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Keywords

Fish domestication, genetic diversity, Lake Genevea, Lake Neuchâtel, Perca Fluviatilis.

Abstract

In this study, the genetic diversity of Eurasian perch Perca fluviatilis was compared between two lakes, Lake Geneva and Lake Neuchâtel, which are only separated by 50 km and often used to establish the broodstock for farming. Perch were sampled in six localities in Lake Geneva, and two localities in Lake Neuchâ-tel. Analyses were performed using twelve microsatellites in June 2012 (spawning period) and September 2012 (early autumn). Results revealed that perch populations in Lake Geneva were genetically different than those of Lake Neuchâtel. Genetic diversity of perch in Lake Neuchâtel (mean number of allele A = 6.91, allelic richness Ar = 5.19 and observed heterozygosity Ho = 0.607) were significantly higher than for perch in Lake Geneva (A = 6.08 Ar = 5.86 and Ho = 0.416). Some private alleles were present and characterize each lake population. According to FST-pairwise estimates, populations of the two lakes were significantly different. Some hypotheses that may explain this difference are discussed: the nature of the watershed and the anthropic pressures, as fishing pressure and aquaculture practices. Even at a fine-local scale, the choice of the origin of a wild population influences the initial genetic variability introduced in the farming system at the first step of domestication

1. Introduction

For two decades, the aquaculture of percid fishes, especially Eurasian perch Perca fluviatilis Linnaeus, 1758, has appeared as a way of diversification for the European inland aquaculture (Fontaine, 2009; Fontaine and Teletchea, 2019) and new fish farms based on intensive Recirculating Aquaculture Systems (RAS) technology were built in Europe, mainly in France, Germany, Ireland and Switzerland (Steen-feldt et al., 2015). The main market targeted by these farms is located in the Alpine region surrounding Switzerland and desired products are whole fish weighing 80-120 g or small fillets of 15-25 g (Toner, 2015). Because fishery activities existed in numerous Alpine lakes for a very long period of time, this niche market is characterized by a strong link between the fish and the local territory as consumers wish to eat perch from local lakes. The Eurasian perch has a large native distribution area and is present in various aquatic ecosystems such as rivers, lakes and ponds (Stepien et al., 2015). It has been demonstrated that the characteristics of habitats influence the quality of the Eurasian perch caught for human consumption (Thomas et al., 2015). For example, the comparison of the quality, which is a complex and multifactorial concept (Thomas et al., 2015), of perch from the estuary of the Rhine River and the Geneva Lake showed that fish morphology and colour, as well as the nutritional quality of the flesh (fillets), were highly related to perch origins (Mairesse et al., 2005, 2006). Also, morphological divergence between near-shore littoral and open-water pelagic perch substantially increased with increasing water transparency (Bartels et al., 2012). That explains why Eurasian perch farms have mainly start their production by catching fertilized egg ribbons in some Alpine lakes, as they want to produce perch with a specific shape and other quality attributes required by consumers in this region.

However, in aquaculture, the control of product quality is not the only stake for fish farmers, the knowledge of the genetic resources is of primary importance to better understand changes in husbandry performance and to assess the potential for further selective breeding programs (Ben Khad-

her et al., 2016). Even if globally, Alpine Eurasian perch populations belong to a same genetic pool (Nesbo et al., 1999), recent studies conducted at a smaller geographical scale (local hydro systems), such as in Lake Constance, Germany (Gerlach et al., 2001), identified different intra-genetic structure of perch populations. In fact, perch populations inhabiting different Alpine lakes, which are connected to different watersheds (Danube, Rhine, Rhône), could display different genetic diversities. Such situation could have consequences on the performance of broodstock in fish farms.

As fish farmers often establish their initial broodstock with fish from Lake Geneva and/or Lake Neuchâtel (Ben Khadher et al., 2016), a study was conducted in order to analyse and compare the genetic diversity and structure of the Eurasian perch populations in these two lakes.

Those lakes were studied during the spawning season (June) and later in September to reveal if genetic patterns change outside spawning period and following juvenile dispersion.

2. Material and Methods

2.1. Sampling location

Lake Geneva is the largest alpine lake located between France and Switzerland (46°26'N, 6°33'E) with a surface area of 580 km2 and a maximum depth of 309 m (International Committee for the Protection of Lake Geneva: Commission Internationale pour la Protection des Eaux du lac Léman, CIPEL). It is divided into two sub-lakes: the eastern Upper Lake and the western Lower Lake (CIPEL, 2005). Lake Geneva belongs to Rhône watershed. The Rhône begins at the Rhône Glacier in the Swiss Alps and flows into the Mediterranean Sea

Lake Neuchâtel is a pre-alpine lake, located in Switzerland (46°54'N, 6°52'E) and is the nearest lake to Lake Geneva (only 50 km separate them). In contrast to Lake Geneva, Lake Neuchâtel has a smaller surface (215 km2), a maximum depth of 153 m and is not divided into two parts. Lake Neuchâtel belongs to Rhine watershed, which begins in Gotthard massif and flows into the North Sea.

2.2. Fish sampling

Perch were sampled during June 2012 (349 individuals) and September 2012 (329 individuals). Fish were collected around the Lake Geneva and the Lake Neuchâtel, in six and two localities, respectively (Fig 1). Sample sizes varied from 85 in Neuchâtel (Lake Neuchâtel) to 349 in Lake Geneva. Fish were caught by professional fishermen using traps and nets at depth of 5 to 20 m. Size of sampled individuals varied from 8.0 to 40.0 cm and fin clips were stored in 95% ethanol for genetic analyses.

2.3. DNA extraction, amplification, and microsatellitegenotyping

DNA was extracted with a modified high-salt DNA extraction protocol (Aljanabi and Martinez, 1997). Twelve microsatellite markers were used: PflaL1, PflaL2, PflaL4, PflaL6, PflaL9, PflaL10 (Leclerc et al., 2000), and YP60, YP78, YP111 (Li et al., 2007) that were previously developed for yellow perch (Perca flavescens (Mitchill, 1814)); SviL7 (Wirth et al., 1999), and Svi17, Svi18, (Borer et al., 1999) that were developed for walleye (Sander vitreus (Mitchill, 1818)). For each sample, PCR and genotyping were conducted in four multiplex using the QIAGEN Multiplex reactions PCR Plus Kit and fluorescently labelled primers (VIC, NED, 6-FAM and PET). The design of multiplex was based on the size range of the different loci to avoid crosschecking between primers and on the optimised annealing temperatures. PCR reactions were carried out in a total volume of 10 µL containing 1 µL of genomic DNA (40 ng/µL), 5 µL of Master mix (Qiagen), and 1 µL of primer mix at a concentration (0.2 µM of each primer) recommended by the Kit manufacturer. Amplifications were performed in a BioRad DNA thermal cycler as follows: 5 min at 95°C, followed by 30 cycles of 30 s at 95°C, 90 s at the annealing temperature (48 and 55°C), and 30 s at 72°C, with a final extension of 45 min at 60°C. PCR products for each sample (3 µL) were mixed with 15 µL of Hi-DiTM Formamide and 0.2 µL of the size standard GeneScanTM 600 LIZ® (Applied Biosystems). They were then genotyped and visualized using an ABI 3130XL Prism automated sequencer.

2.4. Genetic analysis

Allele sizes were determined with GENEMAPPER 4.0. Potential errors (allelic dropouts, stuttering or null alleles) were investigated with MICROCHEKER (Van Oosterhout et al., 2004). Linkage disequilibrium and conformation to HWE (Hardy-Weinberg Equilibrium) were estimated between loci and at each locus by exact tests with 1,000 Markov Chain iterations under the null hypothesis of identical allelic distribution between samples using GENEPOP 4.2.1 (Raymond and Rousset, 1995). Deviations from HWE for each locus and each site were calculated as a chi-square test of observed and expected heterozygosity.

To assess the level of genetic diversity, mean number of alleles per locus (A), observed heterozygosity (Ho), and expected heterozygosity (He) were determined with GENETIX 4.05 (Nei, 1978; Belkhir et al., 2004). The allelic richness (Ar) and private alleles (Ap) were estimated with HP-RARE 1.1, which is a program that compensates for sampling disparity using rarefaction (Petit et al., 1998; Kalinowski, 2005). Rarefaction method allows to measure the number of alleles per locus in samples of uneven size to produce unbiased estimates of allelic richness (Petit et al., 1998; Kalinowski, 2005). Minimum sample size considered for calculating Ar and Ap was 52. Allelic richness and observed heterozygosity have been tested by ANOVA test with R program and Tukey's post-hoc test (p-value < 0.05).

Global and specific Wright's F-statistics between sites (FIS and FST) were calculated according to Weir and Cock-erham (1984) using GENEPOP and GENETIX. GENETIX was also used for Factorial Correspondence Analysis (FCA), which gives a visual representation of individual genotype clustering. To investigate the genetic differentiation between sites, FST-

pairwise values were calculated according to Weir and Cockerham (1984) and p-values were estimated using the genic differentiation test (Dememorization: 10,000; Batches: 100; Iterations per batch: 5,000) implemented in GENEPOP (Rousset, 2008). Significance levels for HWE and pairwise FST-values were adjusted using Bonferroni corrections (Rice, 1989).

In order to detect possible genetic clusters (K) in Lake Geneva and Lake Neuchâtel, a Bayesian clustering analysis implemented in STRUCTURE 2.3.4 (Pritchard et al., 2000) was run using an admixture model with independent allele frequencies. Different K (ranging from 1 to 7) were tested for each lake separately and then for the two lakes together. Ten independent runs for each K = 1-7 involved a burn-in of 10,000 Markov Chain Monte Carlo (MCMC) iterations, followed by 100,000 replications. Admixture model with independent allele frequencies were assumed. STRUCTURE HARVESTER v0.6.94 (Earl and VonHoldt, 2012) was used to estimate the most likely number of K.

3. Results

3.1. Genetic variability within populations

A total of 682 individuals from 6 sampling sites at two different periods and 173 individuals from 2 sampling sites at two different periods sampled in Lake Geneva and Lake Neuchâtel, respectively, were genotyped at twelve microsatellite loci (Tabs I, II). No scoring errors due to either stuttering or null alleles were observed using MICROCHECKER.

All 12 microsatellite loci were polymorphic in all sampling localities. The allelic richness varied from 2.00 for Svi18, PflaL6 and YP111 to 12.79 for PflaL9 (Tabs I, II).

In Lake Geneva, the number of alleles and observed heterozygosity were not significantly different from June to September with a mean value of 4.39 and 0.416, respectively. However, the mean number of alleles and observed heterozygosity were significantly higher in Lake Neuchâtel, and values were 6.58 and 0.607, respectively (Tab. I).

Each population displayed some private alleles, which did not exist in the other lake (Tab. III). Lake Geneva population had 18 alleles (among a total of 90 alleles), while Lake Neuchâtel population displayed 25 private alleles (among a total of 97) (Tab. III). Such locus presented more private alleles than others, like PflaL9 and YP78. Private alleles of YP78 were present in high frequencies, for example a frequency of 0.7892 in Neuchâtel population (Tab. III).

Observed heterozygosity (Hobs) varied from 0.04 for SviL7 and PflaL4 in Lake Geneva to 0.928 for PflaL9 in Lake Neuchâtel. Excess and deficit of heterozygosity were observed at several loci for the two lakes (Tabs I, II). Individuals sampled during June 2012 showed a highly significant excess of heterozygosity ($p < 0.001$) for both lakes, which could result from relatedness among sampled individuals during the spawning period.

Allele frequencies deviated significantly from HWE at PflaL10 and YP 111 during June 2012 and at Svi17 during September 2012, in Lake Geneva (Tab. i). The linkage disequilibrium test showed that only 0.95% of comparisons deviated significantly. In Lake Neuchâtel, allele frequencies deviated from HWE at PflaL9, YP111 and YP78 ($p < 0.05$). For all loci and all sampling localities combined, allele frequencies did not deviated from HWE ($p = 0.079$) (Tab. i). In Lake Neuchâtel, 4.54% of comparisons did not conform to the Linkage Disequilibrium expectation after Bonferroni corrections (threshold = 5%).

3.2. Differentiation between populations

FST-pairwise comparisons showed that individuals from all sampling localities in Lake Geneva were significantly different from those sampled in Lake Neuchâtel (Tab. iV).

Factorial Correspondence Analysis (FCA) grouped Lake Geneva population and Lake Neuchâtel populations in distinct clusters. Global FST value was 0.0032 in Lake Geneva and 0.1296 in Lake Neuchâtel. The mean value of all pair-wise comparisons between Geneva and Neuchâtel populations was highly significant, with a value of 0.14 ($p < 4.7$ 10–4). Significant divergences were also observed between individuals sampled in Neuchâtel during the two periods (FST = 0.0108; p-value < 0.001) (Tab. IV).

Bayesian clustering analysis showed the presence of a single population in Lake Geneva, whilst two sub-populations were found in Lake Neuchâtel. The determination of the most probable K confirmed the presence of two sub-populations in Lake Neuchâtel. The second cluster was mainly present in sampling locality S8 during September 2012 (NP2) (Fig. 2).

4. Discussion

Previous studies (Ben Khadher et al., 2015) reviewed genetic characteristics of Eurasian perch population in Lake Geneva, however this study provides the first comparison between the two-founder supposed lakes for perch aquaculture.

The populations of perch from these two lakes are genetically different. In addition, each lake population presented some private alleles. In Lake Geneva, sampling localities covered the whole lake, whilst only the downstream part of Lake Neuchâtel was sampled here (only 9 km separated the two sampling localities on both shores). Despite this, genetic variability, number of alleles and observed heterozygosity were higher within Lake Neuchâtel than Lake Geneva populations. These two lakes are geographically close, only 50 km separate them; yet they are located on two different watersheds. Therefore, the two lakes are not connected and thus, fish populations may be genetically different. Previous studies in Lake Constance (Gerlach et al., 2001), which is located on Rhine basin as Lake Neuchâtel, have also found the presence of two sub-populations of perch. Lake Constance is a pre-alpine lake located in Germany, Switzerland and Austria (47°36'N, 9°24'E). Studies on Lake Erken (located in

Sweden, 59°50'N, 18°37'E) have also found the presence of different populations of perch (Bergek and Bjorklund, 2007). These lakes present also different char-acteristics, among which size and shape: Lake Erken has a water surface of 24 km2 and a maximum depth of 21 m and is divided in two parts (Bergek and Bjorklund, 2007); Lake Constance covers 536 km2, has a maximum depth of 254 m and is divided in two parts (Behrmann-Godel and Gerlach, 2008).

Comparing the four lakes, Lake Constance, Lake Erken, Lake Geneva and Lake Neuchâtel, surface area would not be a major factor explaining the genetic diversity of perch populations. In the smallest lake (Lake Erken), several populations were identified, whilst in the largest one (Lake Geneva in this study), only one was found. Besides, in Lake Erken, Bergek and Bjorklund (2007) suggested that open water may constitute a physical barrier to gene flow. In this lake, the major genetic discontinuity was detected between individuals sampled in the centre and littoral sites and were separated by deep sections. However, if open water really presents a barrier, it would restrain perch dispersion in the deepest lake. Yet, in Lake Geneva, physical barrier did not restrict perch dispersion. Moreover, unlike Lake Constance, no clear discontinuity between upper and lower Geneva parts was observed (Ben Khadher et al., 2015).

As mentioned previously, genetic variability for Lake Neuchâtel population was higher than in Lake Geneva. Lake Geneva is located in the upstream of the Rhône, which it is the main inflow with Dranse River in this lake. All its tributaries are cold trout rivers, unfavourable to perch. Consequently, there is probably no supply of perch in Lake Geneva, in exception from the Rhône. In contrast, Lake Neuchâtel is located further downstream of the Rhine, which crosses several lakes before flowing into Lake Neuchâtel. Also, this lake is connected to Lake Morat and Lake Biel. Therefore, perch populations in Lake Neuchâtel are not isolated as those of Lake Geneva.

From 1960, Lake Geneva experienced serious eutrophication period until 2000. During this eutrophication period, perch population in Lake Geneva has increased and was overexploited. Thereafter, perch stocks have suddenly declined in 1975 (Dubois et al., 2008). Since this date, perch stocks continue to decline and fishing captures became unstable. As a consequence, genetic variability has perhaps incurred a sharp reduction due to overfishing (went through a bottleneck) as shown in other species, such as the Atlantic cod Gadus morhua Linnaeus, 1758 (Hutchinson et al., 2003), the northern red snapper Lutjanus campechanus (Poey, 1860) (Saillant and Gold, 2006) or the New Zealand snapper Pagrus auratus (Forster, 1801) (Hauser et al., 2002). For this latter species, populations in both Hauraki Gulf and Tasman Bay (New Zealand) have been overexploited in the mid-1980s. To understand overexploitation effect on New Zealand snapper population, DNA from dried scales from 1950 to 1986 were analyzed, using seven microsatellites. Results showed a significant genetic diversity reduction during its exploitation history, especially for Tasman Bay. In addition, effective population size values were five orders of magnitude lower than census values (Hauser et al., 2002). Therefore, overfishing may also partly explain why genetic variability of perch population in Lake Geneva is low. However, even perch population in Lake Neuchâtel had been fished, but there is no information about the degree of fishing pressure and its influence on perch stocks.

Another hypothesis may explain why genetic variability is higher in Lake Neuchâtel. Floating cages were installed (from 1999 to 2011) in Lake Neuchâtel, containing perch juveniles obtained in hatchery. Those juveniles were supposed to come from the same lake; however, no information about hatchery breeding program can confirm it. In hatchery, there are most often different stocks from different origins that are mixed and thus, we cannot be sure that farmed juveniles are really from Lake Neuchâtel (Ben Khadher et al., 2016). We cannot exclude that perch from populations other than from Neuchâtel were used, and thus may have escaped and introgressed the local population, resulting in an increase of the genetic variability (Youngson et al., 2001; Vandeputte, 2012).

Our study clearly showed that the choice of the natural hydrosystem sampled and consequently, the initial wild individuals as founder populations, highly influences the initial genetic variability introduced in the rearing system, even if hydrosystems are very closed and similar. In the case of Eurasian perch from Alpine lakes, the genetic structure seems to be highly variable from one lake to another, independently to its size. For aquaculture purpose and a better management of the first steps of a domestication process (before closing the broodstock and the application of breeding programs (Teletchea and Fontaine, 2014), an analysis of the genetic structure of perch population at a local scale (intra-lake level) appears necessary to better know the initial genetic variability caught from the hydrosystem. This study provides initial information about the genetic characteristic of Geneva and Neuchâtel populations. Perch farms managers will have the opportunity to identify which population may supplement their stocks and, if necessary, increase the allele's number of their captive population.

Intra- and inter-lakes genetic variability could explain important differences observed in survival, growth and food intake according to geographical origin of perch populations (Mandiki et al., 2004). In future research, the potential of the wild populations, including their genetic structure, should be specified to optimise the domestication process. Lake Neuchâtel populations should not be managed as a single stock, unlike Lake Geneva population.

5. Conclusion

Perch populations of Lake Geneva and Lake Neuchâtel were genetically different. Genetic variability in Lake Gene-va population was lower than Lake Neuchâtel population.

For the domestication of the Eurasian perch, the choice of the initial hydrosystem to establish initial population is very important. A better knowledge of the initial genetic structure of wild populations is required before starting the domestication of a species. This study provides primordial information, for perch farmers, concerning genetic diversity and private alleles, which could be targeted to enhance their stocks. According to farm goals, the choice of founders can differ. If farmers target Geneva "strain" of perch, they must not mix Neuchâtel populations in their stock. However, Neu-châtel populations could represent a s uitable source of diversification and genetic pool gain for captive stocks.

Table 1. Genetic variability for the 12 microsatellite loci studied in Lake Geneva at six sampling localities during June 2012 (LP1) and September 2012 (LP2) for Perca fluviatilis. Number of individuals genotyped (N), number of alleles per locus (A), allelic richness (Ar), private alleles (Ap), expected heterozygosity (Hexp), observed heterozygosity (Hobs), inbreeding coefficient (FIS), p-value of Global Hardy-Weinberg tests (HWE). p-value: * P < 0.05, ** P < 0.01, *** P < 0.001.

Sites		PflaL2	Svi17	SviL7	PflaL4	PflaL9	Svi18	PflaL1	YP60	PflaL6	PflaL10	YP111	YP78	Total
LP1	*N*	281	317	309	349	349	349	326	316	316	349	351	346	349
	A	9	8	9	5	10	2	7	5	3	4	5	3	70
	Ar	8.79	7.31	8.65	4.64	9.28	2.00	6.65	5.8	2.99	3.82	4.48	2.82	5.61
	Ap	0.00	0.82	0.00	0.00	0.00	0.00	0.82	0.00	0.00	0.00	2.48	0.00	0.35
	H_{exp}	0.32	0.33	0.56	0.04	0.55	0.25	0.37	0.71	0.35	0.63	0.37	0.16	0.394
	H_{obs}	0.27	0.35	0.59	0.04	0.58	0.25	0.34	0.70	0.33	0.66	0.39	0.13	0.393
	F_{IS}	0.14**	–0.04*	–0.047	–0.019	–0.059	0.001	0.125**	0.036*	0.052	–0.072	–0.062	0.336**	0.0076***
	HWE	1.000	0.994	0.354	0.691	0.817	0.611	0.523	0.913	0.678	0.005	0.0001	0.985	0.997
LP2	*N*	324	325	311	329	327	328	310	303	319	317	267	317	329
	A	12	8	10	4	10	4	6	6	5	5	2	4	76
	Ar	11.53	7.51	9.79	3.67	9.49	3.82	5.99	5.82	4.97	4.84	2.00	3.99	6.12
	Ap	3.53	0.85	0.00	0.00	1.69	0.97	0.00	0.00	0.004	0.00	0.00	2.17	0.77
	H_{exp}	0.37	0.66	0.04	0.56	0.23	0.38	0.69	0.45	0.66	0.37	0.51	0.45	0.459
	H_{obs}	0.39	0.74	0.04	0.58	0.22	0.40	0.64	0.29	0.68	0.32	0.42	0.43	0.440
	F_{IS}	0.016	–0.04	–0.10*	–0.01	–0.01	0.03	0.03	0.03	0.05***	–0.01	0.01	0.02	0.019
	HWE	0.99	0.04	0.14	0.83	0.31	0.62	0.95	0.87	1.00	0.33	0.54	0.85	0.99

Table 2. Genetic variability for the 12 microsatellite loci studied in Lake Neuchâtel at two sampling localities during June 2012 (NP1) and September 2012 (NP2) for Perca fluviatilis. Number of individuals genotyped (N), number of alleles per locus (A), allelic richness (Ar), private alleles (Ap), expected heterozygosity (Hexp), observed heterozygosity (Hobs), inbreeding coefficient (FIS), p-value of Global Hardy-Weinberg tests (HWE); p-value: * P < 0.05, ** P < 0.01, *** P < 0.001.

Sites		PflaL2	Svi17	SviL7	PflaL4	PflaL9	Svi18	PflaL1	YP60	PflaL6	PflaL10	YP111	YP78	Total
NP1	*N*	79	78	79	84	84	84	83	79	76	84	84	83	85
	A	7	6	11	8	16	2	7	6	5	7	2	3	80
	A_r	4.80	4.57	8.34	5.95	10.48	2.00	4.89	5.32	3.79	4.45	2.00	2.52	4.93
	Ap	0.16	0.97	0.95	2.02	2.45	0.00	0.66	0.24	1.28	0.45	0.00	0.02	0.77
	H_{exp}	0.770	0.514	0.619	0.431	0.752	0.443	0.601	0.739	0.392	0.681	0.497	0.339	0.565
	H_{obs}	0.835	0.615	0.696	0.511	0.928	0.583	0.650	0.683	0.342	0.857	0.821	0.409	0.661
	F_{IS}	–0.08*	–0.198	–0.124	–0.187	–0.237**	–0.319**	–0.082	0.076*	0.129	–0.259***	–0.659***	–0.208*	0.031***
	HWE	0.841	0.098	0.250	0.548	0.125	0.189	0.487	0.947	0.892	0.098	0.014	0.135	0.250
NP2	*N*	87	88	87	89	89	88	81	80	26	77	77	80	89
	A	8	8	11	7	18	4	8	5	2	8	2	5	86
	A_r	6.11	5.08	8.64	5.10	12.79	2.59	6.00	4.97	2.00	5.76	2.00	4.42	5.46
	Ap	0.73	1.30	0.92	1.27	4.34	0.54	1.23	0.00	0.00	1.56	0.00	0.13	1.01
	H_{exp}	0.752	0.509	0.681	0.396	0.766	0.331	0.680	0.757	0.340	0.713	0.488	0.555	0.581
	H_{obs}	0.804	0.500	0.689	0.359	0.775	0.295	0.703	0.650	0.115	0.623	0.545	0.575	0.553
	F_{IS}	–0.069	0.019	–0.012	0.093	–0.011	0.110	–0.034	0.142**	0.665**	0.127	–0.116	–0.036	0.543*
	HWE	0.989	0.117	0.162	0.235	0.039	0.200	0.367	0.966	0.989	0.167	0.00	0.0348	0.079

Locus	Alleles (bp)	Geneva		Neuchâtel	
		LP1	LP2	NP1	NP2
PflaL2	240	0.0000	**0.0028**	0.0000	0.0000
	242	0.0028	0.0085	0.0064	0.0068
	244	0.0138	0.0169	0.0128	0.0135
	246	0.0193	0.0169	0.0000	0.0270
	248	0.0000	**0.0028**	0.0000	0.0000
	250	0.0801	0.0678	0.0833	0.0541
	252	0.0000	**0.0085**	0.0000	0.0000
	254	0.8039	0.7006	0.8462	0.8041
	256	0.0249	0.0198	0.0128	0.0270
	258	0.0083	0.0706	0.0128	0.0000
	260	0.0414	0.0819	0.0256	0.0541
	264	0.0055	0.0000	0.0000	0.0135
	282	0.0000	**0.0028**	0.0000	0.0000
Svi17	110	0.1657	0.1441	0.2564	0.2330
	112	0.0000	0.0000	**0.0128**	**0.0114**
	126	0.0000	**0.0028**	0.0000	0.0000
	130	0.0000	0.0056	0.0000	0.0057
	132	**0.0028**	0.0000	0.0000	0.0000
	134	0.0028	0.0000	0.0000	0.0114
	136	0.7873	0.7994	0.6474	0.6591
	138	0.0028	0.0028	0.0192	0.0057
	140	0.0276	0.0282	0.0577	0.0625
	142	0.0028	0.0028	0.0000	0.0114
	144	0.0000	0.0000	**0.0064**	0.0000
	146	**0.0083**	**0.0141**	0.0000	0.0000
SviL7	224	0.0000	0.0000	**0.0063**	0.0000
	226	0.0000	0.0028	0.0063	0.0172
	228	0.0000	0.0113	0.0443	0.0862
	230	0.0166	0.0056	0.0886	0.0172
	232	0.0028	0.0056	0.0443	0.0115
	234	0.0138	0.0508	0.0253	0.0287
	236	0.5939	0.5085	0.5949	0.5287
	238	0.0470	0.0847	0.1266	0.1609
	240	0.0773	0.1610	0.0316	0.0632
	244	0.2376	0.1610	0.0253	0.0632
	246	0.0028	0.0000	0.0063	0.0115
	248	0.0083	0.0085	0.0000	0.0115
PflaL4	119	0.0000	0.0000	**0.0060**	0.0000
	123	0.0083	0.0056	0.0893	0.1404
	125	0.0000	0.0000	0.0000	**0.0112**
	127	0.0000	0.0000	**0.0893**	0.0000
	129	0.0000	0.0000	**0.0119**	**0.0393**
	131	0.0028	0.0000	0.0179	0.0056
	133	0.9779	0.9887	0.7440	0.7640

Locus	Alleles (bp)	Geneva		Neuchâtel	
		LP1	LP2	NP1	NP2
	135	0.0028	0.0028	0.0179	0.0225
	137	0.0083	0.0028	0.0238	0.0169
PflaL9	197	0.0387	0.0424	0.0833	0.0393
	199	0.0000	0.0000	**0.0060**	0.0000
	201	0.5856	0.5650	0.4464	0.4551
	203	0.0000	**0.0028**	0.0000	0.0000
	205	0.0000	0.0000	0.0000	**0.0169**
	225	0.0000	**0.0028**	0.0000	0.0000
	229	0.0000	0.0000	**0.0119**	**0.0112**
	231	0.0000	0.0000	**0.0060**	**0.0281**
	233	0.1713	0.1469	0.0357	0.0562
	235	0.0028	0.0056	0.0119	0.0056
	237	0.0055	0.0000	0.0298	0.0169
	239	0.0000	0.0000	**0.0774**	**0.0056**
	241	0.0000	0.0000	**0.0060**	**0.0506**
	245	0.0000	0.0000	0.0000	**0.0112**
	247	0.0028	0.0000	0.0060	0.0056
	249	0.0028	0.0028	0.0000	0.0281
	251	0.1740	0.2175	0.1845	0.1011
	253	0.0138	0.0056	0.0476	0.0787
	255	0.0028	0.0085	0.0060	0.0618
	257	0.0000	0.0000	**0.0357**	**0.0169**
	261	0.0000	0.0000	**0.0060**	**0.0112**
Svi18	155	0.0000	**0.0056**	0.0000	0.0000
	161	0.8646	0.8277	0.3274	0.1932
	165	0.0000	0.0000	0.0000	**0.0057**
	169	0.1354	0.1638	0.6726	0.7955
	171	0.0000	0.0028	0.0000	0.0057
PflaL1	120	**0.0028**	0.0000	0.0000	0.0000
	122	0.0000	0.0198	0.0000	0.0309
	124	0.7459	0.7684	0.3735	0.4012
	126	0.0138	0.0085	0.0060	0.0000
	128	0.0083	0.0085	0.0000	0.0062
	130	0.2072	0.1751	0.5060	0.3827
	132	0.0193	0.0198	0.0783	0.1111
	134	0.0028	0.0000	0.0120	0.0062
	136	0.0000	0.0000	**0.0120**	**0.0123**
	138	0.0000	0.0000	**0.0120**	**0.0494**
YP60	233	0.0028	0.0028	0.063	0.0000
	237	0.3204	0.3531	0.0886	0.0562
	241	0.0387	0.0056	0.1456	0.1625
	245	0.2265	0.2458	0.2468	0.3063
	249	0.3343	0.3136	0.4051	0.3125
	253	0.0773	0.0791	0.1076	0.1625

Table 3. Alleles frequencies at 12 variable loci across Geneva and Neuchâtel population of Perca fluviatilis sampled during June (P1) and September (P2). Private alleles are identified in bold type.

Locus	Alleles (bp)	Geneva		Neuchâtel	
		LP1	LP2	NP1	NP2
PflaL6	135	0.2167	0.2486	0.1908	0.2115
	143	0.0000	0.0000	**0.0066**	0.0000
	145	**0.0083**	**0.0169**	0.0000	0.0000
	147	0.0000	0.0113	0.0132	0.0000
	149	0.7750	0.7175	0.7566	0.7885
	151	0.0000	0.0056	0.0329	0.0000
PflaL10	210	0.0000	0.0000	0.0000	**0.0065**
	220	0.0000	0.0000	**0.0060**	**0.0195**
	222	0.0000	0.0028	0.0060	0.0130
	224	0.5138	0.3955	0.3512	0.3506
	226	0.2403	0.3277	0.3690	0.2987
	228	0.2431	0.2627	0.2500	0.2792
	230	0.0028	0.0113	0.0119	0.0260
	232	0.0000	0.0000	**0.0060**	**0.0065**

Locus	Alleles (bp)	Geneva		Neuchâtel	
		LP1	LP2	NP1	NP2
YP111	247	0.2182	0.2062	0.5536	0.5844
	250	**0.0028**	0.0000	0.0000	0.0000
	253	**0.0028**	0.0000	0.0000	0.0000
	256	0.7735	0.7938	0.4464	0.4156
	259	**0.0028**	0.0000	0.0000	0.0000
YP78	209	0.9006	0.0000	0.0000	0.0188
	212	0.0967	0.0000	0.0000	0.0313
	215	0.0000	0.0000	**0.1988**	**0.3500**
	218	0.0000	0.0000	**0.7892**	**0.5688**
	221	0.0000	0.0798	0.0120	0.0313
	224	0.0000	**0.4322**	0.0000	0.0000
	227	**0.0028**	**0.5367**	0.0000	0.0000
	230	0.0000	**0.0113**	0.0000	0.0000

Table 3. Continued

	LP1	LP2	NP1	NP2
LP1		NS	*	**
LP2	0.1156		*	**
NP1	0.2127	0.1783		**
NP2	0.2153	0.1815	0.0108	

Table 4. Genetic distance (FST) comparisons between Lake Geneva (LP1 and LP2) and Lake Neuchâtel (NP1 and NP2) Eura-sian perch populations. FST-pairwise values are below diagonal and correspond statistical test are above diagonal. p-value: * P < 0.05), P < 0.01, *** P <0.001.**

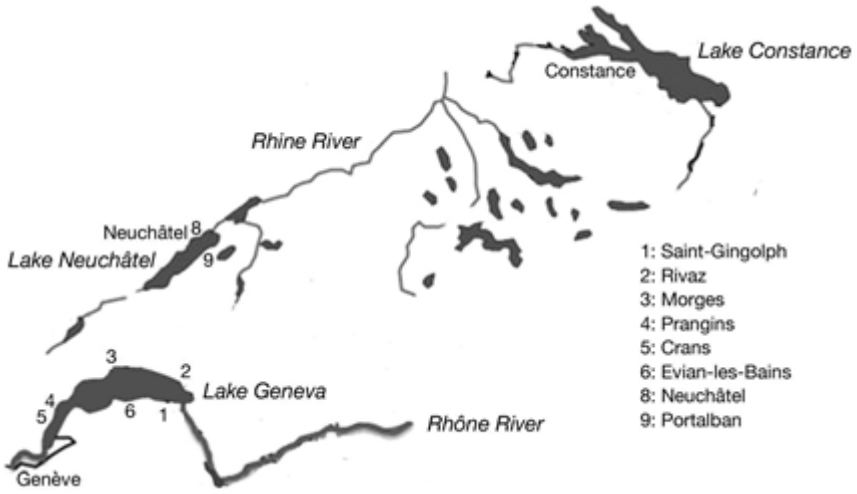

Figure 1. Maps of the studied lakes depicting sampling localities of Eura-sian perch (Perca fluviatilis).

Cliquez ou appuyez ici pour entrer du texte.

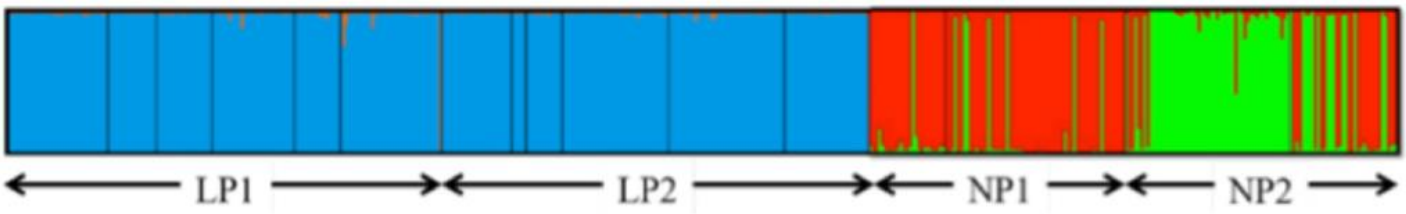

Figure 2. Bayesian clustering analy¬sis of Eurasian perch population in Lake Geneva (LP1, LP2) and Lake Neuchâtel (NP1, NP2), during June 2012 (P1) and September 2012 (P2).

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