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Tatyana Gebauer (Vanina)

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CONTENT

CHAPTER 1

GENERAL INTRODUCTION

1.1. Growth of human population and wild stock exploitation

"Ten percent of the big fish still remain. There are still some blue whales. There are still some krill in Antarctica. There are a few oysters in Chesapeake Bay. Half the coral reefs are still in pretty good shape, a jewelled belt around the middle of the planet. There's still time, but not a lot, to turn things around."

– Sylvia Earle

During the 20th century, the human population had increased from about 1.6 billion in 1900 to over 6 billion in 2000 (Ramankutty et al., 2002; Cohen, 2003; Blanco et al., 2009). Moreover, it has been projected that the population will reach over 9 and 10 billion by 2050 and 2100, respectively (Borlaug, 2002; Roberts, 2011; Roser and Ortiz-Ospina, 2017). In 2009, an estimated 1.02 billion of people were undernourished (Pogge, 2016). If the population does grow by the projected pace, nourishing a population of 9 to 10 billion people seems to be a big challenge (Moffitt and Cajas-Cano, 2014). In order to feed this projected world population, 70% increase of global food production would be needed by 2050 (Roth, 2011). Hand in hand with increasing human population and the food supply, the world resources are under significant stress from over-exploitation, pollution and habitat destruction (Godfray et al., 2010; Tester and Langridge, 2010; Alexandratos and Bruinsma, 2012; Crist et al., 2017).

The evidence suggest that fish and seafood seems to be a better alternative to nourish the human population due to higher protein and energy retention (Björkli, 2002; Ytrestøyl et al., 2015) as well as lower carbon- and water- footprints (Mekonnen and Hoekstra, 2011; Ziegler et al., 2013; Béné et al., 2015). Furthermore, fish and other sea products provide excellent nutritional value, including high-quality easily-digestible protein, essential fatty acids, and wide variety of vitamins and minerals required by human body (Willett, 1994; Lichtenstein et al., 2006; Mozaffarian and Rimm, 2006; FAO, 2014). Nowadays, around 17% of global population's animal protein intake is covered by fisheries (FAO, 2018). Per capita fish consumption increased almost two times from 10 kg to 19 kg from 1960 to 2012 (FAO, 2014). It means, that expansion of human population and economic development will increase future world's demand for fish protein products (Merino et al., 2012).

The increased demand for fish products resulted in significant pressure on wild fish stocks (Stokes and Law, 2000; Jørgensen et al., 2007; Agnew et al., 2009; Helyar et al., 2014). According to FAO (2009), around 30% of wild stocks are already overfished, 60% reached their maximum feasible limit, and only 10% are being fished under their limit. In other words, the oceans cannot continue to supply the world's increasing demand for fish. Indeed, capture production has stabilized at about 90 million metric tons of fish since the late 1980s (FAO, 2018). Hence, aquaculture, defined as the farming of fish, crustaceans, molluscs, aquatic plants, algae, and other organisms, is increasingly considered to be a potential solution in the global malnutrition crisis and in the face of continued overexploitation of wild fish stocks (Naylor et al., 2000; Bostock et al., 2010). Tidwell and Allan (2001) stated that further fish supplies for human consumption is expected to come mainly from aquaculture.

1.2. Aquaculture growth – Europe has been side-lined

"Give a man a fish and you feed him for a day; teach a man to fish and you feed him for a lifetime."

– Chinese wisdom

Aquaculture is the fastest-growing food production sector globally, with an average increase of 8% in production of animal crops per year since 1970 (FAO, 2018). Indeed, over the past 50 years, aquaculture has grown dramatically and become an important part of overall global food production (Fontaine et al., 2009; Bostock et al., 2010). In 2014, aquaculture produced around 45% of all fish for human consumption and Msangi et al. (2013) modelled that the production would reach 93.6 million metric tons of fish and shellfish products by 2030, which is an increase of almost 25% of that reported by FAO (2016). To meet future demands for fish and shellfish products, aquaculture production would need to reach 140 million metric tonnes by 2050 (Waite et al., 2014).

While global aquaculture is growing steadily and a further growth is expected (Bostock et al., 2010), the European sector has been stagnating for the last decades (FAO, 2018) despite repeated policy initiatives to launch new growth in the industry (Nielsen et al., 2016). Large-scale growth of aquaculture in Europe has been hampered by a shortage of suitable sites and the ecological carrying capacity of existing ones (Simard et al., 2008), limited fresh water availability (Badiola et al., 2012), public criticism based on perceived environmental impact (Kaiser and Stead, 2002) as well as strict environmental regulation and bureaucracy (Nielsen et al., 2016). Therefore, innovative solutions offering long-term environmental, economic and social sustainability are required in order to increase aquaculture production (Alexander et al., 2015). Solutions such as integrated multi-trophic aquaculture, bio-floc technology and recirculating aquaculture systems (RAS) perform well across most indicators of productivity as well as environmental resources utilization (Waite et al., 2014; Alexander et al., 2015). Recirculating systems provide opportunities to reduce water usage (*e.g.* less than 1m^3 of water per kg sea bass, *Dicentrarchus labrax*, produced in RAS) (Metaxa et al., 2006) and to improve waste management and nutrient recycling, making RAS an intensive fish production system that is compatible with environmental sustainability (Timmons and Ebeling, 2007; Martins et al., 2010). This is particularly pronounced for freshwater RAS where the waste may be treated in regional waste water treatment facilities or may be used for agricultural purposes in the form of fertilizer or compost, while treatment options for waste from marine RAS are more limited (van Rijn, 2013). Furthermore, the energetic costs of osmoregulation in marine species ranging from 10% up to 50% of energy intake (Kirschner, 1993; Morgan and Iwama, 1999) makes favour the use of freshwater fishes in the RAS technology (Boeuf and Payan, 2001).

High capital costs are one of the biggest challenges to RAS calling for higher productive capacity to reduce payback period and operation costs (De Ionno et al., 2006; Martins et al., 2010; Dalsgaard et al., 2013). Another aspect improving the profitability is increasing the sale price of the product (De Ionno et al., 2006) supporting the rearing of highly valued species. Because over 75% of the European freshwater fish production is formed by two low/medium value species – common carp, *Cyprinus carpio* L., and rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) (Chiu et al., 2013; Dalsgaard et al., 2013; Żarski et al., 2017), the diversification of European aquaculture is inevitable (Fontaine et al., 2009; Schmidt et al., 2011). Indeed, Le François et al. (2010) pronounced the diversification of aquaculture as a necessary prerequisite for ensuring a sustainable development of the industry.

1.3. Diversification of European aquaculture

The main issue concerning the aquaculture diversification is the rational selection of suitable species for particular market (Le François et al., 2010). Naylor et al. (2000) proposed rearing of low-trophic species for development of sustainable aquaculture justified by significantly lower needs for valuable fish meal and fish oil in nutrition of herbivorous species. However, several difficulties come up with rearing of the herbivorous species. According to Behrens and Lafferty (2007) herbivorous species possess physiological limitation in digestibility of plant protein at low temperatures and, therefore, display better performances at higher temperatures. Moreover, hand in hand with economic growth, the consumer preference is shifted towards higher-trophic carnivorous species making herbivorous species less desirable and requested in European market (Le François et al., 2010; Waite et al., 2014).

The diversification of aquaculture may also collide with national legislation that prevents introduction of non-native species due to protection of native biodiversity. Furthermore, alien species may not show good growth performances or be socially acceptable in their new environment as in their home range (Harvey et al., 2017). While native species may require investments (*e.g.* development of rearing protocols, new technologies), their usage may be still less demanding compared to the introduction and the transfer of non-native species. Moreover, selling the species that consumers are already familiar with is easier than promoting a non-native species (Harvey et al., 2017).

Higher-trophic species native in Europe, therefore, seems to be the right fit for European aquaculture diversification. In the last decades, European perch, *Perca fluviatilis* L. has been referred to as one of the promising candidates for freshwater aquaculture diversification in Europe (Kestemont and Mélard, 2000; Watson, 2008).

1.4. European perch, *Perca fluviatilis*, general information

The European perch is the most common and widely distributed member of the perch family (Thorpe, 1977; Stepien and Haponski, 2015). Originally widespread throughout Europe and Asia, European perch has been also successfully introduced in other parts of the world including South Africa, Australia, New Zealand, Siberia and Southern Europe (Collette and Bănărescu, 1977; Thorpe, 1977; Stepien and Haponski, 2015). The introduction of the European perch into a broad variety of habitats located in different latitudes was allowed by its high phenotypic plasticity and tolerance to wide ranging environmental conditions (Karås and Hudd, 1993; Nesbø et al., 1999; Stepien et al., 2015).

European perch is important both commercially and ecologically (Pukk, 2016). The flesh display excellent dietetic and sensory qualities reflecting high market demands particularly in Alpine and Nordic areas of Europe (Ljunggren et al., 2003; Stejskal et al., 2009; Król and Zieliński, 2015). Additionally, European perch is a targeted game species throughout Europe (Heermann et al., 2013; Vainikka et al., 2016). European perch is also appreciated by ecologists due to its biomeliorative capacity for the regulation of zooplanktivores (*e.g.* roach *Rutilus rutilus* (L.)., bream *Abramis brama* (L.), topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846) and ruffe *Gymnocephalus cernua* (L.) in production ponds (Adámek et al., 2010). Indeed, in the Baltic coastal zone, the formerly dominant European perch has shown strong regional declines since the early 1990s (Nilsson et al., 2001; Adjers et al., 2006) resulting in an increase of the primary production because of the disrupted top-down control (Eriksson et al., 2009).

1.5. European perch production and market

The European perch capture production remains stable and does not exceed 34 000 metric tonnes (FAO, 2016). The main producers are the Russian Federation (42%; 13 196 tonnes in 2016), Finland (30%; 9 382 tonnes in 2016), Sweden (10%; 3 318 tonnes in 2016), Estonia (8%; 2 407 tonnes in 2016) and Poland (4%; 1 114 tonnes in 2016). Although Finland produces almost one third of the global European perch production, the majority of the production is designated for home market needs, while only a small fraction of the production is exported to French and Swiss markets (Toner, 2015; FAO, 2016).

The European perch aquaculture production amounted 585 metric tonnes in 2016 (FAO, 2016). The large part of this production was from Switzerland, the Russian Federation and Kazakhstan (together 549 tonnes), while the rest of the production came from the EU countries (Bulgaria, Czech Republic, Denmark, Italy, Romania). According to Toner (2015), the biggest European perch farms in Europe are Valperca SA in Switzerland, Lucas Perche in France and Clune Fisheries Ltd in Ireland, however the data on European perch production are not available for France and Ireland in the FAO report (2018). Therefore, it is possible that the actual European perch aquaculture production is higher than reported by FAO (2018).

According to FAO (2018), the price for 1 kg of perch has considerably increased from 2007 to 2016. In 2007, the price of European perch was 2.08 USD per 1 kg (311 metric tonnes with a production value of 647 000 USD), while in 2016, the price was 6.36 USD per 1 kg (585 metric tonnes with a production value of 3 741 000 USD), *i.e.* a 3 fold increase in the relative production value of the European perch. This increase might be caused by boosted market demands for this species due to customers' preferences.

Nowadays, the European perch is appreciated by consumers throughout Europe and particularly in Alpine areas and can be supplied as fillets or whole fish depending on regional demands (Tamazouzt et al., 1993). The size of fish required by Alpine markets (Switzerland, and parts of France, Italy, Germany, and Austria) is usually <150 g, while bigger fish (>250 g) are preferred in Nordic markets (Finland, Iceland, Norway, Denmark and Sweden). A comparison of perch prices in various retail stores in the main European markets showed that retail prices for European perch products in EU supermarkets varied considerably by country and by product form. One of the highest prices for frozen pre-packaged fillets were recorded in Finland (€27.50–28.30), Germany (€22.00) and Italy (€21.30). Frozen European perch fillets were sold for €14.00 in Greece and €11.00 in Portugal, while fresh perch (loose, not pre-packaged) could be found for €9.40 in Poland (Eurofish, 2017).

1.6. European perch aquaculture systems

In general, European perch can be reared using three different production systems, *i.e.* extensive ponds, semi-intensive cages, and intensive RAS (Kestemont et al., 2008; Policar et al., 2008). Furthermore, combination of production systems during different ongrowing phases was successfully employed in many countries including Sweden (Őberg, 2008), Germany (Schmidt and Wedekind, 2008) and the Czech Republic (Policar et al., 2009).

1.6.1. Extensive pond culture

Traditionally, the European perch has been cultured extensively in ponds with other fish species, mainly with cyprinids (*e.g.* in the Czech Republic, Slovakia, Poland). In these polycultures, European perch represents about 2-5% of fish stock (Kestemont et al., 1996). However, in some cases (fingerling production), European perch is a highly undesirable fish

species because it competes for food with commercially important fishes or predates on their early life stages (Kestemont et al., 2008). In ponds, the European perch is harvested generally twice per year during autumn and spring (Adámek et al., 2012; Kratochvíl, 2012), *i.e.* such production does not meet the year-round supply. Nowadays, the European perch is produced both in polycultures with other species and in monocultures in small ponds (*e.g.* in France, Czech Republic, Ireland). Considerable share of European perch production in polyculture comes from ponds in Russia, Romania, Latvia, Italy and Bulgaria (Policar et al., 2008).

The benefits of pond culture include the maintenance of broodstock on natural food source and the suitability of pond-reared fish for restocking programmes (Kestemont et al., 2008). On the other hand, the disadvantages lie in the slow growth, sensitivity to water quality and pathogens (Policar et al., 2009; Żarski et al., 2017).

1.6.2. Semi-intensive cage culture

Semi-intensive cage production of European perch has not been widely used in a full commercial operation but it was applied in Switzerland, Sweden and in France as an experimental pilot scale at the fishfarm (Tamazouzt et al., 1996; Kestemont et al., 2008; Policar et al., 2015).

Despite the fact that this rearing method has several advantages (*e.g.* low production cost, maintenance in natural environment), it is not suitable for large-scale year-round commercial production due to slow growth induced by water quality fluctuations and low survival rates caused by disease and parasite outbreaks as well as cannibalism (Policar et al., 2015). Indeed, Fontaine et al. (1996) highlighted that usage of cage system can be economically applicable for a short production cycle from June to September. Ceccuzzi et al. (2010) found the cage culture to be beneficial for the production of fingerlings for restocking programmes.

1.6.3. Intensive RAS culture

Recirculating systems have been proven successful for the production of freshwater and marine species as they enable intensive predictable year-round production by means of water quality control, out-of-season reproduction, effective hygiene and disease management while decreasing the environmental pollution (Martins et al., 2010). Stable RAS conditions enable a) to increase the production level (*e.g.* by reducing water consumption, control of recycling of nutrients and improving waste management, stable temperature maintenance, better hygiene and disease management) b) easier monitoring and preventing fish escapes compared to ponds and cages c) more predictable production, reducing the fish stress and controlling of cannibalism d) culture fish during all year and completely control of the rearing process (Piedrahita, 2003; Tal et al., 2006; Verdegem et al., 2006; Kestemont et al., 2008; Summerfelt et al., 2009; Martins et al., 2010).

European perch was introduced in RAS in the early 1990s (Toner, 2015). These systems offer wide range of benefits limiting the success of previous rearing methods, such as faster growth rate, higher survival rate and shorter cycle production by reducing time to reach the marketable size (80–100 g) from 14 months to 9 months (Policar et al., 2015; Żarski et al., 2017).

Despite these advances, the production of European perch in RAS conditions still fails to meet the market demands (Kestemont et al., 2015). One of the reasons of limited European perch production in RAS is the lack of clear and standardized reproductive and rearing protocols (Kestemont and Mélard, 2000; Żarski et al., 2017). Moreover, the development of the European perch culture is hindered by several critical factors in the life cycle and breeding

performance of the current stocks. These hindrances include asynchronous spawning, small size and fragility of the larvae, their dependence on live food, small mouth gape size, high larval mortality, swim bladder inflation failure, high growth heterogeneity and cannibalism (Overton and Paulsen, 2005; Policar et al., 2008; Rougeot and Mélard, 2008; Kestemont and Henrotte, 2015).

1.7. Bottlenecks in intensive culture of European perch

1.7.1. Survival and growth rates

It is widely accepted that the survival and growth rates of the European perch are influenced by the water temperature. Significantly higher growth rate was observed with increasing temperature up to 22 to 24°C. Indeed, Karås and Thoresson (1992) showed higher feed intake between 23°C and 28°C. On the other hand, low temperature (17°C) was found to increase the survival rate and reduce the cannibalism occurrence of the European perch (Mélard et al., 1996; Kestemont et al., 2003). In RAS, the European perch cultured at 23°C could reach the minimal commercial marketable size (100 g for Alpine countries) in 9 months (Mélard, 2008). The European perch was also successfully reared at lower temperatures (ranging from 11°C to 20°C), however these temperature ranges are not suitable for intensive productions due to significant reduction in growth rate (Kestemont and Mélard, 2000).

Tank colour has been proven as an important factor influencing the food intake and consequently growth and survival rates of the European perch. According to Tamazouzt et al. (2000) higher growth and survival rates were obtained in white and light grey tanks. Strand et al. (2007) documented that food intake was significantly higher in white and grey tanks compared to black ones due to increased feed visibility caused by higher contrast in lighter tanks. Both results were obtained under low light intensity around 250 lx. Contrary, Jentoft et al. (2006) recorded higher growth rate in European perch larvae reared in black tanks. Finally, Staffan (2004) found no significant difference in growth rate among white, grey and black wall tank colours, however it was noticed that lower light intensity is preferable for reducing stress in perch. Kestemont et al. (2003) also noted that the light intensity did not significantly affect the survival, cannibalism and size heterogeneity.

Survival and growth rates in the European perch are also improved with increasing photoperiod (Kestemont et al., 2003). Jourdan et al. (2000) confirmed that increased day length from 12L:12D to 18L:6D or 24L:0D induced significantly higher specific growth rate and lower coefficient of variation in weight, without any differences between the latter two light regimes. However, continuous daylight slightly decreased the survival rate. Therefore, the photoperiod from 12L:12D to 18L:6D with light intensity of 250 lx at water surface were cited as favourable for the European perch rearing conditions in intensive aquaculture and were widely used in other studies (Jacquemond, 2004b; Strand et al., 2007; Stejskal et al., 2009). Improving rearing performances trough increasing day length had also been shown in yellow perch *Perca flavescens* (Mitchill, 1814) (Huh et al., 1976), Atlantic cod *Gadus morhua* L. (Folkvord and Otterå, 1993) and rabbitfish *Siganus guttatus* (Bloch, 1787) (Duray and Kohno, 1988).

1.7.2. Growth heterogeneity and cannibalism

Size heterogeneity of newly hatched European perch sibling larvae is shown to be low (Babiak et al., 2004). Relatively small larvae (5.4 mm and 0.7-0.8 mg) are dependent on specific high quality live food because they are visual predators (Craig, 1987). Under intensive aquaculture conditions the European perch larvae are fed with *Artemia* spp. nauplii during the first feeding but according to Kestemont et al. (1996), *Artemia* spp. nauplii is not optimal feed due to not appropriative size for the mouth gape of the larvae. Although feeding the European perch larvae using the *Artemia* spp. nauplii presents advantages such as overall market availability and easy culture (Vlavonou et al., 1999), only 60 to 70% of the larvae are able to ingest the *Artemia*. Low feeding level or starvation may induce high level of mortality and size heterogeneity among larvae boosting the cannibalism activity and disease susceptibility (Mélard et al., 1996; Lahnsteiner and Kletzl, 2018). European perch larvae also accept rotifers and formulated dry feed, however they are not widely used due to lower growth and survival rates compared to those obtained with *Artemia* nauplii (Tamazouzt et al., 1998; Overton and Paulsen, 2005).

Cannibalism at the larval stage is more dramatic compared to the juvenile stage. This stems from the fact that the larvae have a large mouth gape relative to their body size and they can prey on larvae that are just a little smaller (Baras, 1998). In European perch larvae rearing, cannibalism-induced losses can amount to more than 50% of the initial density (Baras et al., 2003; Babiak et al., 2004; Król et al., 2015). According to Kestemont et al. (2003), in the first several days post-hatching (dph), when the size heterogeneity among larvae is low, type I cannibalism prevails (incomplete ingestion of prey, mainly abdomen or tail), while older larvae and juveniles shift to cannibalism type II (total prey ingestion). Cannibalism is facilitated by the size heterogeneity but at the same time it contributes to more heterogeneous fish stock, since larger individuals consume smaller ones while growing faster (Brabrand, 1995; Baras and Jobling, 2002; Kestemont et al., 2003). It has therefore been proposed, that removal of the larger fish decreases the size heterogeneity and consequently the cannibalism rate (Baras and Jobling, 2002). However, Kestemont et al. (2003) and Mandiki et al. (2007) have shown that the frequent removal of larger individuals did not mitigate the cannibalism rate and did not improve neither the survival nor the growth rates, probably due to re-establishment of new hierarchies. Hence, effectiveness of the size-sorting practices in hatchery of the European perch is a highly discussed issue.

Nowadays, cannibalism is identified as a foraging strategy and rather influenced by environmental factors (*e.g.* food availability, size heterogeneity, stock density, size-sorting) than genetic ones (Svenning and Borgstrøm, 2005; Baras et al., 2013; Król et al., 2014; Król and Zieliński, 2015). According to Mélard et al. (1996), higher cannibalism rate was observed at low stocking densities due to the development of dominance and hierarchies among the European perch larvae resulting from the number of available territories in a limited space. On the other hand, with higher stocking density, the cannibalism decreases while the survival and growth rates increase (Kestemont et al., 1996; Kestemont et al., 2003). In contrast, Król and Zieliński (2015) found that higher density did not result in reduction of cannibalistic behaviour.

1.7.3. Swim bladder inflation

Swim bladder inflation (SBI) is an important process in the larval phase of the European perch. The individuals with non-inflated swim bladder (NISB) display poor growth and low survival rate and often develop malformations of the vertebral skeleton (Jacquemond, 2004b). Fish with NISB make substantial effort to maintain neutral buoyancy position and spend more energy for swimming and capturing the food, which often results in starvation (Summerfelt, 1996). Moreover, due to poor swimming ability and unbalanced swimming behaviour, the individuals with NISB become easy prey for cannibals (McElman and Balon, 1979). The failure of SBI was also reported in larvae of other fishes, such as the yellow perch, the pikeperch *Sander lucioperca*I (L.), walley *Stizostedion vitreum* (Mitchill, 1818), the striped bass *Morone saxatilis* (Walbaum, 1792), the gilthead sea bream *Sparus aurata* L., the Japanise amberjack *Seriola quinqueradiata* Temminck and Schlegel, 1845 and many other fish species (Chapman et al., 1988; Chatain and Ounais-Guschemann, 1990; Marty et al., 1995; Sakakura and Tsukamoto, 1998; Demska-Zakes et al., 2003; Czesny et al., 2005).

Swim bladder inflation takes place after the initial exogenous feeding (about 3rd–4th dph in the European perch). The larvae swim towards the water surface and try to gulp air bubble to fill the swim bladder connected with the digestive system through the pneumatic duct (Egloff, 1996). It has been conjecture to state that the SBI ended with atrophy of the pneumatic duct, in fact the pneumatic duct is still present when SBI ceases (Marty et al., 1995). Although Egloff (1996) considered that the inflation status of the European perch was found to be fixed after 21st dph, the observations of Jacquemond (2004b) showed that the European perch juveniles were able to inflate their swim bladder beyond the 30th dph. Late SBI, however, resulted in lower growth rate (Jacquemond, 2004a; Jacquemond, 2004b).

The SBI failure is often caused by the contamination of water surface by oil increasing the surface water tension and preventing the fish larvae to gulp air bubbles (Boggs and Summerfelt, 1996; Laramée et al., 2016). An alternative reason of SBI failure results from bacterial aerocystitis, an inflammation of the swim bladder epithelium due to ingesting partially decomposed feed which is heavily contaminated with microbes and fungi (Marty et al., 1995). Nowadays, spray flow and surface skimmers are employed in order to avoid the accumulation of an oil film at the water surface while reducing the risk of NSBI and skeletal deformities (Kestemont et al., 2008). The disadvantage of using surface skimmer devices lies in the creation of turbulence at the surface that may lead to high larvae mortality as the larvae become disoriented in the skimmers.

According to Woolley and Qin (2010) effectiveness of SBI varies with changes in photoperiod, light intensity and temperature. Palińska-Żarska et al. (2019) observed higher SBI rate and survival in European perch larvae reared in black tanks at 15°C with a photoperiod of 24L:0D and the light intensity of 1500 lx at the water surface compared to white tanks at 20°C and 25°C. These rearing conditions are recommended for at least 12 dph in order to achieve the highest effectiveness of SBI rate.

1.8. Variation of key traits among different European perch populations

Several studies have determined that presence of traits desirable for aquaculture can vary between geographically distinct wild populations, *e.g.* in Coho salmon *Oncorhynchus kisutch* (Walbaum, 1792) and striped bass (Nicieza et al., 1994a; Nicieza et al., 1994b; Conover et al., 1997; Brown et al., 1998). The geographic differentiation of key traits for aquaculture means that choosing wild European perch population displaying optimum survival, growth, and cannibalism rates in aquaculture conditions may be important for the establishment or enhancement of fish broodstock, as was already shown for yellow perch (Rosauer et al., 2011; Rosburg, 2017). The selection of stock(s) with better growth traits may ultimately help to overcome current bottlenecks in the European perch aquaculture.

Several hypotheses have been put forward to explain geographic differentiations of the phenotypic traits desirable for aquaculture (Mandiki et al., 2004; Rosauer et al., 2011). Population differences in specific traits could be linked to phenotypic plasticity (due to differences in habitat environment, feeding regime, predation pressure, competition *etc.*) and heritable differences or genetics among isolated populations (Purchase et al., 2005; Olsson and Ragnarsson, 2006; Pigliucci et al., 2006; Tremblay et al., 2008; Parker et al., 2009; Wang et al., 2009) or their combination (Avise, 2000; DeWitt and Scheiner, 2004). In wild populations, phenotypic plasticity and adaptive differentiation allow the fish to adapt to changing conditions and stressors such as predators, competitors, and habitat change (Stearns, 1989; Hori, 1993; Magnhagen and Heibo, 2004; Olsson and Eklöv, 2005), however, long-term selection pressure can lead to genetic specialization and development of differing genetic stocks even at small spatial scales (Scheiner, 1993; Smith, 1993; Gerlach et al., 2001; Olsson, 2006; Bergek and Björklund, 2009; Bergek and Olsson, 2009).

To find out whether differences in growth traits are due to genetic differentiation or due to phenotypic plasticity, common garden experiment or capture of different populations in standardised conditions should be applied (West-Eberhard, 2003; West-Eberhard, 2005). Since allopatric populations are placed in the same environment, one would expect phenotypic variation and potential consequent differences in aquaculture performance to occur among genetically differentiated populations (see section 1.9 about genetic differentiation in European perch populations).

Earlier studies comparing survival, growth, cannibalism and SBI success among allopatric European perch populations have used common garden conditions which reduced environmental effect (Mandiki et al., 2004; Pimakhin and Zák, 2014). Study of Mandiki et al. (2004) highlighted significant differences in growth performances between four geographically different European perch stocks reared in RAS at 23°C. At the larval- and juvenile-stages, survival rate and body weight were significantly higher in populations from Belgium and North-East France than in South-West France and North Italy. In another experiment, the comparison of the European perch stocks growth performances from Finland and Belgium showed higher growth rate and feed intake in Finish stock at the end of juvenile stage (Mandiki et al., 2004). Similarly, differences in growth and SBI success between twenty two allopatric populations were found by Pimakhin and Zák (2014). However, previous studies did not assess the genetic differentiation between studied populations.

1.9. Evolution and genetic differentiation of European perch

According to the DNA data the *Perca* genus separated out the European perch from nearest relatives the yellow perch and the Balkhash perch *Perca schrenkii* Kessler, 1874 (Stepien et al., 2015). Recent fossil record calibration data presented by Stepien et al. (2015) indicated that ancestral *Perca* originated approximately 19.8 million years ago during the Miocene Epoch what is consistent with the age of the oldest fossil perch records in the Crimea (Lebedev, 1952) and France (Mein et al., 1983). Therefore, it was suggested by Collette and Bănărescu (1977) and Stepien et al. (2015) that ancestral perch first appeared in the waters of Europe. However, Carney and Dick (2000) assumed the North America or Europe as an option of the first ancestral perch appearance based on the hypothesis and fossil evidences of *Perca* origin and distribution. Three different hypothesis were proposed in order to explain the origin and distribution of *Perca* genera ancestors.

McPhail (1970) and Collette and Bănărescu (1977) believed that perch ancestors moved east from Europe to Siberia and from there dispersed into North America over the Beringia Land Bridge. The presence of perch in the Eastern Siberia was supported by archaeological records of *Perca* fossil and is estimated at the Pleistocene Epoch. Despite this *Perca* fossil found in Siberia, Carney and Dick (2000) questioned the hypothesis of *Perca* penetration to the North America over the Beringia Land Bridge due to glaciation periods during the Pleistocene Epoch. Carney and Dick (2000) alluded that it was improbable to use this route for farther dispersal of the ancestral perch from Siberia to the North America since the glaciers presented a barrier for its movement over the Beringia Land Bridge.

Another hypothesis shown ancestor perch migrating to the North America from Europe when the North Atlantic Land Bridge between Europe and North America still existed, this dispersion has given a boost to the differentiation between European perch and yellow perch linage. Afterwards, the North Atlantic Land Bridge between continents was interrupted and percid fauna evolved independently. During the Oligocene Epoch with the disappearance of the Oblik Sea between Europe and Asia, the ancestral perch moved east to Siberia (Stepien et al., 2015).

The last hypothesis, was referred to Percidae as a widespread Laurasian clade when North America and Europe were still connected across the North Atlantic (Wiley, 1992; Carney and Dick, 2000). This hypothesis required ancestral perch to be at least as old as early Oligocene Epoch when Europe was still separated from Asia by the Oblik Sea but was connected to the North America through Greenland. Additionally, the evidence of most fossils find of freshwater species including *Perca* were found located in the Western North America whose existence was estimated to be between the late Cretaceous and early Quaternary (Carney and Dick, 2000). Therefore, *Perca* may have inhabited in the North America and Europe what makes complicated the determination of *Perca* origin in the North America or European landmass.

Due to the most recent Pleistocene Ice Age perches as well as other aquatic species migrated to south waters of the ice sheets and concentrated in restricted areas known as glacial refugia (Hocutt and Wiley, 1986). These glacial refugia shaped the habitats of the European perch and influenced broad scale patterns of genetic diversity (Nesbø et al., 1999). Mitochondrial DNA and RAPD markers analyses of different European perch populations over Europe and one from Siberia revealed relatively recent ancestral recolonization patterns in connection with Pleistocene period of glaciations. Four main European perch colonization refugia were allocated by Nesbø et al. (1999). Phylogenetic analyses depicted the Danube haplotype as the most ancient haplotype and it is presumed that Danubian origin is plausible for the whole present perch linages presented in Nesbø et al. (1999). Low level of differentiation was found between Siberian and Eastern European perch populations what might be attributed

to recent dispersal of this population from Europe. This is in agreement with the hypothesis of geographical distribution of perch (Carney and Dick, 2000; Stepien and Haponski, 2015). However, only one Siberian population was used in the study and therefore other sampling sites from Siberia are required.

1.10. Objectives of the Ph.D. thesis

The present Ph.D. thesis is devoted to the comparison of growth traits of European perch from different Central and North populations in standardised RAS conditions and assessment of the hypothesis that aquaculture performances differ between genetically differentiated fish groups. Following specific objectives guided our study:

1. Highlighting the geographic differentiation in keys traits for aquaculture.
2. Estimation of the genetic differentiation between populations using four mitochondrial markers.
3. Comparison of survival, growth parameters, and cannibalism among allopatric European populations through a transplant experimental design placing each population in the same standardized conditions.

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CHAPTER 2

SEEKING FOR THE INNER POTENTIAL: COMPARISON OF LARVAL GROWTH RATE BETWEEN SEVEN POPULATIONS OF *PERCA FLUVIATILIS*

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EUROPEAN PERCID FISH CULTURE

Seeking for the inner potential: comparison of larval growth rate between seven populations of *Perca fluviatilis*

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Abstract

Larval rearing is a crucial step in fish production. However, issues in larval production, such as low growth/survival rate, impede the aquaculture development of many species including *Perca fluviatilis*. Since allopatric populations of *P. fluviatilis* exhibit different growth rates for first-life stages, basing fish stocks on populations displaying optimal features in aquaculture conditions could overcome some of these issues. Here, we (i) compare the growth rate in standardised re-circulating aquaculture system conditions and (ii) assess the genetic differentiation using four mitochondrial markers between seven allopatric populations. Our results confirm that key features for aquaculture can vary at the intraspecific level. However, we do not highlight any clear aquaculture trait differences related to genetic differentiation. Therefore, we cannot assess the genetic basis of growth rate differentiation between populations. This paves the way to future studies on aquaculture performances of genetically distinct populations in *P. fluviatilis*.

Keywords European perch · Genetic differentiation · Growth rate · mtDNA · Origin · Population

Introduction

Nowadays, a trend to diversify the aquaculture industry through new species production is emerging (Fontaine et al. 2009). It aims at promoting the sustainability of aquaculture and

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meeting today's and tomorrow's challenges (e.g. adaptation to environmental and consumer demand fluctuations, food security promotion) (FAO 2016). Such a diversification implies controlling the life cycle of new species in captive environments which is often challenging (Teletchea and Fontaine 2014). Larval rearing is one of the most crucial steps in this control. Indeed, issues in larval production impede the production development of many species including several percid fishes (Szkudlarek and Zakęś 2007; Dąbrowski et al. 2000). The European perch (*Perca fluviatilis*) exemplifies the difficulty and the importance of larval rearing.

The *P. fluviatilis* aquaculture development started during the last decades of the second millennium (Kestemont et al. 2015). Most of its current production relies on intensive re-circulating aquaculture systems (RAS) (Toner 2015). Despite an increasing consumer interest, this production fails to meet market demands (Kestemont et al. 2015). This is mainly due to several bottlenecks in life cycle completion in captivity and rearing performances, especially at first-life stages: low growth rate, low survival rate, high cannibalism rate, as well as dependence on live food of larvae (Kestemont et al. 2015).

In order to overcome larval rearing issues, one solution could rely on choosing wild or farmed populations displaying optimal survival, growth, and cannibalism rates in aquaculture conditions to create farmed stocks. Indeed, European perch populations from different geographic areas exhibit different growth rates and feed efficiencies for first-life stages (Mandiki et al. 2004). Similarly, differences in growth and swim bladder inflation rate are known between different larvae populations (Pimakhin and Žák 2014). Therefore, using fishes from populations with better performances at the larval stage could improve nursery of *P. fluviatilis* and allow choosing the best fish stocks for fish farming selective–breeding program. However, few *P. fluviatilis* populations have been compared to date (i.e. Mandiki et al. 2004; Pimakhin and Žák 2014). Moreover, the genetic distinctiveness of these previously studied populations has not been investigated (Mandiki et al. 2004; Pimakhin and Žák 2014) even though such information would be the first hint that population-specific aquaculture performance could be potentially heritable.

Here, we compare the growth rate at first-life stage of *P. fluviatilis* from seven different Central and North European populations in standardised RAS conditions. Furthermore, we estimate the genetic differentiation between populations using four mitochondrial markers in order to assess the hypothesis that aquaculture performances differ between genetically differentiated fish groups.

Materials and methods

Sampling and rearing

In May 2017, we sampled egg ribbons (i.e. 10 ribbons per population) of wild European perch from seven wild locations (Fig. 1). All ribbons were transported by car except for Finnish populations which were transported by plane (see the transport length in Table 1). These ribbons were transported (in oxygenated polyethylene bags filled with 1/3 of water, 2/3 of oxygen; 16 ± 1 °C and placed in thermobox) to the Institute of Aquaculture and Protection of Waters, Faculty of Fisheries and Protection of Waters (University of South Bohemia, Czech Republic). After transportation, we determined the development stage by randomly sampling 150 eggs per population and comparing them to a background developmental table

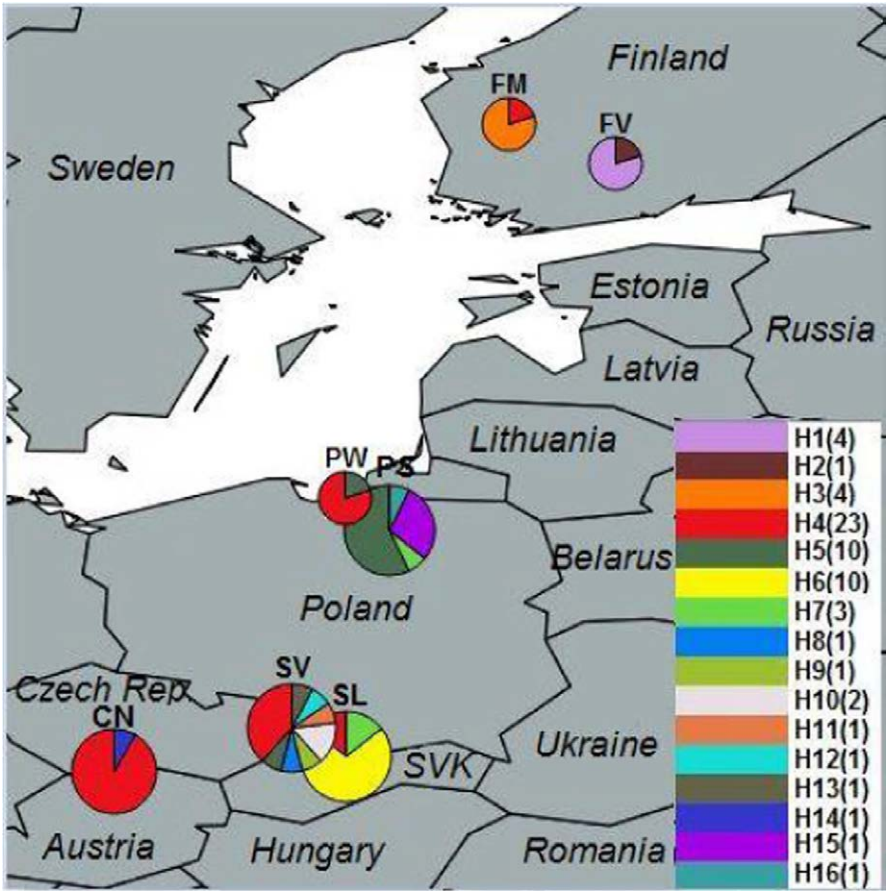

Fig. 1 Sampling areas and haplotype distribution of seven European perch populations in Europe: FV, Valkea-Kotinen Lake (61° 14′ 32.1″ N, 25° 03′ 47.1″ E Finland); FM, Majajärvi Lake (62° 03′ 57.2″ N, 22° 53′ 40.6″ E Finland); PS, Stary Dwór Lake (53° 44′ 51.6″ N, 20° 27′ 11.8″ E Poland); PW, Wiślany Lagoon (54° 22′ 36.4″ N, 19° 31′ 38.4″ E Poland); CN, Nové Hrady Pond (48° 47′ 33.8″ N, 14° 48′ 32.3″ E Czech Republic); SV, River Váh (49° 07′ 29.7″ N, 18° 27′ 26.2″ E Slovakia); SL, Liptovská Mara Reservoir (49° 5′ 20.1″ N, 19° 34′ 38.3″ E Slovakia). SVK, Slovakia. Different colours correspond to different haplotypes. Haplotype size refers to the number of individuals studied in each population. Numbers in brackets indicate the number of specimens sharing the haplotype

(Alix et al. 2015) (see Table 1). After temperature acclimatisation, eggs were incubated in 200-L transparent tanks (tank size of 50 × 50 × 80 cm) with a water flow made by aeration. Tanks were equipped with hatching cages as described by Żarski et al. (2017) until 3 days post-hatching (dph). Water parameters in hatching apparatuses were maintained at 17 °C ± 0.8, pH = 7 ± 0.5, oxygen > 90% with 50% daily water exchange. The light intensity was 200–250 lx at the water surface. The photoperiod was constant at 12L:12D.

For each population, we mixed larvae originating from 10 ribbons (total of about 12,060 larvae) at 3 dph and divided them in triplicate with a density of 67 individuals L^{-1} in 60-L light grey (tank size of 22.5 × 30 × 89 cm) with a water flow through averaging 1 L/min. Temperature was gradually raised from 17 °C ± 0.8 to 23 °C ± 0.5 (1 °C per day) and kept stable.

Table 1 Transport length, egg development stage, survival rate of embryos, egg diameter, body weight, total length and specific growth rate of European perch larvae from Valkea-Kotinen Lake, Finland (FV); Majajärvi Lake, Finland (FM); Stary Dwór Lake, Poland (PS); Wiślany Lagoon, Poland (PW); Nové Hrady Pond, Czech Republic (CN); River Váh, Slovakia (SV); Liptovská Mara Reservoir, Slovakia (SL) stocks on the 3, 10, 17 and 24 dph. O, organogenesis steps 1 and 2. G, gastrulation step 2. Values expressed as mean ± SD. Values (in row) with different superscript letters are significantly different (p value < 0.05)

	FV	FM	PS	PW	CN	SV	SL
Transport length (hours)	6	6	10	10	1	6	6
Obtained developmental egg stage	O1	O1	O1	G2	O2	O1	G2
Survival rate of embryos (%)	76.1 ± 6.3^{c}	29.1 ± 5.3^{d}	77.4 ± 10.8^{bc}	94.1 ± 4.9^{ab}	79.2 ± 3.9^{abc}	96.2 ± 0.4^{a}	$93.1. \pm 4.9^{abc}$
Egg diameter (mm)	2.15 ± 0.08^{a}	1.53 ± 0.09^{d}	1.69 ± 0.08^{cd}	1.89 ± 0.09^{b}	1.78 ± 0.07^{c}	1.92 ± 0.08^{b}	1.96 ± 0.09^{b}
Body weight (mg)							
3rd DPH	0.8 ± 0.2^{c}	1.1 ± 0.1^{abc}	0.9 ± 0.1^{c}	1.0 ± 0.1^{bc}	1.4 ± 0.1^{a}	1.3 ± 0.1^{ab}	1.0 ± 0.3^{bc}
10th DPH	7.3 ± 4.2^{a}	2.6 ± 0.9^{abc}	1.0 ± 0.1^{c}	2.1 ± 1.4^{bc}	3.3 ± 1.2^{ab}	2.4 ± 1.0^{abc}	2.7 ± 1.2^{abc}
17th DPH	14.7 ± 5.2^{ab}	19.1 ± 7.8^{a}	8.3 ± 1.8^{b}	7.3 ± 3.9^{b}	17.3 ± 5.7^{a}	10.5 ± 4.4^{ab}	16.2 ± 2.9^{a}
24th DPH	71.1 ± 17.4^{a}	63.8 ± 29.7^{ab}	23.0 ± 8.6^{c}	39.1 ± 8.5^{abc}	43.3 ± 25.5^{abc}	28.3 ± 10.5^{c}	30.7 ± 6.3^{bc}
Total length (mm)							
3rd DPH	6.2 ± 0.1^{ab}	6.4 ± 0.5^{a}	6.7 ± 0.1^{a}	6.2 ± 0.3^{ab}	5.3 ± 0.3^{bc}	5.2 ± 0.3^{bc}	5.2 ± 0.3^{c}
10th DPH	9.9 ± 1.5^{ab}	11.4 ± 0.6^{a}	10.6 ± 0.7^{ab}	10.6 ± 0.9^{ab}	10.1 ± 2.1^{ab}	8.8 ± 0.7^{b}	8.8 ± 0.7^{b}
17th DPH	13.5 ± 1.6^{abc}	14.6 ± 2.5^{abc}	18.6 ± 2.6^{a}	15.3 ± 2.2^{ab}	17.1 ± 3.0^{a}	10.9 ± 0.9^{c}	12.4 ± 1.1^{bc}
24th DPH	19.0 ± 1.2^{abc}	19.7 ± 2.9^{ab}	20.5 ± 0.9^{a}	16.9 ± 1.1^{bcd}	19.0 ± 1.8^{ab}	15.5 ± 1.5^{cd}	15.0 ± 1.1^{d}
Specific growth rate (day%$^{-1}$)							
3rd to 24th DPH (total)	20.99 ± 0.55^{a}	19.40 ± 0.9^{ab}	15.69 ± 0.59^{c}	17.27 ± 0.74^{bc}	16.05 ± 1.75^{c}	14.64 ± 0.68^{c}	16.67 ± 1.61^{bc}

Oxygen saturation (> 90%) and pH level (7 ± 0.5) were monitored twice a day with a multimeter (Hach Lange HQ40d, Germany); ammonium (0.05 ± 0.01 mg L^{-1}) and nitrite (0.05 ± 0.02 mg L^{-1}) concentrations twice a week (DR 2800, Hach Company, USA). The light intensity was 200–250 lx at the water surface and the photoperiod was constant at 12L:12D with light period from 7am to 7pm.

Feeding with *Artemia* was performed between 3 and 24 dph. During the first 7 days of feeding, larvae were hand-fed five times a day in 2-h intervals with micro-*Artemia* nauplii of 350–380 μm (Ocean Nutrition; ration of 700 nauplii per larvae per day; cca 9 nauplii per mL). Micro-*Artemia* nauplii were subsequently replaced with *Artemia* nauplii of 430–460 μm (hatching rate above 260,000 nauplii g^{-1}; Ocean Nutrition; rations of 35% of fish biomass for the second week and 10% for the last third week) (Kestemont et al. 2015). During the weaning period (21 to 24 dph), *Artemia* nauplii were progressively replaced by commercial pelleted food BioMar Larviva Pro Wean 100 (80–200 μm; Nersac, France) over the course of 4 days, hand-fed in 2-h intervals from 8am to 6pm. Daily rations were for the first day 10% *Artemia* nauplii of fish biomass + 2% of compound feed; for the second day, 5% *Artemia* nauplii of fish biomass + 30% of compound feed; for the third day, 5% *Artemia* nauplii of fish biomass + 60% of compound feed; and 100% of compound feed on 24 dph (Kestemont and Mélard 2000).

Initial assessment of fish egg quality

For calculation of embryo survival rate, eyed eggs (n = ca 150 eggs) from each egg ribbon were photographed under a Leica Z6-APO stereoscopic microscope (Leica Microsystems, Switzerland). Embryo survival rate was determined as the percent survived embryos of the total number of eggs in each sample. At the eyed stage, we measured inner diameter of swelled oocytes of 100 randomly chosen eggs from each ribbon by averaging the length of vertical and horizontal diameter of each egg (Żarski et al. 2011). Measured eggs were not returned back into tanks.

Assessment of aquaculture performance/key traits

Larvae from all populations were weighed (BW) and measured at 3, 10, 17 and 24 dph with respect to different timing of hatching among the tested populations. For each sampling point, 15 individuals per tank were killed by lethal dose of oil clove concentration (Hamackova et al. 2006) and weighted (OHAUS Explorer EX224M, NJ, USA) to nearest 0.1 mg. For determination of total length (TL), fish were photographed and measured in ImageJ software (Rueden et al. 2017). The specific growth rate (SGR; %/day) was calculated according to the following equation: $SGR = 100*(\ln W2 - \ln W1)*\Delta T^{-1}$, where $W1$ and $W2$ are the initial and final mean body weights, respectively, and ΔT is the time interval (days) between sampling points.

Statistical analyses

All statistical analyses were performed with Statistica version 13.3 (TIBCO Software Inc., CA, USA). Comparison of aquaculture performances for embryo survival rate, egg size, SGR, TL and BW among studied populations was performed through analysis of variance. The assumptions of ANOVA were checked and when they were not met, the Kruskal-Wallis test was performed. Afterwards, Tukey HSD (for ANOVA) or multiple comparisons of mean ranks (for

Kruskal-Wallis test) with Bonferroni correction were done for identification of pairwise significant differences.

Assessment of genetic differentiation

We collected fin clips from 68 larvae at 30 dph (see the number of sequenced individuals per population in Table S1) and stored them in ethanol (96%) prior to DNA extractions using a commercial E.Z.N.A. tissue DNA kit (Macherey-Nagel, Germany). We estimated potential genetic differentiation between populations through analyses of four mitochondrial regions: cytochrome b (Cytb), D-loop of control region (D-loop), 16S rRNA (16S) and cytochrome oxidase I (COI). These DNA regions have commonly been used in fish to study intraspecific genetic patterns (Makhrov and Bolotov 2006; Baharum 2012), including European perch (e.g. Nesbø et al. 1998a; Nesbø et al. 1998b; Nesbø et al. 1999). Gene fragments were amplified using primers L14724F/H15918R (Cytb; Irwin et al. 1991), HV2/CSBD (D-loop; Nesbø et al. 1998b), 16Sar/16Sbr (16S; Palumbi 1996) and jgLCO1490/jgHCO2198 (COI; (Vrijenhoek 1994). Mitochondrial genes were amplified using polymerase chain reaction (PCR): 10-pmol primers, PPP MasterMix (Top Bio), DNA and distilled water. An initialization step of 5 min at 95 °C was followed by 38 cycles of denaturation at 94 °C for 40 s; 50-s annealing at 55.8 °C for 16S, 49 °C for COI and 55 °C for Cytb and D-loop; and 1-min extension at 72 °C plus a 10-min final extension at 72 °C. The PCR products were purified with the E.Z.N.A. gel extraction kit (Macherey-Nagel, Germany) following manufacturer's protocol. Primers CSBD, 16Sbr, jgLCO1490 and H15918R were used for single-strand sequencing (Macrogen Inc., Amsterdam, Netherlands).

Sequences were aligned and manually checked using GENEIOUS 10.1.3 (Kearse et al. 2012). For coding genes, nucleotide sequences were translated into amino acids. The identity of each sequence was checked using BLAST (Altschul et al. 1997). The aligned sequences for D-loop (351 bp) and COI (641 bp) showed seven variable sites with six unique haplotypes in each, 16S (541 bp) showed six variable sites with five unique haplotypes and Cytb (541 bp) showed one variable site with two unique haplotypes. Unique haplotype sequences are available in GenBank (see Table S1). Since all genes belong to the mitochondrial genome, the four markers were concatenated within a single alignment for genetic differentiation analyses using Mesquite 3.31 (Maddison and Maddison 2015). We obtained 16 unique haplotypes in the concatenated matrix (1931 bp) which included 21 variable sites.

Concatenated haplotype map for each stock was created using QGIS software 2.18.3 (QGIS Development Team 2009). Analysis of molecular variance (AMOVA, 100,000 number of permutations) and estimation of the fixation index FST and pairwise FST were conducted in SPADS v. 1.0 (Dellicour and Mardulyn 2014).

Results

Initial state of the stocks

The survival rate of embryos was higher than 77% in all tested populations except population from FM where the survival rate was 29% (see population acronym meaning in Table 1).

The inner diameter of swelled oocytes at eyed egg stage showed significant differences among tested populations (Table 1). The highest and the lowest diameters were observed for Finnish populations ($F_{6,693} = 544.7$, p value < 0.05, Table 1).

Aquaculture traits among perch stocks

At 3 dph, we observed an inter-populational differentiation of initial BW: CN, SV, and FM had significantly higher values (except for the comparison between SV with PW and SL, and FM with all populations) (chi-square = 56.43, p value < 0.05, df = 6, Table 1). This result, however, changed during the ongoing growth periods, and at the end of the experiment, the highest values were observed in other populations (chi-square = 43.66, p value < 0.05, df = 6, Table 1). For SGR results, FV displayed significantly higher values compared to non-Finnish populations ($F_{6,14} = 12.77$, p value < 0.05, Table 1).

Finish and Polish populations showed the highest TL at 3 dph and most of them remained among the populations with the highest TL at the end of the experiment (chi-square = 62.33, p value < 0.05, df = 6, Table 1).

Genetic differentiation among perch stocks

The geographic distribution of haplotypes (Fig. 1) suggested a genetic differentiation among populations: some haplotypes were restricted to some populations (e.g. H1 in Finland, Fig. 1) while the frequency of other haplotypes differed between populations. Overall, the AMOVA confirmed this differentiation between populations (i.e. FST = 0.501, p value < 0.01). Pairwise AMOVA highlighted significant differentiations between most populations (Table 2). Strong genetic differentiations were observed between Finnish (especially FM) and all other populations (Table 2). In contrast, differences between central Europe populations were not significant or lower (Table 2).

Discussion

Our results show that there are differentiations in growth performances between the studied populations (Table 1). Overall, the Finnish populations tend to have higher performances (Table 1). Similar results were observed by Mandiki et al. (2004) during their comparison of juveniles from Poland and Finland. One could expect that the different initial state of eggs (i.e. egg diameter and egg survival rate) could explain the differences of growth (Table 1). Indeed, a relationship is known between egg size (linked to female size) and larval size/weight at hatching (Moodie et al. 1989; Olin et al. 2012). However, our data showed no such

Table 2 Pairwise FST values from mtDNA sequence data of European perch populations. FV, Valkea-Kotinen Lake (Finland); FM, Majajärvi Lake (Finland); PS, Stary Dwór Lake (Poland); PW, Wiślany Lagoon (Poland); CN, Nové Hrady Pond (Czech Republic); SV, River Váh (Slovakia); SL, Liptovská Mara Reservoir (Slovakia)

	SV	CN	PS	PW	SL	FV
SV						
CN	*0.048*					
PS	*0.224*	*0.394*				
PW	−0.032	0.012	*0.158*			
SL	*0.243*	*0.424*	*0.526*	*0.414*		
FV	*0.252*	*0.632*	*0.556*	*0.600*	*0.671*	
FM	*0.623*	*0.885*	*0.788*	*0.885*	*0.884*	*0.875*

Significant values in italics, p value < 0.01

relationship (Table 1). Therefore, the observed divergences could be explained by (i) population-specific environment before the experiment (including parental effect), (ii) local adaptation based on genetic differentiation, or (iii) both (Wolf and Wade 2009).

Our experimental design (i.e. transplant experiment in which all populations undergo the same standardised RAS and rearing practices) allows minimising the effect of environment on growth performances. However, we cannot rule out potential effect of pre-experiment environment on our results. Indeed, we collected egg ribbons in the wild meaning that they can undergo different environmental pressures. Such pressures can lead to responses during development and extend through all or part of the life of an organism (Fusco and Minelli 2010; Wiens et al. 2014). Moreover, environmental conditions in which parent fish lived as well as the parent features (e.g. age, maternal size; Olin et al. 2012) can impact the offspring performance (Mousseau and Fox 1998). Without information about the parents of the sampled egg ribbons, we cannot exclude such parental effects (Youngson and Whitelaw 2008).

Alternatively, different environmental pressures applied over several generations can lead to local adaptations based on genetic divergences (e.g., Losos and Ricklefs 2009). Our analyses showed that the most genetically divergent populations (i.e. Finnish with higher FST values) tend overall to have more distinct growth performances (Tables 1 and 2). This could suggest a genetic basis of the observed growth differentiation and, consequently, a potential heritability of this pattern as it has already been highlighted for several fish species (e.g. Rosenau and McPhail 1987; Nicieza et al. 1994; Brown et al. 1998). However, genetically undifferentiated populations (i.e. PW, CN and SV) also presented distinct growth rates (Tables 1 and 2). The lack of genetic differentiation of these populations should be further assessed by higher resolution analyses (e.g. microsatellites since mitochondrial markers are quite conserved and, thus, we could underestimate genetic divergences).

Finally, potential biases induced by our experimental design can be noticed. First, ribbon transportation can have influenced embryo development and thus larvae performances. However, we tried to minimise such an impact by transporting egg ribbons during less sensitive egg development stages (e.g. gastrulation and organogenesis, see Table 1) (Woynarovich and Horváth 1980). Overall, the length and the mean of transport as well as the development stage of our samples do not seem to influence our results (Table 1). Second, we did not evaluate feed intake because such an assessment on larvae remains methodologically difficult/time-consuming. Although, tested populations were reared in optimal conditions according to literature (Kestemont and Mélard 2000; Tamazouzt et al. 2000; Kestemont et al. 2008; Kestemont et al. 2015), we cannot rule out potential influence of feed intake on growth differentiation. Whether such a population-specific feed intake exists, it should be considered as a population-dependent feature potentially valuable for aquaculture.

Our study confirms that key features for aquaculture can vary at the intraspecific level which could be beneficial to improve European perch production. However, we do not highlight any clear aquaculture trait differences related to genetic differentiation. Therefore, we cannot estimate the contribution of pre-experiment population-specific environment and potential local adaptation based on genetic differentiation on our results. This could be solved by performing similar experiment over several generations.

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Author contributions JK, VS and TV conceived original idea. JK, VS and TV carried out the sampling. TV, RG and BD contributed to rearing process. TL, LT, MB and TV contributed to laboratory genetic analyses. RG performed statistical analyses. TL, LT, RG, VS, MB, BD and TV discussed the results and contributed to the final manuscript, revising it critically for important intellectual content.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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CHAPTER 3

GENETIC AND AQUACULTURE PERFORMANCE DIFFERENTIATION AMONG WILD ALLOPATRIC POPULATIONS OF EUROPEAN PERCH (PERCIDAE, *PERCA FLUVIATILIS*)

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Genetic and aquaculture performance differentiation among wild allopatric populations of European perch (Percidae, *Perca fluviatilis*)

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ABSTRACT

Present research suggests that phenotypic variations and consequent potential differences in suitability for commercial culture are more likely to occur among genetically diverse populations. We investigated diversity in traits important to aquaculture and assessed genetic differentiation based on four mitochondrial markers in three European populations of *Perca fluviatilis*. Using a transplant approach to standardize conditions and minimize environmental effects on phenotype expression, we compared survival, cannibalism, growth rate, growth heterogeneity, and specific growth rate of the populations to assess whether difference in aquaculture performance (i.e. expression of phenotypical traits that facilitate the rearing of fish and impact the productivity of the farming) is more likely between genetically differentiated populations than between genetically similar populations. We found key traits of performance to differ among allopatric populations, suggesting value in considering geographic source of broodstock. The largest aquaculture performance disparities were observed among genetically differentiated populations. Some lesser differences were observed between allopatric genetically similar populations, possibly the consequence of pre-collection environment, or transgenerational effects.

1. Introduction

Aquaculture is one of the fastest growing food-producing sectors (FAO, 2016), with current fish production involving a small number of species (Teletchea and Fontaine, 2014). This low diversity leads to negative consequences with respect to (1) wild environments (non-native species invasion triggered by translocations of the few produced species out of their natural range for production or trade purpose; (Garibaldi and Bartley, 1998), (2) food security via high epizooty hazard for key species in the human food supply (Godoy et al., 2008), and (3) economic prospects due to low potential to adapt to changes in environment/consumer demand (Fontaine et al., 2009). The diversification of fish production to increase aquaculture sustainability (Fontaine et al., 2009) is an emerging trend including the development of European perch (*Perca fluviatilis* L.) culture (Kestemont et al., 2015).

The European perch is a widespread freshwater predatory species (Stepien and Haponski, 2015). This is a polytypic species that displays geographic differentiation in genetic (Nesbø et al., 1999) and phenotypic traits (Mandiki et al., 2004; Pimakhin and Žák, 2014) throughout its distribution range. Its high market value along with increasing consumer demand make it commercially important in some European countries (i.e. especially in France and Switzerland) where over 500 t are produced annually (Toner, 2015; FAO, 2016). Nowadays, most of the production relies on fish bred in intensive aquaculture systems (i.e. re-circulating aquaculture systems, RAS) and harvested at 80–100 g (Toner, 2015). The RAS production development began early in the large scale *P. fluviatilis* aquaculture since this farming system allows improving (i) efficiency and profitability of culture by reducing time to marketable weight, (ii) water consumption, (iii) waste management, (iv) disease control, and (v) stable temperature maintenance (Żarski et al., 2017). However, production of European perch still fails to meet market demands (Kestemont et al., 2015). Indeed, several obstacles in the life cycle and breeding performance of the current European perch stock hinder culture development: asynchronous spawning, high larval mortality, low growth rate, high growth heterogeneity, and high rates of cannibalism among larvae (Brabrand, 1995; Tamazouzt et al., 2000; Baras et al., 2003; Policar et al., 2008; Rougeot and Mélard, 2008).

Several studies have determined that presence of traits desirable for aquaculture can vary between geographically distinct wild populations, i.e., in Coho salmon (*Oncorhynchus kisutch*) (Rosenau and McPhail, 1987) and striped bass (*Morone saxatilis*) (Brown, 1994; Conover et al., 1997; Brown et al., 1998). Growth, survival, larval malformation, and

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cannibalism (so-called zootechnical traits) have also been shown to differ among wild allopatric populations of European perch (Mandiki et al., 2004; Pimakhin and Žák, 2014). The geographic differentiation of key traits for aquaculture means that choosing wild perch from areas displaying optimum survival, growth, and cannibalism rates in aquaculture conditions may be important for the establishment or enhancement of fish farming broodstock, as was shown for *P. flavescens* (Rosauer et al., 2011). Since known geographic differentiation of *P. fluviatilis* traits included features involved in current bottlenecks of its aquaculture, this may ultimately help to overcome current challenges in European perch aquaculture.

Although some hypotheses have been put forward to explain geographic differentiations of phenotypic traits desirable for aquaculture (e.g., Mandiki et al., 2004, Rosauer et al., 2011). Population differences in specific traits can be shaped by genetic differentiation fostered by gene flow reduction among separated or isolated populations or by phenotypic plasticity, the capacity of a genotype to vary in phenotype depending on environmental or developmental conditions (Pigliucci et al., 2006), or their combination (Avise, 2000; DeWitt and Scheiner, 2004; Bergek and Björklund, 2009). Earlier studies comparing survival, cannibalism, and growth rates of allopatric *P. fluviatilis* populations have employed an experimental transplant approach (Mandiki et al., 2004; Pimakhin and Žák, 2014), which reduces environmental effects. Since allopatric populations are placed in the same environment, one would expect phenotypic variation and potential consequent differences in aquaculture performance to occur among genetically differentiated populations (see genetic differentiation in European populations in Nesbø et al., 1999). However, previous studies did not assess the genetic differentiation between studied populations and investigated only early life stages derived from eggs collected from the wild. Since environmental impact on gene expression and resulting phenotypes may or may not be consistent throughout life and can also affect succeeding generations, it is not known if observed differences among populations are genetically- or environmentally-induced.

In this study, we aim at (i) highlighting the geographic differentiation in keys traits for aquaculture and (ii) investigating the genetic basis of this potential differentiation in *P. fluviatilis*. To this end, we develop a comparison of survival, growth parameters, and cannibalism in three allopatric European populations through a transplant experimental design, placing each population in the same standardized conditions, coupled with a genetic assessment based on four mitochondrial markers.

2. Materials and methods

2.1. Wild fish stock and initial egg assessment

Egg ribbons of three wild allopatric fish populations were collected from three localities in different drainage basins (Table 1) corresponding to areas where occur genetically different populations according to Nesbø et al. (1999). The egg ribbons were sampled at the beginning of the European perch spawning season (i.e. this beginning was determined by collaborators' population monitoring; from the end of April and beginning of May). We transported egg ribbons by car to the experimental facility of the Faculty of Fisheries and Protection of Waters, South Bohemia University. Eggs were held in oxygenated polyethylene bags (filled 1/3 of water, 2/3 of oxygen, t-16 ± 1 °C) placed in a thermo box: 10 ribbons from Poland, 11 ribbons from the Czech Republic, and 12 ribbons from Slovakia. After the transportation, we determined the developmental advancement of ribbons by randomly choosing 150 eggs per population, photographing them, and comparing them to references from Żarski et al. (2011). Polish and Slovakian populations were on 6 days post-fertilization (dpf) while the Czech population was on approximately 8 dpf. At the facility, bags were placed into separate 200 L hatching tanks filled with dechlorinated tap water (17 °C ± 0.5, pH = 7 ± 0.5, oxygen >90%) for temperature acclimatization. When temperature in the bag and hatching tank equalized, egg ribbons were placed onto the net bottom of hatching cages Żarski et al. (2017) until three days post-hatching (dph). During this period, 50% of water volume was replaced daily. Water temperature, pH, and oxygen saturation were maintained at 17 ± 0.8 °C, 7 ± 0.5, and > 90%, respectively.

After temperature acclimatization, 150 randomly chosen eggs per population were sampled to assess fertilization rate according to (Křišťan et al., 2012). At the eyed stage, the inner diameter, not including the gelatinous coat, of 100 randomly sampled eggs was measured following Żarski et al. (2011) using a Leica Z6-APO scope (Leica Microsystems, Switzerland). The eggs from Poland (PL), Czech Republic (CZ), and Slovakia (SK) hatched on 2, 9, and 12 May 2017, respectively.

2.2. Pre-experiment rearing protocol

All populations were reared in the same conditions. At 3 dph, larvae were transferred into an RAS. We mixed larvae from 10 ribbons per each population in this system. The light grey tanks sized 22.5 × 30 × 89 cm, 60 L with water flow-through averaging 1 L/min in each tank till 31th DPH (17 ± 0.8 °C, pH = 7 ± 0.5, oxygen >90%). We used a density of 67 specimens L^{-1}. The feeding was initiated 3 days after hatching with *Artemia* nauplii up to day 24 (Tamazouzt et al., 2000; Jentoft et al., 2006). During the first seven days of feeding, larvae were fed manually at 2 h intervals from 08.00–18.00 h with micro-*Artemia* nauplii of 350–380 μm (Ocean Nutrition) in ration 700 nauplii per larvae. Micro-*Artemia* nauplii was subsequently replaced with *Artemia* nauplii with hatching >260,000 nauplii g^{-1} (Ocean Nutrition) at rations for the second week 35% of fish biomass and 10% for the last third week, respectively (Kestemont et al., 2015). At 21 dph, *Artemia* nauplii were progressively replaced with commercial pelleted BioMar Larviva Pro Wean 100 (Nersac, France) over the course of four days, manually fed at 2 h intervals from 08:00–18:00 h with a daily ration for the first day 10% *Artemia* nauplii of fish biomass +2% of compound feed, for the second day 5% *Artemia* nauplii of fish biomass +30% of compound feed, for the third day 5% *Artemia* nauplii of fish biomass +60% of compound feed and 100% of compound feed on the 24 dph (Kestemont and Mélard, 2000). From 25 dph juveniles were fed only commercial pellets with the size of pellets which progressively increased according to mean body weight (in ration 0,01 g – 9, 3%; 0,22 g – 7, 4%; 0,73 g – 5, 1%; from 1,56 g – 4.5%) (Fiogbé and Kestemont, 2003). Dead larvae were removed daily. After 3 dph the temperature was gradually increased from 17 °C to 23 °C (+1 °C per day) and kept stable. Temperature, oxygen saturation, and pH were measured twice daily in the pre-experimental period with a multimeter (Hach Lange HQ40d, Germany). The light intensity ranged 200–250 lx at the water surface. The photoperiod was constant at 12 L: 12D.

Table 1
Sampling sites of European perch populations.

Country	Locality	Habitat	Basin	Latitude(N)/Longitude (E) WGS84
Poland	Stary Dwór Lake	Small lake	Baltic Sea	53°44′51.6″N 20°27′11.8″E
Czech Republic	Nové Hrady	pond	North Sea	48°47′33.8″N 14°48′32.3″E
Slovakia	River Váh	River	Black Sea	49°07′29.7″N 18°27′26.2″E

2.3. Experimental rearing protocol

Prior to the experiment (i.e. after pre-experiment rearing), the initial body weight and mortality rate were assessed at 30th day: (1) initial body weight: 0.11 ± 0.02 for Slovakians, 0.13 ± 0.02 for Czechs, and 0.04 ± 0.01 for Polishes; (2) mortality rate: 75%; 62.5%; 55%, respectively. The experiment was initiated at 31 dph with feed-trained juveniles, a time when digestive enzymes are expected to be fully developed (Cuvier-Péres and Kestemont, 2001) and mortality associated with feed changes declined (Kestemont et al., 1996; Ljunggren et al., 2003). Juveniles were redistributed into 60 L light rectangular grey tanks size 22.5 × 30 × 89 with water flow-through of 2 L/min in each tank (150 specimens per tank; 2.5 specimens L^{-1}) (Mélard et al., 1996) in triplicate RAS (~4000 L) with dechlorinated tap water. The rearing experiment lasted 84 days, from the 31 to 115 dph. Dead fish were immediately removed from the tanks and numbers recorded daily. Juveniles were fed manually at 2 h intervals from 08:00–18:00 h with a daily ration (Fiogbé and Kestemont, 2003). Concentration of oxygen, pH, and temperature were monitored twice daily. Ammonium and nitrite concentrations were recorded twice weekly. Dissolved oxygen was maintained above 90% and pH at 7 ± 0.5. Concentrations of ammonium were 0.05 ± 0.01 mg L^{-1}, while nitrites were 0.05 ± 0.02 mg L^{-1} measured with portable spectrophotometer (DR 2800, Hach Company, USA). The light intensity ranged 200–250 lx at the water surface. The photoperiod was constant at 12 L: 12D.

2.4. Assessment of aquaculture performance of fish populations

2.4.1. Measurements

All fish were weighed and measured at 31, 59, 87, and 115 dph for body weight, specific growth, and growth heterogeneity. At each sampling date, 15 specimens per tank (45 per population) were anaesthetized using clove oil solution at 0.015 mg L^{-1} and weighed (OHAUS Explorer EX224M, NJ, USA) to the nearest 0.1 mg. Specific growth rate (SGR, %/day) was calculated by $SGR = 100*(\ln W_2 - \ln W_1)*\Delta T^{-1}$, in which W1 and W2 are the initial and final mean body weight, and ΔT is the time interval between samplings in days. Growth heterogeneity (GH) was calculated from CV_{FBW}/CV_{IBW}, where CV is the coefficient of variation (100*SD/mean) and IBW and FBW are the initial and final body weight.

Mortality rate (MR, %) was calculated from number of dead fish as D_f*100/Ni, in which D_f is number of dead fish and N_i is the number of initial stocked fish per tank. This rate was calculated for four time periods (31–59 dph, 59–87 dph, 87–115 dph, and 31–115 dph). The number of dead fishes was recorded daily.

Cannibalism rates (i.e. cannibalism type II) were recorded at the end of experiment at 115 dph. Cannibalism rate (CR, %) was calculated as $CR = ((N_i - N_d - N_f)/Ni) * 100$, where Ni and Nf are the initial and final numbers of fish, respectively, and N_d is the number of dead fish counted during the experiment (Kestemont et al., 2003; Mandiki et al., 2004; Ljubobratović et al., 2015).

2.4.2. Statistical analyses

Statistical analyses compared the mean values of each factor among the tree fish populations (i.e. using populations as statistical units). Since each group sample was not drawn from a normally distributed population according to the Shapiro-Wilk test, the assumptions for one-way analysis of variance were not met, and the Kruskal-Wallis test by rank was used to assess differences in growth rate, growth heterogeneity, mortality, and cannibalism. When significant differences were detected, Dunn's multiple comparison test was used to identify specific population differences. Statistical analyses were conducted in R v. 3.4.4 (R Development Core Team, 2018).

2.5. Assessment of genetic differentiation among fish populations

To estimate genetic differentiation, fin clips were collected from 15 perch of each population and stored in pure ethanol (99%). The DNA extraction used a commercial E.Z.N.A. Tissue DNA kit (Macherey-Nagel, Germany). Fragments of four mitochondrial regions, cytochrome *b* (Cytb), D-loop of control region (D-loop), 16S rRNA (16S), and cytochrome oxidase I (COI) were amplified using primers L14724F/H15918R (Irwin et al., 1991), HV2/CSBD (Nesbø et al., 1998), 16Sar/16Sbr (Palumbi, 1996), and jgLCO1490/jgHCO2198 (Vrijenhoek, 1994), respectively. These DNA regions are commonly used for determining genetic differences at the intraspecific level (Lecocq et al., 2013) including in European perch (Nesbø et al., 1999). The conditions of the polymerase chain reaction (PCR) were 10 pmol primers, PPP MasterMix (Top Bio), DNA, and distilled water. An initialization step of 5 min at 95 °C was followed by 38 cycles of denaturation at 94 °C for 40 s; 50 s annealing at 55.8 °C for 16S, 49 °C for COI, and 55 °C for Cytb and D-loop; and 1-minuts extension at 72 °C plus a 10-minuts final extension at 72 °C. The PCR products were purified with the E.Z.N.A Gel extraction kit (Macherey-Nagel, Germany) following manufacturer's protocol. The products were sequenced by Macrogen Europe (Amsterdam, Netherlands) on a 3730XL (Applied Biosystems) using primers H15918R, CSBD, 16Sbr, and jgLCO1490.

Nucleotide sequences were manually checked using GENEIOUS 10.1.3 (Kearse et al., 2012). There was no uncertainty in the consensus sequences. For coding genes (COI and Cytb), translation to proteins using the vertebrate mitochondrial DNA genetic code was performed on Mesquite 3.31 (Maddison and Maddison, 2015) to verify that there was no stop codon in coding regions. The fish origin of each sequence was checked with BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). The unique haplotypes found were deposited in GenBank (Table S1).

The alignments were conducted in MAFFT v. 6.0 using FFT-NS-2 algorithm default parameters (Katoh et al., 2017). The four markers were concatenated within a single alignment for the genetic differentiation analyses using Mesquite 3.31. A concatenated haplotype map for each population was created with QGIS software 2.18.3 (https://qgis.org/en/site/). Analysis of molecular variance (AMOVA, 100,000 permutations) based on allele frequency and estimate of the fixation index F_{ST} and pairwise F_{ST} were calculated in Arlequin v. 3.5 (Excoffier et al., 2005) with 10,000 random permutations.

3. Results

3.1. Egg assessment

Fertilization rates of the CZ, SK, and PL populations were 80 ± 2.3%, 90 ± 4.2%, and 88 ± 4.1%, respectively. Egg diameter (mm) differed significantly among populations tested (Kruskal-Wallis, $P < .01$) with mean ± SD of 1.89 ± 0.1, 1.77 ± 0.07, and 1.69 ± 0.08 for SK, CZ, and PL populations, respectively.

3.2. Aquaculture performance

At 31 dph, initial body weight differed significantly among populations (Kruskal-Wallis test, $P < .01$, Table 2). At 59 and 87 dph, SK and PL populations showed significantly lower body weight than CZ (Kruskal-Wallis test, $P < .01$, Table 2). At 115 dph, the CZ population showed significantly higher body weight than SK and PL populations.

Throughout the experiment, the SGR was significantly higher in the PL population at most sampling times (Table 2). The CZ population did not differ from SK population at 115 dph. (Table 2).

Mortality rates of the populations were similar at most sampling times (Table 2). Kruskal-Wallis test *P*-values 0.05 (31 to 59 dph), 0.19 (59 to 87 dph), < 0.05 (87 to 115 dph; (pairwise results Table 2), and 0.24 (31 to 115 dph). There was no significant difference in survival among the populations throughout the study period (Table 2).

Table 2
Body weight, specific growth rate, mortality rate, growth heterogeneity, and cannibalism rate (mean ± standard deviation) of tree populations of European perch juveniles at 31, 59, 87, and 115 dph. Different superscripts within a row indicates significant difference. SK = Slovakia, CZ = Czech Republic, PL = Poland.

	SK	CZ	PL
Body weight (g)			
31 dph	0.11 ± 0.02^{b}	0.13 ± 0.02^{c}	0.04 ± 0.01^{a}
59 dph	0.38 ± 0.04^{a}	0.60 ± 0.07^{b}	0.30 ± 0.03^{a}
87 dph	2.22 ± 0.22^{a}	4.12 ± 0.40^{c}	3.07 ± 0.33^{b}
115 dph	5.98 ± 0.46^{a}	8.95 ± 3.14^{b}	6.70 ± 0.46^{a}
Specific growth rate (% day^{-1})			
31–59 dph	4.29 ± 0.31^{a}	5.41 ± 0.25^{a}	7.26 ± 0.61^{b}
59–87 dph	10.66 ± 0.34^{a}	12.28 ± 0.29^{b}	15.57 ± 0.53^{c}
87–115 dph	14.20 ± 0.49^{a}	14.89 ± 0.79^{a}	18.36 ± 0.67^{b}
Mortality rate (%)			
31–59 dph	46.67 ± 10.35^{a}	36.89 ± 2.78^{a}	40.00 ± 9.26^{a}
59–87 dph	4.44 ± 3.01^{a}	5.11 ± 1.68^{a}	1.11 ± 0.38^{a}
87–115 dph	0.22 ± 0.38^{a}	1.78 ± 0.77^{b}	0.44 ± 0.38^{ab}
31–115 dph (total)	51.33 ± 8.82^{a}	43.78 ± 3.79^{a}	41.56 ± 9.48^{a}
Growth heterogeneity			
31–59 dph	1.66 ± 0.45^{b}	0.95 ± 0.24^{ab}	0.82 ± 0.25^{a}
59–87 dph	1.26 ± 0.18^{a}	1.07 ± 0.32^{a}	1.47 ± 0.64^{a}
87–115 dph	1.22 ± 0.16^{a}	0.85 ± 0.22^{a}	1.30 ± 0.33^{a}
31–115 dph (total)	2.47 ± 0.28^{b}	0.81 ± 0.20^{a}	1.42 ± 0.54^{a}
Cannibalism rate (%)			
31–115 dph (total)	26.44 ± 5.55^{a}	28.22 ± 5.00^{a}	28.89 ± 0.77^{a}

Growth heterogeneity differed significantly between SK and PL groups from 31 to 59 dph), with the PL population exhibiting the lowest GH (Table 2). However, no significant difference in GH was detected at later sampling points at 87 dph and 115 dph.

Cannibalism was detected in all groups. The cannibalism rate was not significantly different in all groups (Table 2).

3.3. Genetic differentiation among fish populations

Sequencing data was obtained from 39 perch of the three populations (Table S1). The data matrix for D-loop (350 bp), 16S (541 bp), and COI (641 bp) contained four, five, and four unique haplotypes, respectively. The CytB (399 bp) data matrix was not polymorphic and presented only one previously reported haplotype (accession number KC819836) (Haponski and Stepien, 2013). The information of haplotype distribution is presented in Fig. 1.

The aligned sequences of the concatenated matrix (1931 bp) from 39 European perch exhibited 16 variable sites, defining 12 unique haplotypes with the two most common being H3, shared by 16 specimens recorded from SL, CZ, as well as H4 in 9 specimens from PL and SK (Fig. 1). The coefficient of genetic differentiation diversity among populations was 0.365 ($P < 0.01$). The concatenated matrix was characterized by high haplotype diversity ($H_d = 0.780$). AMOVA results demonstrated 22.84% of the genetic variation to be among populations and 77.16% of the genetic variation within populations.

The F_{ST} value was 0.228 (AMOVA, $P < .01$), indicating significant population genetic structure. Pairwise F_{ST} indicated strong differentiation of the PL population from the other populations (Table 3). The SK and CZ were weakly differentiated with low F_{ST} values and no significant differentiation in AMOVA.

4. Discussion

4.1. Geographic variation in aquaculture performance

The aquaculture performance of the three studied fish populations suggests differences in potential for fish farming (Table 2). Populations differed in SGR, growth heterogeneity, traits currently impacting

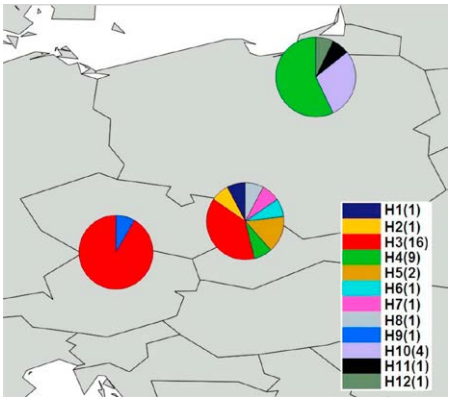

Fig. 1. Sampling areas and haplotype distribution of European perch populations. Different colours indicate different haplotypes. Numbers in brackets indicate the number of specimens sharing the haplotype.

Table 3
Pairwise F_{ST} values from the mitochondrial dataset of European perch populations. SK = Slovakia, CZ = Czech Republic, PL = Poland.

	SK	CZ
SK		
CZ	0.048	
PL	**0.224**	**0.394**

Significant values in bold, $P = .01$.

European perch culture (Kestemont et al., 2015). Such population-specific aquaculture performance has been reported in European perch from other geographic areas (Mandiki et al., 2004; Pimakhin and Žák, 2014). Therefore, consideration of differences among allopatric populations is important for the establishment or enhancement of European perch broodstock, as has been the case with other fish species (Rosenau and McPhail, 1987; Brown, 1994; Conover et al., 1997; Brown et al., 1998). Further comparative studies of other European perch populations are required to allow identifying the population(s) best suited to aquaculture.

4.2. Sources of geographic variation in aquaculture performance

Knowledge of the source of aquaculture performance differences among fish populations is critical to fish farming. However, establishing the origin of variation among allopatric fish populations is not straightforward. Differences can be explained by genetic differentiation (Avise, 2000) or phenotypic plasticity (DeWitt and Scheiner, 2004; Bergek and Björklund, 2009).

Past demographic events such as population movements triggered by climate cycles (Bernatchez and Wilson, 1998) and former/current geographic barriers (Bergek and Björklund, 2009) are important factors shaping within-species genetic differentiation. These factors can lead to a decrease or interruption of gene flow among allopatric conspecifics that fosters local genetic specificity through processes including genetic drift (Avise, 2000). Isolated gene pools may occur with diverse habitats, eco-climatic conditions, population densities, or food availability producing variation in selective pressure (Mayr, 1963). In this scenario, phenotypic variation can result as a consequence of genetic adaptations to the local environment (Losos and Ricklefs, 2009), for instance, to

abiotic factors (temperature, levels of dissolved oxygen, ammonia, nitrites, salinity, photoperiod, food availability, and quality) as well as biotic factors (degree of competition, predation, and population density) (Hansson, 1984; Przybylski, 1996; Pierce et al., 2003).

Our study revealed genetic differences among specimens inhabiting different areas, especially with respect to the PL group vs. other populations (Table 2). The genetic differentiation is in agreement with Nesbø et al. (1999). The results obtained in the PL population compared to the other groups conforms to the hypothesis that genetically different populations are likely to display variation in characteristics affecting their potential for aquaculture. However, we also observed variation in aquaculture performance among fish of genetically similar populations. This could be explained by an underestimation of the genetic variation based on analysis of only four mitochondrial markers. Phenotypically distinct organisms are not always characterized by large genetic differences (Ferguson, 2002; Salvato et al., 2002; Rheindt et al., 2011), making quantification of genetic differentiation challenging without further analyses of nuclear genes or of the entire genome. Alternatively, differences in any morphological, physiological, or behavioural trait among non-genetically similar fish populations could be a consequence of phenotypic plasticity (DeWitt and Scheiner, 2004).

Phenotypic plasticity is a ubiquitous phenomenon in living organisms in response to environmental conditions (DeWitt and Scheiner, 2004). It is predicted that high gene flow in an allopatric gene pool as suggested among CZ and SK populations by AMOVA, should favour the development and maintenance of phenotypic plasticity over local genetically-based adaptations (Crispo, 2008; Bergek and Björklund, 2009). Applying similar environmental conditions to different fish populations through transplant experiments, as in our study, minimizes potential effects of phenotypic plasticity on the studied traits and suggests a genetic basis for the variation (West-Eberhard, 2003; Rosburg, 2017). We collected specimens at the egg stage to rule out a potential phenotypic plasticity effect. Alteration in phenotype as a response to environmental cues can occur during development and extend through all or part of the life of an organism (Fusco and Minelli, 2010; Wiens et al., 2014). Ruling out a potential phenotypic plasticity effect would require breeding sequential generations of desired strains under similar conditions, requiring long term transplant experiments, which may be costly and time-consuming.

4.3. Potential limitations

In addition to genetic or phenotypic plasticity as a source of the observed differences in aquaculture performance, we cannot exclude possible sampling bias. First, we did not conduct an initial assessment of pathogens in the specimens. Although mortality rates were similar among populations, pathogens may have affected performance of a population without leading to increased mortality.

Second, the wild egg ribbons were collected from unknown broodstock. Therefore, observed interpopulational divergences could be differences between genetic pool families that can affect the offspring husbandry performances. However, we argue that our sampling design minimizes such an effect. We minimize the risk of studying individuals with a high degree of kinship by mixing larvae from different egg ribbons (i.e. one ribbon is laid by on female) for each population. Third, environmental conditions such as diet, parasites, and water temperature experienced by the parent fish may be important in shaping offspring phenotype (Mousseau and Fox, 1998): Past environmental circumstances may contribute as much as current conditions to performance (Devevey et al., 2010). Such a transgenerational effect is not determined by the offspring's genome but instead by the environmental experience of its parents (Youngson and Whitelaw, 2008). Therefore, fish obtained from parents with high condition through a resource-rich/pathogen-low environment may acquire the parent condition and thus perform better under any environmental conditions than does offspring of poor quality parents (Valtonen et al., 2012). Performance of European perch larvae can be impacted by maternal size (Olin et al., 2012). Since we have no information about the parents of the sampled egg ribbons, we cannot exclude such a transgenerational or maternal effect.

5. Conclusion

According to our result, we suggest that aquaculture performance differs among allopatric populations, as previously stated for other fish species. Therefore, quantification of geographic variation in key traits could have potential for overcoming current issues in European perch aquaculture. The differences were mainly observed between genetically differentiated populations but lower divergences where recorded between genetically undifferentiated populations. These latter differences could be a consequence of different health status, pre-collection environment, or transgenerational effects. Further studies are needed to assess the importance of these factors in geographic differentiation of aquaculture performance.

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Author contributions

JK, VS, RG, and VT conceived the original idea. JK, VS, and TV carried out the sampling and transport of egg ribbons. TV and RG contributed to the rearing process. TL, LT, MB, and VT contributed to laboratory genetic analyses. TL and MR performed statistical analyses. TV, RG, LT, and TL led the writing. All authors discussed the results and contributed to the final manuscript, revising it critically for content.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2018.12.071.

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CHAPTER 4

WHEN BEHAVIOURAL GEOGRAPHIC DIFFERENTIATION MATTERS: INTER-POPULATIONAL COMPARISON OF AGGRESSIVENESS AND GROUP STRUCTURE IN THE EUROPEAN PERCH

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EUROPEAN PERCID FISH CULTURE

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

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Abstract

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

Keywords Aggression · Aquaculture · Behaviour · Cannibalism · Intraspecific differentiation · Larvae · *Perca fluviatilis* · Social structure

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Introduction

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

Among behavioural traits, inter-individual relationships, group structure and activity can affect directly the ability of a species to be domesticated and efficiently produced in intensive monoculture conditions. Tolerance to conspecifics in a limited area is an essential parameter for production (Kristiansen et al. 2004) since it affects individual welfare (Huntingford 2004; Ashley 2007). Selecting populations which present an aggregative and cohesive group structure, therefore limiting stress, would be favouring welfare. However, living in group is not costless as it can trigger for instance competition for resources (Pitcher and Parrish 1993; Martins et al. 2012; Ward and Webster 2016). In culture conditions, this can lead to the emergence of aggressive behaviours (Damsgård and Huntingford 2012), such as attacks or bites, leading in some cases to cannibalism (Baras 2013). These aggressive behaviours have several potentially negative consequences in fish culture such as mortalities, stress, immune suppression or uneven competition for food (Damsgård and Huntingford 2012 and references therein). Cannibalism (type I: prey is caught tail first and ingested partially; type II: prey is caught by the head or tail and fully ingested; Baras et al. 2003; Baras 2013) is a major bottleneck in finfish aquaculture (Naumowicz et al. 2017) since it can lead to important losses (Baras et al. 2003; Huntingford et al. 2012). For example, cannibalism can cause up to 50% losses in *Perca fluviatilis* (Baras et al. 2003; Kestemont et al. 2003). Finally, activity is also an important factor in aquaculture as it contributes to the total energetic budget (e.g. up to 40% of *Perca flavescens* budget; Boisclair and Leggett 1989). Moreover, less active taxa could contribute to lower potential contacts and subsequent potential aggressive interactions. Therefore, in domestication processes, it is necessary to take into account the ability for taxa to present the most suitable group structure, low aggressive interaction rate, as well as lower activity. Yet, there is an intraspecific differentiation (differentiation between allopatric populations of conspecific individuals; Mayr 1963) which could further help to improve domestication processes.

Behavioural intraspecific differentiation and its potential for selection of founder populations have been poorly investigated to date. However, intraspecific differences in aggressive behaviour (Magurran and Seghers 1991; Mandiki et al. 2004; Bell 2004), time spent foraging in an open habitat (Bell 2004; Magnhagen 2006), schooling (Magurran and Seghers 1991), or boldness (Wright et al. 2003) have been already assessed for a few species (see also Foster 1999). Abiotic factors can

influence social behaviours (e.g. temperature, light, population density; Baras et al. 2003; Kestemont et al. 2003), yet a genetic basis was also suggested since allopatric populations or geographically distinct strain differentiations were demonstrated for a few species (Amundsen et al. 1999; Damsgård and Huntingford 2012; Magnhagen et al. 2015). Therefore, considering such behavioural intraspecific differentiation could allow improving aquaculture for species for which production is still limited by behavioural bottlenecks.

The European perch, *Perca fluviatilis* L., is one of the fish species involved in the European aquaculture diversification (Kestemont et al. 2015). Its long-standing socioeconomic interest (high market value and recreational interest) led to the development of its aquaculture in the 1990s (Kestemont and Mélard 2000; Kestemont et al. 2015). However, its production is still limited due to several bottlenecks, including some aspects related to fish behaviour such as aggressiveness and high cannibalism and subsequent mortalities (Kestemont et al. 2015). However, geographic differentiation has been previously observed for some of problematic behavioural traits (e.g. cannibalism rate, Mandiki et al. 2004). Therefore, we aim in this study at (i) assessing if European perch allopatric populations present differentiation for group structure and activity, as well as for aggressive interactions during first-life stages, and (ii) identifying populations presenting behavioural advantages for production.

Material and methods

Rearing conditions

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

Egg ribbons were obtained during the 2018 spawning season (May 2018) from lakes Geneva (GEN; Switzerland; 46° 26′ N, 6° 33′ E), Valkea-Müstajärvi (VAL; Finland; 61° 13′ 08″ N, 25° 07′ 05″ E) and Iso-Valkjärvi (ISO; Finland; 60° 57′ 21″ N, 26° 13′ 3″ E). After transport, 19 egg ribbons per lake were incubated at the Experimental Platform of Aquaculture (Unit of Animal Research and Functionality of Animal Products, University of Lorraine, Vandœuvre-lès-Nancy, France) in incubators (110 × 64 × 186 cm; one incubator per population), containing nine racks each (45 × 7 × 12 cm), at 13 °C. Each incubator had its own temperature control and recirculated water (flow rate of 4 m^3 h^{-1}) system, and water was UV sterilised. Oxygen rate (10.5 ± 0.2 mg L^{-1}) and temperature (13.0 ± 0.3 °C) were checked daily, while pH was measured three times a week (8.0 ± 0.1). Ammonium (lower than 0.05 mg L^{-1}) and nitrite concentrations were monitored three times a week until hatching (lower than 0.01 mg L^{-1}). Photoperiod was 12L/12D and light intensity was 400 lx at the water surface.

Two independent experiments were performed in order to ensure availability of larvae across the rearing period: experiment I from hatching until the end of weaning (26 days post-hatching (dph)) and experiment II from 27 dph until 60 dph. All populations were reared in independent structures.

Concerning experiment I, after hatching, larvae from the different egg ribbons were mixed and transferred to three green internal wall 71-L cylindro-conical tanks (three replicates per population; recirculated aquaculture system (RAS)) at a density of 50 larvae L^{-1}. Temperature was gradually increased during 2 weeks to 20 °C, photoperiod was 12L/12D and light intensity

was 400 lx. Larvae were fed with newly hatched *Artemia* naupli (Sep-Art, INVE) every 1 h 30 from 3 dph until weaning. At 16 dph, *Artemia* ration was decreased by 25% every 3 days and dry feed ration (BioMar, 300 μm until 21 dph, then 500 μm) was increased by the same ratio. After 25 dph, larvae were only fed with dry feed ad libitum (BioMar 500 μm, then 700 μm at 44 dph until the end of the experiment). At 26 dph, the larvae in cylindro-conical tanks were removed to start experiment II.

For experiment II, larvae not used for experiment I were held after hatching in 2-m^3 tanks (RAS) under the same temperature, feeding, light intensity and photoperiod regimes as individuals of the experiment I. At 27 dph, these larvae were transferred at a density of 19 larvae L^{-1} to the three cylindro-conical tanks in order to start experiment II. Light intensity was 80 lx at water surface, all else remaining equal to experiment I (except for density).

During the two experiments, oxygen concentration (8.7 ± 2.3 mg L^{-1}) and temperature (20.0 ± 0.6 °C) were checked daily for all tanks. Ammonium (0.14 ± 0.1 mg L^{-1}), pH (7.2 ± 0.9 mg L^{-1}), and nitrite concentrations (0.08 ± 0.08 mg L^{-1}) were monitored three times a week. Tanks were cleaned daily after first feeding, and dead individuals were removed every morning. Survival rate for ISO, VAL and GEN was respectively 40.1% (± 12.0), 29.4% (± 14.5) and 6.6% (± 3.4) for experiment I (26 dph; statistical difference between Geneva Lake and the two Finnish populations; $F = 7.2$, df = 2, $P < 0.05$) and 31.5% (± 4.3), 28.0% (± 11.1) and 37.4 (± 8.1) for experiment II (60 dph; no statistical difference between the three populations; $F = 0.98$, df = 2, $P = 0.42$). These ranges of survival rates were comparable to what is found in literature (e.g. Tamazouzt et al. 2000; Baras et al. 2003; Fiogbé and Kestemont 2003).

Group structure and activity

For each population, three replicates for each cylindro-conical tank were performed over 2 days (25 and 26 dph). At 24 and 25 dph, a total of 90 individuals ($n = 30$ for each cylindro-conical tank, 10 individuals per replicate) were sampled for each population and transferred to three aquaria (58 L; one aquarium per cylindro-conical tank; order of cylindro-conical replicates randomly assessed over 2 days; see Appendix 1) with an 80 lx light intensity and a temperature of 20.0 °C (± 0.5). Individuals were not fed from the moment they were transferred to the beginning of the experiment the following day in order to have individuals in the same energetic state. After one night of acclimatisation, individuals were tested by groups of ten in circular arenas. Groups of ten individuals might not reflect faithfully what occurs in cylindro-conical tanks. However, evaluation cannot be performed directly in the tanks, and this method was previously validated (e.g. Colchen et al. 2016). Three circular arenas (30-cm diameter with 1.5 cm of water depth) were used to investigate group structure and activity (Colchen et al. 2016). Water in the arena was the same as in the aquaria; room temperature was maintained at 20.0 °C (± 0.6), and arenas were lit at 10 lx from underneath in order to avoid shadows during recording. For each replicate, individuals were transferred from the aquarium to the arena with a beaker and a siphon. After 30-min acclimatisation, individuals were filmed for 30 min using camcorders (Sony, Handycam, DCR-SR72E) located 50 cm above the arena. The three arenas were filmed simultaneously, and the order of replicates tested was randomly assessed. After 1 h, individuals were euthanised with an overdose of MS-222 following European rules and kept in formalin 4% for later length measurements. Larvae tested from ISO, VAL and GEN were respectively 14.05 ± 0.55 mm, 12.90 ± 0.62 mm and 13.87 ± 0.26 mm. This full experiment was performed again during experiment II with fish sampled from cylindro-conical tanks at 44 and 45 dph. For this second test, individuals from ISO, VAL

and GEN were respectively 26.74 ± 1.67 mm, 26.28 ± 1.99 mm and 22.97 ± 1.08 mm (no statistical difference between populations for the two experiments: experiment I: $F = 0.712$, df = 2, $P = 0.528$ and experiment II: $F = 1.68$, df = 2, $P = 0.263$).

Group structure analysis was performed using the ImageJ software. Images were extracted from videos at 3-min interval (11 images per video). From each image, exact coordinates of each individual were noted using the middle point between the eyes. Three parameters were evaluated to assess the group structure: the nearest neighbour distance, the mean of inter-individual distances and the variance of these inter-individual distances (Buske and Gerlai 2011a). Nearest neighbour distance represents the distance between a focal fish and its closest neighbour and is an indicator of the group aggregation. The mean of inter-individual distances corresponds to the mean of distances between a focal fish and all the other fish of the group, and the average of values from all group members is an indicator of the group cohesion. Finally, the average of variances of inter-individual distances from each fish represents the homogeneity of distribution (Buske and Gerlai 2011a). Activity was also calculated in ImageJ. One image per second was extracted for six consecutive seconds every 5 min. Coordinates of each individual were noted for each image, and then, distance swam was calculated every second during the 5 s then averaged to obtain the mean distance swam for each individual per second.

All statistical analyses were performed in R 3.0.3 (R Core Team 2017). To test the normality of distributions, a Shapiro-Wilk test (R Core Team 2017) was used and homogeneity of variances was tested using the Levene test (Gastwirth et al. 2015). Then, linear mixed models were used with distances and activity as fixed factors and cylindro-conical tanks as random factor (Bates et al. 2004). There was no influence of the cylindro-conical tank on all models. Therefore, one-way analyses of variance (ANOVA F test) followed by Tukey post hoc tests were used to evaluate differences between populations (R Core Team 2017).

Quantification of aggressive interactions

Daily observations were carried out at different moments of the day previous to this experiment but did now allow identifying a cannibalism peak during the photophase. Therefore, we hypothesised that the beginning of the photophase would correspond to the cannibalism peak since individuals were not fed between 5.30 p.m. and the next morning, that they were used to be fed during the photophase and that European perch is a visual predator (Graeb et al. 2005; Kestemont et al. 2008). Therefore, observations were performed after first feeding with a 5-min acclimatisation to the presence of the observer and 5 min of focal sampling (Colchen et al. 2019). Daily observations were carried out between 8.30 a.m. and 10 a.m. from 10 dph until the end of experiment I (26 dph). For experiment II, observations were carried out every 3 days (Appendix 1). One replicate per population was observed per day, and the same person performed all observations. Since hatching times were asynchronous between populations, the order of populations or tanks observed was randomly assigned. Several aggressive behaviours were noted: (i) pursuit: an individual heads towards a conspecific, gets close and follows it when the conspecific moves; this involves a change of direction of the two individuals; (ii) attack: when an individual heads towards a congener and gets rapidly close to it without necessarily contact between the two individuals; (iii) bite: when an individual catches with its mouth a part of a conspecific's body and then releases it; and (iv)

capture: when an individual ingests a part or the whole conspecific (type I and II cannibalisms). Taking into account all these aggressive interactions, a global daily aggressive interaction rate was calculated relatively to the initial number of individuals in the tank. Enucleation, being a specific indicator of aggressiveness in perch (Jourdan et al. 2000), was also evaluated by counting daily the number of dead individuals enucleated. Enucleation rate was calculated relatively to the initial number of individuals in the tank. For phase II, type II cannibalism rate was estimated by subtracting from the initial number of individuals the number of survivors and dead individuals over phase II and calculating a rate relatively to the initial number of individuals in the tank. Cannibalism rate could not be evaluated for experiment I as a precise monitoring of mortality was not possible the first week due to fast degradation of dead larvae. Finally, mortality rates attributed to cannibalism and enucleation were also calculated. In order to meet assumptions of normality (Shapiro-Wilk test, R Core Team 2017) and homogeneity of variances (Levene test, Gastwirth et al. 2015), data for all aggressive parameters was transformed (i.e. $\log(x + 1)$). One-way analyses of variance (ANOVA F test) followed by Tukey post hoc tests were used to evaluate differences between populations (R Core Team 2017). When assumptions were not respected (only for the aggressiveness rate during experiment I), Kruskal-Wallis H tests (R Core Team 2017) were used followed by Dunn post hoc tests (Pohlert 2015).

Results

Group structure and activity

Experiment I (25–26 dph)

Inter-individual distances ($F = 7.8$, df = 2, $P < 0.05$), variance of inter-individual distances ($F = 9.9$, df = 2, $P < 0.05$) and activity ($F = 8.2$, df = 2, $P < 0.05$) are significantly lower for GEN compared to VAL and ISO (Fig. 1). There is no statistical difference between VAL and ISO. There is no statistical difference between populations for the nearest neighbour distance ($F = 1.4$, df = 2, $P = 0.2$; Fig. 1).

Experiment II (45–46 dph)

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

Quantification of aggressive interactions

The first cases of cannibalism (type II only) were observed at 26 dph for ISO and at 51 dph for GEN. No cannibalism case was observed for VAL. There is no difference of daily aggressive interaction rate in experiment I ($H = 0.60$, df = 2, $P = 0.74$; Fig. 1), but in experiment II, these behaviours were significantly higher in GEN than ISO and VAL ($F = 7.21$, df = 2, $P < 0.05$; Fig. 2). There is no statistical difference between ISO and VAL. Enucleation rate, which is null in experiment I for all populations, is significantly higher in GEN compared to VAL and ISO ($F = 70.74$, df = 2, $P < 0.05$;

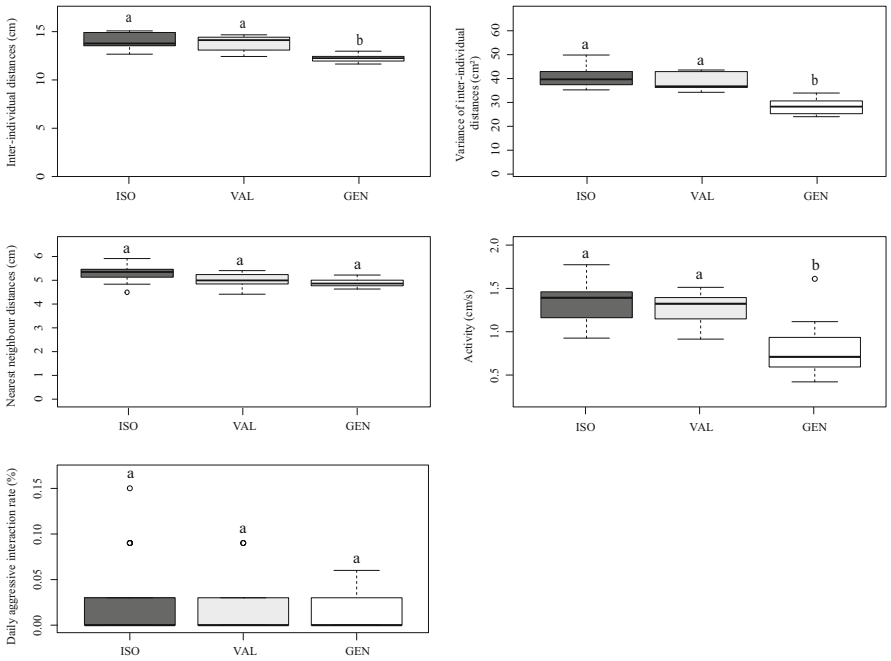


Fig. 1 Box plots representing group structure and aggressive interaction results for experiment I ($n = 3330$). Four measures of group structure are presented: inter-individual distances, variance of inter-individual distances, nearest neighbour distances and activity. The black line represents the median;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

Fig. 2) in experiment II. Cannibalism rate is not statistically different between populations ($F = 0.018$, df = 2, $P = 0.98$; Fig. 2). Mortality rate attributed to cannibalism and enucleation is not statistically different between the three populations ($F = 0.69$, df = 2, $P = 0.59$; Fig. 2).

Discussion

Inter-populational differentiation in behavioural traits and its potential causes

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

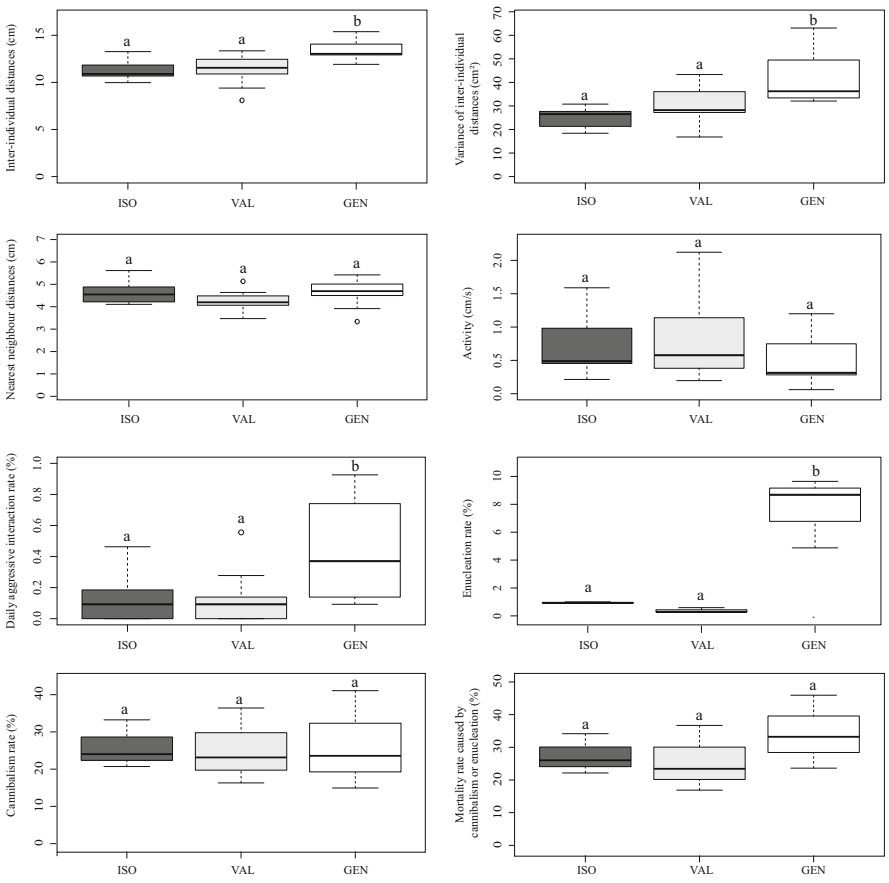


Fig. 2 Box plots representing group structure and aggressive interaction results for experiment II ($n = 1080$). Four measures of group structure are presented: inter-individual distances, variance of inter-individual distances, nearest neighbour distances and activity. Aggressive interaction results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

Intraspecific differentiation in group structure and aggressive behaviours has been already highlighted for several fish species (Rosenau and McPhail 1987; Magurran and Seghers 1991; Amundsen et al. 1999; Lahti et al. 2001; Huizinga et al. 2009; Wark et al. 2011; Song et al. 2011). Here, a more cohesive and homogeneous structure is demonstrated for Finnish populations compared to GEN at 45–46 dph (Fig. 2). These results, associated with a similar nearest neighbour distance, indicate a structure in sub-groups in all populations but with a distance between these groups higher for GEN at 45 dph. The less homogeneous group structure of GEN at 45 dph is quite congruent with the higher aggressiveness highlighted for this population. Indeed, although daily aggressive interaction rate seems low (0.1–0.9%; Fig. 2), the congruence between aggressive interaction patterns and enucleation rate supports the higher aggressiveness of GEN compared to the two Finnish populations. The absence of difference in cannibalism rate indicates that aggressive interactions are not necessarily followed by type II cannibalism. Therefore, our study is not congruent with Mandiki et al. (2004) who

showed a difference in intracohort cannibalism rate between different European perch allopatric populations (but with different populations than the ones investigated here). Here, we highlight differences in aggressive interactions aside from cannibalism rate. Inter-populational behavioural differences can be shaped by genetic differentiation, by phenotypic plasticity, or by their combination.

On the one hand, the observed inter-populational behavioural differences could be shaped by genetic differentiation. Indeed, population-specific demographic histories and potential local adaptations fostered by particular selective pressures can lead to the acquisition of distinct behavioural phenotypic traits or development rates between allopatric conspecific populations (Foster and Endler 1999; Foster 1999). For instance, it was shown a link between aggressiveness and the level of predation of the natural living site (Huntingford 1982; Magurran and Seghers 1991) as well as other environmental factors such as food availability and water current velocity (Lahti et al. 2001 and references therein). The occurrence of inherited differences in aggressive interactions was assessed for several species (Huntingford et al. 2012; Damsgård and Huntingford 2012). Similarly, inter-populational differences in activity were found to be connected to prey size distribution, total prey biomass and water transparency (Boisclair and Leggett 1989). Unfortunately, we do not have enough information on the different lakes' abiotic and biotic parameters to make any assessment. Another explanation of inter-populational differences could be divergences in development rates potentially triggered by genetic specificities. Indeed, we compare the populations at the same age, but we do not know if the compared fishes are at the same developmental stage (i.e. the lack of development table for larval and juvenile stages of *P. fluviatilis* prevents us to assess if the development is synchronous between populations). The populations might have divergent development rates, which can trigger inter-populational differences in parameters investigated. For instance, the higher aggressiveness in experiment II might be related to the development of muscular and nutritional structures through the larval stage (Kestemont et al. 1996; Vlavonou 1996). It can also be related to the development of visual structures since the visual acuity, essential for capture of prey, increases until metamorphosis (Guma'a 1982). In addition, the aggregation in sub-groups might be due to several factors such as kinship (Behrmann-Godel et al. 2006), the nature of interactions (e.g. aggressive interactions), spatial distribution, or differential sizes (Hinde 1976). Since these two last factors are sensitive to developmental stage, group structure is also influenced by development rate.

On the other hand, phenotypic plasticity (i.e. the ability of a genotype to produce more than one phenotype when exposed to different environments; Pigliucci et al. 2006; Kelly et al. 2012) is an alternative explanation of the observed behavioural differentiations between populations (DeWitt and Scheiner 2004) with behaviour reflecting the strategy adopted under the influence of environmental factors. This was suggested as the driving factor for cannibalism in *P. fluviatilis* (Krol et al. 2015 and references therein) as well as in other species (e.g. Svenning and Borgstrøm 2005). Since we have used an experimental transplant approach (common environment), we speculate that we have minimised the effect of the environment (West-Eberhard 2003). Nevertheless, influences of past environmental conditions (i.e. before the beginning of our experiment) cannot be ruled out. On the one hand, we have collected individuals at the egg stage in the wild, and phenotypic response to environmental conditions could have occurred during development (Swain and Lindsey 1986). On the other hand, environmental conditions experienced by the parents might have influenced offspring phenotype (Mousseau and Fox 1998; Youngson and Whitelaw 2008). At last, it was also shown an influence of maternal size on larvae performance (Olin et al. 2012). Since we have no information on the parents of egg sampled, we cannot exclude the influence of maternal effects which were demonstrated in *P. fluviatilis* for other traits (Babiak et al. 2004; Krol et al. 2015).

Overall, we cannot assess the importance of genetic differentiation, phenotypic plasticity and specific development rates in population-specific behaviour. Behavioural differentiation

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

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

For each population, we observe a behavioural differentiation between the two studied ages. Such a differentiation has been previously observed in other species. For instance, development of shoaling (increasing protection against predators, foraging efficiency and mate encounters) with age through a decrease of inter-individual and nearest neighbour distances has already been observed in zebrafish (Buske and Gerlai 2011b; Buske and Gerlai 2012). We observe similar development for ISO and VAL populations. In contrast, the opposite pattern observed for GEN population is unexpected and corresponds to the establishment of a less homogeneous group with age. Mechanisms underlying the age-dependent changes in group structure are so far unknown. Differential ontogenies of sensory development might play a role into differences at the different ages (Buske and Gerlai 2012). Several neuroanatomical, physiological. or biochemical factors have been suggested to be involved (Buske and Gerlai 2012). There might also be some group regulation mechanisms subsequent to weaning, which can potentially increase competition for resources linked for instance to bioenergetic needs or physiological shifts. This competition could explain the higher occurrence of aggressive interactions in experiment II.

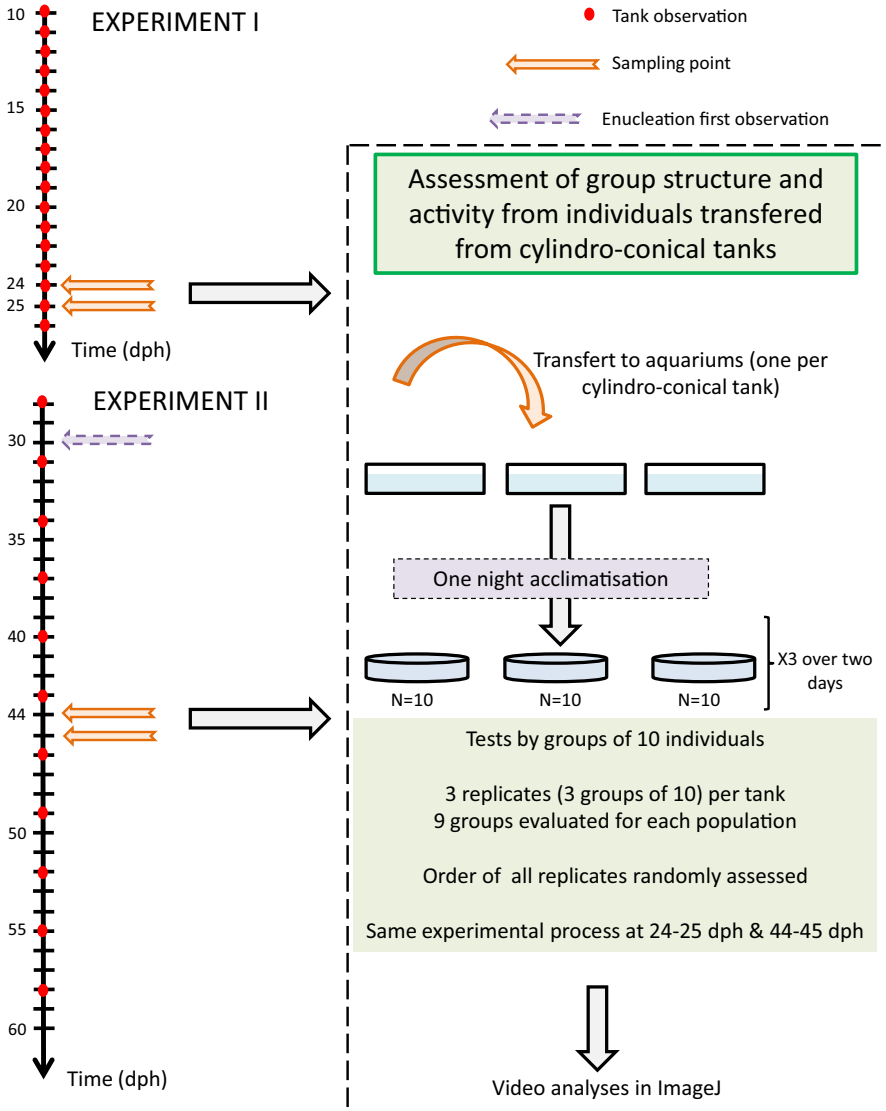
Integrating inter-populational behaviour differentiation: a way to improve aquaculture production?

The variability occurring in behaviour at the intraspecific level offers the opportunity to select fishes whose behaviours make them more suitable for aquaculture production (Huntingford et al. 2012). In the European perch, the lack of population-specific activity tends to make this trait useless to select best populations for aquaculture purpose. In contrast, difference in aggressiveness (i.e. and its consequences: losses due to aggressive interactions ranged from about 20 to 40% depending on the population; experiment II, Fig. 2) is a potential selection criterion for farmers since such interactions are highly detrimental for fish production. Similarly, the population-specific group structure should be considered as highly important information to highlight most suitable populations for intensive aquaculture. Based on our result, the more cohesive group structure and less aggressive interactions of Finnish *P. fluviatilis* make them the most suitable populations for aquaculture. However, more populations need to be compared in order to identify populations of interest across the species range. Moreover, we cannot exclude the future potential impact of domestication since behavioural traits are modified by this process (Kohane and Parsons 1988). Yet, taking into account behavioural intraspecific differentiation would allow starting domestication program on populations presenting the best behavioural pre-disposition.

Selecting best populations for aquaculture production cannot be made through only behavioural trait comparisons. Indeed, selective breeding for low stress responsiveness has for instance been applied in several fish species, but these low-stress response fish were also

the ones which were more aggressive (Huntingford et al. 2012). Intraspecific differentiation has been already assessed for several other traits of interest such as growth (e.g. Mandiki et al. 2004; Leithner and Wanzenböck 2015), feed conversion efficiency (e.g. Imsland et al. 2000; Jonassen et al. 2000), or disease resistance (e.g. Imsland et al. 2002; Overturf et al. 2003). Therefore, the choice of the founder population must then be based on a multi-function and multi-trait approach rather than a single-trait decision framework.

Appendix



Appendix 1 Material and methods workflow

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Compliance with ethical standards

All along experimental procedures, individuals were handled as little as possible. All procedures were in accordance with the national and international guidelines for protection of animal welfare (Directive 2010/63/EU). This study was conducted with the approval of Animal Care Committee of Lorraine (CELMA no. 66) and the Ministry of Higher Education, Research, and Innovation (APAFIS13368-2018020511226118).

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors.

Abbreviations *GEN*, Lake Geneva; *VAL*, Lake Valkea-Müstajärvi; *ISO*, Lake Iso-Valkjärvi; *RAS*, Recirculated Aquaculture System

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CHAPTER 5

GENERAL DISCUSSION

Introducing a new species into aquaculture presents a risk for fish farmers due to low experience with the rearing and the reproduction of this new species. Despite substantial research effort put into intensive production of European perch in the last decades (Fontaine et al., 1996; Fiogbé and Kestemont, 2003; Żarski et al., 2011), many commercial fish farmers are still not convinced of the economic sustainability of European perch culture (Steenfeldt et al., 2015). The production yields of the European perch could be enhanced by implementing biotechnological practices, *e.g.* domestication and selective breeding, which are reported to increase desirable zootechnical traits (*e.g.* growth rate, feed conversion efficiency) and therefore reduce production costs (Liao and Huang, 2000; Gjedrem, 2012; Gjedrem et al., 2012). Nevertheless, prior to starting the genetic improvement practices, researches should focus on selection of suitable strain(s) for aquaculture as they can display considerable variations in zootechnical traits (Mandiki et al., 2004; Pimakhin and Žák, 2014) and therefore considerably improve the development of profitable percid industry in the near future (Kestemont and Mélard, 2000).

The difference in aquaculture performances between various populations was documented for several fish species (Rosenau and McPhail, 1987; Conover et al., 1997; Brown et al., 1998). Previous studies on European perch showed that populations from different geographic areas exhibit different growth rates and feed efficiencies, with outperforming of the more northern populations (Mandiki et al., 2004; Pimakhin and Žák, 2014). However, previous studies did not assess the genetic differentiation between studied populations, hence, it is not known if observed differences among populations were genetically- induced.

Past demographic events such as population movements triggered by climate cycles (*e.g.* Pleistocene glaciations) (Martinson et al., 1987; Dawson, 1992; Bernatchez and Wilson, 1998) and former/current geographic barriers (Bergek and Björklund, 2009) are important factors shaping within-species genetic differentiation. Habitat conditions in refugia and postglacial lakes changed on a regular basis, as their locations and boundaries and, consequently, species with different ecological characteristics and dispersal abilities responded differently to events (Pielou, 1992). Ecological differentiation has led to the formation of reproductively isolated taxa and species pairs (Bernatchez and Wilson, 1998). These factors can lead to a decrease or interruption of gene flow among allopatric conspecifics that fosters local genetic specificity through processes including genetic drift (Avise, 2000). Isolated gene pools may occur with diverse habitats, eco-climatic conditions, population densities, or food availability producing variation in selective pressure (Mayr, 1970). In this scenario, different environmental pressures (*e.g.* abiotic and biotic factors) applied over several generations can lead to local adaptations based on genetic divergences (Hansson, 1984; Przybylski, 1996; Pierce et al., 2003; Losos and Ricklefs, 2009).

Based on F_{ST} value, the Finish (FV, FM in Chapter II) and Polish (PL in Chapter III) populations were the most genetically divergent. The genetic differentiation is in line with previous findings of Nesbø et al. (1999). Moreover, our results revealed that the most genetically divergent Finish (FV and FM) populations tend to have one of the highest specific growth rates (SGR; Chapter II). Similarly in Chapter III, our results showed higher SGR in genetically differentiated PL population compared to CZ and SK populations. These results support the hypothesis that genetically different populations are likely to display variation in characteristics affecting their potential in aquaculture. This could suggest a potential heritability of this pattern as it has already been highlighted for several fish species (Nicieza et al., 1994; Bell, 2005).

In Chapter II, the two northernmost Finnish populations showed higher growth performances. This is in line with Mandiki et al. (2004), who observed that Finish population

outperformed the Polish one (different populations from the ones investigated in our study). Indeed, environmental conditions vary along the latitudinal gradient, where growth rate in fish was shown to decrease with latitude (Beverton, 1987; Lobón-Cerviá et al., 1996; Belk and Houston, 2002; Quist et al., 2003). This phenomenon may be due to the hypothesis that northern fish compensate for their shorter growing season and higher investments in annual reproduction (Blanck and Lamouroux, 2007) by increasing growth rate more rapidly with temperature than do southern fish (Conover and Present, 1990). Thus, intraspecific variation in traits of the European perch at larger spatial scales could also be related to latitudinal clines.

Higher growth performances could be also partly attributed to behavioural traits such as group structure and aggressive interactions (Li and Brocksen, 1977). More cohesive and homogenous group structures were demonstrated in both Finish (VAL and ISO) populations compared to French (GEN), which, on the other hand, showed higher aggressive interactions (Chapter IV). These inter-population differences in behavioural traits could be also shaped by genetic differentiation. Intraspecific differentiation in group structure and aggressive behaviours has been already highlighted for several fish species (Magurran and Seghers, 1991; Lahti et al., 2001; Huizinga et al., 2009; Wark et al., 2011).

One could expect that the different initial state of eggs (*i.e.* egg diameter and egg survival rate) could explain the differences of growth. Indeed, a relationship is known between egg size (linked to female size) and larval size/weight at hatching (Moodie et al., 1989; Chambers and Leggett, 1996; Johnston et al., 2007; Olin et al., 2012). However, our data showed no such relationship. According to Andree et al. (2015) maternal effects seem to be highly variable and complex and the initial larvae weight does not always correlate with the egg size and the initial larvae body weight. Marshal et al. (2010) have also alluded that the particular trend between eggs and larvae characteristics may be inconsistent and vary among environments and year classes.

The observed differences in zootechnical and behavioural traits could be explained by (i) population-specific environment before the experiment (including parental effect), (ii) local adaptation based on genetic differentiation, or (iii) their combination (Wolf and Wade, 2009). However, we also observed variation in aquaculture performance among genetically undifferentiated fish populations (*i.e.* the larvae from populations PW, CN, SV in Chapter II and juveniles from populations CZ and SK in Chapter III). Although four DNA regions were commonly used for determining genetic difference at the intraspecific level for several fish species (*e.g.* the burbot *Lota lota* (L.), the European whitefish *Coregonus lavaretus* (L.), the Atlantic salmon *Salmo salar* L.) (Makhrov and Bolotov, 2006; Costedoat and Gilles, 2009; Baharum, 2012; Patwardhan et al., 2014) including the European perch (Nesbø et al., 1998a; Nesbø et al., 1998b; Nesbø et al., 1999), this method is rather conservative and could underestimate genetic divergences (Wan et al., 2004). Therefore, the genetic differentiation of undifferentiated populations should be further assessed by higher resolution analyses (*e.g.* microsatellites). Phenotypically distinct organisms are not always characterized by large genetic differences (Ferguson, 2002; Salvato et al., 2002; Rheindt et al., 2011), making quantification of genetic differentiation challenging without further analyses of nuclear genes or the entire genome. Alternatively, differences in any morphological, physiological, or behavioural traits among non-genetically differentiated fish populations could be a consequence of phenotypic plasticity (DeWitt and Scheiner, 2004).

Potential biases induced by our experimental design cannot be ruled out. First, ribbons transportation could affect the embryo development as well as subsequent larvae growth performances. In order to minimize such impact, we transported the egg ribbons during less sensitive egg development stages (*e.g.* gastrulation and organogenesis) (Woynarovich

and Horváth, 1980). In fact, the length and the mean of transport as well as developmental stage of our samples did not seem to affect our results (see Chapter II). Second, although our daily observations suggest that in general most larvae in all populations started to feed, we did not measure the feeding intake because such an assessment in larvae stage remains methodologically difficult/time-consuming. Therefore, despite the fact that all tested populations were reared under the same optimal conditions (Kestemont and Mélard, 2000; Tamazouzt et al., 2000; Kestemont et al., 2008; Kestemont et al., 2015), we cannot exclude potentially biased feed intake. Whether such a population-specific feed intake exists, it should be considered as a population-specific feature potentially valuable for aquaculture.

Furthermore, the wild egg ribbons were collected from unknown broodstock with different environmental pressures, therefore the zootechnical traits of the European perch can be also impacted by maternal size (Olin et al., 2012). Egg size and number vary within and among females and also depending on the environmental conditions experienced by the female and reflecting the nutrient status and age (Solemdal, 1997). Since we have no information about the parents of the sampled egg ribbons, we cannot exclude such a transgenerational or maternal/parental effect. Thus, observed inter-population differences could be caused by genetic pool families that can affect the offspring husbandry performances. However, we argue that our sampling design limited such an effect, because we mixed larvae from ten different egg ribbons (one ribbon is laid by one female) for each population, thus, we minimized the hazard of studying individuals with a high degree of kinship. Furthermore, biotic and abiotic conditions such as diet, parasites and water temperature experienced by the parent fish may be important in shaping offspring phenotype and development (Mousseau and Fox, 1998; Fusco and Minelli, 2010; Wiens et al., 2014). Indeed, past environmental circumstances may contribute at the same degree as the current conditions to growth performance (Mousseau and Fox, 1998; Devevey et al., 2010). Such a transgenerational effect is not determined by the offspring's genome but instead by the environmental experience of its parents (Youngson and Whitelaw, 2008). Therefore, fish obtained from parents with high condition through a resource-rich/pathogen-low environment may acquire the parental condition and thus perform better under any environmental conditions than does offspring of poor quality parents (Henderson et al., 2000; Valtonen et al., 2012).

In addition, we did not conduct an initial assessment of pathogens in the specimens. Although mortality rates were similar among populations (see Chapter III), pathogens may have affected performance of the populations without leading to increased mortality.

Although in Chapter III, SGR of juveniles from PL population was significantly higher compared to the remaining populations (from the CZ and SK), in Chapter II, the growth rate of larvae from the same population (PL) was among the lowest. This could be related to the durations of both experiments (24 days in Chapter II vs. 84 days in Chapter III) meaning that 24 days might not be long enough for the expression of the genetic growth differences, that was reached in longer experiment (Chapter III).

Aggressive behaviour observations have been recorded after first feeding, but cannibalism peaks with aggressions might occur at different period of the day between populations and calculated cannibalism rate might also include dead individuals eaten by siblings, which can lead to biases in the estimation of cannibalism rates. However, the temporal differentiation in cannibalism peaks has not been reported to date and the cannibalism estimation method, widely used across the literature (Kestemont et al., 2003; Mandiki et al., 2004; Ljubobratović et al., 2015), allows us to compare populations. Therefore, we argue that biases related to observations of inter-population behavioural differentiations were minimized.

In our studies, we compared the populations at the same age (Chapters II, III, IV), but we do not know if the fishes were in the same developmental stage (*i.e.* the lack of development

table for larval and juvenile stages of *P. fluviatilis* prevents us to assess if the development is synchronous between populations). The populations might have divergent development rates, which can trigger inter-population differences in investigated parameters. For instance, the higher aggressiveness in experiment II, Chapter IV might be related to the development of muscular and nutritional structures through the larval stage (Kestemont et al., 1996; Vlavonou et al., 1999). It can also be related to the development of visual structures since the visual acuity, essential for capture of prey, increases until metamorphosis (Guma'a, 1982). Additionally, in present thesis we studied different populations (Chapters II, III, IV) which could have different body shapes. These differences in shapes have already been highlighted at the intraspecific level in the European perch (Mairesse et al., 2005). Furthermore, evidence suggested that linear and weight growths are regulated by different endocrine systems in fish and may not necessary happened at the same time (Björnsson et al., 2012), however, liner and weight differentiation in growth between different European perch populations have not been reported to date.

Additionally, phenotypic plasticity is a ubiquitous phenomenon in living organisms in response to environmental conditions and the variation of aquaculture performances among SK and CZ (Chapter III) could be caused by high gene flow in an allopatric gene pool among these populations, that was favoured for the development and maintenance of phenotypic plasticity over local genetically-based adaptations (DeWitt and Scheiner, 2004; Crispo, 2008; Bergek and Björklund, 2009). Applying similar environmental conditions to different fish populations through transplant experiments, as in our study, minimizes potential effects of phenotypic plasticity on the studied traits and suggests a genetic basis for the variation (West-Eberhard, 2003; Rosburg, 2017). However, alteration in phenotype as a response to environmental cues can occur during the development and extend through all or part of the life of an organism (Fusco and Minelli, 2010; Wiens et al., 2014). Ruling out a potential phenotypic plasticity effect would require breeding sequential generations of desired strains under similar conditions, requiring long-term transplant experiments, which may be costly and time-consuming.

Conclusion

This thesis includes three publications where we highlighted the geographic differentiation in key traits for aquaculture of the European perch. Our study confirms that key zootechnical and behavioural traits can vary at the intraspecific level, which could be beneficial for improving the production of the European perch.

- Higher growth and better behaviour performances were observed in the northernmost populations (Chapters II, III and IV).
- Better growth performances were shown in both Finish (Chapter II) and one Polish (Chapter III) populations.
- More cohesive and homogenous group structure were demonstrated in two Finish populations compared to French population (Chapter IV).
- The populations showing better growth performances in RAS conditions were the most genetically differentiated populations.
- Variation in aquaculture performance was also observed among genetically lower- or un-differentiated populations (Chapters II and III).
- This variation could be a consequence of different food level intake, health status, body shapes, development stage or pre-collection environment.

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ENGLISH SUMMARY

Growth, genetic and morphological characteristics of different perch (*Perca fluviatilis*) populations in intensive aquaculture

Tatyana Gebauer (Vanina)

Growing human population and demands for quality protein sources resulted in fully- or over-exploitation of 90% of the world's fish stocks. This has led to continuous growth of global aquaculture production being the fastest growing food-producing sector. However, this is not true for the European aquaculture sector which has been stagnating for the last decades. Large-scale growth of European aquaculture has been hampered by a shortage of suitable sites and the ecological carrying capacity of existing ones, public criticism based on perceived environmental impacts as well as strict environmental regulations and bureaucracy. Modern solution such as recirculating aquaculture systems (RAS) perform well across most indicators of productivity as well as environmental resources utilization. Higher capital costs of the RAS call for higher productive capacity reducing operation costs and culture of highly valued species increasing the sale price. Since over 75% of the European freshwater fish production is formed by two low/medium value species (common carp and rainbow trout), the diversification of European aquaculture is inevitable. Diversification of aquaculture is therefore crucial in order to fulfil the sustainable development, while the European perch (*Perca fluviatilis* L.) is one of promising candidates. Despite the fact that the species has been introduced in RAS more than two decades ago, the volume of European perch production is still not high enough to meet the market demand. Poor growth capacity, small size and fragility of the larvae, size heterogeneity and cannibalism rate (*i.e.* zootechnical traits) as well as inter-individual relationships in population (*i.e.* behavioural traits) are usually cited as the main limiting factors.

Zootechnical and behavioural traits can vary substantially among wild allopatric European perch populations. Choosing wild European perch population(s) showing higher growth rate, lower cannibalism and size heterogeneity with specific behavioural traits such as low aggressive interaction rate and homogeneous spatial distribution in rearing units are crucial for the establishment of the European perch broodstock and subsequent selective breeding programs. Therefore, knowledge of the zootechnical and behavioural traits relative to geographic origin supported by genetic analyses may ultimately help to overcome current challenges and bottlenecks of European perch aquaculture.

Population differences in zootechnical and behavioural traits can be shaped by genetic differentiation, phenotypic plasticity, or by their combination. However, it is not clear whether the inter-population differences are genetically- or environmentally-induced. Therefore, we explored the zootechnical traits of geographically different European perch populations at larval- (two Finish, two Polish, two Slovakian, one Czech; Chapter II) and juvenile-stages (Polish, Czech, Slovakian; Chapter III) in the same standardized conditions reducing the environmental effect. Additionally, we provided a genetic-based assessment on four mitochondrial markers: cytochrome b, D-loop of control region, 16S rRNA, and cytochrome oxidase I (Chapters II, III). In Chapter IV, we observed behavioural traits of larvae and juveniles from two Finish and one French populations.

In Chapter II, we corroborate previous findings documenting higher growth rate of northern populations of the European perch (*i.e.* both Finnish populations), which are, at the same time, most genetically divergent compared to other tested populations. This could suggest a genetic basis of the observed growth differentiation and, consequently, a potential heritability

of this pattern. Higher growth rate could be partly attributed to behavioural interactions as we found more cohesive and homogenous group structure in both Finish compared to French population which, on the other hand, showed higher aggressive behaviour (Chapter IV). However, European perch larvae from genetically lower- or un-differentiated populations (*i.e.* Polish, Slovakian and Czech) showed various growth rates as well. This could be caused by potentially biased feed intake, even though the larvae were reared in optimal standardized conditions. However, the feed intake was not evaluated due to methodological difficulties. Moreover, the effects of pre-experimental environmental conditions cannot be eliminated as well, because tested populations were sampled at egg stage and therefore the information about the size or past environmental circumstance of parents is not available.

In Chapter III, we observed significantly higher specific growth rate of juveniles from genetically distinct Polish population compared to the rest populations (Czech and Slovakian). Although in Chapter II the growth rate of larvae from the same Polish population (Stary Dwór Lake) was among the lowest, in the Chapter III the specific growth rate and body weight of Polish juveniles were one of the highest. This could be related to the durations of both experiments (24 days in Chapter II vs. 84 days in Chapter III) meaning that 24 days might not be long enough for expression of the genetic-induced growth difference, which was reached in longer experiment (Chapter III). Cannibalism and mortality rates were similar at the end of the experiment among all populations in Chapter III excluding influence of genetic basis on these parameters. However, we also observed slight variation in zootechnical traits among fish from genetically similar Czech and Slovakian populations. This might be caused by underestimation of the genetic variation based on analysis of only four mitochondrial markers, a consequence of different health status, pre-collection environment, or transgenerational effects.

In conclusion, higher growth rates were mainly observed in the most genetically differentiated populations (Chapters II, III). We also corroborate previous findings documenting higher growth rate of northern populations of the European perch. At the same time, northern populations display lower aggression and more cohesive social behaviour (Chapter IV). However, we also observed variation in aquaculture performance among genetically lower divergent or genetically similar populations. The variation could be a consequence of different food intake, health status, pre-collection environment, transgenerational effect and usage of conservative mitochondrial markers. Further studies are needed to assess the importance of these factors in geographic differentiation of aquaculture performance.

CZECH SUMMARY

Růst, genetické a morfologické charakteristiky různých populací okouna říčního (*Perca fluviatilis*) v intenzivní akvakultuře

Tatyana Gebauer (Vanina)

Rostoucí lidská populace a s tím spojené zvýšené požadavky na proteinové zdroje způsobily, že 90 % světových populací ryb jsou loveny na hranici jejich ekologické kapacity, nebo tuto hranici dokonce překračují. To vedlo k nepřetržitému růstu globální akvakultury, která se stala nejrychleji rostoucím sektorem potravinářského průmyslu. Akvakultura v Evropě však, na rozdíl od globální akvakultury, v posledních 20 letech stagnuje. Růst produkce evropské akvakultury je limitován nedostatkem vhodných a vyčerpanou ekologickou kapacitou existujících lokalit, kriticky vnímanými dopady na životní prostředí, ale i složitou a přísnou legislativou. Řešením můžou být moderní technologie, jako např. recirkulační akvakulturní systémy (RAS), které se vyznačují vysokou produktivitou i efektivitou využití zdrojů. Z důvodu vysokých vstupních nákladů RAS je však nezbytné zajistit vysokou intenzitu chovu ryb (vyšší produkční kapacita a hustoty obsádek), ale také zaměřit se na druh s vyšší tržní hodnotou. Vzhledem k tomu, že více než 75 % produkce sladkovodních ryb v Evropě tvoří dva druhy s nízkou/středně vysokou tržní hodnotou (kapr obecný a pstruh duhový), je diverzifikace evropské akvakultury nevyhnutelná. Diverzifikace je klíčovým nástrojem pro naplnění udržitelného vývoje akvakultury, přičemž okoun říční (*Perca fluviatilis* L.) se jeví jako slibný kandidát pro diverzifikaci evropské sladkovodní produkce. Navzdory tomu, že počátky chovu okouna říčního v RAS sahají do 90. let 20. století, se objem produkce zásadně nezvýšil a v současnosti nedokáže uspokojit poptávku trhu. Jako hlavní faktory limitující růst produkce okouna říčního z RAS jsou uváděny pomalý růst, malá velikost a vysoká senzitivita larev, růstová heterogenita a kanibalizmus (tj. zootechnické vlastnosti), jakožto i vysoká agresivita (tj. behaviorální vlastnosti).

Zootechnické a behaviorální vlastnosti se můžou významně lišit mezi divokými alopatrickými populacemi okouna říčního. Výběr populací, které vykazují rychlejší růst, nižší kanibalizmus a růstovou heterogenitu a specifické behaviorální vlastnosti vhodné pro podmínky akvakultury (nízká míra agresivity, homogenní struktura hejna), je tedy klíčovou podmínkou pro založení chovných hejn a následné šlechtitelské programy. Znalosti o zootechnických a behaviorálních vlastnostech v závislosti na různém geografickém původu a genetické diferenciaci tedy můžou v konečném důsledku pomoci překonat současné problémy a limitace chovu okouna říčního.

Interpopulační rozdíly v zootechnických a behaviorálních vlastnostech můžou být způsobeny genetickou diferenciací, fenotypovou plasticitou nebo jejich kombinací. Není však jasné, zda jsou tyto rozdíly mezi populacemi vyvolané geneticky, nebo environmentálními vlivy. Zkoumali jsme proto zootechnické vlastnosti alopatrických populací u larev (po dvou populacích z Finska, Polska a ze Slovenska a jedna z ČR; kapitola II) a juvenilů okouna říčního (po jedné populaci z Polska, ČR a Slovenska; kapitola III) ve stejných standardizovaných podmínkách snižujících efekt environmentálních vlivů. Dále jsme provedli genetické analýzy založené na čtyřech mitochondriálních markerech: cytochromu b, D-loop kontrolní oblasti, 16S rRNA a cytochromoxidáze I (kapitoly II, III). V kapitole IV jsme pozorovali behaviorální rysy larev a juvenilů u třech populací okouna říčního (dvě z Finska a jedna z Francie).

Výsledky kapitoly II potvrzují dřívější vědecké poznatky dokumentující rychlejší růst u severních populací okouna říčního (tj. obě populace z Finska), které jsou zároveň nejvíce geneticky diferenciované od ostatních testovaných populací. To naznačuje, že pozorované rozdíly v zootechnických vlastnostech mají genetický základ, a tudíž jsou potenciálně dědičné. Rychlejší růst severních populací by mohl být částečně připsán behaviorálním interakcím,

protože pozorování v kapitole IV prokázalo, že obě populace z Finska projevují méně agresivních interakcí a více homogenní strukturu hejna ve srovnání s populací z Francie. Larvy okouna říčního z geneticky méně nebo nediferencovaných populací (tj. z Polska, Slovenska a ČR) však také vykazovaly rozdíly v některých zootechnických vlastnostech. To by mohlo být způsobeno rozdíly v příjmu krmiva, a to navzdory tomu, že byly larvy chovány v optimálních standardizovaných podmínkách. Příjem krmiva však v kapitole II nebyl hodnocen z důvodu metodických problémů těchto analýz. Rovněž nemůžeme vyloučit efekt environmentálních podmínek v pre-experimentální periodě i vliv velikosti a kondice rodičů, protože testované populace byly získány z přírodních lokalit ve stadiu jiker.

V kapitole III jsme pozorovali signifikantně vyšší specifickou rychlost růstu juvenilů okouna říčního z geneticky diferenciované populace z Polska ve srovnání s ostatními populacemi (z ČR a Slovenska). Přitom v kapitole II byl růst larválních stadií u stejné populace (jezero Stary Dwór) jeden z nejpomalejších mezi testovanými populacemi. To by mohlo souviset s dobou trvání obou experimentů (24 dní v kapitole II vs. 84 dní v kapitole III), ve smyslu, že 24 dní nemusí být dostatečně dlouhá doba pro expresi geneticky vyvolaného rozdílu v zootechnických vlastnostech, který byl dosažen v delším experimentu (kapitola III). Kanibalizmus a mortalita juvenilů byly na konci experimentu podobné u všech populací vylučující vliv genetického základu na tyto parametry. Nicméně i u geneticky podobných populací (ČR a Slovenko) jsme pozorovali rozdíly v některých zootechnických vlastnostech. To může být způsobeno podhodnocením analýz genetické diferenciace založené pouze na čtyřech mitochondriálních markerech, odlišným zdravotním stavem nebo transgeneračními efekty.

Na základě uvedených experimentů jsme dospěli k závěru, že rychlejší růst byl pozorován především u nejvíce geneticky diferenciovaných populací okouna říčního (kapitoly II, III). Rovněž můžeme potvrdit výsledky dřívějších studií dokumentující rychlejší růst u severních populací. Zároveň jsme pozorovali, že u severních populací docházelo k méně častým agresivním interakcím a mají více homogenní strukturu hejna (kapitola IV). Zaznamenali jsme však také rozdíly v zootechnických vlastnostech mezi geneticky méně diferenciovanými nebo podobnými populacemi. Tyto variace by mohly být důsledkem odlišného příjmu potravy, zdravotního stavu, environmentálních podmínek před sběrem jiker, transgeneračního účinku a použití konzervativních mitochondriálních markerů. K posouzení významu těchto faktorů na zootechnické vlastnosti okouna říčního jsou zapotřebí další studie.

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Vanina, T., Gebauer, R., Stejskal, V., Toomey, L., Rutegwa, M., Kouřil, J., Bláha, M., Lecocq, T., 2019. Genetic and aquaculture performance differentiation among wild allopatric populations of European perch (Percidae, *Perca fluviatilis*). Aquaculture 503: 139–145. https://doi.org/10.1016/j.aquaculture.2018.12.071 (IF 2017 = 2.71)

Vanina, T., Gebauer, R., Toomey, L., Stejskal, V., Drozd, B., Bláha, M., Kouřil, J., Lecocq, T. 2019. Seeking for the inner potential: comparison of larval growth rate between seven populations of *Perca fluviatilis*. Aquaculture International 27: 1055–1064. https://doi.org/10.1007/s10499-019-00384-4 (IF 2018 = 1.455)

Stejskal, V., Matoušek, J., Šebesta, R., Prokešová, M., **Vanina, T.**, Podhorec, P., 2018. Prevalence of deformities in intensively reared *Coregonus* peled and comparative morphometry with pond-reared fish. Journal of Fish Diseases 41: 375-381. https://doi.org/10.1111/jfd.12695 (IF 2017 =2.00)

Vanina, T., Stejskal, V., 2017. A new record of *Cottus spinulosus* in the Talas River watershed Kazakhstan Central Asia. Journal of Ichthyology 57: 547–552. https://doi.org/10.1134/S003294521704018X (SIR 2016 = 0.33)

Abstracts and conference proceedings

Vanina, T., Gebauer, R., Stejskal, V., Bláha, M., Kouřil, J., 2018. Growth differences among geographically distinct populations in European perch juveniles under RAS conditions: preliminary data. In: EAS (eds.), Aquaculture Europe 2018 Abstracts. Montpellier, France, August 25–29, 2018, 772 (Poster).

Lundova, K., Matousek, J., Prokesova, M., Sebesta, R., **Vanina, T.**, Stejskal, V., 2017. The effect of timing of photoperiod prolongation on postponement of puberty in brook trout (*Salvelinus fontinalis*). In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018, 686 (Poster).

Stejskal, V., Matousek, J., Prokesova, M., Novikova, K., **Vanina, T.**, Sebesta, R., Gasko, L., 2017. The effect of different insect meal (Hermetia ilucens) inclusion on growth performances of European perch (*Perca fluviatilis*, L.). In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018, 1100 (Poster).

Vanina, T., Stejskal, V., Bláha, M., Kouřil, J., 2017. Patterns in growth performance of geographically distinct European perch (*Perca fluviatilis*) populations reared under controlled conditions. In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018, 1220 (Poster).

TRAINING AND SUPERVISION PLAN DURING STUDY

Name	Tatyana Gebauer (Vanina)
Research department	2015–2019 – Laboratory of controlled reproduction and intensive fish culture of FFPW USB
Supervisor	Prof. Jan Kouřil
Period	29th October 2015 until 18th September 2019

Ph.D. courses	**Year**
Basic of scientific communication	2016
Applied hydrobiology	2017
Ichthyology and fish taxonomy	2016
Pond aquaculture	2016
Biostatistics	2017
English language	2015

Scientific seminars	**Year**
Seminar days of FFPW	2015 2016 2017 2018

International conferences	**Year**
Vanina, T., Stejskal, V., Bláha, M., Kouřil J., 2017. Patterns in growth performance of geographically distinct European perch (*Perca fluviatilis*) populations reared under controlled conditions. In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018, 1220 (Poster).	2017
Stejskal, V., Matousek, J., Prokesova, M., Novikova, K., **Vanina, T.**, Sebesta, R., Gasko, L., 2017. The effect of different insect meal (*Hermetia ilucens*) inclusion on growth performances of European perch (*Perca fluviatilis*, L.). In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018, 1100 (Poster).	2017
Lundova, K., Matousek, J., Prokesova, M., Sebesta, R., **Vanina, T.**, Stejskal, V., 2017. The effect of timing of photoperiod prolongation on postponement of puberty in brook trout (*Salvelinus fontinalis*). In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2018,686 (Poster).	2017
Vanina, T., Gebauer, R., Stejskal, V., Bláha, M., Kouřil, J., 2018. Growth differences among geographically distinct populations in European perch juveniles under RAS conditions: preliminary data. In: EAS (eds.), Aquaculture Europe 2018 Abstracts. Montpellier, France, August 25–29, 2018, 772 (Poster).	2018

Foreign stays during Ph.D. study at FFPW	**Year**
Prof. Dariusz Kucharczyk, Department of Lake and River Fisheries, University of Warmia and Mazury, Olsztyn, Poland (1 month, Histological structure of European perch, *Perca fluviatilis*, organs kept under different temperatures in tanks)	2016
Assoc. Prof. Thomas Lecocq, University of Lorraine, Faculty of Sciences and Technologies, Nancy, France (2 months, studying methods of fragment analysis outputs using of various software packages for data processing)	2017
Prof. Dr. Werner Kloas, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany (6 months, development of fish feed with alternative ingredients replacing the fish meal)	2019

Pedagogical activities	Year
Leadership of laboratory work with PhD student Lola Toomey (France)	2017–2018
Consultancy of Homola Ondřej B.Sc. thesis	2018
Participation in the Aquaexcel project "Is there a geographic differentiation in the performances for aquaculture production between allopatric populations of *Perca fluviatilis*?"	2018
Leadership of Kana Sumikawa (Japan) summer school project "Genetic identification and differences among European perch (*Perca fluviatilis*) populations reared in pond aquaculture in the Czech Republic"	2018
Leadership of Adrián Villar Montalt (Spain) summer school project "Effects of different feeding management on sterlet *Acipenser ruthenus* swimming behaviour"	2019

CURRICULUM VITAE

PERSONAL INFORMATION

Name: Tatyana
Surname: Gebauer (Vanina)
Title: MSc.
Born: 14th February, 1989, Almaty, KZ
Nationality: Kazakhstan
Languages: Russian (native), Czech, English (B2, IELTS certificate)
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EDUCATION

2015 – present	Ph.D. student, Fishery, Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses (CENAKVA), Czech Republic
2011–2013	M.Sc., Fishery, Faculty of Biology and Biotechnology, Al-Farabi Kazakh National University, Almaty, Kazakhstan
2007–2011	B.Sc., Fishery, Faculty of Biology and Biotechnology, Al-Farabi Kazakh National University, Almaty, Kazakhstan
1996–2007	Shormanova School, Issyk, Kazakhstan

COMPLETED COURSES

2011	A course of lectures on cell biology at the University of SunWay, Kuala Lumpur, Malaysia
2012	International Seminar on identification of microorganisms and plant species by genotyping methods, Urumqi, China
2015	Abroad training in the Centre for Environmental Health and Toxicology, College of Public Health, UNMC, University of Nebraska at Omaha, USA

RESEARCH STAY AND COLLABORATIONS

2016	Prof. Dariusz Kucharczyk, Department of Lake and River Fisheries, University of Warmia and Mazury, Olsztyn, Poland
2017	Assoc. Prof. Thomas Lecocq, University of Lorraine, Faculty of Sciences and Technologies, Nancy, France
2019	Prof. Werner Kloas, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

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