



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

Lola Toomey, Martin Bláha, Emilie Mauduit, Tatyana Vanina, Margot Baratçabal, Yannick Ledore, Sami Vesala, Pascal Fontaine, Alain Pasquet,  
Thomas Lecocq

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18      **the European perch**

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20    Short title: Behavioural geographic differentiation in *Perca fluviatilis*

21    Lola Toomey<sup>1\*</sup>, Martin Bláha<sup>2</sup>, Emilie Mauduit<sup>1</sup>, Tatyana Vanina<sup>2</sup>, Margot Baratçabal<sup>1</sup>,  
22    Yannick Ledoré<sup>1</sup>, Sami Vesala<sup>3</sup>, Pascal Fontaine<sup>1</sup>, Alain Pasquet<sup>1, 4</sup>, Thomas Lecocq<sup>1\*</sup>

23    <sup>1</sup> Université de Lorraine, Inra, URAFPA, F-54000 Nancy, France

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

27    <sup>3</sup> Natural Resources Institute Finland, Helsinki, Finland

28    <sup>4</sup> CNRS (Centre national de la Recherche Scientifique)

29

30    \* Corresponding Authors

31    lola.toomey@univ-lorraine.fr +33372745200

32    thomas.lecocq@univ-lorraine.fr +33372745696

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

35 **ABSTRACT**

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

48

49 **KEYWORDS**

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

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56 **INTRODUCTION**

57 Increasing the agriculture sustainability, including aquaculture, relies partly on the  
58 production and domestication of new species (Gepts et al. 2012). Domestication is  
59 considered as the process in which populations are bred in man-controlled environment and  
60 modified across successive generations from their wild ancestors in ways making them more  
61 useful to humans who control, increasingly during the process, their reproduction and food  
62 supply (Lecocq, 2018). However, domestication remains a difficult, long, and expensive  
63 process ridden by unfruitful outcomes, mostly due to zootechnical issues or taxon intrinsic  
64 features (Liao and Huang 2000; Diamond 2002; Teletchea and Fontaine 2014). This is  
65 particularly acute in intensive aquaculture (i.e. nowadays, intensive monoculture is the  
66 primary aquaculture) in which many new species domestication trials are hampered by  
67 several bottlenecks and end up being abandoned (Teletchea and Fontaine 2014). For  
68 instance, some fish species display low resistance to diseases or low food conversion  
69 efficiency, which impede or slow down their domestication (Liao and Huang 2000; Otton  
70 2004). Conversely, other traits are favouring domestication such as fast growth rate and  
71 acceptance of artificial feeds, and consequently make taxon production an economically  
72 viable initiative (Liao and Huang 2000; Le François et al. 2010). Among these features, some  
73 behavioural traits are particularly essential since they can deeply facilitate domestication  
74 (Liao and Huang 2000; Jobling 2010; Le François et al. 2010) and subsequent aquaculture  
75 production (Huntingford et al. 2012).

76 Among behavioural traits, inter-individual relationships, group structure, and activity can  
77 affect directly the ability of a species to be domesticated and efficiently produced in  
78 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.

124 **MATERIAL AND METHODS**

125 **Rearing conditions**

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

131 Egg ribbons were obtained during the 2018 spawning season (May 2018) from lakes Geneva  
132 (GEN; Switzerland; 46°26'N, 6°33'E), Valkea-Müstajarvi (VAL; Finland; 61°13'08"N,  
133 25°07'05"E), and Iso-Valkjärvi (ISO; Finland; 60°57'21"N, 26°13'3"E). After transport, 19 egg  
134 ribbons per lake were incubated at the Experimental Platform of Aquaculture (Unit of  
135 Animal Research and Functionality of Animal Products, University of Lorraine, Vandœuvre-  
136 lès-Nancy, France) in incubators (110x64x186cm; one incubator per population), containing  
137 nine racks each (45x7x12cm), at 13°C. Each incubator had its own temperature control and  
138 recirculated water (flow rate of  $4\text{m}^3.\text{h}^{-1}$ ) system and water was UV sterilised. Oxygen rate  
139 ( $10.5 \pm 0.2\text{mg.L}^{-1}$ ) and temperature ( $13.0 \pm 0.3^\circ\text{C}$ ) were checked daily while pH was  
140 measured three times a week ( $8.0 \pm 0.1$ ). Ammonium (lower than  $0.05\text{mg.L}^{-1}$ ) and nitrite  
141 concentrations were monitored three times a week until hatching (lower than  $0.01\text{mg.L}^{-1}$ ).  
142 Photoperiod was 12L:12D and light intensity was 400 lx at the water surface.

143 Two independent experiments were performed in order to ensure availability of larvae  
144 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<sup>-1</sup>. 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 2m<sup>3</sup> 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<sup>-1</sup> 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  $0.6^\circ\text{C}$ ) 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 % ( $\pm 12.0$ ), 29.4 % ( $\pm 14.5$ ) and 6.6  
167 % ( $\pm 3.4$ ) for experiment I (26 dph; statistical difference between Geneva Lake and the two

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

172 **Group structure and activity**

173 For each population, three replicates for each cylindro-conical tank were performed over  
174 two days (25 and 26 dph). At 24 and 25 dph, a total of 90 individuals ( $n=30$  for each cylindro-  
175 conical tank, 10 individuals per replicate) were sampled for each population and transferred  
176 to three aquaria (58 L; one aquarium per cylindro-conical tank; order of cylindro-conical  
177 replicates randomly assessed over two days; see appendix 1) with an 80lx light intensity and  
178 a temperature of 20.0°C ( $\pm 0.5$ ). Individuals were not fed from the moment they were  
179 transferred to the beginning of the experiment the following day in order to have individuals  
180 in the same energetic state. After one night of acclimatisation, individuals were tested by  
181 groups of ten in circular arenas. Groups of ten individuals might not reflect faithfully what  
182 occurs in cylindro-conical tanks. However, evaluation cannot be performed directly in the  
183 tanks and this method was previously validated (e.g. Colchen et al. 2016). Three circular  
184 arenas (30 cm diameter with 1.5cm of water depth) were used to investigate group structure  
185 and activity (Colchen et al. 2016). Water in the arena was the same as in the aquaria, room  
186 temperature was maintained at 20.0 °C ( $\pm 0.6$ ) and arenas were lit at 10lx from underneath  
187 in order to avoid shadows during recording. For each replicate, individuals were transferred  
188 from the aquarium to the arena with a beaker and a siphon. After 30min acclimatisation,  
189 individuals were filmed for 30min using camcorders (Sony, Handycam, DCR-SR72E) located  
190 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  $14.05 \pm 0.55$ mm,  $12.90 \pm 0.62$ mm, and  $13.87 \pm 0.26$ 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  $26.74 \pm 1.67$ mm,  $26.28 \pm 1.99$ mm, and  $22.97 \pm 1.08$ 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 now 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:

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

258 **Compliance with ethical standards**

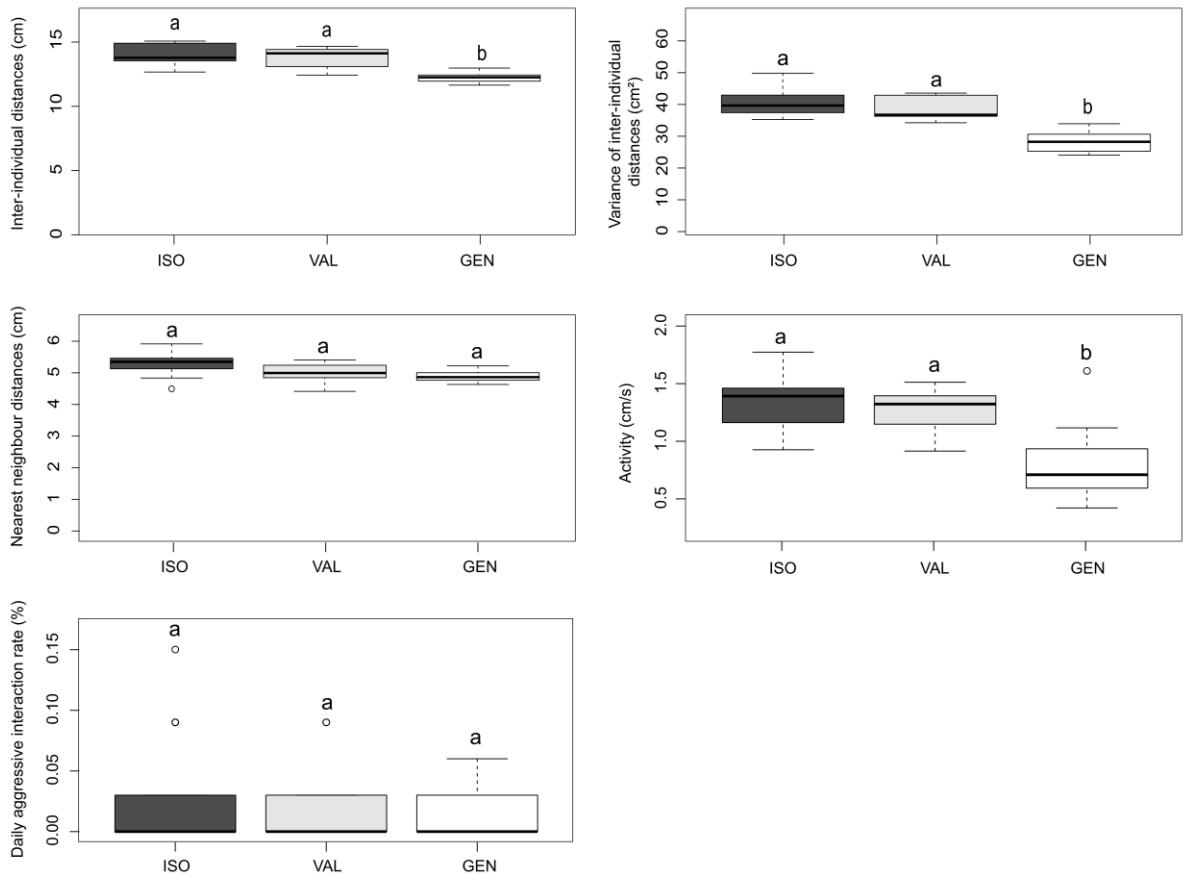
259 All along experimental procedures, individuals were handled as little as possible. All  
260 procedures were in accordance with the national and international guidelines for protection  
261 of animal welfare (Directive 2010/63/EU). This study was conducted with the approval  
262 Animal Care Committee 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).



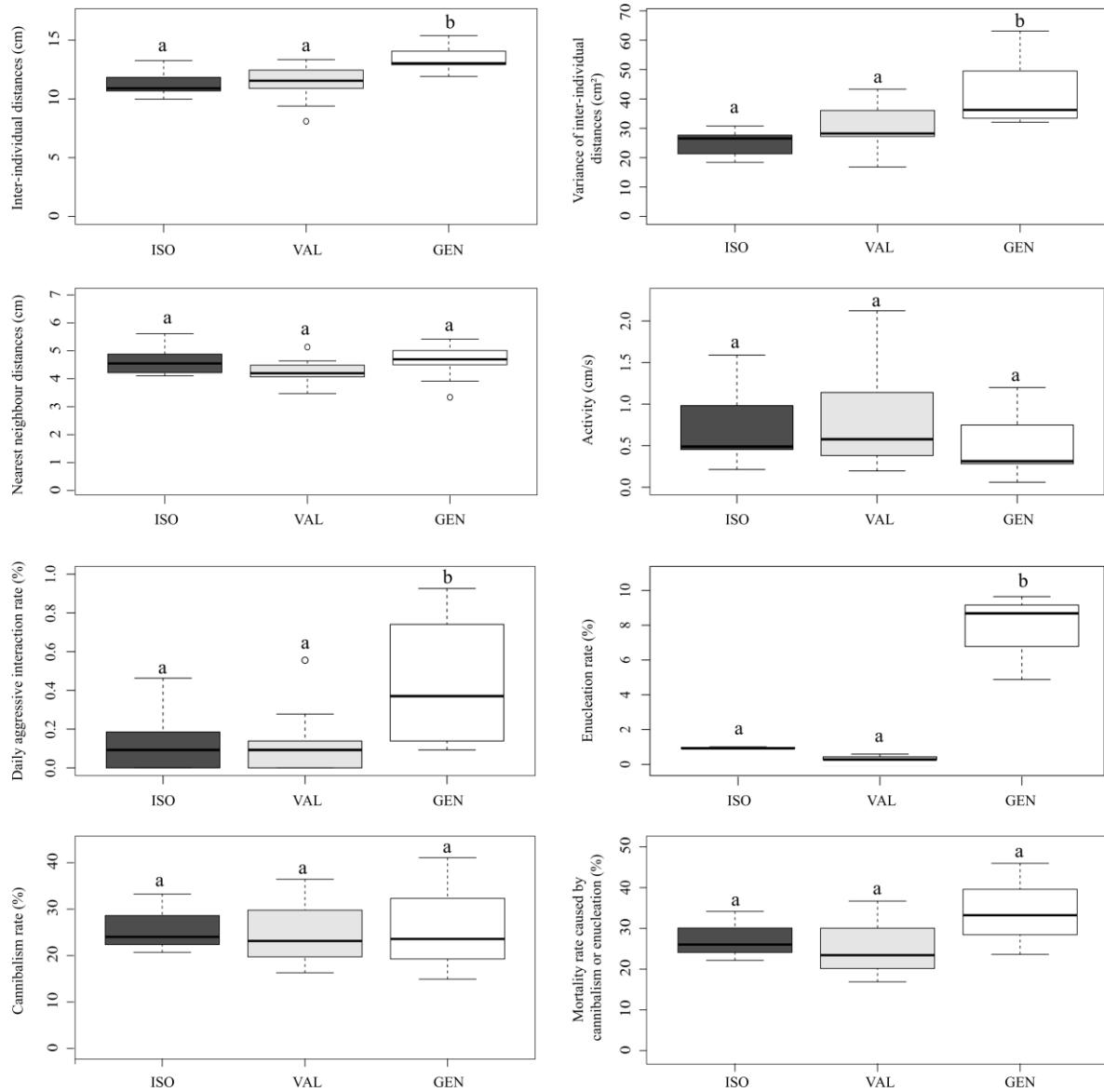
272 **Fig. 1:** Boxplots representing group structure and aggressive interaction results for  
 273 experiment I (n=3330). Four measures of group structure are presented: inter-individual  
 274 distances, variance of inter-individual distances, nearest neighbour distances, and activity.  
 275 The black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

279 Experiment II (45-46 dph)

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

285   **Quantification of aggressive interactions**

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



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

305 **DISCUSSION**

306 **Inter-populational differentiation in behavioural traits and its potential causes**

307 In this study, we highlight intraspecific differentiation between the two Finnish populations  
308 and GEN for group structure (experiments I and II) and aggressive interactions (only  
309 experiment II) while activity does not differ. We cannot exclude some potential biases in our  
310 experiments. For instance, (i) aggressive behaviour observations have been made after first  
311 feeding but cannibalism peaks (and aggressions) might occur at different moments of the  
312 day between populations and (ii) calculated cannibalism rate might also include dead  
313 individuals eaten by conspecifics which can blur differences in cannibalism rates. However,  
314 since (i) temporal differentiation in cannibalism peaks has not been reported to date and (ii)  
315 the cannibalism estimation method, widely used across literature (e.g. Kestemont et al.  
316 2003; Mandiki et al. 2004), allows to compare populations, we argue that bias related to  
317 observations of inter-populational behavioural differentiations at two ages are limited.

318 Intraspecific differentiation in group structure and aggressive behaviours has been already  
319 highlighted for several fish species (Rosenau and McPhail 1987; Magurran and Seghers 1991;  
320 Amundsen et al. 1999; Lahti et al. 2001; Huizinga et al. 2009; Wark et al. 2011; Song et al.  
321 2011). Here, a more cohesive and homogeneous structure is demonstrated for Finnish  
322 populations compared to GEN at 45-46 dph (Fig. 2). These results, associated with a similar  
323 nearest neighbour distance, indicate a structure in sub-groups in all populations but with a  
324 distance between these groups higher for GEN at 45 dph. The less homogeneous group  
325 structure of GEN at 45 dph is quite congruent with the higher aggressiveness highlighted for  
326 this population. Indeed, although daily aggressive interaction rate seems low (0.1-0.9 %; Fig.  
327 2), the congruence between aggressive interaction patterns and enucleation rate supports

328 the higher aggressiveness of GEN compared to the two Finnish populations. The absence of  
329 difference in cannibalism rate indicates that aggressive interactions are not necessarily  
330 followed by type II cannibalism. Therefore, our study is not congruent with Mandiki et al.  
331 (2004) who showed a difference in intra-cohort cannibalism rate between different  
332 European perch allopatric populations (but with different populations than the ones  
333 investigated here). Here, we highlight differences in aggressive interactions aside from  
334 cannibalism rate. Inter-populational behavioural differences can be shaped by genetic  
335 differentiation, by phenotypic plasticity, or by their combination.

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

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

364 On the other hand, phenotypic plasticity (i.e. the ability of a genotype to produce more than  
365 one phenotype when exposed to different environments; Pigliucci et al. 2006; Kelly et al.  
366 2012) is an alternative explanation of the observed behavioural differentiations between  
367 populations (DeWitt and Scheiner, 2004) with behaviour reflecting the strategy adopted  
368 under the influence of environmental factors. This was suggested as the driving factor for  
369 cannibalism in *P. fluviatilis* (Krol et al. 2015 and references therein) as well as in other  
370 species (e.g. Svenning and Borgstrøm 2005). Since we have used an experimental transplant  
371 approach (common environment), we speculate that we have minimized the effect of the  
372 environment (West-Eberhard 2003). Nevertheless, influences of past environmental  
373 conditions (i.e. before the beginning of our experiment) cannot be ruled out. On the one

374 hand, we have collected individuals at the egg stage in the wild and phenotypic response to  
375 environmental conditions could have occurred during development (Swain and Lindsey  
376 1986). On the other hand, environmental conditions experienced by the parents might have  
377 influenced offspring phenotype (Mousseau and Fox 1998; Youngson and Whitelaw 2008). At  
378 last, it was also shown an influence of maternal size on larvae performance (Olin et al. 2012).  
379 Since we have no information on the parents of egg sampled, we cannot exclude the  
380 influence of maternal effects which were demonstrated in *P. fluviatilis* for other traits  
381 (Babiak et al. 2004; Krol et al. 2015).

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

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

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

397 2012). We observe similar development for ISO and VAL populations. In contrast, the  
398 opposite pattern observed for GEN population is unexpected and corresponds to the  
399 establishment of a less homogeneous group with age. Mechanisms underlying the age-  
400 dependant changes in group structure are so far unknown. Differential ontogenies of  
401 sensory development might play a role into differences at the different ages (Buske and  
402 Gerlai 2012). Several neuroanatomical, physiological or biochemical factors have been  
403 suggested to be involved (Buske and Gerlai 2012). There might also be some group  
404 regulation mechanisms subsequent to weaning, which can potentially increase competition  
405 for resources linked for instance to bioenergetic needs or physiological shifts. This  
406 competition could explain the higher occurrence of aggressive interactions in experiment II.

407 **Integrating inter-populational behaviour differentiation: a way to improve aquaculture  
408 production?**

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

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

426 Selecting best populations for aquaculture production cannot be made through only  
427 behavioural trait comparisons. Indeed, selective breeding for low stress responsiveness has  
428 for instance been applied in several fish species but these low-stress response fish were also  
429 the ones which were more aggressive (Huntingford et al. 2012). Intraspecific differentiation  
430 has been already assessed for several other traits of interest such as growth (e.g. Mandiki et  
431 al. 2004; Leithner and Wanzenböck 2015), feed conversion efficiency (e.g. Imsland et al.  
432 2000; Jonassen et al. 2000), or disease resistance (e.g. Imsland et al. 2002; Overturf et al.  
433 2003). Therefore, the choice of the founder population must then be based on a multi-  
434 function and multi-trait approach rather than a single-trait decision framework.

435

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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

456

457

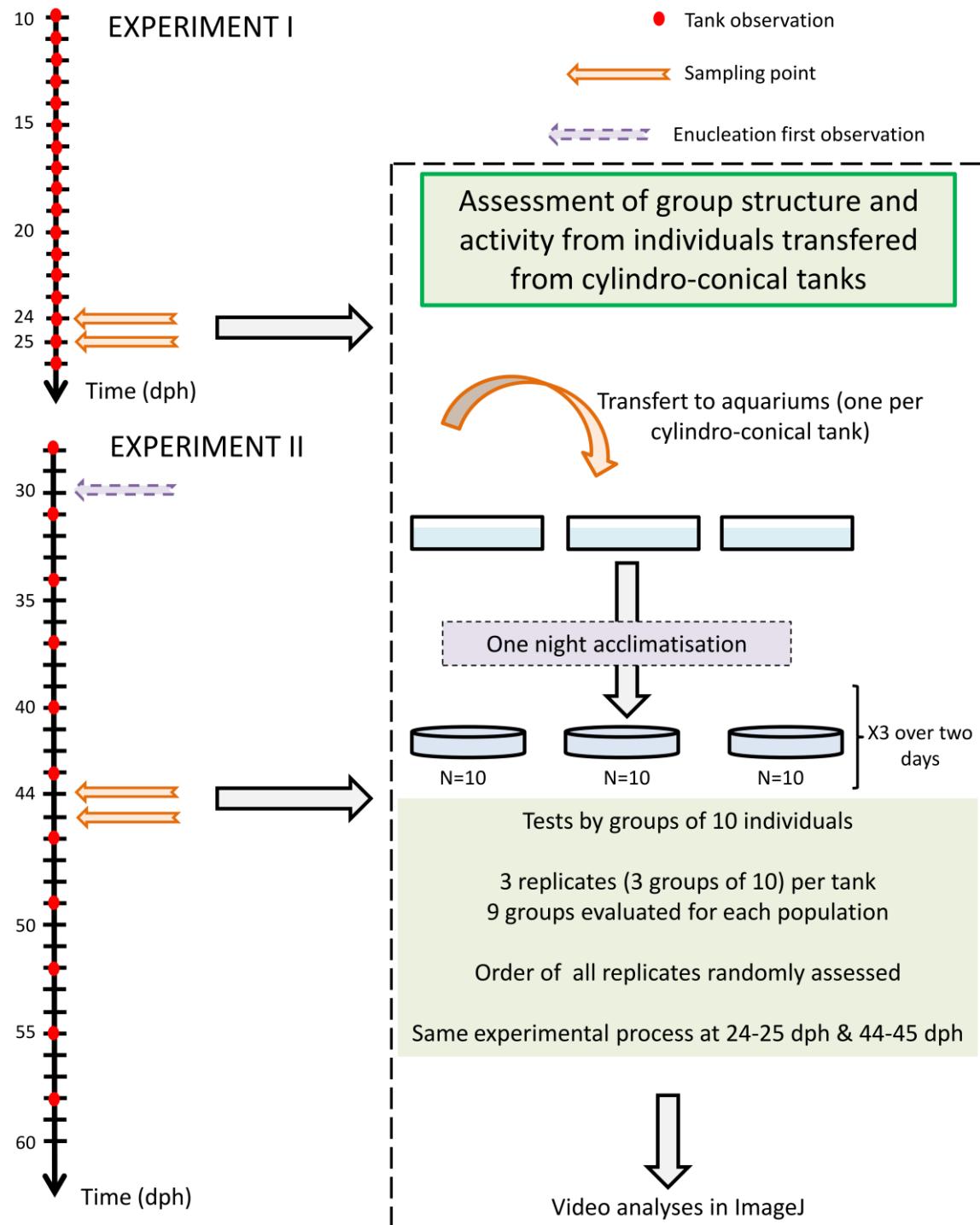
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461 APPENDIX

462 Appendix 1: Material and methods workflow.



463

464

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