

Genetic effects of supportive stockings on native pikeperch populations in boreal lakes – three cases, three different outcomes

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The genetic consequences and gene flow of pikeperch (*Sander lucioperca*) stocking were assessed in three boreal lakes based on admixture model analysis and comparison of the pre- and post-release patterns of genetic variability at 9 DNA microsatellite loci in the recipient populations. In two out of the three cases, the releases of fish from foreign populations caused significant changes in the genetic structure of the recipient population. The largest changes were observed in Lake Oulujärvi, where the post-release sample was almost identical to the released Lake Vanajanselkä population, and about 90% of the catch was composed of the released population. The genetic composition of Lake Lohjanjärvi pikeperch also shifted markedly towards that of the released Lake Vanajanselkä population, and about half of the later catch was of released Vanajanselkä origin. In Lake Vanajanselkä, in contrast, releases of pikeperch from lakes Painio and Averia had only a small impact on the genetic structure of the pikeperch population. These results indicate that the current stocking practices create an effective artificial gene flow that may strongly shape and reduce the genetic differentiation among the remaining native pikeperch populations. A common feature of all three cases was the lack of prior appraisal of the potential genetic and ecological risks in relation to the expected benefits of the release programmes.

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The native distribution of pikeperch (*Sander lucioperca*) in northern Europe is assumed to be related to the *Lake Ancylus* (freshwater) stage of the present Baltic Sea (LÖNNBERG 1899; LEHTONEN et al. 1996), which ca 9200–9000 BP (BJÖRCK 1995) provided the species a distribution path to areas covered by the former lake, up to 100–150 m above the present water level of the Baltic Sea. Since the initial colonization, adaptive selection, gene flow and drift have shaped the patterns of genetic diversity within the species, resulting in a relatively high level of genetic variability (BJÖRKLUND et al. 2007; SÄISÄ et al. 2010) comparable to that reported in Scandinavian whitefish (*Coregonus lavaretus*, SÄISÄ et al. 2008), grayling (*Thymallus thymallus*, KOSKINEN et al. 2000), perch (*Perca fluviatilis*, NESBØ et al. 1999) and Atlantic salmon populations (*Salmo salar*, SÄISÄ et al. 2005).

Since the late 1800s, the distribution and genetic diversity of pikeperch has also been shaped by human-influenced gene flow through introductions and hatchery releases. In Denmark, the first introduction took place in 1898, and since then pikeperch have been established in over 70 water bodies (DAHL 1982). In Sweden, Norway and Finland the pikeperch is a native species, but has also been the most commonly introduced non-salmonid fish (TAMMI et al. 2003). In Finland, the pikeperch is native in ca 650 lakes, but due to introductions, the present distribution

includes ca 2300 lakes (LAPPALAINEN and TAMMI 1999). The expansion of pikeperch has been exclusively regarded as a positive phenomenon, unlike in Turkey, the UK and Denmark, for instance, where the expansion has in some cases involved undesirable ecological effects (CRIVELLI 1995; COWX et al. 1997; JEPSEN et al. 2000).

Until the mid-1900s, introductions in Finland were mostly carried out using repeated transfers of adult fish or fertilized eggs (HALME 1961, 1962), a method that seems to have been quite effective in transferring genetic material (SÄISÄ et al. 2010). Some of the most vital naturally reproducing pikeperch populations in Finland stem from these early introductions, including two major source stocks of current hatchery production. Apart from the stocking pressure (no. of stocking events and individuals released; KOLAR and LODGE 2001) and the traits of the species, the success of the early introductions may relate to the availability of favourable habitats at altitudes above the *Lake Ancylus* water level, and to the fact that the source stocks were usually located close to the recipient lakes. In the Rhône delta of France, the invasive success of pikeperch has similarly been explained by the traits of the species and the stocking pressure, maintaining a high level of genetic variability in the introduced populations (POULET et al. 2008).

A new era of pikeperch stocking was catalyzed by the collapse of several important pikeperch stocks during the

1960s and early 1970s (COLBY and LEHTONEN 1994). The management strategy devised in this situation was based on the stocking of young-of-the-year (YOY) pikeperch. More efficient rearing methods were developed (RUUHJÄRVI and HYVÄRINEN 1996), increasing the production of YOY pikeperch to ca 10 million year⁻¹ (ANON. 2004). The production was mainly directed to new introductions and re-stocking projects aiming at re-establishing lost pikeperch populations. In recent years, the fish have mainly been used in various enhancement projects aimed at the mitigation of reproduction failures or the effects of over-fishing, or simply at improving fishing possibilities.

The popularity of enhancement programmes has raised questions about their sustainability. Despite the high costs of the programmes, their economic benefits have often not been properly evaluated. Stocking also has been a tempting solution in many cases, as it reduces the need for strict fishing regulation. The main concern, however, is the potential adverse effect of releases of foreign genetic material on the genetic diversity and adaptability of the species as a whole. Due to insufficient control and planning, practically all stocking programmes in Finland have relied on three to four source stocks, all of them with a southern origin. The possibly small effective population size of the broodstocks used has also raised concerns, as it causes loss of diversity (RYMAN and LAIKRE 1991). During the last two decades, practically all remaining indigenous freshwater pikeperch stocks are likely to have been subjected to the flow of foreign southern genes through hatcheries. The genetic effects of releases such as competition between native and introduced species or stocks, the replacement of native stocks, mixing of stocks and extinction of native stocks have been widely discussed (COWX et al. 1997).

In this study, we assessed the genetic consequences of pikeperch stockings for indigenous native populations in three boreal lakes in Finland: Lake Lohjanjärvi, Lake Vanajanselkä and Lake Oulujärvi. Genetic information was available from the three recipient pikeperch populations before releases, from the three released hatchery populations and also the admixed populations in each lake after the releases, allowing us to assess the proportion of new genetic material in the native populations after the releases. Finally, to address the overall sustainability of current stocking practices, we contrasted the observed genetic effects of the three stocking programmes with their expected socioeconomic benefits.

MATERIAL AND METHODS

Study lakes

Lake Lohjanjärvi

The indigenous pikeperch is recreationally and economically one of the most important fish species in Lake

Lohjanjärvi (area 89 km², mean depth 13 m), southern Finland (Fig. 1). In mail surveys, reported pikeperch catches from 1981–2002 varied from 4–21 tons year⁻¹ (SALMINEN and RUUHJÄRVI 2004). About 90% of the catches have been taken by gillnets, while trolling accounts for 10% of the total yield. The catches are mainly used for household needs, but some fishermen also sell fish.

LEHTONEN and MIINA (1988) reported high fishing mortality and a low age at recruitment (4–6 years) for Lake Lohjanjärvi pikeperch. Growth over-fishing was regarded as evident and recruitment over-fishing possible. A larger gill-net mesh size (50–55 mm, bar length) and a larger minimum landing size (MLS; 40–42 cm) were suggested and in 1992 also implemented to increase the age at recruitment. Releases of YOY pikeperch were also expanded to increase and stabilize catches, and in the 1990s they reached the level of 100 000 individuals year⁻¹ (ca 11 ind. ha⁻¹, Fig. 2).

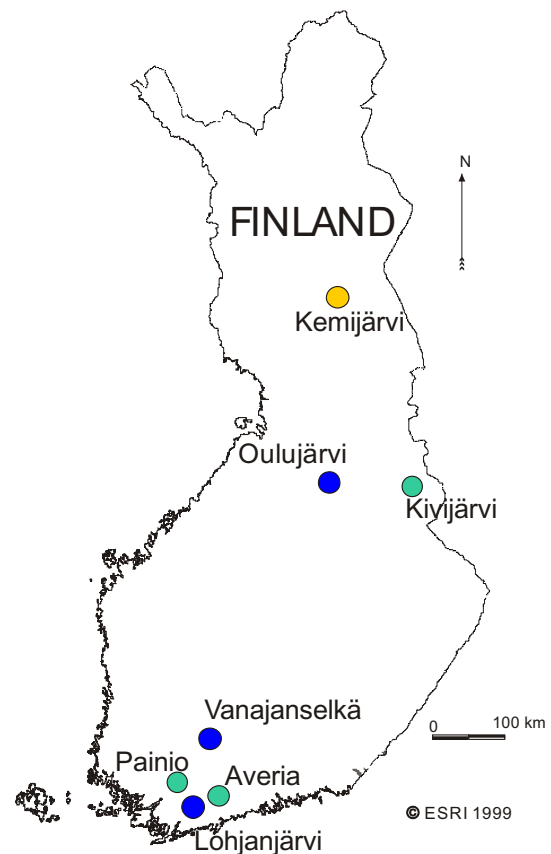


Fig. 1. The location of the three study lakes (blue dots; Lakes Lohjanjärvi, Vanajanselkä and Oulujärvi) and the three pikeperch populations additionally used in the releases (green dots; Lakes Averia, Painio and Kivijärvi). The pikeperch population of Lake Kemijärvi (yellow dot) was used as an outgroup in the genetic distance analyses.

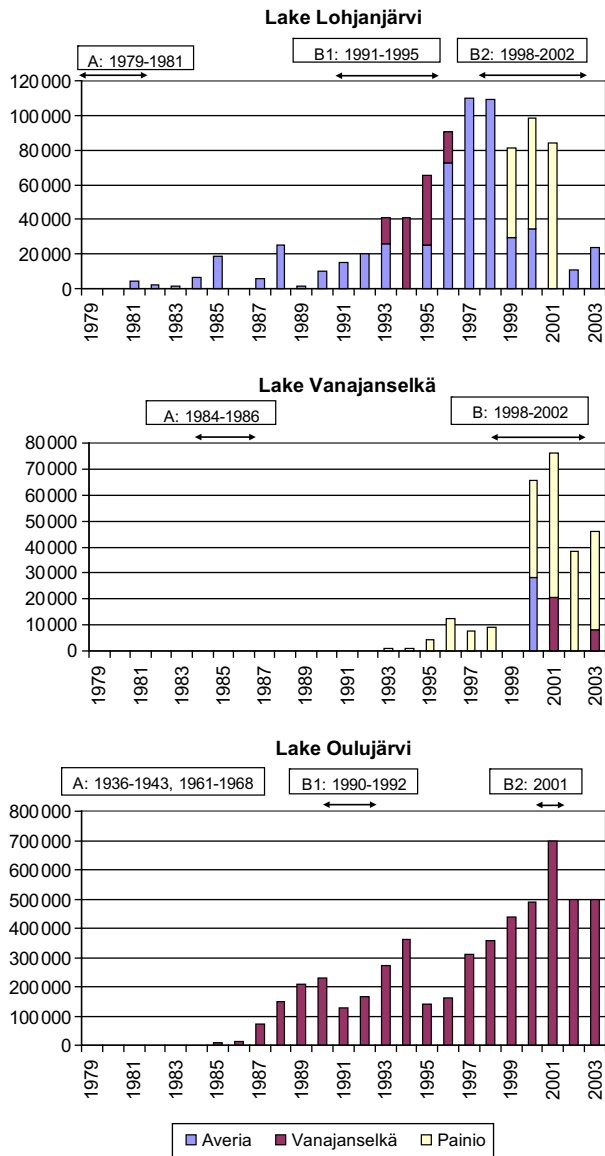


Fig. 2. Releases of YOY pikeperch according to the year-class (1979–2003) and source stock in Lake Lohjanjärvi, Lake Vanajanselkä and Lake Oulujärvi. Arrows indicate the year-classes of pre- (A) and post-stocking (B) samples (Table 1).

Lake Vanajanselkä

Lake Vanajanselkä is the largest lake (103 km², mean depth 8 m) of the Vanajavesi watercourse in the River Kokemäenjoki basin. The relatively strong and stable indigenous pikeperch population (TOIVONEN et al. 1981) supports important pikeperch fisheries and has also served as a source for early transfers of adult fish and eggs (HALME 1961, 1962; RUUHIJÄRVI and SALMINEN 1992), and since the 1980s also for large-scale YOY production (RUUHIJÄRVI and HYVÄRINEN 1996). Pikeperch catches of recreational fishermen have recently been ca 20 tons year⁻¹. Seven professional fishermen (in 2006, Pekka Korhonen pers.

comm.) also fish pikeperch in the lake, their catch being 5–10 tons year⁻¹.

Gill-netting with mainly 45 mm nets accounts for ca 90% of the pikeperch catch, the rest being caught mainly by trollers (KIVINEN 2009). Despite the good growth rate of Lake Vanajanselkä pikeperch, the recommended rises in the minimum landing size (present 37 cm) and gill-net mesh size have not been implemented. Instead, enhancement releases have been carried out (Fig. 2), despite the good recruitment of the native population.

Lake Oulujärvi

Until the late 1950s, Lake Oulujärvi (area 928 km², mean depth 7.6 m) pikeperch sustained a flourishing fishery, with catches amounting to 100–150 tons year⁻¹ (SUTELA and HYVÄRINEN 2002). Thereafter, catches began to decline and the bottom, less than 100 kg year⁻¹, was reached in the early 1980s. In the 1990s, catches began to recover and have recently been around 100 tons year⁻¹. Pikeperch are mainly taken by recreational gill-netters and anglers, but also provide an important target for the 32 professional fishermen operating in the lake (in 2006, Pekka Korhonen pers. comm.).

Potential causes for the collapse of the pikeperch stock and catches in Lake Oulujärvi, as in numerous other boreal lakes, were the declining temperatures in 1940–1970 combined with increasing exploitation caused by the shift from cotton to more efficient nylon monofilament gill-nets (COLBY and LEHTONEN 1994). Enhancement stocking was the main management action recommended in this situation (SALOJÄRVI et al. 1981), and based on this recommendation releases were started in 1985, reaching the level of 500 000 individuals year⁻¹ in the 2000s (Fig. 2, ca 5 ind. ha⁻¹).

The production and releases of hatchery pikeperch

The production of YOY pikeperch relies on the annual capture of wild spawners from the spawning areas using trap-nets (SALMINEN and RUUHIJÄRVI 1991; RUUHIJÄRVI and HYVÄRINEN 1996). After hatching the larvae are stocked at 20 000–40 000 ind. ha⁻¹ into 1–2 ha dams producing natural food. The average harvest in late August–September, i.e. after 3–4 months of rearing, is about 10 000 YOY pikeperch ha⁻¹, ranging in total length from 60–80 mm.

As the background of YOY pikeperch has not been an issue among the managers, the production of larvae has concentrated on a limited number of dense source populations, all with a southern origin. Another factor potentially influencing the genetic consequences of releases is family size, i.e. the number of juveniles produced per female. Given the high fecundity in artificial rearing (SALMINEN et al. 1992) and high survival during rearing, one large female may produce up to 200 000 juveniles, which may

then constitute a large part of or even the whole year-class stocked in one or two larger or several smaller lakes. To prevent this, hatcheries have been advised to mix the offspring of females that spawn at approximately the same time, but it is not known to what extent this actually happens.

Our three study lakes offer typical examples of the complex transfers of pikeperch from one water-body to another:

- 1) In Lake Lohjanjärvi, three foreign populations were used in the releases (Fig. 3, Table 1). Two of them (Lake Averia and Lake Painio) are genetically close to Lake Lohjanjärvi pikeperch (SÄISÄ et al. 2010), as they have their roots in early (1930s) transfers from the same Lake Lohjanjärvi, while the third source population (Lake Vanajanselkä) is genetically more distant (SÄISÄ et al. 2010).
- 2) In Lake Vanajanselkä, both its own indigenous population, and the populations of Lake Averia and Lake Painio have been used in the releases (Fig. 3, Table 1).
- 3) In Lake Oulujärvi, pikeperch from Lake Vanajanselkä have been stocked, mostly via a special brood-fish lake (Lake Kivijärvi) housing a pikeperch population established in the late 1980s by transferring

493 (0.5–3.0 kg) adult fish from Lake Vanajanselkä (Fig. 3, Table 1) (SUTELA et al. 1995).

Pikeperch samples

The analysis of genetic impacts was based on admixture modelling and the comparison of genetic variability within the three recipient populations in Lakes Lohjanjärvi, Vanajanselkä and Oulujärvi, before and after stocking. From all three lakes, one pre-stocking sample and one or two (in Lake Oulujärvi) post-release admixture samples were analyzed (Table 1). The three pikeperch populations additionally used in the releases (from lakes Averia, Painio and Kivijärvi) were also sampled for the DNA analyses. The pikeperch population of Lake Kemijärvi was used as an outgroup in the genetic distance analyses (SÄISÄ et al. 2010).

In the case of Lohjanjärvi it was possible to organize an additional test, independent of the genetic data, as the juveniles (from Lake Averia and Lake Vanajanselkä) released there in 1991–1995 were marked using hot-branding (SAURA 1996; SALMINEN and RUUHJÄRVI 2004), allowing the identification of their stock of origin (Table 1, Fig. 2). Their stock-specific proportions were recorded among adult pikeperch sampled in 1994–2000.

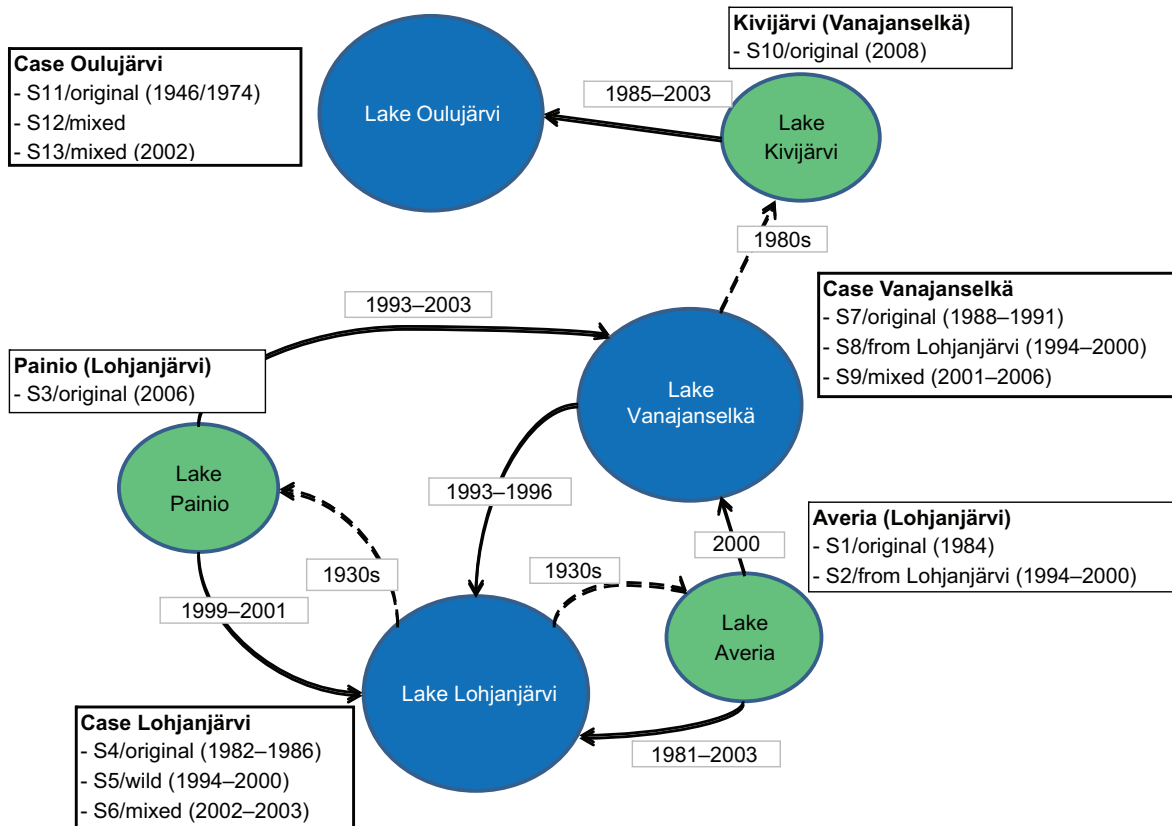


Fig. 3. Genetic background and population transfer history of the sampled Finnish pikeperch populations. Dashed lines indicate transfers of adult fish, solid lines transfers of YOY. Sample numbers (S) refer to Table 1.

Table 1. Analysed pikeperch samples. Sample number, genetic background of the population, sampling site (Fig. 1), sampling period (*A* = pre-stocking, *B* = post-stocking), sample size (*n*), catch year, year class and status of studied pikeperch samples. *Individuals for the sample were recognized from hot branding marks.

Sample	Genetic background	Sampling lake	Sampling period	n	Catch year	Year class	Status
S1	Lohjanjärvi (broodstock)	Averia	–	63	1984	1979–1982	original/source
S2	Lohjanjärvi	Lohjanjärvi	B1	59	1994–2000	1991–1993	Lake Averia origin*
S3	Lohjanjärvi (broodstock)	Painio	–	74	2006	1985–2005	original/source
S4	Lohjanjärvi	Lohjanjärvi	A	60	1982–1986	1979–1981	Original
S5	Lohjanjärvi	Lohjanjärvi	B1	60	1994–2000	1991–1995	wild*
S6	Lohjanjärvi and Vanajanselkä	Lohjanjärvi	B2	200	2002–2003	1998–2002	current, mixed
S7	Vanajanselkä	Vanajanselkä	A	60	1988–1991	1984–1986	original
S8	Vanajanselkä	Lohjanjärvi	B1	60	1994–2000	1993–1995	Vanajanselkä origin*
S9	Vanajanselkä and Lohjanjärvi	Vanajanselkä	B	208	2001–2006	1998–2002	current, mixed
S10	Vanajanselkä (broodstock)	Kivijärvi	–	31	2008	1992–1998	original/source
S11	Oulujärvi	Oulujärvi	A	8, 15	1946, 1974	1936–1943, 1961–1968	original
S12	Oulujärvi and Vanajanselkä	Oulujärvi	B1	100	1990s	1990–1992	mixed
S13	Oulujärvi and Vanajanselkä	Oulujärvi	B2	100	2002	2001	current, mixed

DNA analysis and calculations

DNA extraction and microsatellite laboratory analysis were conducted according to the description of SÄISÄ et al. (2010). Variation in the following nine microsatellite loci was determined: *PflaL3*, *PflaL8* (LECLERC et al. 2000), *Svi4*, *Svi6*, *Svi18*, *Svi33* (BORER et al. 1999), *SviL7*, *SviL8* and *SviL11* (WIRTH et al. 1999).

The number of alleles in samples was compared using a rarefaction-based allelic richness measure (EL MOUSADIK and PETIT 1996; PETIT et al. 1998), which was calculated with FSTAT software ver. 2.9.3 (GOUDET 2001). The program calculates allelic richness for the smallest number of individuals typed for any locus. Each locus was calculated separately with the same number over all populations, and the mean was calculated over loci. Population differentiation was analyzed with the GENEPOP (ver. 4.0) software package (RAYMOND and ROUSSET 1995; ROUSSET 2008) with Markov chain parameters, 300 batches and 3000 iterations. The Bonferroni correction (RICE 1989) was applied to correct for the number of tests in the H-W equilibrium. The potential occurrence of null alleles was also checked by GENEPOP. Indication of a null allele in locus *Svi33* could be seen, but it was still included in the analysis, as indication of null alleles may result from Hardy-Weinberg deviations as well.

The expected heterozygosity level in each sample was calculated using Popgene ver. 1.32 (YEH and BOYLE 1997). Differences in the mean heterozygosities and allele richness's

between populations were assessed by the *t*-test for paired observations (NEI 1987). Analysis of the differences between samples was based on allele frequency differences, using pairwise F_{st} values (WEIR and COCKERHAM 1984), which were estimated with FSTAT ver. 2.9.3 (GOUDET 2001). Standard deviations and confidence intervals were estimated through bootstrapping. Genetic distances between samples were calculated using Nei's D_A distances (NEI et al. 1983). A phylogenetic tree was constructed using a neighbour joining (NJ) algorithm (SAITOU and NEI 1987) with DISPAN software (OTA 1993). Bootstrapping with 1000 replicates was used to test the statistical strength of the branches.

To analyse the population mixtures in the recipient lakes, Bayesian clustering algorithms were used in the program STRUCTURE (ver. 2.2.3) (PRITCHARD et al. 2000; FALUSH et al. 2003; PRITCHARD and WEN 2004). The program assigns individual fish to one or more groups, with their relative frequency of predicted membership totalling 1.00. This allowed analyses of admixed populations with prior information from the source populations. In all cases, the options of using population information and applying the admixture model for the unknown catch sample were used. Moreover, *alpha*, describing the amount of population mixing, was allowed to vary in all cases and was different for each population. The total length of the runs was 150 000 iterations, with a burn-in of 100 000 iterations and the last 50 000 iterations being used for the estimates.

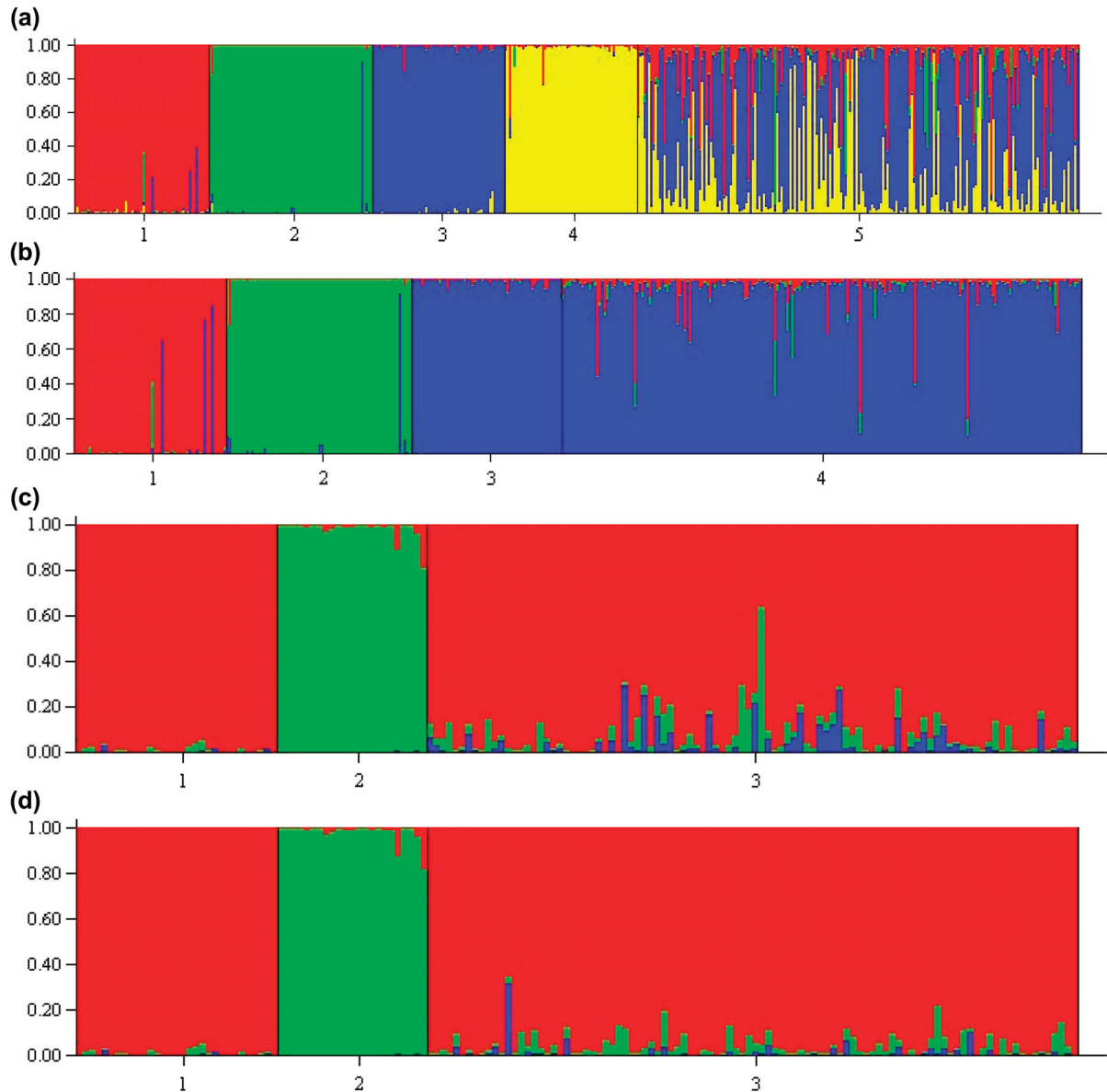


Fig. 4a–d. Estimated population structure of pikeperch from Bayesian STRUCTURE analysis for four catch mixtures. Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent its estimated population group membership fractions. Black lines separate individuals from different numbered samples. Sample names and numbers are given separately for each case. **(a)** Lake Lohjanjärvi 2000, Population 1 = Aperia, red (S1), 2 = Painio, green (S3), 3 = Vanajanselkä, blue (S7), and 4 = original Lohjanjärvi, yellow (S4), 5 = catch mixture of Lake Lohjanjärvi in 2000 (S6). **(b)** Lake Vanajanselkä 2000, (Population 1 = Aperia, red (S1), 2 = Painio, green (S3) and 3 = original Vanajanselkä, blue (S7), 4 = catch mixture from Lake Vanajanselkä in 2000 (S9). **(c)** Lake Oulujärvi 1990. Population 1 = Kivijärvi, red (S10), 2 = Oulujärvi original, green (S11) and 3 = catch mixture from Lake Oulujärvi in the 1990s (S12). **(d)** Lake Oulujärvi 2000. Population 1 = Kivijärvi (S10), 2 = Oulujärvi original (S11) and 3 = catch mixture from Lake Oulujärvi in 2000 (S13). Numbers in brackets refer to Table 1, sample number.

Convergence of all runs was checked. In all cases, the number of contributing populations, K , was known, which simplified the analyses. Several runs were carried out for each admixture and the consistency of the runs was assessed. Changes in K were also tested with K values of one more or less than the known number of populations,

and results with the greatest posterior probabilities are presented.

Admixture analysis was also performed with maximum likelihood estimation by WANG (2003), included in the LEADMIX software. This is based on the principle that allele frequencies of the admixed populations should be

Table 2. The genetic diversity of the pikeperch samples for the three cases, the sampling lake, catch year, status of the population, mean sample size for nine loci, mean expected heterozygosity (H_e) and its standard error (SE), and average allelic richness (A_r) for nine DNA microsatellite loci.

Sample	Sampling lake	Catch year	Status	Mean n/locus	H_e	SE	A_r
Case Lohjanjärvi							
S1	Broodstock, Aperia,	1984	original/source	58.0	0.41	0.08	3.7
S2	Lohjanjärvi	1994–2000	Aperia, origin	56.6	0.46	0.08	3.9
S3	Broodstock, Painio	2006	original/source	69.9	0.45	0.08	3.6
S4	Lohjanjärvi	1982–1986	original	59.1	0.44	0.09	3.6
S5	Lohjanjärvi	1994–2000	wild	59.4	0.45	0.08	4.0
S6	Lohjanjärvi	2002–2003	current, mixed	195.0	0.51	0.08	4.4
Case Vanajanselkä							
S7	Vanajanselkä	1988–1991	original	58.7	0.49	0.09	4.3
S8	Lohjanjärvi	1994–2000	Vanajanselkä, origin	58.4	0.48	0.09	4.1
S9	Vanajanselkä	2001–2006	current, mixed	204.2	0.53	0.08	4.5
Case Oulujärvi							
S10	Broodstock, Kivijärvi	2008	original/source	30.7	0.52	0.09	4.6
S11	Oulujärvi	1946, 1974	original	14.6	0.54	0.07	3.8
S12	Oulujärvi	1990s	Mixed	95.3	0.46	0.10	4.0
S13	Oulujärvi	2002	current, mixed	98.4	0.47	0.09	4.2
	Mean				0.51	0.08	4.1

linear combinations of those of the contributing parental populations at the time when admixture occurs. In addition to some previous programs, it also takes into account genetic drift that has potentially occurred in parental populations and in admixture populations since the admixture, and even the potential drift of the parental populations before admixture occurred. The program additionally gives 95% confidence intervals for the admixture proportions. Results of the STRUCTURE and LEADMIX analysis were compared with the population grouping analysis based on genetic distances.

Analysis was carried out for four catch mixture populations: Lohjanjärvi 2000 (Table 1, S6), Vanajanselkä 2000 (Table 1, S9) Oulujärvi 1990s (Table 1, S12) and Oulujärvi 2000 (Table 1, S13). For the Lake Lohjanjärvi case, the potential additional contributors were the populations from Lakes Painio, Aperia and Vanajanselkä, and for Lake Vanajanselkä, the populations from Lakes Painio and Aperia, (Fig. 3). For the Lake Oulujärvi case, the only potential contributing foreign population was the Kivijärvi brood stock of Vanajanselkä origin.

RESULTS

Genetic diversity in pikeperch samples

The overall expected mean heterozygosity (H_e) of all samples was 0.51 and the mean allelic richness over all samples was 4.1 alleles loci⁻¹. The F_{ST} over all populations was as high as 0.08. The highest allele richness was observed in the Lake Kivijärvi broodstock population (S10), with 4.6 alleles loci⁻¹, and highest expected

heterozygosity ($H_e = 0.54$) in the pre-stocking sample of Lake Oulujärvi (S11; Table 2). The lowest allelic richness (3.6 alleles) was observed in the Lake Painio population (S3) and in the pre-stocking sample from Lake Lohjanjärvi (S4), and the lowest expected heterozygosity in the original Lake Aperia population (S1; 0.41). The genotype distributions of the three native populations in lakes Lohjanjärvi, Oulujärvi and Vanajanselkä did not deviate from Hardy–Weinberg equilibrium after Bonferroni correction.

The genetic diversity was in general relatively high in all cases both before and after stock transfers (Table 2), and no decrease in genetic diversity could be observed as a result of stocking. In all three cases, allelic richness was actually somewhat higher after releases than in the original pre-stocking population. In Lakes Lohjanjärvi and Vanajanselkä, the mean heterozygosity was also higher in the contemporary than in the native population.

The only statistically significant difference in the mean heterozygosity was between the Lake Painio population (S3) and the contemporary admixed population of Lake Lohjanjärvi (S6), which had a higher diversity. Allelic richness was also statistically significantly higher in the contemporary Lohjanjärvi sample (S6) than in the samples from Lake Aperia (S1), Lake Painio (S3) and even in the sample from the native Lake Lohjanjärvi population (S4).

Samples S2 and S8 from Lake Lohjanjärvi, both representing three consecutive year-classes of adult F_1 fish identified to their stock of origin (Lake Aperia and Lake Vanajanselkä, correspondingly) by marking, showed genetic diversity comparable to that in their source populations (S1 and S7), indicating that genetic diversity was

Table 3. Mean proportions (%) of individuals assigned to each of the pre-defined populations from each of the four admixed pikeperch samples by the Bayesian STRUCTURE program (Bayes estimate), and stock proportion estimates with their 95% confidence intervals (CI) from the maximum-likelihood estimation of the LEADMIX program (MLE estimate).

		Bayes estimate %	MLE estimate %	5% CI	95% CI
S1	Lohjanjärvi 2000	6.4	10.2	0.0	20.9
	Averia				
S3	Painio	5.4	0.0	0.0	12.3
S7	Vanajanselkä 1980	47.8	54.6	45.8	72.5
S4	Lohjanjärvi 1980	40.5	35.2	14.8	43.6
	Vanajanselkä 2000				
S1	Averia	6.0	10.8	10.7	10.8
S3	Painio	2.2	3.1	3.1	3.2
S7	Vanajanselkä 1980	91.8	86.2	86.1	86.2
	Oulujärvi 1990				
S10	Kivijärvi-Vanajanselkä	89.0	99.9	92.8	100.0
S11	Oulujärvi, original	2.7	0.0	0.0	8.5
S12	Oulujärvi 1990	8.3	–	–	–
	Oulujärvi 2000				
S10	Kivijärvi-Vanajanselkä	89.8	98.3	89.9	100.0
S11	Oulujärvi, original	6.5	1.7	0.0	11.8
S13	Oulujärvi 2000	3.7	–	–	–

in this case quite efficiently transferred through rearing and stocking from the source lakes to the recipient population.

Admixture analysis of three pikeperch populations

Lake Lohjanjärvi

In the Lake Lohjanjärvi case, a marked genetic contribution could be observed as result of the releases. The admixed catch sample was mainly composed of both Lake Vanajanselkä and Lake Lohjanjärvi populations (Table 3, Fig. 4a). A large proportion of individuals were admixtures. Vanajanselkä pikeperch comprised at least about half of the catch in Lake Lohjanjärvi. The maximum likelihood estimate for the contribution of Vanajanselkä was 54.6% (95% confidence interval (CI), 45.8–72.5%), and that of indigenous Lake Lohjanjärvi pikeperch was correspondingly only 35.2% (CI: 14.8–43.6%) (Table 3). The Bayesian estimate for the contribution of Vanajanselkä was slightly less, being 47.8%, and for Lohjanjärvi somewhat more, 40.5%. In all cases, the Bayesian estimates were within the 95% confidence intervals of the maximum likelihood estimates.

The estimated contribution of the Vanajanselkä population in the admixture was somewhat less than the observed contribution of marked Vanajanselkä pikeperch (62–72%)

to Lake Lohjanjärvi catch samples from year-classes 1993–1995 (SALMINEN and RUUHIJÄRVI 2004).

The most commonly released stock in Lake Lohjanjärvi has been Lake Averia pikeperch (Fig. 2). The latest releases have been carried out with Lake Painio pikeperch, but very little genetic effect of these releases could be observed, despite the relatively large numbers of released fish. The larger contribution from the Lake Painio pikeperch releases could be excluded (shown in Fig. 4a as green), but releases from Lake Averia were possibly contributing to the catch sample, as the maximum likelihood estimate was 10% with a probability interval of 0–20% for the Averia stock contribution. The more successful Lake Vanajanselkä fish were only released in 1993–1995, and also in much smaller numbers.

Lake Vanajanselkä

In the Lake Vanajanselkä case, very little genetic contribution could be seen as a result of the releases (Fig. 4b), and the original Vanajanselkä pikeperch still accounted for the majority of the catch. According to the Bayesian estimate, 91.8% of the admixture gene pool originated from the indigenous Vanajanselkä population, and with the maximum likelihood estimation the proportion was somewhat less, being 86.2% (Table 3). About 10% originated from

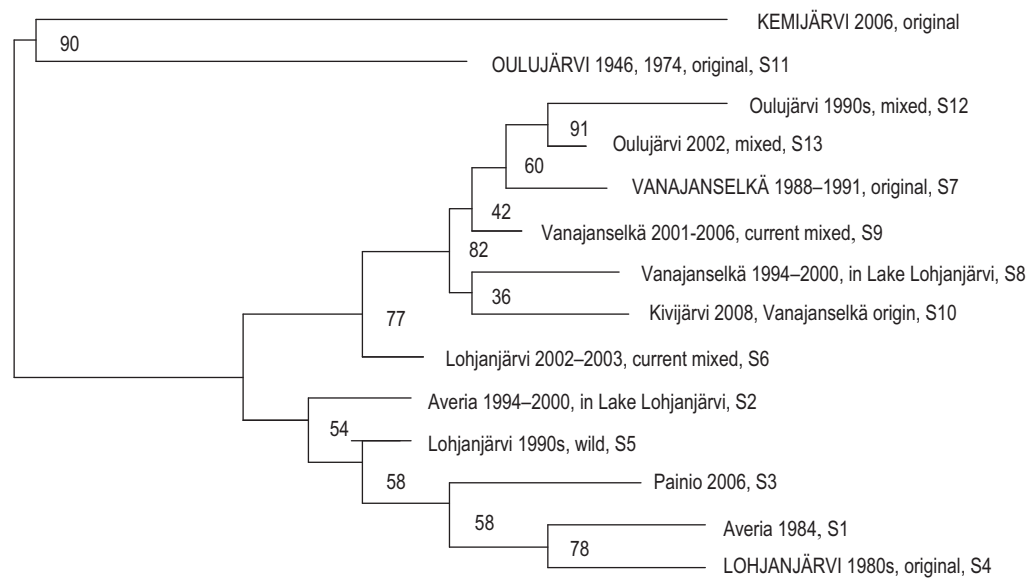


Fig. 5. Genetic distances based on nine microsatellite DNA loci. Names of indigenous populations in capital letters. Sample numbers (S) refer to Table 1.

the Averia population releases, and hardly any from the Painio population releases, although this population was the more commonly used stock in releases, and easily distinguishable from other populations. The 95% confidence interval for the MLE estimate was narrow, and the Bayesian estimate did not fall within these limits.

Lake Oulujärvi

In the case of Lake Oulujärvi pikeperch, the indigenous population has nearly disappeared. The results show that a large majority of the contemporary Lake Oulujärvi pikeperch population originated from the releases of Kivijärvi-Vanajanselkä pikeperch. In both mixed samples, from 1990 and 2000, the proportion of fish originating from the releases was about 90% when estimated with the Bayesian method (Table 3, Fig. 4c–d). When the potential effect of genetic drift was included in the maximum-likelihood method, the proportion of the original Vanajanselkä population increased very close to 100% (Table 3). For both Oulujärvi mixed samples, the posterior probabilities were higher in the Bayesian method when the number of contributing populations was set to three rather than to two, indicating that the admixture could not completely be explained by the two populations, and the results are therefore given accordingly.

Genetic differentiation among stocks before and after stocking

According to genetic distances, the populations grouped into three main groups, where Lakes Averia, Painio and the original Lohjanjärvi samples formed the first group

(Lohjanjärvi group), Lakes Vanajanselkä, Oulujärvi mixed samples, Kivijärvi and Lohjanjärvi samples the second group (Vanajanselkä group) and the two northern native populations from Lakes Kemijärvi and Oulujärvi the third group (Fig. 5). The genetic differentiation between allele frequencies of the populations before and after releases remained statistically significant within all these groups, and in fact all pair wise comparisons between populations were statistically significant.

The mean genetic distance within the Lohjanjärvi group was 0.06 and within the Vanajavesi group 0.04. The original Lake Oulujärvi sample was the most distinct of the other samples and grouped together with the sample of indigenous pikeperch from the northern Lake Kemijärvi (Fig. 1), which was used as an outgroup in the analysis. In general, the results on the genetic structure confirmed the changes observed in the recipient populations in admixture analysis, and results from both analyses were congruent for all cases.

Lake Lohjanjärvi

Five of the six samples originating from Lake Lohjanjärvi pikeperch grouped into the same branch in the dendrogram (Fig. 5). The Averia 1984 sample was most similar to the original Lohjanjärvi sample, Painio had some unique features and the catch sample from the 1990s (wild fish identified by marking) had also shifted somewhat from the original population. The most distinctive was, however, the last sample, the admixture from the years 2002 and 2003, which grouped into the Vanajanselkä group instead of the Lohjanjärvi group. The F_{ST} between the Lohjanjärvi

Table 4a. Estimates of F_{ST} values between pairs of pikeperch samples in the case of Lake Lohjanjärvi.

F_{ST}	S1. L.	S2. L.	S3. L.	S4. L.	S5. L.	S6. L.	S7. L.
	Averia	Lohjanjärvi B1	Painio	Lohjanjärvi A	Lohjanjärvi B1	Lohjanjärvi B2	Vanajanselkä A
S2. L. Lohjanjärvi B1	0.02						
S3. L. Painio	0.16	0.15					
S4. L. Lohjanjärvi A, original	0.02	0.03	0.17				
S5. L. Lohjanjärvi B1	0.01	0.01	0.16	0.01			
S6. L. Lohjanjärvi B2, catch	0.05	0.04	0.14	0.04	0.02		
S7. L. Vanajanselkä A, original	0.10	0.07	0.18	0.09	0.05	0.03	
S8. L. Vanajanselkä B1	0.10	0.08	0.19	0.10	0.06	0.02	0.02

and Vanajanselkä pikeperch decreased from the original level of 0.09 to 0.03 for the last admixture population, also showing the increase in similarity (Table 4a).

Lake Lohjanjärvi was only stocked with Lake Vanajanselkä pikeperch in 1993–1996, whereas our samples represented later year-classes of 1998–2002. The marked impact of Lake Vanajanselkä pikeperch on the genetic composition of these year-classes thus indicates that these foreign pikeperch have successfully reproduced in Lake Lohjanjärvi.

Lake Vanajanselkä

In the case of Lake Vanajanselkä, the releases of Lake Painio and Lake Averia pikeperch had no strong effects on the genetic structures of the sampled year classes (1998–2002). The original Vanajanselkä population was very similar to the Kivijärvi broodstock founded from it, with the later sample caught from Lake Lohjanjärvi (identified by marking) and also with the latest sample from Lake Vanajanselkä itself. The F_{ST} between Lake Vanajanselkä pikeperch and the released source populations decreased slightly after releases, for the Averia stock from 0.10 to 0.08 and for Painio from 0.18 to 0.16 (Table 4b). These changes confirmed the results of the admixture analysis, indicating that small genetic changes had taken place in the Vanajanselkä pikeperch population since the releases of foreign pikeperch began. This was also partly expected as, in contrast to the Lake

Lohjanjärvi case, only relatively small-scale releases of foreign pikeperch (and only from Lake Painio) had been carried out in year-classes preceding the sampling period (Fig. 2).

The stocked Lake Vanajanselkä pikeperch sampled as adult fish from Lake Lohjanjärvi (covering all three stocked and marked year-classes of 1993–1995) grouped close to their source population, confirming the temporal stability of the population, and the difference from the Lake Lohjanjärvi population.

Lake Oulujärvi

The post-stocking pikeperch population of Lake Oulujärvi grouped tightly together with the mediating stock of Lake Kivijärvi and with the original source population of Lake Vanajanselkä (Fig. 5). The genetic distance between the indigenous and the new post-release Oulujärvi populations was large (D_A 0.15). As a result of releases, the F_{ST} between Lake Oulujärvi and Lake Vanajanselkä pikeperch, as well as that between Lake Oulujärvi and Lake Kivijärvi pikeperch, decreased markedly (from 0.08 to 0.01 and from 0.06 to 0.02, respectively), indicating a clear increase in similarity (Table 4c). These results suggest that the indigenous stock had in this case practically been replaced by the introduced stock.

The pikeperch population of Lake Kivijärvi, established in the 1980s by transferring adult fish (493 individuals in the late 1980s) from Lake Vanajanselkä, was nearly as variable as, and grouped close to the original population (Table 2, Fig. 5). This indicated that successful introductions can be carried out with this old-fashioned approach, which had also been applied earlier, for instance, in the introductions of pikeperch into Lakes Averia and Painio in the 1930s (SÄISÄ et al. 2010).

In the cases of Lake Oulujärvi and Lohjanjärvi, the current hatchery and stocking procedures also appeared to be successful in transferring genetic material, i.e. foreign genes. In the former, the YOY pikeperch were produced using spawners captured from the 2nd generation pikeperch stock of Lake Kivijärvi. The resultant post-release

Table 4b. Estimates of F_{ST} values between pairs of pikeperch samples in the case Lake Vanajanselkä.

F_{ST}	S1. L. Averia	S3. L. Painio	S7. L. Vanajanselkä A
S3. L. Painio	0.16		
S7. L. Vanajanselkä A, original	0.10	0.18	
S9. L. Vanajanselkä B, catch	0.08	0.16	0.01

Table 4c. Estimates of F_{ST} values between pairs of pikeperch samples in the case Lake Oulujärvi.

F_{ST}	S7. L. Vanajanselkä A	S10. L. Kivijärvi	S11. L. Oulujärvi A	S12. L. Oulujärvi B1
S10. L. Kivijärvi	0.01			
S11. L. Oulujärvi A, original	0.08	0.06		
S12. L. Oulujärvi B1, catch 1990	0.03	0.02	0.10	
S13. L. Oulujärvi B2, catch 2000	0.01	0.02	0.08	0.02

population in Lake Oulujärvi was very close to, and almost as diverse as, the original source population of Lake Vanajanselkä.

DISCUSSION

Genetic consequences of pikeperch stock enhancement

Our results indicate that the ongoing enhancement activities have created effective artificial gene flow that, if not properly controlled, may strongly shape and reduce the remaining genetic differentiation among pikeperch populations in northern Europe. The use of foreign source stocks in stock enhancement programs may lead to significant admixing or, as in the case of Lake Oulujärvi, the remaining indigenous pikeperch stocks can be replaced.

Given the long history and large scale of human-induced gene flow between pikeperch populations, the current level of genetic diversity among populations is actually surprisingly high (the present study; BJÖRKLUND et al. 2007; SÄISÄ et al. 2010). This may be because in the early introductions, fish were not usually transferred to water bodies where the species already existed. Most of the indigenous pikeperch stocks, including those of Lakes Oulujärvi, Lohjanjärvi and Vanajanselkä, thus remained intact until the new large-scale enhancement projects were commenced in the late 1980s.

In general, the genetic diversity in Scandinavian pikeperch seems to be somewhat lower than that reported for the walleye (*Sander vitreus*), the North American sibling species. The mean heterozygosity of walleye populations for 10 microsatellite loci was 0.70 among all sites in a study by STEPIEN et al. (2009), while in our data from pikeperch (*Sander lucioperca*) for nine loci it was 0.51. BJÖRKLUND et al. (2007) observed similar diversity levels in Scandinavian pikeperch.

When native fish stocks become mixed with all-around hatchery stocks, the overall genetic diversity among populations inevitably decreases. Besides endangering the future adaptation of the species to potential environmental changes, this may also lead to the loss of important local adaptations and to the reduction of viability within the

stocks that were to be enhanced. To our knowledge, there is no clear evidence of local ecological adaptations in pikeperch, but the long isolation history and the magnitude of the between-population differentiation (SÄISÄ et al. 2010) suggests that such adaptations are very likely. Coping, for instance, with the deep north-south cline in the length of the growing season, even within Finland, along the northern distribution of the species probably requires appropriate genetic characteristics.

Large lakes and coastal areas of the Baltic Sea have pikeperch stocks consisting of subpopulations spawning in different areas. This has been proven by behavioural (LEHTONEN et al. 1996, KESKINEN et al. 2005) and recently by genetic studies (DANNEWITZ et al. 2010). The closely related walleye has a similar population structure in the Laurentian Great Lakes of North America (STEPIEN et al. 2009). The homing behaviour and potential subpopulations make the effects of stocking foreign or even native pikeperch in large lakes even more unpredictable. Some studies have detected very weak effects on the genetic structure of the indigenous populations (STEPIEN and TAYLOR 2004, the Vanajanselkä case in this study). One explanation can be that the fry have been stocked in unsuitable areas lacking spawning grounds or nursery areas, and they therefore have a limited possibility to reproduce successfully when homing to stocking site to spawn.

One of the genetic concerns related to enhancement programmes is the risk of inbreeding. Hatcheries tend to rely on a limited number of breeders and large family sizes, a combination that may markedly reduce the genetic variability of hatchery fish. In the cases of Lakes Oulujärvi and Lohjanjärvi, genetic variability was quite effectively transferred from the source to the recipient stocks, suggesting that inbreeding may not pose a high risk in the present production system of pikeperch juveniles. As in these two cases, most stock enhancement programmes extend over several year-classes, thus increasing the effective population size and reducing the probability of inbreeding. The genetic variability within each year-class is also often increased by populating each rearing dam with a mixture of larvae from several different families.

The genetic effects of fish stockings have previously been studied especially from brown trout populations

(HANSEN 2002, HANSEN et al. 2006, HANSEN and MENSBERG 2009). A poor performance and low viability of released hatchery trout has sometimes been reported (HANSEN 2002), but in general the reproduction success of released fish has been unpredictable, and obviously depends at least on the state of the native population and the release intensity, but also on the genetic characteristics of the released fish, defining their ability to adapt to the new environment. Nevertheless, it is important for future management plans to be able to assess the extent to which the transferred stock has changed the native stocks. Methods such as LEADMIX allow estimates of the proportions of contributing stocks in admixtures, and individual-based analysis such as STRUCTURE can be used even at the individual level to assess the most likely contributions and even possibly identify indigenous individuals in admixed populations (HANSEN et al. 2006). The use of genetic methods in assessing relative contributions to stocks is limited by the often large genetic similarity among the contributing populations. This provides an ultimate limit for the analysis, but to some extent the resolution can be increased by adding new DNA markers and also by using linkage map information (HANSEN et al. 2009).

Genetic/ecological versus socio-economic aspects in fish stock management

The Finnish Fisheries Act (available at < www.finlex.fi >) implicitly recognizes the value of genetic diversity in fish stocks by prohibiting 'actions that may harmfully influence nature or its balance'. A license from the regional fisheries authority is also required in the case where non-native species or stocks are used in stocking. In the absence of real sanctions, these regulations have, however, had little steering effect on stocking activities at the local level, where economic (profits to the fishery) and social (employment, participation) aspects generally override the genetic and ecological constraints in decision-making.

The invasion of pikeperch into new water bodies has in many cases involved marked changes in the native fish communities (COWX et al. 1997; JEPSEN et al. 2000; SCHULZE et al. 2006). The most dramatic example of negative changes is Lake Egredir in Turkey, where five indigenous fish species, including two endemic ones, disappeared after the introduction of pikeperch in 1955 (CRIVELLI 1995). An example of positive changes is the Finnish Lake Vesijärvi, where introduced pikeperch have been used in biomanipulation to reduce the stocks of unwanted fish species and to improve water quality (PELTONEN et al. 1996, RUUHJÄRVI et al. 2005), also resulting in a flourishing pikeperch fishery comparable to that in Lake Vanajanselkä, the source population of Lake Vesijärvi pikeperch. As our three lakes were already inhabited by native pikeperch, neither negative nor positive ecological impacts were

expected. In Lake Oulujärvi, however, the re-appearance of pikeperch after being nearly absent for two decades, may be regarded as restoration of the fish community.

Economically, pikeperch releases in Lake Oulujärvi and Lake Lohjanjärvi have been considered successful. In Lake Oulujärvi, pikeperch catches have increased from nearly zero in the 1970s to the present level of 100 tons year⁻¹ (SUTELA and HYVÄRINEN 2002), offering fishing opportunities for both recreational and professional fishermen. The entire catch improvement is generally thought to be attributable to the releases and the newly-established natural reproduction of pikeperch in the lake, a perception that receives support from our genetic analysis. The economic profits and costs of the releases have not been specifically evaluated, but the pikeperch is generally thought to be one of the key species maintaining the thriving professional fisheries in the lake. In 2006, over 10% (13.3 tons) of the total pikeperch catch was taken by the 32 professional fishermen operating in the lake, and pikeperch was their second most important target species after vendace (*Coregonus albula*) (122 tons; Pekka Korhonen pers. comm.).

In Lake Lohjanjärvi, the results of the releases were monitored by marking 157 000 hatchery juveniles released in 1991–1995 (SALMINEN and RUUHJÄRVI 2004). These releases contributed markedly to pikeperch catches and fisheries in the lake in 1995–2000. The contribution peaked in 1998, when 60% of the catches were of hatchery origin. In a net-present-value analysis (NPV), the investments in the releases in 1991–1995 emerged as economically profitable when the costs of the releases and fishing, the value of the catch, and the time value of money were taken into account (SALMINEN et al. 2005). The present analyses indicate that the Lake Vanajanselkä pikeperch stocked in 1993–1995, in particular, have been highly successful in economic terms, whereas the more recent stockings of Lake Averia and Lake Painio pikeperch have been much less successful, despite the higher numbers of stocked fish.

A different example is offered by Lake Vanajanselkä, where enhancement has been carried out since 1993, with neither clearly-defined objectives nor any obvious benefits. Pikeperch is the most important target for the numerous recreational and the seven professional fishermen operating in the lake, but their catches have shown no clear response to the releases (KIVINEN 2009). This view is also supported by the present study, showing that the genetic structure of the stock has not been markedly altered, despite the releases of Lake Averia and Lake Painio pikeperch with their clearly different genetic constitution.

The main reason for the weaker contribution of the pikeperch releases to the stock and catches in Lake Vanajanselkä than in Lake Lohjanjärvi is probably the combination of a lower stocking density and stronger natural

recruitment. Another contributing factor may be the smaller stocking size in Lake Vanajanselkä (mostly < 7 cm) than in Lake Lohjanjärvi (7–9 cm). In Lake Vesijärvi, 4- to 21-times higher survival rates have been reported for 8.8–9.6 cm than for 7.1–7.3 cm long pikeperch juveniles (RUUHIJÄRVI and SALMINEN 2004). In natural populations, a positive relationship between fingerling size at the end of the first summer and survival has been demonstrated by BUIJSE and HOUTHUIZEN (1992).

When a stocking programme is planned, the possible effects should be carefully examined (COWX 1994). According to the local and regional management plans, a common feature of all our cases was the lack of prior appraisal of the potential benefits vs the genetic and ecological risks of the enhancement programmes (KORHONEN 1989; MARTTINEN 1990; NIINIMÄKI 1989). The strong belief in the benefits, and disregard for or ignorance of the negative effects of fish stocking are largely shared by all stakeholder groups. Critical opinions are rare, the most frequently expressed desire concerning stocking being 'stock more' (VEHANEN et al. 2000, UUDENMAAN TE-KESKUS 2009). The only sceptical comments have been expressed by Lake Oulujärvi vendace trawlers, who are afraid that the releases of predatory fish, especially those of brown trout, may reduce their catches (VEHANEN et al. 2000). The stocking-inclined approach to fisheries management also receives strong backing from the regional advisory bodies that in many cases additionally act as suppliers of fish for stocking. Finally, for fish farmers, large production numbers and the low price of the fish may be generally more important issues than their origin. With this attitude, ecological and genetic concerns are easily overridden by the short-term socio-economic arguments, compromising the sustainability of the stocking programmes.

Can stock enhancement be sustainable?

According to CHARLES (2001), sustainable development requires a balance between the ecological, economic and social aspects of sustainability. This perception implies that the genetic/ecological aspects may be compromised if the economic and social arguments are strong enough. This may be necessary in some contexts, but in our view probably not in pikeperch stock enhancement. Despite the three somewhat negative cases discussed in this study, our findings also suggest that enhancement can be carried out in a sustainable way without strongly compromising the genetic diversity of pikeperch populations.

In Lake Lohjanjärvi and Lake Oulujärvi, the economic and social criteria of sustainability were relatively well met, but unnecessary genetic risks were taken when foreign source stocks were used in the releases. In Lake Oulujärvi, obtaining indigenous breeders might have been difficult but probably not impossible, despite the poor

state of the native stock. And in case it had proven impossible, the next best alternative would have been one of the closer northern native stocks, instead of the distant southern population of Lake Vanajanselkä. In Lake Lohjanjärvi there is similarly no relevant excuse for the use of Vanajanselkä pikeperch in the releases, as breeders would have been readily available from the genetically closer populations of Lakes Averia and Painio and also from the indigenous stock itself.

The least sustainable of the three cases was Lake Vanajanselkä, where the only criterion of sustainability that was seemingly met was a social one: the enhancement programme has not been openly criticized, despite its uncertain contribution to the stock or catches, and the unwarranted use of a foreign source stock in the releases, causing unnecessary risks to the integrity of the native stock. The vital pikeperch stock probably does not require any enhancement at all, and if it does, indigenous breeders are readily available. A potentially better way to improve the ecological, social and economic sustainability of the pikeperch fishery in Lake Vanajanselkä is to introduce more efficient fishing regulation, for example the implementation of a higher minimum landing size and a larger gill net mesh size, a procedure successfully implemented in many lakes (RUUHIJÄRVI et al. 2005; DEGERMAN et al. 2008).

In general, the supplementation of natural fish populations by the releases of hatchery-reared juveniles has been criticized because of 1) the potential threats to local adaptations, 2) the loss of genetic variation, and 3) the negative effects of hatchery selection and domestication (COWX 1994). Hatchery fish also usually suffer from higher mortality than their wild conspecifics (OLLA et al. 1994; KOSTOW 2004), due to their lack of experience of the natural physical environment, food, competitors and predators 4).

Surprisingly, our results suggest that if local wild breeders are used as a source in stockings to avoid the threat to local adaptations 1), most of the other problems can also be avoided: 2) genetic variation can be preserved and successfully transferred if the releases extend over several year-classes and if each year-class consists of a sufficiently large effective population size; and 3) neither the wild breeders nor the pond-reared juveniles are subjected to other types of domestication than the inevitable selection of the breeding pairs. Moreover, 4) in the lake-like rearing dams pikeperch juveniles learn to use natural food, find natural shelter and in most cases also avoid avian and in some cases even fish predators. To our knowledge, this is more than any other hatchery-based enhancement system can offer.

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