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How does a domestication process modulate oogenesis and reproduction performance in Eurasian perch?

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ABSTRACT

The domestication process is accompanied by adaptation of the animals to captive conditions. It induces changes at different levels thereby affecting a variety of biological functions. While there is abundant literature on the domestication effects on growth and stress response in teleosts, the effects on reproduction have received limited attention. In this work, we investigated the domestication effect on the reproductive ability of Eurasian perch (*Perca fluviatilis* L.), a promising candidate for the development of European aquaculture and whose reproductive physiological processes through the domestication history have not been questioned yet.

To address this question, two populations of F1 and "domesticated" females were subjected to a photothermal program allowing the control of gonadogenesis advancement. Gonadosomatic index, 17β-Estradiol levels, and oocyte diameter were significantly higher in the "domesticated" population than in F1 population. In contrast, testosterone, 11-ketotestosterone, and vitellogenin levels were found to be higher in F1 females than in their "domesticated" counterparts. Lower reproductive performance was observed in the "domesticated" population compared to the F1 population in terms of embryo survival, percentage of eyed-stage larvae, hatching and percentage of malformation rates. In conclusion, this study shows that despite a positive effect on advancing gonadogenesis and vitellogenesis, this domestication route negatively affected the reproductive performance under our conditions.

Statement of relevance: This work will give information to producers to choose good broodstock populations (wild or domesticated) to have optimal reproductive performances in Eurasian perch, and thus improve fish production.

1. Introduction

Price (1984) defined domestication as "the process whereby a population of animals becomes adapted to humans and captivity conditions through one or several combinations of genetic changes throughout the generations". Digard (2003) proposed to define domestication as "the action that is exerted by humans on the animals they own, even if just raising them". Thus, the list of "domesticated" fish species goes from 25 to 30 species with the first definition to >200 species with the second definition. This shows that the concept of domestication is still divisive in the scientific community. However, everyone agrees that fish populations may undergo, through the domestication process, changes in their genomes due to adaptation to environmental stressors, genetic selection (deliberate or not), or inbreeding phenomena (Balon, 2004; Price, 1984). It induces changes at anatomical, physiological, and molecular levels thereby affecting a variety of biological functions (e.g. Brummett et al., 2004). There is abundant literature on the domestication effects on growth (Withler and Beacham, 1994; Hassin et al., 1997; Tymchuk et al., 2006) and stress response in teleosts (Pickering and Pottinger, 1989, 1997; Vandeputte and Prunet, 2002; Douxfils et al., 2011). On the one hand, it has been shown that, on the whole, domestication reduces fish stress response, making them less fearful as shown in salmonids (Pickering and Pottinger, 1989, 1997; Vandeputte and Prunet, 2002), or less sensitive to acute handling stressors in Eurasian perch (Douxfils et al., 2011). But in European sea bass (*Dicentrarchus labrax*) it has been shown that heritability of cortisol response to stress was low (Volckaert et al., 2012). On the other hand, domestication seems to boost growth performance (Withler and Beacham, 1994; Hassin et al., 1997; Tymchuk et al., 2006).

Contrary to growth and stress response, the effects of the domestication process on reproduction have received limited attention. Moreover,

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it appears that research in the field has yielded conflicting results. In ide (*Leuciscus idus*), Krejszeff et al. (2009) showed that domestication positively influenced ovulatory responses following Ovopel™ hormonal treatment. In contrast, they showed that domestication exhibited a negative effect on embryo survival. More recently, a study on the same species showed different results by pointing out a lower ovulatory response to Ovopel™ in the pond-cultured group compared to wild fish (Ciesla et al., 2013) and no domestication effect was observed on the embryo survival. Besides, the effect of domestication can be different from one species to another. In Atlantic salmon (*Salmo salar*), domestication led to an 83% decrease in hatching rates (Jonsson and Jonsson, 2006). In cod (*Gadus morhua*), domestication negatively affected fertilization rates, hatching, and larvae survival (Salze et al., 2005). In brown trout (*Salmo trutta*), domestication negatively affected sperm quality (Dannewitz et al., 2004) but had a positive effect on spawning and egg weight (Randák et al., 2005). Consequently, notable differences also exist between fish families, fish species, and fish populations. These differences led us to investigate the domestication effects on the reproductive ability of Eurasian perch (*Perca fluviatilis*), a species whose domestication history is still recent and which belongs to a poorly investigated fish family. Indeed, according to Teletchea and Fontaine (2014) *Perca fluviatilis* is considered at the 4th level of domestication as the entire life cycle is closed in captivity without wild inputs, but no selective breeding program is used.

Eurasian perch is a freshwater fish species valuable in Europe (Fontaine, 2009). Although the perch market is local, the current production of market-size perch in Europe cannot meet the demand, which is mainly centered in the Alpine region (Setälä et al., 2008; Watson, 2008). It has been shown that in Geneva Lake, there was a decrease of perch yield from 1600 t to 800 t in the 80s due to intensive fisheries (Dubois et al., 2008), this yield stabilized since 1990, when the aquaculture of this species appeared. To meet the increasing demand for small sized perch especially in Switzerland, intensive perch culture has been developed in the past two decades in France, Switzerland, Germany and in Scandinavian countries and reached 500 t in 2014 (Fontaine et al., 2015), even if the demand is mainly supplied by the fisheries (30,000 t/year).

To date, only one study has examined the effect of domestication on Eurasian perch reproduction (Kristan et al., 2012). Results showed a positive effect of domestication on fertilization rates, but a negative effect on ovulation and hatching. However, no detailed study has ever investigated the influence of domestication on both the mating performance and the reproductive mechanisms underlying these effects. Our hypothesis is that disruption in the level of the endocrine actors that control the reproductive cycle explains the changes in reproductive performance along the domestication process.

The aim of this study was to compare two perch populations (F1 and "domesticated"), exposed to a special photothermal program allowing the control of gonadogenesis advancement, in terms of morphological parameters (gonadosomatic index, hepatosomatic index), levels of GnRH and gonadotropin gene expression, sexual steroids and vitellogenin, oocyte developmental stages, and reproductive performance.

2. Materials and methods

2.1. Fish

Two populations of F1 and "domesticated" perch were studied in this experiment, both originating from Lake Geneva (French-Swiss border). F1 breeders came from wild broodstock (F0) collected as eggs directly from Lake Geneva. "Domesticated" breeders were provided by a local producer (Lucas Perches, Hampont, France) as captive-bred fish from several generations, although introduction of wild individuals during reproduction seasons could not be totally excluded. The domestication history of these fish is thus a "black box". The F1 and "domesticated" breeders were obtained by artificial reproduction conducted on November 1st, 2011 and were then raised at the producer's premises, before being sent to the URAFPA-MAN facilities located in Nancy (France) on February 6th, 2012, where they were placed in two 6000 L tanks for growth. On arrival at our facilities, fish of both populations were 3 months old. From hatching onward, the two studied fish populations (F1 and "domesticated") were raised under equal and standardized husbandry conditions, at the Lucas Perches facilities, at a temperature range of 18 °C–20 °C with a photoperiod of 13 L/11 D with a blue or red light. At the URAFPA-MAN facilities fish were kept at 20 °C with a photoperiod of 16 L/8 D during the growth period. Fish were daily fed to apparent satiation during the growth period and throughout the experiment (Le Gouessant pellets n°5, proteins 47%, lipids 13%, ash 6.90%, and fiber 2.2%). Fish were handled in accordance with national and international guidelines for the protection of animal welfare.

2.2. Experimentation and water quality management

The experiment began on May 17th, 2013, with 18-month-old fish which had never spawned before. Breeders of both populations were transferred to 500 L independent experimental tanks (3 tanks per population with 48 fish per tank), each tank had its own filtration system and 25% of the water was changed every month. At the beginning of the experiment, fish weights ranged from 67 to 137.8 g for "domesticated" fish and from 70.4 to 129.8 g for F1 fish. Both populations were exposed to a photothermal program able to induce and drive gonadogenesis (Fontaine et al., 2015) (Fig. 1).

In each tank, water quality was measured three times a week. pH was maintained between 7.0 and 7.5 by $NaCO_3$ additions. Dissolved oxygen was maintained above 6 mg/L. Total ammonia nitrogen (0.36 ± 0.53 mg/L) and nitrite nitrogen (0.08 ± 0.12 mg/L) were measured using a CARY I spectrophotometer and always remained below 1 mg/L.

Fish were sampled at days T0, T35 (start of temperature decrease), T157 (start of chilling period), and T295 (increase in temperature) after the start of the photothermal program (Fig. 1). Six females per tank were collected at each sampling time. The first sampling occurred just before the initial photoperiod decrease. At each sampling date, fish were anesthetized in a Tricaine methanesulfonate (MS-222) bath (120 mg/L, Sigma). Blood was sampled from the caudal vein using a syringe, then stored on ice in heparinized microtubes until centrifuged at 3000*g* for 10 min (Centrifuge Jouan C-412). Aliquots of plasma were stored at −80 °C until ELISA analysis was performed. Then, each fish was euthanized by over-anesthetizing it in Tricaine methanesulfonate (MS-222) bath (240 mg/L), weighed, and dissected for gonad and liver weighing and calculation of the gonadosomatic index (GSI = 100× gonad weight/total fish weight) and hepatosomatic index (HSI = 100× liver weight/total fish weight). For gene expression analysis, the whole brain and pituitary were snap frozen (separately) in liquid nitrogen and stored at −80 °C.

2.3. Gonadal histology

Samples of ovaries were stored in a Bouin-Holland solution for one week, washed once with water and twice with 70% ethanol, and stored in absolute ethanol (Abdulfatah et al., 2010). Then, fragments of gonads were cut into 6 mm thick slices, dehydrated with OTTIX solution (DIAPATH SpA, Italy/MM France), and embedded in a paraffin substitute dubbed Diawax (DIAPATH SpA, Italy/MM France) (adapted from Langeron, 1942). Sections of 6 μm were cut out from the Diawax block and stained with Masson's trichrome–hematoxylin Gill III (Merck, Darmstadt, Germany), 0.5% phloxine B (VWR, California, USA), and 0.5% light green (Sigma, Saint-Quentin-Fallavier, France) according to Rinchard and Kestemont (1996). The stage of oocyte development was determined according to Wallace and Selman (1981).

Observations were completed with a light upright optical microscope (Nikon Eclipse Ni-U) and Nikon BR software (Nikon France, Champigny-sur-Marne, France).