Larval pikeperch Sander lucioperca cannibals are more efficient predators on zebrafish Danio rerio than non-cannibals

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Highlights

- Cannibalism is an intra-specific predation resulting in massive mortality in fish
- Pikeperch is a predatory freshwater fish with precocious onset of piscivory
- Predatory behavioral sequence is more efficient in cannibals than in non-cannibals
- The shift to piscivory involved a change from a S-shape to an attack without S-shape
- Cannibalism is linked to the onset of an efficient piscivory behaviour

Abstract

Cannibalism is an intra-specific predation often resulting in massive mortality in intensive cultured fish species. In piscivorous species, the onset of predation is inevitable. This study explored the link between predation abilities and the onset of cannibalism in pikeperch larvae, a top predator species, with a potential for the European inland aquaculture. Cannibals and non-cannibals, aged between 17 to 34 days-post-hatching, were tested to compare their predatory behavior using zebrafish and pikeperch larvae as prey. Each tested fish was confronted with three other fish (pikeperch or zebrafish) (n = 204 tests) in an arena (20 x 7 x 4 cm with 2 cm of water height, 280 mL) and their behavior was recorded for 20 minutes. The normal predatory behavioral sequence (orientation, approach, attack and capture) was much more efficient in cannibals (calculated as the ratio of number of captures on the number of attacks) than in non-cannibals in both the predation (0.31 ± 0.28 *vs.* 0.05 ± 0.15; $p_{adjust} < 0.0001$) and the cannibalism (0.21 ± 0.29 *vs.* 0.02 ± 0.08; $p_{adjust} = 0.0006$) tests. The shift to a piscivorous diet involved a modification of the attack tactic, replacing a "S-shape" by an attack without "S-shape" but with a tail propulsion. This second tactic developed earlier in cannibals whereas non-cannibals are only able to perform the "S-shape" attack used during the first days of life. Cannibalism was linked to the onset of an efficient piscivory behavior.

Keywords: piscivory, intra-specific predation, behavior, freshwater carnivorous fish.

1. Introduction

Pikeperch *Sander lucioperca* has high potential for inland aquaculture diversification in Europe (Lappalainen et al., 2003; Wang et al., 2009; Policar et al., 2019). The reproduction control (Kucharczyk et al., 2007) and the bio-economic feasibility of its intensive rearing are established (Steenfeldt and Lund, 2008; Steenfeldt et al., 2015). Its demand has been strengthened by the strong decline of wild catches from approximately 50.000 tons in 1950 to 20.000 tons in 2020 (FAO, 2021). Currently, in Europe, the number of pikeperch farms has increased and the production is estimated to 1000-1500 tons per year. Intracohort cannibalism is one of the major bottleneck for the inland aquaculture of piscivorous percid species particularly during the larval stages of pikeperch (Steenfeldt, 2015), walleye *Sander vitreus* (Cuff, 1980) and perch *Perca fluviatilis* (Kestemont et al., 2003). For pikeperch, cannibalistic predation can start a few days after hatching (between 14 and 17 dph) and between individuals of similar size (9.3 ± 1.0 mm; Colchen et al., 2019). In pikeperch larvae, cannibalism could induce up to 53 % at 37 days post-hatching (dph) of mortality in farm (density: 17 larvae.L^{-1}, temperature: 18°C, feeding regime: 3 *Artemia* nauplii.mL^{-1}; Steenfeldt et al., 2011). Cannibalism started as early as 14 dph (9.3 ± 1.0 mm total length (TL)) and was always observed after 80 dph (Colchen et al., 2019).

Pikeperch is a predatory freshwater fish, which become piscivorous during its development. Predation includes all behavioral items required to find, catch, kill and ingest prey (Curio, 2012). Over time, a predator improves its searching tactics, visual and olfactory prey recognition and attack strategies; conversely prey improve camouflage and avoidance abilities. From an energetical perspective, predation has often been associated with the optimal foraging theory (MacArthur and Pianka, 1966; Krebs and Davies, 2009). Considering that cannibalism is an intra-specific predation (Polis, 1981), the transition between predator

and cannibal status could be viewed as a shift between a more generalist to a specialist predator, and it should depend on biotic conditions as prey presence or density. When prey are lacking or scarce, predator would target conspecifics as prey substitute. Among pikeperch, predatory behavior increases progressively during ontogeny (Colchen et al. 2020a). The transition from embryonic stage to larval stage is characterized by the start of exogeneous feeding (5.87 ± 0.77 mm TL; Ott et al., 2012), during which pikeperch feed first on zooplankton with a typical predatory behavior called “S-shape” attack marked by a stop of the fish and the formation of a “S” with his body before the propulsion towards prey (Colchen et al., 2019; Houde, 2001). After that, pikeperch larvae progressively become piscivorous developing an attack without “S-shape”. In this sequence, pikeperch move slowly towards the prey and attack it with a fast tail movement projecting it rapidly forwards (Turesson et al., 2002). Piscivorous behavior in a pikeperch population, can appears very early for some individuals (11.0 ± 1.3 mm TL, 21 dph; Colchen et al., 2020a). It is exhibited by all individuals four months post-hatching (70-80 mm; Persson and Brönmark, 2008). This suggests that the precocious piscivores could become cannibals under farming conditions because they have no other fish prey in their environment except their conspecifics.

In nature, pikeperch is an active predator during low light intensity (dawn and dusk; Dörner et al., 2007) with a perfect visual acuity (Ali et al., 1977; Colchen et al., 2020b). The transition to a piscivorous diet is governed by both anatomical modifications and the availability of prey (Buijse and Houthuijzen, 1992; Claessen et al., 2002; Ribeiro et al., 2021). Adult pikeperch prefer smaller prey than their body size (predator-prey length ratio: 0.23 on average; Dörner et al., 2007) due to their anatomical (large gape) and digestive (presence of enzymes) abilities. This prey/predator size ratio is the “predation window”, which could

fluctuate with available prey (Claessen et al., 2002) and, thus, impact the shift to the piscivorous diet.

The main objective of this study was to test the possible link between cannibalism on pikeperch and the onset of piscivorous behavior on a non-conspecific species, zebrafish *Danio rerio,* known to display escape behavior and has a reactive distance for avoiding perciform predators (Dill, 1974a; b). We hypothesized that a non-cannibal at a given time is not able to display an efficient piscivorous behavior. This statement assumes that to be cannibal, pikeperch larvae needs to be able to realize a full behavioral sequence to capture a fish prey (describe in Colchen et al., 2019). We hypothesize that in larval and juvenile captive populations of pikeperch, cannibalism could be based on the presence of early piscivorous fish. As pikeperch is a strictly piscivorous fish, in a single-species farm conditions the onset of piscivory means the onset of cannibalism, and consequently suggests that cannibalism is unavoidable.

2. Materials and Methods

2.1. Ethical note

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

2.2. Origin and larval rearing conditions

Eggs of pikeperch came from two mature females fertilized by one male in a fish farm (SARL Asialor, Pierrevillers, Moselle, France). After hatching (1st March, 2017), larvae were reared at the Aquaculture Experimental Platform (AEP, registration number for animal experimentation C54-547-18) belonging to the URAFPA lab located at the Faculty of Sciences and Technologies of the University of Lorraine (Nancy-France) in a Recirculating Aquatic System (RAS). They were reared until 14 dph in 700L tanks. Artificial lighting (50 lx at the water surface) followed a 12L/12D cycle with light on from 08.00 am to 8.00 pm with 30 min simulation of dawn and dusk. The water was maintained at 16°C during the first two days and increased by 1°C per day until reaching 20°C. At 14 dph, larvae were transferred from 700L tanks to four 300L independent incubators at 20.0°C ± 0.0°C each containing nine enclosures (38 cm x 7 cm x 11 cm of deep each enclosure with 2.5 L of water). Three enclosures per incubators contained 100 pikeperch larvae for cannibalism observations and the six other ones contained cages (four cages per enclosure) for cannibals and non-cannibals larval rearing. Each incubator was a recirculating water system (110 x 64 x 186 cm) with a flow rate of 4 $m^3.h^{-1}$ and water was UV sterilized (for more information about the experimental facilities, see Réalis-Doyelle et al., 2016; 2022). Incubators were cleaned every morning. Water parameters (mean ± standard deviation, SD) were measured once a week: dissolved oxygen (8.28 $\pm$ 0.98 $mg.L^{-1}$); pH (7.83 $\pm$ 0.05); ammonia (NH_4^+, 0 $mg.L^{-1}$); nitrite ($NO2^-$, 0.32 $\pm$ 0.14 $mg.L^{-1}$). Larvae were fed live prey and commercial inert feed seven times per day as follows: *Artemia* nauplii (550-600 μm, Catvis, Hertogenbosch, Pays-Bas) from 4 to 18 dph, then, Larviva PROWEAN 100, 300, 500, 700 μm (BioMar®, France) until 35 dph and INICIOplus 0.8 mm (BioMar®, France) after 35 dph.

2.3. Selection of cannibals and non-cannibals

For this experiment, predatory behaviors of cannibals were compared to those of non-cannibals. To obtain cannibals, larvae were reared in three enclosures located in each incubator and were identified during observation sessions from above view by focal sampling of five minutes each hour during the light period (a density of 100 larvae per enclosure was used). Cannibals were identified by the presence of a prey in its mouth. If cannibalism was observed, the cannibal, which tends to swim at the surface of the tank with the prey in its mouth, was captured and transferred with a fine mesh dip net into an individual cage (9 cm diameter x 10 cm of height, with 7 cm of water depth and 0.45 L of water) set up in the other six enclosures of each incubator. To obtain non-cannibals, other pikeperch larvae were reared in a cage (9 cm diameter x 10 cm of height, with 7 cm of water depth and 0.45 L of water) in groups of four individuals, and mortality was observed every day for 17 days. If all four larvae were alive the day of the test, they were all considered as non-cannibal for the test. As a total, 96 cages with four larvae were used at the beginning of the experiment to obtain non-cannibals.

We obtained 59 cannibals and 59 non-cannibals aged of 17 to 34 dph (between L5 and L6 stages; Ott et al., 2012). Two cannibals died during the isolation period, one cannibal and one non-cannibal died between the two tests and four videos could technically not be used. Consequently, eight pairs of cannibals and non-cannibals were deleted from the analysis. In total, behaviors of 51 cannibals (mean of TL ± SD: 19.4 ± 4.7 mm) and 51 non-cannibals (mean of TL ± SD: 17.1 ± 2.6 mm) were analyzed. Total length was significantly different between cannibals and non-cannibals ($U = 1647$; $p = 0.006$). The behavioral tests started when the first case of cannibalism was observed.

2.4. Behavioral tests

Two behavioral tests were conducted: a predation test and a cannibalism test. For each trial, one cannibal and one non-cannibal of the same age were each isolated in a cage and not fed during a 24-hour period before the test, then introduced into two rectangular arenas (20 x 7 x 4 cm with 2 cm of water height, 280 mL): one arena for cannibal and one arena for non-cannibal. These arenas were identical and both divided in two equal zones by an opaque removable divider. Cannibal and non-cannibal were introduced, respectively, in the first zone of each rectangular arena and acclimatized for 30 minutes. The type of test depended of individuals introduced in the second zone at the same time of tested larvae.

For predation test, three non-conspecific prey (zebrafish larvae, mean of TL ± SD: 4.0 ± 0.8 mm) were introduced in the second zone of each arena and let for the same acclimatization period than tested larvae. After 30 minutes, the divider of each arena was removed allowing the tested larva (cannibal or non-cannibal) and the three zebrafish of each arena to explore it. For cannibalism test, three conspecifics, which were non-cannibals, (pikeperch larvae, mean of TL ± SD: 14.3 ± 2.3 mm) were introduced in the second zone of each rectangular arena and acclimatized for 30 minutes. After 30 minutes, the divider of each arena was removed allowing the tested larva (cannibal or non-cannibal) and the three conspecifics of each arena to explore it.

For each tested larva, the test order was randomized. After the first test (predation or cannibalism test), pikeperch, cannibal and non-cannibal, were put back in their own cage and the second test (predation or cannibalism in function of the first conducted test) was conducted 24 hours later. The fish behaviors were video recorded with two camcorders (Sony, Handycam, DCR-SR72E) positioned 80 cm above each arena for 20 minutes. The acclimatization period was not considered. For each test, measured parameters concerning the predator or the cannibal were: the number of orientations, approaches, attacks (with “S-

shape" and without "S-shape"), pursuits and captures (for the definitions see **Table 1**). The cannibal or non-cannibal performance was calculated as follows: number of captures/number of attacks.

2.5. Statistical analyses

The total length of larvae of each group was statistically compared with a Mann-Whitney U-test, and the influence of the test order (cannibalism test then predation test and vice versa) was tested on all behavioral parameters by Generalized Linear Model, (package 'glmmADMB'; Zuur et al., 2009).

Data did not fit with normality (Shapiro-Wild test, shapiro.test (R Core Team, 2017)) and variance homogeneity (leveneTest package "car" (Fox and Weisberg, 2016)) for behavioral parameters: the number of orientations, approaches, attacks with "S-shape" or without "S-shape", captures, pursuits and performance. Comparisons of behavioral responses between cannibals and non-cannibals were analyzed with Mann-Whitney U-test for independent data and comparisons between the cannibalism and predation test were analyzed with Wilcoxon test for dependent data. To compare the number of attacks with "S-shape" with attacks without "S-shape", a model based on rank transformation was used with a tested interaction Tests*Types where 'Tests' corresponding to cannibalism and predation tests and 'Types' corresponding to attacks with or without the "S-shape" behavior (packages "ordinal" (Christensen, 2015) and "ART" (Villacorta, 2015)). When a significant interaction was found, a pairwise comparison using Tukey-Kramer-Nemenyi with Tukey-Dist approximation was performed (package "PMCMRplus" (Pohlert, 2022)). All statistical analyses were performed using the free software Rstudio (version 2021.09.2). Results were presented by mean ± SD. The level of significance used in all tests was $p_{adjust} < 0.05$.

3. Results

3.1. Comparisons between cannibals and non-cannibals

First of all, behavioral responses were independent of the test sequence (**Table 2**).

In the predation test on zebrafish, behaviors differed significantly between cannibals and non-cannibals. Cannibals compared to non-cannibals displayed fewer orientations (14 ± 11 *vs.* 30 ± 20; W = 640; $p_{adjust} < 0.0001$; **Fig. 1A; Table 3**), less approaches (9 ± 7 *vs.* 17 ± 12; W = 704; $p_{adjust} = 0.0002$; **Fig. 1B; Table 3**), less attacks (9 ± 8 *vs.* 19 ± 15; W = 758; $p_{adjust} = 0.0008$; **Fig. 1C; Table 3**), but they caught more zebrafish (2 ± 1 *vs.* 0 ± 1; W = 2004; $p_{adjust} < 0.0001$; **Fig. 1D; Table 3**). There was no difference for the number of pursuits between cannibals and non-cannibals (W = 1027; $p_{adjust} = 0.1$; **Fig.1E; Table 3**). Cannibals were significantly more efficient than non-cannibals (0.31 ± 0.28 *vs.* 0.05 ± 0.15; W = 1872; $p_{adjust} < 0.0001$; **Fig. 1F; Table 3**).

In the cannibalism test, the number of approaches (23 ± 21 *vs.* 17 ± 21; W = 1622; $p_{adjust} = 0.03$; **Fig. 1B**), attacks (4 ± 4 *vs.* 3 ± 6; W = 1660; $p_{adjust} = 0.01$; **Fig. 1C**), captures (1 ± 1 *vs.* 0 ± 0; W = 1683; $p_{adjust} = 0.0001$; **Fig. 1D**) and the performance (0.21 ± 0.29 *vs.* 0.02 ± 0.08; W = 700; $p_{adjust} = 0.0006$; **Fig. 1F**) were higher among cannibals than non-cannibals. Number of orientations and pursuits did not differ significantly between the two groups (W = 1602; $p_{adjust} = 0.05$; **Fig. 1A; Table 3** and W = 1418; $p_{adjust} = 0.2$; **Fig. 1E; Table 3**, respectively).

3.2. Comparisons of behavioral performances in predation and cannibalism tests

Cannibals performed more orientations and approaches to congeners in the cannibalism test than to prey in the predation test (**Table 3**). They realized also more attacks, captures and pursuits in the predation than in the cannibalism test (**Table 3**). Cannibals

exhibited better performance in the predation than in the cannibalism test (**Table 3**). Non-cannibals realized more attacks, captures and pursuits in the predation test than in the cannibalism test (**Table 3**). For non-cannibals, all others analyzed behaviors did not differ (**Table 3**).

Cannibals displayed more attacks with "S-shape" in the predation test (mean ± SD: 6 ± 6) than in cannibalism test (mean ± SD: 2 ± 3; W = 120; $p_{adjust} < 0.0001$) and also more attacks without "S-shape" in predation test (mean ± SD: 3 ± 5) than in the cannibalism test (mean ± SD: 2 ± 2; W = 178; $p_{adjust} = 0.002$). Non-cannibals displayed more attacks with "S-shape" in the predation test (mean ± SD: 12 ± 9) than in the cannibalism test (mean ± SD: 2 ± 6; W = 57.6; $p_{adjust} < 0.0001$) and also more attacks without "S-shape" in the predation test (mean ± SD: 7 ± 10) than in the cannibalism test (mean ± SD: 1 ± 2; W = 56; $p_{adjust} < 0.0001$).

3.3. Comparisons between both types of attacks in each test for cannibals and non-cannibals

For cannibals in the cannibalism test, there was no difference between the number of attacks with "S-shape" and without "S-shape" (q = 2.1; $p_{adjust} = 0.12$; **Fig. 2A**). However, in the predation test they significantly displayed more attacks with "S-shape" than without (q = 4.5; $p_{adjust} = 0.001$; **Fig. 2A**). Non-cannibals displayed significantly more attacks than cannibals using "S-shape" in the two tests (cannibalism test: q = 3.4; $p_{adjust} = 0.02$; predation test: q = 4.8; $p_{adjust} = 0.0007$; **Fig. 2B**).

4. Discussion

This study highlights a direct link between the onset of piscivory and cannibalism in pikeperch larvae. Cannibals capture both prey and conspecifics with higher performance

whereas non-cannibals catch little prey with lower efficiency and no conspecifics (**Fig. 1**). Cannibals were better predators in the predation test than in the cannibalism test (**Table 3**). Overall, cannibals were better predators than non-cannibals whatever the prey tested, developing predatory behavioral items for piscivory before their conspecifics. These results contribute to the understanding of cannibalism, a major bottleneck for rearing of pikeperch, a commercially important species.

The foraging bouts of piscivorous fish correspond to a similar sequence across species: prey search, recognition and localization (defined by orientation and approach in the present study), attack, capture and ingestion (Holling, 1965; Endler, 1991). The present study demonstrates this sequence in pikeperch larvae, which is known to be a prerequisite for predator and particularly for fish larvae (e.g. common carp *Cyprinus carpio* and Northern pike *Esox Lucius* (Drost, 1987)). Behaviors implied in this behavioral sequence were few studied in a piscivory context (Howick and O'Brien, 1983; Turesson and Brönmark, 2004). In our study, we showed that non-cannibals did not fully control the behavioral sequence for fish capture contrary to cannibals of the same age. They displayed lot of orientations and approaches without attacking or when they attacked, they do not succeed to capture potential fish prey. Non-cannibal larvae were still in a learning process, particularly the acquisition of a good attack behavior. Such an optimal attack distance to succeed a capture was already demonstrated in chain pickerel *Esox niger* (Rand and Lauder, 1981) and pikeperch (Colchen et al., 2020a). This estimation of the best attack distance, correlated with fish age and development, is not an innate process and predators try several times to attack a prey before being able to control it (Colchen et al., 2020a).

Piscivorous fishes develop different tactics for capturing prey, such as ambushing, stalking and chasing (Takeuchi, 2009), in parallel with morphological traits, such as oral jaw

283 teeth, which are crucial for both capture and handling prey in 12 fish species (Muruga et al.,
284 2022). These diverse predator tactics could be related to the wide range of behavioral
285 adaptations for avoiding capture, among which escape behavior in roach *Rutilus rutilus*
286 (Ranåker et al., 2012), freezing in glow light tetras *Hemigrammus erythrozonus* (Brown and
287 Dreier, 2002) or attacks to the predator as mobbing in French grunt *Haemulon flavolineatum*
288 (Hein, 1996). In our tests, zebrafish and pikeperch larvae have different abilities to defend
289 themselves against a predator. Zebrafish use the escape behavior and their reactive distance
290 for avoiding largemouth bass *Micropterus salmoides*, a real predator, and artificial predators
291 (model predator and a film of an approaching object) depends on both the size and velocity
292 of the predator and not on the distance from the predator or the predator itself (Dill, 1974a;
293 b). Here, pikeperch larvae used as prey were between L5 and L6 stages, with spiny rays on
294 dorsal fins, and a complete development of fins and teeth (Ott et al., 2012) whereas
295 zebrafish larvae had neither developed dorsal fin nor teeth at 4 mm (Parichy et al., 2009),
296 which could partly explain the difference between predation and cannibalism tests. Piscivory
297 was not only reliant on predator selectivity, but also, how prey influence their relative
298 catchability, implying for predator modifications of their capture strategy (Mihalitsis et al.,
299 2021). For a cannibal, it is arguably riskier to attack a conspecific than a non-conspecific prey
300 with less risky structures (fin rays and body spines), such as zebrafish. Cannibals displayed lot
301 of orientations and approaches towards conspecifics, as non-cannibals in predation test
302 towards prey, before attacking. Even if the behavioral sequence to attack and capture a
303 conspecific or a non-conspecific prey seems to be similar, there are quantitative differences
304 in displayed behaviors, with more orientations, approaches and attacks in the cannibalism
305 test, showing that cannibals are probably able to identify a conspecific as potentially
306 dangerous. Consequently, it seems that cannibals choose an attack tactic with less risks

against a conspecific. To attack non-conspecific prey, cannibals used “S-shape”. However, to attack conspecific prey, they used “S-shape” but also no “S-shape” tactic. It highlights that cannibals try to shift to a better capture method but without a complete control of it. The attack with “S-shape”, imposing a pause before attack, is characteristic for some fish larvae attacking zooplankton and invertebrates and represented an important part of type of attack: 50 % in pikeperch larvae (34.6 ± 9.4 mm TL; Colchen et al., 2019; 2020a) and 31.25 % in European whitefish *Coregonus lavaretus* larvae (15.5 ± 0.3 mm TL; Mahjoub et al., 2008). In diet transition, there is a gap from zooplankton and invertebrates to fish (piscivory) feeding implying behavioral changes (Sánchez-Hernández et al., 2019) already described in pikeperch or in walleye (Persson and Brönmark, 2002; Graeb et al., 2005). When pikeperch shift to a piscivorous diet, they need to change their capture method, by switching to an attack without “S-shape” marked by a tail propulsion (appearing between 35 and 40 dph, 32.7 ± 4.2 mm TL, unpublished data), corresponding to the attack without “S-shape” (Sullivan and Atchinson, 1978). Hunting behavioral transition was mentioned in some marine fish larvae where the time spent poised in a striking posture (*i.e.* “S-shape” position) is much longer during first feeding than in later larval stages, and gradually the strike becomes integrated with swimming movements (as attack without “S-shape”) (Hunter, 1980). A poised striking posture seems to be a common tendency in young larvae and declines as larvae grow up suggesting that it could be an adaptation to low feeding success (Hunter, 1980). On one hand, the absence of difference between both types of attacks for cannibals showed that they were in progress to change their attack method (from “S-shape” to non “S-shape” tactic), due to the probably decreasing success to catch prey with the first tactic. On the other hand, by using “S-shape” behavior to attack indistinctly conspecific or non-conspecific, non-cannibals showed that they did not acquire the good attack tactic to

capture fish prey. Nevertheless, the success of capture for non-cannibals in predation test with “S-shape” attacks, even if prey were fish, could be explained by the small size of zebrafish larvae. Indeed, handling times to capture zebrafish could consider as negligible like for zooplankton (Hunter, 1980). Furthermore, there is a favorite size range of prey for predatory fishes. In function of species, maximal prey consumed size observed was between 35 and 78 % of predatory size (Persson et al., 2000; Ribeiro and Qin, 2013). It was previously suggested that 50 % of size difference could be the threshold to initiate intracohort cannibalism in Barramundi *Lates calcarifer* (Ribeiro and Qin, 2013). In pikeperch larvae, this ratio was not known to us but in the present study the ratio between prey size and predator size was 0.8 ± 0.1 for cannibals and non-cannibals in cannibalism test and 0.2 ± 0.0 in predation test. We can conclude that cannibals and non-cannibals had the same size abilities to capture congeners and zebrafish larvae. However, for larger fish prey, as conspecifics, it requires a new set of motor patterns associated with grasping prey and presence of anatomical characteristics (e.g.: teeth or mouth gape; Galarowicz and Wahl, 2005).

Therefore, under monospecific farming conditions, piscivorous feeding was reported to start very early in development of several fish species like perch (10-13 mm; Hunter, 1980; Brabrand, 1995) or walleye (30 mm; Graeb et al., 2005). The present study demonstrated that cannibalism is linked to the onset of available piscivory and not to the onset of predatory behavior that was already controlled when larvae catch zooplankton. Previously, it was demonstrated that very early in the development, pikeperch larvae could capture *Artemia* nauplii but are not able to capture fish prey (Colchen et al., 2020a). Here, we highlighted that all fish able to capture fish prey are potentially cannibals, or at least, that early piscivorous fish have a high probability to become cannibals.

5. Conclusions

To conclude, our study showed that cannibalism is linked to the onset of piscivory and to the acquisition of the behavioral sequence of predation. This statement could explain that when cannibalism is established in a pikeperch population in farming conditions, it is probably irreversible (Baras et Jobling, 2002; Steenfeldt et al., 2015). Are there solutions to avoid cannibalism in pikeperch larvae? Cannibals showed a faster development and are rapidly larger than their conspecifics. A first solution is to practice the sorting of the individuals and to eliminate the largest ones (Naumowicz et al., 2017). This method, helping to reach higher survival rates, mainly due to lower losses caused by cannibalism (Szczepkowski et al., 2011), needs to be repeated frequently (every 10 days for 0.7-8.2 g fish and afterwards at 21 days intervals (Policar et al., 2016)) because larger fish appear quickly in the population. The second method consists to eliminate the fish that exhibit a cannibalistic behavior. This method could be based on a genetic process with individual selection based on later ichthyophagy (*i.e.* Norton et al., 2011; Jensen, 2015).

In order to select fishes whose behaviors make them more suitable for aquaculture production, this study could be useful to investigate in wild and domestic strains behavioral parameters implied in cannibalism (i.e. aggressiveness; Toomey et al., 2019) to establish an early diagnosis of the cannibal potential of a population. This investigation is supported by that cannibalistic behavior was already showed as genetically-based to a great extent in hybrid catfish *Silurus meridionalis-asotus* (Yang et al., 2015) and that aggressiveness can be attributed to the combination or interaction of genotypic variation and environmental difference in sticklebacks *Gasterosteus aculeatus* (Bakker's, 1986). In pikeperch, producing a population with the lowest cannibal potential is the ultimate goal. However, there is a huge variability in behavior at the intraspecific level (Toomey et al., 2019; 2020).

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Author Contributions

All authors have given their approval to the final version of the manuscript. TC FT PF AP: conceived and designed the experiment. YL: took care of fish and lead routine maintenance of rearing facilities. TC: performed the experiments. TC: analyzed the behavioral video recordings. TC AP: analyzed the behavioral and morphological data. TC YL FT PF AP: wrote the paper.

Conflict of interest statement

The authors declare no competing interests.

621 **Figures captions**

622

623 **Figure 1**: Comparisons of the number of orientations (A), approaches (B), attacks (C),
624 captures (D), pursuits (E), and performance (F) between larval pikeperch *Sander lucioperca*
625 cannibals and non-cannibals confronted to three pikeperch larvae in cannibalism tests and
626 to three zebrafish *Danio rerio* larvae in predation tests (see definitions in Table 1). The trial
627 duration was 20 minutes after 30 minutes of acclimatization period.
628 Black lines represented median, black triangles mean and black points outliers. Different
629 letters indicated a statistical difference at $p_{adjust} < 0.05$ between cannibals and non-cannibals
630 in each test (predation and cannibalism) for each behavior.

631

632 **Figure 2**: Comparisons for larval pikeperch *Sander lucioperca* (A) cannibals and (B) non-
633 cannibals between the number of attacks with "S-shape" and without "S-shape" displayed in
634 each test (cannibalism with three pikeperch larvae and predation with three zebrafish *Danio*
635 *rerio* larvae). The trial duration was 20 minutes after 30 minutes of acclimatization period.
636 Black lines represented median, black triangles mean and black points outliers. Different
637 letters indicated a statistical difference at $p_{adjust} < 0.05$ between the two types of attacks
638 (with or without "S-shape") in each test (predation and cannibalism) for each status
639 (cannibals and non-cannibals).

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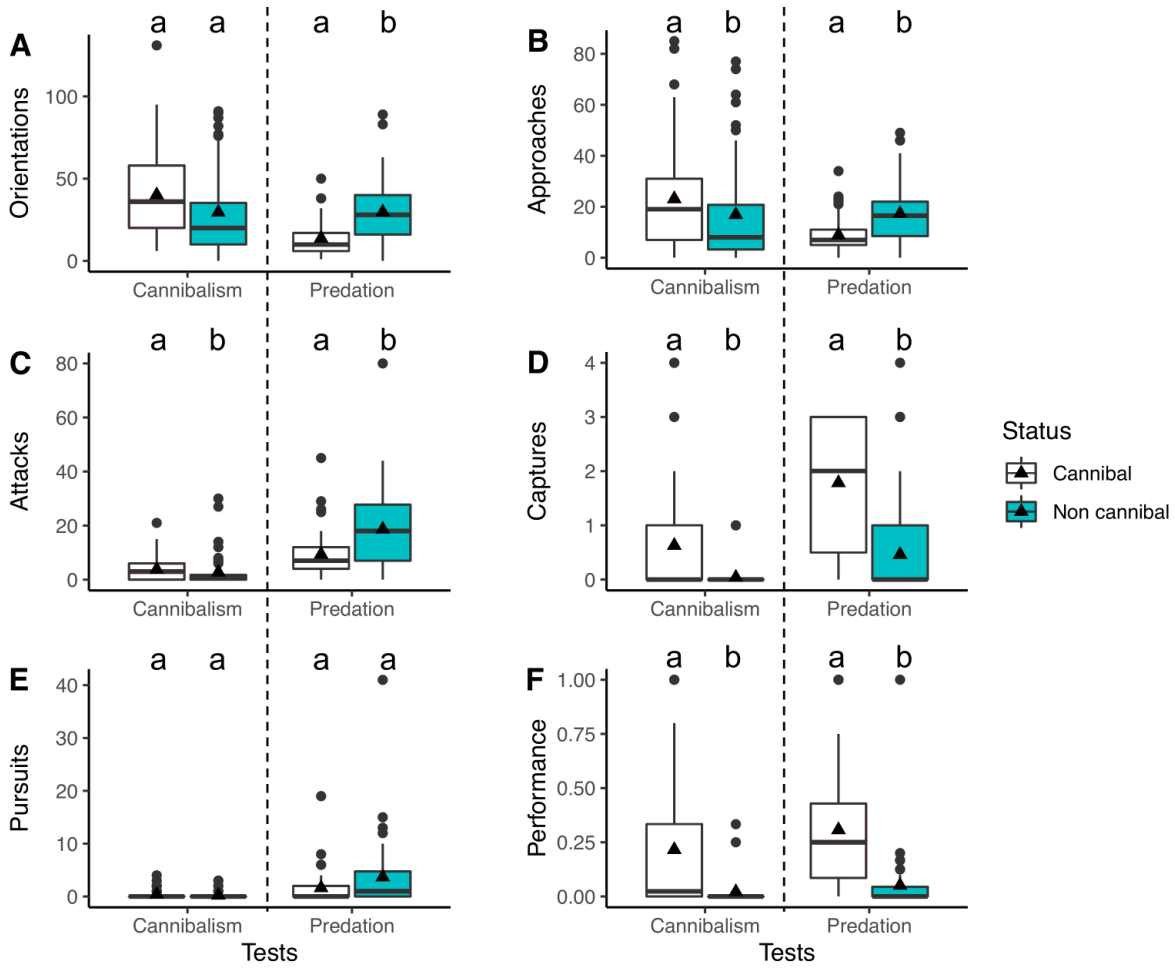
641 Figure 1.



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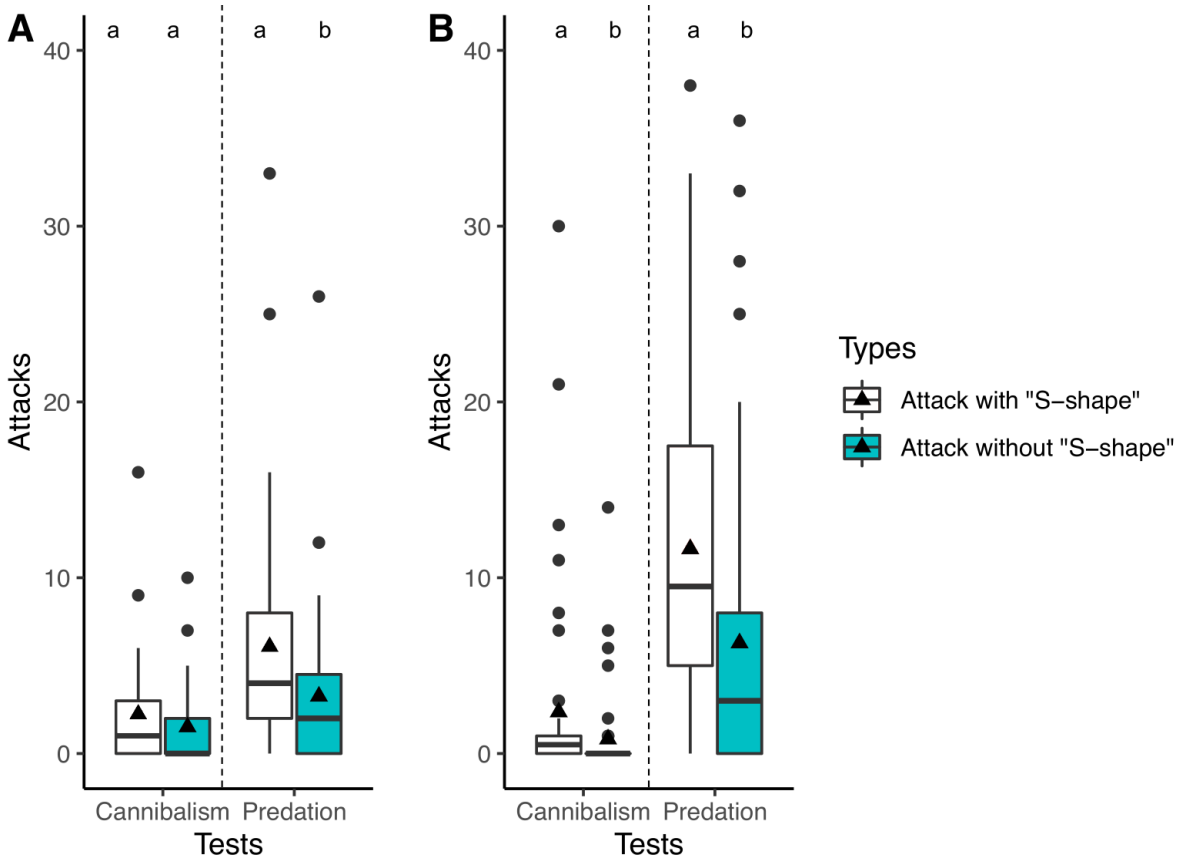
644 Figure 2.



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647 **Table 1.** Definitions of studied behaviors in pikeperch larvae.

Behaviors	Definitions
Orientation	Predator turn its head toward prey or conspecific and eye tracked it (Bell and Sih, 2007).
Approach	Predator movement toward prey or conspecific with slow swimming (Colchen et al., 2017).
Attack without "S-shape"	Predator move toward prey or conspecific and attack with a small and fast tail beat, projecting it rapidly (Sullivan and Atchinson, 1978).
Attack with "S-shape"	A fast movement of predator toward prey or conspecific, with an open mouth (Colchen et al., 2019). The attack is marked by a stop of the fish and the formation of a S-shape with his body before a fast movement (Houde, 2001).
Capture	Predator bite to catch the prey or the conspecific (Colchen et al., 2020a).
Pursuit	When capture failed, predator rapidly swim to catch up the prey or the conspecific.

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650 **Table 2.** Impact of the order and status*order on behaviors (number of orientations,
651 approaches, attacks and captures). The order corresponds to the order in which pikeperch
652 larvae were tested first cannibalism or predation) and status designs whether the individuals
653 are either cannibals or non-cannibals.

654

	Orientations	**Approaches**	**Attacks**	**Captures**
Order	χ^2 = 1.83; p = 0.18	χ^2 = 2.14; p = 0.14	χ^2 = 0.29; p = 0.59	χ^2 = 0.004; p = 0.95
Status x Order	χ^2 = 0.99; p = 0.32	χ^2 = 0.98; p = 0.32	χ^2 = 0.42; p = 0.52	χ^2 = 1.25; p = 0.26

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Table 3. Comparisons between predation and cannibalism tests for cannibals and non-cannibals for all behaviors. The trial duration was 20 minutes after 30 minutes of acclimatization period. Each behavior implied in a predation sequence (orientation, approach, attack, capture, pursuit) was represented and the performance was calculated as the number of succeed captures on the total number of attacks. W is the value of Wilcoxon test and the p-value is adjusted. All results were represented by their means and Standard Deviation (SD).

Behaviors	**Orientation**	**Approaches**	**Attacks**	**Captures**	**Pursuits**	**Performance**
Cannibals						
Mean ± SD in predation test	14 ± 11	9 ± 7	9 ± 8	2 ± 1	2 ± 3	0.31 ± 0.28
Mean ± SD in cannibalism test	40 ± 28	23 ± 21	4 ± 4	1 ± 1	0 ± 0	0.21 ± 0.29
Comparison between both tests	W = 1185; **p_{adjust} < 0.0001**	W = 1056; **p_{adjust} < 0.0001**	W = 148; **p_{adjust} < 0.0001**	W = 50; **p_{adjust} < 0.0001**	W = 66.5; **p_{adjust} = 0.001**	W = 122; **p_{adjust} = 0.02**
Non-cannibals						
Mean ± SD in predation test	30 ± 20	17 ± 12	19 ± 15	0 ± 1	4 ± 7	0.05 ± 0.15
Mean ± SD in cannibalism test	30 ± 26	17 ± 21	3 ± 6	0 ± 0	0 ± 1	0.02 ± 0.08
Comparison between both tests	W = 517; p_{adjust} = 1	W = 458; p_{adjust} = 0.7	W = 521; **p_{adjust} < 0.0001**	W = 14; **p_{adjust} = 0.004**	W = 3.5; **p_{adjust} < 0.0001**	W = 23; p_{adjust} = 0.4