Current genetic structure of European vendace *Coregonus albula* (L.) populations in Latvia after multiple past translocations

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Abstract

Current genetic structure of European vendace Coregonus albula *(L.) populations in Latvia after multiple past translocations*. The European vendace *Coregonus albula* (L.), also known as the European cisco, is a widespread fish species in northern Europe, often regarded as an example of a glacial relict. It is an economically valuable fish and has been artificially propagated in Latvia since 1900. Despite past translocations of larvae and fry and its current protection status, it can be found in only 15 Latvian lakes. We used nine microsatellite markers to study vendace populations from nine Latvian lakes. A higher mean allelic richness and private allelic richness in Lake Riču suggest that this population may be indigenous. Three complementary clustering methods revealed similar grouping into three distinct genetic groups. According to the results, European vendace populations in the Latvian lakes studied may currently be a mixture of several other populations after multiple translocations.

Key words: Population genetics, Fish transfer, Indigenous population, Divergence, Translocation

Resumen

Estructura genética de las poblaciones actuales de Coregonus albula *(L.) como posible respuesta a múltiples translocaciones en el pasado.* El corégono blanco Coregonus albula (L.) es una especie abundante en Europa septentrional que se suele considerar un ejemplo de vestigio de la era glaciar. El corégono blanco es una especie de alto valor económico y, en consecuencia, ha sido propagada artificialmente en Letonia desde 1900. A pesar de las translocaciones de larvas y alevines realizadas en el pasado y el actual estado de protección del corégono blanco, esta especie solo se puede encontrar en 15 lagos de Letonia. En el presente estudio utilizamos nueve marcadores de microsatélites para analizar las poblaciones de corégono blanco de nueve de estos lagos. La mayor riqueza alélica media y riqueza de alelos privados del lago Riču sugiere que esta población de corégono blanco puede ser autóctona. Se utilizaron tres métodos complementarios de agrupación que dieron resultados similares y revelaron la existencia de tres grupos genéticos diferenciados. De acuerdo con los resultados, es posible que las poblaciones europeas de corégono blanco de los lagos estudiados en Letonia sean en la actualidad una mezcla de distintas poblaciones tras múltiples translocaciones.

Palabras clave: Genética de poblaciones, Transferencia de peces, Población autóctona, Divergencia, Translocación

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Introduction

European vendace *Coregonus albula* (L.) is a widespread species in northern Europe. It appeared in North–eastern Europe after the last glacial period and is often regarded as a textbook example of a glacial relict (Mansfelds, 1936; Skrzypczak and Mamcarz, 2006; Borovikova and Makhrov, 2012). European vendace shows a high degree of morphological and genetic variability (Heikinheimo and Mikkola, 2004; Czerniejewski and Rybczyk, 2008; Umbrasaite et al., 2012; Borovikova et al., 2013; Dierking et al., 2014; Delling and Palm, 2019); and together with other whitefish and salmonids, it is considered an economically valuable fish.

The occurrence of European vendace in Latvia was mentioned in reports from the 19th century (Lake Puzes and Lake Usmas) (Kawall, 1858), and a survey of Latvian fish conducted in the 1930s showed that vendace could be found in about 30 lakes, mainly in Eastern Latvia (Mansfelds, 1936). Vendace populations later declined rapidly; they were found in only 11 lakes in the 1950–60s and in five lakes (Ežezers, Lejas, Nirzas, Rāznas and Usmas) in the 1990s (Plikšs and Aleksejevs, 1998). Consequently, European vendace was included in the list of specially protected species in Latvia in 2000 (Regulation no. 396 of the Cabinet of Ministers of the Republic of Latvia, November 14, 2000).

Due to its economic importance, European vendace has been artificially propagated in Latvia since 1900, being stopped only between 1916 and 1922 and between 1941 and 1946 because of the world wars. For artificial propagation, European vendace eggs were collected from Lake Peipus and Lake Ladoga up to 1959 and from Lake Rāznas and Lake Drīdzis ever since 1955 (Mosevich and Kumsare, 1955; Nikanorov and Nikanorova, 1956). Altogether, Peipus and Ladoga vendace larvae, fry and fingerlings, Ladoga ripus larvae (*Coregonus albula infraspecies Ladogae* (Prawdin, 1938 in Kottelat et al., 2005), whitefish (*Coregonus lavaretus maraenoides* (Poljakow, 1874)) and whitefish–ripus hybrids were released successively to many Latvian lakes in different years (1922–1941, 1946–1948, 1955–1959) (Kotov et al., 1958; Andrušaitis, 1960; Burmakin, 1963). As a result of these actions, the industrial catch of European vendace reached up to 13 tons in the 1930s, which was quite substantial for Latvian lakes. Yet despite past translocations of larvae and fry and current European vendace protection status, the species can be found in no more than 15 Latvian lakes. Furthermore, its share in the Latvian fishery is small, with rather insignificant and unstable catches (Aleksejevs, 2015, 2019).

Nowadays, the European vendace populations of West and East Europe have been relatively well investigated using various morphological features and molecular genetic markers (Vuorinen, 1984; Sendek, 2002; Huuskonen et al., 2004; Schulz et al., 2006; Oreha and Škute, 2009; Mehner et al., 2010; Borovikova et al., 2013; Præbel et al., 2013a, 2013b; Sendek et al., 2013; Delling and Palm, 2019). Microsatellite genotyping is particularly useful for detecting genetic structure in closely related populations, regardless of whether they are in evolutionary equilibrium or not, and have been applied, for instance, in the study of the population genetic structure of whitefish all over the world. There are few similar studies on European vendace (Huuskonen et al., 2004; Schulz et al., 2006; Præbel et al., 2013a, 2013b), and little is known about the genetic structure of the European vendace populations in Baltic countries (Kaupinis et al., 2004; Škute and Oreha, 2016). In the present research, nine microsatellite markers were used to study European vendace populations from nine Latvian lakes. We hypothesized that their genetic structure in Latvian lakes might reveal the traces of translocated gene pools. We aimed to decipher whether vendace translocations in the middle of the last century, the consequent population flourishing, and the following decline had an impact on the genetic variability and genetic structure of vendace in Latvian lakes.

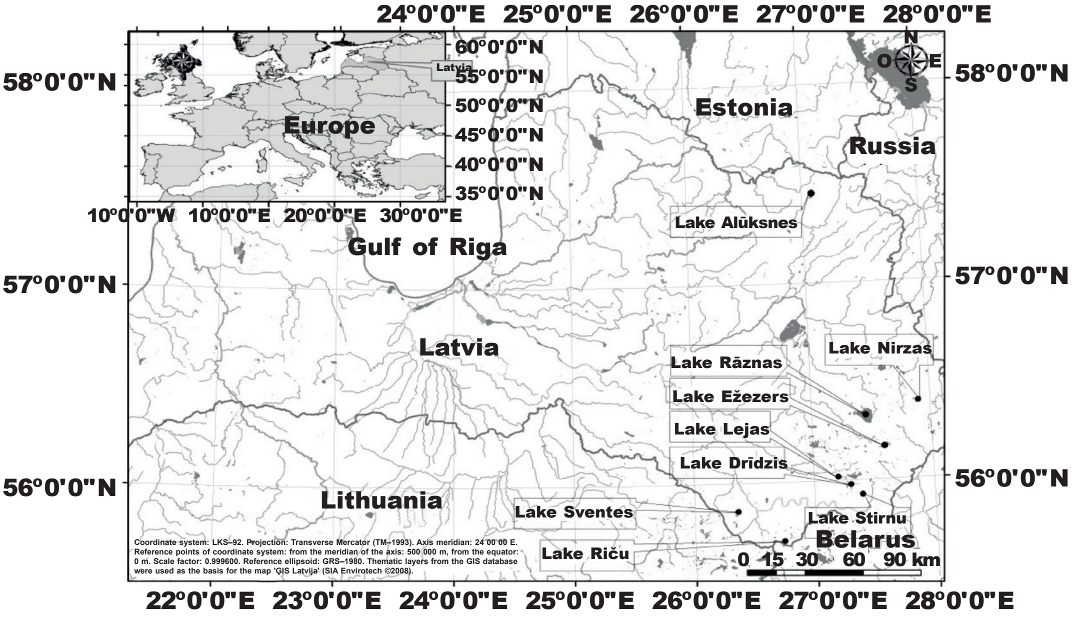
Material and methods

Sampling

Between 2007 and 2016 European vendace samples were collected in Latvia with the help of specialists from the Latvian Fish Resources Agency as part of the sampling efforts of its monitoring plan. Specimens were captured with 20 mm mesh size bottom–set gill nets, each measuring 70 m in length and 6 m in height. The material was collected from nine Latvian lakes (Alūksnes, Nirzas, Ežezers, Rāznas, Lejas, Drīdzis, Stirnu, Sventes and Riču; see locations, surface areas and depths of lakes in fig. 1, table 1). All studied lakes are eutrophic or meso–eutrophic and support commercial and recreational fishing, although commercial activities are currently insignificant and non–profitable. It is notable that fishing with a seine net is restricted in all lakes of Latvia (Regulation No. 159 of the Cabinet of Ministers of the Republic of Latvia, 2001). As the contribution of European vendace to the fishery is not large and the catch is insignificant and unstable, sample sizes taken for research purposes differed in each lake (table 1). Samples of fish tissue (skeletal muscles) were taken and stored at –80 ºC.

Microsatellite analysis

DNA was purified from skeletal muscle tissue according to the salt–extraction method of Aljanabi and Martinez (1997). The quality and quantity of DNA samples were determined using spectrophotometer BioSpec–Nano (Shimadzu). The extracted DNA was stored at –20 ºC. For subsequent molecular analysis, DNA was diluted to a final concentration of 20 ng/µL. Microsatellite amplification was performed using the ABI 9700 thermocycler. PCR (polymerase chain reaction) with fluorescently marked primers (the forward primer in each pair being labelled with the fluorescent label NED, HEX or FAM). PCR mixture components in a final volume of 12 µL were: 100 ng



Coordinate system: LKS–92. Projection: Transverse Mercator (TM–1993). Axis meridian: 24 00 00 E. Reference points of coordinate system: from the meridian of the axis: 500 000 m, from the equator: 0 m. Scale factor: 0.999600. Reference ellipsoid: GRS–1980. Thematic layers from the GIS database were used as the basis for the map 'GIS Latvija' (SIA Envirotech ©2008).

Fig. 1. Map showing sampling locations of nine European vendace populations.

Fig. 1. Mapa de los puntos de muestreo de nueve poblaciones de corégono blanco.

of DNA sample, 10mM Tris–HCl buffer with 50mM KCl, 1.5 mM $MgCl_2$, 2mM dNTPs mix, 0.06 U/µL Taq DNA polymerase, 0.4 µmol/µL of each primer. The individuals were genotyped at nine microsatellite loci: six of the nine were were dinucleotide repeat loci (*Cisco106*, *Cisco90*, *Cisco126*, *Cisco157*, *Cisco200*, *BWF1*; Patton et al., 1997; Turgeon et al., 1999) and three were tetranucleotide repeat loci (*Clatet6*, *Clatet9*, *Clatet13*; Winkler and Weiss, 2008). The PCR thermal cycling program had an initial denaturation at 94 ºC for 5 min, followed by 25 cycles with denaturation at 94 ºC for 30 s, annealing at locus specific temperature (see table 2) for 30 s, and extension at 72 ºC for 60 s, followed by a 7–min final extension at 72 ºC, and cooling at 4 ºC. Both positive and negative controls were used during PCR amplification.

PCR products were separated on an ABI 310 automated analyzer (Applied Biosystem) using Genescan ROX 500 size standard (Applied Biosystem), and alleles were scored with GeneMapper 3.7 software (Applied Biosystem). The Micro–Checker 2.2.3 program was used to check the data for typographic errors and to identify the null allele and genotyping errors: short allele dominance (large allele dropout) and scoring of stutter peaks (Van Oosterhout et al., 2004).

The following standard indices of genetic variation were measured: number and frequency of alleles per locus, occurrence of private alleles in each population, and observed (Ho) and expected (He) heterozygosity levels at each locus. The differences and statistical (χ^2) significance between observed and expected heterozygosity values were calculated using POPGENE 1.32 (Yeh et al., 1999) and GeneAlex 6.41 software (Peakall and Smouse, 2006). Richness of alleles and private alleles in each population were determined, accounting for differences in the size of samples. The rarefaction procedure was used for the smallest sample size as implemented in the software HP–RARE 1.0 (Kalinowski, 2005).

In order to estimate and visualize the genetic structure and differentiation of the studied European vendace populations we used the computer programs STRUCTURE 2.3 (Hubisz et al., 2009) and STRUCTURE HARVESTER (Earl and von Holdt, 2012). A model assuming admixture and correlated allele frequencies between K populations (Burn–ins of 100,000 replications and 300,000 Markov chain Monte Carlo (MCMC) replicates) was used. Sampling locations were used as prior information to assist the structuring (the LOCPRIOR model) as recommended for weak signals of structuring (Hubisz et al., 2009). Values of K between one and nine were tested, running STRUCTURE ten times for each K and using Evanno's ΔK method to determine the most suitable number of clusters (Evanno et al., 2005). The most likely (highest ln Pr(X|K)) grouping was visualized using STRUCTURE HARVESTER (Earl and von Holdt, 2012).

The genetic relatedness of the populations was estimated with Nei's index of genetic distance (D; Nei et al., 1983) using the computer program Populations 1.2.32 (Langella, 2005). The corresponding dendrogram was created according to the neighbor–joining (NJ) method using the computer program TreeView (Page, 1996). Genetic divergence was estimated using pairwise F_{ST} values (Weir and Cockerham, 1984) with GeneAlex 6.41 software (Peakall and Smouse,

Table 1. Characteristics of the Latvian lakes where European vendace were collected, acclimatization actions, and sampling dates: A, area in km^2; Depht, average depth (max depth in m); Date, sampling date; [1] Andrušaitis (1960); [2] Kotov et al. (1958); [3] Burmakin (1963); [4] mention of vendace release but no specific data found.

Tabla 1. Los datos relativos al muestreo y las actuaciones de aclimatación, las principales características de los lagos de Letonia en los que se encontró el corégono blanco: A, área en km^2; Depht, profundidad media (profundidad máxima en m) ; Date, fecha de muestreo; [1] Andrušaitis (1960); [2] Kotov et al. (1958); [3] Burmakin (1963); [4] mención de la liberación de corégono blanco pero no se encontraron datos específicos.

Lake	Location	Water drainage	A	Depht	Action of acclimatization, release dates and material	Date	N
Lejas	56º10'N 27º12'E	Daugava River	1.77	8.2 (34)	1948[2] (vendace larvae)	IX 2012	21
Riču	55º41'N 26º43'E	Daugava River	12.84	9.7 (39.7)	No data[4]	VIII 2016	30
Rāznas	56º19'N 27º26'E	Daugava River	57.56	7 (17)	1930–1941[1] (vendace larvae) 1946[2] (vendace caviar) 1956[3] (Ladoga ripus, ripus and whitefish hybrid larvae) 1957[1] (Ladoga ripus) 1959[1] (Ladoga ripus and Peipus whitefish hybrid)	VIII 2010	7
Sventes	55º51'N 26º21'E	Daugava River	7.35	7.8 (38)	1930–1941[1] (vendace larvae, caviar)	IX 2012	30
Drīdzis	55º58'N 27º17'E	Daugava River	7.53	12.8 (65.1)	1930–1941[1] (vendace larvae) 1946[2] (vendace larvae) 1947–1948[2] (vendace larvae) 1957–1959[1] (vendace larvae)	IX 2012	32
Stirnu	55º55'N 27º23'E	Daugava River	1.48	7.7 (25.8)	1930–1941[1] (vendace larvae) 1946[2] (vendace larvae) 1948[2] (vendace larvae) 1959[1](vendace larvae)	VI 2012	32
Alūksnes	57º27'N 27º50'E	Daugava River	15.44	7.1 (20)	1955[3] (Ladoga ripus and Peipus whitefish hybrid) 1958[1] (Ladoga ripus) 1959[1] (Peipus vendace larvae)	IX 2007	32
Ežezers	56º10'N 27º36'E	Daugava River	9.88	6.4 (21)	No precise data[4]	IX 2008	32
Nirzas	56º23'N 27º54'E	Velikaya River	5.52	8.2 (32)	No precise data[4]	XI 2007	13

2006). The P–values for the pairwise F_{ST} values were corrected for multiple comparisons using the Bonferroni correction (BFC) following Rice (1989). In addition, we estimated structuring of the studied European vendace populations with the principal component analysis (PCA) using GeneAlex 6.41 software (Peakall and Smouse, 2006). The computer program Bottleneck 1.2.02 (Cornuet and Luikart, 1997) was used to detect bottleneck effects on studied populations.

Results

Quality control of genotypic data

Microsatellite genotypic data had no typographic errors or large allele dropout. However, heterozygosity deficits due to the presence of null alleles were detected at 6 loci. Heterozygosity deficits were indicated at *Cisco106* for samples from Lakes Lejas, Riču, Rāznas, Sventes,

Table 2. Main characteristics of the eight microsatellite loci used for the analysis of European vendace *Coregonus albula* populations: TA, annealing temperature; N_A, observed number of alleles in each locus; F_{ST}, the global differentiation per locus; N, mean number of migrants; Ho, observed heterozygosity; He, expected heterozygosity.

Tabla 2. Principales características de los ocho loci de microsatélites utilizados para analizar las poblaciones de Coregonus albula*: TA, temperatura de hibridación;* N_A*, número observado de alelos en cada locus;* F_{ST}*, diferenciación general por locus; N, promedio de migrantes; Ho, heterocigosidad observada; He, heterocigosidad esperada.*

Locus	Size range (bp)	TA (ºC)	N_A	F_{ST}	N	Ho	He
Cisco200	174–340	58	44	0.051	4.609	0.764	0.900
Cisco126	201–209	58	5	0.197	1.020	0.443	0.529
Cisco157	101–165	58	15	0.116	1.906	0.581	0.488
BWF1	203–283	58	23	0.122	1.791	0.530	0.662
Cisco90	108–140	58	15	0.192	1.049	0.763	0.723
Clatet6	184–200	61	9	0.363	0.438	0.249	0.509
Clatet9	165–289	61	24	0.069	3.384	0.820	0.876
Clatet13	214–294	57	19	0.159	1.321	0.772	0.738

Drīdzis, Alūksnes, Ežezers and Nirzas; at *Clatet6* for samples from Lakes Lejas, Riču, Drīdzis, Stirnu, and Alūksnes; at *Cisco200* for samples from Lakes Riču, Drīdzis, Stirnu and Ežezers; at *BWF1* for samples from Lakes Rāznas and Alūksnes; at *Clatet9* for samples from Lake Lejas; and at *Cisco126* for samples from Lake Stirnu. STRUCTURE analyses were performed with and without those loci showing the most heterozygote deficits across populations (*Cisco106, Clatet6, Cisco200*). The number of inferred clusters and the population structure were found to differ when comparing results without *Cisco106* locus but not without *Clatet6* and *Cisco200* (fig. 1s and 2s in supplementary material). Therefore, the locus *Cisco106* was excluded from further analysis.

Genetic variation

Table 2 and table 1s in supplementary material show details of analysed microsatellite loci. The number of alleles at each microsatellite locus was variable. The greatest number of alleles (44) was found at locus *Cisco200*. The minimum numbers of alleles, namely five and nine, were found at loci *Cisco126* and *Clatet6*, respectively. Accordingly, the differentiation values (F_{ST}) at these loci were the smallest. The number of migrants (Nm value) was < 1 only in locus *Clatet6* and > 3 in two loci (*Cisco200* and *Clatet9*). The estimated gene flow was > 1 in five loci (*Cisco126*, *Cisco157*, *BWF1*, *Cisco90*, *Clatet13*) (table 2). Ho and He differed at each locus. The largest values were found at loci *Cisco200* and *Clatet9*. The smallest values were detected at loci *Clatet6* and *Cisco126*. A heterozygote deficit was revealed at five out of eight estimated loci (*Cisco200, Cisco126, BWF1, Clatet6, Clatet9*) and heterozygote excess at three loci (*Cisco157, Cisco90, Clatet13*). However, the differences in Ho and He were not significant ($p > 0.05$).

The standard parameters of genetic variation in studied Latvian populations of European vendace are shown in table 3 and 1s in supplementary material. A total of 154 alleles from among eight microsatellite loci were determined in nine European vendace populations. Allele number in different populations varied from 46 to 84. The mean number of alleles per locus or allelic richness (N_{RA}) varied from 4.24 (Lake Stirnu) to 6.22 (Lake Riču). The mean number of private alleles (N_{RPA}) varied from 0.29 (Lake Stirnu) to 0.87 (Lake Riču). Ho and He varied from 0.507 (Lake Nirzas) to 0.758 (Lake Riču) and from 0.526 (Lake Nirzas) to 0.787 (Lake Riču), respectively. The individual locus tests (for each population) displayed that 20 cases out of 72 had significant deviations of genotype frequencies from Hardy–Weinberg equilibrium (HWE) before and after BFC. Table 4 shows the significant and non–significant deviations of HWE. No significant deviations from HWE were detected in Lake Nirzas only. A significant deviation from HWE was revealed at locus *BWF1* for Lake Rāznas and Lake Alūksnes, at loci *Cisco200* and *Clatet6* for Lake Sventes and Lake Drīdzis, and at three loci for Lake Lejas (*Cisco126, Clatet6, Clatet9*), Lake Stirnu (*Cisco200, Cisco126, Clatet6*) and Lake Ežezers (*Cisco200, Cisco157, BWF1*). Significant deviations from HWE were detected at five out of eight loci in Lake Riču (*Cisco200*, *Cisco157*, *BWF1*, *Clatet6*, *Clatet9*). A heterozygote deficit was detected in 17 out of 20 cases of significant HWE deviations. The deficit

Table 3. Summary of genetic statistics of the studied European vendace populations: N_A, total number of detected alleles; N_{RA}, mean allelic richness; N_{RPA}, private allelic richness; Ho, observed heterozygosity; He, expected heterozygosity.

Tabla 3. Resumen de los parámetros estadísticos genéticos de las poblaciones de corégono blanco estudiadas: N_A, número total de alelos detectados; N_{RA}, riqueza alélica media; N_{RPA}, riqueza de alelos privados; Ho, heterocigosidad observada; He, heterocigosidad esperada.

Populations	N_A	N_{RA}	N_{RPA}	Ho	He
Lejas	59	5.14	0.39	0.554	0.700
Riču	84	6.22	0.87	0.758	0.787
Rāznas	46	5.75	0.6	0.536	0.647
Sventes	70	5.43	0.51	0.708	0.735
Drīdzis	78	5.56	0.47	0.615	0.715
Stirnu	53	4.24	0.29	0.532	0.614
Alūksnes	80	5.84	0.81	0.681	0.738
Ežezers	63	4.85	0.41	0.647	0.640
Nirzas	52	4.76	0.58	0.507	0.526

at 12 of these 17 cases was due to the presence of null alleles. Heterozygote excess was detected at three (Lake Riču, *Cisco157*; Lake Ežezers, *Cisco157*, *BWF1*) out of 20 cases of significant HWE deviations.

Population structure and spatial variation

Table 5 shows the pairwise F_{ST} estimates of genetic differentiation between the studied European vendace populations of Latvia. The pair Lake Sventes–Lake Riču displayed the smallest differentiation (0.048, $p \leq 0.001$), whereas the pair Lake Nirzas–Lake Alūksnes had the highest F_{ST} value (0.159, $p \leq 0.001$). Little genetic differentiation was revealed for Lake Drīdzis–Lake Lejas and Lake Alūksnes–Lake Riču pairs (0.051, $p \leq 0.001$). For all other pairs, moderate genetic differentiation was shown: the F_{ST} values varied from 0.062 to 0.133 ($p \leq 0.001$) (table 5). The sequential BFC did not change the significance level (p value) from the pairwise F_{ST} comparisons.

Table 4. Significance of departure from Hardy–Weinberg equilibrium after sequential Bonferroni corrections: ns, not significant; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

*Tabla 4. Significación de la desviación del equilibrio Hardy–Weinberg tras correcciones de Bonferroni sucesivas: ns, no significativa (*P < 0,05; **P < 0,01; ***P < 0,001).*

	Cisco200	*Cisco126*	*Cisco157*	*BWF1*	*Cisco90*	*Clatet6*	*Clatet9*	*Clatet13*
Lejas	ns	**	ns	ns	ns	***	***	ns
Riču	*	ns	***	*	ns	**	**	ns
Rāznas	ns	ns	ns	*	ns	ns	ns	ns
Sventes	***	ns	ns	ns	ns	**	ns	ns
Drīdzis	***	ns	ns	ns	ns	***	ns	ns
Stirnu	***	*	ns	ns	ns	***	ns	ns
Alūksnes	ns	ns	ns	***	ns	ns	ns	ns
Ežezers	*	ns	***	**	ns	ns	ns	ns
Nirzas	ns	ns	ns	ns	ns	ns	ns	ns

Table 5. F_{ST} values obtained during the pair comparison of European vendace samples from the studied lakes. The smallest and the highest F_{ST}–values are shown in bold; a value lying in the range between 0 and 0.05 indicates little genetic differentiation; a value between 0.05 and indicates 0.15, moderate differentiation; a value between 0.15 and 0.25, high differentiation; and values above 0.25, very high genetic differentiation (Wright, 1978; Hartl and Clark, 2007).

Tabla 5. Valores de F_{ST} *obtenidos durante la comparación pareada de las muestras de corégono blanco de los lagos estudiados. Los valores mínimos y máximos de* F_{ST} *se muestran en negrita; un valor entre 0 y 0,05 indica poca diferenciación genética; un valor entre 0,05 y 0,15 indica diferenciación moderada; un valor entre 0,15 y 0,25 indica diferenciación elevada, y los valores superiores a 0,25 indican diferenciación genética muy elevada (Wright, 1978; Hartl y Clark, 2007).*

Sample	Lejas	Riču	Rāznas	Sventes	Drīdzis	Stirnu	Alūksnes	Ežezers	Nirzas
Lejas		0.001	0.010	0.001	0.001	0.001	0.001	0.001	0.001
Riču	0.067		0.001	0.001	0.001	0.001	0.001	0.001	0.001
Rāznas	0.067	0.075		0.001	0.001	0.001	0.001	0.001	0.001
Sventes	0.079	**0.048**	0.093		0.001	0.001	0.001	0.001	0.001
Drīdzis	**0.051**	0.062	0.084	0.068		0.001	0.001	0,001	0.001
Stirnu	0.056	0.099	0.109	0.110	0.063		0.001	0.001	0.001
Alūksnes	0.067	**0.051**	0.103	0.067	0.077	0.117		0.001	0.001
Ežezers	0.115	0.071	0.133	0.115	0.100	0.133	0.080		0.001
Nirzas	0.132	0.119	0.114	0.141	0.129	0.152	**0.159**	0.107	

The PCA plot by population (fig. 2) revealed four groups of populations. The first group combined specimens from Lakes Alūksnes, Sventes, and Riču. Populations from Lakes Stirnu, Lejas, Rāznas, and Drīdzis were included in the second group. Lakes Nirzas and Ežezers formed the third and fourth groups, respectively. Bayesian clustering partitioned populations into three genetic groups (K = 3; fig. 1s in supplementary material), placing lakes Alūksnes, Sventes and Riču in the first group; Lakes Stirnu, Lejas and Drīdzis in the second group; and Lakes Nirzas and Ežezers in the third group (instead of separated as in the PCA; fig. 2). Importantly, the European vendace population from Lake Rāznas showed a clear admixture of genotypes, and thus its genetic affiliation was unclear (fig. 3).

The NJ tree branched out into three main groups (fig. 4). Populations from Lakes Nirzas and Ežezers were separated as a single group as in Bayesian clustering (fig. 3). Those from Lake Rāznas branched out into a separate group. The populations from the remaining six lakes made up a third group, which had two main branches that separated lakes into two groups: Lakes Drīdzis, Lejas and Stirnu in the first group, and Lakes Riču, Sventes and Alūksnes in the second group.

Discussion

Translocation of freshwater fish of economic importance between rivers and lakes is a common procedure in many countries. However, such transfer could represent a serious threat if the recipient river or lake has an indigenous or even endemic population. Mixing of gene pools may reduce fitness due to out–breeding depression and loss of local adaptations (Avise and Hamrick 1996). On the other hand, translocations are also widely used in conservation efforts (Rummel et al., 2016; Resende et al., 2020), and in such cases, genetic identification is of crucial importance both for the source populations and for the receiving community (Præbel et al., 2013a). Microsatellites are successfully used for genetic studies of different *Coregonus* species, as well as for the monitoring, protection and management of these species (Huuskonen et al., 2004; Schulz et al., 2006; Præbel et al., 2013a; Dierking et al., 2014; Delling and Palm, 2019). Here, genetic diversity and possible divergence in European vendace populations from nine Latvian lakes were analysed to determine the genetic diversity and differentiation of the investigated populations.

The Latvian lake populations of European vendace showed a high level of He. Some loci showed a deficit of heterozygotes whereas others showed an excess (table 2). At the same time, the Ho and He in total at all loci in each of the lakes showed no significant difference (table 3). Disequilibrium may be caused mainly by the presence of null alleles. The use of microsatellite primers developed from a related species can result in non–amplification in the target species ('null' alleles; Rogers et al., 2007; Teterina et al., 2007), and the actual heterozygosity level may be underestimated in

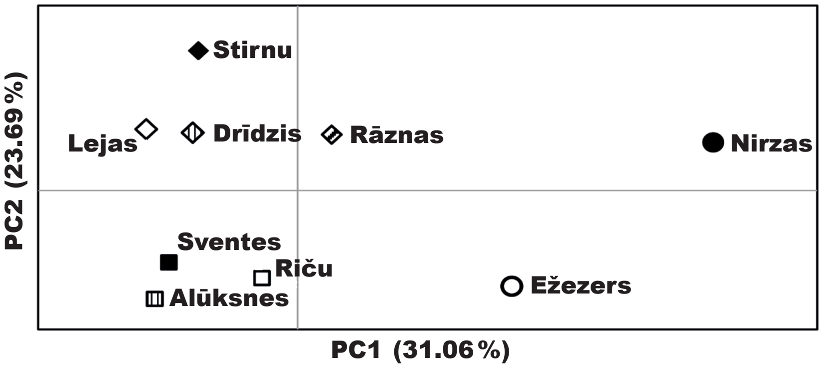


Fig. 2. Principal component analysis (PCA) plot of the genetic structuring among the nine European vendace populations. PC1 and PC2 explain 31.06 % and 23.69 % of the total variation, respectively.

Fig. 2. Gráfico del análisis de componentes principales (PCA) de la estructura genética entre las nueve poblaciones de corégono blanco. PC1 y PC2 explican el 31,06 % y el 23,69 % de la variación total, respectivamente.

the studied populations (Ramstad, 2006). In our study, the level of heterozygosity was quite high, though the nine used microsatellite primers were developed for *Coregonus artedi*, *Coregonus nasus* and *Coregonus lavaretus* species (Patton et al., 1997; Turgeon et al., 1999; Winkler and Weiss, 2008). Similar quite high heterozygosity levels have been reported in whitefish populations (0.485–0.553, Fopp–Bajat et al., 2015; 0.433–0.455, Præbel et al., 2021). Relatively high levels of heterozygosity could also be recovered long after translocation (at least 16 years; Præbel et al., 2021) or may point to the existence of genetic drift effects rather than the loss of alleles in translocated populations.

A relatively large and stable indigenous population tends to have a greater level of genetic variability than a transferred or stocked population (Huuskonen et al., 2004; Præbel et al., 2013a; Adams et al., 2016; Præbel et al., 2021). In the present study, the largest allele count was revealed at six loci for Lake Alūksnes and Lake Riču vendace populations and at three loci for Lake Drīdzis. The mean allelic richness and private allelic richness was higher in the European vendace population of Lake Riču than in any other populations studied, likely indicating that Lake Riču has an indigenous European vendace population (table 3). This assumption may be indirectly confirmed by the fact that data about any European vendace translocation in Lake Riču are lacking. A similar study on whitefish

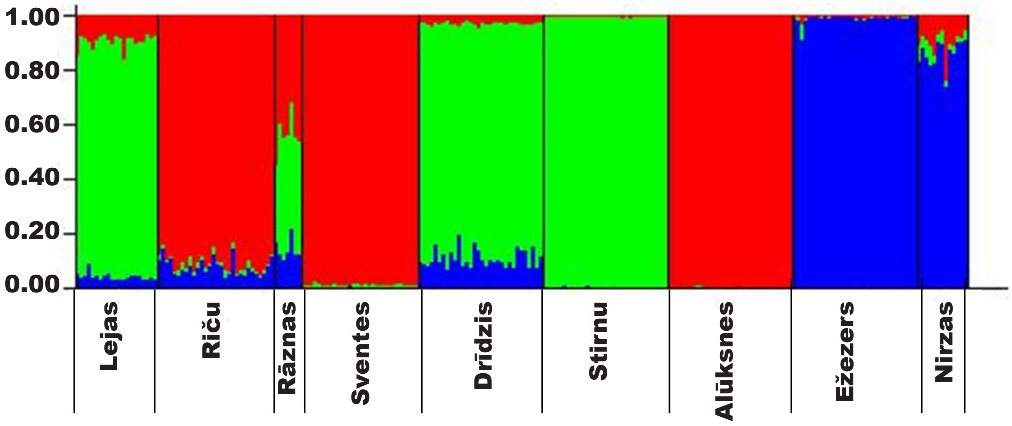


Fig. 3. Bayesian clustering of all individuals using STRUCTURE (Hubisz et al., 2009).

Fig. 3. Agrupamiento bayesiano de todos los individuos utilizando STRUCTURE (Hubisz et al., 2009).

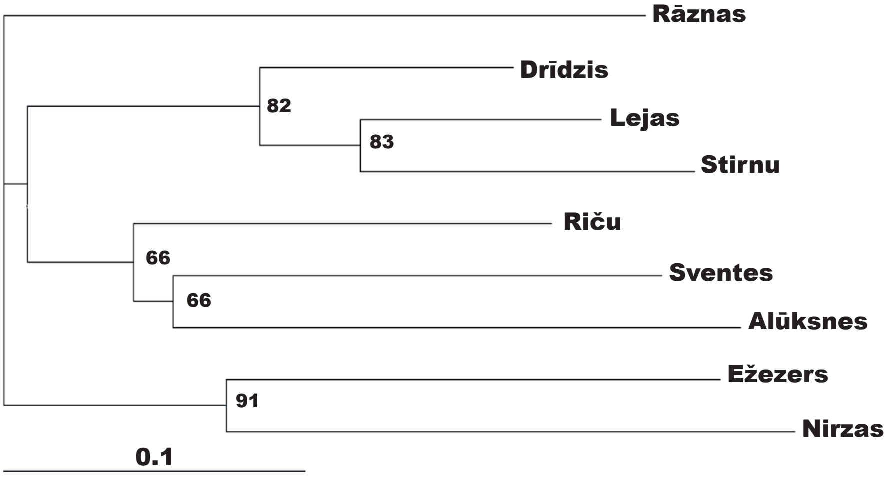


Fig. 4. Genetic differentiation of nine European vendace samples from Latvian lakes as revealed by a neighbour–joining tree using Nei et al. (1983) genetic distance.

Fig. 4. Diferenciación genética de las nueve muestras de corégono blanco procedentes de lagos de Letonia obtenida con un árbol elaborado mediante el método de unión de vecinos utilizando la distancia genética de Nei et al. *(1983).*

in Poland also recorded a higher number of private alleles in one of the studied populations, which was also assumed to have an indigenous population (Fopp–Bajat et al., 2015). A smaller private allelic richness was revealed in the European vendace population in Lake Alūksnes, but in this case, there are historical data on three cases of vendace and ripus release (table 1). A local population with either an indigenous gene pool or a mixture of indigenous and translocated gene pools could explain this pattern. The transferred fish could be genetically identical to the indigenous gene pool or introduce favourable traits for adaptation and survival. In addition, recent research pointed out that in translocated populations, new alleles can arise *de novo,* creating novel genotypes (Præbel et al., 2021). Therefore, the European vendace population of Lake Alūsknes most likely has an overall genetic mixture that fits within the general indigenous genofond. In comparison with recent European vendace population studies based on similar microsatellite loci (Delling and Palm, 2019, Præbel et al., 2021), the count of alleles in European vendace populations in Latvian lakes is not low, and it is at a level that is typical for both native and translocated populations.

The PCA plot, Bayesian clustering and NJ tree showed that individuals could be partitioned into three distinct genetic groups. All three methods grouped the populations of Lakes Riču, Alūksnes and Sventes together (fig. 2–4). As shown in table 1, translocation actions were conducted in lakes Alūksnes and Sventes at different times. It is known that vendace larvae from Lake Peipus were released in Lake Alūksnes whereas the origin of the material released in Lake Sventes is unknown (data were not provided in the original publication; Andrušaitis, 1960). Therefore, it is possible that different gene pools were released in these two lakes. At the present time, it is most likely that populations in Lakes Alūksnes and Sventes have a mixture of indigenous and translocated gene pools, with most of the population having an indigenous gene pool similar to that of the Lake Riču population. Furthermore, similar moderate F_{ST} values were also reported for native whitefish populations in Scotland (Adams et al., 2016).

The second group combined populations from Lakes Drīdzis, Lejas and Stirnu. These lakes are located close to each other (the distances between them vary from 7 to 15 km) and they are connected by canals and small rivers. There are also data about European vendace translocations into these lakes (table 1). Moreover, these lakes have a smaller private allelic richness than that in Lakes Riču and Alūksnes. Lake Drīdzis was used as a source of material for vendace propagation between 1946 and1959 (Andrušaitis, 1960). Altogether, our results indicate that the populations from Lakes Drīdzis, Lejas and Stirnu have similar gene pools, formed as the result of mixing indigenous and translocated gene pools and possible random migrations. There is ample literature reporting small pairwise F_{ST} values between recently diverged populations. For example, F_{ST} = 0.011 was reported between two European vendace populations after recent invasion in water bodies in Finland (Præbel et al., 2013a). A low level of genetic difference (F_{ST} = 0.021) was also reported between two lakes in Finland after European vendace stock transfers (Huuskonen et al., 2004). The level of genetic difference between donor populations and two translocated *Coregonus lavaretus* populations was also low (F_{ST} = 0.014 and 0.027; Præbel et al., 2021). Finally, very similar values were reported between whitefish populations from different localities within the same lake in Scotland (F_{ST} = 0.001–0.024; Adams et al., 2016). In the present study, pairwise F_{ST} values also show a moderate but somewhat higher genetic differentiation, most likely a result of translocation and mixing with the indigenous gene pool.

The third genetic group included populations from Lakes Nirzas and Ežezers. Although these lakes have witnessed similar historical translocations, their populations show a moderate to high level of genetic differentiation compared to all other investigated populations as well as one from each other. Such high F_{ST} levels are typical among native postglacial coregonid populations in northern Fenoscandia (Østbye et al., 2006; Saisa et al., 2008; Præbel et al., 2013a, 2013b). Thus, it can be considered that European vendace populations of Lake Nirzas and Lake Ežezers have indigenous gene pools.

The European vendace population from Lake Rāznas showed unclear genetic affiliation to any of the above–mentioned genetic groups as the three clustering methods rendered different results. One potential explanation for this pattern is that once translocated to Lake Rāznas, the introduced gene pool diverged enough to become quite distinct from the indigenous gene pool. However, it is most likely that the small sample size of the population from Lake Rāznas could explain the observed inconsistencies.

Unfortunately, our data on past translocations are incomplete. As a result, we were unable to analyse historical samples of European vendace that could help conclude whether or not the genetic differentiation of the nine vendace populations analysed is the result of translocations alone. Other studies have rendered mixed results, as some show that transferred fish may have a minor effect on the indigenous European vendace population (Lake Höytiäinen in Finland; Huuskonen et al., 2004), whereas others show that the translocated gene pool can often displace native species, subspecies or populations. For example, the native whitefish (*C. holsatus*) of Lake Schaal in Germany disappeared from the lake, and the specimens currently found in Lake Schaal and in three adjacent lakes are identified as *C. maraenoides* introduced from Lake Peipsi (Mehner et al., 2018). Thus, we can only suppose that the vendace populations in the investigated Latvian lakes are a mix of several populations and may not therefore be fully indigenous. As the genetic differentiation among studied population shows quite a high value for local populations and migration is possibility limited, we consider that we have ecologically distinct populations in the studied lakes. This assumption can be supported by morphometric trait studies in European vendace populations in Latvian lakes, which showed that while morphological properties did not exceed the limits of variability, in almost every Latvian reservoir, due to their plastic (morphometric) variability, European vendace created a local form depending on the certain environmental conditions (Oreha, 2016).

The results of our study suggest each studied local population be considered a different management unit and may contribute to the development of an optimal strategy for their effective conservation and management, taking into account the peculiarity of each separate European vendace population. The European vendace populations with the highest genetic variability could serve as a potential genetic resource to enhance populations of the species in all Latvian lakes in the future.

Conclusions

The level of genetic variability differs among the populations studied. Such differences may be caused by translocations or a genetic drift, which influence the allele frequencies in different ways, and could be driven by environmental factors. Our present results could be useful in the design and monitoring of conservation programs of vendace populations in Latvian lakes.

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Supplementary material

Table 1s. Allelic variability at eight microsatellite loci in vendace populations in nine Latvian lakes: N, number of samples; N_A, number of alleles at each locus; Ho, observed heterozygosity; He, expected heterozygosity.

Tabla 1s. Variabilidad alélica en ocho loci de microsatélites en las poblaciones de corégono blanco procedentes de nueve lagos de Letonia: N, número de muestras; N_A*, número de alelos en cada locus; Ho, heterocigosidad observada; He, heterocigosidad esperada.*

Populations		*Cisco200*	*Cisco126*	*Cisco157*	*BWF1*	*Cisco90*	*Clatet6*	*Clatet9*	*Clatet13*
Lejas	N	20	21	21	20	20	12	21	20
	N_A	15	3	3	6	8	4	14	6
	Ho	0.900	0.143	0.667	0.600	0.850	0.000	0.524	0.750
	He	0.906	0.468	0.571	0.595	0.815	0.639	0.857	0.751
Riču	N	28	30	30	30	30	29	30	30
	N_A	20	4	5	8	10	7	18	12
	Ho	0.714	0.667	0.933	0.700	0.933	0.379	0.867	0.867
	He	0.915	0.668	0.600	0.777	0.865	0.728	0.922	0.818
Rāznas	N	7	7	7	7	7	7	7	7
	N_A	12	3	4	5	5	2	10	5
	Ho	0.857	0.429	0.429	0.143	0.571	0.286	0.857	0.714
	He	0.908	0.622	0.367	0.745	0.673	0.245	0.878	0.735
Sventes	N	30	30	30	30	30	30	30	30
	N_A	16	4	4	5	7	6	14	14
	Ho	0.833	0.667	0.567	0.667	0.733	0.500	0.833	0.867
	He	0.891	0.704	0.588	0.602	0.725	0.618	0.879	0.869
Drīdzis	N	32	32	32	32	32	30	32	32
	N_A	22	4	4	7	11	5	15	10
	Ho	0.594	0.563	0.406	0.750	0.969	0.167	0.813	0.656
	He	0.912	0.609	0.389	0.757	0.857	0.627	0.914	0.651
Stirnu	N	31	32	32	32	32	22	32	32
	N_A	16	4	3	5	8	3	9	5
	Ho	0.677	0.188	0.563	0.656	0.938	0.045	0.781	0.406
	He	0.860	0.420	0.461	0.670	0.822	0.460	0.824	0.396
Alūksnes	N	31	30	32	31	32	26	32	32
	N_A	19	5	6	10	8	5	14	13
	Ho	0.839	0.567	0.688	0.226	0.906	0.346	0.938	0.938
	He	0.917	0.567	0.661	0.708	0.707	0.574	0.880	0.890
Ežezers	N	31	32	32	32	32	28	32	32
	N_A	18	3	4	5	5	2	14	12
	Ho	0.710	0.531	0.750	0.563	0.656	0.214	0.844	0.906
	He	0.908	0.488	0.537	0.497	0.653	0.293	0.873	0.869
Nirzas	N	12	13	13	13	13	13	13	13
	N_A	13	3	4	5	5	5	10	7
	Ho	0.750	0.231	0.231	0.462	0.308	0.308	0.923	0.846
	He	0.882	0.210	0.213	0.604	0.391	0.393	0.855	0.663

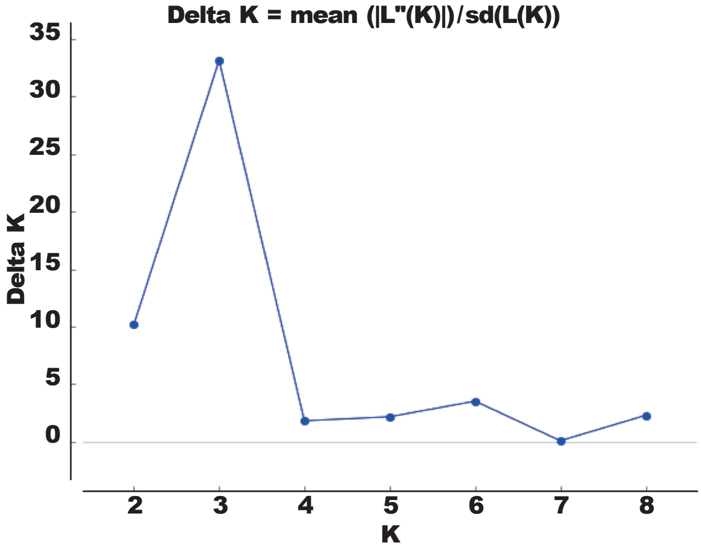

Fig. 1s. Results from STRUCTURE for inferring K populations among the nine studied European vendace *Coregonus albula* (L.) populations when omitting one of three loci (*Cisco106*) that may be associated with null alleles (Delta K values; Evanno et al., 2005).

Fig. 1s. Resultados obtenidos con STRUCTURE de inferir K poblaciones entre las nueve poblaciones estudiadas de corégono blanco Coregonus albula *(L.) cuando se omite uno de los tres loci* (Cisco106) *que puede estar asociado a alelos nulos (valores de Delta K; Evanno* et al.*, 2005).*

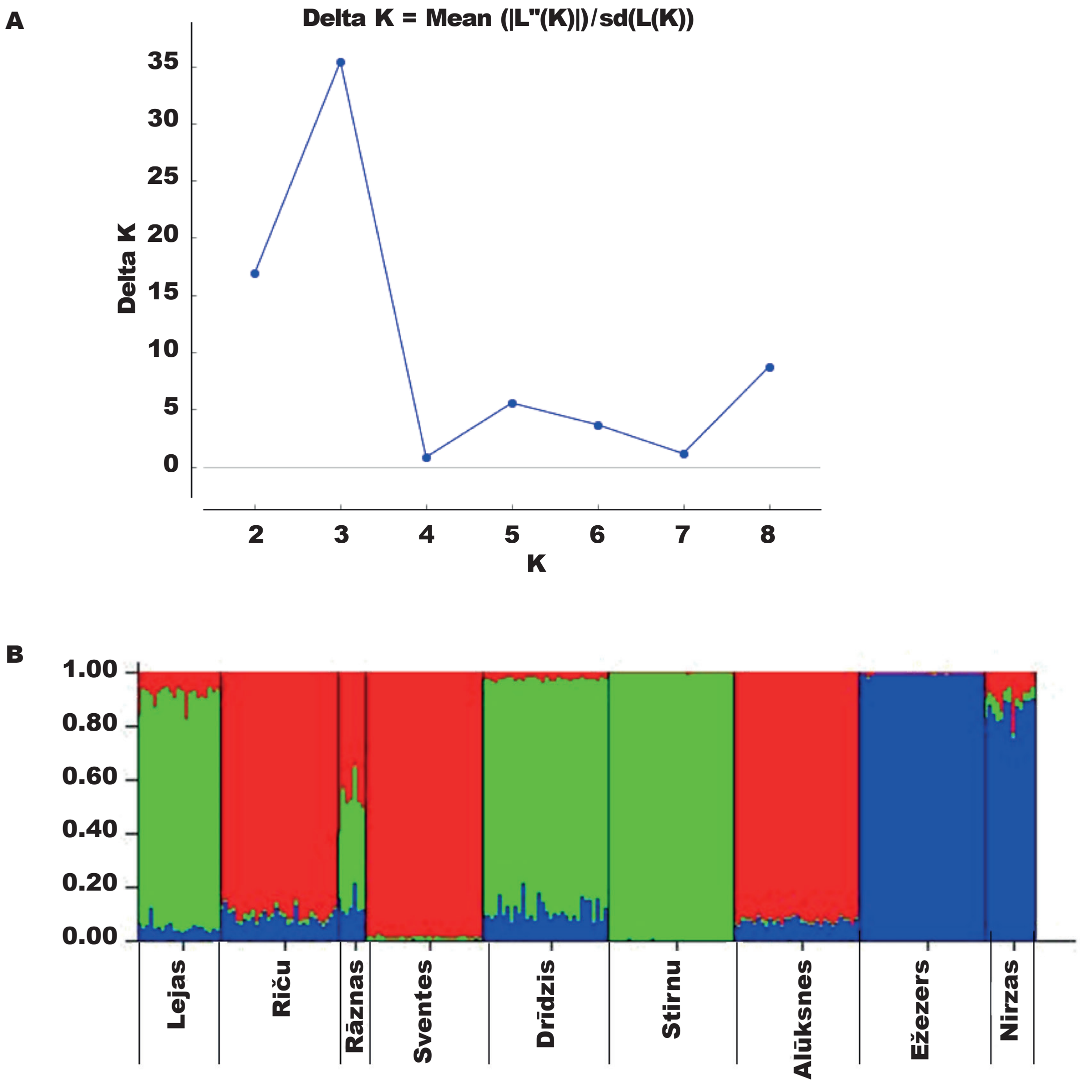

Fig. 2s. Results from STRUCTURE for inferring K populations among the nine studied European vendace populations when omitting three loci (*Cisco106, Cisco200* and *Clatet6*) that may be associated with null alleles: A, Delta K values (Evanno et al., 2005); B, the genetic structure among nine studied vendace populations (Bayesian clustering assuming three genetic clusters of individuals, K = 3). In the STRUCTURE analysis, black lines separate individuals from different sampling sites and each individual is represented by a thin horizontal line, which is partitioned into K–colored segments representing the individual's estimated membership fractions in K clusters.

*Fig. 2s. Resultados obtenidos con STRUCTURE de inferir K poblaciones entre las nueve poblaciones estudiadas de corégono blanco cuando se omiten tres loci (*Cisco106, Cisco200 *y* Clatet6*) que pueden estar asociados a alelos nulos: A, valores de Delta K (Evanno* et al.*, 2005); B, estructura genética de las nueve poblaciones estudiadas de corégono blanco (agrupamiento bayesiano suponiendo tres grupos genéticos de individuos, K = 3). En el análisis STRUCTURE las líneas negras separan a los individuos de diferentes sitios de muestreo y cada individuo se representa con una fina línea horizontal, que está dividida en segmentos de K coloreados que representan la proporción estimada de individuos en los grupos K.*