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Finding a rare gem: Identification of a wild biological unit with high potential
for European perch larviculture

Short title: Potentials within European perch

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ABSTRACT

Potential for aquaculture can differ among allopatric wild populations of a species of interest. This makes relevant to seek best candidates for fish farming at the intraspecific level. Here, we compare the aquaculture potential among allopatric population groups of the European perch, a species of interest for fish farming. More specifically, we aim at finding population groups with the best performance in larviculture through an integrative approach that allows considering geographic differentiation in domestication processes. A multi-function/trait assessment was performed on three genetically differentiated groups of European perch populations: (i) Danube, (ii) Eastern Europe, and (iii) European Plain. A geographic differentiation was highlighted for six important traits for perch larviculture: survival rate, swim bladder inflation rate, deformity rate, length at hatching, mean of interindividual distances, and change in activity following a stress event. Along with fish farmer-advice-based weighting of the traits, the calculation of an aquaculture potential score allowed identifying the populations from the Danube region as the most interesting to potentially overcome current bottlenecks in European perch larviculture.

Key words: Aquaculture - Differentiation - Domestication - Intraspecific - Multi-trait - *Perca fluviatilis*.

1. INTRODUCTION

Geographic differentiation (Mayr, 1942) between conspecific allopatric populations is a common phenomenon in the wild (e.g. Delarue et al., 2009; Lecocq et al., 2015; Yeates-Burghart et al., 2009). It is defined as any genetic and/or phenotype interpopulational differentiation shaped by divergence processes within the species distribution range. Geographic differentiation results from distinct demographic histories, random genetic drift, limited gene flow, and/or local adaptations (Avice, 2000; Mayr, 1963).

Geographic differentiation of wild species has been considered as an important phenomenon to be considered in domestication (*sensu* Lecocq, 2020) for fish aquaculture (e.g. Mandiki et al., 2004; Gjedrem 2012; Vandeputte et al., 2014; Toomey et al., 2020a,b). Indeed, geographic differentiation patterns are already known for many key traits for aquaculture such as growth rate (e.g. Svåsand et al., 1996; Chavarie et al., 2010), inter-individual interactions (e.g. Rosenau and McPhail, 1987; Wark et al., 2011), or resistance to diseases (e.g. Imsland et al., 2002; Khanh Doan et al., 2017). Therefore, some populations of a species of concern can display key traits' expressions (i.e. aquaculture performances) facilitating domestication (e.g. a high growth rate) while others can impede this process (e.g. a high aggressiveness towards conspecifics). This means that domestication processes can be enhanced by choosing the population(s) with the most suitable performances for aquaculture (Toomey et al., 2020b). It could especially be useful to help the diversification of the aquaculture production promoted by international institutions (e.g. FAO 2018), which requires new species domestication (Teletchea and Fontaine 2014). A three-step integrative approach has been recently developed to facilitate the domestication of new species by taking into consideration geographic differentiation (Toomey et al., 2020b). The first step classifies wild populations by merging those that are most likely undifferentiated and by separating population groups for which aquaculture performance differentiation could be expected, the so called prospective units

(PU; Toomey et al., 2020b). This classification is based on a differentiation proxy (i.e. a measured variable used to infer the differentiation of aquaculture performances) such as genetic marker information. It allows to avoid to randomly choose populations, which could result in (i) unnecessary aquaculture potential assessment through the comparison of undifferentiated populations or (ii) missing a potentially important group of populations. The second step compares the aquaculture performances of populations from different PU. The variance of a phenotype being determined by genetic factors, environmental factors, and the interaction between these two factors (Falconer and Mackay, 1996), phenotypic specificities observed in the wild may not be maintained under controlled aquaculture conditions (e.g. Vandeputte et al., 2002). Therefore, the assessment of populations' performances must be performed *ex-situ* in the same domestication environment (i.e. close to farming conditions; de Villemereuil et al., 2016). Moreover, because the aquaculture potential (i.e. potential to be successfully domesticated and produced; Toomey et al., 2020b) of a fish stock relies on several trait expressions and biological functions, this assessment has to be based on a multi-function and multi-trait approach. Finally, the last step aims at identifying the unit with the highest potential for aquaculture through the weighting of the different traits evaluated (i.e. not all traits have the same importance to stakeholders) and the calculation of an aquaculture potential score. The aquaculture potential score allows making a synthesis of results obtained at the multi-function and multi-trait levels.

The European perch (Actinopterygii, Percidae, *Perca fluviatilis*) is an example of a species for which considering the wild geographic differentiation could enhance its aquaculture production. This could be especially important since it is seen as a candidate of interest for European inland aquaculture diversification (Fontaine and Teletchea, 2019). The European perch is a widespread freshwater species occurring across Eurasia (Stepien et al., 2015). Its economic and recreational interests led to start domesticating this species in the 1990's

(Fontaine and Teletchea, 2019). However, the production is still limited because of numerous bottlenecks, particularly in the first-life stages (e.g. low survival rate, growth heterogeneity; Fontaine and Teletchea, 2019; Policar et al., 2019). Yet, a geographic differentiation was previously highlighted between wild populations for *P. fluviatilis* at the genetic level (Nesbø et al., 1999; Toomey et al., 2020a), as well as at the phenotypic level in controlled conditions regarding behaviour (Mandiki et al., 2004; Toomey et al., 2019), growth and survival rates (Mandiki et al., 2004; Vanina et al., 2019a, 2019b), and development (Pimakhin and Zak, 2014). However, these previous studies highlighted geographic differentiation for a limited number of traits/biological functions. In addition, they focused on random populations without a justification about why these populations were selected.

Here, we aim at assessing if some wild population groups would be less impacted by known bottlenecks of *P. fluviatilis* production during the larval production stage. We used the above mentioned three-step integrative approach in order to go beyond the limits of previous studies because it allows (i) avoiding randomly pick populations by using an intraspecific classification and (ii) leading a multi-function and multi-trait evaluation. Ultimately, we aim at providing a new insight to fish farmers to improve European perch production.

2. MATERIAL AND METHODS

2.1 First step of the integrative approach: intraspecific classification

Several proxies are suggested in Toomey et al. (2020b). Here, the genetic proxy was chosen to perform an intraspecific classification. Indeed, groups of populations with divergent demographic histories are likely to have acquired some phenotypic specificities, including for key traits for aquaculture (Toomey et al., 2020b). A phylogeographic classification was already available for *P. fluviatilis* in literature. Toomey et al. (2020a) showed the occurrence of five PU based on phylogeographic methods: (i) European Plain, (ii) Eastern Europe, (iii)

Danube and Alpine foreland (hereafter called Danube), (iv) Northern and Western Fennoscandia, and (v) Balkans. Only the three first PU could be sampled in this work.

2.2 Second step of the integrative approach: Performance evaluation

2.2.1 Compliance with ethical standards

Individuals were handled as little as possible all along the experiment. All procedures used were in accordance with international and national guidelines for protection of animal welfare (Directive 2010/63/EU). This work was led with the approval Animal Care Committee of Lorraine (CELMA n°66) and the Ministry of Higher Education, Research, and Innovation (APAFIS13368-2018020511226118, APAFIS17164-2018101812118180).

2.2.2 Biological material collection and pre-experiment rearing conditions

Egg ribbons (one ribbon corresponding to one female) were obtained across two years during spawning seasons (May 2018 – April and May 2019; Figure 1). One lake representative of the Danube unit was collected: Lake Balaton (BAL; 2019, Hungary; 46°54'23.375"N, 18°2'43.119"E). Regarding the two other PU, several lakes were collected for each PU because of the large size of these units. This allowed considering potential differentiation within each unit. In this way, two populations were collected for the Eastern Europe unit: Lakes Valkea-Müstajärvi (VAL; 2018, Finland; 61°13'08"N, 25°07'05"E) and Iso-Valkjärvi (ISO; 2018, Finland; 60°57'21"N, 26°13'3"E). Four lakes were sampled for the European Plain which is the largest prospective unit: Lakes Geneva (GEN; 2019, France; 46°22'7.20"N, 6°27'14.73"E), Bourget (BOU; 2019, France; 45°44'12.469"N, 5°52'1.617"E), Kierzlinskie (KIE; 2019, Poland; 53°47'54"N, 20°44'45"E), and Hohen Sprenzer (HOH; 2019, Germany; 53°55'10.369"N, 12°13'6.005"E). After transportation, 13 to 32 egg ribbons per lake were incubated at the experimental platform of aquaculture (Unit of Animal Research and Functionality of Animal Products, University of Lorraine, Vandœuvre-lès-Nancy, France) at

13°C in incubators (1-2 independent incubators per population; for details on incubators see Toomey et al., 2019). Photoperiod was set to 12L:12D and light intensity to 400 lx at the water surface. Oxygen rate ($9.8 \pm 0.7 \text{ mg.L}^{-1}$) and temperature ($13 \text{ °C} \pm 0.5 \text{ °C}$) were checked daily while pH (8.0 ± 0.3) and ammonium and nitrite concentrations (lower than 0.05 mg.L^{-1}) were monitored three times a week until hatching.

Figure 1: Map representing the approximate geographic range of the different prospective units and the different populations sampled. Prospective units are represented by colored areas: blue for Danube, yellow for European Plain, and green for Eastern Europe. Populations are represented by black circles: ISO, VAL, BAL, KIE, HOH, GEN, and BOU correspond to Lakes Iso-Valkjärvi, Valkea-Mustajärvi, Balaton, Kierzlinskie, Hohen Sprenger, Geneva, and Bourget, respectively.

2.2.3 *Experimental rearing conditions*

Spawning seasons of the different wild populations are shifted in time. Therefore, all populations were reared separately using the same rearing protocol in independent structures, in which there is a precise control of temperature and photoperiod. Given the increasing concerns about Perhabdovirus in Europe (Bigarré et al., 2017), all populations were tested for the occurrence of this virus (*Laboratoire Départemental d'Analyses du Jura*, Poligny, France). All results were negative to the presence of the Perhabdovirus. The experimental phase started at one day-post hatching (dph) until after weaning, at 26 dph.

Rearing conditions in a Recirculated Aquaculture System (RAS) were the same as Toomey et al. (2019). Briefly, for each lake, all larvae from the different egg ribbons were mixed after hatching and transferred to three green (RGB: 137, 172, 118) internal-wall 71 L cylindro-conical tanks (three replicates per population; RAS) at a density of 50 larvae.L^{-1} . Light intensity was 400 lx at the water surface and photoperiod was 12L:12D (with a simulation of

dawn and dusk for 30 min). Temperature was gradually increased during the first two weeks from 13 °C to 20 °C (one-degree Celsius rise per day). Larvae were hand-fed with newly hatched *Artemia* nauplii (Sep-Art, INVE) from three dph until at 16 dph, seven times a day (every 90 min, from 8.30 am to 5.30 pm). At 16 dph, weaning (i.e. transition from live feed to inert dry artificial diet) started. *Artemia* ration was decreased by 25 % every three days and dry feed ration (BioMar, 300 µm until 21 dph, then 500 µm) was increased by the same ratio. After 25 dph, larvae were only fed with dry feed *ad libitum* (BioMar 500 µm). Temperature (20.0 ± 0.4 °C) and oxygen concentration (8.6 ± 1.4 mg.L⁻¹) were checked daily in all cylindro-conical tanks. Ammonium and nitrite concentrations (means inferior to 0.1 mg.L⁻¹) and pH (7.8 ± 0.4 mg.L⁻¹) were monitored three times a week. Every day after first feeding, tanks were cleaned and dead individuals removed.

2.2.4 Larviculture performance assessment

In this study, a trait expression value is considered at the replicate (i.e. cylindro-conical tank) level. Each trait expression value is obtained from the average of individual values. All traits studied refer to important traits listed in Toomey et al. (2020b).

Growth traits are important to study in larviculture production, particularly growth rate, final length (Kestemont et al., 2015), larval size at hatching (Teletchea and Fontaine, 2010), and growth heterogeneity (Fontaine and Le Bail, 2004; Kestemont et al., 2015). In order to evaluate these traits, 30 larvae per population (i.e. ten larvae per cylindro-conical tank) were sampled at one and 26 dph. Individuals were euthanized with an overdose of MS-222 and kept in formalin 4%. Larvae were measured (total length; ± 0.01 mm) using ImageJ (Schneider et al., 2012). Specific growth rate (SGR) was calculated using the following formula: $SGR = 100 * (\exp^{[(\ln(L_f) - \ln(L_i)) / \Delta T]} - 1)$ where L_i and L_f are the average initial and final length, respectively, and ΔT the duration of the experiment (Crane et al., 2019). Final growth heterogeneity was calculated using the formula: CV_{L_f} / CV_{L_i} where CV is the coefficient of

variation ($100 \times \text{standard deviation/mean}$) and L_i and L_f the initial and final length, respectively.

Survival rate is one of the key traits for larviculture production (Kestemont et al., 2015; Conceicao and Tandler, 2018). It was calculated for each cylindro-conical tank based on the final count of larvae using the following formula: $N_f \times 100 / (N_i - N_s)$, where N_f is the final number of fish counted at 26 dph, N_i the initial number of fish, and N_s the number of fish sampled along the phase (i.e. for growth measurements and behaviour experiment, see below).

Developmental traits are also essential for larviculture, including swim bladder inflation rate (Polcar et al., 2019), deformity rate (Kestemont et al., 2015; Alix et al., 2017), and the volume of the yolk sac (Trabelsi et al., 2013). Swim bladder inflation rate was calculated at 26 dph on all remaining larvae following the protocol used in Jacquemond (2004a, 2004b; 20 g.L⁻¹ of sea salt and 70 mg.L⁻¹ of MS-222) and using the formula: $100 \times (SB+ / N_f)$ with $SB+$ the number of larvae with swim bladder and N_f the final number of larvae at 26 dph. Deformity rate was calculated in the final counting at 26 dph using the following formula: $100 \times (N_m / N_f)$ with N_m the number of deformed larvae (only visible column deformities) and N_f the final number of larvae counted. Finally, the yolk sac volume was calculated in the following way: $\pi/6 \times YSL \times YSH^2$, where YSH is the yolk sac height and YSL the yolk sac length (Bagarinao, 1986).

The ability of fish larvae to be efficiently produced in intensive conditions (i.e. high rearing densities) also depends on several behavioural factors (Toomey et al., 2020b, 2019), namely: (i) inter-individual relationships (i.e. here more particularly aggressiveness) and inter-individual distances (Huntingford, 2004; Kristiansen et al., 2004; Kestemont et al., 2015; Naumowicz et al., 2017), (ii) activity (Boisclair and Leggett, 1989; Ashley, 2007 and references within), and (iii) the ability to tolerate stress (Schreck et al., 1997; Colson et al.,

2015). Aggressiveness was assessed through the consideration of cannibalism (Baras, 2012) and enucleation, a specific aggressive behaviour in *P. fluviatilis* (Jourdan et al., 2000). It was evaluated based on the daily examination of dead larvae using the following formula: $(N_e + N_t) / N_d$ where N_e is the number of enucleated larvae, N_t the number of truncated larvae (type I cannibalism), and N_d the number of dead larvae counted between five and 26 dph (not possible to count the number of dead larvae between one and five dph due to their rapid decomposition, but aggressive interactions are reported to start at later stages; Baras et al., 2003; Kestemont et al., 2015). The protocol to evaluate inter-individual distances (Buske and Gerlai, 2011) and activity was adapted from Colchen et al. (2017) and Toomey et al. (2019). Each population was evaluated at 25 and 26 dph. For each population, 90 larvae (i.e. 30 larvae per cylindro-conical tank) were sampled the day before the experiment and transferred to aquaria (58 L; 80 lx) at 20 °C. After one night of acclimatization, populations were tested by groups of ten larvae in circular arenas (10 lx, 30 cm diameter, 1.5 cm of water depth). Behaviour of individuals was recorded (three arenas tested simultaneously; three replicates per cylindro-conical tanks, three cylindro-conical tanks per population). After 30 min acclimatization, the following 30 min were used to assess inter-individual distances and activity. After one hour, a sudden event test (adapted from Colson et al. [2015] and Millot et al. [2009]) was performed to evaluate the tolerance to stress through the evaluation of activity before and after the sudden stress. Changes in behaviour, including activity, have been shown as an accurate stress indicator in fish (Schreck et al., 1997; Ashley, 2007). A 1 cm marble was released (from distance, experimenter in an adjacent room) in the center of the arena. The fall was driven by an electromagnet placed 47.5 cm above the bottom of the arena. Activity was recorded after the drop of the marble for 30 min and the first ten seconds were analyzed (initial response to stress being often triggered in terms of seconds; Schreck et al., 1997). At the end of the behavioural experiment, larvae were euthanized with an overdose of MS-222

for further length measurements. Averaged total lengths of larvae tested from VAL, ISO, BAL, KIE, GEN, BOU, HOH, and were 12.90 ± 0.62 mm, 14.05 ± 0.55 mm, 10.62 ± 0.47 mm, 10.90 ± 0.73 mm, 11.81 ± 1.01 mm, 11.77 ± 0.48 mm, and 11.35 ± 0.72 mm, respectively. Before the sudden stress, images were extracted from videos every five minutes (six images per video) to evaluate inter-individual distances (i.e. mean of distances between a focal individual and all the other individuals of the group; group cohesion indicator; Buske and Gerlai, 2011). All image analyses were performed in ImageJ (Schneider et al., 2012). For each image, coordinates (using the middle point between the eyes) of each individual were noted. This allowed measuring distances between a given individual and the other members of the group. All these distances were averaged to get one value per individual. Means obtained for all members of the group were averaged per image. The mean between all image values allowed obtaining a mean value of inter-individual distances per replicate (Colchen et al., 2017). Concerning activity, one image per second was extracted for six consecutive seconds every five minutes before the sudden stress test. After the drop of the marble, images were extracted every second for the first six seconds. Distance swam every second was calculated and the mean allowed obtaining the distance swam per second for each individual. The mean between individual values allowed obtaining an activity for each image series. To calculate activity before stress, which is based on several sampling times, the mean between image series allowed calculating the activity per replicate. For post-stress evaluation, for each cylindro-conical tank, the difference delta in activity was calculated between the median value of activity before stress and the median value of activity after stress (over the six seconds post-stress).

2.2.5 Inter-PU statistical analyses

All statistical analyses were performed in R 3.0.3 (R Core Team, 2020) using values from each cylindro-conical tank (three replicates per population). Homogeneity of variances and

normality of distribution were tested using the Levene test (R-package *lawstat*; Gastwirth et al., 2015) and a Shapiro-Wilk test, respectively. When assumptions were not met, data were transformed (log-transformation for deformity rate, activity, and activity difference delta; inverse-transformation for length at one dph and specific growth rate). In order to check if the cylindro-conical tank or population had an influence on results, Corrected Akaike Information Criterion (R-package *qpcR*, Spiess, 2018) were used to compare linear mixed models (biological traits as fixed factors; cylindro-conical tank and/or population as random factor(s); R-package *lmer* Kuznetsova et al., 2017) and linear model (biological traits as fixed factors, no random factor). When there was no influence of random factors (for deformity rate, final length heterogeneity, length at hatching, activity, activity difference delta, interindividual distances, and specific growth rate), one-way analyses of variance (ANOVA F test) followed by Tukey post hoc tests were used to evaluate differences between PU. When the effect of one (for survival rate, swim bladder inflation rate, length at hatching, yolk sac volume) was significant, the ANOVA was performed on the linear mixed model and estimated marginal means were calculated (R-package *emmeans*; Lenth, 2019). When assumptions were not respected (only for aggressiveness rate), the effects of the two random factors were checked using the R-package *ARTool* (Kay and Wobbrock, 2020). Since there was no effect of random factors, a Kruskal-Wallis H test was used followed by Dunn post-hoc test (R-package *PMCMR*; Pohlert, 2014). All post-hoc results were corrected relatively to the number of comparisons using Benjamini-Hochberg procedure.

2.3 Third step of the integrative approach: Evaluation of the aquaculture potential

Only traits for which a statistical differentiation between PU was observed (P-value $[P] < 0.05$) were considered for the calculation of the aquaculture potential score. The first step of this score calculation consists of calculating an average weight coefficient for each trait based on the investigation led in Toomey et al. (2020b) among percid farmers (Appendix S1). Then,

since value ranges are different among traits, the second step aims at standardizing data for the different traits (centering and scaling [mean of zero and standard deviation of one] and translating to avoid negative and zero values) for each replicate (i.e. cylindro-conical tank). The last step consists of calculating the aquaculture potential score for each replicate (calculation details in Appendix S1). The formula is adapted from the selective index used in quantitative genetics (Moreira et al., 2019). Caution should be paid to the trait expression expected. For instance, while for most traits the highest value is the most interesting (e.g. growth rate, survival rate), for some other traits the lowest values are of higher interest (i.e. activity, inter-individual distances, deformity rate, activity difference delta). Therefore, for these traits, for which the lowest values are of interest, the standardized values were multiplied by “-1”. Overall, the aquaculture potential score (ranging from $-\infty$ to ∞) is defined as indicated in Formula 1.

Formula 1:

$$\text{Aquaculture potential score} = \sum_{i=1}^n (\text{Weighting coefficient}(i) * \text{Standardized value}(i))$$

Where: n corresponds to the number of traits, i=1 the first trait evaluated, i the trait considered, n = the last trait considered, the *weighting coefficient* corresponds to the weight attributed to each trait by perch farmers, and the *standardized value* corresponds to the centered-scaled and translated value attributed to the population replicate for each trait. The biological unit with the highest score is the one with the highest potential for aquaculture.

From scores obtained on all replicates from all populations, statistical analyses were performed to evaluate the statistical differentiation in scores between PU. Homogeneity of variances and normality of distribution were tested using the Levene test (R-package *lawstat*) and a Shapiro-Wilk test, respectively. Assumptions being respected, a one-way analysis of

variance (ANOVA F test) was performed followed by Tukey post hoc test to evaluate differences between PU. P were corrected for multiple comparisons using Benjamini-Hochberg procedure.

3. RESULTS

There was no differentiation between PU for specific growth rate in length ($F_{(2,4)}$; where 2 corresponds to the first degree of liberty [number of PU-1] and 4 to the second degree of liberty [total number of populations-number of PU])= 2.30 , $P=0.13$), final length heterogeneity ($F_{(2,4)}=0.81$, $P=0.46$), final length ($F_{(2,4)}=0.45$, $P=0.67$), yolk sac volume ($F_{(2,4)}=0.49$ $P=0.65$), aggressiveness rate ($K=4.59$, $df=2$, $P=0.10$), and activity ($F_{(2,4)}=2.56$, $P=0.11$)

There was a statistically significant differentiation between PU for survival rate ($F_{(2,4)}=8.04$, $P<0.05$), swim bladder inflation rate ($F_{(2,4)}=68.93$, $P<0.05$), deformity rate ($F_{(2,4)}=20.94$, $P<0.05$), length at hatching ($F_{(2,4)}=13.62$, $P<0.05$), inter-individual distances ($F_{(2,4)}=25.26$, $P<0.05$), and activity difference delta ($F_{(2,4)}=3.87$, $P<0.05$) (Figure 2).

Figure 2: Barplots representing results obtained for traits for which a statistically significant difference was found between prospective units. D refers to Danube unit, P to European Plain unit, and E to Eastern Europe unit. Colors for each prospective unit refer to colors used in Figure 1. Different letters indicate significant differences between PU ($p\text{-value}<0.05$) using post-hoc tests. + indicates the optimal expected value according to fish farmers and – the least optimal value.

The calculation of the aquaculture potential score allowed to show a significant statistical differentiation between all PU ($F_{(2,18)}=29.98$, $P<0.05$). It allowed identifying the Danube as the best PU for larviculture of *P. fluviatilis* while the European plain unit presents the lowest score (Table 1; Appendix S1). When looking at the population level, the same pattern is

observed with populations belonging to the European Plain group having lower score than those belonging to Danube and Eastern units (Table 1).

Table 1: Aquaculture potential score for each population/Prospective Unit (PU). Different letters indicate statistically significant differences (p-value<0.05) between PU using Tukey post-hoc test.

Population	VAL	ISO	BAL	KIE	HOH	GEN	BOU
Average score per	93.96 ±	41.21 ±	340.72 ±	-152.61	-80.26 ±	-171.94	-212.02 ±
population ± s.d.	35.15	92.97	138.58	± 99.61	152.48	± 148.26	152.14
PU	Eastern		Danube		European Plain		
Average score per			340.72 ^b				
PU ± s.d.	67.59 ^a ± 69.18		±138.58		-154.21 ^c ± 143.24		

4. DISCUSSION

4.1 Geographic differentiation between PU

In this study, a geographic differentiation was highlighted at PU level for six traits out of 12. We cannot exclude that geographic differentiation in growth rate, final size, and growth heterogeneity appear latter during the fish development as observed during the on-growing period by other studies (Mandiki et al., 2004). Similarly, the absence of differentiation in aggressiveness could also be explained by the timing of the experiment, since the change in feeding regime during weaning increases the incidence of aggressive interactions (Mandiki et al., 2004; Toomey et al., 2019). Nevertheless, our results highlight the potential usefulness of considering wild geographic differentiation for aquaculture development. Indeed, large differentiations between PU have been highlighted in major traits for larviculture. This appears as particularly interesting for survival rate, swim bladder inflation rate, and deformity

rate, which were shown as major bottlenecks in European perch larviculture (Fontaine and Teletchea, 2019; Kestemont et al., 2015; Policar et al., 2019). A geographic differentiation in controlled conditions has already been reported for European perch, at the populational level, regarding several important traits (Mandiki et al., 2004; Pimakhin and Zak, 2014; Pimakhin et al., 2015; Toomey et al., 2019; Vanina et al., 2019a;2019b). However, comparison of our results with previous studies is difficult since different rearing conditions were used. A geographic differentiation for important traits was also previously reported for other species (e.g. Jonassen et al., 2000; Rosauer et al., 2011; Vandeputte et al., 2014).

A differentiation can also be seen at lower levels than PU. Indeed, for the two PU for which several populations were sampled, inter-populational differences can be seen in the score for aquaculture potential (Table 1). This would be expected since the first step classification of the used approach aims at merging populations with very similar aquaculture performances but not exactly the same ones. However, the statistical differentiation for six major traits for larviculture indicates that the differentiation within PU is overall lower than the differentiation between PU making the assessment at the PU level relevant.

4.2 Implications for *Perca fluviatilis* larviculture

As observed in figure 2, the PU identified as the best for larviculture might be different according to the trait considered (e.g. length at hatching would highlight the Eastern European group as the best while swim bladder inflation rate would characterize the Danube unit as the most interesting). Overall, the Danube group seems the most interesting from results obtained in the second step of the approach. Yet, these results do not take into consideration the potential differential weight of the different traits according to fish farmers. Conversely, the aquaculture potential score used in the third step (Formula 1) allows integrating the differential importance of the traits. This score presents the limit to not take into consideration statistical differentiation between PU since it is calculated based on the trait value. However,

it presents the advantage to simplify the decision-making regarding conclusions drawn to identify the unit with the highest potential for aquaculture. The use of this score confirmed that the Balaton unit was the most interesting for *Perca fluviatilis* larviculture.

The lowest potential for aquaculture was highlighted for the European Plain unit. It is worth noting that individuals from this unit (i.e. more specifically Lake Geneva) were supposedly at the origin of the founder stocks of several perch farms (Ben Khadher et al., 2016). Nevertheless, previous genetic assessment of farmed populations showed that Lake Geneva genotypes were poorly represented in farmed stocks (Ben Khadher et al., 2016). This means that several introductions of individuals from different geographic origins have likely occurred during the domestication of these farmed lineages (Ben Khadher et al., 2016). Although the geographic origin of wild populations introduced in farmed stocks is still unknown, it suggests that fish farmers would have already, and possibly unconsciously, reaped the benefit of wild geographic differentiation within the European perch to develop their production.

Our results suggest that the use of populations from the Danube group could allow overcoming bottlenecks tied to first-life stages, which could be partly linked to the previous use of a suboptimal unit. Overall, production efficiency is one of the major bottlenecks limiting the expansion of the sector. Improving zootechnical performances appears as an efficient solution to reduce production costs for European perch culture. Nevertheless, potential benefits of replacing or integrating Danube populations in current fish farmer stocks cannot be assessed because we did not compare their aquaculture performances with those of currently farmed strains. A comparison in the same controlled conditions between the Balaton unit and currently farmed stocks would allow pointing out advantages of using this specific unit to overcome bottlenecks of the European perch production.

Beside the zootechnical performances assessment, caution should be paid to the environmental risks of using non-local populations (Toomey et al., 2020a). Indeed, even in indoor aquaculture, risks of escapees cannot be ruled out (Summerfelt and Vinci, 2009). These escapees can trigger negative consequences on the genetic integrity and fitness of locally adapted populations (e.g. genetic homogenization/introgression, competition for resources, or pathogen introduction; Arechavala-Lopez et al., 2013; Danancher and Garcia-Vazquez, 2011; Laikre et al., 2005). The impact of escapees are particularly well known in Salmonids, particularly for *Salmo salar* (e.g. Fleming et al., 2000; McGinnity et al., 2003) but should not be neglected for Percid culture, even though the risk of escapees is much lower in RAS culture than for sea cages used in *S. salar* culture. Overall, the choice of the founder stock should be based on a trade-off between risks for local populations and benefits regarding the potential divergences. The decision-making should be based on a consensus between all stakeholders involved in the perciculture sector and rearing systems should be designed in a way to minimize escapee risks.

4.3 Limitations in the performance evaluation

Populations were compared in the same standardized aquaculture conditions in order to highlight genetically based differentiations in performances (de Villemereuil et al., 2016). However, in this experiment, egg ribbons were collected in the wild and have already experienced an influence from the wild environment. Therefore, the potential impact of phenotypic plasticity, including transgenerational effects, on performances cannot be completely ruled out (Pigliucci et al., 2006; Youngson and Whitelaw, 2008). Yet, we argue that such potential biases are minimized thanks to (i) the collected of 13-32 egg ribbons per population, which minimizes female specificity and transgenerational effect biases and (ii) the comparison in the same experimental environment, which limits the impact of phenotypic plasticity. Moreover, completely avoiding such biases is still difficult since it would imply

breeding individuals over several generations (i.e. at least 2.5 years long bioassays for *P. fluviatilis*).

More specifically for the behavioural traits, it is worth noting that the low density used could make the result poorly reflective of what happens in industrial larviculture. However, behavioural assessment on larvae at high density is still hard to achieve (i.e. increases the complexity of tracking and image analyses).

4.4 Perspectives

Overall, this study highlights that there can be a substantial impact in the choice of the founder population for perch farming. These results are first insights, which could be helpful for *P. fluviatilis* larviculture, but these results are specific to our RAS system. Indeed, the potential interaction between genotype and environment was not assessed (Sae-Lim et al., 2016). The presence of such interaction implies that the PU for our rearing system may not be as interesting in different rearing conditions (i.e. a particular genotype presenting different phenotypes in different rearing environments). This could prevent the election of a specific PU as the best universal biological unit. Therefore, this interaction remains to be tested before extending conclusions to other domestication systems. Moreover, three PU out of five were tested here. Evaluating aquaculture potential for the two other PU (i.e. Balkans, Northern and Western Fennoscandia) could eventually lead to the identification of a PU with a higher potential for aquaculture. Furthermore, this work was led on the first phase of larviculture but remains to be performed for the rest of the production cycle to check if the best PU for the initiation of larviculture remains the best for the rest of the production cycle. Therefore, further traits need to be taken into account such as traits linked to other life stages and important traits for production (e.g. size at sexual maturity, fertilisation rate; filleting yield), along with traits essential for future selective breeding programmes (e.g. genetic variation) (Toomey et al., 2020b). Finally, differences in aquaculture potential between PU remain to

best tested in fish farms conditions in order to evaluate economic consequences of differentiation between PU and subsequent choice of the founder population.

Supplementary data

Appendix S1: Calculation of the aquaculture potential score. The first step consists of calculating an average weight coefficient for each trait taking into account farmers' opinions (step A). Then, for each replicate, standardized values are calculated for each trait when a significant statistical differentiation between prospective units was highlighted (Step B). Finally, a score per trait and per replicate/population/PU is calculated by multiplying the average weighting coefficient by the (average) standardized value (Step C). A coefficient of -1 is used for traits for which the lowest value is the one expected by fish farmers. The sum of all these results allows to calculate for each replicate/population/PU an aquaculture potential score.

Declaration of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

TL, AP, PF, and LT designed the study and collected biological material. LT performed the bioassays and the analyses. TL and LT wrote the manuscript. All authors read and approved the final manuscript.

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