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**When behavioural geographic differentiation matters: inter-
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When behavioural geographic differentiation matters: inter-population comparison of aggressiveness and group structure in the European perch

Short title: Behavioural geographic differentiation in *Perca fluviatilis*

Lola Toomey^{1*}, Martin Bláha², Emilie Mauduit¹, Tatyana Vanina², Margot Baratçabal¹,
Yannick Ledoré¹, Sami Vesala³, Pascal Fontaine¹, Alain Pasquet^{1, 4}, Thomas Lecocq^{1*}

¹ Université de Lorraine, Inra, URAFPA, F-54000 Nancy, France

² Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of
Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in Ceske
Budejovice, Zátisí 728/II, CZ-389 25 Vodňany, Czech Republic

³ Natural Resources Institute Finland, Helsinki, Finland

⁴ CNRS (Centre national de la Recherche Scientifique)

* Corresponding Authors

lola.toomey@univ-lorraine.fr +33372745200

thomas.lecocq@univ-lorraine.fr +33372745696

University of Lorraine, Boulevard des Aiguillettes, BP 70239, 54506 VANDOEUVRE-LES-
NANCY CEDEX FRANCE

ABSTRACT

Domestication is still a long and difficult process and it is particularly impacted by species behavioural traits. Indeed, tolerance to high densities in intensive cultures and sociability are major features which facilitate domestication and influence the effectiveness of aquaculture production. Moreover, behavioural domestication predispositions could change at the intraspecific level. Here, we investigate three essential behavioural traits: aggressive interactions, group structure, and activity between three allopatric populations of *Perca fluviatilis*, a fish species at its nascent stage of production. We highlight inter-population differences in group structure and aggressive interactions but not in activity. A more cohesive and homogeneous group structure was demonstrated for Finnish populations compared to Lake Geneva at 45-46 days post-hatching. In addition, Lake Geneva presented a higher aggressiveness. These inter-population differences could be used in European perch aquaculture in order to improve production as well as welfare of individuals.

KEYWORDS

Aggression - aquaculture - behaviour - cannibalism - intraspecific differentiation - larvae - *Perca fluviatilis* - social structure

INTRODUCTION

Increasing the agriculture sustainability, including aquaculture, relies partly on the production and domestication of new species (Gepts et al. 2012). Domestication is considered as the process in which populations are bred in man-controlled environment and modified across successive generations from their wild ancestors in ways making them more useful to humans who control, increasingly during the process, their reproduction and food supply (Lecocq, 2018). However, domestication remains a difficult, long, and expensive process ridden by unfruitful outcomes, mostly due to zootechnical issues or taxon intrinsic features (Liao and Huang 2000; Diamond 2002; Teletchea and Fontaine 2014). This is particularly acute in intensive aquaculture (i.e. nowadays, intensive monoculture is the primary aquaculture) in which many new species domestication trials are hampered by several bottlenecks and end up being abandoned (Teletchea and Fontaine 2014). For instance, some fish species display low resistance to diseases or low food conversion efficiency, which impede or slow down their domestication (Liao and Huang 2000; Otton 2004). Conversely, other traits are favouring domestication such as fast growth rate and acceptance of artificial feeds, and consequently make taxon production an economically viable initiative (Liao and Huang 2000; Le François et al. 2010). Among these features, some behavioural traits are particularly essential since they can deeply facilitate domestication (Liao and Huang 2000; Jobling 2010; Le François et al. 2010) and subsequent aquaculture production (Huntingford et al. 2012).

Among behavioural traits, inter-individual relationships, group structure, and activity can affect directly the ability of a species to be domesticated and efficiently produced in intensive monoculture conditions. Tolerance to conspecifics in a limited area is an essential

79 parameter for production (Kristiansen et al. 2004) since it affects individual welfare
80 (Huntingford 2004; Ashley 2007). Selecting populations which present an aggregative and
81 cohesive group structure, therefore limiting stress, would be favouring welfare. However,
82 living in group is not costless as it can trigger for instance competition for resources (Pitcher
83 and Parrish 1993; Martins et al. 2012; Ward and Webster 2016). In culture conditions, this
84 can lead to the emergence of aggressive behaviours (Damsgård and Huntingford 2012), such
85 as attacks or bites, leading in some cases to cannibalism (Baras 2013). These aggressive
86 behaviours have several potentially negative consequences in fish culture such as
87 mortalities, stress, immune-suppression, or uneven competition for food (Damsgård and
88 Huntingford 2012 and references therein). Cannibalism (type I: prey is caught tail first and
89 ingested partially; type II: prey is caught by the head or tail and fully ingested; Baras et al.
90 2003; Baras 2013) is a major bottleneck in finfish aquaculture (Naumowicz et al. 2017) since
91 it can lead to important losses (Baras et al. 2003; Huntingford et al. 2012). For example,
92 cannibalism can cause up to 50% losses in *Perca fluviatilis* (Baras et al. 2003; Kestemont et al.
93 2003). Finally, activity is also an important factor in aquaculture as it contributes to the total
94 energetic budget (e.g. up to 40% of *Perca flavescens* budget; Boisclair and Leggett 1989).
95 Moreover, less active taxa could contribute to lower potential contacts and subsequent
96 potential aggressive interactions. Therefore, in domestication processes, it is necessary to
97 take into account the ability for taxa to present the most suitable group structure, low
98 aggressive interaction rate, as well as lower activity. Yet, there is an intraspecific
99 differentiation (differentiation between allopatric populations of conspecific individuals;
100 Mayr 1963) which could further help to improve domestication processes.

101 Behavioural intraspecific differentiation and its potential for selection of founder
102 populations have been poorly investigated to date. However, intraspecific differences in
103 aggressive behaviour (Magurran and Seghers 1991; Mandiki et al. 2004; Bell 2004), time
104 spent foraging in an open habitat (Bell 2004; Magnhagen 2006), schooling (Magurran and
105 Seghers 1991), or boldness (Wright et al. 2003) have been already assessed for a few species
106 (see also Foster 1999). Abiotic factors can influence social behaviours (e.g. temperature,
107 light, population density; Baras et al. 2003; Kestemont et al. 2003), yet a genetic basis was
108 also suggested since allopatric populations or geographically distinct strain differentiations
109 were demonstrated for a few species (Amundsen et al. 1999; Damsgård and Huntingford
110 2012; Magnhagen et al. 2015). Therefore, considering such behavioural intraspecific
111 differentiation could allow improving aquaculture for species for which production is still
112 limited by behavioural bottlenecks.

113 The European perch, *Perca fluviatilis* L., is one of the fish species involved in the European
114 aquaculture diversification (Kestemont et al 2015). Its long standing socio-economic interest
115 (high market value and recreational interest) led to the development of its aquaculture in
116 the 90's (Kestemont and Mélard 2000; Kestemont et al. 2015). However, its production is
117 still limited due to several bottlenecks including some aspects related to fish behaviour such
118 as aggressiveness and high cannibalism and subsequent mortalities (Kestemont et al. 2015).
119 However, geographic differentiation has been previously observed for some of problematic
120 behavioural traits (e.g. cannibalism rate, Mandiki et al. 2004). Therefore, we aim in this study
121 at (i) assessing if European perch allopatric populations present differentiation for group
122 structure and activity, as well as for aggressive interactions during first-life stages, and (ii)
123 identifying populations presenting behavioural advantages for production.

MATERIAL AND METHODS

Rearing conditions

Rearing parameters were chosen according to trade-offs between abiotic culture conditions used in literature (e.g. Vlavonou 1996; Kestemont et al. 2003; Kestemont et al. 2015), our practices, and fish farming practices. The rearing protocol was tested and validated with a domesticated population from the fish farm “Lucas Perches” (Hampont, France) comparing growth and survival results to literature (e.g. Vlavonou 1996; Fiogbé and Kestemont 2003).

Egg ribbons were obtained during the 2018 spawning season (May 2018) from lakes Geneva (GEN; Switzerland; 46°26'N, 6°33'E), Valkea-Müstajärvi (VAL; Finland; 61°13'08"N, 25°07'05"E), and Iso-Valkjärvi (ISO; Finland; 60°57'21"N, 26°13'3"E). After transport, 19 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) in incubators (110x64x186cm; one incubator per population), containing nine racks each (45x7x12cm), at 13°C. Each incubator had its own temperature control and recirculated water (flow rate of 4m³.h⁻¹) system and water was UV sterilised. Oxygen rate (10.5 ± 0.2mg.L⁻¹) and temperature (13.0 ± 0.3°C) were checked daily while pH was measured three times a week (8.0 ± 0.1). Ammonium (lower than 0.05mg.L⁻¹) and nitrite concentrations were monitored three times a week until hatching (lower than 0.01mg.L⁻¹). Photoperiod was 12L:12D and light intensity was 400 lx at the water surface.

Two independent experiments were performed in order to ensure availability of larvae across the rearing period: experiment I from hatching until the end of weaning (26 days

145 post-hatching, dph) and experiment II from 27 dph until 60 dph. All populations were reared
146 in independent structures.

147 Concerning experiment I, after hatching, larvae from the different egg ribbons were mixed
148 and transferred to three green internal-wall 71L cylindro-conical tanks (three replicates per
149 population; recirculated aquaculture system (RAS)) at a density of 50 larvae.L⁻¹. Temperature
150 was gradually increased during two weeks to 20°C, photoperiod was 12L:12D and light
151 intensity was 400lx. Larvae were fed with newly hatched *Artemia* naupli (Sep-Art, INVE)
152 every 1h30 from 3 dph until weaning. At 16 dph, *Artemia* ration was decreased by 25% every
153 three days and dry feed ration (BioMar, 300µm until 21 dph, then 500µm) was increased by
154 the same ratio. After 25 dph, larvae were only fed with dry feed *ad libitum* (BioMar 500µm,
155 then 700µm at 44 dph until the end of the experiment). At 26 dph, the larvae in cylindro-
156 conical tanks were removed to start experiment II.

157 For experiment II, larvae not used for experiment I were held after hatching in 2m³ tanks
158 (RAS) under the same temperature, feeding, light intensity, and photoperiod regimes as
159 individuals of the experiment I. At 27 dph, these larvae were transferred at a density of 19
160 larvae.L⁻¹ to the three cylindro-conical tanks in order to start experiment II. Light intensity
161 was 80 lx at water surface, all else remaining equal to experiment I (except for density).

162 During the two experiments, oxygen concentration ($8.7 \pm 2.3 \text{ mg.L}^{-1}$) and temperature ($20.0 \pm$
163 $0.6 \text{ }^{\circ}\text{C}$) were checked daily for all tanks. Ammonium ($0.14 \pm 0.1 \text{ mg.L}^{-1}$), pH ($7.2 \pm 0.9 \text{ mg.L}^{-1}$),
164 and nitrite concentrations ($0.08 \pm 0.08 \text{ mg.L}^{-1}$) were monitored three times a week. Tanks
165 were cleaned daily after first feeding and dead individuals were removed every morning.
166 Survival rate for ISO, VAL and GEN were respectively 40.1 % (± 12.0), 29.4 % (± 14.5) and 6.6
167 % (± 3.4) for experiment I (26 dph; statistical difference between Geneva Lake and the two

Finnish populations; $F=7.2$, $df=2$, $P<0.05$) and 31.5 % (± 4.3), 28.0 % (± 11.1) and 37.4 (± 8.1) for experiment II (60 dph; no statistical difference between the three populations; $F=0.98$, $df=2$, $P=0.42$). These ranges of survival rates were comparable to what is found in literature (e.g. Tamazouzt et al. 2000; Baras et al. 2003; Fiogbé and Kestemont 2003).

Group structure and activity

For each population, three replicates for each cylindro-conical tank were performed over two days (25 and 26 dph). At 24 and 25 dph, a total of 90 individuals ($n=30$ for each cylindro-conical tank, 10 individuals per replicate) were sampled for each population and transferred to three aquaria (58 L; one aquarium per cylindro-conical tank; order of cylindro-conical replicates randomly assessed over two days; see appendix 1) with an 80lx light intensity and a temperature of 20.0°C (± 0.5). Individuals were not fed from the moment they were transferred to the beginning of the experiment the following day in order to have individuals in the same energetic state. After one night of acclimatisation, individuals were tested by groups of ten in circular arenas. Groups of ten individuals might not reflect faithfully what occurs in cylindro-conical tanks. However, evaluation cannot be performed directly in the tanks and this method was previously validated (e.g. Colchen et al. 2016). Three circular arenas (30 cm diameter with 1.5cm of water depth) were used to investigate group structure and activity (Colchen et al. 2016). Water in the arena was the same as in the aquaria, room temperature was maintained at 20.0 °C (± 0.6) and arenas were lit at 10lx from underneath in order to avoid shadows during recording. For each replicate, individuals were transferred from the aquarium to the arena with a beaker and a siphon. After 30min acclimatisation, individuals were filmed for 30min using camcorders (Sony, Handycam, DCR-SR72E) located 50cm above the arena. The three arenas were filmed simultaneously and the order of

replicates tested was randomly assessed. After 1h, individuals were euthanised with an overdose of MS-222 following European rules and kept in formalin 4% for later length measurements. Larvae tested from ISO, VAL and GEN were respectively $14.05 \pm 0.55\text{mm}$, $12.90 \pm 0.62\text{mm}$, and $13.87 \pm 0.26\text{mm}$. This full experiment was performed again during experiment II with fish sampled from cylindro-conical tanks at 44 and 45 dph. For this second test, individuals from ISO, VAL and GEN were respectively $26.74 \pm 1.67\text{mm}$, $26.28 \pm 1.99\text{mm}$, and $22.97 \pm 1.08\text{mm}$ (no statistical difference between populations for the two experiments; experiment I: $F=0.712$, $df=2$, $P=0.528$; experiment II: $F=1.68$, $df=2$, $P=0.263$).

Group structure analysis was performed using the ImageJ software. Images were extracted from videos at 3-min interval (11 images per video). From each image, exact coordinates of each individual were noted using the middle point between the eyes. Three parameters were evaluated to assess the group structure: the nearest neighbour distance, the mean of inter-individual distances, and the variance of these inter-individual distances (Buske and Gerlai 2011a). Nearest neighbour distance represents the distance between a focal fish and its closest neighbour and is an indicator of the group aggregation. The mean of inter-individual distances corresponds to the mean of distances between a focal fish and all the other fish of the group and the average of values from all group members is an indicator of the group cohesion. Finally, the average of variances of inter-individual distances from each fish represents the homogeneity of distribution (Buske and Gerlai 2011a). Activity was also calculated in ImageJ. One image per second was extracted for six consecutive seconds every five minutes. Coordinates of each individual were noted for each image and then distance swam was calculated every second during the five seconds then averaged to obtain the mean distance swam for each individual per second.

214 All statistical analyses were performed in R 3.0.3 (R Core Team 2017). To test the normality
215 of distributions, a Shapiro-Wilk test (R Core Team 2017) was used and homogeneity of
216 variances was tested using the Levene test (Gastwirth et al. 2015). Then, linear mixed
217 models were used with distances and activity as fixed factors and cylindro-conical tanks as
218 random factor (Bates et al. 2004). There was no influence of the cylindro-conical tank on all
219 models. Therefore, one-way analyses of variance (ANOVA F test) followed by Tukey post hoc
220 tests were used to evaluate differences between populations (R Core Team 2017).

221 **Quantification of aggressive interactions**

222 Daily observations were carried out at different moments of the day previous to this
223 experiment but did not allow identifying a cannibalism peak during the photophase.
224 Therefore, we hypothesised that the beginning of the photophase would correspond to the
225 cannibalism peak since individuals were not fed between 5.30pm and the next morning, that
226 they were used to be fed during the photophase and that European perch is a visual
227 predator (Graeb et al. 2005; Kestemont et al. 2008). Therefore, observations were
228 performed after first feeding with a five-minute acclimatisation to the presence of the
229 observer and five minutes of focal sampling (Colchen et al., 2019). Daily observations were
230 carried out between 8.30am and 10am from 10 dph until the end of experiment I (26 dph).
231 For experiment II, observations were carried out every three days (see Appendix 1). One
232 replicate per population was observed per day and the same person performed all
233 observations. Since hatching times were asynchronous between populations, the order of
234 populations or tanks observed were randomly assigned. Several aggressive behaviours were
235 noted: (i) Pursuit: an individual heads towards a conspecific, gets close and follows it when
236 the conspecific moves; this involves a change of direction of the two individuals, (ii) Attack:

when an individual heads towards a congener and gets rapidly close to it without necessarily contact between the two individuals, (iii) Bite: when an individual catches with its mouth a part of a conspecific's body and then releases it, and (iv) Capture: when an individual ingests a part or the whole conspecific (type I and II cannibalisms). Taking into account all these aggressive interactions, a global daily aggressive interaction rate was calculated relatively to the initial number of individuals in the tank. Enucleation, being a specific indicator of aggressiveness in perch (Jourdan et al. 2000), was also evaluated by counting daily the number of dead individuals enucleated. Enucleation rate was calculated relatively to the initial number of individuals in the tank. For phase II, type II cannibalism rate was estimated by subtracting from the initial number of individuals the number of survivors and dead individuals over phase II and calculating a rate relatively to the initial number of individuals in the tank. Cannibalism rate could not be evaluated for experiment I as a precise monitoring of mortality was not possible the first week due to fast degradation of dead larvae. Finally, mortality rates attributed to cannibalism and enucleation were also calculated. In order to meet assumptions of normality (Shapiro-Wilk test, R Core Team 2017) and homogeneity of variances (Levene test, Gastwirth et al. 2015), data for all aggressive parameters was transformed (i.e. $\log(x+1)$). One-way analyses of variance (ANOVA F test) followed by Tukey post hoc tests were used to evaluate differences between populations (R Core Team 2017). When assumptions were not respected (only for the aggressiveness rate during experiment I), Kruskal-Wallis H tests (R Core Team 2017) were used followed by Dunn post-hoc tests (Pohlert 2015).

Compliance with ethical standards

259 All along experimental procedures, individuals were handled as little as possible. All
260 procedures were in accordance with the national and international guidelines for protection
261 of animal welfare (Directive 2010/63/EU). This study was conducted with the approval
262 Animal Care Committee of Lorraine (CELMA n°66) and the Ministry of Higher Education,
263 Research, and Innovation (APAFIS13368-2018020511226118).

264 **RESULTS**

265 **Group structure and activity**

266 Experiment I (25-26 dph)

267 Inter-individual distances ($F=7.8$, $df=2$, $P<0.05$), variance of inter-individual distances ($F=9.9$,
268 $df=2$, $P<0.05$), and activity ($F=8.2$, $df=2$, $P<0.05$) are significantly lower for GEN compared to
269 VAL and ISO (Fig. 1). There is no statistical difference between VAL and ISO. There is no
270 statistical difference between populations for the nearest neighbour distance ($F=1.4$, $df=2$,
271 $P=0.2$; Fig. 1).

Fig. 1: Boxplots representing group structure and aggressive interaction results for experiment I (n=3330). Four measures of group structure are presented: inter-individual distances, variance of inter-individual distances, nearest neighbour distances, and activity. The black line represents the median, the outsider box corresponds to lower and upper quartile values and white dots correspond to most extreme values within 1.5 times the interquartile range from the ends of the box. Different letters indicate significant differences between populations ($P < 0.05$) using post hoc tests.

Experiment II (45-46 dph)

Inter-individual distances ($F=7.8$, $df=2$, $P<0.05$) and variance of inter-individual distances ($F=9.9$, $df=2$, $P<0.05$) are significantly higher for GEN compared to VAL and ISO (Fig. 2). There is no statistical difference between ISO and VAL. There is no statistical difference between populations for the nearest neighbour distance ($F=1.4$, $df=2$, $P=0.3$) and activity ($F=1.2$, $df=2$, $P=0.3$; Fig. 2).

Quantification of aggressive interactions

The first cases of cannibalism (type II only) were observed at 26 dph for ISO and at 51 dph for GEN. No cannibalism case was observed for VAL. There is no difference of daily aggressive interaction rate in experiment I ($H=0.60$, $df=2$, $P=0.74$; Fig. 1) but in experiment II these behaviours were significantly higher in GEN than ISO and VAL ($F=7.21$, $df=2$, $P<0.05$; Fig. 2). There is no statistical difference between ISO and VAL. Enucleation rate, which is null in experiment I for all populations, is significantly higher in GEN compared to VAL and ISO ($F=70.74$, $df=2$, $P<0.05$; Fig. 2) in experiment II. Cannibalism rate is not statistically different between populations ($F=0.018$, $df=2$, $P=0.98$; Fig. 2). Mortality rate attributed to cannibalism and enucleation is not statistically different between the three populations ($F=0.69$, $df=2$, $P=0.59$; Fig. 2).

Fig.2: Boxplots representing group structure and aggressive interaction results for experiment II (n=1080). Four measures of group structure are presented: inter-individual distances, variance of inter-individual distances, nearest neighbour distances and activity. Aggressive interactions results include aggressive interaction rate, enucleation rate, cannibalism rate, and mortality rate caused by aggressive interactions. The black line represents the median, the outsider box corresponds to lower and upper quartile values and white dots correspond to most extreme values within 1.5 times the interquartile range from the ends of the box. Different letters indicate significant differences between populations ($P < 0.05$) using post hoc tests.

DISCUSSION

Inter-populational differentiation in behavioural traits and its potential causes

In this study, we highlight intraspecific differentiation between the two Finnish populations and GEN for group structure (experiments I and II) and aggressive interactions (only experiment II) while activity does not differ. We cannot exclude some potential biases in our experiments. For instance, (i) aggressive behaviour observations have been made after first feeding but cannibalism peaks (and aggressions) might occur at different moments of the day between populations and (ii) calculated cannibalism rate might also include dead individuals eaten by conspecifics which can blur differences in cannibalism rates. However, since (i) temporal differentiation in cannibalism peaks has not been reported to date and (ii) the cannibalism estimation method, widely used across literature (e.g. Kestemont et al. 2003; Mandiki et al. 2004), allows to compare populations, we argue that bias related to observations of inter-populational behavioural differentiations at two ages are limited.

Intraspecific differentiation in group structure and aggressive behaviours has been already highlighted for several fish species (Rosenau and McPhail 1987; Magurran and Seghers 1991; Amundsen et al. 1999; Lahti et al. 2001; Huizinga et al. 2009; Wark et al. 2011; Song et al. 2011). Here, a more cohesive and homogeneous structure is demonstrated for Finnish populations compared to GEN at 45-46 dph (Fig. 2). These results, associated with a similar nearest neighbour distance, indicate a structure in sub-groups in all populations but with a distance between these groups higher for GEN at 45 dph. The less homogeneous group structure of GEN at 45 dph is quite congruent with the higher aggressiveness highlighted for this population. Indeed, although daily aggressive interaction rate seems low (0.1-0.9 %; Fig. 2), the congruence between aggressive interaction patterns and enucleation rate supports

the higher aggressiveness of GEN compared to the two Finnish populations. The absence of difference in cannibalism rate indicates that aggressive interactions are not necessarily followed by type II cannibalism. Therefore, our study is not congruent with Mandiki et al. (2004) who showed a difference in intra-cohort cannibalism rate between different European perch allopatric populations (but with different populations than the ones investigated here). Here, we highlight differences in aggressive interactions aside from cannibalism rate. Inter-populational behavioural differences can be shaped by genetic differentiation, by phenotypic plasticity, or by their combination.

On the one hand, the observed inter-populational behavioural differences could be shaped by genetic differentiation. Indeed, population-specific demographic histories and potential local adaptations fostered by particular selective pressures can lead to the acquisition of distinct behavioural phenotypic traits or development rates between allopatric conspecific populations (Foster and Endler 1999; Foster 1999). For instance, it was shown a link between aggressiveness and the level of predation of the natural living site (Huntingford 1982; Magurran and Seghers 1991) as well as other environmental factors such as food availability and water current velocity (Lahti et al. 2001 and references therein). The occurrence of inherited differences in aggressive interactions was assessed for several species (Huntingford et al. 2012; Damsgård and Huntingford 2012). Similarly, inter-populational differences in activity were found to be connected to prey size distribution, total prey biomass, and water transparency (Boisclair and Leggett 1989). Unfortunately, we do not have enough information on the different lakes abiotic and biotic parameters to make any assessment. Another explanation of inter-populational differences could be divergences in development rates potentially triggered by genetic specificities. Indeed, we compare the populations at

the same age but we do not know if the compared fishes are at the same developmental stage (i.e. the lack of development table for larval and juvenile stages of *P. fluviatilis* prevent us to assess if the development is synchronous between populations). The populations might have divergent development rates, which can trigger inter-population differences in parameters investigated. For instance, the higher aggressiveness in experiment II might be related to the development of muscular and nutritional structures through the larval stage (Kestemont et al. 1996; Vlavanou 1996). It can also be related to the development of visual structures since the visual acuity, essential for capture of prey, increases until metamorphosis (Guma'a 1982). In addition, the aggregation in sub-groups might be due to several factors such as kinship (Behrmann-Godel et al. 2006), the nature of interactions (e.g. aggressive interactions), spatial distribution, or differential sizes (Hinde 1976). Since these two last factors are sensitive to developmental stage, group structure is also influenced by development rate.

On the other hand, phenotypic plasticity (i.e. the ability of a genotype to produce more than one phenotype when exposed to different environments; Pigliucci et al. 2006; Kelly et al. 2012) is an alternative explanation of the observed behavioural differentiations between populations (DeWitt and Scheiner, 2004) with behaviour reflecting the strategy adopted under the influence of environmental factors. This was suggested as the driving factor for cannibalism in *P. fluviatilis* (Krol et al. 2015 and references therein) as well as in other species (e.g. Svenning and Borgstrøm 2005). Since we have used an experimental transplant approach (common environment), we speculate that we have minimized the effect of the environment (West-Eberhard 2003). Nevertheless, influences of past environmental conditions (i.e. before the beginning of our experiment) cannot be ruled out. On the one

hand, we have collected individuals at the egg stage in the wild and phenotypic response to environmental conditions could have occurred during development (Swain and Lindsey 1986). On the other hand, environmental conditions experienced by the parents might have influenced offspring phenotype (Mousseau and Fox 1998; Youngson and Whitelaw 2008). At last, it was also shown an influence of maternal size on larvae performance (Olin et al. 2012). Since we have no information on the parents of egg sampled, we cannot exclude the influence of maternal effects which were demonstrated in *P. fluviatilis* for other traits (Babiak et al. 2004; Krol et al. 2015).

Overall, we cannot assess the importance of genetic differentiation, phenotypic plasticity, and specific development rates in population-specific behaviour. Behavioural differentiation might be the result of the interaction of all factors (see for instance for cannibalism, Baras and Jobling 2002; Yang et al. 2015). Moreover, effects of experience on behaviour cannot be ruled out as it was previously suggested as an important factor for the behavioural variation (Hellström and Magnhagen 2011; Magnhagen 2015). Further analyses over several generations with populations under identical rearing conditions as well as the establishment of a development table for larval and juvenile stages of *P. fluviatilis* are needed to assess the importance of each factor in the geographic differentiation of behaviour.

Differences in group structure and aggressive interactions between the two different ages

For each population, we observe a behavioural differentiation between the two studied ages. Such a differentiation has been previously observed in other species. For instance, development of shoaling (increasing protection against predators, foraging efficiency, and mate encounters) with age through a decrease of inter-individual and nearest neighbour distances has already been observed in zebrafish (Buske and Gerlai 2011b; Buske and Gerlai

2012). We observe similar development for ISO and VAL populations. In contrast, the opposite pattern observed for GEN population is unexpected and corresponds to the establishment of a less homogeneous group with age. Mechanisms underlying the age-dependant changes in group structure are so far unknown. Differential ontogenies of sensory development might play a role into differences at the different ages (Buske and Gerlai 2012). Several neuroanatomical, physiological or biochemical factors have been suggested to be involved (Buske and Gerlai 2012). There might also be some group regulation mechanisms subsequent to weaning, which can potentially increase competition for resources linked for instance to bioenergetic needs or physiological shifts. This competition could explain the higher occurrence of aggressive interactions in experiment II.

Integrating inter-population behaviour differentiation: a way to improve aquaculture production?

The variability occurring in behaviour at the intraspecific level offers the opportunity to select fishes whose behaviours make them more suitable for aquaculture production (Huntingford et al. 2012). In the European perch, the lack of population-specific activity tends to make this trait useless to select best population for aquaculture purpose. In contrast, difference in aggressiveness (i.e. and its consequences: losses due to aggressive interactions ranged from about 20% to 40% depending on the population; experiment II, Fig. 2) is a potential selection criterion for farmers since such interactions are highly detrimental for fish production. Similarly, the population-specific group structure should be considered as highly important information to highlight most suitable populations for intensive aquaculture. Based on our result, the more cohesive group structure and less aggressive interactions of Finnish *P. fluviatilis* make them the most suitable populations for

aquaculture. However, more populations need to be compared in order to identify populations of interest across the species range. Moreover, we cannot exclude the future potential impact of domestication since behavioural traits are modified by this process (Kohane and Parsons 1988). Yet, taking into account behavioural intraspecific differentiation would allow starting domestication program on populations presenting the best behavioural pre-disposition.

Selecting best populations for aquaculture production cannot be made through only behavioural trait comparisons. Indeed, selective breeding for low stress responsiveness has for instance been applied in several fish species but these low-stress response fish were also the ones which were more aggressive (Huntingford et al. 2012). Intraspecific differentiation has been already assessed for several other traits of interest such as growth (e.g. Mandiki et al. 2004; Leithner and Wanzenböck 2015), feed conversion efficiency (e.g. Imsland et al. 2000; Jonassen et al. 2000), or disease resistance (e.g. Imsland et al. 2002; Overturf et al. 2003). Therefore, the choice of the founder population must then be based on a multi-function and multi-traits approach rather than a single-trait decision framework.

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447 **CONFLICT OF INTEREST AND ETHICAL STATEMENT**

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

449 Ethical approval: “All applicable international, national, and/or institutional guidelines for
450 the care and use of animals were followed by the authors.”

451 **ABBREVIATIONS**

452 GEN: Lake Geneva

453 VAL: Lake Valkea-Müstajärvi

454 ISO: Lake Iso-Valkjärvi

455 RAS: Recirculated Aquaculture System

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APPENDIX

Appendix 1: Material and methods workflow.

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