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Genetic characterization and relatedness of wild and farmed Eurasian perch (*Perca fluviatilis*): Possible implications for aquaculture practices

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ABSTRACT

Aquaculture of the Eurasian perch, *Perca fluviatilis*, in recirculating systems has emerged over the past decades to become a significant way of diversification for inland areas in Europe. The development of such a production relies partly on the improvement of growth performance (i.e., reducing production costs), which requires suitable genetic management of broodstocks and the development of selective breeding programs. In this context, the present study was undertaken assessing for the first time the genetic diversity of farmed stocks of perch. Twelve microsatellite loci were used to investigate the genetic diversity of nine farmed stocks (547 individuals) from two perch farms located in France and their supposedly wild founder population from Lake Geneva (394 individuals). First, the wild population displayed the lowest genetic diversity and differed genetically from all farmed populations except one, XB2. Second, genetic diversity did not decrease between farmed breeders and their potential offspring. However, in the three groups of broodstock-offspring the number of alleles decreased by 10%, 21%, and 15%, respectively. In addition, effective population size decreased in all offspring groups. A family structuring was also observed among broodstocks and their offspring, with an unequal family contribution being suspected. In the absence of parental information, these results attest to the utility of genetic tools to evaluate genetic diversity and the necessity of a monitoring program to maintain genetic variability among farmed perch. Genetic variability among farmed stocks appears to be sufficient for perch production to be sustainable and selective breeding programs to be developed.

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1. Introduction

The Eurasian perch, *Perca fluviatilis*, is a common European freshwater fish species that is particularly appreciated and consumed in Alpine areas (Fontaine, 2004). It is extensively fished in large lakes or reservoirs (Gillet et al., 2013; Ben Khadher et al., 2015) or reared in ponds for both human consumption and recreational angling (Kestemont et al., 2009). Fishery production varies considerably between years and does not meet the current demand for human consumption (Fontaine, 2004). The good quality of the product (fillet) and the high demand from local markets (e.g., Switzerland, eastern France, and northern Italy) have led to consider perch as a promising candidate for inland aquaculture (Fontaine et al., 1993; Kestemont and Dabrowski, 1996; Mairesse et al., 2005).

The onset of perch domestication occurred in the early 1990s. A key progress was made when the reproductive cycle (sexual maturation and spawning) was controlled in captivity and a hormonal injection protocol to obtain out-of-season spawning was developed (Kucharczyk et al., 1996; Kouřil et al., 1997; Migaud et al., 2002, 2004; Fontaine et al., 2006; Abdulfatah et al., 2011, 2013). In addition, other studies have enabled rearing protocols to be improved for this species, including broodstock management, husbandry conditions (Jourdan et al., 2000; Kestemont et al., 2003), nutritional requirements (Kestemont et al., 2001; Mathis et al., 2003), gamete quality (Żarski et al., 2011; Shaliutina et al., 2012), and larval quality (Henrotte et al., 2010). Nowadays, intensive production of perch is successfully obtained in monoculture within recirculating systems (Fontaine et al., 2009) and the entire life cycle of perch is effectively controlled in captivity, most often without wild inputs (Teletchea and Fontaine, 2014). In other words, from a wild population (F0), successive generations (F1–F3, etc.) can be produced with or without the introduction of additional wild perch (eggs, juveniles, or breeders). Despite such substantial advances,

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no selective breeding programs have been implemented so far to improve perch zootechnical performance (higher growth rate, lower growth heterogeneity, lower cannibalism rate, higher filleting yield, etc.). Manipulations of genetic features have only focused on sex control to produce female-only populations (Rougeot et al., 2002, 2004) or triploid populations (Rougeot et al., 2003) in order to increase growth rate and reduce growth heterogeneity.

Eurasian perch was recently classified at the fourth level of domestication as defined by Teletchea and Fontaine (2014). At this level, behavioral, physiological, and morphological changes in farmed fish can be observed as compared with their wild congeners (Lorenzen et al., 2012). For perch, the domestication process seems to have increased their resistance to chronic stress, growth, and immune status (Douxfils et al., 2011). In addition, their adaptation to rearing systems (extensive, semi-extensive, and intensive systems) has led to changes in morphological indices related to shape (head, mouth, and compactness), color, and physiology (gonadosomatic, hepatosomatic, viscerosomatic, and perivisceral fat indexes) (Mairesse et al., 2005). On the other hand, a possible negative result of domestication on perch is that they might have low reproductive success (absolute and relative fecundity, hatching rate), as was found in one population of farmed perch in comparison with their wild counterparts (Křišťan et al., 2012). This might be linked to a relationship between genetic diversity and reproductive performance, which has been established for some fish species (Overturf et al., 2003; Porta et al., 2006; Borrell et al., 2011). For the Senegalese sole, *Solea senegalensis*, poor reproductive performance of a hatchery stock, which was composed of both wild and first generation offspring (F1) individuals mixed together, might have been the result of genetic depression after the use of offspring in the whole stock. More than 50% of the decrease in allelic richness was observed in F1, in addition to heterozygosity reduction (Porta et al., 2006). By studying the genetic diversity among five different strains of rainbow trout, *Oncorhynchus mykiss*, it was found that strains with the lowest average of gene diversity displayed the lowest feed conversion ratio and the highest specific growth rate (Overturf et al., 2003). Knowledge of genetic resources is thus of primary importance to better understand changes in husbandry performance and to assess the potential for further selective breeding programs.

The aims of this study were to (i) compare the genetic variability between wild perch coming from Lake Geneva, which was mainly used to establish the broodstocks of French farms (Ledore et al., 2010; Ben Khadher et al., 2015), and (ii) evaluate the genetic variability within different farmed stocks, using twelve microsatellites.

2. Materials and methods

2.1. Fish samples

Farmed individuals were sampled in May 2014 from two commercial perch farms located in the northeastern part of France. Origin and stock affiliation information were provided by fish farmers. The first farm Y had two broodstocks YB1 and YB2 and their respective first generation offspring YF1B1 and YF1B2. From the second farm X, five stocks were sampled: a broodstock and its first generation offspring, XB1 and XF1B1, respectively, another broodstock XB2, and two stocks of mixed origin XFD and XM (Table 1).

Besides farmed individuals, 395 wild perch were sampled in Lake Geneva during the spawning period (June 2012) and previously analyzed in Ben Khadher et al. (2015).

2.2. Microsatellite amplification and genotyping

For each farmed stock, between 48 and 72 individuals were sampled (Table 1) among approximately 500 farmed perch for the two farms. DNA was extracted from each fin clip sample using a modified high salt DNA extraction protocol according to Aljanabi and Martinez (1997). Amplification was performed for all samples (wild and farmed) using twelve microsatellite markers: *PflaL*1, *PflaL*2, *PflaL*4, *PflaL*6, *PflaL*9, and *PflaL*10 (Leclerc et al., 2000); *YP*60, *YP*78, and *YP*111 (Li et al., 2007) previously developed for yellow perch (*Perca flavescens*); *SviL*7 (Wirth et al., 1999), and *Svi*17 and *Svi*18 (Borer et al., 1999) developed for walleye (*Sander vitreum*). Four multiplex reactions were carried out for each sample using QIAGEN Multiplex PCR Plus Kit and fluorescently labeled primers (VIC, NED, 6-FAM, and PET). Polymerase chain reaction was performed in a total volume of 10 μL: 1 μL of genomic DNA, 5 μL of Master mix (Qiagen), and 1 μL of primer mix. Amplifications were carried out in a BioRad DNA engine as follows: 5 min at 95 °C, followed by 30 cycles of 30 s at 95 °C, 90 s at the annealing temperature (48 °C and 55 °C), and 30 s at 72 °C, with a final extension of 45 min at 60 °C. Amplified fragments were separated and visualized on an ABI 3130XL Prism automated sequencer and scored with GeneMapper 4.0 software.

Table 1
Number of sampled individuals for the nine farmed stocks (N), number of alleles per locus (A), allelic richness (A_r), observed and expected heterozygosity (H_{obs}/H_{exp}), effective size (N_e) and their confidence interval (CI), and inbreeding rate (F).

	N	A	A_r	H_{obs}/H_{exp}	N_e (CI)	$F = 1/2\ N_e$
XB1	60	8.66	8.57	0.60/0.63	202.02 (123.00–465.70)	0.002
XF1B1	60	7.33	7.30	0.65/0.63	81.02 (55.41–162.45)	0.006
XB2	72	4.75	4.52	0.42/0.43	48.22 (32.15–94.84)	0.010
XFD	58	7.33	7.31	0.67/0.70	62.02 (43.22–112.61)	0.008
XM	60	6.58	6.54	0.61/0.61	49.37 (35.25–86.51)	0.010
YB1	60	6.16	6.00	0.54/0.62	51.93 (35.50–116.80)	0.009
YF1B1	48	5.58	5.52	0.63/0.58	30.42 (24.10–42.30)	0.016
YB2	72	6.58	6.11	0.62/0.62	72.36 (47.50–164.90)	0.006
YF1B2	58	5.25	5.12	0.56/0.55	46.40 (33.07–89.43)	0.010

2.3. Data analysis

Allelic dropout, scoring errors, and the potential presence of null alleles were assessed using MICRO-CHECKER software (Van Oosterhout et al., 2004). Genetic diversity was assessed for each stock separately and for the whole sampled fish population by calculating the following coefficients: number of alleles per locus (A), allelic richness (A_r), and private allelic richness (A_p) determined with HP-RARE 1.1 program that compensates for sampling disparity using rarefaction (Kalinowski, 2005), as well as observed heterozygosity (H_o) and expected heterozygosity (H_e) (Nei, 1978) calculated using GENETIX 4.05 software (Belkhir et al., 2004). Possible genetic differences (A, A_r, H_o, and H_e) between the ten stocks were determined using ANOVA test followed by Tukey's post-hoc test at p-value <0.05. These statistical analyses were conducted with STATISTICA 10 software.

Divergence among group pairs was estimated with F_{ST}-pairwise (Weir and Cockerham, 1984) and significance levels were evaluated with an exact test for genic differentiation (dememorization: 10,000; batches: 100; iterations per batch: 5000) using GENEPOP 4.2.1 software (Raymond and Rousset, 1995; Rousset, 2008). Significance levels for F_{ST}-pairwise values were adjusted using Bonferroni corrections (Rice, 1989). Inbreeding coefficients F_{IS} (Wright, 1969) were estimated as a Weir and Cockerham (1984) parameter implemented in GENEPOP.

Hardy–Weinberg equilibrium (HWE) and genotypic linkage disequilibrium (LD) between pairs of loci for each sample were tested using GENEPOP 4.2.1 (Raymond and Rousset, 1995). Both tests were conducted using 10,000 dememorizations, 100 batches, and 5000 iterations. The significance level was $\alpha = 0.05$ and Bonferroni

adjustment of p-values was used for multiple testing correction (Rice, 1989).

The possible genetic clusters between wild and farmed populations and within each farm stocks were determined with Bayesian clustering analysis implemented in STRUCTURE 2.3.4 program (Pritchard et al., 2000). Individuals were assigned to one group among a predefined number of genetic clusters (K), under the assumptions of Hardy–Weinberg, without prior information about their origin. Ten independent runs for each $K = 1–10$ involved a burn-in of 10,000 Markov Chain Monte Carlo (MCMC) iterations, followed by 100,000 replications. An admixture model with independent allele frequencies was assumed. The most likely number of K was estimated as the change in the ln probability values [ln P(D)] between successive values of K following the ΔK method of Evanno et al. (2005). STRUCTURE HARVESTER 0.6.94 was used to infer this procedure (Earl and vonHoldt, 2012). For farmed individuals, STRUCTURE was run separately for each broodstock and their putative offspring.

Factorial correspondence analysis (FCA) was also performed with all samples using GENETIX (Belkhir et al., 2004) to discriminate possible differences between stock farms and wild populations.

2.4. Patterns of relatedness

Average relatedness (r) between all pairs of individuals (Queller and Goodnight, 1989) was calculated using two software programs to compare the results. The linear-regression approach of Queller and Goodnight's (1989) moment estimator implemented in COANCESTRY (Wang, 2011) was used to quantify relatedness coefficients. Relatedness values allow each pair of individuals to be assigned to one of eight types of relationships, among which three were studied here: full-sibs, half-sibs, and unrelated. In addition, to evaluate whether average relatedness and inbreeding were higher in offspring compared to broodstocks and between all broodstocks, the bootstrapping method of Wang (2011) was applied using 10,000 replications and at 95% confidence intervals. Relatedness was also evaluated using ML-RELATE (Kalinowski et al., 2006), which calculates maximum likelihood estimates of pairwise relatedness between individuals. This program generates absolute (non-negative) estimates and can accommodate null alleles. It also allows the user to determine the relationship for each pair of individuals (parent-offspring "PO", full-sibling "FS", half-sibling "HS", and unrelated "U"). The most likely relationship between individuals was determined by testing a putative relationship (the highest likelihood value) and an alternative relationship (the second highest likelihood value) based on 10,000 simulations.

For paternity reconstruction and determination of minimum parent number, two approaches were used. A likelihood method implemented in COLONY 2.0 (Jones and Wang, 2010) was used for family reconstruction and to estimate the minimum number of parents and sibling relationship. COLONY was run for independent cohorts, assuming random mating without inbreeding and without clone, dioecious, and diploid individuals. Among the three available analysis methods, runs were of medium length using the full likelihood method with medium likelihood of precision. A second maximum likelihood parentage reconstruction method implemented in Pedigree 2.0 (Herbinger, 2005) was used for confirmation of parental groups when no parental information was available. The program was run 10 times, applying the full-sib constraint (FSC) with: 1,000,000 iterations, a weight of one, a temperature (speed of the algorithm) of 10, and a random seed.

Effective sizes (N_e) of each stock were estimated using ONeSAMP 1.2 program (Tallmon et al., 2008). This program infers the effective size of the population from a single sample using summary statistics in an approximate Bayesian computation. In a closed population, the inbreeding produced in a single generation, measured by a decrease in heterozygosity, is calculated from this equation: $F = 1/2N_e$ (Douglas, 1986).

3. Results

3.1. Comparison between wild and farmed populations

Each of the sampled stocks was polymorphic at the 12 microsatellites (Table 2). The total number of alleles ranged from 5 (*Pfla L6*) to 26 (*Pfla L9*). Allelic richness ranged from 2.00 (*Svi18*) to 10.80 (*Pfla L2*) in the wild population and from 1.78 (*PflaL6* for YF1B2) to 16.72 (*PflaL9* for XB1, see Table 2) in the nine farmed stocks. This variability was significantly higher ($p < 0.05$) within farmed stocks than in the wild population for 10 out of the 12 loci (Table 2).

The average frequency of homozygous individuals was higher in the wild population ($H_{obs} = 0.41$) than in the farmed broodstocks (XB1; 0.60), (YB1; 0.54), and (YB2; 0.62). Linkage disequilibrium deviated from Hardy–Weinberg, even after Bonferroni corrections, for XB1, XB2, XFD, XM, YB1, and YB2 in 10, 1, 12, 1, 14, and 5 out of 66 comparisons for the 12 microsatellites analyzed, respectively.

Besides, the three farmed broodstocks (XB1, YB1, and YB2) belonged to a different genetic cluster from that of their putative wild counterparts (Fig. 1). Only XB2 individuals were genetically close to the wild individuals (Fig. 1).

3.2. Farmed stocks

3.2.1. Farm X

3.2.1.1. Genetic variability and structure. All sampled stocks followed expected frequencies under Hardy–Weinberg equilibrium except *SviL7* that showed significant departure from the latter ($p < 0.0001$). After sequential Bonferroni corrections, the linkage disequilibrium test was significant in only 7.57% comparisons (25 out of 330 comparisons) at $p < 0.05$, which is above the expected threshold (5%). Broodstock XB1 did not show any differences in allelic richness and observed heterozygosity when compared to their offspring XF1B1 (Table 1). However, a 15% decrease in the total number of alleles was observed between XB1 and XF1B1, resulting from 37.5% allelic loss versus 22% allelic gain. Moreover, broodstock XB1 showed a significant heterozygosity deficiency ($F_{IS} = 0.04$; $p < 0.001$), while their direct offspring exhibited a significant heterozygosity excess ($F_{IS} = -0.03$; $p < 0.001$) (Table 2). The second broodstock XB2 was characterized by the lowest allelic richness (A_r), mean number of private alleles (A_p), and observed heterozygosity (H_{obs}) (4.52, 0.15, and 0.42, respectively), and by a significant heterozygosity deficiency ($F_{IS} = 0.03$; $p < 0.001$) (Table 2). Effective population size (N_e) was higher in broodstock XB1 than in their offspring XF1B1, thus inbreeding was higher within offspring (Table 1).

F_{ST}-pairwise values showed significant differentiation between the five stocks (Table 3) with a global value of 0.14. STRUCTURE analysis determined $K = 3$ as different genetic clusters (Fig. 2a). Broodstock XB2 formed a single cluster that was different from the other two. The second cluster included Broodstock XB1 and more than 50% of individuals from stock XFD. Broodstock XB1 and their offspring XF1B1 belonged to two different clusters (Fig. 2a). Indeed, the third cluster included offspring XF1B1 and stock XM.

3.2.1.2. Genetic relatedness. Both ML-RELATE and COANCESTRY supported "unrelated" as the most probable relationship for the five stocks. XB2 presented the lowest proportion of "unrelated" and the highest rate of full-sibs (Table 4).

Comparison between XB1 and their putative offspring XF1B1 showed no differences in relatedness coefficient (r) ($r = 0.120$ and

Table 2
Genetic variability for the 12 microsatellite loci in nine farmed stocks (farm X and Y) and wild population of Lake Geneva for *Perca fluviatilis*. Number of genotyped individuals (N), number of alleles per locus (A), allelic richness (A_r), private allelic richness (A_p), expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}), inbreeding coefficient (F_{IS}), p-value of Global Hardy–Weinberg tests (*HWE*). *($P<0.05$), **($P<0.01$), ***($P<0.001$)

	PflaL2	Svi17	SviL7	PflaL4	PflaL9	Svi18	PflaL1	YP60	PflaL6	PflaL10	YP111	YP78	Total
XB1													
N	59	60	60	60	60	59	59	58	60	60	60	60	60
A	12	7	10	7	17	5	11	9	3	10	4	9	8.66
A_r	11.84	6.92	9.92	6.86	16.72	4.94	10.94	8.96	3.00	9.85	3.93	5.85	8.57
A_p	4.12	2.93	2.21	3.15	3.93	0.00	1.94	1.96	0.00	1.01	0.0008	1.00	1.86
H_{exp}	0.63	0.68	0.76	0.40	0.88	0.46	0.80	0.74	0.31	0.77	0.44	0.68	0.63
H_{obs}	0.64	0.70	0.86	0.41	0.70	0.44	0.69	0.68	0.33	0.73	0.43	0.61	0.60
F_{IS}	−0.02	−0.02*	−0.12	−0.04	0.21***	0.04	0.13*	0.07*	−0.06	0.05*	0.03	0.10	0.04***
HWE													0.99
XF1B1													
N	57	58	56	59	59	59	58	56	57	57	57	57	60
A	9	7	7	4	13	6	10	6	3	13	3	7	7.33
A_r	8.94	6.99	7.00	3.99	12.86	5.92	9.96	6.00	2.99	12.98	3.00	6.96	7.30
A_p	0.98	0.99	0.06	0.00	1.93	1.92	0.0002	0.00	0.00	0.07	0.00	0.98	0.58
H_{exp}	0.55	0.58	0.81	0.20	0.82	0.73	0.86	0.78	0.06	0.77	0.60	0.70	0.63
H_{obs}	0.59	0.60	0.96	0.18	0.86	0.69*	0.96	0.78	0.07	0.78	0.57	0.61	0.65
F_{IS}	−0.07	−0.03	−0.19*	0.09	−0.05	0.05	−0.12*	0.005	−0.01	–	0.04	0.13	−0.03***
HWE										0.02***			0.59
XB2													
N	72	72	72	72	70	72	72	72	66	72	72	71	72
A	5	4	6	4	9	4	4	6	2	6	2	5	4.75
A_r	4.55	3.72	5.77	3.75	8.54	3.77	3.55	5.94	2.00	5.54	2.00	4.99	4.52
A_p	0.0009	0.00	0.0002	0.003	1.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
H_{exp}	0.29	0.34	0.59	0.09	0.53	0.60	0.24	0.70	0.29	0.64	0.31	0.55	0.43
H_{obs}	0.31	0.40	0.66	0.09	0.55	0.38	0.22	0.75	0.28	0.70	0.33	0.33	0.42
F_{IS}	−0.08	−0.15	−0.12	−0.02	−0.04	0.35***	0.09	−0.05	0.007	−0.09	−0.05	0.39***	0.03***
HWE													0.87
XFD													
N	58	58	58	58	58	58	58	58	58	58	58	58	58
A	6	7	8	5	15	4	8	8	4	12	4	7	7.33
A_r	6.00	7.00	7.96	5.00	14.89	4.00	7.99	8.00	3.99	11.92	3.99	6.96	7.31
A_p	0.002	0.0009	0.00	0.00	1.96	0.01	0.00	1.00	1.00	1.00	0.06	0.06	0.43
H_{exp}	0.69	0.75	0.79	0.69	0.87	0.69	0.79	0.83	0.39	0.73	0.54	0.59	0.70
H_{obs}	0.55	0.74	0.93	0.81	0.86	0.51	0.79	0.67	0.41	0.65	0.53	0.56	0.67
F_{IS}	0.20**	0.02	−0.17**	−0.17	0.01***	0.26***	0.006	0.19***	−0.04	0.11***	0.01*	0.03	0.04***
HWE													0.95
XM													
N	60	60	59	60	60	60	60	60	57	60	60	58	60
A	6	6	6	4	11	4	9	7	3	12	3	8	6.58
A_r	5.92	5.99	6.00	4.00	10.93	4.00	8.99	6.93	3.00	11.80	3.00	7.89	6.54
A_p	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.96	0.24
H_{exp}	0.44	0.48	0.81	0.28	0.80	0.71	0.82	0.80	0.11	0.77	0.57	0.70	0.61
H_{obs}	0.48	0.46	0.91	0.31	0.81	0.60	0.85	0.83	0.10	0.81	0.61	0.46	0.61
F_{IS}	−0.08	0.04	−0.13	−0.11	−0.01	0.16*	−0.03	−0.03*	0.11	–	−0.08	0.34***	0.009***
HWE										0.04***			0.27
YB1													
N	57	57	56	58	58	58	59	59	59	59	59	59	60
A	9	5	8	8	12	4	4	7	3	8	2	4	6.16
A_r	8.69	4.94	7.96	7.45	11.21	3.98	3.76	6.98	3.00	7.97	2.00	3.99	6.00
A_p	0.80	0.07	0.96	1.07	1.97	0.00	0.76	0.00	0.00	0.01	0.00	0.00	0.47
H_{exp}	0.75	0.46	0.68	0.52	0.80	0.67	0.54	0.76	0.48	0.73	0.50	0.52	0.62
H_{obs}	0.49	0.45	0.82	0.53	0.72	0.51	0.44	0.64	0.44	0.69	0.38	0.42	0.54
F_{IS}	0.35***	0.00	−0.20	−0.01	0.10***	0.23***	0.18*	0.15	0.10	0.05***	0.22	0.18	0.12***
HWE													1.00
YF1B1													
N	48	48	48	48	48	48	46	45	48	48	48	48	48
A	9	4	8	6	6	5	5	5	3	7	2	7	5.58
A_r	8.74	3.99	7.81	5.87	5.87	4.99	4.97	5.00	3.00	6.99	2.00	6.99	5.52
A_p	1.88	0.00	0.00	0.94	0.00	0.36	1.00	0.00	0.00	0.00	0.00	1.00	0.43
H_{exp}	0.66	0.34	0.60	0.45	0.64	0.73	0.67	0.55	0.53	0.66	0.48	0.62	0.58
H_{obs}	0.83	0.35	0.77	0.54	0.68	0.64	0.76	0.66	0.47	0.83	0.50	0.56	0.63
F_{IS}	−0.25**	−0.002	−0.28*	−0.18	−0.07*	0.11*	−0.13**	−0.19*	0.10	–	−0.03	0.09*	−0.08***
HWE										0.25***			0.19
YB2													
N	48	49	49	72	70	71	72	72	72	72	71	62	72
A	6	6	7	8	13	5	5	8	3	9	2	7	6.58
A_r	5.87	5.83	6.99	6.72	11.21	4.63	4.24	7.62	3.00	8.19	2.00	6.92	6.11
A_p	1.00	0.05	0.00	0.90	1.97	0.002	0.62	0.00	0.00	0.62	0.00	0.92	0.43
H_{exp}	0.67	0.51	0.67	0.43	0.78	0.71	0.49	0.79	0.42	0.71	0.45	0.72	0.62
H_{obs}	0.66	0.55	0.73	0.47	0.81	0.60	0.59	0.81	0.51	0.77	0.39	0.59	0.62

Table 2 (*Continued*)

	PflaL2	Svi17	SviL7	PflaL4	PflaL9	Svi18	PflaL1	YP60	PflaL6	PflaL10	YP111	YP78	Total
F_{IS}	0.01*	−0.03	−0.08*	−0.09	−0.03	0.15**	−0.21	−0.03	−0.19	–	0.12	0.17***	−0.01***
HWE										0.09***			0.92
YF1B2													
N	51	53	51	58	53	53	56	58	57	58	58	57	58
A	6	6	5	5	9	4	5	7	2	7	3	4	5.25
A_r	5.75	5.95	5.00	4.55	8.99	3.97	4.80	6.98	1.78	6.72	2.95	4.00	5.12
A_p	0.92	2.05	0.0004	1.33	1.59	0.00	0.39	0.37	0.00	0.004	0.95	0.00	0.64
*H*exp	0.58	0.70	0.67	0.36	0.87	0.31	0.65	0.83	0.01	0.68	0.30	0.62	0.55
H_{obs}	0.62	0.66	0.78	0.32	0.98	0.35	0.75	0.81	0.01	0.63	0.36	0.40	0.56
F_{IS}	−0.07	0.37**	−0.15**	0.09**	−0.12*	−0.15	−0.14	0.02***	0.00	0.06***	−0.19	0.35**	−0.002***
HWE													0.88
Geneva													
N	323	359	351	391	391	391	366	358	356	391	393	275	395
A	11	10	10	6	11	2	10	8	4	5	5	4	7.16
A_r	10.80	9.00	9.69	5.10	9.92	2.00	8.67	7.48	3.89	4.67	4.09	4.00	6.61
H_{exp}	0.34	0.34	0.57	0.05	0.57	0.25	0.40	0.72	0.33	0.62	0.37	0.17	0.3982
H_{obs}	0.32	0.36	0.59	0.05	0.62	0.25	0.39	0.71	0.32	0.68	0.43	0.15	0.4102
F_{IS}	0.065***	−0.059	−0.029	−0.025	−0.095	0.025	0.023	0.004	0.028	−0.092	−0.187***	0.052	−0.0369***
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

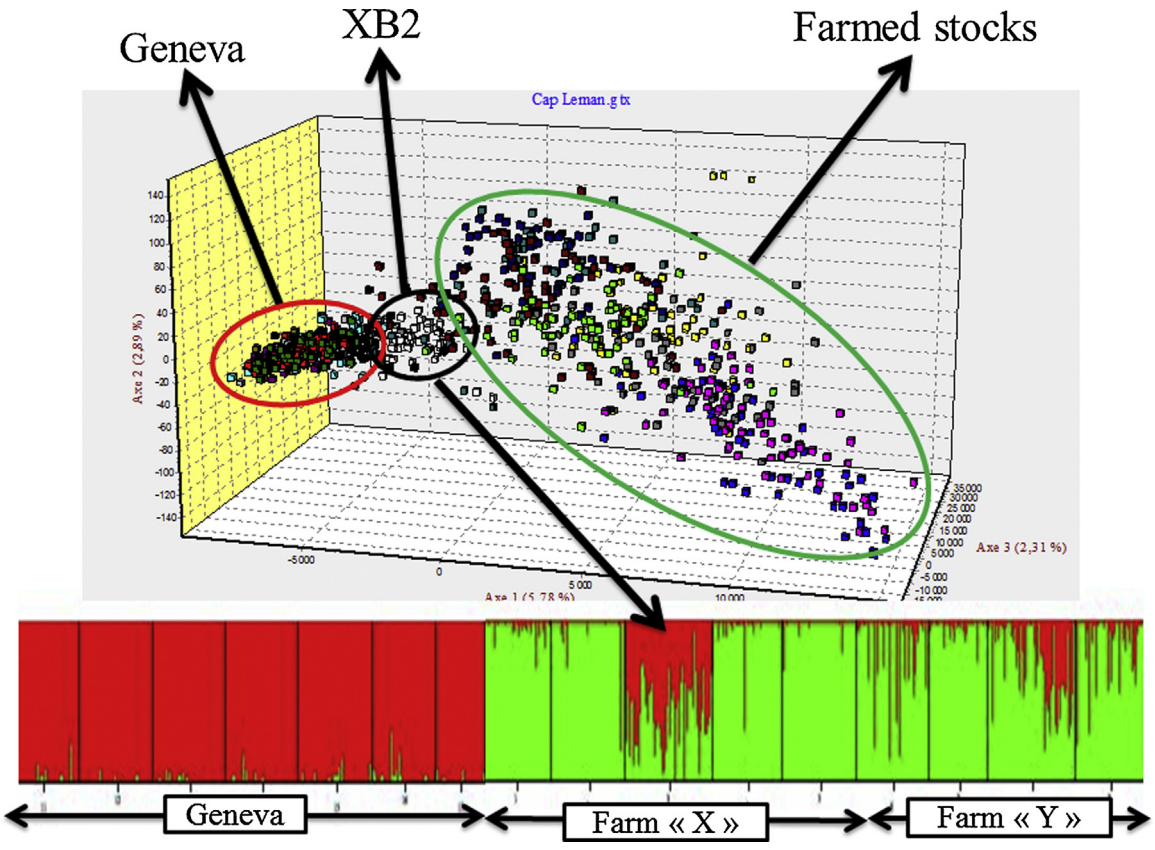


Fig. 1. Factorial correspondence analysis (FCA) of the genetic variability based on 12 microsatellite loci in wild and captive Eurasian perch (*Perca fluviatilis*): red circle indicates Geneva Lake population, green circle indicates captive stocks and black circle indicates (XB1) broodstock.

0.105, respectively) (Fig. 3a). However, relatedness within XB2 was significantly higher (CI = 95%) than in the other four stocks (Fig. 3b).

Family structuring was characterized for XB2 and XF1B1 stocks of Farm X. Offspring were more family structured than their breeders and presented a smaller family size (Fig. 4). Breeders had 13 families, as opposed to 20 families for offspring.

3.2.2. Farm Y

3.2.2.1. Genetic variability and structure. All sampled stocks at all loci had frequencies in agreement with HWE expectations ($p < 0.05$). Among the 264 tests performed for linkage disequilibrium and after Bonferroni corrections, only 29 (10.98%) were significant ($p < 0.05$). MICRO-CHECKER software showed that this disequilibrium was induced by the presence of null alleles ($p < 0.05$) at *PflaL2*, *Svi18*, and *YP78*. Five loci displayed a deficit in heterozygosity ($p < 0.001$) and four displayed an excess in heterozygosity ($0.05 < p < 0.001$).

There were no differences in allelic richness and observed heterozygosity between broodstocks YB1 and YB2 and their offspring YB1F1 and YB2F1, respectively (Table 1). YB1 exhibited a heterozygote deficit while YF1B1, YB2, and YB2F1 were characterized by a heterozygote excess ($p < 0.001$) (Table 2). Both offspring YB1F1

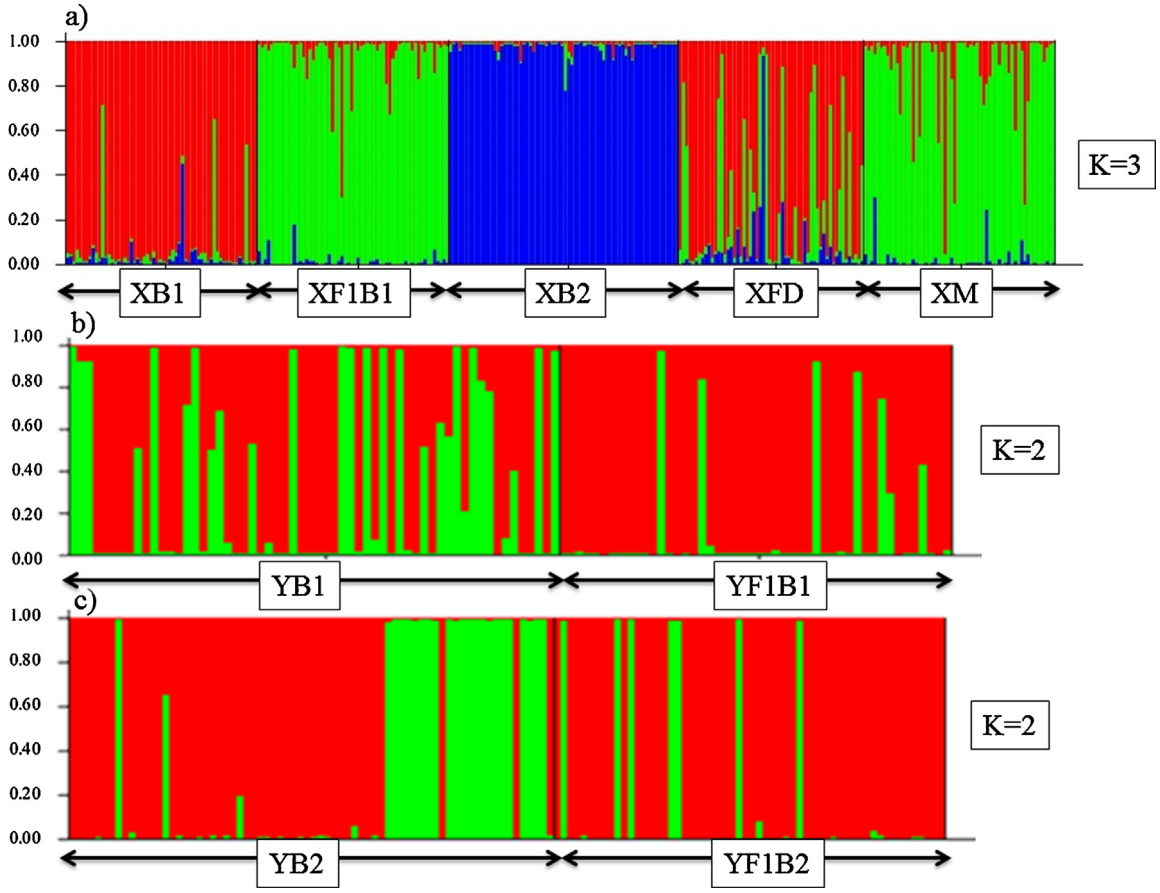


Fig. 2. Bayesian clustering analysis in STRUCTURE program for breeders-offsrpring combination in farm 'Y' and farm 'X'. Each vertical bar denotes one individual. (a) The five stocks of farm (X). (b) $K = 2$ for (YB1) breeders and their putative offspring (YF1B1). (c) $K = 2$ for (YB2) breeders and their putative offspring (YF1B2).

Table 3
Pairwise F_{ST} values between nine farmed stocks from two farms of Eurasian perch (below diagonal) and Lake Geneva population, and significance levels from genotypic differentiation test (above diagonal). *p*-value: HS: highly significant.

	XB1	XF1B1	XB2	XFD	XM	YB1	YF1B1	YB2	YF1B2	Geneva
XB1		HS	HS	HS	HS	HS	HS	HS	HS	HS
XF1B1	0.08		HS	HS	HS	HS	HS	HS	HS	HS
XB2	0.23	0.27		HS	HS	HS	HS	HS	HS	HS
XFD	0.06	0.07	0.21		HS	HS	HS	HS	HS	HS
XM	0.06	0.004	0.28	0.07		HS	HS	HS	HS	HS
YB1	0.09	0.14	0.13	0.07	0.14		HS	HS	HS	HS
YF1B1	0.11	0.17	0.22	0.11	0.17	0.02		HS	HS	HS
YB2	0.07	0.12	0.14	0.07	0.12	0.004	0.03		HS	HS
YF1B2	0.04	0.12	0.20	0.08	0.11	0.09	0.14	0.07		HS
Geneva	0.48	0.50	0.56	0.45	0.50	0.47	0.48	0.48	0.52	

Table 4
Mean relatedness *r* (±SE) of all stocks according to Queller and Goodnight (1989) and relationship percentage.

	r (Queller and goodnight)	Relationship percentage		
		Unrelated	Half-sibs	Full-sibs
XB1	0.120 ± 0.0006	82.99%	11.41%	5.59%
XF1B1	0.105 ± 0.0006	80.16%	14.57%	5.25%
XB2	0.490 ± 0.001	76.05%	12.87%	11.06%
XFD	0.021 ± 0.0007	82.51%	11.79%	5.68%
XM	0.151 ± 0.0005	81.63%	13.84%	4.51%
YB1	0.002 ± 0.002	76.68%	13.46%	9.84%
YF1B1	0.120 ± 0.001	76.41%	11.08%	12.49%
YB2	0.131 ± 0.001	77.30%	12.87%	9.81%
YF1B2	0.201 ± 0.001	76.70%	12.64%	10.64%

and YB2F1 showed a 10% and 21% decrease, respectively, in the total number of alleles compared to their breeders. These decreases resulted from a combination of lost and new alleles. Some loci (*Svi*17, *PflaL*4, and *YP*111) showed a higher value of private alleles in YF1B2 than in Y2 (Table 2). Alleles which were not found within offspring stocks always showed the lowest frequency (e.g., allele 220 in *PflaL*2, frequency = 0.0088).

Concerning the effective population size (N_e), broodstocks YB1 and YB2 showed higher values than their respective offspring YF1B1 and YF1B2 (Table 1). Besides, inbreeding (*F*) was higher in offspring than in their breeders (Table 1).

The mean global F_{ST} for all farm Y stocks was 0.059 and all F_{ST}-pairwise comparisons were significantly different ($p < 0.001$) showing that the two broodstocks YB1 and YB2 and their direct offspring were genetically different (Table 3). The analysis for determining the most probable number of genetic clusters indicated the existence of two different clusters ($K = 2$) for each breeder-offspring combination. When analyzing YB1 and YF1B1 together (or YB2 and YF1B2), two genetic clusters were found in different proportions in both stocks (Fig. 2b and c). The first broodstock YB1 was composed of 37% of the first cluster (Fig. 2b) and 63% of the second cluster (Fig. 2b). Their offspring YF1B1 corresponded to 10% of the first cluster and 90% of the second cluster. Similarly, the second broodstock YB2 corresponded to 33% of the first cluster and 67% of the second one. Their offspring YF1B2 corresponded to 12% of the first cluster and 88% of the second cluster (Fig. 2c).

3.2.2.2. Genetic relatedness. Relationship tests performed using ML-RELATE and COANCESTRY software supported "unrelated" as the most probable relationship for all pairs of individuals and for all stocks (Table 4). From broodstock (YB1) to their putative

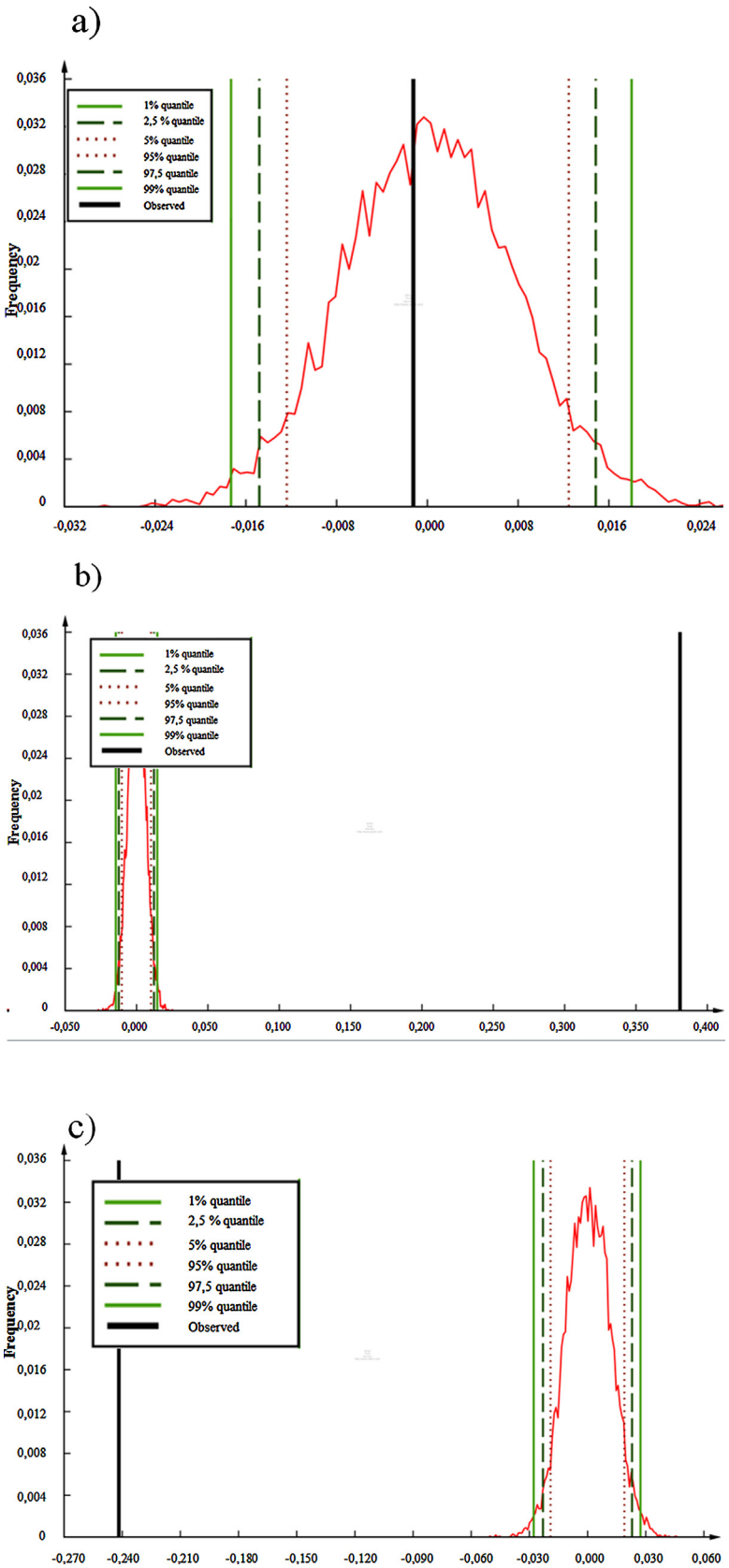


Fig. 3. Mean difference in relatedness (r) between (a) XB1 and their putative offspring XF1B1 (b) XB2 and all other groups and (c) YB1 and their putative offspring YF1B1.

offspring (YF1B1), the number of full-sibs increased from 9.84% to 12.49% (Table 4). Relatedness comparison between (YB1) and their putative offspring (YF1B1) showed that the observed (r) value increased significantly ($r = 0.002$ and 0.12, respectively; $p < 0.01$) (Fig. 3c).

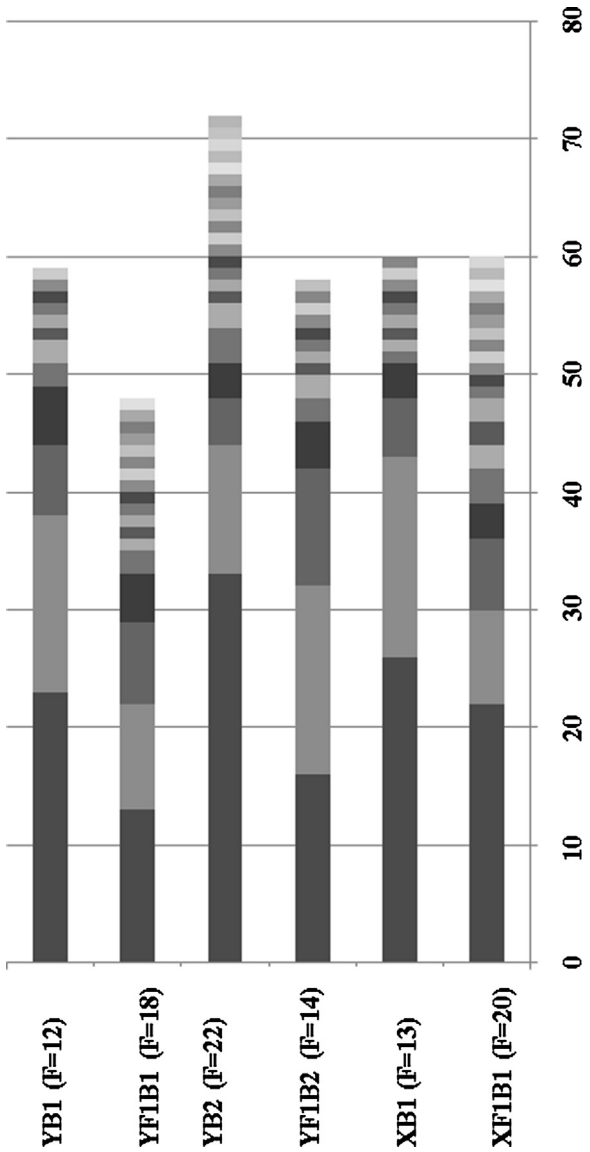


Fig. 4. Family distribution within broodstocks and their offspring. Each vertical bar represents the number of families and each color within the bar represents number of individuals per family identified in six broodstocks of the farm X and Y.

As for farm X, different families were detected in all stocks of farm Y. Fig. 4 shows the number of families per stock and the number of individuals per family. Each stock included large-, medium-, and small-sized families. The number of families and their proportion changed between breeders to offspring (Fig. 4).

4. Discussion

In this study, twelve microsatellite markers were used to evaluate the effect of domestication on the evolution of the genetic diversity of Fx and Fx + 1 perch compared to their putative wild congeners.

4.1. Wild and farmed populations

Farmed stocks from the two perch farms, except XB2, were genetically distinct from the wild population of Lake Geneva, and genetic diversity was higher within farmed stocks. These results and the presence of new alleles within offspring suggest that perch reared in these two farms at the time of the study came from different geographic areas (yet unknown) and not only from Lake Geneva, even though, according to fish farmers, most founder individuals were supposedly from that lake. Besides, the heterozygote deficit observed in farmed broodstocks, known as the Wahlund effect, is probably caused by a subdivision of the population (Wahlund, 1928; Khrustaleva et al., 2014). Such a deficit could also be expected when mixing individuals from different populations results in reduced fitness of hybrid offspring and in outbreeding depression. The outbreeding depression hypothesis could not be tested here. Furthermore, individuals originating from related parents exhibited higher homozygosity. As we did not have any homozygous individuals with rare alleles and as their putative parents did not share the same rare allele, the hypothesis of non-random aggregation between related individuals was rejected.

The low number of individuals belonging to the Lake Geneva population in the two farms may also be partly due to the effect of geographic origin on the survival, growth, and food intake of perch during larval and juvenile stages (Mandiki et al., 2004). That could explain why some populations were over-represented in the farms at the time of the study because they had survived better than the putative original population from Lake Geneva. Such a hypothesis could be tested by rearing egg strands originating from Lake Geneva and from farmed breeders under the same conditions and for at least two generations, and by genotyping the survival of offspring, a method known as the common garden experiment. This method was used, for example, to test for local adaptation in early life stages of two different capelin *Mallotus villosus* populations and it showed that no local adaptation to thermal environment occurred at both beach and demersal spawning sites (Penton and Davoren, 2013).

Adding wild inputs into farmed stocks and swapping breeders between farms is common practice in aquaculture, most often to avoid inbreeding (Vandeputte and Launey, 2004; Teletchea and Fontaine, 2014). For the Atlantic salmon, *Salmo salar*, a reduction in genetic variability was detected between the first farmed population and their wild founders (Cross and King, 1983; Stahl, 1983; Crozier and Moffett, 1989; Koljonen, 1989). A few years later, Cross and Challanain (1991) analyzed five domestic strains that represented 90% of the Irish salmon production in 1990 and a wild population. They found that four strains shared the same level of genetic diversity as the wild population and only one strain had a lower level of genetic diversity. Such an increase in the genetic variability of domestic stocks resulted from swapping individuals with farms of different countries (Youngson et al., 2001). Similarly, fish swapping between farms and regular introduction of wild individuals in farmed stocks resulted, on average, in higher genetic variability of domestic populations of brown trout, *Salmo trutta*, compared to their original wild populations (Chevassus et al., 1992).

As with most species, our findings suggest the probable input of wild individuals into farmed stocks of perch and the possible swapping of individuals between farms, including fish produced in research facilities. These inputs could explain the higher genetic variability found in these farms compared to their "supposed" wild congeners from Lake Geneva.

4.2. Farmed populations

4.2.1. Genetic diversity

As inferred from estimates of observed heterozygosity and allelic richness, XB2 breeders were clearly less variable than all the other farmed stocks. The observed heterozygosity, with values ranging from 0.54 to 0.67, was considered as moderate when compared to the mean value ($H_{obs} = 0.54 \pm 0.25$) calculated for 13 farmed freshwater fish species (DeWoody and Avise, 2000). In order to maintain such a number of heterozygote fish, special care must be taken when managing farmed stocks as fish

domestication is most often accompanied by a reduction in genetic diversity (Jackson et al., 2003; Porta et al., 2006; Exadactylos et al., 2007). When comparing the breeders with their putative offspring, no reductions in allelic richness or heterozygosity were recorded. However, farm Y showed a 10% and 21% decrease in the number of alleles for each offspring stock (YF1B1 and YF1B2, respectively) compared to their respective breeders, and farm X showed a 15% decrease in the number of alleles for offspring XF1B1. Additionally, as a consequence of a reduction in effective population size, inbreeding increased (not significant) in one generation. These results were in accordance with previous findings. For the Atlantic halibut, *Hippoglossus hippoglossus*, Jackson et al. (2003) suggested that a large decrease in the total number of alleles (26%) and in effective population size N_e (from 27 in parents to 13 in offspring) per generation resulted in a challenging reduction in genetic diversity for the future broodstock (F1). Other farmed fish species showed even more critical reductions. The Senegalese sole, *Solea senegalensis*, showed a more than 50% decrease in the number of alleles per locus, as well as 16% and 26% reductions in heterozygosity after only one generation in captivity (Porta et al., 2006). A domesticated turbot, *Scophthalmus maximus,* from a sea farm in the Irish Sea, displayed an 86% loss of genetic variation (Exadactylos et al., 2007). For the Eurasian perch, the small reduction in the total number of alleles did not seem to be a problem as genetic diversity did not differ between breeders and their offspring. Different production strategies and husbandry conditions can affect the genetic variability from one farm to another. Moreover, the control of parental contribution, especially that of the female-parent, is usually easier for perch than for other species, because perch spawn egg strands and not individual eggs.

The observed heterozygosity was higher than expected in offspring. Similar results were obtained by Herbinger et al. (2006) studying microsatellite markers for the Atlantic salmon, *Salmo salar*. The authors hypothesized that this was due to the small effective number of breeders and chance differences in allele frequencies between male and female parents producing the offspring (Herbinger et al., 2006). Therefore, our results would suggest the same explanation since the effective number of parents decreased from one generation to the next, but the hypothesis of differences in allele frequencies between the two sexes still has to be checked.

Besides, alleles with the lowest frequency among breeders often disappear within offspring, which might be a result of genetic drift (Crow and Kimura, 1970). Some loci displayed more private alleles within offspring, but these values were low (maximal $A_p = 2.05$) and sampled breeders represented only 10% of the whole stock, which was insufficient to conclude that wild fish were added to produce the first generation. Further studies should be performed on the second offspring generation (F2) derived from the first one (F1), in order to monitor how genetic diversity evolves through domestication.

4.2.2. Families structuring

Farmed perch showed no high relatedness or high half- and/or full-sibling relationships. This result suggests that kin aggregation does not automatically appear as a result of mating within farmed stocks. Despite these low relatedness values, the different stocks (broodstocks and offspring) were structured into either large or small families. The family size (number of individuals composing each family) was smaller for offspring than for broodstocks. This might be due to the fact that if individuals from large families mate with several individuals from small families, offspring families would be represented by only few individuals. In the case of the greater amberjack, *Seriola dumerili*, parental contribution was lower than the real number of available parents, which was explained by a probable influence of family variance (Rodriguez-Barreto et al., 2013). In their study, these authors calculated the contribution of each parent to the next generation and they suggested an unequal parental contribution. In the present study, the contribution of each parent could not be calculated because only part but not the entire parent stock was sampled. Therefore, the hypothesis of an unequal contribution of parents to the next generation leading to a reduction in the effective population size could only be checked by genotyping the whole stock of parents, and/or if more parental information was available.

4.2.3. Comparisons between farms and application to aquaculture

This study showed three cases of first generation (F1) offspring production in two perch farms. Each case provided an example of the effects of aquaculture practices on genetic diversity. For the two breeder-offspring combinations of farm Y, two different genetic groups were found within both breeders and offspring. However, the number of families increased for the first offspring group and decreased for the second one. For farm X, the breeders and their putative offspring belonged to two different genetic groups, and the number of families was higher in offspring than in breeders. These differences may be explained by different hypotheses. First, the two farms may use wild fish of different origin to establish their broodstocks. Then, each farm may provide different husbandry conditions, which could affect the survival rate of the various strains that exist. The same population of perch may thus survive better in one farm than in the other. Finally, each fish farm has its own reproductive protocol (choice of breeders, sex ratio, protocol for artificial spawning, etc.) that could affect offspring composition.

For Eurasian perch, farmed stocks must be managed with caution to avoid inbreeding (Novel et al., 2013). Data from the present study will help farmers in their breeding programs, in spite of the lack of pedigree information. First of all, it is essential to underline that all stocks display suitable genetic variability able to produce several generations without any further inputs of wild congeners. For the stability of such variability, producing several generations with an equal breeders' contribution using a factorial mating design (Vandeputte et al., 2009) seems to be a suitable strategy. The design can be supplemented by the optimal contribution strategy that takes into account breeding values of breeders and their relationship (Meuwissen, 1997). As suggested for the European sea bass, *Dicentrarchus labrax*, this strategy minimizes the increase in inbreeding and the reduction in genetic variability, while allowing the selection of targeted traits (Novel et al., 2013).

5. Conclusions

Genetic diversity was higher for farmed stocks than for the Lake Geneva population, which was genetically distinct. As the development of perch aquaculture is recent, it is likely that broodstocks from other drainage areas had been introduced regularly alongside with the founder broodstocks, as already observed for other better known species, such as sea bass (Vandeputte et al., 2009). Besides, breeding strategies differed between the two farms and some perch farmers preferred adding wild individuals to avoid inbreeding or to compensate for the low levels of production (i.e., the shortage of offspring at certain times during the year). Therefore, the genetic differences between the founder populations and the studied farmed broodstocks could not be clearly defined, especially without pedigree traceability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aqrep.2015.12.003.

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