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14 **Is a cannibal different from its conspecifics? A behavioural, morphological, muscular and**  
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33 **Highlights**

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35

- Visual processing was linked to the onset of cannibalism in pikeperch.

36

- Two retinal layers (ganglion cell layer and inner nuclear layer) were thicker for cannibals.

37

- The non behavioural differences could explain asynchrony in the onset of cannibalism.

38

- Cannibalism would be driven by rearing condition-dependent individual development.

39

40 **Abstract**

41 Cannibalism is defined as the act of killing and consuming the whole, or major part, of an individual  
42 belonging to the same species, irrespective of its stage of development. Intra-cohort cannibalism in  
43 fish larval or juvenile stages, which is a major economic problem, has been widely studied in captive  
44 fish populations. In our study, we investigated the influence of animal personality (with cross-maze  
45 and conspecific choice tests) on intra-cohort cannibalism using pikeperch *Sander lucioperca* as a  
46 model species. Furthermore, we investigated the morphological (geometric morphological analysis)  
47 and anatomical (histological analysis of retinal and muscle tissue sections) differences between  
48 cannibal (C) fish (TL =  $34.6 \pm 9.4$  mm, n = 25) and conspecific fish randomly sampled from rearing  
49 tanks, herein called 'potential non-cannibal fish' (PNC) (TL =  $31.4 \pm 10.5$  mm, n = 42). We did not  
50 find any behavioural differences (swimming activity, exploration, conspecific choice) between  
51 cannibal and potential non-cannibal fish that could explain asynchrony in the onset of cannibalism.  
52 Moreover, we did not observe any morphological differences between the two groups (C and PNC  
53 fish). However, we did detect anatomical differences in two retinal layers (ganglion cell layer and  
54 inner nuclear layer) that were thicker for cannibals. These two layers are involved in the collection of  
55 information by photoreceptors and allow the shapes, colours and movements of objects to be detected  
56 in the water column. The onset of cannibalism therefore appears to be linked to environmental  
57 condition-dependent individual development, with some individuals exhibiting precocious anatomical,  
58 and probably physiological, development, rather than to individual personality.

59

60

61 **Keywords:** cannibalism; multi-trait approach; fish; freshwater species; *Sander lucioperca*

## 62           1. Introduction

63 Cannibalism could be considered as a predatory strategy that involves capturing, killing and eating a  
64 part or the whole of individuals of the same species (Polis, 1981; Elgar and Crespi, 1992). It has been  
65 recorded in more than 500 vertebrate species (Soulsby, 2013). Among them, about 200 species are  
66 fishes (Smith and Reay, 1991), for which cannibalism has been reported in the wild and under farming  
67 conditions. The most commonly farmed fish species are piscivorous predators: out of 26 fish species  
68 commonly found in rearing systems, 18 are classified as carnivorous and piscivorous and only 8 are  
69 considered as omnivorous and do not feed on other fish species). In the wild, cannibalism can be  
70 considered as ‘a lifeboat mechanism’ defined as the survival of a cannibalistic population when food  
71 for the adults is too scarce to support a non-cannibalistic population (van den Bosch et al., 1988).  
72 Under farming conditions, where yet there is usually no food limitation since fish are fed *ad libitum*,  
73 larviculture performance is also often affected by intra-cohort cannibalism. Intra-cohort cannibalism in  
74 fish larval or juvenile stages has been widely studied in captive fish populations since such a  
75 behaviour is a major economic problem in farmed piscivorous species (Naumowicz et al., 2017;  
76 Pereira et al., 2017).

77 In order to explain intra-cohort cannibalism, size heterogeneity has been largely documented. Indeed,  
78 it is known that the cannibal is larger in size than its prey, reflecting differences in development. Two  
79 types of cannibalism have been described during fish larval and early juvenile development stages:  
80 Type I, which occurs generally during the larval stage, does not imply any size difference between the  
81 cannibal and its prey, which is not entirely ingested (Baras, 2013); Type II, which occurs at a later  
82 stage, is characterized by the entire consumption of the prey and greater size heterogeneity between  
83 the cannibal and its prey (Baras and Jobling, 2002). However, even though size heterogeneity  
84 facilitates cannibalism, and many studies have attempted to identify environmental or population  
85 factors that could affect it (for review, see Pereira et al., 2017). To our knowledge, however, very few  
86 studies have used a multi-trait approach to identify the traits that could be involved in the onset of  
87 cannibalism (e.g. Baras and Jobling, 2002).

88 In fish, cannibalism implies performing as a piscivorous predator with particular characteristics. First,  
89 it is necessary for a piscivorous fish to have physical abilities to detect (i.e. visual cues), pursue and

90 capture (developing jaw and trunk musculature), and digest (digestive enzyme function) a prey  
91 (Sakakura and Tsukamoto, 1996; Cahu and Zambonino Infante, 2001). It is easier for a cannibal  
92 because its prey, belonging to the same species, has the same movement abilities. Finally, for fish, the  
93 mouth size is a limiting factor for ingesting a prey, particularly for Type II cannibalism (Hetch and  
94 Appelbaum, 1988; Sogard and Olla, 1994). The size of the mouth could be a consequence of an  
95 allometric growth of the mouthparts (Baras and Jobling, 2002). In Type II cannibalism, the mouth  
96 must be large enough to ingest the prey headfirst, in order to avoid the spiny dorsal fin and pectoral  
97 rays that may cause injury or even death of the cannibal (Qin et al., 2004). These morphological and  
98 anatomical characteristics have been largely studied by comparing cannibals and their prey (Baras and  
99 Jobling, 2002; Baras, 2012), and the former authors have concluded that the cannibals have a larger  
100 mouth gape, stronger musculature and better vision than their prey (Baras, 1998; Baras, 2012).  
101 However, the behavioural differences between cannibals and conspecifics have received less attention,  
102 which may be due to the difficulties in setting up these kinds of experimental designs.

103 Behavioural traits of personality allowed to reveal consistent behavioural differences over time and/or  
104 in different contexts between individuals of the same population (Koolhaas et al., 1999; Sih et al.,  
105 2004; Réale et al., 2007). This concept of personality makes the difference between bold individuals,  
106 which take risks, and are more aggressive, and shy individuals, which are less active and more  
107 sociable. Within a population, individuals may be classified between these two extremes of  
108 behavioural profiles along the bold-shy axis (Bell, 2007). Personality plays an important role in the  
109 onset of several behaviours during ontogeny, among which foraging performance in birds (Kurvers et  
110 al., 2009; Patrick and Weimerskirch, 2014), mammals (Mella et al., 2015) and fish (Cutts et al., 1998;  
111 2001; Wilson and McLaughlin, 2007). In fish, foraging abilities are correlated to individual's level of  
112 activity in the Atlantic Salmon *Salmo salar* L. (Cutts et al., 1998), and the Arctic charr *Salvelinus*  
113 *alpinus* L. (Cutts et al., 2001). In this context, it seems that bold individuals were the best performing  
114 foragers (Conrad et al., 2011). In light of these findings, as personality could influence foraging  
115 performances, we can hypothesize that in a population, cannibals and non-cannibals lie at different  
116 points on the bold-shy continuum.

117 In our study, we investigated the influence of animal personality on intra-cohort cannibalism using

118 pikeperch *Sander lucioperca* as a fish model. This freshwater fish exhibits a high degree of  
119 cannibalism (<50%) under intensive rearing conditions (Molnár et al., 2004; Kestemont et al., 2007).  
120 However, it is necessary to understand what may differentiate a cannibal (C) from the other  
121 conspecifics (called ‘potential non-cannibal fish’ (PNC) in this study) to regulate this major bottleneck  
122 in pikeperch farming (Kestemont et al., 2007; 2015). Cannibalism mainly occurs in early  
123 development, when pikeperch larvae are between 14 and 17 days post-hatching (dph), and there is a  
124 first peak between 32 and 42 dph at 20°C (Colchen et al., 2019). In order to complete the comparison  
125 between cannibals and their conspecifics, we also investigated morphological (body shape by  
126 geometric morphometric analysis) and anatomical differences (retina and muscle development by  
127 histological analysis). Thereby, we wanted to determine whether there were behavioural,  
128 morphological and/or anatomical differences between cannibals and their conspecifics. Using  
129 behavioural, morphological and anatomical traits evolving during the ontogenetic development to  
130 compare cannibal fish with potential non-cannibal fish of pikeperch, we can hypothesize that  
131 cannibals should (i) be bolder, (ii) have more developed caudal musculature and a larger gape size,  
132 and (iii) have better visual abilities. These predictions mean that, if cannibalism depends on animal  
133 personality, some individuals will never be cannibals in this population.

134

## 135 **2. Materials and methods**

### 136 **2.1. Rearing of the fish**

137 The experiment was carried out at the Aquaculture Experimental Platform (AEP, registration number  
138 for animal experimentation C54-547-18) belonging to the URAFPA lab and located at the Faculty of  
139 Sciences and Technologies of the University of Lorraine (Nancy - France). Eggs came from two  
140 mature females (2.7 and 2.9 kg) previously injected with sGnRH $\alpha$  (25 and 50  $\mu\text{g}\cdot\text{kg}^{-1}$ , respectively;  
141 ovaRH, Syndel laboratories, Ltd) and fertilized by one male in a fish farm (SARL Asialor,  
142 Pierrevillers, Moselle, France). At their arrival at the AEP on 1<sup>st</sup> February 2016, just before hatching,  
143 the fertilized eggs were transferred into eight 700 L tanks where larvae hatched and developed until 52  
144 dph. Artificial lighting (50 lx) followed a 12L/12D cycle with light on from 08:00 to 20:00 with 30



145 min simulation of dawn and dusk. The water was maintained at 16°C until hatching and then increased  
146 by 1°C per day until reaching 20°C. Water parameters (mean ± standard deviation, SD) were  
147 measured once or twice a week: dissolved oxygen =  $8.0 \pm 0.5 \text{ mg.L}^{-1}$ , pH =  $6.9 \pm 0.8$ , salinity =  $0.2 \pm$   
148  $0.05 \text{ g.L}^{-1}$ , ammonia ( $\text{NH}_4^+$ ) =  $5.3 \pm 1.0 \text{ mg.L}^{-1}$  and nitrite ( $\text{NO}_2^-$ ) =  $0.08 \pm 0.07 \text{ mg.L}^{-1}$ . Fish were fed  
149 seven times per day between 8:30 and 17:30 during light period every one and a half hours. They were  
150 fed live prey and a commercial inert feed as follows: firstly, nauplii of *Artemia* (550-600 µm, Sep-Art  
151 *Artemia* cyst) from 4 to 16 dph, then Larviva PROWEAN 100, 300, 500, 700 µm (BIOMAR®,  
152 France) and INICIOplus 0.8 mm (BIOMAR®, France), following the protocol used by Schram and  
153 Philipsen (2003) for weaning.

154

## 155 2.2. Sampling of the fish

156 Our aim was to compare traits (anatomical, morphological and behavioural) between cannibal and  
157 potential non-cannibal fish, as we can be sure that at the sampling time fish were not cannibal, but we  
158 have no information about their attack activity on conspecifics before the sampling. In order to detect  
159 fish displaying cannibalism, 5 min observations were made at each tank every morning (after 9:40  
160 a.m.) from 10 to 52 dph. When a case of cannibalism was observed, the observer attempted to capture  
161 the cannibal with a dip net. Out of 192 observed cases of cannibalism, 25 cannibals were sampled  
162 (total length (mean ± SD) =  $34.6 \pm 9.4 \text{ mm}$ ). To allow for comparison, each time we captured a  
163 cannibal, we also captured one or two fish randomly (potential non-cannibal fish) of similar size (total  
164 length (mean ± SD) =  $31.4 \pm 10.5 \text{ mm}$ ). For these potential non-cannibal fish (n = 42), we verified that  
165 they were not eating a conspecific or that there was no other fish in their digestive tube. All fish  
166 (potential non-cannibals and cannibals) were transferred into individual cages (15 x 12 x 11 cm) in a  
167 52.5 L aquarium (50 x 35 x 30 cm) for 24 hours before their use in behavioural tests. The light cycle  
168 and the water temperature were the same as those in the 700 L tanks.

169

## 170 2.3. Behavioural tests

171 To establish the personality of pikeperch larvae and early juveniles, two behavioural tests were used: a  
172 cross-maze test to analyse swimming activity, exploration and boldness, and a choice test between  
173 conspecifics or not to analyse the relationship behaviours.

174 The cross maze apparatus (16 x 5 cm with 2.5 cm of water) consisted of four arms, divided into five  
175 zones (**Fig. 1A**) and placed on a translucent table with a light below (50 lx). Fish were tested one by  
176 one. Each fish was placed in an acclimatization zone (7 x 5 cm) separated from the maze by a vertical  
177 divider (**Fig. 1A**). After a 30 min acclimatization period, the divider was removed and fish behaviour  
178 was video recorded for 20 min. Several independent behavioural measures were analysed: i) the  
179 individual latency to emerge from the acclimatization zone (E\_LS) (in seconds), if a fish did not  
180 emerge from the acclimatization zone (AZ) during the 20 min period, a latency period of 1,200 s was  
181 attributed. ii) the total number of visited zones (E\_NVZ) and iii) swimming activity (E\_SA) (in  
182 seconds). All variables were analysed over the entire 20 min period except E\_SA, which was  
183 calculated over three periods of time: from the 1<sup>st</sup> to the 3<sup>rd</sup> minute, from the 9<sup>th</sup> to the 11<sup>th</sup> minute and  
184 from the 17<sup>th</sup> to the 19<sup>th</sup> minute (adapted from Pasquet et al., 2015).

185 The conspecific choice tests were realized in the same type of device. The apparatus consisted of four  
186 arms divided into five zones (**Fig. 1B**). Three arms of the cross-maze were separated from the central  
187 zone by transparent dividers perforated with small holes (less than 1 mm in diameter). These holes  
188 allowed constant water flow between the arms of the cross-maze. The three zones contained zero,  
189 three, and six pikeperch larvae of the same age and reared under the same conditions as the tested fish,  
190 and unknown from the tested fish. The main goal was to determine if a cannibal prefer stay near  
191 conspecifics or not and if the size of the group impact the choice. Each tested fish was placed in an  
192 acclimatization zone (7 x 5 cm) separated from the maze by a vertical divider (**Fig. 1B**). After 30 min  
193 of acclimatization, the divider between the acclimatization zone and the cross-maze was removed. The  
194 behaviour of the tested larvae was video recorded for 20 min. Five variables were taken into account  
195 during this period: the latency to emerge from the acclimatization zone (S\_LS) (in seconds) and the  
196 time spent close (less than 1 cm from the divider) to the groups of zero (S\_Z0), three (S\_Z3) or six  
197 conspecifics (S\_Z6), and aggressive behaviours (e.g. the attack attempts against the transparent  
198 divider). This last behaviour was never observed, consequently only the first four variables have been

199 considered in the statistical analyses.

200

#### 201 2.4. Geometric morphological analysis

202 After the behavioural tests, all larvae (cannibal and potential non-cannibal fish) were euthanatized  
203 with an overdose of tricaine methane-sulfonate (MS-222, Sigma; 240 mg.L<sup>-1</sup>). The right side of each  
204 fish was photographed with a digital camera (Panasonic, DMC-FZ18). For each photographed fish,  
205 total length (TL) was measured and the coordinates of 15 morphological landmarks (LMs) were  
206 recorded (**Fig. 2**), using tpsDig 2.16 (Rohlf, 2008). The scale was calibrated for each photograph. The  
207 LMs were selected to provide a definition of the fish morphology in which the LMs are given as *x* and  
208 *y* coordinates. The distances and angles between specific LMs were determined from their coordinates.  
209 The LMs were digitized on the lateral side of each fish by the same observer (**Fig. 2**). Body shape was  
210 analysed using LM-based geometric morphometric methods (Rohlf, 1990; Bookstein, 1991). The LMs  
211 were superimposed to have a common centroid and rotated to minimize the distances between  
212 corresponding LMs. Once all the fish were aligned, the mean configuration of LMs was computed  
213 (consensus or reference shape). At that time, LM 11 and 12 were excluded because of the inaccuracy  
214 of their positions for each fish, and so were all spine-malformed fish (*n* = 29) and fish with one LM  
215 missing (*n* = 5). Finally, we compared the geometrical morphologies of 16 cannibal fish and 17  
216 potential non-cannibal fish. Fish were projected to a tangent space by orthogonal projection where the  
217 distances between shapes were linear functions. This process then permitted the use of multivariate  
218 statistical methods to evaluate shape variation. Principal component analysis (PCA) was performed  
219 after computing the variance-covariance matrix of the procruster shape coordinates and projecting the  
220 data onto the corresponding eigenvectors. All geometric morphometric-related analyses were carried  
221 out with R (version 3.5.3) with ‘shapes’ (Dryden, 2018) and ‘factoextra’ (Kassambara and Mundt,  
222 2017) packages. Thin-plate spline deformation grids of fish body shape to compare cannibal fish with  
223 potential non-cannibal fish were generated on MorphoJ<sup>®</sup> software (Klingenberg, 2011).

224

#### 225 2.5. Histological data

226 After taking pictures of each fish for the morphological analysis, larvae were fixed in 10% buffered  
227 formalin (Sigma-Aldrich, HT501128-4L). Twenty-five cannibals and 18 potential non-cannibal fish  
228 were used for this histological study, whose steps were all conducted at IRTA (Aquaculture Program,  
229 Sant Carles de la Rapita, Spain). Two types of fish tissue were analysed: the eyes, because vision is  
230 key to the development of predatory behaviour, and the muscles, which are essential for mobility to  
231 pursue and capture prey. To perform the various analyses, an eye and caudal muscles (vertical cut just  
232 behind the anus) were collected from each larva. All samples (eyes and muscles) were dehydrated  
233 with graded series of ethanol (from 50% to 100%) and embedded in paraffin with a Histolab ZX-  
234 60Myr automatic tissue processor (Especialidades Médicas MYR SL, Spain). Then, paraffin blocks  
235 were prepared in an AP280-2Myr station and cut into serial sagittal sections (3  $\mu\text{m}$  thick) with a  
236 Microm HM automatic microtome (Leica RM2155 Microsystems Nussloch GmbH, Nussloch,  
237 Germany). Paraffin-embedded eyes and muscle sections were kept at 40°C overnight. Then, samples  
238 were deparaffined with graded series of xylene and stained by means of Hematoxylin (5 min) and  
239 Eosin (5 min). Stained sections were examined using an upright optical light microscope (Nikon  
240 Eclipse Ni-U) at 40x magnification (Nikon France, Champigny-sur-Marne, France).

241 For each cannibal (n = 19) and potential non-cannibal (n = 10) fish, the thickness of the seven retinal  
242 layers (Ganglion Cell Layer (GCL), Inner Plexiform Layer (IPL), Inner Nuclear Layer (INL), Outer  
243 Plexiform Layer (OPL), Outer Nuclear Layer (ONL), Photoreceptor Layer (P) and Pigmentary  
244 Epithelium (PE)) was measured using Nikon BR software (**Fig. 3**). Furthermore, the number of muscle  
245 fibres was counted on four defined zones for each cannibal (n = 16) and potential non-cannibal (n = 9)  
246 fish, and maximal and minimal diameters measured on 40 fibres for each fish (**Fig. 3**). The muscle  
247 fibres were classified as large (> 30  $\mu\text{m}$ ) or small (< 30  $\mu\text{m}$ ) depending on their diameters.

248

## 249 2.6. Statistical analysis

250 For the behavioural variables, we calculated the mean and standard deviation (SD) to assess the  
251 variability of pikeperch behavioural responses. For each variable of interest, in each group (cannibal  
252 and potential non-cannibal fish), inter-individual variability was assessed by calculating the coefficient

253 of variation (CV, % = SD/mean x 100) as a normalized measure of dispersion. We checked the  
254 normality of the data (Shapiro-Wilk test, R Core Team, 2017) and the homogeneity of the variances  
255 (Levene's test; Fox and Weisberg, 2016). For each group, we assessed the correlation between the  
256 values of each variable of interest between fish with Spearman correlations. Furthermore, comparisons  
257 of the same variables between cannibal and potential non-cannibal fish were carried out with a  
258 parametric Student's t-test for independent data. A multifactorial analysis (PCA) was conducted taking  
259 into account all the behavioural variables (FactoMineR; Husson et al., 2019) and all the individuals  
260 were projected on the graph of the PCA analysis. Data analyses were performed using R software  
261 (version 3.0.3) and the level of significance used in all tests was  $P < 0.05$ .

262 For the morphological analysis, all the coordinates of the landmarks obtained on cannibal and  
263 potential non-cannibal juveniles were analysed with a generalized procrustes analysis (GPA), with  
264 MorphoJ® software (Klingenberg, 2011). This procedure allowed us to eliminate all variations due to  
265 translation, rotation and scale effects. Then, the standardized coordinates obtained with this method  
266 were analysed with the Relative Warp Analysis (Rohlf, 1993), which is a principal component  
267 analysis (PCA).

268 For the histological parameters, as the data fitted the normality and the homogeneity of the variances,  
269 we used an ANCOVA, taking the TL of each individual as covariate. The analysis was performed with  
270 R software (version 3.5.3) and the level of significance used in all tests was  $P < 0.05$ .

271

## 272 2.7. Ethical note

273 During all procedures, we took care to minimize handling and stress as much as possible for the study  
274 animals. All fish treatments and procedures used in this study were in accordance with the guidelines  
275 of the Council of the European Union (2010/63/UE) and the French Animal Care Guidelines (Animal  
276 approval No. APAFIS#1813-2015111618046759v2).

277

## 278 3. Results

### 279 3.1. Behavioural analyses of each group: cannibal and potential non-cannibal fish.

#### 280 3.1.1. Inter-individual variability

281 The analysis of coefficients of variation revealed considerable inter-individual variability in the  
282 variables measured in both tests carried out for cannibal and potential non-cannibal fish (**Table 1**),  
283 indicating that there was a high level of behavioural variability in both groups of fish.

284

### 285 3.1.2. Correlations between behavioural variables

286 Regarding cannibal fish, swimming activity was positively correlated to the total number of visited  
287 zones and the time spent near three conspecifics (S\_Z3) (**Table 2**). Then, the time spent near six  
288 conspecifics was negatively correlated to the latency to emerge from the acclimatization zone (S\_LS)  
289 in the conspecific choice test and positively correlated to the time spent near three conspecifics  
290 (S\_Z3). Finally, the total number of visited zones was positively correlated to the time spent near three  
291 conspecifics (**Table 2**). For potential non-cannibal fish, swimming activity was positively correlated to  
292 the total number of visited zones, to the time spent near the zone without conspecifics (S\_Z0), to the  
293 time spent near three conspecifics (S\_Z3) and to the time spent near six conspecifics (S\_Z6) (**Table**  
294 **2**). Then, the total number of visited zones was positively correlated to the time spent near three and  
295 six conspecifics (**Table 2**). Finally, the latency to emerge from the acclimatization zone in the  
296 conspecific choice test was negatively correlated to the time spent near the zone without conspecifics  
297 (S\_Z0), to the time spent near three conspecifics (S\_Z3) and to the time spent near six conspecifics  
298 (S\_Z6) (**Table 2**).

299

## 300 3.2. Comparison between cannibal and potential non-cannibal fish.

### 301 3.2.1. Behavioural test analysis

302 In the cross-maze test, the swimming activity (E\_SA) of cannibal fish was similar to that of potential  
303 non-cannibal fish ( $t = 1.22$ ;  $df = 65$ ;  $p = 0.23$ ; **Table 1**). The time to emerge from the acclimatization  
304 zone (E\_LS) was similar between cannibal and potential non-cannibal fish ( $t = 0.64$ ;  $df = 65$ ;  $p = 0.52$ ;  
305 **Table 1**). Cannibal fish visited statistically as many maze zones (E\_NVZ) as potential non-cannibal  
306 fish did ( $t = 0.95$ ;  $df = 65$ ;  $p = 0.34$ ; **Table 1**).

307 Regarding the conspecific choice test, cannibal fish emerged nearly as rapidly as potential non-

308 cannibal fish from the acclimatization zone (S\_LS) ( $t = -1.06$ ;  $df = 65$ ;  $p = 0.29$ ; **Table 1**). Values of  
309 S\_Z0 ( $t = -0.4$ ;  $df = 65$ ;  $p = 0.69$ ; **Table 1**), S\_Z3 ( $t = -0.11$ ;  $df = 65$ ;  $p = 0.91$ ; **Table 1**) and S\_Z6 ( $t$   
310  $= 1.32$ ;  $df = 65$ ;  $p = 0.2$ ; **Table 1**) were similar between cannibal and potential non-cannibal fish.

311 When all these variables were analysed using a PCA, the first two axes of the PCA represented 56.4%  
312 of the total variance (first axis = 39.0%, second axis = 17.4%; **Fig. 4**). The first axis contrasted the  
313 time to emerge from the acclimatization zone in both behavioural tests from swimming activity and  
314 conspecifics choice variables. This axis highlighted a bold-shy continuum with fish, which emerged  
315 rapidly from the acclimatization zone and were more active and attracted by conspecifics. The second  
316 axis was represented by the time spent near the zone without conspecific fish. Swimming activity  
317 (E\_SA) was positively correlated to the total number of visited zones (E\_NVZ) ( $r = 0.81$ ;  $p < 0.001$ ;  
318 **Fig. 4A**) and to the time spent near zones with conspecifics (S\_Z3:  $r = 0.44$ ;  $p < 0.001$  and S\_Z6:  $r =$   
319  $0.33$ ;  $p < 0.01$ ; **Fig. 4A**). The time to emerge from the acclimatization zone (S\_LS) in the conspecific  
320 choice test was negatively correlated to swimming activity (E\_SA) ( $r = -0.32$ ;  $p < 0.01$ ; **Fig. 4A**) and  
321 to the time spent near zones with conspecifics (S\_Z3:  $r = -0.34$ ;  $p < 0.01$  and S\_Z6:  $r = -0.34$ ;  $p <$   
322  $0.01$ ; **Fig. 4A**). Projection of individuals on axes highlighted that cannibal and potential non-cannibal  
323 fish were equally distributed on both axes and consequently did not demonstrate a difference on  
324 behavioural traits (**Fig. 4B**).

325

### 326 3.2.2. Geometric morphological analysis

327 The PCA of aligned coordinates for the 13 selected landmarks yielded 10 principal components (PCs;  
328 **Fig. 5A**). The first two axes (PC1 and PC2) explained 38.1% and 22.8% of the body phenotypic  
329 variability, respectively, which accounted for 60.9% of the total variance. In contrast, the third axis  
330 (PC3) only accounted for 13.4% of the variance and, consequently, this axis and the subsequent ones  
331 were not included in further analyses. In addition, the morphospace (ellipses) from each group  
332 revealed no clear separation between cannibal and potential non-cannibal fish, with a total overlap  
333 between groups (**Fig. 5B**). A transformation grid for visualizing changes in body shape for cannibal  
334 and potential non-cannibal fish did not reflect changes in both relative shifts and body shape in  
335 pikeperch juveniles (**Fig. 5C**; **Supplementary materials**).

336

337 3.2.3. Histological analyses

338 Regarding the retina, the ganglion cell layer (GCL) and the inner nuclear layer (INL) were much  
339 thicker in cannibal fish than in potential non-cannibal fish (**Fig. 3; Table 3**). There were no marked  
340 differences in the thickness of all other layers between the two groups (**Table 3**), and fish size (TL)  
341 had no effects on all morphological parameters taken into account ( $p > 0.05$ ). Considering trunk  
342 musculature, cannibal and potential non-cannibal fish exhibited similar diameters and numbers of  
343 muscle fibres. Both parameters were however found to be significantly affected by fish size (TL) ( $p <$   
344  $0.05$ ; **Fig. 3; Table 3**).

345

346 **4. Discussion**

347 Inter-individual variability, which is behaviourally, anatomically, morphologically and physiologically  
348 observable, characterizes the pikeperch population analysed in our study. Such variability is clearly  
349 visible under farming conditions leading for example to size heterogeneity, which may be regulated by  
350 control of environmental parameters. Under farming conditions, the existence of intra-cohort  
351 cannibalism has been shown repeatedly in various pikeperch populations (Ljubobratović et al., 2015;  
352 Steinfeldt, 2015; Król and Zakęś, 2016; Molnár et al., 2018). In our study, we investigated  
353 behavioural, morphological and anatomical potential differences between individuals of a population  
354 in order to explore such differences between a cannibal and its conspecifics and, consequently, the  
355 traits that could be involved in its differentiation from other individuals of the population.

356 It is well known that rearing factors such as population density, light intensity, feeding frequency,  
357 water turbidity or presence of alternative prey could affect the cannibalism rate (for review, see  
358 Naumowicz et al., 2017; Pereira et al., 2017), and result in individual behaviour changes (Coppens et  
359 al. 2010). These studies have demonstrated a range of individual responses directly influenced by  
360 environmental stimuli that could be associated with behavioural plasticity. Indeed, cannibals react to  
361 environmental stimuli by decreasing or increasing their cannibalism rates (Smith and Reay, 1991;



362 Hecht and Piennar, 1993; Folkvord, 1997), but it seems that no biotic or abiotic factors can eradicate  
363 cannibalism (Baras and Jobling, 2002). Rather than focusing on individual behavioural plasticity to  
364 understand why an individual becomes a cannibal at a given time of its development, our study looked  
365 at the differences in several traits between cannibals and other individuals of the population. Thus, it  
366 has provided results on several parameters (behaviour, morphology and anatomy) to highlight  
367 differences between cannibals and their conspecifics of a given population in order to evaluate  
368 whether a specific trait could differentiate them.

369 The study of personality allowed us to work on behavioural differences between individuals and look  
370 for differences between cannibal fish and their conspecifics (Torres et al., 2017; Meager et al., 2018).  
371 In our study, we demonstrated that there are no behavioural differences between cannibals and  
372 conspecifics. For several years, a number of behavioural differences observed under fish farming  
373 conditions have been explained by the personality paradigm, such as self-feeding triggering (Ferrari et  
374 al., 2014), aggressive behaviour (Martins et al., 2012), susceptibility to infection (Kittilsen et al.,  
375 2009a, b) or resuming feeding after transfer to a new tank (Vaz-Serrano et al., 2011). To our  
376 knowledge, no previous studies have compared the personality of cannibals with that of conspecifics,  
377 but several studies characterized personality first and then observed cannibalism rates in different  
378 groups composed of shy, bold or mixed individuals (Sih et al., 2004; McGhee and Travis, 2010; Réale  
379 et al., 2010; Colléter and Brown, 2011; Dahlbom et al., 2011; Mesquita et al., 2016). A recent study on  
380 catfish larvae *Lophiosilurus alexandri* showed that when sorting larvae by personality traits, there was  
381 a higher cannibalism rate in bold and mixed groups than in shy groups (Torres et al., 2017), thus  
382 suggesting a link between personality and cannibalism. However, our results were in disagreement  
383 with those of the above-mentioned authors, since we did not find any differences in personality traits  
384 associated with cannibalism. In our study, the non-difference between the two groups could be  
385 explained by the fact that some cannibals may have been mistakenly classified in the potential non-  
386 cannibal group because they did not display cannibalistic behaviour at the time of observation. We do  
387 not know if all potential non-cannibal fish had already been a cannibal or not. However, we were able  
388 to demonstrate a personality continuum in our pikeperch population with extreme personality as  
389 shown by a uniform repartition of fish personality scores on the first axis of the PCA. These results

390 were in agreement with those previously reported in a study conducted on the same species by our  
391 research group (Colchen et al., 2017). Therefore, even if potential non-cannibal fish were not all non-  
392 cannibals, assuming that cannibals have a different personality from the others, they should be found  
393 on either side of the point cloud when projecting all individuals on the PCA, meaning that cannibals  
394 have extreme personality (bold or shy). As a second argument, there were potentially few cannibals in  
395 the population with  $30.9 \pm 8.6$  jumpers (the biggest fish in a population) per week (in 700 L tanks,  
396 with initial densities of  $100 \text{ larvae.L}^{-1}$ , unpublished data). It was therefore unlikely that we had  
397 captured a large number of cannibals when randomly collecting potential non-cannibal fish. So, we  
398 could hypothesize that, in pikeperch, personality is not a major characteristic for distinguishing  
399 cannibals from other individuals, but it could be associated with anatomical and/or morphological  
400 variables.

401 Cannibalism may not occur at the same time in all individuals because it is a piscivorous behaviour  
402 and, in the particular case of larvae, the shift from a planktivorous to a piscivorous diet requires  
403 morphological, anatomical and physiological modifications (Buijse and van Densen, 1992;  
404 Galarowicz and Whal, 2005; Hart and Ison, 1991; Kaji et al., 2002; Mittelbach and Persson, 1998). It  
405 has been shown that the onset of predation in pikeperch larvae is not synchronic for all individuals in a  
406 population and occurs from three to six weeks after hatching when larvae are reared at  $20^{\circ}\text{C}$  (Colchen  
407 et al., submitted). As cannibalism is an intra-specific predation phenomenon, its onset, like that of  
408 predation, was not synchronic between individuals and therefore could explain the non-behavioural  
409 differences between cannibal and potential non-cannibal fish (fish sampling between 10 and 52 dph).  
410 In pikeperch, cannibalism may have more to do with the onset of piscivory than with personality  
411 differences between individuals in a population.

412 Furthermore, our results demonstrated that there were no morphological differences between cannibals  
413 and other individuals in the population. In other species, morphological differences between cannibals  
414 and non-cannibals have already been shown such as in salamander (Pfennig and Collins, 1993). At the  
415 early juvenile stage, coloration was the only missing pattern for our pikeperch specimens to look like  
416 adults, they were therefore assumed to be already morphologically developed. Thus, we could  
417 hypothesize that at larval stages morphological differences (e.g. mouth development) may be a good

418 visual guide for distinguishing a cannibal from another conspecific, but at juvenile stages visual  
419 differentiation is not possible because fish are fully morphologically developed. Moreover, there were  
420 no differences in trunk musculature development between cannibal and potential non-cannibal fish.  
421 Under farming conditions, where high animal density is common practice, we can assume that capture  
422 conditions may not be complicated, so fish do not need to have developed musculature, they just have  
423 to catch smaller, deformed or sick fish. However, there appeared to be anatomical differences in the  
424 retina between cannibal and potential non-cannibal fish. Although there was the same number of  
425 layers for the two groups, two layers were thicker in cannibals: the ganglion cell layer and the inner  
426 nuclear layer. These two layers are involved in the collection of information by photoreceptors and  
427 allow shapes, colours and movements to be detected, which is useful for prey detection. These retina  
428 layers may therefore play an important role in prey capture. We can speculate that cannibals had better  
429 visual abilities with high detection accuracy. Fish have retinas that keep growing after embryogenesis  
430 (Lyall, 1957 ; Fernald, 1989), so the retinal layers increase in size continuously throughout  
431 development. The inner nuclear layer has the cell bodies of Müller cells (Mack et al., 1998), which are  
432 able to undergo a change and multiply in order to maintain glial functions and improve visual  
433 performance in growing fish (Mack et al., 1998). When larvae grow up, the density of Müller cells  
434 decreases but their total number increases compensating the thickening of the inner nuclear layer to  
435 keep visual performance at its maximum (Mack et al., 1998). It seems that in pikeperch larval  
436 cannibals this compensation was maximal allowing for better vision. Piscivory feeding habits  
437 (including cannibalism) require more refined detection and sensory-motor abilities compared to  
438 planktivory and microzooplankton feeding habits (Smith and Reay, 1991; Margulies, 1997). In  
439 pikeperch cannibals the ontogeny of the visual system appeared to be more advanced, which may have  
440 contributed significantly to a rapid improvement in their predatory abilities and the development of  
441 early piscivory, and thus to cannibalism. In order to complete the present study, it could also be  
442 interesting to look at differences in the development of the digestive systems of cannibal and potential  
443 non-cannibal fish to assess their abilities to digest fish prey.

444

## 445 **5. Conclusion**

446 Under the present experimental conditions there were no behavioural differences between cannibal  
447 and potential non-cannibal fish that could explain asynchrony in the onset of piscivory in pikeperch.  
448 Furthermore, no external morphological differences were found between the two groups. However, we  
449 did observe anatomical differences in the development of the eyes with two thicker retinal layers  
450 (ganglion cell layer and inner nuclear layer) in cannibals, which are involved in the collection of  
451 information by photoreceptors and allow the shapes, colours and movements of objects to be detected  
452 in the water column. These findings have led us to conclude that cannibalism would be driven by  
453 rearing condition-dependent individual development, with some individuals exhibiting precocious  
454 anatomical and probably physiological developments, rather than by individual personality traits  
455 governed by genetic determinism (Stamps, 2007).

456

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464

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657 **Figure captions**

658 **Figure 1:** Experimental set-up for behavioural tests. (A) Cross-maze test with an acclimatization zone  
659 (AZ) and four zones for exploration. (B) Conspecific choice test with an acclimatization zone (AZ), an  
660 entry zone (EZ), a central zone (CZ) and three zones with no (0), three (3) or six (6) conspecifics. The  
661 asterisk (\*) represents a divider that was removed after the acclimatization period.

662  
663 **Figure 2:** Landmarks collected on pikeperch larvae. 1. Tip of the premaxillary; 2. Insertion of the  
664 operculum on the profile; 3. Anterior insertion of anal fin; 4. Posterior insertion of anal fin; 5,7.  
665 Insertion of caudal fin; 6. Posterior extremity of the lateral line; 8. Posterior insertion of second dorsal  
666 fin; 9. Anterior insertion of second dorsal fin; 10. Posterior insertion of first dorsal fin; 11. Anterior  
667 insertion of first dorsal fin; 12. Insertion of the operculum on the profile; 13, 14, 15. Posterior  
668 extremity, anterior extremity and centre of eye.

669  
670 **Figure 3:** Frontal histological sections of retina and muscles. (A) Retina: Lens (L), Ganglion Cell  
671 Layer (GCL), Inner Plexiform Layer (IPL), Inner Nuclear Layer (INL), Outer Plexiform Layer (OPL),  
672 Outer Nuclear Layer (ONL), Photoreceptor Layer (P) and Pigmentary Epithelium (PE). (B) Muscles.  
673 The black squares represent the focus and expansion carried out to count and measure muscle fibres.  
674 (C-D) Expansions of parts of muscles. The yellow asterisks (\*) represent small fibres and the yellow  
675 arrows represent large fibres.

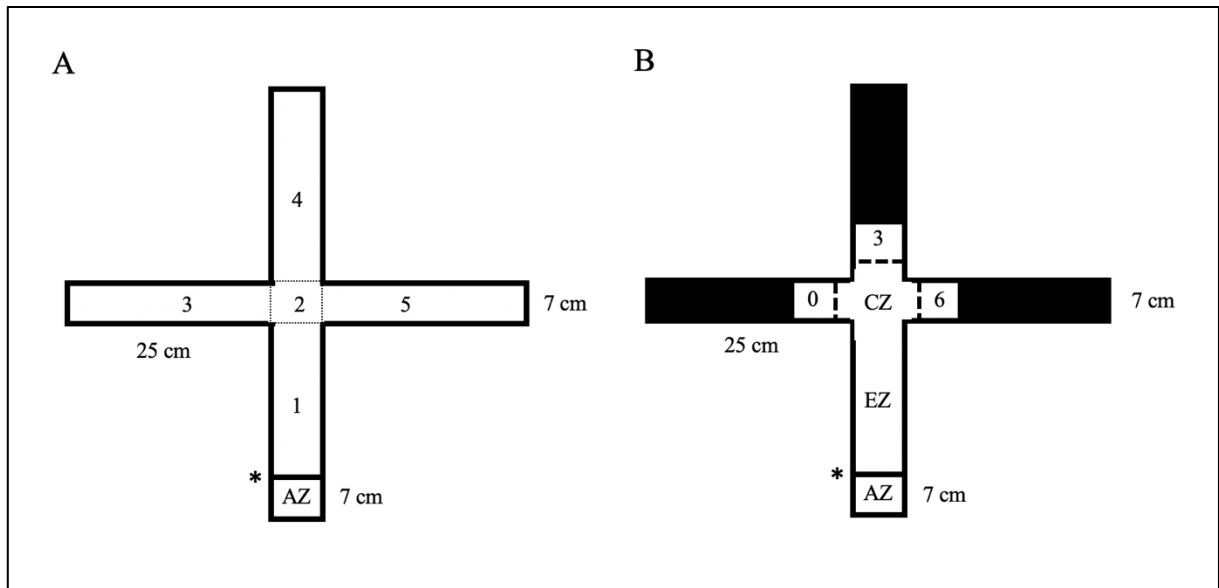
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677 **Figure 4:** (A) PCA conducted with seven behavioural variables of the two tests (cross-maze and  
678 conspecific choice tests). For the cross-maze test: Swimming activity (E\_A), Latency to emerge from  
679 the acclimatization zone (E\_LS), Total number of visited zones (E\_NVZ); for the conspecific choice  
680 test: Latency to emerge from the acclimatization zone (S\_LS), Time spent near the zone without  
681 congeners (S\_Z0), Time spent near three congeners (S\_Z3), Time spent near six congeners (S\_Z6).  
682 (B) Projection of individuals of each group: cannibal and potential non-cannibal fish as a function of  
683 PCA variables. The white dots represent cannibal fish and the black dots potential non-cannibal fish.

684

685 **Figure 5:** Results of the geometric morphological analysis of cannibal and potential non-cannibal  
686 pikeperch considering the set of 13 landmarks (LM). (A) Percentage variance explained by various  
687 principal components (PC) obtained by the principal component analysis (PCA). PC1 and PC2  
688 explained 38.1% and 22.8% of the phenotypic variability, respectively. (B) Bivariate plot of the PCA  
689 scores obtained from cannibal (blue dots) and potential non-cannibal (red dots) fish on the  
690 morphospace depicted by PC1 and PC2; barycentre and 95% ellipses are shown for both fish groups.  
691 (C) Thin-plate spline deformation grid of fish body shape to compare cannibal with potential non-  
692 cannibal fish.  
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694 **Figure 1. Colchen et al.**

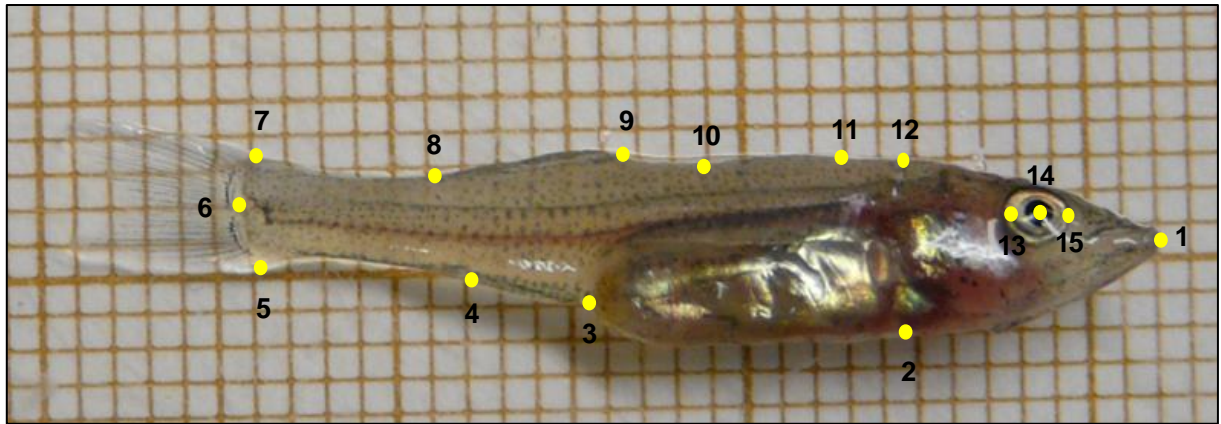
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698 **Figure 2. Colchen et al.**

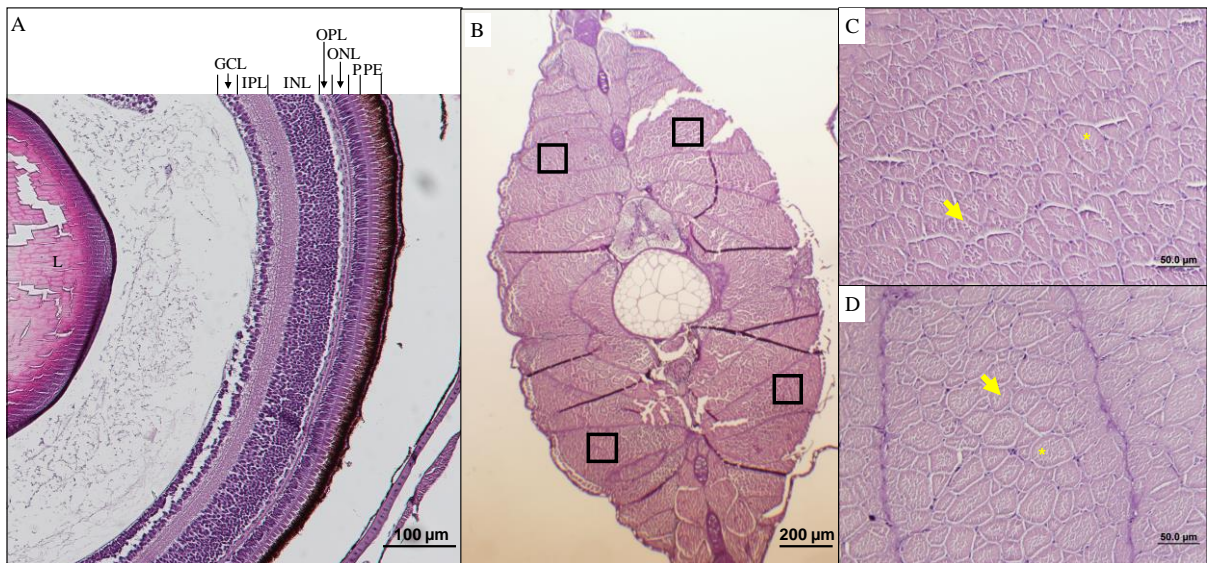
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702 **Figure 3. Colchen et al.**

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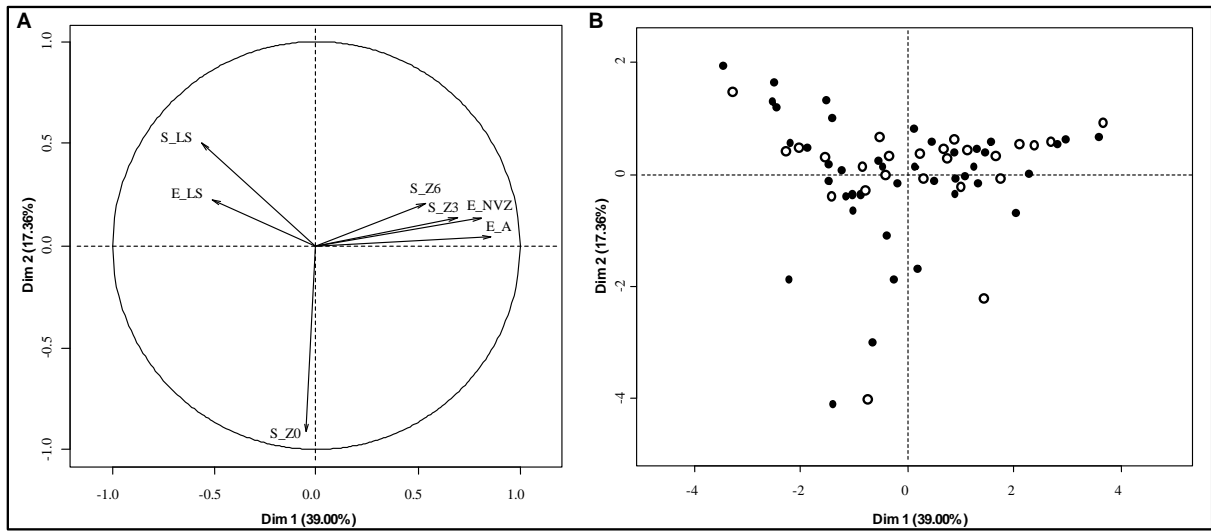
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706 **Figure 4. Colchen et al.**

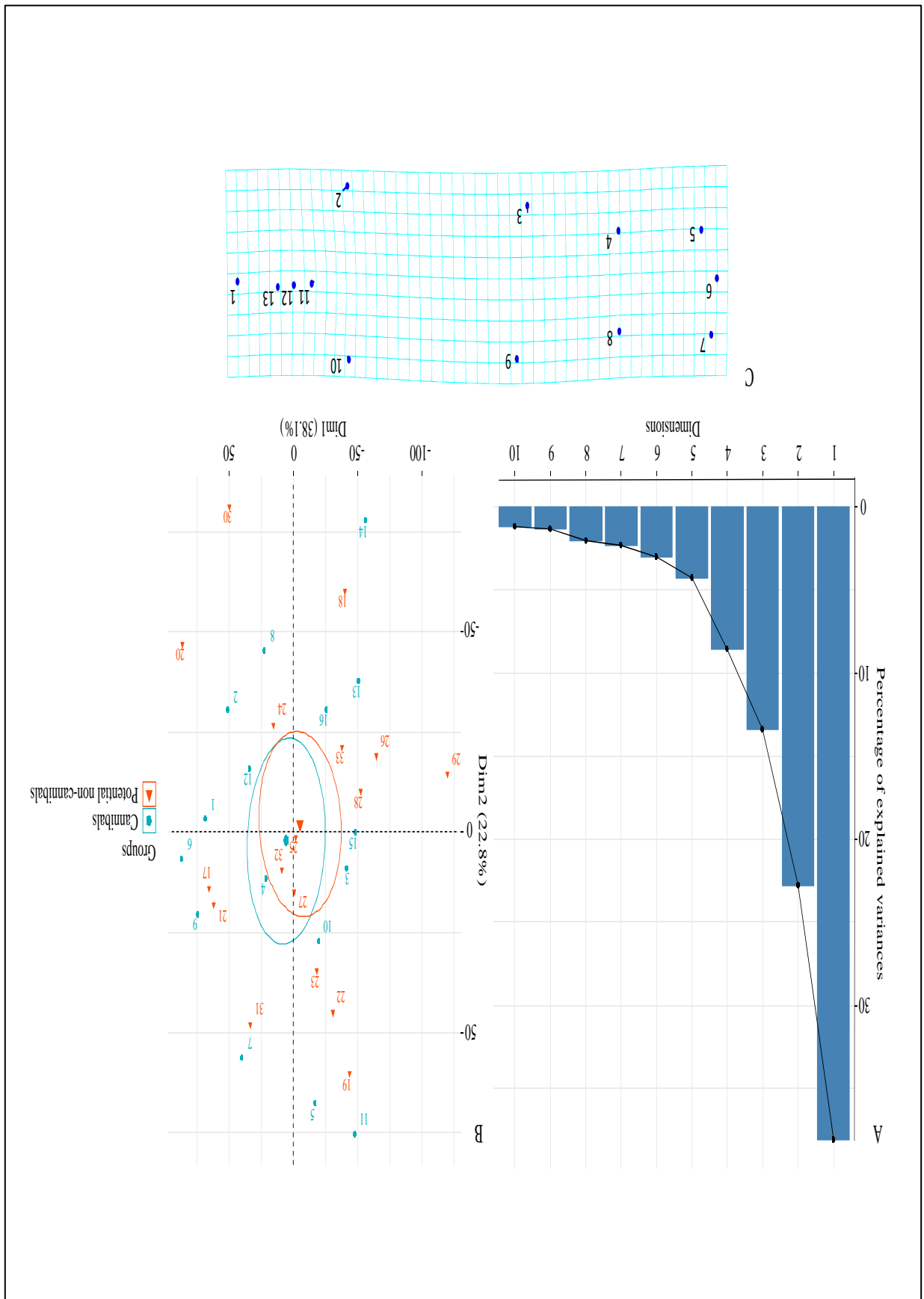
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713 **Table 1:** Mean ( $\pm$  SD) of the variables of interest measured in cross-maze and conspecific  
714 choice tests for cannibal and control fish; inter-individual variation is represented by the  
715 coefficient of variation (CV).

716

Behavioural test	Variables	Cannibal fish		Potential non-cannibal fish	
		Mean $\pm$ SD	CV (%)	Mean $\pm$ SD	CV (%)
Cross-maze test	Swimming activity (E_A)	171.7 $\pm$ 110.3	64.2	137.5 $\pm$ 111.9	81.3
	Latency to emerge from the acclimatization zone (E_LS)	237.3 $\pm$ 346.1	145.9	182.0 $\pm$ 335.5	184.3
	Total number of visited zones (E_NVZ)	68.8 $\pm$ 74.9	108.9	52.1 $\pm$ 65.4	125.4
Conspecific choice test	Latency to emerge from the acclimatization zone (S_LS)	159.0 $\pm$ 233.1	146.6	251.6 $\pm$ 395.1	157.0
	Time spent near zone without congener (S_Z0)	124.6 $\pm$ 271.0	217.4	152.4 $\pm$ 271.4	178.1
	Time spent near three congeners (S_Z3)	126.4 $\pm$ 134.0	106.0	130.8 $\pm$ 177.0	135.3
	Time spent near six congeners (S_Z6)	257.7 $\pm$ 267.4	103.8	176.0 $\pm$ 229.6	130.4

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720 **Table 2:** Correlations (Spearman correlations) between behavioural variables in both tests:  
721 cross-maze and conspecific choice tests for cannibal and potential non-cannibal fish. For  
722 exploration and boldness, three variables were analysed: the individual latency to emerge  
723 from the acclimatization zone (E\_LS) (in seconds), the total number of visited zones  
724 (E\_NVZ) and swimming activity (E\_SA) (in seconds). For sociability test, four variables  
725 were analysed: the latency to emerge from the acclimatization zone (S\_LS) (in seconds) and  
726 the time spent close (less than one centimetre of the divider) to the groups of 0 (S\_Z0), three  
727 (S\_Z3) or six conspecifics (S\_Z6).

Variables	E_A	E_LS	E_NVZ	S_LS	S_Z0	S_Z3	S_Z6
	Cannibal fish						
<b>E_A</b>	/	S=3151.4; p=0.3; rho=-0.21	S=259.3; <b>p&lt;0.0001</b> ; rho=0.90	S=3339.3; p=0.1; rho=-0.28	S=1808.3; p=0.14; rho=0.30	S=1237.2; <b>p=0.007</b> ; rho=0.52	S=1688.3; p=0.08; rho=0.35
<b>E_LS</b>	S=12058; p=0.88; rho=0.02	/	S=3337.5; p=0.16; rho=-0.28	S=2862.9; p=0.63; rho=-0.10	S=2656; p=0.92; rho=-0.02	S=2842.7; p=0.66; rho=-0.09	S=2500.9; p=0.85; rho=0.04
<b>E_NVZ</b>	S=2826.5; <b>p&lt;0.0001</b> ; rho=0.77	S=13181; p=0.66; rho=-0.07	/	S=3094.7; p=0.36; rho=-0.19	S=1874.3; p=0.18; rho=0.28	S=1359.6; <b>p=0.01</b> ; rho=0.48	S=1816.1; p=0.14; rho=0.30
<b>S_LS</b>	S=13205; p=0.66; rho=-0.07	S=9915.2; p=0.21; rho=0.19	S=12388; p=0.98; rho=-0.004	/	S=3174.3; p=0.28; rho=-0.22	S=2984.6; p=0.48; rho=-0.15	S=3855.1; <b>p=0.01</b> ; rho=-0.48
<b>S_Z0</b>	S=8626.2; <b>p=0.05</b> ; rho=0.30	S=12744; p=0.84; rho=-0.03	S=9003.5; p=0.08; rho=0.27	S=17760; <b>p=0.004</b> ; rho=-0.43	/	S=1959.5; p=0.23; rho=0.25	S=2439.7; p=0.77; rho=0.06
<b>S_Z3</b>	S=6702.6; <b>p=0.002</b> ; rho=0.46	S=15232; p=0.13; rho=-0.23	S=6575.4; <b>p=0.002</b> ; rho=0.47	S=16360; <b>p=0.03</b> ; rho=-0.32	S=9539.1; p=0.15; rho=0.23	/	S=983.2; <b>p=0.0009</b> ; rho=0.62
<b>S_Z6</b>	S=7090.2; <b>p=0.005</b> ; rho=0.42	S=12789; p=0.81; rho=-0.04	S=7750.3; <b>p=0.01</b> ; rho=0.37	S=16526; <b>p=0.02</b> ; rho=-0.33	S=9303.6; p=0.12; rho=0.24	S=5294.6; p<0.0001; rho=0.57	/
	Potential non-cannibal fish						

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730 **Table 3:** Means  $\pm$  SD of different layers of retina (Ganglion Cell Layer (GCL), Inner  
731 Plexiform Layer (IPL), Inner Nuclear Layer (INL), Outer Plexiform Layer (OPL), Outer  
732 Nuclear Layer (ONL), Photoreceptors Layer (P) and Pigmentary Epithelium (PE)) and  
733 numbers and diameters of muscles measured on histological cuts for cannibal and control fish  
734 and statistical results of comparison between both groups.

735

Variables		Cannibal fish (Mean $\pm$ SD)	Potential non- cannibal fish (Mean $\pm$ SD)	F	p
Retina	Thickness of GCL ( $\mu\text{m}$ )	35.69 $\pm$ 15.24	24.60 $\pm$ 6.51	3.90	<b>0.05</b>
	Thickness of IPL ( $\mu\text{m}$ )	48.61 $\pm$ 16.40	53.46 $\pm$ 20.27	0.49	0.49
	Thickness of INL ( $\mu\text{m}$ )	61.90 $\pm$ 23.05	45.44 $\pm$ 9.43	4.98	<b>0.03</b>
	Thickness of OPL ( $\mu\text{m}$ )	15.59 $\pm$ 10.91	17.54 $\pm$ 7.42	0.27	0.61
	Thickness of ONL ( $\mu\text{m}$ )	24.02 $\pm$ 11.73	23.21 $\pm$ 5.39	0.04	0.83
	Thickness of P ( $\mu\text{m}$ )	21.78 $\pm$ 13.96	21.49 $\pm$ 7.65	0.004	0.95
	Thickness of PE ( $\mu\text{m}$ )	36.84 $\pm$ 23.17	43.31 $\pm$ 15.44	0.72	0.40
Muscles	Number of large fibres	27.62 $\pm$ 7.19	25.58 $\pm$ 6.27	0.74	0.40
	Number of small fibres	22.28 $\pm$ 9.69	29.00 $\pm$ 10.78	2.64	0.12
	Maximal diameter of fibres ( $\mu\text{m}$ )	35.84 $\pm$ 6.31	34.95 $\pm$ 5.76	0.33	0.57
	Minimal diameter of fibres ( $\mu\text{m}$ )	24.46 $\pm$ 4.75	23.53 $\pm$ 5.82	0.76	0.39

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