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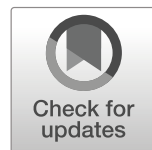
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Seeking for the inner potential: comparison of larval growth rate between seven populations of *Perca fluviatilis*

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Abstract

Larval rearing is a crucial step in fish production. However, issues in larval production, such as low growth/survival rate, impede the aquaculture development of many species including *Perca fluviatilis*. Since allopatric populations of *P. fluviatilis* exhibit different growth rates for first-life stages, basing fish stocks on populations displaying optimal features in aquaculture conditions could overcome some of these issues. Here, we (i) compare the growth rate in standardised recirculating aquaculture system conditions and (ii) assess the genetic differentiation using four mitochondrial markers between seven allopatric populations. Our results confirm that key features for aquaculture can vary at the intraspecific level. However, we do not highlight any clear aquaculture trait differences related to genetic differentiation. Therefore, we cannot assess the genetic basis of growth rate differentiation between populations. This paves the way to future studies on aquaculture performances of genetically distinct populations in *P. fluviatilis*.

Keywords European perch · Genetic differentiation · Growth rate · mtDNA · Origin · Population

Introduction

Nowadays, a trend to diversify the aquaculture industry through new species production is emerging (Fontaine et al. 2009). It aims at promoting the sustainability of aquaculture and

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meeting today's and tomorrow's challenges (e.g. adaptation to environmental and consumer demand fluctuations, food security promotion) (FAO 2016). Such a diversification implies controlling the life cycle of new species in captive environments which is often challenging (Teletchea and Fontaine 2014). Larval rearing is one of the most crucial steps in this control. Indeed, issues in larval production impede the production development of many species including several percid fishes (Szkudlarek and Zakęś 2007; Dąbrowski et al. 2000). The European perch (*Perca fluviatilis*) exemplifies the difficulty and the importance of larval rearing.

The *P. fluviatilis* aquaculture development started during the last decades of the second millennium (Kestemont et al. 2015). Most of its current production relies on intensive recirculating aquaculture systems (RAS) (Toner 2015). Despite an increasing consumer interest, this production fails to meet market demands (Kestemont et al. 2015). This is mainly due to several bottlenecks in life cycle completion in captivity and rearing performances, especially at first-life stages: low growth rate, low survival rate, high cannibalism rate, as well as dependence on live food of larvae (Kestemont et al. 2015).

In order to overcome larval rearing issues, one solution could rely on choosing wild or farmed populations displaying optimal survival, growth, and cannibalism rates in aquaculture conditions to create farmed stocks. Indeed, European perch populations from different geographic areas exhibit different growth rates and feed efficiencies for first-life stages (Mandiki et al. 2004). Similarly, differences in growth and swim bladder inflation rate are known between different larvae populations (Pimakhin and Žák 2014). Therefore, using fishes from populations with better performances at the larval stage could improve nursery of *P. fluviatilis* and allow choosing the best fish stocks for fish farming selective-breeding program. However, few *P. fluviatilis* populations have been compared to date (i.e. Mandiki et al. 2004; Pimakhin and Žák 2014). Moreover, the genetic distinctiveness of these previously studied populations has not been investigated (Mandiki et al. 2004; Pimakhin and Žák 2014) even though such information would be the first hint that population-specific aquaculture performance could be potentially heritable.

Here, we compare the growth rate at first-life stage of *P. fluviatilis* from seven different Central and North European populations in standardised RAS conditions. Furthermore, we estimate the genetic differentiation between populations using four mitochondrial markers in order to assess the hypothesis that aquaculture performances differ between genetically differentiated fish groups.

Materials and methods

Sampling and rearing

In May 2017, we sampled egg ribbons (i.e. 10 ribbons per population) of wild European perch from seven wild locations (Fig. 1). All ribbons were transported by car except for Finnish populations which were transported by plane (see the transport length in Table 1). These ribbons were transported (in oxygenated polyethylene bags filled with 1/3 of water, 2/3 of oxygen; 16 ± 1 °C and placed in thermobox) to the Institute of Aquaculture and Protection of Waters, Faculty of Fisheries and Protection of Waters (University of South Bohemia, Czech Republic). After transportation, we determined the development stage by randomly sampling 150 eggs per population and comparing them to a background developmental table

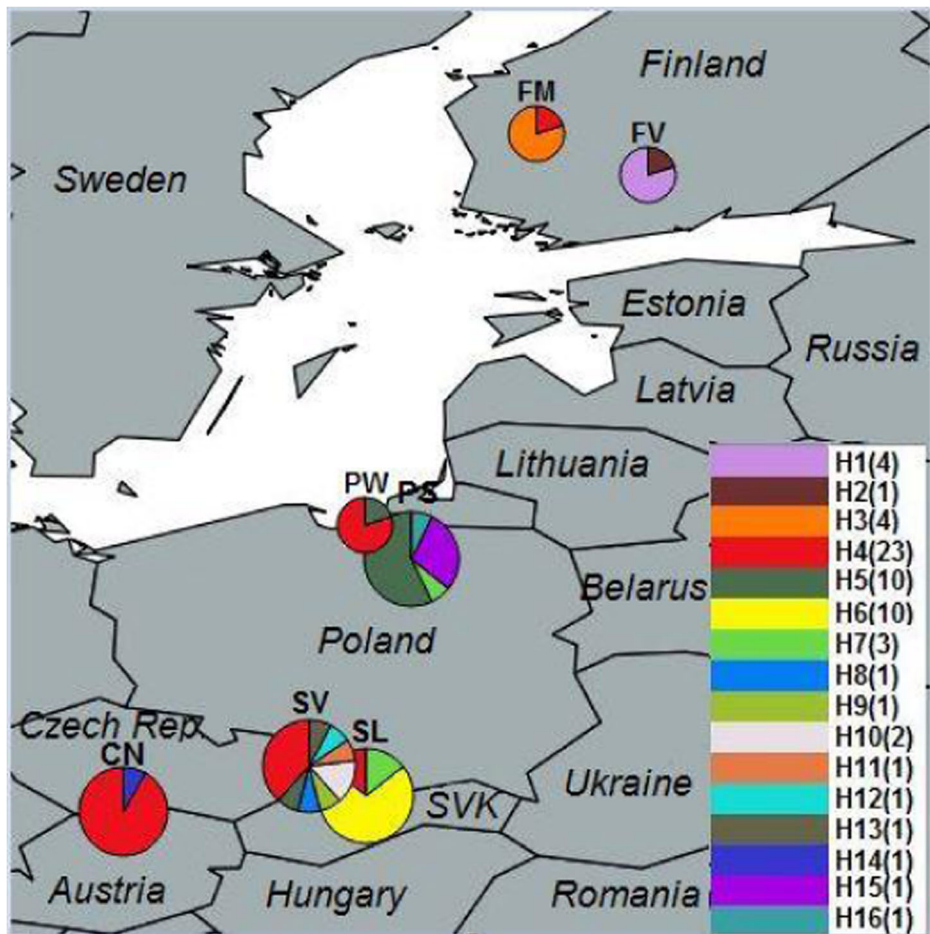


Fig. 1 Sampling areas and haplotype distribution of seven European perch populations in Europe: FV, Valkea-Kotinen Lake (61° 14' 32.1" N, 25° 03' 47.1" E Finland); FM, Majajärvi Lake (62° 03' 57.2" N, 22° 53' 40.6" E Finland); PS, Stary Dwór Lake (53° 44' 51.6" N, 20° 27' 11.8" E Poland); PW, Wiślany Lagoon (54° 22' 36.4" N, 19° 31' 38.4" E Poland); CN, Nové Hrády Pond (48° 47' 33.8" N, 14° 48' 32.3" E Czech Republic); SV, River Váh (49° 07' 29.7" N, 18° 27' 26.2" E Slovakia); SL, Liptovská Mara Reservoir (49° 5' 20.1" N, 19° 34' 38.3" E Slovakia). SVK, Slovakia. Different colours correspond to different haplotypes. Haplotype size refers to the number of individuals studied in each population. Numbers in brackets indicate the number of specimens sharing the haplotype

(Alix et al. 2015) (see Table 1). After temperature acclimatisation, eggs were incubated in 200-L transparent tanks (tank size of 50 × 50 × 80 cm) with a water flow made by aeration. Tanks were equipped with hatching cages as described by Żarski et al. (2017) until 3 days post-hatching (dph). Water parameters in hatching apparatuses were maintained at 17 °C ± 0.8, pH = 7 ± 0.5, oxygen > 90% with 50% daily water exchange. The light intensity was 200–250 lx at the water surface. The photoperiod was constant at 12L:12D.

For each population, we mixed larvae originating from 10 ribbons (total of about 12,060 larvae) at 3 dph and divided them in triplicate with a density of 67 individuals L⁻¹ in 60-L light grey (tank size of 22.5 × 30 × 89 cm) with a water flow through averaging 1 L/min. Temperature was gradually raised from 17 °C ± 0.8 to 23 °C ± 0.5 (1 °C per day) and kept stable.

Table 1 Transport length, egg development stage, survival rate of embryos, egg diameter, body weight, total length and specific growth rate of European perch larvae from Valkeakotinen Lake, Finland (FV); Majärvi Lake, Finland (FM); Stary Dwór Lake, Poland (PS); Wislany Lagoon, Poland (PW); Nové Hrády Pond, Czech Republic (CN); River Váh, Slovakia (SV); Liptovská Mara Reservoir, Slovakia (SL) stocks on the 3, 10, 17 and 24 dph. O, organogenesis steps 1 and 2. G, gastrulation step 2. Values expressed as mean \pm SD. Values (in row) with different superscript letters are significantly different (p value < 0.05)

	FV	FM	PS	PW	CN	SV	SL
Transport length (hours)	6	6	10	10	1	6	6
Obtained developmental egg stage	O1	O1	O1	G2	O2	O1	G2
Survival rate of embryos (%)	76.1 \pm 6.3 ^c	29.1 \pm 5.3 ^d	77.4 \pm 10.8 ^{bc}	94.1 \pm 4.9 ^{ab}	79.2 \pm 3.9 ^{abc}	96.2 \pm 0.4 ^a	93.1 \pm 4.9 ^{abc}
Egg diameter (mm)	2.15 \pm 0.08 ^a	1.53 \pm 0.09 ^d	1.69 \pm 0.08 ^{cd}	1.89 \pm 0.09 ^b	1.78 \pm 0.07 ^c	1.92 \pm 0.08 ^b	1.96 \pm 0.09 ^b
Body weight (mg)							
3rd DPH	0.8 \pm 0.2 ^c	1.1 \pm 0.1 ^{abc}	0.9 \pm 0.1 ^c	1.0 \pm 0.1 ^{bc}	1.4 \pm 0.1 ^a	1.3 \pm 0.1 ^{ab}	1.0 \pm 0.3 ^{bc}
10th DPH	7.3 \pm 4.2 ^a	2.6 \pm 0.9 ^{abc}	1.0 \pm 0.1 ^c	2.1 \pm 1.4 ^{bc}	3.3 \pm 1.2 ^{abc}	2.4 \pm 1.0 ^{abc}	2.7 \pm 1.2 ^{abc}
17th DPH	14.7 \pm 5.2 ^{ab}	19.1 \pm 7.8 ^a	8.3 \pm 1.8 ^b	7.3 \pm 3.9 ^b	17.3 \pm 5.7 ^a	10.5 \pm 4.4 ^{ab}	16.2 \pm 2.9 ^a
24th DPH	71.1 \pm 17.4 ^a	63.8 \pm 29.7 ^{ab}	23.0 \pm 8.6 ^c	39.1 \pm 8.5 ^{abc}	43.3 \pm 25.5 ^{abc}	28.3 \pm 10.5 ^c	30.7 \pm 6.3 ^{bc}
Total length (mm)							
3rd DPH	6.2 \pm 0.1 ^{ab}	6.4 \pm 0.5 ^a	6.7 \pm 0.1 ^a	6.2 \pm 0.3 ^{ab}	5.3 \pm 0.3 ^{bc}	5.2 \pm 0.3 ^{bc}	5.2 \pm 0.3 ^c
10th DPH	9.9 \pm 1.5 ^{ab}	11.4 \pm 0.6 ^a	10.6 \pm 0.7 ^{ab}	10.6 \pm 0.9 ^{ab}	10.1 \pm 2.1 ^{ab}	8.8 \pm 0.7 ^b	8.8 \pm 0.7 ^b
17th DPH	13.5 \pm 1.6 ^{abc}	14.6 \pm 2.5 ^{abc}	18.6 \pm 2.6 ^a	15.3 \pm 2.2 ^{ab}	17.1 \pm 3.0 ^a	10.9 \pm 0.9 ^c	12.4 \pm 1.1 ^{bc}
24th DPH	19.0 \pm 1.2 ^{abc}	19.7 \pm 2.9 ^{ab}	20.5 \pm 0.9 ^a	16.9 \pm 1.1 ^{bcd}	19.0 \pm 1.8 ^{ab}	15.5 \pm 1.5 ^{cd}	15.0 \pm 1.1 ^d
Specific growth rate (day ⁻¹)							
3rd to 24th DPH (total)	20.99 \pm 0.55 ^a	19.40 \pm 0.9 ^{ab}	15.69 \pm 0.59 ^c	17.27 \pm 0.74 ^{bc}	16.05 \pm 1.75 ^c	14.64 \pm 0.68 ^c	16.67 \pm 1.61 ^{bc}

Oxygen saturation ($> 90\%$) and pH level (7 ± 0.5) were monitored twice a day with a multimeter (Hach Lange HQ40d, Germany); ammonium ($0.05 \pm 0.01 \text{ mg L}^{-1}$) and nitrite ($0.05 \pm 0.02 \text{ mg L}^{-1}$) concentrations twice a week (DR 2800, Hach Company, USA). The light intensity was 200–250 lx at the water surface and the photoperiod was constant at 12L:12D with light period from 7am to 7pm.

Feeding with *Artemia* was performed between 3 and 24 dph. During the first 7 days of feeding, larvae were hand-fed five times a day in 2-h intervals with micro-*Artemia* nauplii of 350–380 μm (Ocean Nutrition; ration of 700 nauplii per larvae per day; cca 9 nauplii per mL). Micro-*Artemia* nauplii were subsequently replaced with *Artemia* nauplii of 430–460 μm (hatching rate above 260,000 nauplii g^{-1} ; Ocean Nutrition; rations of 35% of fish biomass for the second week and 10% for the last third week) (Kestemont et al. 2015). During the weaning period (21 to 24 dph), *Artemia* nauplii were progressively replaced by commercial pelleted food BioMar Larviva Pro Wean 100 (80–200 μm ; Nersac, France) over the course of 4 days, hand-fed in 2-h intervals from 8am to 6pm. Daily rations were for the first day 10% *Artemia* nauplii of fish biomass + 2% of compound feed; for the second day, 5% *Artemia* nauplii of fish biomass + 30% of compound feed; for the third day, 5% *Artemia* nauplii of fish biomass + 60% of compound feed; and 100% of compound feed on 24 dph (Kestemont and Mélard 2000).

Initial assessment of fish egg quality

For calculation of embryo survival rate, eyed eggs ($n = \text{ca } 150$ eggs) from each egg ribbon were photographed under a Leica Z6-APO stereoscopic microscope (Leica Microsystems, Switzerland). Embryo survival rate was determined as the percent survived embryos of the total number of eggs in each sample. At the eyed stage, we measured inner diameter of swelled oocytes of 100 randomly chosen eggs from each ribbon by averaging the length of vertical and horizontal diameter of each egg (Żarski et al. 2011). Measured eggs were not returned back into tanks.

Assessment of aquaculture performance/key traits

Larvae from all populations were weighed (BW) and measured at 3, 10, 17 and 24 dph with respect to different timing of hatching among the tested populations. For each sampling point, 15 individuals per tank were killed by lethal dose of oil clove concentration (Hamackova et al. 2006) and weighted (OHAUS Explorer EX224M, NJ, USA) to nearest 0.1 mg. For determination of total length (TL), fish were photographed and measured in ImageJ software (Rueden et al. 2017). The specific growth rate (SGR; %/day) was calculated according to the following equation: $\text{SGR} = 100 * (\ln W_2 - \ln W_1) * \Delta T^{-1}$, where W_1 and W_2 are the initial and final mean body weights, respectively, and ΔT is the time interval (days) between sampling points.

Statistical analyses

All statistical analyses were performed with Statistica version 13.3 (TIBCO Software Inc., CA, USA). Comparison of aquaculture performances for embryo survival rate, egg size, SGR, TL and BW among studied populations was performed through analysis of variance. The assumptions of ANOVA were checked and when they were not met, the Kruskal-Wallis test was performed. Afterwards, Tukey HSD (for ANOVA) or multiple comparisons of mean ranks (for

Kruskal-Wallis test) with Bonferroni correction were done for identification of pairwise significant differences.

Assessment of genetic differentiation

We collected fin clips from 68 larvae at 30 dph (see the number of sequenced individuals per population in Table S1) and stored them in ethanol (96%) prior to DNA extractions using a commercial E.Z.N.A. tissue DNA kit (Macherey-Nagel, Germany). We estimated potential genetic differentiation between populations through analyses of four mitochondrial regions: cytochrome b (Cytb), D-loop of control region (D-loop), 16S rRNA (16S) and cytochrome oxidase I (COI). These DNA regions have commonly been used in fish to study intraspecific genetic patterns (Makhrov and Bolotov 2006; Baharum 2012), including European perch (e.g. Nesbø et al. 1998a; Nesbø et al. 1998b; Nesbø et al. 1999). Gene fragments were amplified using primers L14724F/H15918R (Cytb; Irwin et al. 1991), HV2/CSBD (D-loop; Nesbø et al. 1998b), 16Sar/16Sbr (16S; Palumbi 1996) and jgLCO1490/jgHCO2198 (COI; (Vrijenhoek 1994). Mitochondrial genes were amplified using polymerase chain reaction (PCR): 10-pmol primers, PPP MasterMix (Top Bio), DNA and distilled water. An initialization step of 5 min at 95 °C was followed by 38 cycles of denaturation at 94 °C for 40 s; 50-s annealing at 55.8 °C for 16S, 49 °C for COI and 55 °C for Cytb and D-loop; and 1-min extension at 72 °C plus a 10-min final extension at 72 °C. The PCR products were purified with the E.Z.N.A. gel extraction kit (Macherey-Nagel, Germany) following manufacturer's protocol. Primers CSBD, 16Sbr, jgLCO1490 and H15918R were used for single-strand sequencing (Macrogen Inc., Amsterdam, Netherlands).

Sequences were aligned and manually checked using GENEIOUS 10.1.3 (Kearse et al. 2012). For coding genes, nucleotide sequences were translated into amino acids. The identity of each sequence was checked using BLAST (Altschul et al. 1997). The aligned sequences for D-loop (351 bp) and COI (641 bp) showed seven variable sites with six unique haplotypes in each, 16S (541 bp) showed six variable sites with five unique haplotypes and Cytb (541 bp) showed one variable site with two unique haplotypes. Unique haplotype sequences are available in GenBank (see Table S1). Since all genes belong to the mitochondrial genome, the four markers were concatenated within a single alignment for genetic differentiation analyses using Mesquite 3.31 (Maddison and Maddison 2015). We obtained 16 unique haplotypes in the concatenated matrix (1931 bp) which included 21 variable sites.

Concatenated haplotype map for each stock was created using QGIS software 2.18.3 (QGIS Development Team 2009). Analysis of molecular variance (AMOVA, 100,000 number of permutations) and estimation of the fixation index F_{ST} and pairwise F_{ST} were conducted in SPADS v. 1.0 (Dellicour and Mardulyn 2014).

Results

Initial state of the stocks

The survival rate of embryos was higher than 77% in all tested populations except population from FM where the survival rate was 29% (see population acronym meaning in Table 1).

The inner diameter of swelled oocytes at eyed egg stage showed significant differences among tested populations (Table 1). The highest and the lowest diameters were observed for Finnish populations ($F_{6,693} = 544.7$, p value < 0.05, Table 1).

Aquaculture traits among perch stocks

At 3 dph, we observed an inter-population differentiation of initial BW: CN, SV, and FM had significantly higher values (except for the comparison between SV with PW and SL, and FM with all populations) (chi-square = 56.43, p value < 0.05, df = 6, Table 1). This result, however, changed during the ongoing growth periods, and at the end of the experiment, the highest values were observed in other populations (chi-square = 43.66, p value < 0.05, df = 6, Table 1). For SGR results, FV displayed significantly higher values compared to non-Finnish populations ($F_{6,14} = 12.77$, p value < 0.05, Table 1).

Finish and Polish populations showed the highest TL at 3 dph and most of them remained among the populations with the highest TL at the end of the experiment (chi-square = 62.33, p value < 0.05, df = 6, Table 1).

Genetic differentiation among perch stocks

The geographic distribution of haplotypes (Fig. 1) suggested a genetic differentiation among populations: some haplotypes were restricted to some populations (e.g. H1 in Finland, Fig. 1) while the frequency of other haplotypes differed between populations. Overall, the AMOVA confirmed this differentiation between populations (i.e. $F_{ST} = 0.501$, p value < 0.01). Pairwise AMOVA highlighted significant differentiations between most populations (Table 2). Strong genetic differentiations were observed between Finnish (especially FM) and all other populations (Table 2). In contrast, differences between central Europe populations were not significant or lower (Table 2).

Discussion

Our results show that there are differentiations in growth performances between the studied populations (Table 1). Overall, the Finnish populations tend to have higher performances (Table 1). Similar results were observed by Mandiki et al. (2004) during their comparison of juveniles from Poland and Finland. One could expect that the different initial state of eggs (i.e. egg diameter and egg survival rate) could explain the differences of growth (Table 1). Indeed, a relationship is known between egg size (linked to female size) and larval size/weight at hatching (Moodie et al. 1989; Olin et al. 2012). However, our data showed no such

Table 2 Pairwise F_{ST} values from mtDNA sequence data of European perch populations. FV, Valkea-Kotinen Lake (Finland); FM, Majajärvi Lake (Finland); PS, Stary Dwór Lake (Poland); PW, Wiślany Lagoon (Poland); CN, Nové Hradky Pond (Czech Republic); SV, River Váh (Slovakia); SL, Liptovská Mara Reservoir (Slovakia)

	SV	CN	PS	PW	SL	FV
SV						
CN	<i>0.048</i>					
PS	<i>0.224</i>	<i>0.394</i>				
PW	−0.032	0.012	<i>0.158</i>			
SL	<i>0.243</i>	<i>0.424</i>	<i>0.526</i>	<i>0.414</i>		
FV	<i>0.252</i>	<i>0.632</i>	<i>0.556</i>	<i>0.600</i>	<i>0.671</i>	
FM	<i>0.623</i>	<i>0.885</i>	<i>0.788</i>	<i>0.885</i>	<i>0.884</i>	<i>0.875</i>

Significant values in italics, p value < 0.01

relationship (Table 1). Therefore, the observed divergences could be explained by (i) population-specific environment before the experiment (including parental effect), (ii) local adaptation based on genetic differentiation, or (iii) both (Wolf and Wade 2009).

Our experimental design (i.e. transplant experiment in which all populations undergo the same standardised RAS and rearing practices) allows minimising the effect of environment on growth performances. However, we cannot rule out potential effect of pre-experiment environment on our results. Indeed, we collected egg ribbons in the wild meaning that they can undergo different environmental pressures. Such pressures can lead to responses during development and extend through all or part of the life of an organism (Fusco and Minelli 2010; Wiens et al. 2014). Moreover, environmental conditions in which parent fish lived as well as the parent features (e.g. age, maternal size; Olin et al. 2012) can impact the offspring performance (Mousseau and Fox 1998). Without information about the parents of the sampled egg ribbons, we cannot exclude such parental effects (Youngson and Whitelaw 2008).

Alternatively, different environmental pressures applied over several generations can lead to local adaptations based on genetic divergences (e.g., Losos and Ricklefs 2009). Our analyses showed that the most genetically divergent populations (i.e. Finnish with higher F_{ST} values) tend overall to have more distinct growth performances (Tables 1 and 2). This could suggest a genetic basis of the observed growth differentiation and, consequently, a potential heritability of this pattern as it has already been highlighted for several fish species (e.g. Rosenau and McPhail 1987; Nicieza et al. 1994; Brown et al. 1998). However, genetically undifferentiated populations (i.e. PW, CN and SV) also presented distinct growth rates (Tables 1 and 2). The lack of genetic differentiation of these populations should be further assessed by higher resolution analyses (e.g. microsatellites since mitochondrial markers are quite conserved and, thus, we could underestimate genetic divergences).

Finally, potential biases induced by our experimental design can be noticed. First, ribbon transportation can have influenced embryo development and thus larvae performances. However, we tried to minimise such an impact by transporting egg ribbons during less sensitive egg development stages (e.g. gastrulation and organogenesis, see Table 1) (Wojnarovich and Horváth 1980). Overall, the length and the mean of transport as well as the development stage of our samples do not seem to influence our results (Table 1). Second, we did not evaluate feed intake because such an assessment on larvae remains methodologically difficult/time-consuming. Although, tested populations were reared in optimal conditions according to literature (Kestemont and Mélard 2000; Tamazouzt et al. 2000; Kestemont et al. 2008; Kestemont et al. 2015), we cannot rule out potential influence of feed intake on growth differentiation. Whether such a population-specific feed intake exists, it should be considered as a population-dependent feature potentially valuable for aquaculture.

Our study confirms that key features for aquaculture can vary at the intraspecific level which could be beneficial to improve European perch production. However, we do not highlight any clear aquaculture trait differences related to genetic differentiation. Therefore, we cannot estimate the contribution of pre-experiment population-specific environment and potential local adaptation based on genetic differentiation on our results. This could be solved by performing similar experiment over several generations.

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Author contributions JK, VS and TV conceived original idea. JK, VS and TV carried out the sampling. TV, RG and BD contributed to rearing process. TL, LT, MB and TV contributed to laboratory genetic analyses. RG performed statistical analyses. TL, LT, RG, VS, MB, BD and TV discussed the results and contributed to the final manuscript, revising it critically for important intellectual content.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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