

# GENETIC AND MORPHOLOGICAL VARIABILITY OF SMALL VENDACE (*COREGONUS ALBULA* (LINNAEUS, 1758)) POPULATION IN THREE LATVIAN LAKES

Natalja Škute, Jeļena Oreha, Aleksandra Morozova

Škute N., Oreha J., Morozova A. 2016. Genetic and morphological variability of small vendace (*Coregonus albula* (Linnaeus, 1758)) population in three Latvian lakes. *Acta Biol. Univ. Daugavp.*, 16 (1): 99–110.

Vendace (*Coregonus albula*) is a widely spread species in Holarctic waters. In Latvia vendace is included in the list of specially protected species in Latvia. In this research there were studied the some morphological changes in three small vendace populations after more than 50 years since the last studies. In addition, the genetic variability based on allozymes and RAPD markers was studied. It was shown that there are changes of meristic characteristics that have occurred since the previous studies. It was shown that the level of polymorphism and heterozygosity in three lakes' vendace populations are quite high, but the number of alleles per locus is quite small. The PCA plot revealed grouping of studied populations by the RAPD markers data better than those by the allozyme markers data.

Key words: *Coregonus albula*, allozymes, RAPD, polymorphism, genetic diversity.

Natalja Škute, Jeļena Oreha, Aleksandra Morozova. Department of Ecology, Institute of Life Sciences and Technology, Daugavpils University, Parādes 1A St., Daugavpils, LV-5401, Latvia, natalja.skute@du.lv

## INTRODUCTION

The vendace (*Coregonus albula*) is a widely spread species in Holarctic waters. It has reached Northwestern Europe after glaciation. The vendace is a polymorphic species of circumpolar distribution composed of several intraspecific forms. The vendace exhibits a great variation in morphological characteristics, at the population level as well. At the beginning of the last century, *Coregonus albula* was artificially introduced from Lake Peipus and Lake Ladoga to more than 30 Latvian lakes. In the 1990s, the vendace was detected only in five out of 30 lakes.

At the present moment it can be found in some Latvian lakes; however, the catch is insignificant and unstable. This species is included in the list of specially protected species with restricted use in Latvia (Regulation No 396 of the Cabinet of Ministers of the Republic of Latvia 14.11.2000).

Because of a high degree of variability of the vendace it seems to be important to determine the morphological changes in vendace populations that have occurred since the last studies of mid-twentieth century. The lack of basic data on biology and population status of the local vendace populations hinders sustainable utilization of this fish and efforts to manage its reproduction in Latvian lakes.

Morphological characteristics of the Latvian vendace were last studied in the 1950s-1960s (Laganovska 1957, Nikanorov 1964). The genetic study of the local population of vendace did not take place till the present moment. The assessment of the genetic variability is the first step in the evaluation of the long-term conservation status of species in natural habitats. This is an important issue for species with low population sizes exposed to the effects of inbreeding and genetic drift.

There are many types of molecular markers for study of genetic structure of populations: allozymes, RAPD, ALFP, microsatellites, regions of mitochondrial DNA and others. In this part of our study, we used such nuclear DNA markers as allozymes and RAPD. The enzyme gene variability has been widely applied in studies of fish population genetics (Cordes et al. 2005, Kumus et al. 2003). The genetics of vendace (*Coregonus albula*) has mainly been studied in Finland, Russia and Lithuania, using traditional allozymes markers (Vuorinen 1984, Vuorinen et al. 1991, Kaupinis et al. 2004, Kaupinis & Bukelskis 2010, Sendek 2004, 2011). This allows comparing our data with other genetic studies of

vendace populations living in similar conditions. As the RAPD markers are spread all over the genome (Williams et al. 1990), this technique is particularly useful in order to quickly find new changeable markers associated with visible indications, and especially for those species, on whose genome there is no or little information (Lynch & Milligan 1994, Corley-Smith et al. 2005). The RAPD-analysis can serve as a singular express method for detection the level of genetic polymorphism, which is particularly useful for little-studied taxonomic groups. Koljonen and Jurvelius, evaluated the success of vendace transfer into Lake Puruvesi in eastern Finland by enzyme electrophoresis and RAPD markers (Koljonen & Jurvelius 1995).

The aim of the present studies was to analyse not only some morphological changes that have occurred since the previous studies, but to perform preliminary analysis of genetic structure of small vendace populations from three different lakes of Latvia using allozymes and RAPD markers as well. These lakes, namely Nirzas, Rāznas and Sventes, are different by their areas, depths and trophic status. Nevertheless, nowadays the vendace practically does not occur in these lakes.



Fig. 1. The location of sampling sites. - Lake Sventes, Lake Nirzas and Lake Rāznas.

## MATERIAL AND METHODS

### Study sites and sample collection

Vendace (*Coregonus albula*) samples were collected from 3 Latvian lakes (two medium deep and one deep lake), namely Nirzas, Rāznas and Sventes, in 2007 (see location of lakes on Fig. 1) with the help of the Latvian Fish Resources Agency specialists. The features of the lakes under study are as follows: Nirzas (area 552 ha, maximum depth 21m) is a medium deep eutrophic lake, Rāznas (area 5756.4 ha, maximum depth 17 m) is a medium deep eutrophic lake as well, and Sventes (area 34.8 ha, maximum depth 38 m) is a deep meso-eutrophic lake, one of the deepest reservoirs in Latvia. For the genetic analysis the samples of fish tissue like skeletal muscles and liver were used. For the morphological and genetic analysis 30 vendace samples were examined. The samples of fish tissue were stored at -20°C until the allozyme analysis and the DNA extraction.

### Morphological analysis

The collected ichthyological material was measured using the whitefish measurement methods described by Pravdin (1966) and commonly used nowadays (Lajus 2001, Pereskokov & Rogozin 2001, Lajus 2003, Kaupinis & Bukelskis 2004, Gurichev & Belousov 2005). In order to evaluate the variation in some morphometric parameters (number of the perforated scales on lateral line (LL), number of gill rakes on the first left gill arch (sp.br.), anal fin ray number (RA)) that has occurred during the last 50 years, our data were compared to those collected from Lake Rāznas (Laganovska 1957), Lake Nirzas and Lake Sventes (Nikanorov 1964). The Student criterion was used to determine the significant differences. The difference between samples was considered to be significant, when  $P < 0.05$ .

The fish condition was assessed by analysing parameters  $k$  and  $n$  of the total length ( $L$ )-weight ( $W$ ) relationship ( $L$ - $W$ ):  $W = k \times L^n$ , where  $W$  - total fish weight (g),  $L$  - total fish length (mm),

$k$ ,  $n$  - constant parameters, calculated based on empirical data (Wootton 1996).

### Allozyme analysis

For the allozyme analysis the homogenate of skeletal muscles and liver tissue was used. The samples of tissue were homogenized in buffer 0.2 M Tris-HCl, pH 8, 0; 0.01 mg/ml Triton X-100; 4 mg/ml  $MgCl_2$ ; 0.2 mg/ml NADP at ratio 1:2 and analysed using polyacrylamide gels (5% or 10%) (Palauskas & Tubelyte-Kirdiene 2002) in two buffer systems (a): Tris- $H_3BO_3$ , pH 8.3 (Palauskas & Tubelyte-Kirdiene 2002) and (b): Tris-Glycine, pH 8.3 (Pobezhimova et al. 2004). Ten isoenzyme systems were analysed: aspartate aminotransferase (E.C. 2.6.1.1, Aat), superoxide dismutase (E.C. 1.15.1.1, Sod), alcohol dehydrogenase (E.C. 1.1.1.1, Adh), lactate dehydrogenase (E.C. 1.1.1.27, Ldh), malic enzyme (E.C. 1.1.1.40, Me), malate dehydrogenase (E.C. 1.1.1.37, Mdh), esterase D (E.C. 3.1.1.1, EstD), esterases (E.C. 3.1.1., Est), glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49, G6pdg), glycerol-3-phosphate dehydrogenase (E.C. 1.1.1.8, G3pdg). Histochemical staining was done by standard methods (Korochkin et al. 1977). The enzyme nomenclature by Shaklee recommendation (Shaklee 1990) was used. The enzyme and gene abbreviation was used according to Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology on the Nomenclature and Classification of Enzymes by the Reactions they catalyse. The isoenzyme loci were identified according to Vuorinen (1984) and Sendek (2000). Alleles were identified basing on relative electrophoretic mobility of allozymes and were designated in alphabetical order with "A" being the most anodally migrating allele. For the statistical analysis the computer program GeneAlex 6.41 (Peakall & Smouse 2006) was used. There were estimated the standard parameters of the gene diversity: percent of polymorphic loci (95%) ( $P$ ), number of alleles ( $N_a$ ), observed ( $H_{obs}$ ) and expected ( $H_{exp}$ ) heterozygosity. Deviations from Hardy-Weinberg equilibrium (HWE) were tested by  $\chi^2$ -test.

## RAPD analysis

The DNA was extracted from skeletal muscle tissue according to a salt-extraction method by Aljanabi (Aljanabi et al. 1997) standard protocol. In order to make the RAPD-RCR analysis the DNA was diluted to 10 ng/μl concentration. In the present analysis, there were used eight decanucleotide primers from sets A and B (Carl Roth, Germany). The amplifications were carried out in the thermal cycler ABI 9700 programmed for 35 cycles of 30 s at 94 °C, 30 s at 38 °C, and 30 s at 72 °C. RAPD-PCR reactions were performed at the volume of 12 μl on 0.2 ml 96-well plate (PCR reaction buffer with KCl, 25mM MgCl<sub>2</sub>, 0.7U Taq DNA polymerase (MBI Fermentas, Vilnius, Lithuania), 0.1% Triton X-100, 2mM dNTP mix, and DNA template). The PCR products were separated using the 1.4% agarose gel (Sigma) in TBE buffer (0.045 M Tris-borate and 0.001M EDTA). The gels were stained with ethidium bromide, and the DNA fragments were visualized using UVP Imaging system. The size of the DNA fragments was estimated by comparing them to 100bp DNA Lader Plus (MBI Fermentas, Vilnius, Lithuania) using Vision WorksLS Software. In order to confirm the reproducibility of the selected polymorphic bands the analysis of the same samples was made at least three times. The calculation of the genetic parameters of populations were calculated from the band presence-absence matrix by the program POPGENE V1.31 (Yeh et al. 1999).

## RESULTS AND DISCUSSION

The data on the current populations of vendace in Latvian lakes can provide information about the results of the vendace adaptation, and morphometric features may show changes since the previous studies. Some authors have noted radical changes in fish exterior features as a result of its acclimatization in new reservoirs (Burmakin 1963, Reshetnikov 1980). In order to compare the variation of some morphometric properties of *Coregonus albula* for the last 50 years, the data from Lake Rāznas and Lake Sventes populations (Laganovska 1957) and the

data from Lake Nirzas population (Nikanorov 1964) were used. Study of the changes in meristic parameters was made concerning such parameters as RA, LL, and sp. br. The obtained results are presented in Table 1. Essential changes of such parameters as RA and sp.br were revealed in all lakes except Nirzas. In the latter, the essential difference in average values is observed only in the RA parameter. The number of rays of the anal fin has increased in all lakes ( $p < 0.05$ ), whereas the number of gill rakers has diminished in all studied vendace populations ( $p < 0.05$ ).

Concerning the LL parameter in Lake Nirzas compared to the fish of Lake Rāznas and Lake Sventes the fish had smaller number of scales in the lateral line. Regarding the RA parameter the vendace in Lake Sventes had larger number of rays of the anal fin than the fish in Lake Rāznas and Lake Nirzas. The sp.br parameter of vendace revealed that the fish in Lake Nirzas had larger number of gill rakers than the fish in other lakes. Unfortunately, the data on environmental conditions and food reserves in these lakes 50 years ago are not available. It is known that variation in fish is particularly strongly influenced by the temperature (Burmakin 1963), which can affect a number of rays in unpaired fins, gill rakers and scales in the lateral line. In other words, in the lakes, where the incubation temperature on the spawning grounds is lower, the above mentioned parameters are increasing in number. The number of rays in the anal fin increased in all investigated vendace populations, while the number of gill rakers decreased (see Table 1) as it was mentioned above. Some authors believe that alongside the temperature the variation in the number of gill rakers is influenced by the quality of food reserve. Nikanorov (1964), for example, points out that the vendace has more gill rakers in water body with poorer food reserves. According to other studies, the vendace has a smaller number of gill rakers in the lakes, where it consumes larger zooplankton organisms (Reshetnikov 1980). It was shown that some meristic features of vendace and morphological parameters of lakes significantly correlated in studied vendace populations in Lithuania (Kaupinis & Bukelskis 2010). Therefore, the changes of meristic

Table 1. Morphometric characteristics of vendace in three Latvian lakes

Lakes	Date of sampling	RA		LL		SP.BR.	
		mean±se	P value	mean±se	P value	mean±se	P value
Nirzas	2007	12.92±0.14	*	78.31±1.11	ns	42±0.82	ns
	1964	11.22±0.04		80.31±0.2		40.8±0.17	
Sventes	2007	13.78±0.22	*	90.33±0.53	ns	39.8±0.17	*
	1957	12.19±0.06		90±0.33		44.3±0.17	
Raznas	2007	13±0.32	*	83±1.02	ns	36±1.29	*
	1957	11.48±0.09		83.26±0.22		40.9±0.35	

(RA, number of ray in anal fin; LL, number of scales on the lateral line; sp.br., number of gill rakers; ns, not significant differences ( $P > 0.05$ ); \* -  $P < 0.05$ )

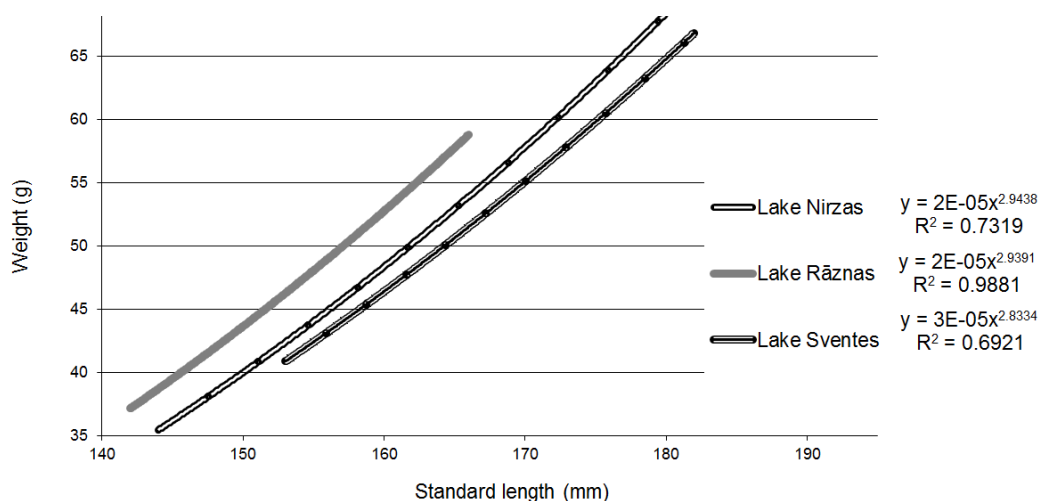


Fig. 2. Relationship between the total length and weight of vendace individuals in studied lakes.

characteristics can be considered as a result of adaptation of local vendace populations to the conditions of Latvian lakes that has been taking place during the last 50 years. In Lake Nirzas and Lake Rāznas the living conditions are more homogeneous, properties of lake are less variable, spawning grounds are concentrated in one place, and the simple relief provides homogeneous and quite stable conditions for vendace development and life. The adaptation of vendace populations to specific environmental conditions leads to changes in their morphological features, which has been proved by introduction of the vendace into new water bodies (Sirotkin 1990).

The fish condition was assessed by length-weight (L-W) dependence. Normally the individual's body length-weight (L-W) dependence was understood as growth rate of individuals. The fish growth rate from Lake Rāznas, Lake Nirzas and Lake Sventes is shown in Fig. 2. The growth rate of the vendace varies among lakes. The parameter  $n$  of the power function ordinarily shows that there are environmental conditions favourable or unfavourable for the vendace (it may be result of lower or higher production in these lakes). The length-weight relationship is usually a power function. The function exponent depends on fish body shape; in the "slender", fish the exponent is lower than 3 and becomes



Table 2. Level of heterozygosity in *Coregonus albula* populations in studied Latvian lakes

	Sventes	Nirzas	Rāznas
Hobs	0.23	0.19	0.17
Hexp	0.19	0.20	0.18
$\chi^2$ -test	ns	*	ns

(Hobs - Mean level of observed heterozygosity ; Hexp - Mean level of expected heterozygosity;  $\chi^2$ -test - significance level of differences between Hobs and Hexp; ns-not significant differences; \* -  $P < 0.05$ )

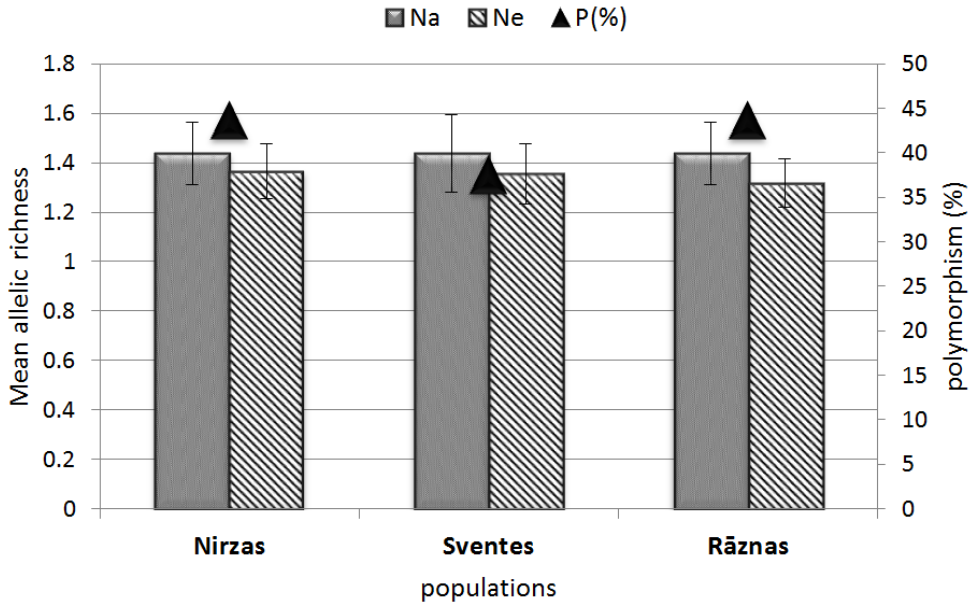


Fig.3. Allelic richness and polymorphism in *Coregonus albula* populations in studied lakes based on allozyme markers.

higher in the “stout” fish (Wootton 1996). The exponent in the vendace normally amounts to about 3 (Christianus 1995, Czerniejewski & Filipiak 2002), thus indicating an isometric growth of the species. In some crustacean plankton-rich lakes, the exponent is close to 3.5 (Winfield et al. 1996), but it may drop below 2.5 in the lakes characterised by environmental conditions that are not advantageous for the vendace growth (Czerniejewski & Filipiak 2002). The mean values of the coefficient  $n$  of the length-weight relationship of vendace from Lake Nirzas and Lake Rāznas were analogical (~2.94). Only in Lake Sventes the coefficient  $n$  of the length-weight relationship of vendace was

a bit smaller (~2.83), than in other our studied vendace populations. The exponent in the our studied vendace populations was similar to data reported by the some authors (e.g., Sutton et al. 2000, Czerniejewski et al. 2007) and bigger than in other vendace populations in commercially exploited lakes in Western Pomerania (Poland) (2.2 - 2.3) (Czerniejewski & Rybczyk 2008). It is noteworthy that the exponent  $n$  in our studied vendace populations indirectly indicated that the population being in good condition and that there are environmental conditions favourable for the vendace (it may be result higher production in these lakes). The vendace in Lake Sventes and Lake Nirzas was characterised by a higher

value of fish standard length and weight (Fig. 2). The smallest vendace individuals were in Lake Rāzna.

The study of genetic variability is the first step towards the understanding of process, which can influence the ecological stability of the local vendace population. Ten isoenzyme systems were studied. 20 enzyme loci of these systems were analysed. The analysed isoenzyme systems were analogical in studied vendace populations. There were nine monomorphic loci and ten polymorphic loci in vendace populations in Lake Rāznas and Lake Nirzas. However, 11 monomorphic loci and nine polymorphic loci were detected in vendace population in Lake Svantes. There were differences in superoxide dismutase system, e.g., one polymorphic locus was detected in vendace populations from Lake Rāznas and Lake Nirzas, and two monomorphic loci were detected in the vendace population from Lake Svantes.

Allelic richness and polymorphism in *Coregonus albula* populations in studied lakes based on

allozyme markers are shown in Fig.3. The total level of polymorphism based on the investigated isoenzyme polymorphic loci is 37.5 % (vendace from the deep Lake Svantes) and 43.8% (vendace from medium deep Lake Rāznas and Lake Nirzas). The total level of polymorphism in vendace population in Russian watercourses was about 40 - 50% (Sendek 2004.). However, the number of polymorphic loci varied from 25 to 75% in Lithuanian lakes' vendace populations (Kaupinis & Bukelskis 2010). The number of alleles per locus and effective number of alleles per locus are similar in all studied populations (Fig. 3), however is quite small in comparison with the number of alleles per locus in analogical studies in vendace populations from watercourse in Russian and Finland (Vuorinen 1984, Vuorinen et al. 1991, Sendek 2004, 2011). Perhaps it could be result of "founder effect", that may occur as result of vendace introduction in Latvian lakes.

It is considered that changes in level of heterozygosity in isoenzyme loci are associated with the fluctuations in population size (Nei & Graur 1984). The expected and observed level

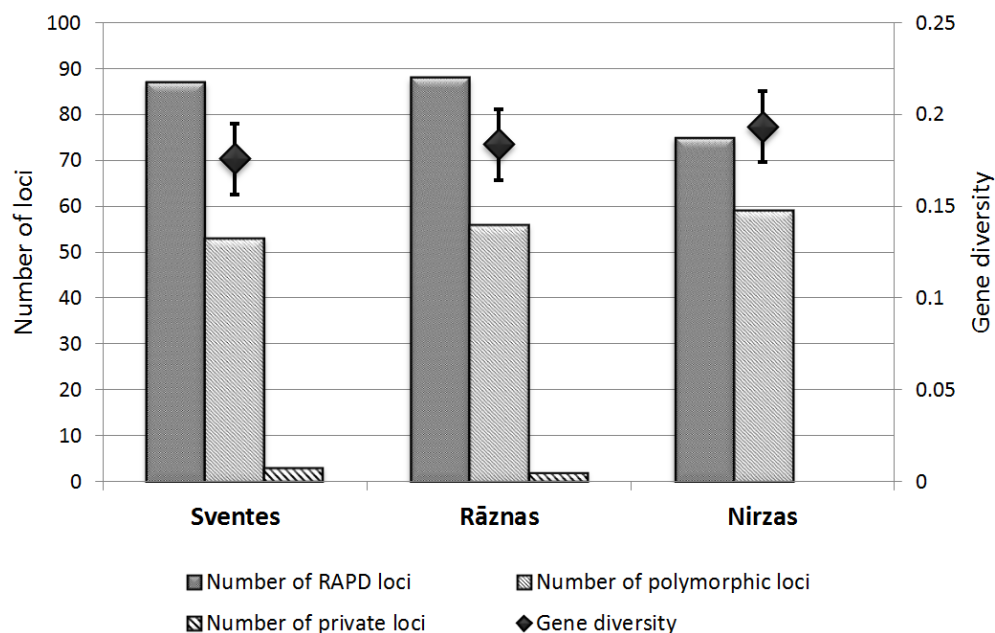


Fig. 4. Number of RAPD loci and gene diversity of *Coregonus albula* in three Latvian lakes, based on RAPD markers.

of heterozygosity (by HWE) in three vendace populations is shown in Table 2. As we can see, the observed level of heterozygosity slightly differs in studied vendace populations. The level of heterozygosity is variable in different loci. However, the average level of the observed heterozygosity is quite high (0.17 to 0.22) compared to other studies, where this parameter varies from 0.048 to 0.104 in the vendace populations in Finland watercourses (Vuorinen 1984) and from 0.095 to 0.099 in the vendace population from the Lake Ladoga in Russia (Sendek 2002).

It is suggested (Williams et al. 1990) that RAPD analysis gives more accurate estimates between closely related populations. The results of RAPD analysis indicated that 58 loci (bands) were marked for all studied populations, 23 of them were polymorphic, 16 were monomorphic for all studied vendace populations and 19 loci varied in different populations as monomorphic or polymorphic.

The number of RAPD loci and gene diversity of *Coregonus albula* populations in three Latvian lakes are shown in Fig. 4. The percentage of the polymorphic loci ranged from 49.35% in Lake

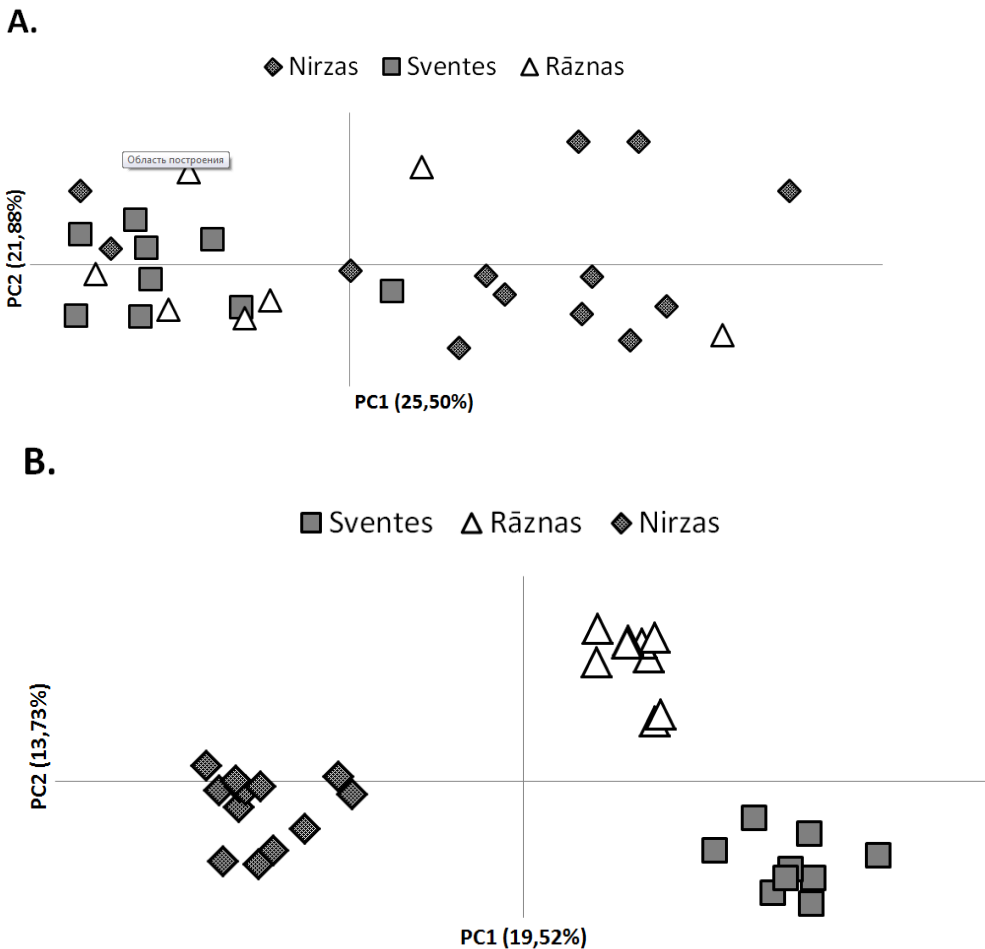


Fig.5. Principal component analysis (PCA) plot of the genetic structuring among the three vendace populations. A). PC1 and PC2 explain 25.50% and 21.88% of the total variation, respectively (by allozyme markers); B). PC1 and PC2 explain 19.52% and 13.73% of the total variation, respectively (by RAPD markers).



Sventes vendace population to 61.04% in Lake Nirzas population. The level of polymorphism in Lake Rāznas had an intermediate value (55.84%). It can be seen (Fig. 4) that there are eight private loci in Lake Sventes' vendace population, however there are no private loci at all in Lake Nirzas' vendace population. Possibly, it could be associated with significant fluctuation in population size in Lake Nirzas and with not so significant fluctuations in Lake Rāznas, which could cause such differences in the number of private alleles.

Principal component analysis (PCA) plots of the genetic structuring among the three vendace populations are shown in Fig. 5. The PCA plot by allozyme markers revealed grouping of Lake Sventes, Lake Rāznas and Lake Nirzas (figure 4 (A)). Each axis, PC1 and PC2, explained 25.50% and 21.88% of the total variation, respectively. The PCA plot by RAPD markers revealed all studied vendace populations separately (Figure 5 (B)). Each axis, PC1 and PC2 explain 19.52% and 13.73% of the total variation, respectively. As could be seen the PCA plot by RAPD markers revealed grouping more obvious. Probably this is because of bigger DNA region was scanned by RAPD markers, than it done by allozyme markers.

As a result of the fact that studied lakes differ by their morphometric characteristics, the influence of environment factors could have a different effect on the studied vendace populations. Furthermore, this effect could be reflected on vendace populations' genetic structure.

## CONCLUSION

The mean level of protein polymorphism in vendace populations in Latvia is 41.67%, but the mean level of polymorphism based on RAPD is 55.41%. The level of heterozygosity is quite high in all investigated populations. It's possible that the little differences between observed and expected level of heterozygosity in particular loci in investigated populations can be caused by the genetic drift. In particular, it is worth to

notice that a possibility of migrants from the other lakes is limited. The investigated populations are closely related to each other (according to enzyme systems), but genetic grouping based on RAPD marker assays are more obvious for studied vendace populations. Obtained private loci (based on RAPD markers) give the opportunity to develop markers for identification of vendace individuals of these populations.

The recognized morphological features' changes in three Latvian lakes' vendace populations possibly show its adaptation to specific environmental conditions.

## REFERENCES

- Aljanabi S. M., Martinez, I. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research.*, 25(22): 4692–4693.
- Corley-Smith G.E., Wennerberg L., Schembri J.A., Lim C.J., Cooper K.L., Brandhorst B.P. 2005. Assignment of Sockeye Salmon (*Oncorhynchus nerka*) to spawning sites using DNA markers. *Marine Biotechnology*, 7(5): 440-448.
- Burmakin E.V. 1963. Akklimatizacija presnovodnyh ryb v SSSR. (Acclimatization of freshwater fishes in USSR). *Izvestija gosudarstvennogo nauchno – issledovatel'skogo instituta ozernogo i rechnogo rybnogo hozjajstva*, LIII: 314 s. (In Russian).
- Christianus J. 1995. Age and growth of selected vendace (*Coregonus albula* L.) populations in Poland. *Archiv für Hydrobiologie. Special Issues in Advanced Limnology*, 46: 97-102.
- Cordes J.F., Perkins D.L., Kincard H.L., May B. 2005. Genetic analysis of fish genome and allozymes variation within and among Atlantic salmon from Downeast river of Maine. *Journal of Fish Biology*, 67(Suppl. A): 104-117.

- Czerniejewski P., Wawrzyniak W., Stepanowska K. 2007. Variability of Length and Weight growth rates in the vendace *Coregonus albula* (L.) from some Western Pomeranian lakes. *Acta Sci. Pol., Piscaria*, 6 (3–4): 13–32.
- Czerniejewski, P., Filipiak, J. 2002. Biological and morphological characteristics of vendace, *Coregonus albula* L. from lakes Drawsko and Pelcz. *Acta Ichthyol. Piscat*, 32 (1): 53–69.
- Czerniejewski, P., Rybczyk, A. 2008. Variations in age and length growth rates of vendace, *Coregonus albula* (L.), from selected lakes in Western Pomerania. *Archives of Polish Fisheries*, 16(1): 63–74.
- Gurichev P.A., Belousov I. Ju. 2005. Vnutrividovaja differenciacija siga guby Keret' Belogo morja i priliezhashhih ozer. (Intraspecific differentiation of the whitefish in the White Sea Bay of Keret and adjacent lakes.) *Materialy IX mezhdunarodnoj konferencii: Problemy izuchenija, racional'nogo ispol'zovanija i ohrany resursov Belogo morja*, 87 – 91s. (In Russian).
- Kaupinis A., Bukelskis E. 2004. Vendace (*Coregonus albula* (L.)) growth and morphological diversity in lakes of Lithuania. *Acta Zoologica Lituanica*, 14(1): 3–12.
- Kaupinis A., Bukelskis E. 2010. Morphological and genetic variations in vendace (*Coregonus albula* (L.)) in the lakes of Lithuania. *Acta Zoologica Lituanica*, 20(1): 51–60.
- Kaupinis A., Paulauskas A., Bukelskis E. 2004. Izoenzyme systeme and genotypes in vendace (*Coregonus albula* (Linnaeus, 1758)) from Lithuanian lakes. *Acta Zoologica Lituanica*, 14(2) 3–13.
- Koljonen M.-L., Jurvelius J. 1995. Onkamosta istutettu murkku lisaaty Puruvedessa. *Suamen Kalastuslehte*, 3: 12–15.
- Korockin L.I., Serov O.A., Pudovkin I.I. 1977. *Genetika izofermentov.* (Genetics of isoenzymes.) Moskva: Nauka, 278. (in Russia)
- Kumus I., Ciftci Y., 2003. Fish Population Genetic and Molecular Markers: Fisheries and Aquaculture. *Turkish Journal of Fisheries and Aquatic Sciences*, 3:51–79.
- Laganovska R. 1957. Latvijas PSR ezeru repsis – *Coregonus albula* un ta biologija. *LPSR ZA Vēstis*, 3 (116): 83 – 96.
- Lajus D.L. 2001. Variation patterns of bilateral characters: variation among characters and among populations in the White Sea herring (*Clupea palasi marisalbi*) marisalbi). *Biol. J. Linn. Soc.*, 74: 237–253.
- Lajus D.L., Knust R., Brix O. 2003. Fluctuating asymmetry and other parameters of morphological variation of eelpout *Zoarces viviparus* from different parts of distributional range. *Sarsia*, 88: 247 – 260.
- Lynch M., Milliga, B.G. 1994. Analysis of population genetic structure with RAPD markers. *Molecular Ecology*, 3:91–99.
- Nei M., Graur D. 1984. Exten of protein polymorphism and the neutral mutation theory. *Evolution Biology*, 17:73–118.
- Nei M. 1973. Analysis of gene diversity in subdivided populations. *PNAS*, 70: 3321–3323.
- Nikanorov Ju.I. 1964. Morfologicheskie osobennosti lokal'nyh stad evropejskoj rjapushki *Coregonus albula* v zavisimosti ot uslovij obitanija (Morphological peculiarities of the local populations of European vendace *Coregonus albula* subject to living conditions). *Voprsy ihtiologii*, 4, 3(32), 411 – 422 s. (In Russian).
- Palauskas A., Tubelyte-Kurdiene V. 2002. *Practicum in Genetics. Part III. Genetics*

- p>of isoenzymes. Kaunas. Vytauta Magnus University publishers. (In Lithuanian )
- Peakall R., Smouse P.E. 2006. GENALEX6 genetic analysis in Excel Population genetic software for teaching and research. *Molecular Ecology*, 6: 228-295.
- Pereskokov A.V., Rogozin A.G. 2001. Hekotorye osobennosti chudskogo siga iz ozera Bol'shoe Miassovo (Some peculiarities of the Choud whitefish from the Lake Bolshoje Miassovo). *Izvestija Cheljabinskogo nauchnogo centra*, 4 (13), 68 – 72 s. (In Russian).
- Pobezimova T.P., Kolesnichenko A.V., Grabeljnih O.I. 2004. Elektroforeticheskiye metodi issledovaniya belkov. [Electrophoretic methods of protein study]. V: Metodi izuchenija mitochondrij rastenij. Poljarografija i elektroforez. Moskva: OOO NIK promekobezopasnostj, 37–69. (in Russian).
- Pravdin I. F. 1966. Rukovodstvo po izucheniju ryb (A Gide to Fish Studies). Moskva: Pishhevaja promyshlennost', 375 s. (In Russian).
- Reshetnikov Ju. S. 1980. Jekologija i sistematika sigovyh ryb (Ecology and Systematics of Coregonids). Moskva, Nauka. 300 s. (In Russian).
- Sendek D.S. 2004. The origin of sympatric forms of Eiropian whitefish (*Coregonus lavaretive* L.) in Lake Ladoga based on comparative genetic analysis of populations in North-West Russia. *Annalas Zooligici Fennici*, 41: 25-39.
- Sendek D.S. 2011. Origin of the Coregonid Fish Populations in the Russian Part of the Gulf of Finland (The Baltic Sea). 11th International Symposium on the Biology and Management of Coregonid Fishes, 26-30 September, Mondsee, Austria (poster).
- Sendek D.S. 2000. Phylogenetic analysis of Coregonid fishes by means of allozyme electrophoresis method. PhD thesis. St.Petersburg, 214 pp.
- Shaklee J.B., Allendorf F.W., Shaklee J.B., Allendorf F.W., Morizot D.C., Whitt G.S 1990. Gene nomenclature for protein-coding loci. *Transactions of the American Fisheries Society*, 119: 2-15
- Sirotkin, V.P., 1990. Osobennosti jekologii Ladozhskogo ripusa, akklimatizirovannogo v raznotipnyh ozerah Severnogo Kazahstana. Avtoreferat dissertacii kandidata biologicheskikh nauk. Moskva, MGU (In Russian).
- Sutton S.G., Bult T.P., Haedrich R.L. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. *Transactions of the American Fisheries Society*, 129: 527-538.
- Vuorinen J. 1984. Electrophoretic expression of genetic variation and duplicate gene activity in vendace, *Coregonus albula* (Salmonidae). *Hereditas*, 101: 85-96.
- Vuorinen J.A., Næsje, T.F., Sandlund, O.T. 1991. Genetic changes in a vendace *Coregonus albula* (L.) population, 92 years after introduction. *Journal of Fish Biology*, 39(A): 193-201.
- Williams J.G.K., Kubelik A.R., Lian K.J. Rafalski J.A., Tingey S.V. 1990. DNA polymorphism amplified by arbitrary primers are useful as genetic markers. *Nucl. Acid. Res.*, 18: 6531-6535.
- Winfield I.J., Adams C.E., Fletcher J.M. 1996. Recent introductions of the ruffe (*Gymnocephalus cernuus*) to three United Kingdom lakes containing *Coregonus* species. *Annales Zoologici Fennici*, 33: 459-466.

Wootton R.J. 1996. Ecology of teleost fishes.  
London: Chapman and Hall, 404 pp.

Received: 10.07.2016.

Accepted: 12.05.2016.

Yeh F.C., Yang R., Boyle Y. 1999. POPGENE.  
Version 1.31 Microsoft Window-Based  
Freeware for Population Genetic Analysis  
Quick User Guide University, USA.