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

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

3 Short title: Potentials within European perch

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21 **ABSTRACT**

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

36

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

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## 44 1. INTRODUCTION

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

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

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

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

94 (Fontaine and Teletchea, 2019). However, the production is still limited because of numerous  
95 bottlenecks, particularly in the first-life stages (e.g. low survival rate, growth heterogeneity;  
96 Fontaine and Teletchea, 2019; Policar et al., 2019). Yet, a geographic differentiation was  
97 previously highlighted between wild populations for *P. fluviatilis* at the genetic level (Nesbø  
98 et al., 1999; Toomey et al., 2020a), as well as at the phenotypic level in controlled conditions  
99 regarding behaviour (Mandiki et al., 2004; Toomey et al., 2019), growth and survival rates  
100 (Mandiki et al., 2004; Vanina et al., 2019a, 2019b), and development (Pimakhin and Zak,  
101 2014). However, these previous studies highlighted geographic differentiation for a limited  
102 number of traits/biological functions. In addition, they focused on random populations  
103 without a justification about why these populations were selected.

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

## 110 **2. MATERIAL AND METHODS**

### 111 **2.1 First step of the integrative approach: intraspecific classification**

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

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

## 120 **2.2 Second step of the integrative approach: Performance evaluation**

### 121 *2.2.1 Compliance with ethical standards*

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

### 127 *2.2.2 Biological material collection and pre-experiment rearing conditions*

128 Egg ribbons (one ribbon corresponding to one female) were obtained across two years during  
129 spawning seasons (May 2018 – April and May 2019; Figure 1). One lake representative of the  
130 Danube unit was collected: Lake Balaton (BAL; 2019, Hungary; 46°54'23.375"N,  
131 18°2'43.119"E). Regarding the two other PU, several lakes were collected for each PU  
132 because of the large size of these units. This allowed considering potential differentiation  
133 within each unit. In this way, two populations were collected for the Eastern Europe unit:  
134 Lakes Valkea-Müstajärvi (VAL; 2018, Finland; 61°13'08"N, 25°07'05"E) and Iso-Valkjärvi  
135 (ISO; 2018, Finland; 60°57'21"N, 26°13'3"E). Four lakes were sampled for the European  
136 Plain which is the largest prospective unit: Lakes Geneva (GEN; 2019, France; 46°22'7.20"N,  
137 6°27'14.73"E), Bourget (BOU; 2019, France; 45°44'12.469"N, 5°52'1.617"E), Kierzlinkie  
138 (KIE; 2019, Poland; 53°47'54"N, 20°44'45"E), and Hohen Sprenzer (HOH; 2019, Germany;  
139 53°55'10.369"N, 12°13'6.005"E). After transportation, 13 to 32 egg ribbons per lake were  
140 incubated at the experimental platform of aquaculture (Unit of Animal Research and  
141 Functionality of Animal Products, University of Lorraine, Vandœuvre-lès-Nancy, France) at

142 13°C in incubators (1-2 independent incubators per population; for details on incubators see  
143 Toomey et al., 2019). Photoperiod was set to 12L:12D and light intensity to 400 lx at the  
144 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  
145 daily while pH ( $8.0 \pm 0.3$ ) and ammonium and nitrite concentrations (lower than  $0.05 \text{ mg.L}^{-1}$ )  
146 were monitored three times a week until hatching.

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

### 153 2.2.3 *Experimental rearing conditions*

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

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

166 dawn and dusk for 30 min). Temperature was gradually increased during the first two weeks  
167 from 13 °C to 20 °C (one-degree Celsius rise per day). Larvae were hand-fed with newly  
168 hatched *Artemia* nauplii (Sep-Art, INVE) from three dph until at 16 dph, seven times a day  
169 (every 90 min, from 8.30 am to 5.30 pm). At 16 dph, weaning (i.e. transition from live feed to  
170 inert dry artificial diet) started. *Artemia* ration was decreased by 25 % every three days and  
171 dry feed ration (BioMar, 300 µm until 21 dph, then 500 µm) was increased by the same ratio.  
172 After 25 dph, larvae were only fed with dry feed *ad libitum* (BioMar 500 µm). Temperature  
173 ( $20.0 \pm 0.4$  °C) and oxygen concentration ( $8.6 \pm 1.4$  mg.L<sup>-1</sup>) were checked daily in all  
174 cylindro-conical tanks. Ammonium and nitrite concentrations (means inferior to 0.1 mg.L<sup>-1</sup>)  
175 and pH ( $7.8 \pm 0.4$  mg.L<sup>-1</sup>) were monitored three times a week. Every day after first feeding,  
176 tanks were cleaned and dead individuals removed.

#### 177 *2.2.4 Larviculture performance assessment*

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

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

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

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

199 Developmental traits are also essential for larviculture, including swim bladder inflation rate  
200 (Polcar et al., 2019), deformity rate (Kestemont et al., 2015; Alix et al., 2017), and the  
201 volume of the yolk sac (Trabelsi et al., 2013). Swim bladder inflation rate was calculated at 26  
202 dph on all remaining larvae following the protocol used in Jacquemond (2004a, 2004b; 20  
203  $\text{g.L}^{-1}$  of sea salt and 70  $\text{mg.L}^{-1}$  of MS-222) and using the formula:  $100 \times (SB+ / N_f)$  with  $SB+$   
204 the number of larvae with swim bladder and  $N_f$  the final number of larvae at 26 dph.  
205 Deformity rate was calculated in the final counting at 26 dph using the following formula:  
206  $100 \times (N_m / N_f)$  with  $N_m$  the number of deformed larvae (only visible column deformities) and  
207  $N_f$  the final number of larvae counted. Finally, the yolk sac volume was calculated in the  
208 following way:  $\pi/6 \times YSL \times YSH^2$ , where  $YSH$  is the yolk sac height and  $YSL$  the yolk sac  
209 length (Bagarinao, 1986).

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

216 2015). Aggressiveness was assessed through the consideration of cannibalism (Baras, 2012)  
217 and enucleation, a specific aggressive behaviour in *P. fluviatilis* (Jourdan et al., 2000). It was  
218 evaluated based on the daily examination of dead larvae using the following formula:  $(N_e +$   
219  $N_t) / N_d$  where  $N_e$  is the number of enucleated larvae,  $N_t$  the number of truncated larvae (type  
220 I cannibalism), and  $N_d$  the number of dead larvae counted between five and 26 dph (not  
221 possible to count the number of dead larvae between one and five dph due to their rapid  
222 decomposition, but aggressive interactions are reported to start at later stages; Baras et al.,  
223 2003; Kestemont et al., 2015). The protocol to evaluate inter-individual distances (Buske and  
224 Gerlai, 2011) and activity was adapted from Colchen et al. (2017) and Toomey et al. (2019).  
225 Each population was evaluated at 25 and 26 dph. For each population, 90 larvae (i.e. 30 larvae  
226 per cylindro-conical tank) were sampled the day before the experiment and transferred to  
227 aquaria (58 L; 80 lx) at 20 °C. After one night of acclimatization, populations were tested by  
228 groups of ten larvae in circular arenas (10 lx, 30 cm diameter, 1.5 cm of water depth).  
229 Behaviour of individuals was recorded (three arenas tested simultaneously; three replicates  
230 per cylindro-conical tanks, three cylindro-conical tanks per population). After 30 min  
231 acclimatization, the following 30 min were used to assess inter-individual distances and  
232 activity. After one hour, a sudden event test (adapted from Colson et al. [2015] and Millot et  
233 al. [2009]) was performed to evaluate the tolerance to stress through the evaluation of activity  
234 before and after the sudden stress. Changes in behaviour, including activity, have been shown  
235 as an accurate stress indicator in fish (Schreck et al., 1997; Ashley, 2007). A 1 cm marble was  
236 released (from distance, experimenter in an adjacent room) in the center of the arena. The fall  
237 was driven by an electromagnet placed 47.5 cm above the bottom of the arena. Activity was  
238 recorded after the drop of the marble for 30 min and the first ten seconds were analyzed  
239 (initial response to stress being often triggered in terms of seconds; Schreck et al., 1997). At  
240 the end of the behavioural experiment, larvae were euthanized with an overdose of MS-222

241 for further length measurements. Averaged total lengths of larvae tested from VAL, ISO,  
242 BAL, KIE, GEN, BOU, HOH, and were  $12.90 \pm 0.62$  mm,  $14.05 \pm 0.55$  mm,  $10.62 \pm 0.47$   
243 mm,  $10.90 \pm 0.73$  mm,  $11.81 \pm 1.01$  mm,  $11.77 \pm 0.48$  mm, and  $11.35 \pm 0.72$  mm,  
244 respectively. Before the sudden stress, images were extracted from videos every five minutes  
245 (six images per video) to evaluate inter-individual distances (i.e. mean of distances between a  
246 focal individual and all the other individuals of the group; group cohesion indicator; Buske  
247 and Gerlai, 2011). All image analyses were performed in ImageJ (Schneider et al., 2012). For  
248 each image, coordinates (using the middle point between the eyes) of each individual were  
249 noted. This allowed measuring distances between a given individual and the other members of  
250 the group. All these distances were averaged to get one value per individual. Means obtained  
251 for all members of the group were averaged per image. The mean between all image values  
252 allowed obtaining a mean value of inter-individual distances per replicate (Colchen et al.,  
253 2017). Concerning activity, one image per second was extracted for six consecutive seconds  
254 every five minutes before the sudden stress test. After the drop of the marble, images were  
255 extracted every second for the first six seconds. Distance swam every second was calculated  
256 and the mean allowed obtaining the distance swam per second for each individual. The mean  
257 between individual values allowed obtaining an activity for each image series. To calculate  
258 activity before stress, which is based on several sampling times, the mean between image  
259 series allowed calculating the activity per replicate. For post-stress evaluation, for each  
260 cylindro-conical tank, the difference delta in activity was calculated between the median value  
261 of activity before stress and the median value of activity after stress (over the six seconds  
262 post-stress).

### 263 *2.2.5 Inter-PU statistical analyses*

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

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

### 286 **2.3 Third step of the integrative approach: Evaluation of the aquaculture potential**

287 Only traits for which a statistical differentiation between PU was observed (P-value [ $P$ ] <  
288 0.05) were considered for the calculation of the aquaculture potential score. The first step of  
289 this score calculation consists of calculating an average weight coefficient for each trait based  
290 on the investigation led in Toomey et al. (2020b) among percid farmers (Appendix S1). Then,

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

303 Formula 1:

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

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

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

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

### 316 3. RESULTS

317 There was no differentiation between PU for specific growth rate in length ( $F_{(2,4)}$ ; where 2  
318 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  
319 PU])= $2.30$ ,  $P=0.13$ ), final length heterogeneity ( $F_{(2,4)}=0.81$ ,  $P=0.46$ ), final length ( $F_{(2,4)}=0.45$ ,  $P$   
320  $=0.67$ ), yolk sac volume ( $F_{(2,4)}=0.49$   $P=0.65$ ), aggressiveness rate ( $K=4.59$ ,  $df=2$ ,  $P=0.10$ ),  
321 and activity ( $F_{(2,4)}=2.56$ ,  $P=0.11$ )

322 There was a statistically significant differentiation between PU for survival rate ( $F_{(2,4)}=8.04$ ,  
323  $P<0.05$ ), swim bladder inflation rate ( $F_{(2,4)}=68.93$ ,  $P<0.05$ ), deformity rate ( $F_{(2,4)}=20.94$ ,  
324  $P<0.05$ ), length at hatching ( $F_{(2,4)}=13.62$ ,  $P <0.05$ ), inter-individual distances ( $F_{(2,4)}=25.26$ ,  $P$   
325  $<0.05$ ), and activity difference delta ( $F_{(2,4)}=3.87$ ,  $P <0.05$ ) (Figure 2).

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

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

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

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

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

341

## 342 4. DISCUSSION

### 343 4.1 Geographic differentiation between PU

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

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

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

#### 369 **4.2 Implications for *Perca fluviatilis* larviculture**

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

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

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

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

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

### 417 **4.3 Limitations in the performance evaluation**

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

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

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

#### 434 **4.4 Perspectives**

435 Overall, this study highlights that there can be a substantial impact in the choice of the  
436 founder population for perch farming. These results are first insights, which could be helpful  
437 for *P. fluviatilis* larviculture, but these results are specific to our RAS system. Indeed, the  
438 potential interaction between genotype and environment was not assessed (Sae-Lim et al.,  
439 2016). The presence of such interaction implies that the PU for our rearing system may not be  
440 as interesting in different rearing conditions (i.e. a particular genotype presenting different  
441 phenotypes in different rearing environments). This could prevent the election of a specific  
442 PU as the best universal biological unit. Therefore, this interaction remains to be tested before  
443 extending conclusions to other domestication systems. Moreover, three PU out of five were  
444 tested here. Evaluating aquaculture potential for the two other PU (i.e. Balkans, Northern and  
445 Western Fennoscandia) could eventually lead to the identification of a PU with a higher  
446 potential for aquaculture. Furthermore, this work was led on the first phase of larviculture but  
447 remains to be performed for the rest of the production cycle to check if the best PU for the  
448 initiation of larviculture remains the best for the rest of the production cycle. Therefore,  
449 further traits need to be taken into account such as traits linked to other life stages and  
450 important traits for production (e.g. size at sexual maturity, fertilisation rate; filleting yield),  
451 along with traits essential for future selective breeding programmes (e.g. genetic variation)  
452 (Toomey et al., 2020b). Finally, differences in aquaculture potential between PU remain to

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

455

#### 456 **Supplementary data**

457 **Appendix S1: Calculation of the aquaculture potential score.** The first step consists of  
458 calculating an average weight coefficient for each trait taking into account farmers' opinions  
459 (step A). Then, for each replicate, standardized values are calculated for each trait when a  
460 significant statistical differentiation between prospective units was highlighted (Step B).  
461 Finally, a score per trait and per replicate/population/PU is calculated by multiplying the  
462 average weighting coefficient by the (average) standardized value (Step C). A coefficient of -  
463 1 is used for traits for which the lowest value is the one expected by fish farmers. The sum of  
464 all these results allows to calculate for each replicate/population/PU an aquaculture potential  
465 score.

#### 466 **Declaration of interest**

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

#### 469 **Author contributions**

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

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