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Domestication modulates the expression of genes involved in neurogenesis in high-quality eggs of Sander lucioperca

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Keywords

Aquaculture, microarray, pikeperch, transcriptomics.

Abstract

Pikeperch, Sander lucioperca, is a species of high interest to the aquaculture. The expansion of its production can only be achieved by furthering domestication level. However, the mechanisms driving the domestication process in finfishes are poorly understood. Transcriptome profiling of eggs was found to be a useful tool allowing understanding of the domestication process in teleosts. In this study, using next-generation sequencing, the first pikeperch transcriptome has been generated as well as pikeperch-specific microarray comprising 35,343 unique probes. Next, we performed transcriptome profiling of eggs obtained from wild and domesticated populations. We found 710 differentially expressed genes that were linked mostly to nervous system development. These results provide new insights into processes that are directly involved in the domestication of finfishes. It can be suggested that all the identified processes were predetermined by the maternally derived set of genes contained in the unfertilized eggs. This allows us to suggest that fish behavior, along with many other processes, can be predetermined at the cellular level and may have significant implications on the adaptation of cultured fish to the natural environment. This also allows to suggest that fish behavior should be considered as a very important pikeperch aquaculture selection trait.

1. Introduction

Domestication of animals is one of the most important accomplishments of mankind (Diamond, 2002). This process involves significant modifications of animals' physiology, morphology, and behavior by adapting them to the conditions provided by humans (Price, 1999). Recent concept indicates that in fish, contrary to other animals, domestication is a multistage process starting from transferring wild specimens into captive conditions (Level 0) and ending with establishing selective breeding program (Level 6; Teletchea, 2019). When considering the domestication as a process during which fish adapt to the culture environment, this process starts already at the larval stage during which domestication-related consequences were found to be already profound (Palińska-Żarska et al., 2020). Consequently, successful act of reproduction can be considered as a very important step indicating successful adaptation to the culture conditions enabling further steps of domestication. This aspect—being crucial in developing targeted selective breeding programs—has still been poorly understood and there is still very little information allowing to conclude about key elements conditioning successful domestication of finfishes.

Fish domestication is crucial for sustainable expansion of the aquaculture sector (Teletchea & Fontaine, 2014), it being the

main source of human edible fish worldwide (FAO, 2018). This is especially important in candidate and newly cultured fish species, playing an important role in the diversification offish production and has a huge importance for catering to an evergrowing market demand for high quality, healthy, and fresh animal-based proteins (Fontaine & Teletchea, 2019; Teletchea, 2016). However, as of date, from among ~200 fish species being cultured, only 75 can be considered as domesticated. In many cases, the domestication attempts to fail within the first few years (Teletchea, 2019). This is because of the huge gap in knowledge about the mechanisms of adaptation of fish to the culture environments and closure of life cycle in captivity, which is the first step toward successful domestication (Teletchea & Fontaine, 2014). Thus, the knowledge of the mechanisms driving the domestication in fishes is crucial in targeting traits for selection and consequently develop effective selective breeding programs. In recent years, there has been a growing interest in studying finfish domestication processes from different perspectives. Studies have revealed that besides the positive effect of domestication (evident in increased growth rate and disease and stress resistance; Douxfils et al., 2011; Teletchea & Fontaine, 2014), there are a number of processes that are negatively affected. This includes functionality of the endocrine system (Khendek et al., 2017, 2018) and gamete quality (Křišťan, Stejskal, & Policar, 2012; Lanes, Bizuayehu, de Oliveira Fernandes, Kiron, & Babiak, 2013), which leads to lowered spawning effectiveness and consequently limited production of high-quality progeny and subsequent generations (Migaud et al., 2013; Schaerlinger & Żarski, 2015). The intensification of negative consequences are more apparent whenever the entire life cycle of the fish is closed indoor in intensive production systems (such as recirculating aquaculture systems; RAS). In such cases, all the environmental factors, conditioning the overall performance of fish, are entirely artificial (Fontaine, Wang, & Hermelink, 2015). This is the case, for instance, in pikeperch production, which relies mostly on the fish intensively cultured in RAS (Steenfeldt et al., 2015). Despite huge progress in intensification of its aquaculture technology over the last two decades, captive broodstock of pikeperch are still characterized by highly variable and/or lowered spawning performance, reflected mainly in poor egg quality (Schaefer, Overton, & Wuertz, 2016; Żarski et al., 2019). This limits the successful expansion of its commercial production, and is also associated with several concerns regarding the use of fish coming from such a production to support natural recruitment in open water bodies.

The lower egg quality of domesticated broodstock of percids is related to intrinsic and extrinsic factors, with the latter being associated mainly with the photothermal conditions provided during the annual reproductive cycle (Fontaine et al., 2015). Intrinsic factors related to stress response (Douxfils et al., 2011) and nutritional status (Henrotte et al., 2010) have already been studied. However, in the case of pike-perch the most recent study has shown that there is huge intragroup variability in terms of the quality of eggs (Żarski et al., 2019), suggesting that there are certain individual predispositions for adaptation to the intensive culture conditions. From this perspective, understanding the mechanisms of successful adaptation of particular specimens to captivity is key to elaborate specific husbandry conditions, selective breeding programs, and selection criteria as well as to prepare the potential restocking program for a given population.

The developmental competence of eggs until maternal-to-zygotic transition exclusively relies on maternally derived biomolecules, such as proteins and messenger RNAs (mRNAs; Cheung et al., 2019; Ma, Martin, Dixon, Hernandez, & Weber, 2019). The composition and profile of these molecules, deposited in the eggs during the oogenesis and final oocyte maturation (FOM; Bobe & Labbé, 2010), can be considered as a reflection of the direct response of the female to particular conditions, suggesting potential "molecular programming" of the eggs being adjustable by husbandry practices (Sullivan, Chapman, Reading, & Anderson, 2015). This makes the molecular profiling of eggs an excellent proxy for understanding the processes involved in determining their quality as well as those processes that have modulatory effects on the overall fish performances. This includes the environmental conditions to which fish are exposed—such as extremely different conditions which can be recorded in either open water bodies (in the wild) or aquaculture. Therefore, analysis of molecular profile of ovulated eggs coming from two populations at distinct domestication levels may also allow an understanding of the processes involved in successful domestication.

From among the tools available, we chose the widely applied transcriptomics approach for molecular characterization of fish egg (Bobe, 2015). Hitherto, research has mainly been focused on the exploration of the transcriptome profile of egg quality (Bizuayehu, Mommens, Sundaram, Dhanasiri, & Babiak, 2019; Bonnet, Fostier, & Bobe, 2007; Cheung et al., 2019; Lanes, Fernandes, Kiron, & Babiak, 2012; Mommens et al., 2010; Żarski, Nguyen, et al., 2017). The transcriptome information related to domestication-induced modifications in the eggs is still very limited. Recently, it was reported that domestication had an impact on the expression of the genes involved in immune response of freshly collected eggs of Eurasian perch, Perca fluviatilis (Rocha de Almeida et al., 2019). However, it is not clear whether the modifications in the tran-scriptome observed in that study were a consequence of the domestication process or were caused by the differences in the egg quality recorded, which is a commonly known modulator of the transcriptome in ovulated eggs in teleosts (Bonnet et al., 2007; Żarski, Nguyen, et al., 2017). Besides, information on modifications in the transcriptome caused by domestication in developing embryos are available. The transcriptome analysis of embryos at two- to eight-cell stages or at the eyed-egg-stage (highly advanced embryo, just before hatching) were performed for Atlantic cod (Gadus morhua; Lanes et al., 2013) and Atlantic salmon (Salmo salar; Bicskei, Taggart, Glover, & Bron, 2016), respectively. As of date, there is no information on the transcriptome profile of pikeperch eggs, and also, there are no data allowing the comparison of the transcriptome of ovulated eggs from domesticated and wild fish—both characterized by high quality. Therefore, in the present study, we performed a comparative analysis of the transcriptome profiles of unfertilized pikeperch eggs obtained from either domesticated or wild females. However, because of the nonavailability of the pikeperch genome at the time when this study was conducted, to achieve our goal, we also generated the first multi-tissue transcriptome of pikeperch and designed pikeperch-specific microarrays.

2. Results

2.1.| RNA-seq and de novo transcriptome assembly

Raw sequence data from the HiSeq 2500 sequencer were deposited into the NCBI SRA under the accession no. PRJNA589878. The lowest number of contigs obtained following tissue de novo tran-scriptome assemblies was recorded for eggs (19,575), whereas the highest was for larvae (50,757) and muscles (51,040). Meta-analysis revealed that a total of 43,501 contigs were obtained using the implemented approach (Table 1), from which 35,343 were recognized as unique, which were used for microarray design. Overall, the meta-transcriptome was characterized by 93.8% completeness as indicated by the BUSCO score. This score has been calculated on 4,584 Acti-nopterygii proteins and corresponds to 79.1% complete single copy, 14.7% complete duplicated, 2.7% fragmented, and 3.5% of missing proteins. Further, the process of designing of microarray allowed to include all 35,343 unique probes based on contigs identified during the transcriptome assembly.

2.2. Biological quality of eggs from domesticated and wild fish

Among the 60 egg batches obtained from domesticated females, 8 were found to meet the quality criteria considered for the present study. Among the 15 egg batches obtained from wild females, only 7 were characterized by high quality and were used for further procedures. In effect, eggs selected for analysis from both the populations were characterized by high overall biological quality (Figure 1). There were no statistical differences between the two populations in any of the parameters measured (survival rate [SR], hatching rate [HR], and deformity rate [DR]).

2.3. Microarray analysis

In microarray analysis, successful hybridization was recorded for 17,543 genes, which were further subjected to statistical analysis. A total of 710 differentially expressed genes (DEGs) were identified between eggs obtained from domesticated and wild females; 410 of these genes were upregulated in eggs from domesticated females and 300 were upregulated in eggs from wild females (Table S2). Among the DEGs, protein homologs were not found for 24 genes and these genes were named as uncharacterized (un-prot) or hypothetical (hy-prot) proteins. Clustering analysis allowed the identification of four different clusters, clearly distinguishing the two experimental groups as well as the genes upregulated in eggs from domesticated or wild fish (Figure 2).

2.4. Functional analysis of DEGs

Functional analysis revealed significant enrichment (false discovery rate [FDR] < 0.05) of 462 processes. All the significantly enriched biological processes are presented in Table S3. The top 30 most enriched processes, represented by 376 genes (Figure S1), were clustered into four clearly distinguishable clusters (Figure 3). Among the identified clusters, genes involved in the developmental process (GO:0032502), nervous system development (GO:0007399), regulation of phosphorylation (GO:0042325), and the ones related to cell motility (GO:0048870) together with those related to localization (GO:0051674) were further subjected to STRING analysis. In the cluster expected to take part in the regulation of phosphorylation, two processes were suggested to be involved in phosphorus and phosphate metabolism but were not directly involved in phosphorylation. However, an in-depth analysis of all the significantly enriched processes (see Table S3) revealed the enrichment of 15 phosphorylation- and dephosphorylation-related processes, clearly indicating that this process was significantly modulated by domestication. This cluster was, therefore, considered to represent the "regulation of phosphorylation" process.

STRING analysis of the gene sets representing the four different clusters highlighted many significantly enriched biological processes specific for these clusters identified (Figures 4–7). The analysis of gene set representing "developmental process" (Figure 4) was found to be involved in 997 significantly (FDR < 0.05) enriched biological processes, 70 molecular functions, and 140 cellular components. Among the genes found to be connected with the highest confidence (0.900), 88 were involved in at least five of the most enriched processes (Figure 4), from which 16 were selected for quantitative polymerase chain reaction (qPCR) validation. Additionally, the analysis revealed that this gene set was involved in 46 different, significantly enriched (FDR < 0.05) KEGG pathways. Interestingly, the most significantly enriched one was axon guidance (hsa04360; FDR = 3.69E−08), which is a key stage in the formation of neuronal networks. Second STRING analysis, on the gene set representing the nervous system development, confirmed significant enrichment of the axon guidance (FDR = 1.26E−09) KEGG pathway (being the most enriched among 14 pathways identified with this gene set; Figure 5). Besides, with this gene set, 488 biological processes, 47 molecular functions, and 113 cellular components were found to be significantly enriched (FDR < 0.05). It is noteworthy, that 9 out of 30 most enriched Gene Ontology (GO) terms of the cellular component indicated their direct involvement in the nervous system development, as they were found to be important components of neurons and synapses. Among the gene set analyzed, 30 out of 42 GO terms connected with highest confidence (Figure 5), were found to be involved in at least 5 (out of 10) most significantly enriched biological processes related to nervous system development. Among those genes, ctsz, prkcz, ctnna2, casp3, mapt, camk2b, gabrb1, ntn4, lamb1, and dag1 were chosen for qPCR validation (Figure 5). STRING analysis performed for the set of genes representing protein phosphorylation indicated their involvement in 830 significantly enriched (FDR < 0.05) biological processes, 78 molecular functions, and 73 cellular components. The involvement of 10 of the most enriched biological processes in protein modification processes was confirmed, with phosphorylation being the most important one (Figure 6). For qPCR validation, 13 genes (out of 34 genes connected with highest confidence and taking part in at least five most enriched biological processes) were selected. Among the 57 enriched KEGG pathways, MAPK signaling (hsa04010; FDR = 4.11E−06) and apoptosis (hsa04210; FDR = 3.62E−05) were found to be the most enriched ones (Figure 6). The sets of genes representing cell motility and localization were involved in processes related to controlled and self-propelled movement. However, 41 significantly enriched processes were also directly related to

the neuron and nervous system development, together with the fact that axon guidance was again the most enriched KEGG pathway, suggesting the significant involvement of this set of genes in the development of the nervous system (Figure 7).

2.5. Results of the validation of candidate genes with qPCR

Among the 20 genes whose expression levels were validated with qPCR, 14 (70%) were confirmed to be significantly differentially expressed. Nine genes (camk2b, casp3, mapt, nckap1l, spred1, ctnna2, ctsz, dag1, and ikbkg) were confirmed to be upregulated in eggs from domesticated females and the other five (hras, ccnd2, ntn4, gabrbb1, and prkcz) we confirmed to be upregulated in eggs of wild females (Figure 8). The expression level of six genes (tgfb2, socs5, lamb1, map4k4, fbxw7, and pycard) was similar in the eggs from both the populations. From among successfully validated genes, 10 were found to be involved in nervous system development (camk2b, casp3, mapt, nckap1l, ctnna2, ctsz, dag1, ntn4, gabrb1, prkcz) (Figure S1).

3. Discussion

3.1. RNA Domestication-induced changes in the transcriptome of the eggs of pikeperch

. Comparative analyses of the transcriptome of wild and cultured fish have been reported for several fish species at different steps of embryonic (Lanes et al., 2013) and larval development as well as for juvenile (Bicskei, Bron, Glover, & Taggart, 2014) and adult fish (Chen et al., 2017; Tymchuk, Sakhrani, & Devlin, 2009). Also, one study showed the comparison of transcriptome profile of unfertilized eggs of wild and domesticated fish collected immediately after ovulation (Rocha de Almeida et al., 2019). However, in those studies, the authors compared the eggs of lower quality (maximum HR did not exceed 50%), and the quality was also different between the two groups that were included, which would not allow an objective comparison of their findings with those of the present study. Another approach, potentially comparable to that used in the present study, was of Lanes et al. (2013) who analyzed the transcriptome of only the viable embryos at two- to eight-cell stages in Atlantic cod. However, considering the fact that transcriptomic profile of early-cleaving embryos may differ from the unfertilized eggs by RNAs coming from sperm (Gross, Strillacci, Peñagaricano, & Khatib, 2019) and/or tran-scriptomic status may be changed along with the first cell division in fishes (White et al., 2017), a comparison of the results of Lanes et al. (2013) with the present study is very difficult. Especially, Atlantic cod eggs from domesticated females were of significantly lower quality when compared to the ones obtained from wild females; this could additionally influence the differences in the transcriptome. Therefore, it is highly difficult to compare the overall transcriptome data obtained herein with the ones already published. However, it should be stressed that despite the methodical differences there were some genes that were differentially expressed in both domesticated and wild fish. This applies to plexins (plxb1 and plxnd1 in Atlantic cod and pikeperch, respectively), eukaryotic translation initiation factors (eif6 in Atlantic cod and eif2ak1, eif3a, and eif1b in pikeperch), several zinc finger proteins (represented in pikeperch by znf185, znf347, znf710, znf668, and znf862), tetraspanins (tspan7 in Atlantic cod and tspan17 in pikeperch), and MAP kinase-activated protein kinase (mapkapk5 and mapkapk3 in Atlantic cod and pikeperch, respectively), which constitute a set of potential candidate markers of domestication in finfishes. However, their actual usefulness should be investigated in greater detail, and the interspecies uniformity of these markers should be confirmed.

It should be highlighted that in the present study, three different genes encoding cathepsins (ctsk, ctss, and ctsz) were found among the DEGs; all the three were overexpressed in the domesticated group. In Atlantic cod, cathepsin A (ctsa) was found to be overexpressed in the embryos of the domesticated population (Lanes et al., 2013). In finfishes, cathepsins were reported to be involved in the processing of yolk proteins during oogenesis and FOM (Fabra & Cerdà, 2004) and were found to be correlated with the egg quality in several teleosts (Carnevali et al., 2001; Gwon, Kim, Baek, Lee, & Kwon, 2017), including percids (Kestemont, Cooremans, Abi-Ayad, & Mélard, 1999). For instance, in rainbow trout, ctsz was overexpressed in low-quality egg (Aegerter, Jalabert, & Bobe, 2005), suggesting that it is an egg-quality-associated marker. However, the eggs in the present study were of very high quality in both the populations, eliminating the assumption of modified expression of cathepsins because of egg quality. Fabra and Cerdà (2004) reported that ctsk is more abundant at the previtellogenic stage in Fundulus heteroclitus, whereas expression of ctss and ctsz is relatively constant throughout gonado-genesis. Therefore, modified expression of cathepsins recorded in the present study (expression level of ctsz was also confirmed by qPCR) suggests that domestication affects the process of incorporation and/ or processing of different proteins into the yolk during oogenesis, without clear involvement in any particular stages. This may be because of the different dietary protein sources needed by the fish to process during gonadogenesis. However, further studies are needed for validation of this hypothesis.

3.2. Biological processes modified bydomestication in pikeperch

Comparative transcriptome analysis of different developmental stages and/or tissues from domesticated or wild finfishes usually allows the identification of several biological processes modified in relation to the immune and stress response (Rocha de Almeida et al., 2019; Tymchuk et al., 2009), digestive capacity (Chen et al., 2017), and metabolism of various compounds (Lanes et al., 2013). In the present study, seven significantly enriched GO terms were found to be related to stress and 23 were related to immune response (see Table S3), confirming the importance of modification of these processes during the domestication of finfishes. Additionally, a number of processes related to the metabolism of different compounds were identified, including glutamate, oxoacids, valine, phosphorus, and phospholipids (Table S3). Interestingly, these processes are apparently predetermined in ovulated eggs, potentially influencing the development of the immune system, stress response, and

metabolism from the very beginning of ontogeny. In the present study, no processes related to digestive capacity were identified to be affected by domestication. The fact that in pikeperch, unfertilized eggs were analyzed and not the developed organism, suggests that the modification of the digestive capacity occurs later in ontogenesis. Lanes et al. (2013) also did not find any digestive system-related processes to be significantly modulated at early embryonic development. On the contrary, Palińska-Żarska et al. (2020) reported domestication-driven modifications of the digestion capacity in larvae of Eurasian perch at hatching, which became more evident at the end of larval metamorphosis. Bicskei et al. (2014) reported that the digestive activity was modified by the domestication level in Atlantic salmon not earlier than in the fry that has started exogenous feeding. It can, therefore, be concluded that expression of genes taking part in digestion are evidently different between wild and domestic stocks when this system is already well developed, whereas immune and stress responses are of immense importance even during the earliest developmental stages.

Among the most enriched biological processes noticed in the present study, 274 genes involved in the developmental process were identified. However, the developmental process is a very general ontological term, which includes various highly important processes. Further analysis revealed that 114 of these genes were shared with the process of nervous system development (Figure S2), indicating the huge importance of the latter in the final analysis. Besides, the high enrichment of axon guidance KEGG pathway additionally supports the presumptions that the development of the nervous system is among the most important processes modified by domestication in pikeperch eggs. Generally, it is well established that domestication affects the behavior of farmed animals (Kaiser, Hennessy, & Sachser, 2015), including fish (Drew et al., 2012). These changes are related to the necessity of tolerance to altered conditions provided by humans, leading to modified brain architecture (Brusini et al., 2018). These changes are obviously driven by modification at the level of transcription of crucial genes leading to considerable changes in the transcriptome profile of the brain of domesticated fishes relative to their wild counterparts (Tymchuk et al., 2009). Moreover, the effect of domestication on nervous system development was already observed at earlier stages, such as in yolk-sac fry of Atlantic salmon (Bicskei et al., 2014) or even at two- to eight-cell stages in Atlantic cod (Lanes et al., 2013). In a recent study, Colson et al. (2019) reported that breeders of rainbow trout (Oncorhynchus mykiss) which experienced thermal stress have yielded eggs with modified expression of genes such as auts2, dpysl5, arv1, and plp1 being responsible—among others— for neurodevelopment as well as neural and cognitive disorders. Moreover, Colson et al. (2019) also revealed that the progeny obtained from egg batches exhibiting different expressions of those genes were also exhibiting modified emotional responses and learning performance. Molnár, Csuvár, Benedek, Molnár, and Kabai (2018) who reported that domesticated pikeperch exhibited modified exploratory behavior when compared to their wild counterparts, suggesting the behavior is crucial in adaptability of this species to artificial environment. These observations together with our results suggest that the development of nervous system may already be predetermined by the maternally derived transcriptomic “cargo” incorporated into the oocyte during the oogenesis and FOM, as a consequence of exposure to extrinsic and/or genetic factors.

It is well known that following fertilization maternally derived RNAs are crucial for the development of transcriptionally silent embryo until maternal-to-zygotic transition (MZT; Ren et al., 2020)

Next, the resumed zygotic transcription was shown to be accompanied bydegradation of maternal RNAs (Despic & Neugebauer, 2018). However, the RNA degradation throughout the embryonic development is presumably selective as it may be controlled by internal mechanisms (Alizadeh, Kageyama, & Aoki, 2005; Ren et al., 2020). Especially that many transcripts are considerably expressed from egg to fully developed embryo/larvae (Adrian-Kalchhauser, Walser, Schwaiger, & Burkhardt-Holm, 2018; White et al., 2017). This often applies to very important genes, such as the ones involved in immune response (Ellingsen, Strand, Monsen, Bøgwald, & Dalmo, 2005). In addition, considering that the genes involved in translation were found to be important for developing embryos (Cheung et al., 2019; Żarski, Ngugen, et al., 2017) it may also be expected that RNAs are being translated during the embryonic development into proteins consequently influencing/contributing to formation of particular cells and/or tissues/organs. This can be the case with the genes involved in nervous system development. Especially that Colson et al. (2019) and Kondrychyn, Robra, and Thirumalai (2017) clearly indicates that the neurodevelopment in fishes can be controlled by maternally inherited RNAs. Despite the exact mechanism conditioning influence of the maternally derived transcripts on the nervous system development is still to be explored, the results of our study highlights the possible huge importance of maternal contribution to the behavioral adaptability of finfishes.

Adaptation of every living organism is associated with their ability to respond to internal and external cues. Timely response to the modified environment is a crucial element in such adaptation, which may be considered as successful only if the reproductive capacity is retained. At the molecular level, such a response is conditioned by the capability of cells for sensing, transmitting, storing, and interpreting information received through various pathways (Humphrey, James, & Mann, 2015). In this sense, posttranslational modification (PTM) of proteins is a highly important transducer of the signals received. Phosphorylation, which is involved in almost every cellular process (Cohen, 2002), is among the most important of the PTMs. Protein phosphorylation, and other PTMs, were found to be among the significantly modified processes resulting from domestication of pikeperch (Figure 6). This indicates that the PTMs are certainly important components of the adaptability of fish to intensive culture conditions, as was reported in other fish species (Lanes et al., 2013). However, considering the fact that 29 genes responsible for phosphorylation were also involved in nervous system development (Figure S2) and oxidative phosphorylation was downregulated in the brain of domestic fish (Tymchuk et al., 2009), the genes determined to be involved in the phosphorylation processes in the present study may also play modulatory roles in the development of the nervous system.

3.3. Expression levels of candidate genes

The qPCR-validated genes related to the central nervous system that were significantly upregulated in domesticated fish were reported to be responsible for the protection of neurons

(camk2b; Fang, Feng, Zhao, & Liu, 2014), synaptic plasticity (ctnna2; Terracciano et al., 2011), and were found to be involved in counteracting neuroinflammation (ctsz; Allan et al., 2017). The genes that were upre-gulated in eggs from wild broodstock were reported to regulate thalamocortical axon branching (ntn4; Hayano et al., 2014) and are known to be crucial for normal brain development (gabrb1; Halder et al., 2015). The remaining genes subjected to qPCR validation that were recognized to be involved in the two abovementioned processes were also identified to be involved in the protein phosphorylation process. However, even these genes were reported to be involved in the development and functioning of the nervous system. This includes neuronal programmed cell death (casp3; Roth & D'Sa, 2001), suppression of apoptosis of neurons (nckap1l; Zhong et al., 2019), development of the neurons (prkcz; Hapak, Rothlin, & Ghosh, 2019), formation and maintenance of synapses (dag1; Nickolls & Bönnemann, 2018) as well as modulation of the expression of neuron-associated Tau proteins (mapt; Caillet-Boudin, Buée, Sergeant, & Lefebvre, 2015). All these results indicate that domestication highly affects the nervous system development in finfishes, and the changes are evident in pikeperch even after a single generation in captivity.

Among the genes recognized to be involved in the phosphorylation process, those validated with qPCR were also involved in other processes. Among the genes upregulated in eggs from wild fish, ccnd2 and hras were found to be also involved in cell cycle progression. Importantly, modified expression of these genes led to gonadal (ccnd2; Sicinski et al., 1996; Wang et al., 2016) and cervical (hras; Córdova-Alarcón, Centeno, Reyes-Esparza, García-Carrancá, & Garrido, 2005) cancer. On the contrary, the genes upregulated in eggs of domesticated fish were involved in the reception of ubiqui-tination signals and in the activation of the IKK complex (ikbkg; Israël, 2010; Muller, Baeyens, & Dustin, 2018); these were also involved in the negative regulation of the Ras–ERK pathway (sprØ1; Suzuki, Morita, Hirata, Shichita, & Yoshimura, 2015), confirming that intracellular signaling (involving PTMs) should be considered as crucial in the process of fish domestication.

3.4. Conclusions

The results of the present study provide new insights into the processes that are directly involved in the successful domestication of finfishes. It can be suggested that these processes are predetermined by the maternally derived set of genes contained already in the unfertilized eggs. Our approach confirmed that the immune and stress responses are among the processes modulated during fish adaptation to intensive culture conditions. However, it should be highlighted that, for the first time, we have identified PTMs of proteins as well as the development of the nervous system to be among the most important processes affected by domestication. This allows us to suggest that the behavioral traits, whenever associated with high growth rate and reproductive capacity, may be considered as very important for the selection of pikeperch, and presumably other teleosts, for aquaculture purposes.

4. Material and methods

All experimental procedures related to animal handling, and reproductive procedures undertaken in this study were performed with the compliance of the European legislations for fish welfare and whenever appropriate approved by the Lorraine Ethics Committee for Animal Experimentation (CELMEA; APAFIS-2016022913149909).

The study was performed in two phases—the preparatory phase and the experimental phase. In the preparatory phase, the first complex transcriptome of a pikeperch was obtained, which allowed the designing of a pikeperch-specific microarray. In the experimental phase, a comparative transcriptome profiling of eggs from wild and domesticated stocks was done (Figure 9).

4.1. Preparatory phase: Collection of samples and extraction of RNA for RNA-seq

Three domesticated mature pikeperch males (obtained from fish farm SARL Asialor, Pierrevillers, France) were euthanized by immersion in tricaine methanesulfonate (MS-222; Sigma-Aldrich, Lyon, France) solution (150 mg L–1) for over 20 min. Next, the liver, head kidney, muscles, stomach, and testes were sampled. Additionally, preovulatory oocytes (sampled in vivo by catheterization; that is, flexible catheter was inserted into the genital pore of the fish, and small sample of oocyte was sucked-out with a syringe connected to a catheter; as described by Żarski, Kucharczyk, et al., 2012), ovulated eggs, and freshly hatched larvae from three wild females were also sampled. The samples from these three wild females were obtained in vivo, and fish after the reproduction were released into the earthen pond. The sample choice aimed at having as wide a repertoire of the transcripts as possible. Additionally, the transcripts from preovulatory oocytes collected from wild females upon commercial controlled reproduction operation (caught in Vistula Lagoon, North Poland and further subjected to standard controlled reproduction procedure at the fish farm "Tolkmicko," Tolkmicko, North Poland) until the larval stage ensured the presence of egg-specific transcripts occurring naturally in this species and not affected by the domestication process. Besides, the choice of collecting oocytes, eggs, and larvae from wild fish was dictated by the necessity of having a repertoire of transcripts characterizing high-quality eggs and normal embryonic development and not being potentially biased/ altered by domestication. The tissues/cells/larvae collected were placed into cryotubes immediately after collection and snap-frozen in liquid nitrogen. Larvae before freezing were euthanized by overexposure to MS-222 (20 min at a dose of 150 mg L–1). After transportation to the laboratory, the samples were stored in a freezer (at –80°C) before their use in further procedures. In total, for the preparatory phase of the experiment, three domesticated fish were euthanized, three wild females were exposed to standard reproductive procedures (in vivo), and approximately 600 eggs/em-bryos/larvae were sampled (collected) from them for further analysis.

Total RNA from the tissues was extracted using Total RNA Mini kit (Cat. No. 031-25; A&A Biotechnology, Gdynia, Poland) according to the protocol provided by the manufacturer. For extraction, approximately 50 mg of samples were taken. A NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE) was used to determine the concentration of

the RNA samples. The RNA sample quality was checked using a 2100 Bioanalyzer (Agilent Technologies Inc., Santa Clara, CA), and only those samples exhibiting a RIN (RNA integrity number) value higher than 8.0 were used for sequencing. Before sequencing, RNA was treated with DNA-free DNA Removal Kit (AM 1906; Life Technologies, Carlsbad, CA).

4.2. Preparatory phase: RNA-seq

The sequencing libraries were prepared with TruSeq Stranded mRNA Sample Preparation kit (Illumina, San Diego, CA) according to the manufacturer's instructions. Briefly, polyadenylated RNA was selected using oligo(dT) magnetic beads and was chemically fragmented. First-strand complementary DNA (cDNA) synthesis was performed using random primers and SuperScript II reverse transcriptase in the presence of actinomycin D. Following the cDNA synthesis and adapter ligation, PCR amplification of the generated cDNA was performed. The libraries were sequenced using an Illumina HiSeq 2500 system with 250-base pairs paired-end reads. The sequences were acquired using the Illumina data processing pipeline. The quality control of the samples and screen of contamination was performed using FastQC and FastQ Screen, respectively (both are open-source software available at http://www.bioinformatics. babraham.ac.uk/).

4.3. Preparatory phase: Transcriptome assembly and annotation

The tissue Fastq file pairs were processed in the same way as was done for the Phylofish database (Pasquier et al., 2016). Briefly, the read file for each tissue was assembled with the de novo RNA-Seq Assembly Pipeline (DRAP; Cabau et al., 2017) runAssembly module (version v1.92) using standard parameters following a multi-kmer Oases approach. The contig FASTA files were then merged using the DRAP runMeta module with standard parameters. The resulting contig set was processed with TransDecoder (https://github.com/ TransDecoder/TransDecoder version 5.0.2) to find contigs harboring an open reading frame. The contigs were also quality checked with BUSCO (Simão, Waterhouse, Ioannidis, Kriventseva, & Zdobnov, 2015; version 3.0.0) using the -m trans and -l actinopterygii_odb9 parameters.

4.4. Preparatory phase: Designing ofpikeperch-specific microarray

The pikeperch-specific microarray was designed with the eArray platform of Agilent (available at https://earray.chem.agilent.com/ earray) using the obtained transcriptome. The 8 × 60 k arrays contained 35,343 unique probes. The microarray design is accessible at Gene Expression Omnibus platform under the accession number, GPL27937.

4.5. Experimental phase: Broodstock management and spawning of domesticated broodstock

Domesticated pikeperch broodstock (60 males and 60 females held at Asialor fish farm, Pierrevillers, France) were reared for 6 years in RAS under fully controlled environmental conditions. The system was equipped with biological and mechanical filtration, allowing the maintenance of high water quality parameters (oxygen levels always >80% of the saturation level; ammonia in the 0.2–1.1 mg L−1 and nitrite in the 0.05–0.70 mg L−1 range). Water temperature was maintained automatically within a range of 8–23°C (±0.5°C). Before the collection of samples, the fish were successfully reproduced three times, which made them fully “functional” spawners at the beginning of the experiment, that is, they were capable of successful reproduction every year. The fish were exposed to annual fluctuations of photothermal conditions as described by Fontaine et al. (2015), with modifications as described by Żarski et al. (2019) aimed at changing the wintering conditions (period with the lowest temperature, mimicking the winter period; fish were exposed to temperatures below 10°C for 4 months). The fish were daily fed a compound feed (50% protein, 11% fat, 10% moisture, 1.55% crude fiber, 1.35% phosphorus, 9.5% ash, and 17.9% nitrogen-free extract; Le Goues-sant, France) throughout the year at a rate of 0.2–1% of the biomass, depending on the temperature and appearance of satiation (Żarski et al., 2019).

The sampling operation was performed during the standard commercial reproduction protocol of the fish using the method described by Żarski et al. (2019), wherein females and males were hormonally stimulated (by intraperitoneal injection) with human chorionic gonadotropin (hCG; Chorulon, Intervet, France) at a dose of 500 and 250 IU kg−1, respectively, for ovulation and spermiation. At the time of administering the hormone injection, a sample of oocyte was taken from each female by catheterization to identify their maturation stage (as described earlier by Żarski, Kucharczyk, et al., 2012). At the time of injection, the temperature of water was 12°C and it was kept constant until ovulation. After the induction of ovulation, the photophase of the photoperiod was for 14 hr, during which light was provided with neon tubes. For further procedures, only females at maturation stage I (in the 6-stage classification) were used. After the ovulation was confirmed, eggs were collected by hand stripping in a dry plastic sealable container, separately for each female. Sperm was collected between 5 and 7 days following hormonal stimulation by hand stripping into the dry syringes, separately for each male. The collected sperm was stored at 4°C before further use. Before each handling fish were anesthetized through immersion in MS-222 solution (150 mg L−1; Sigma-Aldrich), as proposed by Kristan, Stara, Turek, Policar, and Velisek (2012). The entire reproduction and sampling procedures were performed in vivo and all the fish used for reproduction survived and were stocked back to the broodstock system from which they were taken.

4.6. Experimental phase: Broodstock management and spawning of wild broodstock

The sampling of eggs from wild broodstock was performed during the commercial reproduction at the fish farm. Wild pikeperch females (n = 15) and males (n = 20) were collected during the spawning season from Vistula Lagoon (North of Poland) with fyke nets when the average daily water temperature in the lagoon reached about 10°C for the first time after wintering. After collection, fish were transported in oxygenated tanks to the Tolkmicko Fish Farm hatchery (Tolkmicko, North Poland), where they were placed in RAS with a controllable photothermal regime. Upon arrival at the hatchery, the fish were scored according to the six-stage

classification of maturation (Żarski, Kucharczyk, et al., 2012). After 24 hr of acclimation to 12°C, fish were administered hCG injection (500 and 250 IU kg−1 administered to females and males, respectively). The temperature during the controlled reproduction was kept constant at 12°C and the photoperiod comprised a photophase of 14 hr. Only females at maturation stage I were used for experiments to conform to the procedures for domesticated broodstock; it has been reported that the maturation stage of females upon injection may have a significant effect on the quality (Żarski, Kucharczyk, et al., 2012) and composition (Żarski, Krejszeff, et al., 2012; Żarski Palińska-Żarska, Łuczyńska, & Krejszeff, 2017) of eggs in percids. After the ovulation was confirmed, the eggs were collected in the plastic sealable containers and were stored for no longer than 30 min before further use. Sperm was collected as described for domesticated broodstock. Before each handling fish were anesthetized through immersion in MS-222 solution (150 mg L−1). The entire reproduction and sampling procedures were performed in vivo, and all the fish used for reproduction survived and were released into the earthen pond. In total, for observation of embryonic development and HR, approximately 3,000 eggs/embryos/larvae (approximately 200 eggs were fertilized from each of 15 females examined) were used.

4.7. Experimental phase: Egg sampling, fertilization, evaluation of egg quality, and selection of samples for transcriptome analysis

Each collected egg portion during both spawning operations (of domesticated and wild fish) was first aliquoted into several cryotubes and then snap-frozen in liquid nitrogen. The remaining eggs were used for evaluation of their quality as described by Roche et al. (2018). Briefly, 5 ml of hatchery water was poured over a glass Petri dish (30 mm diameter). Next, a small portion of eggs (around 100 eggs each time) was placed simultaneously with 50 μl of pooled sperm sample (from three males) on the Petri dish. The contents of the Petri dish were vigorously mixed to promote the contact of eggs with motile spermatozoa and then allowed to stand for few minutes so that the eggs could adhere to the surface of the Petri dish (such adherence is a natural characteristic of pikeperch eggs). Petri dishes with adhered eggs were then washed gently with hatchery water (to remove the excess spermatozoa and other residues) and incubated at 12°C in 500 ml freshwater in plastic cups. First larvae were seen to hatch on Day 9 following fertilization and hatching was recorded for 5 subsequent days. Hatched larvae after the experiment were eu-thanized by overexposure to MS-222 solution (150 mg L−1 for over 20 min).

Freshly collected sperm from several males was always used for fertilization. Each sperm sample, before use in fertilization, was subjectively evaluated under a microscope at ×400 magnification, as described by Cejko et al. (2010). For fertilization, only sperm characterized by the presence of at least 80% motile cells was used. The sperm was used for fertilization within 15 min following hand stripping into 5-ml dry syringes.

During the incubation, the SR of embryos, 72-hr post fertiliza-tion, was determined by direct counting of live and dead embryos from all the eggs being incubated using a stereoscopic microscope at ×4 magnification. The HR was determined by counting all the larvae hatched from each sample. These indices are the most commonly used in reproductive studies (Bobe & Labbé, 2010; Żarski et al., 2019). Additionally, each hatched specimen was verified individually under the stereomicroscope for the occurrence of larval deformity, as described by Alix, Zarski, Chardard, Fontaine, and Schaerlinger (2017), and larval DR (DR = 100 × number of larvae showing deformity/total number of larvae hatched) was estimated.

For transcriptome analysis, eight samples (n = 8; average weight of females 4.07±0.84 kg) from domesticated fish and seven samples (n = 7; average weight of females 3.70±0.99 kg) from wild fish were considered, because only these samples passed the following criteria: SR > 85%, HR > 60%, and DR < 15%. For analysis, only the portions of eggs having high quality were considered important to avoid quality-related bias/alterations of the transcriptomes obtained, because the egg quality is an important modulator of the abundance of mRNAs (Cheung et al., 2019).

4.8. Experimental phase: Transcriptome profiling of eggs coming from domesticated and wild pikeperch females

Total RNA from approximately 50 eggs from each female was isolated as described in Section 4.1. The RNA was aliquoted into two portions and kept frozen at −80°C. One portion was used for gene expression profiling with the high-density oligonucleotide microarray designed as described in Section 2.4. Labeling and hybridization were performed according to the protocol for "One-Color Microarray-Based Gene Expression Analysis (Low Input Quick Amp Labeling)" provided by the manufacturer (Agilent). Briefly, for each sample, 150 ng of total RNA was amplified and labeled using Cy3-CTP. The yield (>1.65 μg cRNA) and specific activity (>9 pmol of Cy3 per μg of cRNA) of Cy3-cRNA produced were checked with the Nanodrop. From the Cy3-cRNA preparation, 1.65 μg was fragmented and hybridized on a subarray. Hybridization was carried out for 17 hr at 65°C in a rotating hybridization oven, and subsequently the array was washed and scanned with an Agilent Scanner (Agilent DNA Microarray Scanner, Agilent Technologies, Massy, France) using the standard parameters for a gene expression 8 × 60 k oligoarray (3 μm and 20 bits). Data were obtained with the Agilent Feature Extraction software (10.7.1.1) according to the appropriate GE protocol and further analyzed with the GeneSpring GX software (Agilent Technologies, Santa Clara, CA). Data were published in the NCBI Gene Expression Omnibus (Edgar, Domrachev, & Lash, 2002) and are accessible through the GEO series accession number, GSE142412. The samples were randomly distributed on the microarray for hybridization. The gene expression data were scale normalized and log(2) transformed before statistical analysis.

DEGs between the groups representing the eggs obtained from domesticated (samples D1–D8) and wild (samples W1–W7) females were identified with the use of the Gene Spring GX software. The differences between the groups were analyzed by unpaired t test after applying filters of a minimum twofold change in expression and a $p < .05$. During the

analysis the Benjamin–Hochberg correction was applied. Average linkage clustering analysis (Gene Cluster 3.0) was performed for the differentially abundant genes (unsupervised linkage).

4.9. Experimental phase: Functional analysis of DEGs

For functional analysis of DEGs, gene symbols for human homologs of each DEG were obtained using basic local alignment search tool (BLAST; available at https://blast.ncbi.nlm.nih.gov/Blast.cgi) and UniProt online tool (available at https://www.uniprot.org/). Briefly, RefSeq number for each DEG was subjected to BLAST (using the "blastp" option) against UniProtKB/Swiss-Prot (Swissprot) database and the unique UniProt accession numbers of best hits were further used for retrieving the gene name using the UniProt Retrieve/ID mapping tool.

The obtained gene symbols were used for enrichment analysis (with cutoff at FDR = 0.05) using the ShinyGO v0.61 online tool (available at http://bioinformatics.sdstate.edu/go/; Ge & Jung, 2018). A hierarchical tree, summarizing the correlation among the 30 most significantly enriched pathways, was also generated using this tool. Further, the connections between the enriched pathways were visualized with the "Network" tool of ShinyGO. This clustering analysis allowed a choice of three groups of genes being clustered into three separate clusters. These clusters were considered for further analysis where genes representing a particular cluster were again subjected to functional enrichment analysis as well as STRING analysis (v 11.0; available at https://string-db.org/). This allowed the generation of functional protein association networks. On the basis of the results obtained using STRING, candidate genes were chosen with highest confidence (minimum required interaction score of 0.900) and excluding the disconnected nodes. Each candidate gene should be recognized to be involved in at least 5 of 10 most enriched processes, taking part in the process identified by clustering analysis.

4.10. Experimental phase: Validation of candidate genes with qPCR

Real-time qPCR was performed for each of the candidate genes chosen. For this purpose, the RNA obtained from eggs of wild and domesticated fish was subjected to reverse transcription using Re-vertAid First Strand cDNA Synthesis Kit (Cat. No. K1622; Thermo Fisher Scientific) according to the manufacturer's protocol with Oligo (dT)18 primers and including the optional step of incubation (5 min at 65°C) for the removal of secondary structures. For synthesis of cDNA, 1.7 ng of total RNA was used.

Real-time qPCR was performed using the Roche Light Cycler 480 II (Roche Molecular Systems Inc., Branchburg, NY). For each qPCR reaction (reaction volume 20 µl), 10 ng cDNA template was used along with DyNAmo HS SYBR Green qPCR Master Mix (Cat. No. F410XL; Thermo Fisher Scientific) and 0.5 µM of each primer (Table S1). The enzyme was activated by incubating at 95°C for 10 min, which was followed by 40 cycles of denaturation at 95°C for 15 s, and annealing and elongation at 60°C for 1 min. After amplification, melting curve analysis was performed according to the manufacturer's recommendations to check the specificity of amplification. Relative expression was calculated using the $2^{-\Delta\Delta Ct}$ method (Livak & Schmittgen, 2001), where for normalization geometric mean of Ct values recorded for four reference genes (agfg1, ankra2, pogz, snx30) was used. The reference genes were the ones exhibiting the most stable expression level (identified using Gene Spring GX as those genes exhibiting the lowest coefficient of variation in expression among all the genes expressed). For each sample, the expression level of each gene was analyzed in triplicates. Finally, the data between the groups (representing eggs obtained from domesticated and wild fish) were analyzed with the t test (Statistica, v.12; StatSoft). Differences between groups were considered significant at $p < .05$.

Table 1. Sequencing outputs and transcriptome de novo assembly statistics of different tissues/cells/larvae of pikeperch, Sander lucioperca

	Preovulatory oocytes	Eggs	Kidney	Larvae	Liver	Stomach	Testis	Muscles	Meta
Number of contigs	31,582	19,575	47,419	50,757	27,646	42,888	45,261	51,040	43,501
Total size of contigs	43,199,232	16,860 312	90,178 490	72,820 225	45,504 505	67,810 599	87,184 042	95,715 818	103,295 281
Longest contig	11,300	15,490	19,597	11,780	15,862	16,872	18,343	18,782	19,597
Shortest contig	251	251	251	251	251	251	251	251	297
Number of contigs >1 k nt	16,356	5,755	30,083	25,316	16,398	23,131	28,683	32,575	32,584
Number of contigs >10 k nt	1	1	129	13	26	43	145	106	243
Mean contig size	1,368	861	1,902	1,435	1,646	1,581	1,926	1,875	2,375
Median contig size	1,045	606	1,422	997	1,247	1,114	1,433	1,403	1,902
N50 contig length	1,971	1,219	2,760	2,193	2,319	2,381	2,806	2,679	3,303
L50 contig count	7,431	4,396	10,481	10,719	6,322	9,023	9,869	11,431	10,239
Contig %A	27.14	27.72	27.16	27.38	26.72	27.31	26.59	27.47	27.49
Contig %C	22.88	22.39	22.85	22.64	23.28	22.71	23.44	22.54	23.26
Contig %G	22.72	22.13	22.77	22.52	23.12	22.57	23.3	22.44	23.67
Contig %T	27.25	27.75	27.2	27.45	26.87	27.39	26.65	27.53	25.56
Contig %N	0.01	0.01	0.02	0.02	0.01	0.02	0.02	0.02	0.02
Contig %non-ACGTN	0	0	0	0	0	0	0	0	0
Number of contig non-ACGTN nt	0	0	0	0	0	0	0	0	0

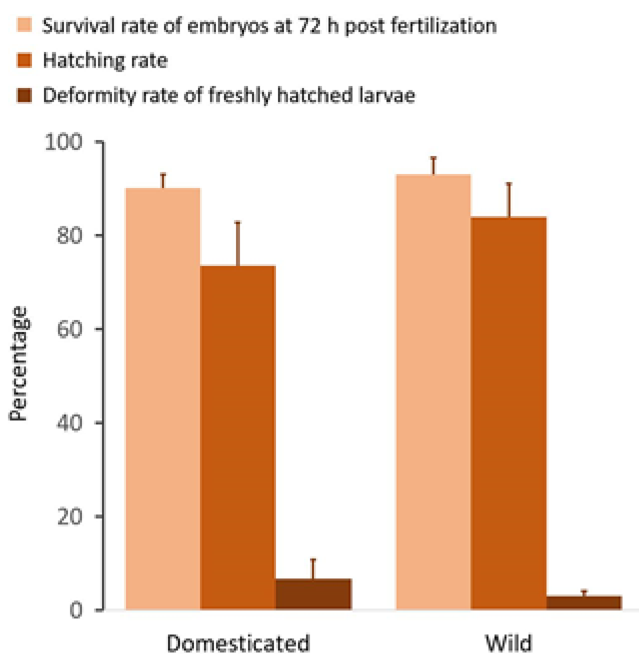


Figure 1. Results of the evaluation of the quality of eggs of pikeperch collected from domesticated or wild broodstock. Data are presented as mean ± SD. SD, standard deviation

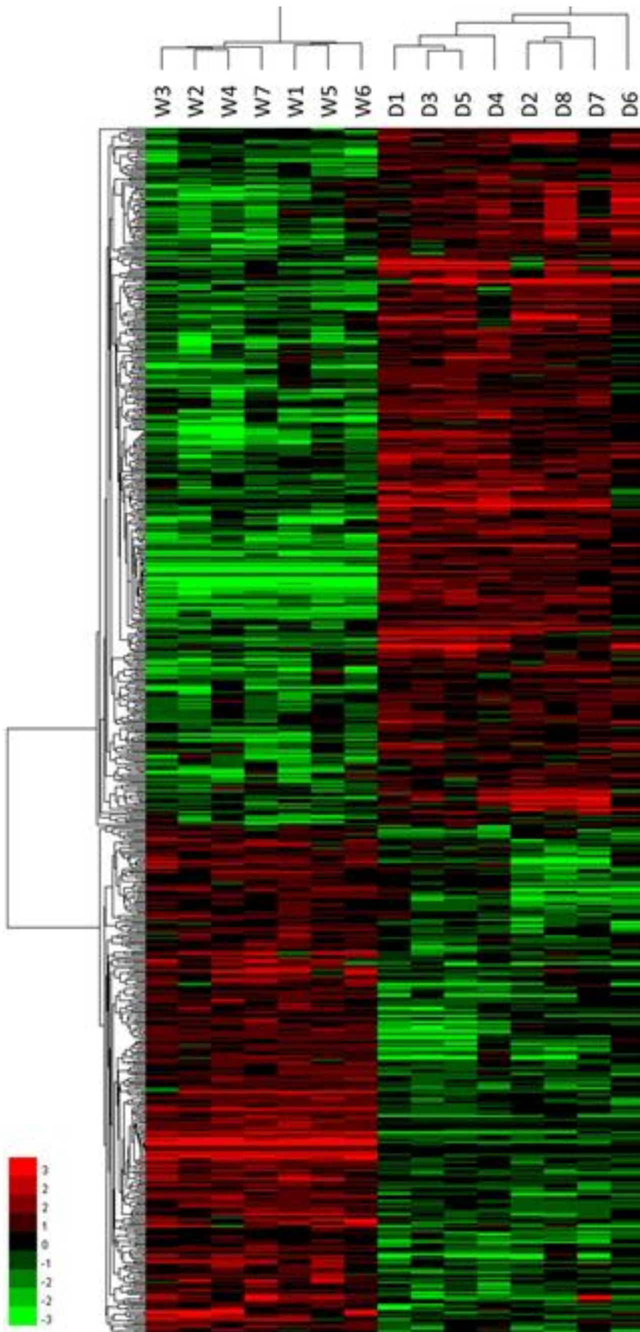


Figure 2. Unsupervised average linkage clustering of 710 differentially expressed genes. Each row represents the same gene, whereas each column represents an RNA sample with its symbol provided above the respective column. Samples W1–W7 represent the expression profile recorded in the wild population, whereas samples D1–D8 are the profiles for the domesticated population. The expression level for each gene is presented using a color intensity scale, where red and green represent over- and under-expression levels, respectively. Black color represents median abundance of the gene

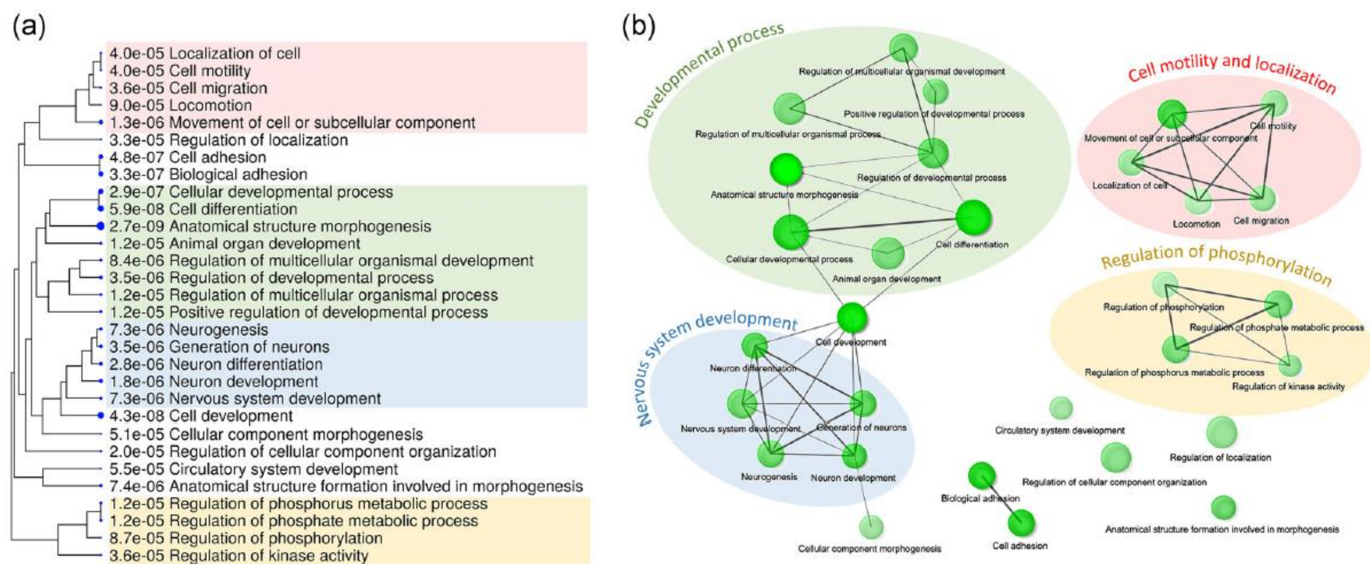
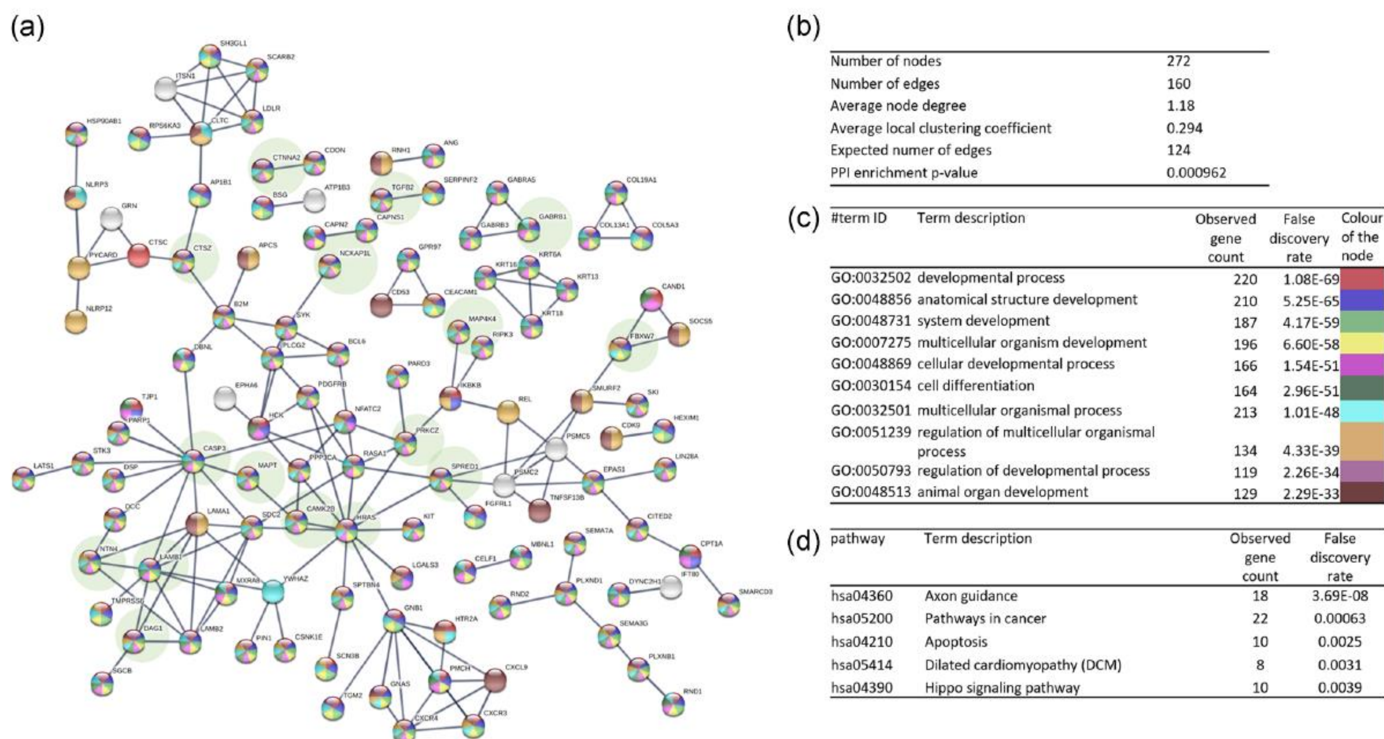


Figure 3. Results of clustering of 30 most enriched biological processes as assessed by gene ontology analysis (for details see Section 4.9),

where (a) shows a hierarchical clustering tree summarizing the correlation among the significant pathways listed in Figure S3 (pathways with many shared genes are clustered together; bigger blue dots indicate the higher significance of p values) and (b) shows the visualization of the relationship between the enriched pathways (two pathways [nodes] are connected if they share 50% or more genes; darker nodes are more significantly enriched gene sets; bigger nodes represent larger gene sets; thicker edges represent more overlapped genes). Areas shaded with the same color in panels a and b represent the same set of enriched pathways



(b)

Number of nodes	272
Number of edges	160
Average node degree	1.18
Average local clustering coefficient	0.294
Expected numer of edges	124
PPI enrichment p-value	0.000962

(c)

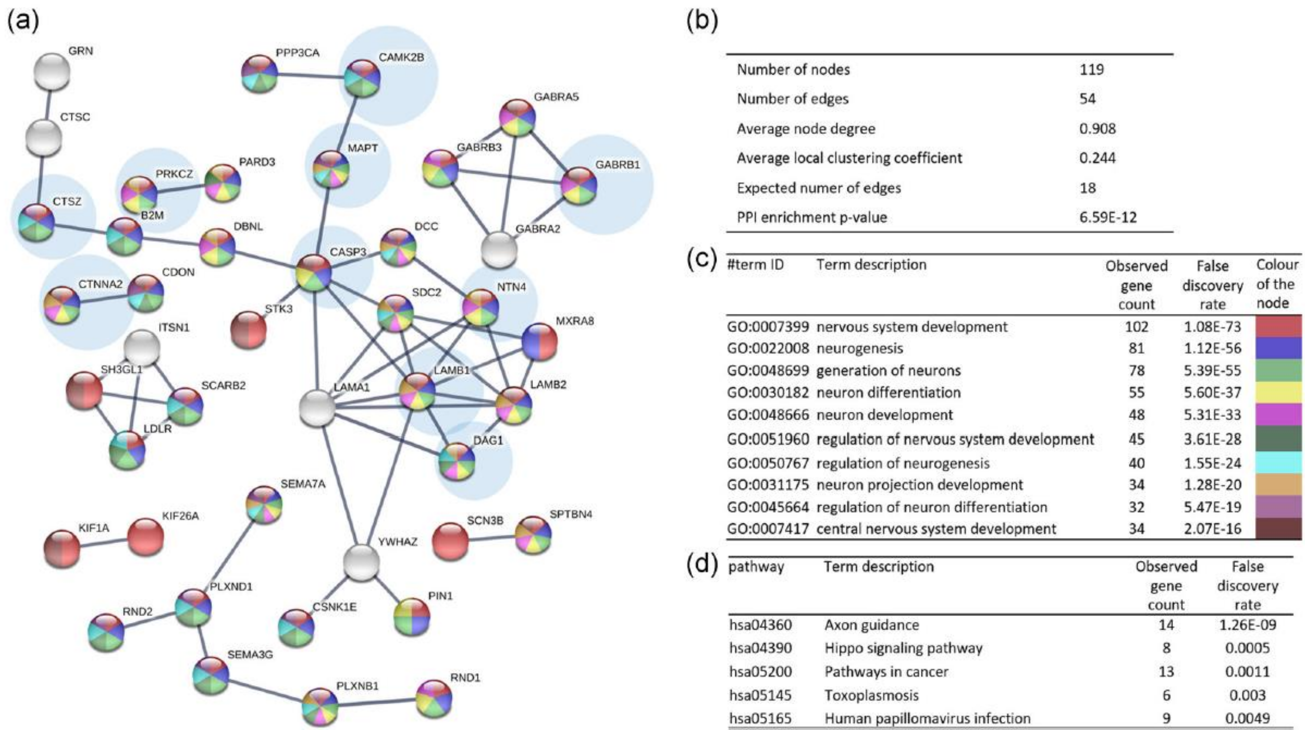
#term ID	Term description	Observed gene count	False discovery rate	Colour of the node
GO:0032502	developmental process	220	1.08E-69	
GO:0048856	anatomical structure development	210	5.25E-65	
GO:0048731	system development	187	4.17E-59	
GO:0007275	multicellular organism development	196	6.60E-58	
GO:0048869	cellular developmental process	166	1.54E-51	
GO:0030154	cell differentiation	164	2.96E-51	
GO:0032501	multicellular organismal process	213	1.01E-48	
GO:0051239	regulation of multicellular organismal process	134	4.33E-39	
GO:0050793	regulation of developmental process	119	2.26E-34	
GO:0048513	animal organ development	129	2.29E-33	

(d)

pathway	Term description	Observed gene count	False discovery rate
hsa04360	Axon guidance	18	3.69E-08
hsa05200	Pathways in cancer	22	0.00063
hsa04210	Apoptosis	10	0.0025
hsa05414	Dilated cardiomyopathy (DCM)	8	0.0031
hsa04390	Hippo signaling pathway	10	0.0039

Figure 4. Results of STRING (v 11.0) analysis

where (a) presents the functional protein association network of gene set recognized for being involved in the developmental process (for details see Figure 3) where nodes and gene names shaded in green indicate the genes chosen for qPCR validation; (b) network statistics; (c) 10 most enriched biological processes with an indication of gene ontology accession number (#term ID), number of genes involved in the particular process (observed gene count), FDR value of the enrichment analysis as well as color scale allowing identification of particular process on the nodes visualized in the association network (part a); (d) five most enriched KEGG pathways. FDR, false discovery rate; qPCR, quantitative polymerase chain reaction

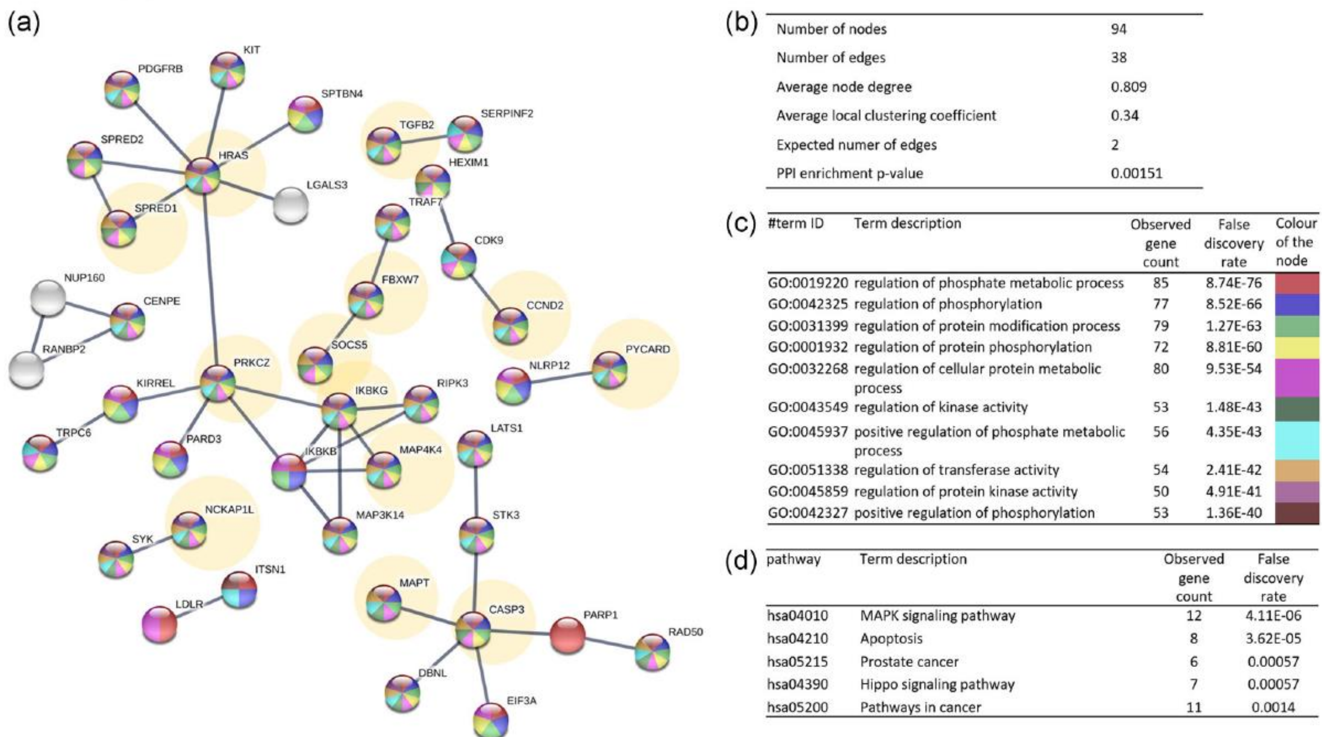


Number of nodes	119
Number of edges	54
Average node degree	0.908
Average local clustering coefficient	0.244
Expected numer of edges	18
PPI enrichment p-value	6.59E-12

#term ID	Term description	Observed gene count	False discovery rate	Colour of the node
GO:0007399	nervous system development	102	1.08E-73	
GO:0022008	neurogenesis	81	1.12E-56	
GO:0048699	generation of neurons	78	5.39E-55	
GO:0030182	neuron differentiation	55	5.60E-37	
GO:0048666	neuron development	48	5.31E-33	
GO:0051960	regulation of nervous system development	45	3.61E-28	
GO:0050767	regulation of neurogenesis	40	1.55E-24	
GO:0031175	neuron projection development	34	1.28E-20	
GO:0045664	regulation of neuron differentiation	32	5.47E-19	
GO:0007417	central nervous system development	34	2.07E-16	

pathway	Term description	Observed gene count	False discovery rate
hsa04360	Axon guidance	14	1.26E-09
hsa04390	Hippo signaling pathway	8	0.0005
hsa05200	Pathways in cancer	13	0.0011
hsa05145	Toxoplasmosis	6	0.003
hsa05165	Human papillomavirus infection	9	0.0049

Figure 5. Results of STRING (v 11.0) analysis
where (a) presents the functional protein association network of gene set recognized for being involved in the nervous system development (for details see Figure 3) where nodes and gene names shaded in blue indicate the genes chosen for qPCR validation; (b) network statistics; (c) 10 most enriched biological processes with an indication of gene ontology accession number (#term ID), number of genes involved in the particular process (observed gene count), FDR value of the enrichment analysis as well as color scale allowing identification of particular process on the nodes visualized in the association network (part a); (d) five most enriched KEGG pathways. FDR, false discovery rate; qPCR, quantitative polymerase chain reaction

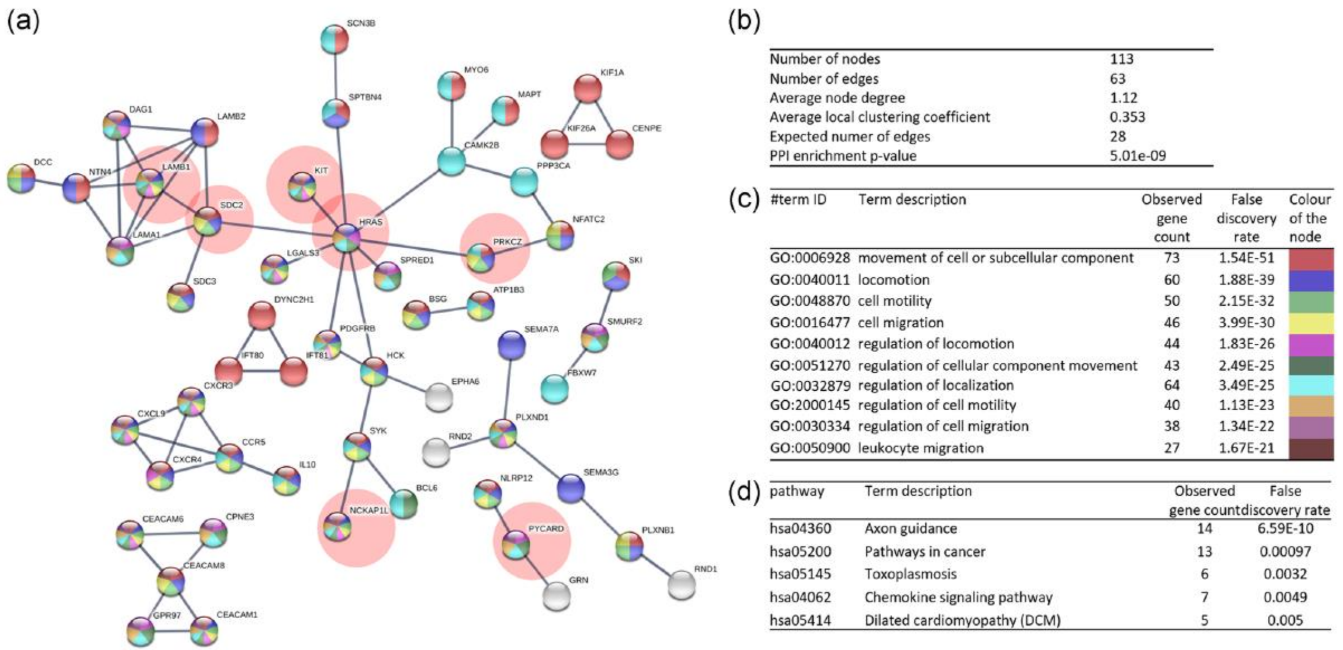


Number of nodes	94
Number of edges	38
Average node degree	0.809
Average local clustering coefficient	0.34
Expected numer of edges	2
PPI enrichment p-value	0.00151

#term ID	Term description	Observed gene count	False discovery rate	Colour of the node
GO:0019220	regulation of phosphate metabolic process	85	8.74E-76	
GO:0042325	regulation of phosphorylation	77	8.52E-66	
GO:0031399	regulation of protein modification process	79	1.27E-63	
GO:0001932	regulation of protein phosphorylation	72	8.81E-60	
GO:0032268	regulation of cellular protein metabolic process	80	9.53E-54	
GO:0043549	regulation of kinase activity	53	1.48E-43	
GO:0045937	positive regulation of phosphate metabolic process	56	4.35E-43	
GO:0051338	regulation of transferase activity	54	2.41E-42	
GO:0045859	regulation of protein kinase activity	50	4.91E-41	
GO:0042327	positive regulation of phosphorylation	53	1.36E-40	

pathway	Term description	Observed gene count	False discovery rate
hsa04010	MAPK signaling pathway	12	4.11E-06
hsa04210	Apoptosis	8	3.62E-05
hsa05215	Prostate cancer	6	0.00057
hsa04390	Hippo signaling pathway	7	0.00057
hsa05200	Pathways in cancer	11	0.0014

Figure 6. Results of STRING (v 11.0) analysis
where (a) presents the functional protein association network of gene set recognized for being involved in the regulation of phosphorylation (for details see Figure 3) where nodes and gene names shaded in yellow indicate the genes chosen for qPCR validation; (b) network statistics; (c) 10 most enriched biological processes with an indication of gene ontology accession number (#term ID), number of genes involved in the particular process (observed gene count), FDR value of the enrichment analysis as well as color scale allowing identification of particular process on the nodes visualized in the association network (part a); (d) five most enriched KEGG pathways. FDR, false discovery rate; qPCR, quantitative polymerase chain reaction



(b)

Number of nodes	113
Number of edges	63
Average node degree	1.12
Average local clustering coefficient	0.353
Expected numer of edges	28
PPI enrichment p-value	5.01e-09

(c)

#term ID	Term description	Observed gene count	False discovery rate	Colour of the node
GO:0006928	movement of cell or subcellular component	73	1.54E-51	
GO:0040011	locomotion	60	1.88E-39	
GO:0048870	cell motility	50	2.15E-32	
GO:0016477	cell migration	46	3.99E-30	
GO:0040012	regulation of locomotion	44	1.83E-26	
GO:0051270	regulation of cellular component movement	43	2.49E-25	
GO:0032879	regulation of localization	64	3.49E-25	
GO:2000145	regulation of cell motility	40	1.13E-23	
GO:0030334	regulation of cell migration	38	1.34E-22	
GO:0050900	leukocyte migration	27	1.67E-21	

(d)

pathway	Term description	Observed gene count	False discovery rate
hsa04360	Axon guidance	14	6.59E-10
hsa05200	Pathways in cancer	13	0.00097
hsa05145	Toxoplasmosis	6	0.0032
hsa04062	Chemokine signaling pathway	7	0.0049
hsa05414	Dilated cardiomyopathy (DCM)	5	0.005

Figure 7. Results of STRING (v 11.0) analysis
where (a) presents the functional protein association network of gene set recognized for being involved in the cell motility and localization (for details see Figure 3) where nodes and gene names shaded in red indicate the genes chosen for qPCR validation; (b) network statistics; (c) 10 most enriched biological processes with an indication of gene ontology accession number (#term ID), number of genes involved in the particular process (observed gene count), FDR value of the enrichment analysis as well as color scale allowing identification of particular process on the nodes visualized in the association network (part a); (d) five most enriched KEGG pathways. FDR, false discovery rate; qPCR, quantitative polymerase chain reaction

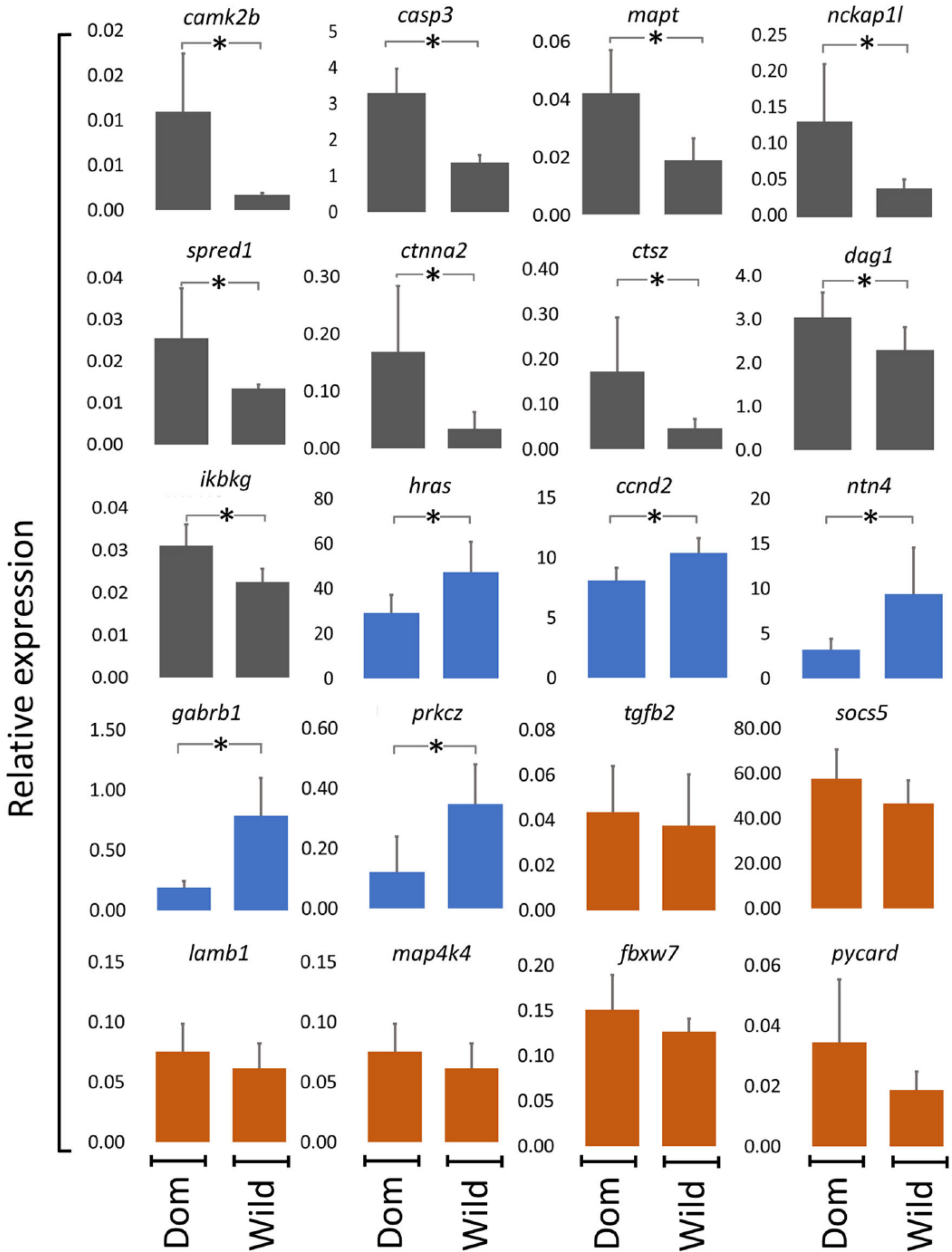


Figure 8. Results of qPCR validation of candidates' genes (as shown in Figures 3–5).
Data, expressed as mean ± SD, marked with an asterisk were statistically different ($p < .05$). Dark-gray and blue bars represent genes upregulated in eggs of domesticated and wild pikeperch, respectively. Orange bars represent genes expressed at a similar level in both—domesticated and wild fish. On the “x”-axis domesticated fish are abbreviated to “Dom”

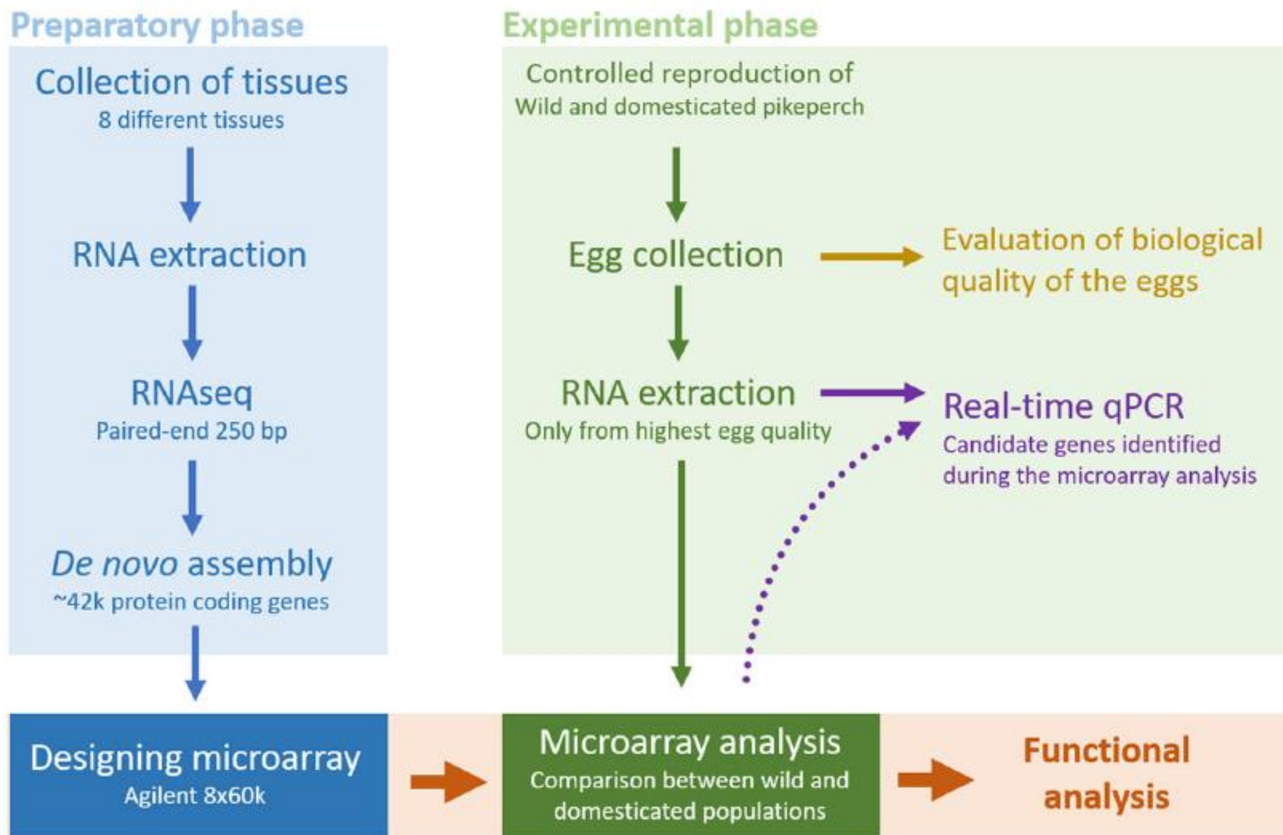


Figure 9. The experimental approach undertaken in the study. qPCR, quantitative polymerase chain reaction; RNA-seq, RNA-sequencing

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6. Acknowledgements

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