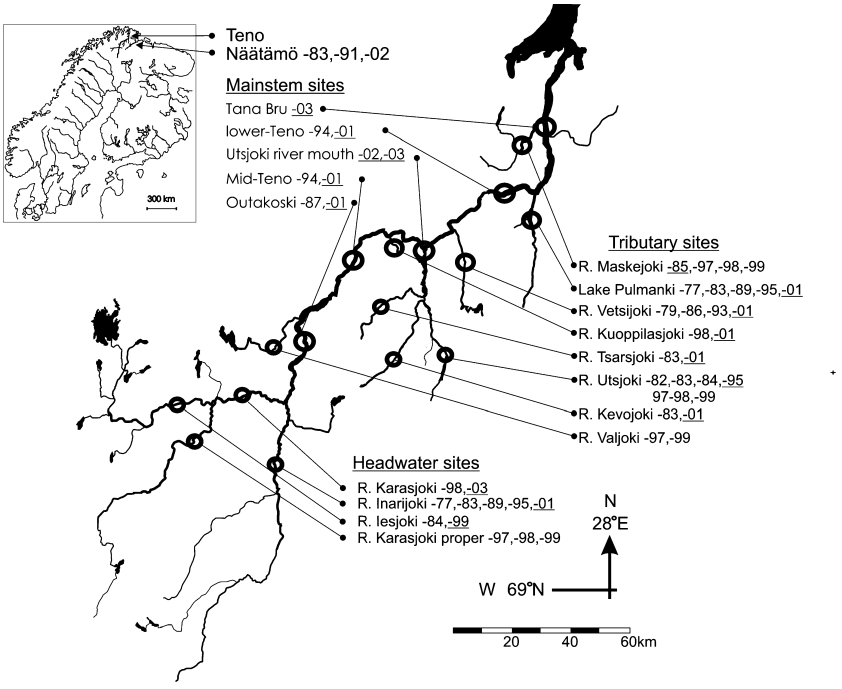

Figure 1 Map showing the location of the rivers Teno and Näätämö in northernmost Europe (nested map). For the Teno river system, sampling sites followed by the year of sampling is shown. Underlined years indicate samples for which the data were obtained from Vähä et al. (2007).

DNA extraction and microsatellite loci

DNA extraction methods and details of the 29 microsatellite loci analyzed were as in Vähä et al. (2007). All but one microsatellite locus (SSOSL311) were amplified by multiplex PCR. Simultaneous amplification of seven or eight loci were carried out in 6 μL reaction volume, which consisted of 1 μL of extracted DNA elute, 1x QIAGEN Multiplex PCR Master Mix solution (Qiagen, GmbH, Hilden, Germany) and varying concentrations (0.1–0.7 μM) of primers (details available at http://users.utu.fi/jpvaha). The locus SSOSL311 was amplified in 10 μL reaction volume, which consisted of 1.5 μL of extracted DNA elute, 0.60 μM of each primer, 1x NH_4 reaction buffer (16 mM $(NH_4)_2SO_4$, 67 mM Tris–HCl (pH 8.8), 0.01% Tween-20, Bioline), 1.5 mM $MgCl_2$, 250 μM dNTP and 0.25 U of BioTaq DNA polymerase (Bioline, GmbH, Luckenwalde, Germany). Thermal cycling profiles for the multiplex protocols were as follows: 15 min at 95°C, followed by 36 cycles of 30 s at 94°C, 90 s at 58–61°C and 60 s at 72°C, followed by final extension step of 10 min at 72°C. For the locus SSOSL311 thermal cycling profile was 3 min at 94°C, followed by 38 cycles of 30 s at 94°C, 60 s at 53°C and 60 s at 72°C and finally an extension step of 5 min at 72°C. Even volumes of the PCR amplified products were pooled and 0.09 μL of GS600LIZ size standard (Applied Biosystems, Foster City, CA) was added as an internal size standard to each sample. Example electropherograms of all loci are available from http://users.utu.fi/jpvaha. Electrophoresis was then performed on ABI 3130*xl* (Applied Biosystems). Allele scoring was performed with GENEMAPPER V3.7 (Applied Biosystems) followed by manual corrections.

Calibration of the data sets and quality control of laboratory and genotyping procedures

To calibrate the data obtained from Vähä et al. (2007), genotyped using GS500LIZ internal size standard, with the current genotyping system (GS600LIZ), a subset of samples were re-amplified and analyzed. This allowed testing the repeatability between the two multiplexing systems. Genotyping error rate calculated the comparison of two multiplexing systems was 0.4% (17 errors/4498 scored alleles). Similarly to our earlier quality control (see Vähä et al. 2007), tests were carried out to evaluate if the current genotyping system of amplifying up to nine loci in one PCR-reaction and injecting amplicons from up to 17 loci in the same capillary resulted in systematic allele drop-outs. More specifically, genotypes obtained with multiplex-PCR (Qiagen) were compared with genotypes obtained utilizing single PCR reaction, where amplicons were also injected into the electrophoresis capillary in sets of seven to nine per capillary. Altogether multi-locus genotypes of 32 samples were compared revealing five miss-scored alleles among the data sets (0.3%). Additionally, 96 samples were re-amplified and analyzed with the current genotyping system. This comparison resulted in an error rate of 0.3% among two replicate analyses. We conclude that the PCR multiplexing of the loci and injecting up to 17 loci in the same capillary did not have a deterministic effect or increase the scoring error in our data. Overall these error rates were low and unlikely to obscure the signal in the data.

Data analyses

Hardy–Weinberg equilibrium, genetic diversity and differentiation indices

Conformity with expected Hardy–Weinberg equilibrium genotypic frequencies for each sample was tested using the randomization test implemented in GENEPOP 3.4 (Raymond and Rousset 1995). We did not perform tests for the genotypic disequilibrium for the pair of loci as these tests were already carried out in Vähä et al. (2007) suggesting the loci being physically unlinked. Genetic diversity was quantified with gene diversity (H_E) and allelic richness (A_R) indices, which was calculated using a rarefaction procedure implemented in HP-RARE 1.0 (Kalinowski 2005). Rarefaction size is shown as x in the subscript $A_{R(x)}$.

Heterogeneity in allele frequency distributions between samples were tested by estimating Fisher's exact P-value for each locus and population pair by Markov chain method and employing Fisher's method to test for joint null hypothesis of no difference as implemented in GENEPOP 3.4 (Raymond and Rousset 1995). The level of genetic variation among populations was estimated by computing F_{ST} values using the $\ominus$ estimator of Weir and Cockerham (1984). To hierarchically assess the molecular variance component attributable to among samples form different sites (spatial) and among samples within sites (temporal) analysis of molecular variance (AMOVA) was performed. AMOVA-analyses were performed with locus-by-locus procedure as implemented in the ARLEQUIN V3.01 software (Excoffier et al. 2005).

Genetic relationships among samples were estimated according to the Nei's genetic distance D_A (Nei et al. 1983) using the POPULATION 1.2.28 software (written by Olivier Langella). D_A has been shown to have good discriminatory power for closely related populations (Nei et al. 1983) and is recommended for microsatellite data (Takezaki and Nei 1996). Genetic relationships were examined by neighbor-joining method (Saitou and Nei 1987) and node support values were obtained by bootstrapping 1000 times over loci. The tree was visualized using TREEVIEW (Page 1996).

Inference of population structure using clustering methods

The underlying population structure was inferred using genetic mixture analysis (Corander et al. 2006a) method followed by the admixture analysis (Corander and Marttinen 2006) implemented in program BAPS 4.14 (Corander et al. 2006b). We chose to utilize this method; because it has superior execution speed compared with Markov Chain Monte Carlo (MCMC) methods, as it uses a stochastic optimization algorithm approach for finding the posterior mode of the genetic structure. Furthermore, BAPS treats the number of populations as an unknown parameter; a feature, which especially in hierarchically structured complex data sets is advantageous (e.g. Vähä et al. 2007). Analyses were performed with a vector of values (20–30) for K each with five replicates. The clustering solution with the highest posterior probability was chosen as the correct partitioning on which the admixture analysis (100 iterations, 200 simulated individuals) was subsequently performed. A P-value ≤ 0.03 was considered as evidence for admixed ancestry (Corander and Marttinen 2005).

As the genetic mixture method provided a clustering solution similar to that described in Vähä et al. (2007), where BAPS was unable to partition MS + HW samples, we utilized the method of 'correlated allele frequency'-model (Falush et al. 2003) implemented in the program STRUCTURE (Pritchard et al. 2000). Hierarchical STRUCTURE analysis, where subsequent runs are performed on partitioned data with individuals of inferred clusters omitted, was performed on the MS + HW samples. For runs estimating ln Pr(X|K) under a certain K, run lengths with 30 000 burn-in and 60 000 total length were used. To adjudicate the correct K we applied the ΔK method (Evanno et al. 2005). The individual assignment patterns were examined using q-value threshold of ≥0.8 to denote nonadmixed membership in the cluster as recommended by Vähä and Primmer (2006).

Using the two above approaches, individuals with nonadmixed ancestry assigned to the population from which it was sampled were selected as a prior reference data: 14 populations (n = 1504 individuals). Assignment of data, was then performed with trained clustering method implemented in BAPS 4.14 (Corander et al. 2006b) followed by admixture analysis (Corander and Marttinen 2006). In the trained clustering each assignment was performed one-by-one. Individuals with admixture P-value ≤ 0.03 were considered as showing significant evidence for admixed ancestry (Corander and Marttinen 2005).

Inference of straying and recent migration rates

Three different estimates of straying/migration were estimated in order to compare the frequency with which individuals were identified in non-natal tributaries, and the frequency with which individuals reproduced successfully in non-natal tributaries: m_{BAPS}, which estimates the frequency with which individuals were identified in non-natal populations, was calculated using BAPS (Corander et al. 2006); m_{BA}, which detects individuals which have very recent (up to two generations back) ancestry in non-native populations, was calculated using BAYESASS (Wilson and Rannala 2003); and m_{MNE}, which estimates gene-flow over the entire sampling interval (in this study, ∼1 to ∼4 generations), was calculated using MNE2 (Wang and Whitlock 2003).

Although BAPS does not explicitly estimate migration rates, a rough point estimate can be obtained by dividing the number of individuals identified as migrants by the sample size (Manel et al. 2005). Considering that admixed individuals (P-value ≤ 0.03) were omitted and adult fish were collected on their spawning grounds, straying (m_{BAPS}) refers to the contemporary year. While all 'miss-assigned' fish in tributaries were considered as strays, an individual in the mainstem was considered a stray from tributary, only if it was collected at a site past the point of joining of the two channels. In the mainstem and headwaters, straying rates were considered only for the headwaters Inarijoki, Iesjoki, and Karasjoki.

Estimates of recent migration rates (m_{BA}) were inferred by the method implemented in the program BAYESASS V1.3 (Wilson and Rannala 2003). The method uses individual multilocus genotypes to estimate rates of recent immigration in Bayesian statistical framework. Joint posterior probability distributions of parameters are estimated by the Markov chain Monte Carlo technique. The implemented method considers migrants up to two generations back and can be applied to nonstationary populations that are neither in genetic equilibrium nor Hardy–Weinberg equilibrium by means of incorporating a separate inbreeding coefficient for each population. Relatively low levels of migration are allowed as the proportion of migrant individuals over two generations into a population cannot exceed 1/3 of the population total. Although the samples from the mainstem sites (Tana $Bru_{(LM)}$ lower $Teno_{(LM)}$, Utsjoki river $mouth_{(LM)}$, middle $Teno_{(LM)}$ and $Outakoski_{(UM)}$) were collected in August 15–31 to maximize the likelihood of sampling individuals, which had completed their spawning migration we considered samples only from the headwaters $Inarijoki_{(HW)}$, $Iesjoki_{(HW)}$ and Karasjoki $proper_{(HW)}$ and pooled samples from lower $Teno_{(LM)}$ and Utsjoki river $mouth_{(LM)}$ to represent Teno mainstem lower (TmsL) population. To increase the sample size given the low level of differentiation and small genetic drift (large N_e, see results) temporal samples were pooled. For tributary populations, recent migration rates were estimated in two periods; 1979–1985 and 1995–2001. Initial trials showed that the convergence

was achieved with a total of 6×10^6 iterations, of which the first 1×10^6 was discarded as burn-in. To estimate the posterior probability distributions of parameters replicate MCMC runs with different seeds were performed. In several runs we observed the MCMC to get stuck on local optimum resulting in a nonmigrant rate of ~67% for the Maskejoki 1985 sample. As additional samples from the early period were not available it was excluded from the analysis. For each population, estimates were averaged over 10 successful replicate runs.

Estimation of effective population sizes and immigration

As gene flow cannot be ruled out in our study system, effective population size estimates were firstly obtained by the likelihood method of and Wang and Whitlock (2003) implemented in the program MNE2 as it provides estimates of the effective population size and immigration rate jointly. For estimating migration (m_{MNE}) into a population over the sampling interval an infinitely large source population providing migrants to the focal population is assumed. For this we considered two source population scenarios (i) all samples other than those from the focal population were combined; (ii) samples from the mainstem and headwaters (MS + HW) were combined as a source when considering a tributary draining to the mainstem or MS + HW and neighboring tributaries when considering Utsjoki river system populations ($Utsjoki_{(T)}$, $Tsarsjoki_{(T)}$, $Kevojoki_{(T)}$).

For estimating N_e of the River Näätämö population, in addition to the two source population scenarios described above, N_e was also estimated assuming a single isolated population adapting to assumptions of the method of Wang (2001) also implemented in MNE2. The estimations were conducted assuming 5000 as a maximum value of N_e. Generation time (G_t) for populations with overlapping generations is suggested to be the mean age of parents (Hill 1979; Miller and Kapuschinski 1997). For each population G_t was estimated as the mean age-at-maturity calculated from the data. Our estimates of generation time are likely to be slightly inflated as the contribution of mature male parr to the reproduction is not accounted for. Thus, the estimates of N_e may be biased downward, but the potential bias is likely of similar magnitude in all populations. When data from more than one sampling site was pooled, in case of the mainstem populations, sampling time was calculated as the weighted mean. Since only integer numbers for the generations between sampling intervals are allowed by the methods, all the estimates were adjusted according the equations provided by Wang and Whitlock (2003).

Assessment of the potential for evolution of local adaptation

We assessed whether local adaptation could occur within the river system, given the estimated effective population sizes and pattern of migration. For this we used the cline theory approach (discussed in detail by Adkison (1995)), formulated by Slatkin (1973) and Nagylaki and Lucier (1980), which has also been applied in e.g. Hansen et al. (2002). Firstly, Slatkin (1973) showed that local adaptation can only occur if the spatial scale of selection is larger than the 'characteristic length' of spatial variation in allele frequencies due to gene flow and selection. Characteristic length (l_c) is defined by $l_c = \sigma_m/\sqrt{s}$, where σ_m is the standard deviation of dispersal distances and s is the strength of selection. Secondly, Nagylaki and Lucier (1980) showed that the relative importance of selection and genetic drift can be captured in a single parameter β and the condition for local adaptation is fulfilled when $\beta >> 1$. The parameter β is defined as $2\sqrt{(2ms)N_e}$, where m = migration rate, s is the strength of selection and N_e is the effective population size. We calculated the standard deviation of dispersal distances σ_m for each population separately using estimates of recent migration rates (m_{BA}) from the later period and geographical distance between presumed mid-points of the habitats. The habitats represent the range which sampling, i.e. angling and netting effort, spanned in each tributary or section of the main stem, and the mid-point has been determined as a geographical mid-point of the section weighed by the distribution and intensity of fishing effort. In other words, the mid-point is located within the most intensive fishing area where the majority of samples have been collected (Erkinaro and Niemelä, unpublished data). Fishing effort has been more concentrated in tributaries, whereas a wider spatial distribution of samples is evident for different sections of the large mainstem. For β, calculations were performed using recent migration rates (m_{BA}) and estimates of m_{MNE} and N_e as obtained with the maximum likelihood method of Wang and Whitlock (2003). Comparing the characteristic length l_c to the spatial scale of selection for each population, the strength of selection, which needs to be invoked in order for local adaptation to occur, was estimated.

Results

Summary statistics of the genetic diversity indices for each locus and sample are provided in Online Supplementary Table S1. Congruence with expected Hardy–Weinberg equilibrium genotype frequencies indicated 12 samples to deviate significantly when tests were combined (Fisher's method) over loci (Table 1). There are two main tributaries draining to the Lake Pulmanki and as expected based on earlier results (Vähä et al. 2007), all five samples collected from Lake Pulmanki showed departure from H–W equilibrium genotype frequencies. In the rest of the samples which showed significant departure from the H–W equilibrium, the cause due to Wahlund effect was

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Table 1. Genetic clustering and diversity indices (as estimated using 29 loci) of Atlantic salmon from 48 samples collected from 17 sites in the River Teno during 1977–2003.

		Assignment to genetic clusters as inferred by BAPS																				Genetic diversity				
Samples		Vet	L. Pulm.		Maskej.		Kev	Tsa	Utsjoki						Kuo	Val	TmsL	TmsU	Ies	Kar	?	na	Adm	H_E	H_O	A_R	N
Vetsijoki-79	T	**25**																1		2							
Vetsijoki-86	T	**27**															1					1	1	0.68	0.67	5.7	30
Vetsijoki-93	T	**33**															1						1	0.68	0.69	5.7	35
Vetsijoki-01	T	**38**															1						1	0.67	0.68	5.5	40
L. Pulm.-77	T		**42**	**8**													1						4	0.64	0.59**	5.0	55
L. Pulm.-83	T		**34**	**15**																			1	0.65	0.65***	5.0	50
L. Pulm.-89	T		**36**	**7**																			2	0.64	0.59**	4.9	45
L. Pulm.-95	T		**36**	**8**																			4	0.65	0.61**	4.9	48
L. Pulm.-01	T		**74**	**12**																			9	0.64	0.60***	5.0	95
Maskej.-85	T				**18**	**6**											1			1			3	0.69	0.67**	5.8	29
Maskej.-97	T				**18**																			0.69	0.69	5.7	18
Maskej.-98	T				**20**																			0.68	0.66	5.4	20
Maskej.-99	T				**14**																			0.66	0.67	5.2	14
Kevojoki-83	T						**35**	7	1		2												7	0.67	0.65***	5.0	52
Kevojoki-01	T						**58**	2															7	0.67	0.66	5.2	67
Kevojoki-83	T							**57**															3	0.62	0.61	4.1	60
Kevojoki-01	T						4	**72**															11	0.63	0.62	4.3	87
Utsjoki-82	T								**4**	**3**													1	0.65	0.65*	-	8
Utsjoki-83	T						2	2	**21**	**8**	**4**						1						2	0.63	0.66***	4.7	40
Utsjoki-84	T						1	3	**4**	**5**	**2**	**5**	**3**										4	0.67	0.64***	5.4	27
Utsjoki-95	T									**24**			**2**							1		1	2	0.67	0.68	5.2	30
Utsjoki-97	T									**8**		**2**												0.67	0.64	-	10
Utsjoki-98	T									**16**			**1**							1			4	0.66	0.67	5.1	22
Utsjoki-99	T							1		**6**							1						1	0.69	0.68	-	9
Kuopp.j.-98	T													**31**			1						1	0.63	0.64	4.7	33
Kuopp.j.-01	T													**34**										0.65	0.67	5.1	34
Valjoki-97	T														**20**					1				0.66	0.63	4.9	21
Valjoki-99	T														**14**					1				0.68	0.67	5.4	15
Tana Bru 03	LM																**13**	11				1		0.70	0.69	6.3	25
Lower Teno-94	LM	1			1					1				1			**39**	12	3	5		4	1	0.69	0.68	6.3	68
Lower Teno-01	LM						1										**21**	3		2		2	1	0.70	0.69	6.4	30
Utsj. Rm 02–03	LM	2						1									**22**	1	1				2	0.70	0.69	6.0	29
Mid Teno -94	LM													1			**24**	11		1		3	1	0.70	0.69	6.3	41
Mid Teno -01	LM	1									1						**18**	7	3		1	1		0.69	0.70	6.3	32
Outakoski -87	UM														1	6	**28**	2	2		2	2	0.69	0.67	6.2	43
Outakoski -01	UM													1	1	11	**29**	2	4		3	5	0.69	0.68	6.2	56
Inarijoki -77	HW															1	**24**		1			1	0.69	0.66	5.9	27
Inarijoki -83	HW	1					1										**30**					2	0.67	0.66	5.8	34
Inarijoki -89	HW															7	**41**	1			1	3	0.69	0.68	5.9	53
Inarijoki -95	HW													1		1	**34**	2				2	0.68	0.66	6.0	40
Inarijoki -01	HW	1														11	**65**	3	4			3	0.69	0.68	6.0	87
Iesjoki -84	HW															2	1	**66**	25		3	2	0.67	0.66	6.0	99
Iesjoki -99	HW	1														2	1	**31**	1			3	0.68	0.67	5.9	39
Karasj. Pr.-97	HW																1		**15**				0.68	0.67	5.8	16
Karasj. Pr.-98	HW														1				**13**				0.68	0.67	6.0	14
Karasj. Pr.-99	HW																		**16**				0.68	0.70	5.8	16
Karasj. -98	HW														1	3	3	27	47		1	6	0.68	0.67	6.1	88
Karasj. -03	HW	1													2	5	2	28	48		1	6	0.69	0.68	6.2	93
Total		131	222	50	71	6	102	145	30	71	9	7	6	69	40	194	305	169	191	1	24	109				1952

For each sample, location is given as T, tributary; LM, lower mainstem; UM, upper mainstem; HW, headwater; ?, Unknown affiliation; n.a., not assigned due to equal ancestry to more than one cluster; Adm., number of individuals showing admixed ancestry ($P \leq 0.03$).

Genetic diversity indices for samples: H_E, expected heterozygosity; H_O, observed heterozygosity and significance test result for deviations from HWE (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$), A_R, allelic richness in 20 genes, N, sample size.

less obvious. As five of these significant tests were observed in the early samples of the temporal replicates we suspected the departure due to technical factors, such as null-alleles or large allele drop-outs related to the usage of degraded and low yield DNA material. For a subset of these samples DNA was re-extracted and for all samples the loci re-amplified and analyzed. Comparison of the electropherograms and genotypes did not reveal significantly elevated genotyping errors or systematic technical artifacts. Although such technical artifacts cannot be ruled out, three aspects convince us to assume that signal from a large number of loci dominated the noise: (i) estimated genotyping error rates were low and did not reveal any systematic artifacts; (ii) the occurrence of individuals from more than one population in a sample was expected; and (iii) relatively strong signal of temporal stability was observed in majority of populations.

Temporal stability of spatial genetic structure

The pattern of differentiation in allele frequencies among samples implied relatively stable genetic constitution of populations over time. Although, 61% of within sampling site comparisons were significant ($P < 0.05$) indicating that change in allele frequencies does occur over time, nearly all (99%) of comparisons between samples from different sites in Teno were significant. All nonsignificant between sites comparisons were among the mainstem (MS) and headwater (HW) samples. Analyses of molecular variance (AMOVA) further corroborated the temporal stability of population structure. Although all permutation tests indicated that both variation components, spatial and temporal, in all tests were highly significant, spatial component was always larger. Overall, 5.2% of genetic variation was among spatial samples while only 0.7% was partitioned among temporal samples. The divergence components were an order of magnitude smaller among the mainstem and headwater samples (MS + HW) samples: the spatial component accounted for 0.8% and the temporal component for 0.2% of the total genetic variation. Considering only tributary populations, the spatial component accounted for 8.5% of the total genetic variation among all samples, while the temporal component of genetic variation was only 1.1%. Temporal variation in allele frequencies was clearly highest in Utsjoki$_{(T)}$ (3.3%), where the largest divergence ($F_{ST} = 0.08$; Online Supplementary Table S2) was found between 1983 and 1997. Excluding Utsjoki$_{(T)}$ samples, the spatial component accounted for 9.2% of the total genetic variation among tributary samples and only 0.7% of the genetic variation was observed between temporal samples.

Genetic relationships of temporal samples and populations were illustrated by the neighbor-joining analysis of D_A between samples (Fig. 2). The neighboring River Näätämö, separated by *c.* 250 km of waterway distance was a distinct group in the tree supported by 100% bootstrap value and used as a root for the tree. The close genetic relationships of temporal samples were generally supported with high bootstrap values separating the clusters. The high divergence of tributary populations was reflected in longer branch lengths compared to those of the mainstem and headwaters. The clustering of the mainstem and Inarijoki$_{(HW)}$ samples in two groups corresponding to populations Teno mainstem lower (TmsL) and Teno mainstem upper (TmsU) inferred in Vähä et al. (2007) was corroborated. The temporal instability of Utsjoki$_{(T)}$ was visible in the phylogenetic tree as it was divided in 'before 1984' and 'after 1995' clusters.

Population assignment and the rate of straying

The final clustering solution including the number of inferred first generation migrants obtained with the trained clustering method implemented in BAPS 4.14 is presented in Table 1. In total, 19 genetic clusters were inferred absorbing 93.2% of samples, while 5.5% of individuals showed admixed ancestry and 1.3% could not be unambiguously assigned. Generally, all temporal replicate samples from tributaries clustered together, apart from Utsjoki$_{(T)}$, Lake Pulmanki$_{(T)}$ and Maskejoki$_{(T)}$ samples. Based on geography and our earlier investigations (Vähä et al. 2007), the division of Lake Pulmanki$_{(T)}$ and Maskejoki$_{(T)}$ samples in more than one cluster was expected, while that of Utsjoki$_{(T)}$ was not. Despite being partitioned to several genetic clusters, they were considered as being of the same origin.

Altogether, 16 strays of mainstem or headwater origin were identified in tributaries resulting in an average straying rate $m_{BAPS} = 0.017$ from the MS + HW to tributaries, while 20 of the fish sampled in MS + HW were of tributary origin, resulting in an average straying rate $m_{BAPS} = 0.023$ from the tributaries to MS + HW. Among tributaries straying was inferred only to occur between the three neighboring rivers, Utsjoki$_{(T)}$, Kevojoki$_{(T)}$ and Tsarsjoki$_{(T)}$, which together constitute the Utsjoki tributary system. Straying rates were high from Tsarsjoki$_{(T)}$ to Kevojoki$_{(T)}$ ($m_{BAPS} = 0.085$) and to Utsjoki$_{(T)}$ ($m_{BAPS} = 0.046$), which also received migrants from the mainstem ($m_{BAPS} = 0.03$).

In the mainstem and headwaters, the inferred straying rates were generally higher as only 76% of the MS+ HW fish were assigned specifically to the assumed population. While only 5.6% the fish caught in the headwaters (Inarijoki, Iesjoki and Karasjoki), were strays from the lower part of Teno mainstem, 26.5% of the lower mainstem fish were of headwater origin.

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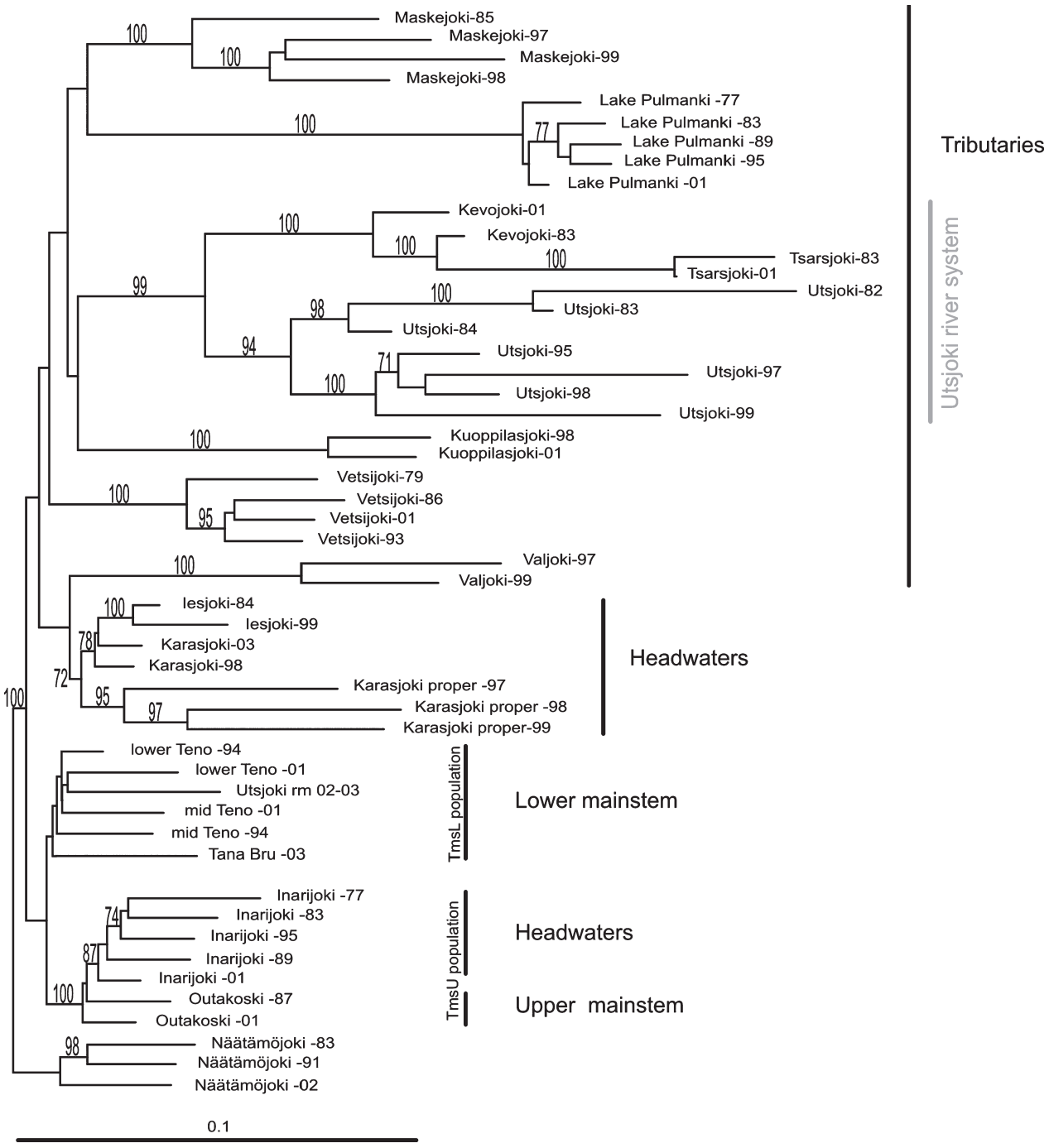

Figure 2 Neighbour-joining tree based on genetic distances (D_A) among samples collected from seventeen sites within Teno river system rooted with samples collected from Näätämö River. Only bootstrap values providing branch support of at least 70% are shown.

Estimates of migration rates

Recent migration rates (m_{BA}) of tributary populations were estimated using BAYESASS from samples collected in two time periods; 1979–1985 and 1995–2001 (Fig. 3, Online Supplementary Table S3). In general, migration rates to tributaries were similar with straying rates. The most significant difference between the two time periods were the elevated levels of migration rates to tributary populations in the earlier period $m_{BA} = 0.10$ than later period $m_{BA} = 0.035$. However, the difference was mainly due to higher migration rates among the populations

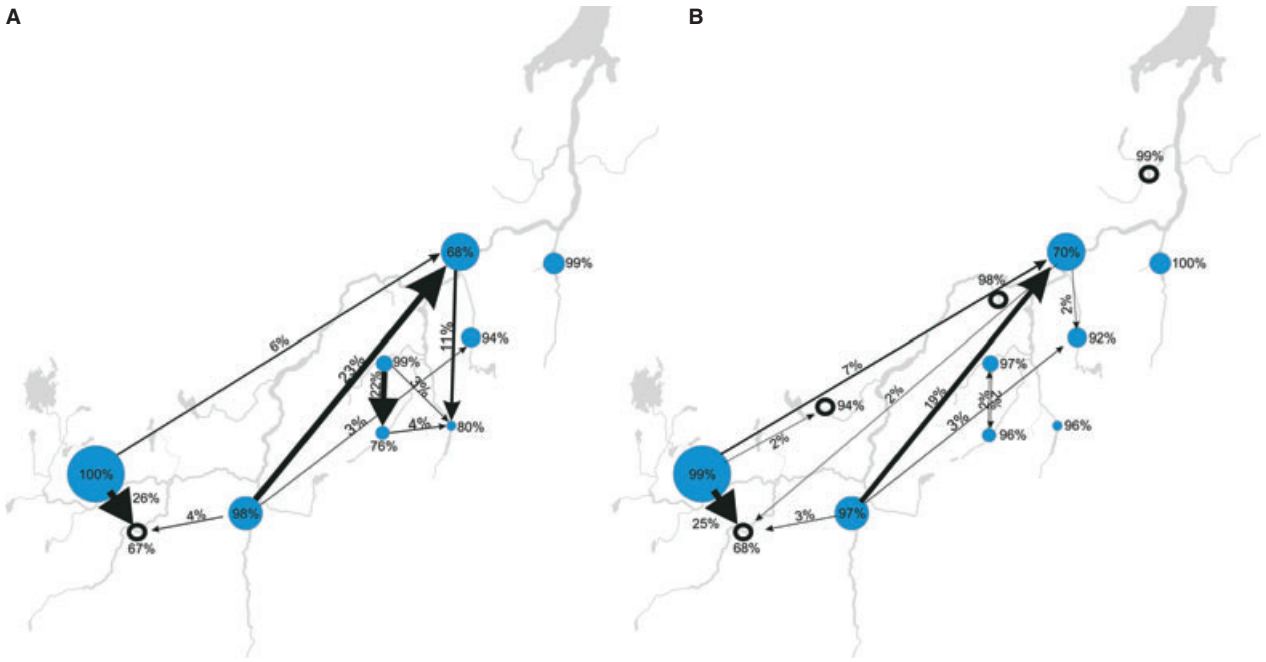

Figure 3 Recent migration rates (*m*) between populations estimated using BAYESASS (Wilson and Rannala 2003) from samples collected (A) during 1979–1985 and (B) during 1995–2001. The numbers next to or within the circles denote the proportion of nonimmigrants within populations. For clarity of presentation *m* values less than 2% are not shown. Surface areas of the circles are proportional to the effective population size, N_e, which was not estimated for populations denoted by open circle.

within Utsjoki river system consisting of Utsjoki$_{(T)}$, Kevojoki$_{(T)}$ and Tsarsjoki$_{(T)}$. More specifically, Kevojoki$_{(T)}$ received migrants (m_{BA} = 0.22) from the neighboring Tsarsjoki$_{(T)}$, while Utsjoki$_{(T)}$ received migrants from the neighboring Kevojoki$_{(T)}$ (m_{BA} = 0.04) and Tsarsjoki$_{(T)}$ (m_{BA} = 0.03) as well as from the mainstem (m_{BA} = 0.11). In the rest of the tributary populations, migration rates were roughly constant over time. Over the thirty year period Lake Pulmanki$_{(T)}$ was the most isolated population, receiving migrants at a rate <1%. In contrast to tributaries, the migration rates to headwaters were incongruent with the estimated straying rates. Whilst the migration rate to Karasjoki$_{(HW)}$ was substantially higher m_{BA} = 0.32–0.33 than straying rate, it was lower to Inarijoki$_{(HW)}$ and Iesjoki$_{(HW)}$, m_{BA} = 0.02–0.03 and m_{BA} = 0.00–0.01, respectively. Similarly to straying rate, the recent migration rate to the lower Teno mainstem was high m_{BA} = 0.30–0.32 with Inarijoki$_{(HW)}$ being the main source of immigrants m_{BA} = 0.19–0.23.

Nevertheless, these straying and recent migration rates were reflected in the estimates for immigration over the total sampling interval (m_{MNE}), which however were substantially lower (Table 2). Generally, the compilation of the source population used in the calculations did not have a substantial effect on the estimates. The largest difference was observed in Vetsijoki$_{(T)}$, for which the immigration rate was m_{MNE} = 0.01 when all samples other than those from the focal population were combined and m_{MNE} = 0.02, when only the samples from the mainstem and headwaters (MS + HW) were considered. Congruently with straying and recent migration rate estimates, the most isolated tributary populations were L. Pulmanki$_{(T)}$ m_{MNE} = 0.004–0.005 and Tsarsjoki$_{(T)}$ m_{MNE} = 0.005–0.006, while the highest estimate was observed in Utsjoki$_{(T)}$ m_{MNE} = 0.048–0.051. The mean rate of gene flow into tributaries was m_{MNE} = 0.018, being slightly less than rates of straying and recent migration. Contrasting with the recent migration rate estimates gene flow to lower parts of Teno mainstem was substantially lower being only m_{MNE} = 0.01–0.014. Again the estimates were lower for the populations higher up in the system: m_{MNE} = 0.002 and m_{MNE} = 0.006–0.009 for Iesjoki$_{(HW)}$ and upper mainstem, respectively.

Effective sizes of the populations

Maximum likelihood estimates of the effective population sizes were substantially larger for the mainstem and headwater populations than for the tributary populations (Table 2). The largest effective population size was estimated for the Iesjoki$_{(HW)}$ population (N_e = 1209,

Table 2. Estimates of effective population size (N_e) and immigration rate (m_{MNE}) for each population, where two or more temporal samples (No. of time points) with time interval (T) exceeding that of generation time (G_t) were available.

Population	T	G_t	No. of time points	Effective population size			Immigration rate		
				N_e	+95%CI	−95% CI	m_{MNE}	+95%CI	−95% CI
Vetsijoki (T)	22	6.2	4	135	237	87	0.010	0.016	0.006
Vetsijoki (T)				112	187	75	0.02	0.03	0.011
Lake Pulmanki (T)	24	6.2	5	165	244	119	0.004	0.005	0.003
Lake Pulmanki (T)				155	233	116	0.005	0.005	0.005
Kevojoki (T)	18	6.2	2	69	99	51	0.019	0.027	0.012
Kevojoki (T)				68	97	51	0.021	0.03	0.014
Tsarsjoki (T)	18	6.9	2	99	150	71	0.005	0.008	0.005
Tsarsjoki (T)				97	155	72	0.006	0.008	0.003
Utsjoki (T)	13.4	6.6	2	35	41	31	0.048	0.061	0.038
Utsjoki (T)				35	41	31	0.051	0.065	0.04
Teno ms Lower[a] (LM)	7.8	6.9	2	618	3696	274	0.010	0.027	0
Teno ms Lower[b] (LM)	7.5	6.9	2	507	3766	228	0.013	0.032	0.001
Teno ms Lower[c] (LM)	7	6.9	2	494	3715	200	0.014	0.038	0.000
Teno ms Upper[a] (HW)	24	6.1	5	338	764	200	0.006	0.010	0.005
Teno ms Upper[b] (UM + HW)	24	6.1	5	431	854	200	0.009	0.015	0.004
Iesjoki (HW)	15	6.7	2	1209	1423	388	0.002	0.005	0.001
Näätämö River*	19	6.3	3	3089	>7588	219	na	na	na
Näätämö River1,†	19	6.3	3	305	1736	158	0.016	0.033	0.003
Näätämö River2,†	19	6.3	3	308	1715	160	0.019	0.039	0.004

Location of the population is denoted in brackets.

LM, lower mainstem; UM, upper mainstem; HW, headwater; T, tributary.

*Estimated using maximum likelihood method assuming a single isolated population.

†Estimated assuming Teno (1 all samples, 2 mainstem and headwater samples) as a source population. Three different sets of samples were used for obtaining parameter estimates for Teno mainstem Lower population: Tana Bru, lower Teno, Utsjoki river mouth and mid Teno (Teno ms Lower[a]); lower Teno, Utsjoki river mouth and mid Teno (Teno ms Lower[b]); lower Teno and mid Teno (Teno ms Lower[c]). Two different sets of samples were used for obtaining parameter estimates for Teno mainstem Upper population: Inarijoki (Teno ms Upper[a]); Inarijoki and Outakoski (Teno ms Upper[b]).

$CI_{-95\%}$ = 388, $CI_{+95\%}$ = 1422). Depending on the samples used in the calculation of N_e for the mainstem populations the estimate varied from N_e = 494 to N_e = 618 for the mainstem lower and N_e = 338 to N_e = 431 for the mainstem upper, being less than half of the size of $Iesjoki_{(HW)}$ population. Estimates of N_e for the tributary populations were generally a magnitude lower than for the mainstem and headwater populations. However, substantial differences was observed also among the tributaries in the estimates of N_e ranging from N_e = 35 in $Utsjoki_{(T)}$ to N_e = 155–165 in Lake $Pulmanki_{(T)}$.

The effective population size of the neighboring Näätämö River was N_e = 3089 with substantial confidence interval ($CI_{\pm 95\%}$ = 219–7518) if migration was not considered. Highlighting the effect of falsely assuming a completely isolated population (Wang and Whitlock 2003), the estimate of N_e for Näätämö salmon was ten-fold smaller N_e = 305–308 ($CI_{\pm 95\%}$ = 158–1736), when Teno was considered as a potential source of migrants. The level of geneflow from the River Teno to Näätämö was however low m_{MNE} = 0.016–0.019.

Assessment of the potential for local adaptation to occur on tributary specific scale

Minimum spatial scales of selection for local adaptation to potentially occur were calculated for each population assuming different strengths of selection (Table 3). The potential for local adaptation to potentially occur was estimated to be feasible with weaker selection for the large mainstem and headwater populations than for tributary populations. For example the salmon population in the long river Iesjoki could potentially respond to spatial variation in selection with strength of s = 0.02 assuming it spans over the 110 km long river. The geographically and genetically relatively isolated lake Pulmanki populations could potentially respond to spatial variation in selection of the strength s = 0.08. Generally, however, for the local adaptation to potentially occur on tributary specific scale, relatively strong selection s = 0.1 (or more) needs to be invoked. The parameter β capturing the relative importance of selection and genetic drift was a less limiting factor for the occurrence of local adaptation given the same strengths of selection values (Table 3).

Table 3. Assessment of the potential for local adaptation based on the approach by Adkison (1995). The strength of selection *s*, which needs to be invoked in order for local adaptation to occur ($\beta >> 1$), was evaluated with m_{BA} and m_{MNE} estimates of migration rates. Local adaptation can exist at the tributary specific level if the spatial scale of selection (*j*) is larger than the 'characteristic length' of spatial variation in allele frequencies due to gene flow and selection.

	β (m_{MNE})	β (m_{BA})		Characteristic length (l_c)					Length of
Population	s = 0.001	s = 0.01	s = 0.001	s = 0.01	s = 0.01	s = 0.02	s = 0.05	s = 0.1	habitat, km (*j*)
Vetsijoki	1.2	3.8	3.5	11.0	382	270	171	121	45
Lake Pulmanki	0.9	2.9	0.9	2.8	93	66	42	29	35
Maskejoki	na	na	na	na	179	127	80	57	65
Kevojoki	0.8	2.7	1.2	3.7	167	118	75	53	40
Tsarsjoki	0.6	1.9	1.6	5.1	140	99	62	44	30
Utsjoki	0.7	2.2	0.6	1.9	270	191	121	85	30
Kuoppilasjoki	na	na	na	na	159	112	71	50	16
Valjoki	na	na	na	na	272	192	122	86	60
TmsL	5.3	16.7	24.5	77.3	825	584	369	261	88
TmsU	3	9.5	5.3	16.8	208	147	93	66	115
Iesjoki	4.3	13.7	8.9	28.0	151	107	67	48	110
Karasjoki	na	na	na	na	576	407	258	182	160

Discussion

Populations show temporal stability in genetic structure

Numerous lines of evidence suggest that the vast majority of Atlantic salmon populations within the Teno river system have been relatively stable over time. Exact tests for heterogeneity in allele frequencies indicated that some change in genetic composition of populations does occur over time (61% of tests significant), but it does not compare to that over space (99% significant). Factorizing the genetic variation into spatial and temporal components by hierarchical AMOVA, we found that 5.2% of genetic variation was among spatial samples while only 0.7% was partitioned among temporal samples.

While a significant spatial component in the genetic variation of anadromous salmon populations appears to be common place, the extent of temporal variation in the genetic structure is less investigated. Several studies applying molecular markers have assessed temporal population structure between rivers with a more than one generation time interval. The main generalization which can be drawn from these studies is that indigenous salmon and trout populations inhabiting relatively large rivers show temporally stable population structure (Nielsen et al. 1997, 1999b; Tessier and Bernatchez 1999; Hansen et al. 2002;), while anadromous brown trout populations in smaller rivers may not (Østergaard et al. 2003; Jensen et al. 2005). Thus, while temporal stability may have been expected for the mainstem and headwaters, the relatively stable genetic structure of the tributary populations was surprising. Despite a statistically significant temporal variation component (1.1%; 0.8% excluding $\text{Utsjoki}_{(T)}$) in the hierarchical analysis of molecular variation (AMOVA), the spatial variation component was more than an order of magnitude larger among tributary populations (8.5%; 9.2% excluding $\text{Utsjoki}_{(T)}$). Given our results, the assumption of temporal stability of anadromous salmonid populations is reinforced and can also occur even within a single river system.

The close genetic relationships of temporal samples from the tributary populations as well as MS + HW sampling sites were also illustrated by the neighbor-joining tree based on Nei's genetic distance (D_A) (Fig. 2). The high divergence of tributary populations was reflected in longer branch lengths compared to those of mainstem and headwater groups of samples. Inclusion of several temporal samples spanning over two decades revealed similar compilations of mainstem and headwater populations as inferred from single point in time samples (Vähä et al. 2007) using Bayesian clustering methods. More specifically, inclusion of temporal replicate samples from the Teno mainstem and $\text{Inarijoki}_{(HW)}$ supported the division in two populations [Teno mainstem lower (TmsL) and Teno mainstem upper (TmsU)].

Dispersal dynamics: from straying to geneflow

Generally, the results from BAPS and BAYESASS provided a similar overview of the asymmetric dispersal patterns within the River Teno: (i) tributaries were surprisingly isolated from the mainstem and headwater populations; (ii) while among MS+HW migration rates appeared higher; and (iii) immigration to specific local populations was intermittent. However, longer term migration, as inferred by MNE2, implied substantially less variation in immigration rates among populations.

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All three estimates of migration rate from the MS + HW to tributaries were of similar magnitude: $m_{BAPS} = 0.017$, $m_{BA} = 0.035$ $m_{MNE} = 0.018$. Thus, there were neither substantial excess of transient individuals in tributaries e.g. exploring males or strong selection against migrants, but salmon encountered in the tributaries contribute effectively to the next generation. However, in light of 5.8% straying rate reported for wild Atlantic salmon from the River Imsa in Norway (Jonsson et al. 2003) the straying rates within the River Teno system were low. Among all the fish caught in tributaries, 4.3% were strays and no strays were detected between tributaries, which are connected to each other through mainstem. The only tributaries that appeared to exchange migrants were those comprising the Utsjoki tributary system: Utsjoki$_{(T)}$, Kevojoki$_{(T)}$ and Tsarsjoki$_{(T)}$. Considering this as one group, the straying rate was 1.7% from the mainstem and headwaters to tributaries. Young and Woody (2007) suggested that tributaries may be easier for salmon to recognize due to unique water chemistry in contrast to the mainstem or entire rivers having similar physical and chemical characteristics and this may then result in higher degree of homing precision by tributary spawning fish. Indeed, some of the tributaries, such as Tsarsjoki and L. Pulmanki do seem to be very isolated in terms of migration, whereas the mainstem and headwaters had higher straying rates. However, the higher migration rates among the MS + HW compared to tributaries were to some extent due to sampling of transient individuals. For example in the lower mainstem, straying and recent immigration rates ($m_{BA} = 0.30$–0.32, Fig. 3) were substantially higher than estimated long term immigration rate ($m_{MNE} = 0.01$–0.014, Table 3). When interpreting the results from method of BAYESASS it is worthwhile keeping in mind that estimating migration among populations with low divergence, such as MS + HW here, convergence problems may be common, but difficult to discern and the estimated migration rates may be inaccurate (Faubet et al. 2007). On the other hand, the estimates for contemporary migration rates from BAYESASS were generally supported by the results from BAPS. Finally, the mean value of gene flow among populations within Teno system was similar ($m_{MNE} = 0.015$–0.019) as that from Teno to Näätämö river system ($m_{MNE} = 0.016$–0.019), which are slightly less than derived from the typical homing accuracy reported for Atlantic salmon (94–98%, Garcia de Leaniz et al. 2007b).

Effective population sizes

The largest effective population size was estimated for the headwater Iesjoki$_{(HW)}$ ($N_e = 1209$), being twice that of the mainstem populations (mean $N_e = 477$) and an order of a magnitude larger than N_e of the tributary populations (mean $N_e = 97$). Thus, as expected, the higher genetic diversity and lower divergence of the MS + HW populations compared to tributaries (Vähä et al. 2007) is due to their high effective population sizes. The N_e of the mainstem populations may in fact be even larger, as inadvertent inclusion of transient individuals in samples would tend to increase the variance in allele frequencies and hence decrease N_e. In wild populations, effects of limited population size on the number of alleles that can be maintained can be much more dramatic than are reductions in heterozygosity or increases in inbreeding depression due to deleterious alleles having being purged (Waples 1990). According to predictions by Waples (1990), a typical tributary population in the River Teno with $N_e \sim 100$, would lose half of the neutral alleles at initial frequency of 0.02 in less than seven generations if drift was not offset by small degree of geneflow from other populations. Coinciding with this theory; Tsarsjoki$_{(T)}$, which was isolated in terms of geneflow, had $N_e \sim 100$, but possessed only ~86% of the allelic richness of Kevojoki$_{(T)}$ with smaller $N_e \sim 70$, but higher geneflow. This clearly illustrates the interplay of geneflow and genetic drift shaping the levels of genetic divergence and diversity of salmon populations and that even in a system with potential for high geneflow, some local populations may be surprisingly isolated. Excluding the two most extreme cases Iesjoki$_{(HW)}$ and Utsjoki$_{(T)}$, our estimates of N_e were of similar magnitude with those reported ($N_e \sim 80$–350) for the Atlantic salmon populations inhabiting rivers (30–100 km) draining to lake Saint-Jean in Canada (Fraser et al. 2007a).

The relationship between N_e and census size is relevant as N_e/N ratio provides information on how well demographic data predicts N_e. There are no census population size estimates available for the whole of the River Teno system. However, in two small tributaries (4 and 6 km) the numbers of adult salmon during the spawning season have been counted by snorkeling observations (Orell and Erkinaro 2007). The harmonic mean of the census sizes over 3 years were 10.8 and 13.6 salmon per kilometer. Extrapolating from these snorkeling counts to approximate the census population sizes of the tributaries investigated in this study and accounting for the generation time, values of the ratio N_e/N lie between 0.01 and 0.07 for tributaries of Teno River. These values are lower than the average $N_e/N = 0.1$ for animal populations (Frankham 1995). Recently, several studies have found evidence for increase in N_e/N ratios in declining populations termed 'genetic compensation' (Ardren and Kapuscinski 2003; Fraser et al. 2007b). In the light of this, low N_e/N values observed in tributary populations could indicate that the status of populations is healthy. However, it is

worthwhile keeping in mind the multitude of factors which may affect values of N_e and N. While fluctuations in population size can substantially reduce N_e, it is especially affected by the cyclic lows (Vucetich et al. 1997; Waples 2002). In the River Teno, numbers of returning salmon are known to oscillate with the ocean climate conditions showing threefold difference between the lowest and highest figures (Niemelä et al. 2004). Given the differences in fecundity, where females can produce 2000–23 000 eggs depending on size at maturity (Erkinaro et al. 1997), variance in reproductive success among individuals may also have a major impact on N_e (e.g. Araki et al. 2007). Yet another important factor affecting N_e is sex-ratio, which in the River Teno salmon appears to be male-biased (*c.* 60:40) even excluding mature male parr (Niemelä et al. 2006a). Due to the low and variable values of the N_e/N ratio, using census data to provide estimates of N_e or vice versa in this system may fail, especially if spatial population structure is not accounted for.

Temporal instability in a local population

A significant exception to the general pattern of temporal genetic structure of populations was observed in the Utsjoki$_{(T)}$ population which exhibited the lowest effective population size, $N_e = 35$ ($CI_{\pm 95\%} = 31–41$). Tests for differences among temporal groups of populations ('before 1984' vs. 'after 1995') for genetic diversity or relatedness indices revealed no statistically significant pattern (e.g. $A_{R(10)} = 3.9$ vs. 4.0, $P_{1\text{-way}} = 0.12$, Rel-c = 0.014 vs. 0.002, $P_{1\text{-way}} = 0.45$) in contrast to expectations in the case of severe bottlenecks (Spencer et al. 2000). The ultimate cause of this temporal instability and small effective population size remained unclear, but two not necessarily mutually exclusive explanations deserve attention: (i) there has been reduction of population size, i.e. bottleneck at or before the time of sampling followed by quick population recovery possibly accompanied with natural supplementation from nearby rivers; (ii) Utsjoki is an incessantly small population subject to strong genetic drift supplemented periodically from nearby rivers, adhering to mainland-island metapopulation dynamics. Our early sampling period (1982–1984) coincides with period of lowest overall catch of salmon in the River Teno since the commencement of monitoring programme (Niemelä et al. 2004). In addition to this, there was exceptionally heavy fishing pressure using nets and weirs along Utsjoki waterway during late 1970's and early 1980's (Niemelä E. personal observations). Spawning grounds in upper Utsjoki$_{(T)}$ have historically been known to support a spawning stock with a relatively large proportion of 2–4SW salmon, while the vast majority of fish in Kevojoki$_{(T)}$ and Tsarsjoki$_{(T)}$ are smaller 1SW salmon. As previous spawners and multi-sea-winter fish, which are highly prized in angling, enter the River Teno earlier than 1SW salmon (Niemelä et al. 2006b) they are subject to a longer fishing period in addition to having to escape more nets and weirs before reaching the spawning grounds. These factors combined likely resulted in a very low number of spawners, which was also reflected in low juvenile densities during this period (Niemelä E. unpublished data). Recovery may have involved migration from nearby populations, as suggested by intermittent migration rates (Fig. 3), which resulted in changes in allele frequencies, but not reduction in total genetic diversity. Such prolonged selective harvesting accompanied by geneflow from nearby populations with different life-history traits (such as Kevojoki$_{(T)}$ and Tsarsjoki$_{(T)}$) therefore has the potential to rapidly increase the proportion of 1SW salmon in the local Utsjoki population.

Overall, the observed changes in genetic structure highlight a fact which is relevant for the conservation and management of highly sub-structured population systems in general: an overall high census size (in the case of Teno salmon, an estimated 30 000–120 000 adults entering the system annually of which 30–60% are not harvested and hence potential spawners; see Karppinen et al. 2004 and references therein) is not necessarily a buffer against population bottlenecks in specific local populations.

Potential for local adaptation

Estimates considering the potential for local adaptation to evolve within the Teno system indicated that it is theoretically possible in mainstem and headwater populations when selection co-efficient exceeds $s = 0.05$ and in tributary populations when $s > 0.1$. However, there were also specific cases where the requirements for the evolution of local adaptation were fulfilled even with much lower selection strengths (e.g. $s = 0.02$ in the headwater river Iesjoki).

Estimation of selection co-efficients in the wild, especially for non morphological characters is inherently difficult (Kingsolver et al. 2001), however selection coefficients of $s \geq 0.1$ are not uncommon (Endler 1986; but see Kingsolver et al. 2001). Similarly, selection co-efficients of this scale have been observed in some salmon populations for traits such as time of emergence from the gravel (Einum and Fleming 2000). To our knowledge, there are no selection co-efficients available for any traits in Teno salmon. However, it is reasonable to expect that strong selection for some traits may exist. One such trait is sea-age at maturity, a trait which shows considerable variation within the Teno system (Niemelä 2004) and has been shown to have a heritable basis in other populations

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(Garcia de Leaniz et al. 2007a). In the River Teno, large MSW females are virtually never found in most small tributaries (Niemelä 2004), and therefore this life history strategy would be expected to be strongly selected against in a number of the tributaries, whilst possibly favored in the mainstem and headwaters. A factor potentially limiting the evolution of fine-scale local adaptation at the tributary specific level in the Teno system is gene flow, which acts to constrain adaptation (Hendry et al. 2002). The most likely result of increased levels of migration, as demonstrated in the Utsjoki system, would be for local adaptations to become more likely to evolve at the tributary system level rather than in single tributaries. It is also important to note that the sampling design of the study can have affected the estimates for local adaptation potential. For example, inclusion of additional tributary populations may change the migration rate estimates in some cases, and estimates of the standard deviation of dispersal distances in the mainstem may not always be accurate. Both of these factors can affect estimations of the scale at which local adaptations may potentially evolve. Regardless, we conclude that there is potential for a number of locally adapted populations or population systems to evolve within the river Teno, as has been suggested for other Atlantic salmon systems (e.g. Landry and Bernatchez 2001) and this should be taken into consideration when developing management strategies.

Demonstrating that there is the potential for local adaptations to evolve does not necessarily imply that the populations currently actually are locally adapted. In order to demonstrate local adaptation a number of criteria should be met (Endler 1986; Taylor 1991; Garcia de Leaniz et al. 2007a): (i) the feature or trait being investigated must have a genetic basis; (ii) differential expression of the trait must be associated with differential survival or reproductive capability among individuals in a common environment; and (iii) a mechanism for selection responsible for maintenance of the trait in a population should be demonstrated. While research in other Atlantic salmon populations suggests that traits such as sea-age at maturity theoretically fulfill these criteria for e.g. adaptation to tributaries versus mainstem in the river Teno, the inference of local adaptation remains speculative without further study in this specific system.

Management implications

Exploitation of salmon originating from the River Teno has been strongly regulated by substantial reductions in marine salmon fisheries during the past couple of decades (Niemelä et al. 2005 and references therein). In addition, the river fisheries have been managed through bilateral agreements between Finland and Norway since late 19th century. These regulations have enabled safeguarding the River Teno salmon, and the total size of the population complex is still today at an exceptional level (see above). However, in addition to the decreasing long-term trend in the number of 3–4SW females, during the past decades the distribution of Atlantic salmon within the River Teno has decreased from *c.* 1200 km to cover only *c.* 1000 km, with some of the higher order tributaries now devoid of salmon (E. Niemelä, unpublished data). Our results indicate that not only are tributaries isolated and harbour potentially locally adapted populations but they are also the most vulnerable to population crashes due to natural or human-induced causes even when the total number of salmon entering and being harvested in the Teno system is very large. In order to regain the historical distribution of salmon and sustain the diversity of life-histories displayed among the populations, establishment of regular fine-scaled monitoring, incorporating both demographic and genetic methodologies, particularly of the tributary populations is recommended. The current bi-laterally (Finland and Norway) run *ex situ* preservation program is based on allozyme information from the 1980s and involves cryo-preservation of milt collected from salmon originating from several of the tributaries within the system (Makkonen et al. 2000). Given the genetic uniqueness of tributary populations illuminated in this study, a more extensive and systematic collection of milt, where each local population is considered as a separate unit for preservation is recommended.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Supplementary Table.

Table S2. Pairwise genetic differentiation measured with F_{ST} (⊖ estimator of Weir and Cockerham 1984).

Table S3. (A) Recent migration rates of tributary populations from samples collected during 1979–1985, estimated using BAYESASS (Wilson and Rannala 2003). Temporal samples for the mainstem and headwater populations are pooled (see Material and methods). (B) Recent migration rates (%) of tributary populations from samples collected during 1995–2001, estimated using BAYESASS (Wilson and Rannala 2003). Temporal samples for the mainstem and headwater populations are pooled (see Material and methods).

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