The estimation of spatial genetic diversity of vendace (Coregonus albula L.) populations in Baltic Lakeland

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Abstract. The vendace (*Coregonus albula*) is native widespread to lakes in northern Eurasia. In the Baltic Lakeland region, populations of local whitefish are the remnants of the Arctic freshwater faunal complex and often regarded as an example of a glacial relict and indicator species of the state of the lake ecosystem. Together with other whitefishes vendace belongs to economically valuable fish species.

The territory of the Baltic Lakeland region is located on the territory of three countries (Latvia, Lithuania and Belarus). The range of the vendace population is declining in waterbodies in Latvia and Belarus, the catch is insignificant and unstable, and this species is included in the list of specially protected fish species. However, in Lithuania this species is widespread and not protected.

The understanding fish population genetic diversity is very important for protection of rare communities and conservation of unique native populations. The estimation of the genetic structure of populations and determining the causes of genetic differentiation and the factors that promote variation between and within populations is fundamental for understanding adaptation and is, therefore, a primary goal of population and conservation genetics. Little is known about the genetic structure of vendace populations in waterbodies in Baltic Lakeland.

In this study eight microsatellite loci were used to investigate the genetic structure within and between populations in six vendace populations from Baltic Lakeland, namely Drivyaty, Rudakova, Strusto, Snudi, Naroch and Drūkšiai. Allelic variation was different in all investigated vendace populations; the observed and expected heterozygosity level was quite high. Bayesian-based STRUCTURE analysis suggested that there are two main genetic groups within our study area, separating Rudakova, Naroch and Strusto into one and others studied populations into the other cluster. These populations would be differentiated due to drift, reduced gene flow and possibly selection that promoting divergence.

Keywords: anthropogenic impact, Baltic Lakeland, genetic differentiation, indigenous population, population decline, population genetics, translocation

I. Introduction

The vendace (*Coregonus albula*) is native widespread to lakes in northern Eurasia around the Baltic Sea, from Germany and Denmark in the west, through Poland to Estonia, Lithuania, Latvia and Russia in the east, and is also found in the slightly brackish waters of the Baltic Sea [1]. In North–eastern Europe populations of local whitefish are the remnants of the Arctic freshwater faunal complex and can be considered as glacial relics [2], [3], [4].

Vendace's ecological importance stems from its position in the food chain of European lakes. As a planktivorous fish, vendace primarily feeds on zooplankton and benthic invertebrates, playing a crucial

role in regulating the abundance and distribution of these lower trophic level organisms [5]. Beyond its role in trophic interactions, vendace is a very plastic species of freshwater whitefish and also serves as a valuable bioindicator species for assessing the health of freshwater ecosystems in Europe. Vendace inhabit in lakes with relatively low trophic conditions and high oxygen levels, so this species also serves as a bioindicator of water quality [6], [7]. Due to its sensitivity to environmental stressors such as pollution, habitat degradation, and climate change in vendace populations can provide early warnings of ecosystem disturbances. Besides this, vendace, together with other whitefishes, belongs to economically valuable fish species. Moreover, *Coregonus albula* is a valuable commercial fish species in Europe [8], [9].

Historically, the territory of the Baltic Lakeland region is located on the territory of three countries (Latvia, Lithuania and Belarus). The management in the past and present, state in nowadays and the factors affecting vendace in different waterbodies differ. So, for example the range of the vendace population is declining in waterbodies in Latvia and Belarus, the catch is insignificant and unstable [10], [11], and this species is included in the list of specially protected fish species. Coregonidae fish species in Latvian lakes has diminished, and vendace have been found only in 13 lakes after 1990 [12]. The habitat of vendace in Belarus is catastrophically declining also. Over the past 50-70 years, the number of lakes inhabited by vendace has decreased from 40-50 to 17 [5], [13]. However, in Lithuania this species is widespread and not protected; vendace was found in 76 lakes [14].

The understanding fish population genetic diversity is very important for protection of rare communities and conservation of unique native populations. The estimation of the genetic structure of populations and determining the causes of genetic differentiation and the factors that promote variation between and within populations is fundamental for understanding adaptation and is,

therefore, a primary goal of population and conservation genetics. Little is known about the genetic structure of vendace populations in waterbodies in Baltic Lakeland [15], [16], [17]. That is why genetic diversity was studied in six vendace populations from Baltic Lakeland, namely Drivyaty, Rudakova, Strusto, Snudi, Naroch and Drūkšiai.

Microsatellites are successfully used for genetic studies of different Coregonus species, as well as for the monitoring, protection and management of these species [18], [19], [20], [21], [22]. In this study eight microsatellite loci were used to investigate the genetic structure within and between populations.

The aim of research was to reveal genetic variability and genetic structure of vendace populations in different waterbodies in Baltic Lakeland and to detect whether the management in the past and present and the factors affecting vendace in different waterbodies had an impact on its genetic variability and genetic structure in present.

II. MATERIALS AND METHODS

A. Sampling

Vendace samples were collected in Baltic Lakeland in 2006 – 2015. The material was collected from seven lakes, namely Lake (further L.) Naroch, L. Snudy, L. Rudakova, L. Strusto, L. Drivyaty, L. Drūkšiai and L. Rāznas (see location, surface area and depth of lakes in Fig. 1, TABLE 1). Classification of the lakes' morphologies was done according to Ancāne [23]. All studied lakes are eutrophic or meso-eutrophic and support commercial and recreational fishing, although commercial activities are currently insignificant and not profitable. Vendace were fished with 20 mm mesh size bottom-set gill nets, each measuring 70 m in length and 6 m in height. As the contribution of vendace to the fishery is not big and the catch is insignificant and unstable, the size samples taken for research purposes differed in each lake (TABLE 1).

Samples of fish tissue (skeletal muscles) were taken and stored at -80ºC to await DNA extraction.

TABLE 1 THE DATA OF SAMPLING AND THE MAIN CHARACTERISTICS OF LAKES IN WHICH THE MATERIAL WAS COLLECTED.

Lake	Location	Water drainage	Area (km²)	Average depth (Max depth),m	Sampling date	N
Naroch	54°86`N, 26°75`E	Viliya River	79.6	8.9(24.8)	11.2014	20
Drivyaty	55°6`N, 27°03`E	Daugava River	459	6.1(12)	11.2014	3
Rāznas	56°19`N, 27°26`E	Daugava River	57.56	7(17)	2006	4
Snudy	55°75`N, 27°06`E	Daugava River	22.0	4.9(16.5)	11.2014	19
Rudakovo	54°89`N, 26°89`E	Daugava River	0.24	11.3(28.6)	11.2014	5
Strusto	55°70`N, 27°04`E	Daugava River	13	7.3(23)	11.2014	4
Drūkšiai	55°64`N, 26°58`E	Daugava River	44.79	7.6(33.3)	07.2015	48

B. Microsatellite analysis

DNA was purified from skeletal muscle tissue according to the salt-extraction method of [24], which earlier was used, in genetic researches of water animals [17], [25]. The quality and quantity of DNA samples was determined using spectrophotometer BioSpec-nano (Shimadzu). The extracted DNA was then stored at -20 ºC to await analysis.

For the analysis, the DNA was diluted to a concentration of 20 ng/μL. Microsatellite amplification was performed using the ABI 9700 thermocycler. PCR was performed with fluorescently marked primers (NED,
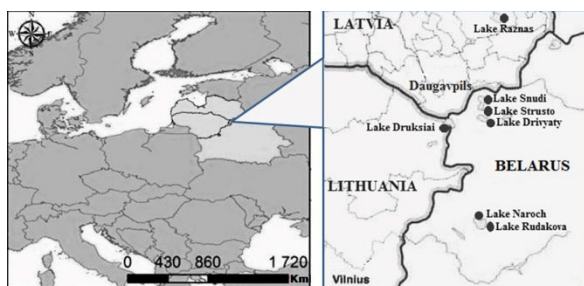

Fig. 1. Map showing sampling locations of seven samples.

HEX, FAM) in a volume of 12 μL. PCR mixture components were: 100 ng of DNA sample, 10mM Tris-HCl buffer with 50mM KCl, 1.5 mM MgCl2, 2mM dNTP mix, 0.06 U/μL Taq DNA polymerase, 0.4 μmol/μL of each primer. The individuals were genotyped at eight microsatellite loci altogether: five of them were dinucleotide repeat loci (*Cisco90, Cisco126, Cisco157, Cisco200, BWF1*) [26], [27] and three tetranucleotide repeat loci (*Clatet6, Clatet9, Clatet13*) [28]. PCR was performed using the thermal cycling program, following an initial denaturation at 94°C for 5 min, 25 cycles were run with denaturation at 94°C for 30 s, annealing at 58°C (for *Cisco126, Cisco157, Cisco200, Cisco90, BWF1*), at 61°C (for *Clatet6, Clatet9*), at 57°C (*Clatet13*) for 30 s, and extension at 72° C for 60 s followed by 7 min extension at 72°C and cooling at 4°C. Amplification was performed three times including a positive and negative control.

The PCR products were separated on ABI 310 automated analyser (Applied Biosystem) using Genescan ROX 500 size standard (Applied Biosystem), alleles were scored in GeneMapper 3.7 software (Applied Biosystem). The given data was verified in the software Micro-Checker 2.2.3 [29]. The Micro-Checker program was used to check out the data for typographic errors, to identify the null allele and genotyping errors: short allele dominance (large allele dropout) and scoring of stutter peaks.

The standard indices of genetic variation were measured: number and frequency of alleles at a locus, occurrence of private alleles in each population, observed and expected heterozygosity level at each locus. Their differences and significance were calculated with the help of χ2 criteria using POPGENE 1.32 [30] and GeneAlex 6.41 software [31]. 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 [32].

In order to estimate and visualize the genetic structure and differentiation of the studied vendace populations and possible relatedness, the computer programs STRUCTURE 2.3 [33] and POPHELPER Structure Web App v 1.0.10. [34] were used. 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) were used. Sampling locations were used as a priori information to assist the structuring (the LOCPRIOR model) as recommended for weak signals of structuring [33]. Values of K between one and seven were tested, running STRUCTURE ten times for each K and using Evanno's ΔK method to determine the most suitable number of clusters [35]. The most likely (highest ln Pr(X|K)) grouping was visualized using POPHELPER Structure Web App v 1.0.10 [34]. The genetic relatedness of the populations was estimated with the help of Nei's [36] index of genetic distance (D) using the computer program Populations 1.2.32 [37]. The dendrogram was created according to the UPGMA method using the computer program TREVIEW [38]. Genetic divergence was estimated by pair-wise F_{ST} values [39] using GeneAlex 6.41 software [31]. The P-values for the pair-wise F_{ST} values was corrected for multiple comparisons by Bonferroni corrections (BFCs) following Rice [40]. Using the computer program Bottleneck 1.2.02 [41] populations were examined for evidence of a bottleneck effect.

III.   RESULTS AND DISCUSSION

A. Genetic variation

The standard parameters of genetic variation in studied Latvian populations of European vendace are shown in TABLE 2. A total of 135 alleles from among eight microsatellite loci were determined in seven studied samples. Allele number in different samples varied from 24 to 98.

TABLE 2 SUMMARY OF GENETIC STATISTICS OF THE STUDIED VENDACE POPULATIONS INCLUDED IN THE STUDY

Populations	N_A	N_{RA}	N_{RPA}	H_O	H_E
Naroch	56	3.34	0.61	0.602	0.657
Snudy	70	3.77	0.63	0.635	0.719
Rudakovo	24	2.54	0.36	0.400	0.440
Strusto	29	3.13	0.36	0.500	0.543
Drivyaty	25	5.13	1.33	0.625	0.514
Drukšiai	98	3.72	0.86	0.589	0.721
Rāznas (*C. lavaretus*)	34	3.67	1.62	0.708	0.672

N_A – total number of detected alleles, N_{RA} - mean allelic richness, N_{RPA} – private allelic richness, H_O – observed heterozygosity, H_E - expected heterozygosity

TABLE 3 F_{ST} VALUES OBTAINED DURING THE PAIR COMPARISON OF EUROPEAN VENDACE SAMPLES FROM THE STUDIED LAKES

Sample	Naroch	Snudy	Rudakova	Strusto	Drivyaty	Drūkšiai	Rāznas
Naroch		0.001/<u>*</u>	0.001/<u>*</u>	0.005/ns	0.001/<u>*</u>	0.001/<u>*</u>	0.001/<u>*</u>
Snudy	0.082		0.001/<u>*</u>	0.297/ns	0.001/<u>*</u>	0.001/<u>*</u>	0.001/<u>*</u>
Rudakova	0.091	0.119		0.227/ns	0.002/<u>ns</u>	0.001/<u>*</u>	0.001/<u>*</u>
Strusto	0.060	0.007	0.024		0.002/ns	0.001/<u>*</u>	0.001/<u>*</u>
Drivyaty	0.154	0.132	**0.309**	0.191		0.001/<u>*</u>	0.001/<u>*</u>
Drūkšiai	0.115	**0.050**	0.193	0.078	0.138		0.001/<u>*</u>
Rāznas	0.232	0.166	0.329	0.239	0.241	0.175	

ns - not significant, * P<0.05, ** P<0.01, *** P<0.001; underlined– significance level after BFCs corrections. 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 [43], [44]

The mean number of alleles per locus or allelic richness (N_{RA}) varied from 2.54 (L. Rudakovo) to 5.13 (L. Drivyaty). The mean number of private alleles (N_{RPA}) varied from 0.36 (L. Rudakovo and L. Strusto) to 1.62 (L. Rāznas).

In recent vendace population research [17] in nine waterbodies from Baltic Lakeland was shown that the

allelic richness ranged from 4.24 to 6.22 and mean number of private alleles varied from 0.29 to 0.87, there was assumed, that waterbodies where was revealed the highest number of private alleles have native vendace population. In our case the highest number of private alleles in L. Rāznas associated with another species in that sample, L. Rāznas sample with *C. lavaretus* indivuduals was taken as outgroup for present research.

The observed and expected heterozygosity for all samples over the eight microsatellite loci varied from 0.400 (Lake Rudakovo) to 0.708 (Lake Rāznas) and from 0.440 (Lake Rudakovo) to 0.721 (Lake Drūkšiai), respectively (TABLE 2). The individual locus tests (for each sample) displayed that eight cases out of 56 had significant deviations of genotype frequencies from Hardy - Weinberg equilibrium (HWE) before BFCs. A significant deviation from HWE was revealed at locus *Clatet6* for L. Naroch, at loci *Cisco200*, *BWF1*, *Cisco90* and *Clatet13* for Lake Snudy, at loci *Cisco200*, *BWF1* and *Clatet9* for Lake Drūkšiai. Significant deviations of genotype frequencies from HWE after BFCs were revealed in two loci in samples from two different lakes. That is, heterozygosity deficits were detected at L. Naroch population in locus *Clatet6* and in L. Drūkšiai in locus *Cisco200*, which was indicated by Micro-Checker as caused by possible presence of null alleles.
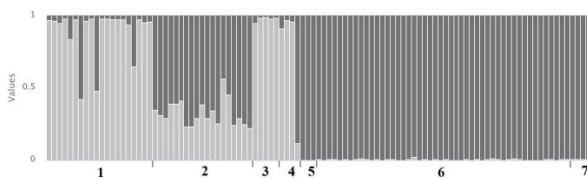

Fig. 2. Bayesian clustering of all individuals using STRUCTURE (1 – L. Naroch, 2 – L. Snudy, 3 – L. Rudakova, 4 – L. Strusto, 5 – L. Drivyaty, 6 – L. Drūkšiai, 7 - L. Rāznas).

The heterozygosity deficit in locus *Clatet6* as caused by the presence of null alleles was observed also in other *Coregonus albula* population study in northern and central Finland [20], central and southeast Finland [8]. The heterozygosity deficit in both loci, as *Cisco200* as *Clatet6*, caused by the presence of null alleles, was mentioned also for *Coregonus albula* populations in different waterbodies in Baltic Lakeland [17]. In present study it was revealed in only one waterbodies for each locus (*Cisco200*, *Clatet6*). Altogether the level of heterozygosity was quite high. So, quite similar heterozygosity levels have been reported for whitefish populations in Poland and Scotland waterbodies (0.485–0.553, [42]; 0.433–0.455, [46], respectively). There were revealed quite high level of heterozygosity. It was shown, that relatively high levels of heterozygosity could also be recovered long after translocations (at least 16 years; [45]). In studied samples there was not been revealed any evidence of a bottleneck effect, which was established by the allele frequency distribution.

In the waterbodies in Baltic Lakeland the number of detected allele fluctuates. For instance, in previous research there were detected 44 alleles in locus *Cisco200* [17], whereas in present research there were detected only 31 alleles in the same locus. However, in some other locus there were revealed more alleles. For instance, there were revealed two more alleles in locus *Clatet13*, five more

alleles in locus *Clatet9* and one more in loci *Cisco126* and *Cisco90*. Despite this, it is one and a half and two times less than in vendace samples from economically valuable fishing areas in central and southeast Finland [8]. The possible reason of it may be that, vendace populations in Baltic Lakeland possibly went through the bottleneck in the past [13], [17], [42].

B. Population structure and spatial variation

The F_{ST} values of genetic differentiation between the studied vendace populations in Baltic Lakeland are shown in TABLE 3. The pair L. Strusto - L. Snudy displayed the smallest differentiation (0.007, p > 0.05), whereas the pairs L. Rudakova - Lake Drivyaty and L. Rudakova - Lake Drūkšiai had the highest F_{ST} values (0.309, p ≤ 0.01; 0.193, p ≤ 0.01 respectively).
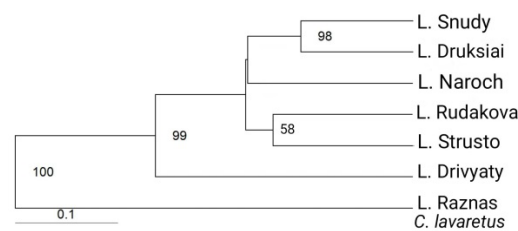

Fig.3. Genetic differentiation of seven studied samples from waterbodies in Baltic Lakeland as revealed by UPGMA tree using Nei et al., (1983) genetic distance (Da).

Besides *C. lavaretus* samples from L. Rāznas, high genetic differentiation shows also pair L. Drivyaty – L. Strusto (0.191, p > 0.05). For all other pairs, moderate genetic differentiation was shown, the FST values varied from 0.05 to 0.154 (p ≤ 0.001) (TABLE 3). The sequential BFC slightly change the significance level (P value) from the pairwise F_{ST} comparisons. Moderate level of genetic differentiation is reported for native whitefish populations in Scotland also have been shown [46]; the same recently was shown for some vendace populations in Baltic Lakeland [17]. So, we can assume, that lakes Naroch, Snudy-Strusto, Rudakova and Drūkšiai are isolated from each other; there is no migration and gene flow.

Little genetic differentiation between L. Strusto and L. Snudy is the smallest, which was revealed between vendace populations in Baltic Lakeland. These two lakes are connected by a channel and little genetic differentiation of vendace samples from these lakes confirms that there is active vendace migration between lakes. Similar little genetic differentiation was reported also for vendace populations after recent invasion in waterbodies in Finland [20]. So we can conclude, that little genetic differentiation between populations is revealed if there is gene flow between. However, Bayesian clustering does not assemble L. Strusto and L. Snudy into one genetic group (Fig. 2.). Earlier was shown also that genetic differentiation between vendace samples from waterbodies which is from different drainage systems is higher than between samples from waterbodies within the same drainage system [9], [17]. However we did not revealed such patterns in present research.

Bayesian clustering partitioned populations into two genetic groups (K=2; Fig. 2), placing lakes Naroch, Strusto and Rudakova in one group; and lakes Rāznas, Drūkšiai, Drivyaty and Snudy in the second group. The

UPGMA tree (Fig. 3) shows following grouping: L. Rāznas and L. Drivyaty were separated as two different branches, other five lakes branch out into separate group. L. Rāznas separated into different branch because it sample constitute of *C. lavaretus* individuals, which was taken as outgroup. Lake Drivyaty separation into different group is unclear; however it may be caused by the small sample size from this lake.

There are five samples from waterbodies which are placed on Belarus area and one from lake, which is placed on Belarus - Lithuanian area. Genetic variability and structure of them do not differ significantly, however all these have different management in the past and present, and the factors affected vendace in past. So, as it has been published earlier [17], [47], due to its economic importance European vendace has been artificially propagated in Latvia. Unfortunately its actions had not been successful, the stocks of vendace decreased and, now, it has protection status. Similarly, European vendace has been artificially propagated in Belarus to increase stocks of this valuable species. However these actions had not been successful [13], vendace's stocks reduced, and it has protection status now [5].

L. Drūkšiai has absolutely different history in this case. It is situated in north-eastern Lithuania. "From 1984, the water of L. Drūkšiai has been used for cooling reactor units of the Ignalina nuclear power plant (INPP). Before the beginning of the construction of the INPP (1950–1975), the fish community of Lake Drūkšiai had been dominated by stenothermal fish species: lake smelt *Osmerus eperlanus* (L.) and vendace *Coregonus albula* (L.), the biomass of which accounted for ca. 40% of the total fish biomass of the lake."[48]. In the first years of exploitation of the INPP (1984–1986) the biomass of vendaces decreased 58.8-fold [49]. During 5 years after the closure of the INPP vendace present one of the core species in the lake fish community [50]. Nowadays, Lake Drūkšiai is a water body of high productivity where both intensive amateur fishing and limited commercial fishing is allowed. The stocks in lake are rather high. So, there is successfully recovered vendace population in L. Drūkšiai. Now, about so substantial fluctuations in population`s size, possibly, indicate only number of alleles in population. Possibly such genetic properties could be formed much earlier.

Taking into account, given genetic diversity in studied vendace samples, can assume that there are various vendace populations in each of studied waterbodies. Vendace populations partially adapted to the changed environmental conditions, but in some of them it is quite fragile. So, it can assume that L. Snudy and L. Strusto vendace populations may be considered as one management unit, taking into account low genetic differentiation between these lakes. However, the Bayesian clustering do not reveals such grouping; so, there is need in additional studies (monitoring). As other studied vendace samples are isolated from each other, it could be considered as different management units to develop optimal strategy for their effective conservation and management.

Conclusion

The level of genetic variability was different in studied populations in Baltic Lakeland. The differences may be caused by genetic drift, which influence allele frequencies in various ways. Changes may be observed on the level of population genetic variability and genetic structure as a result of thermal regime changes and the impact of intensive anthropogenic eutrophication.

Present research could be useful in the design and monitoring of conservation programs of *Coregonus albula* populations in Baltic Lakeland.

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