




Recent progress in European percid fish culture production technology—tackling bottlenecks

Tomas Policar¹  · Fabian J. Schaefer² · Edson Panana³ · Stefan Meyer⁴ · Stefan Teerlinck³ · Damien Toner⁵ · Daniel Źarski⁶

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Abstract

Eurasian perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) have been identified as candidates for production in aquaculture with the potential to deliver products of high quality and value and associated market acceptance. Current aquaculture production of these species predominately targets niche, premium markets, and its up-scaling is still limited due to several bottlenecks. This paper summarizes the most important and recent technological aspects and innovations regarding broodstock management, controlled reproduction, larval and early juvenile stages, nursery, and grow-out culture including methods for the improvement of growth and production in percid fishes. This review study also attempts to identify and outline further prospects and challenges for the future development of the percid aquaculture sector in Europe.

Keywords Broodstock management · Eurasian perch · Hatchery · Innovation · Larviculture · *Perca fluviatilis* · Pikeperch · Production · Reproduction · *Sander lucioperca*

✉ Tomas Policar
policar@frov.jcu.cz

¹ Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in Ceske Budejovice, Zatisi 728/II, 389 25 Vodnany, Czech Republic

² Department of Ecophysiology and Aquaculture, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

³ Inagro, Practical Research Aquaculture Center, Rumbek-Beitem, Belgium

⁴ Institute of Animal Breeding and Husbandry, Christian-Albrechts-University Kiel, Kiel, Germany

⁵ Bord Iascaigh Mhara, Crofton Road, Dún Laoghaire, Co. Dublin, Ireland

⁶ Department of Gametes and Embryo Biology, Institute of Animal Reproduction and Food Research, Polish Academy of Sciences, Olsztyn, Poland

Introduction

The need for and the benefits of diversification of European freshwater aquaculture have long been recognized, e.g., regarding expansion of markets (FEAP 2017), overcoming dependency on imports (Policar and Adámek 2013), addressing challenges associated with climate change (Madenjian 2015), expansion of new (mainly viral and bacterial) diseases (Adamek et al. 2018; Bigarré et al. 2017; Way et al. 2017), and declining wild fishery stocks in combination with changing habitats and overfishing (Zachary and Höök 2015; Olin et al. 2018). European freshwater percids, especially Eurasian perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*), have been identified as prime candidates for production in aquaculture with the potential to deliver products of high quality and value and associated market development (Overton et al. 2015). Current aquaculture production of these species predominately targets niche, premium markets (Toner 2015) and the up-scaling of production is limited (Overton et al. 2015). An integral part of percid aquaculture as with most species is the production of fry for culture as well as restocking in order to support natural recruitment for the purpose of recreational angling, fish population management, i.e., control of small cyprinids and improvement of water quality (Steenfeldt et al. 2015; Kestemont and Mélard 2000). Many aspects of European percid farming have been developed during the last 2–3 decades. However limited and unstable production volumes still persist with sporadic market coverage. While acknowledging the establishment of baseline industry protocols and significant research efforts, percid aquaculture in Europe could still be described as being on the threshold between candidacy and establishment.

According to the FAO (2019), European production of both Eurasian perch and pikeperch amounted to over 46,000 t in 2017, with 95% of total production coming from capture fisheries predominately from Russia, Finland, Sweden, Estonia, Poland, and Ukraine. The current aquaculture production of these two species amounts to ~ 1400 t in Europe. This is nearly a threefold increase since 2000 (~ 490 t). Total percid fish (perch and pikeperch) production by capture fisheries and aquaculture in Europe during the period 1950–2016 is shown in Fig. 1.

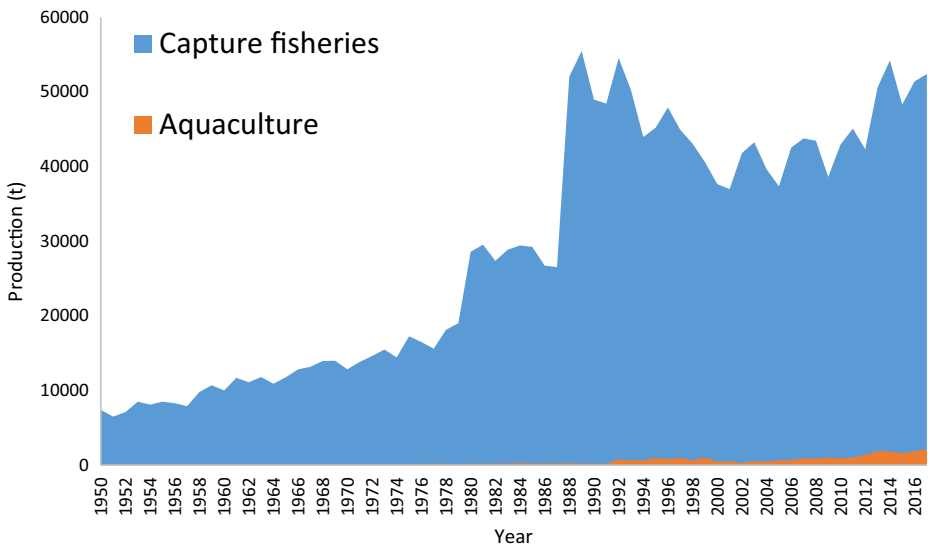


Fig. 1 Total percid fish (perch and pikeperch) production by capture fisheries and aquaculture in Europe during 1950–2016

The total value of aquaculture production of percid fish is estimated to be approx. 8.5 million EUR (FAO 2019), suggesting the average market price of commercial-size fish amounts to over 6 EUR per kg. The sector would appear to have significant potential for development given the rate of expansion and average price. However as with aquaculture production in general, price pressures focuses the priority of R&D activities toward the reduction of production costs which can be addressed by the improvement of production technology. Scientific activities are focused predominantly on the improvement of zootechnical performances of the fish—considering the whole production process—allowing improvement of the overall production efficiency, which is still among the biggest bottlenecks limiting the continued expansion of the sector.

In 2015, the state-of-the-art knowledge of percid biology and aquaculture was collated in a major review “Biology and Culture of Percid Fishes,” edited by Patrick Kestemont, Konrad Dabrowski, and Robert C. Summerfelt. The publication sets a milestone in covering all aspects of biology and aquaculture including a critical review of current bottlenecks, research needs, and the market situation. While a general progress in commercial percid farming can be observed across species and regions, the methodologies in tackling the existing bottlenecks are still diverse. There seems to exist a significant gap between the knowledge provided by academic research and the transfer and implementation of such knowledge in commercial practice, as is the case in many other sectors.

But the sector has progressed since 2015 and significant efforts have been undertaken by both academic and commercial percid professionals, to overcome the issues. The foundation of the European Percid Fish Culture (EPFC) group of European percid professionals and the realization of numerous cooperative projects addressing the identified bottlenecks created a new impetus for the sector. Many of the experiments conducted in national and international projects involved industry partners or semi- to full-scale commercial trials to support applied protocols and the necessary up-scaling of production. This review highlights the progress made since 2015 focusing on bottlenecks addressed mainly in perch and pikeperch from a practitioners’ standpoint. The review focuses on fields such as broodstock management, controlled reproduction, larval and early juvenile culture, juvenile and nursery culture, and grow-out culture, which show potential or have been targeted in order to optimize production of percid fish. Furthermore, the aim is to identify current shortcomings, which require additional efforts to achieve reliable, stable, and predictable production of market-sized percid fish in Europe.

Broodstock management

A solid management of broodstock, also referred to as breeders or spawners, is a vital part of any successful aquaculture venture covering various aspects, such as domestication (under the definition proposed by Teletchea and Fontaine (2014)), rearing environment, nutrition, health, genetic background, and protocols for the induction of gonad maturation. In species new to farming, the broodstock most often derives from wild caught individuals, which have been transferred to the production system. While spontaneous reproduction of such fish can be observed in some species, given suitable water and rearing conditions, this process usually requires a more significant effort, extensive knowledge of the species biology and may frequently result in failure or high variability of results. In temperate species, such as perch and pikeperch, protocols for the induction of gonad maturation are primarily based on the

simulation of natural conditions mimicking the annual fluctuations in water temperature and photoperiod (Fontaine et al. 2015).

Consequently, elaborated protocols for broodstock rearing for the purpose of reproduction have been established for several percid species, mainly perch and pikeperch, which allow for advanced, delayed, or even entirely out-of-season spawning in indoor facilities (Fontaine et al. 2015; Źarski et al. 2015a). These protocol developments address a crucial bottleneck in overcoming the species candidate status since reproduction of these percids under natural environmental conditions, e.g., in outdoor ponds, occurs only during one dedicated annual spawning period. Thus, without controlled and multi seasonal production, the availability of larvae, fingerlings, and juveniles is a limiting factor toward expanded and broader culture of the species. While reproduction of broodstock reared under natural environmental conditions can be shifted by a certain time period (usually a couple of weeks; Blecha et al. 2015), further market development and increased production volumes will need to be based on or complemented by year-round production in RAS.

Despite having progressed substantially, broodstock management, defined here as the rearing period until final or acceptable oocyte stage for hormonal treatment or spawning, of freshwater percids still requires substantial attention. In 2015, a number of bottlenecks were identified related to high variability in reproductive performance (Fontaine et al. 2015; Schaerlinger and Źarski 2015). These include limited knowledge of the effects of broodstock characteristics and rearing on the reproductive traits, as well as the lack of reliable and predictive biomarkers for gamete quality. In recent times, several studies have targeted issues concerning broodstock management. Reviewing the recent literature allows the identification and comparison of regional and production type dependent dynamics and for the analysis of sources of variability in reproductive performance as well as future trends.

Effects of broodstock origin, domestication level and rearing environment have received significant attention. A number of farms and research institutes have established broodstocks, which today mainly consist of f-generation fish both from RAS or ponds (Blecha et al. 2016a; Malinovskyi et al. 2018; Policar et al. 2019; Khendek et al. 2017, 2018; Schaefer et al. 2018a, b; Źarski et al. 2019). This should be considered as significant step toward domestication. However, studies showed that the domestication process negatively affected the reproductive performance in pikeperch and perch, as previously suggested by Křiřtan et al. (2012). In perch, fish kept over several generations showed higher gonadosomatic indexes (GSI), 17β -estradiol levels, and oocyte diameters compared to RAS-cultured broodstock (F1 domesticated generation), but the reproductive performance in terms of hatching rate and larval quality was lower (Khendek et al. 2017). In comparison to RAS-cultured pikeperch broodstock (F0 domesticated generation), pond-cultured breeders showed higher spawning success, GSI, and elevated LH and FSH transcript levels in females and males, respectively (Khendek et al. 2018). In addition, Chen et al. (2017) indicated effects of the domestication process on the immune (up-regulation of 412 genes related to immune system development) and digestive system (down-regulation of 218 genes associated with the digestive system) in perch. Ljubobratović et al. (2017a) have successfully used wintering of RAS-reared broodstock in outdoor ponds. The broodstock origin or history also affects subsequent life stages as shown by Ljubobratović et al. (2018). For perch, it has been suggested to consider the geographic origin of broodstock since differences among allopatric populations can affect key traits of performance with largest performance differences detected among genetically distant populations (Vanina et al. 2019). The issue of genetic diversity in perch was further elucidated by Khadher et al. (2016), who detected higher genetic variability in two farmed perch stocks compared to the supposed founder population. This variability was stable over the

first generation, but inbreeding rate increased. In addition to benefits regarding offspring performance, conservation of genetic diversity, and the control of inbreeding (Blonk and Komen 2015), these studies highlight the need for an optimized selection of broodstock regarding traits associated with the stabilization of reproductive performance, which most often remains highly variable.

Selection of adequate breeder traits also improve animal welfare under controlled culture conditions, because broodstock origin and level of domestication are known to affect stress levels and post-spawning mortalities (Łuczyński et al. 2007; Zakeš and Demska-Zakeš 2009; Krištan et al. 2012; Zakeš et al. 2013; Douxfils et al. 2015; Ljubobratović et al. 2017a; Malinovskyi et al. 2019). Generally, less domesticated percids showed higher sensitivity, stress response, and post-spawning mortality rate compared to more domesticated fish (Zakeš and Demska-Zakeš 2009; Krištan et al. 2012; Douxfils et al. 2015). Of course, such measures will need to be accompanied in combination with proper handling protocols and skilled staff, emphasizing the human component in any successful commercial application. Practical training workshops and tuition videos were implemented in 2017 and 2018 (see www.epfc.net). The spawning technique, spontaneous spawning in tanks or ponds versus manual stripping of gametes, can further affect mortality in both species with higher mortalities in strip-spawned fish compared to spontaneous tank spawners, which might be mitigated through a post-spawning salt treatment for 144 h with concentration of 2.5–10 g L⁻¹ in pikeperch (Policar et al. 2008, 2019; Źarski et al. 2013). From a practical point of view, the use of different anesthesia, such as Propiscin, 2-phenoxyethanol, clove oil, and MS-222, in perch and pikeperch can lower handling stress even further (Velišek et al. 2009; Kristan et al. 2012, 2014; Rožyński et al. 2016, 2018a, b). A joint approach of broodstock selection and optimized handling protocols will most likely result in benefits for animal welfare and lead to an improved reproductive performance.

It has been suggested that stress in broodstock may exert an influence on female reproductive performance and biochemical egg composition, mainly in terms of egg fatty acid (FA) contents, subsequently affecting rates of embryo development in pikeperch (Schaefer et al. 2016a; Schaefer et al. 2018b). However, it is not yet clear whether observed egg cortisol levels are associated with maternal stress. As highlighted by Schaerlinger and Źarski (2015), the egg FA composition holds potential to serve as a marker for the future embryo and larval development. Schaefer et al. (2018b) could identify specific aspects of FA profiles (polar fraction: stearic acid, eicosapentaenoic acid - EPA; neutral fraction: ratio of docosahexaenoic acid – DHA to EPA) being associated with pikeperch early embryo development, which in turn suggest potential for the optimization of broodstock diets, but high variability in FA profiles limits the predictive value. Such considerations regarding the development of specific broodstock feed were supported by Ljubobratović et al. (2017a). Similarly, Ljubobratović et al. (2019) detected differences in pikeperch egg FA profiles (total n-6 and linolenic acid, ratio of n-3 to n-6 FA) being affected by varying hormonal treatment (human chorionic gonadotropin, hCG; salmon gonadoliberine analogue, sGnRH_a) but without effect on the larval performance. Generally, not only polyunsaturated FA (PUFA), mainly DHA, EPA, arachidonic acid, and possibly their precursors, but also stearic acid should be considered due to their functional roles not only in pikeperch, but also in perch as reviewed by Źarski et al. (2017a). Other attempts to identify such markers targeting effects of oxidative stress (mtDNA fragmentation) led to a dead end (Schaefer et al. 2016a). It will be helpful to follow a holistic approach in the future considering differences, such as genetic background, production system, or rearing history, in order to identify predictive biomarkers

and to optimize broodstock diets. It might be necessary to accept that there is not one, perfect marker for predicting future offspring performance and rather varying broodstock and rearing protocols require adapted methodological approaches.

Similarly, photothermal protocols for the induction of gonad maturation differ between species, but may also need to be adjusted for different broodstock with different levels of domestication and history which could explain variable reproductive results. Until now, photothermal protocols, which are regarded as the foundation of successful broodstock management, have been optimized (Blecha et al. 2015; Hermelink et al. 2017; Ljubobratović et al. 2017a, 2019). These improvements include manipulation of the photoperiod (8-, 10-, 12-, and 14-h light), combination of pond- and RAS-rearing (transfer of spawners from ponds to RAS in autumn or spring), and application of varying cold water periods (122 to 223 days at 2.2 to 2.5 °C). It has however been argued that an entirely out-of-season reproduction may inflict negative influence on reproductive performance, but Schaefer et al. (2018a) found that individual traits (size) of RAS-reared pikeperch females might rather be associated with the observed variability in fecundity and egg quality. Consequently, individual characteristics may exert influences under seemingly similar conditions, which have yet to be taken into account when selecting breeders highlighting a substantial lack in knowledge about these effects.

In summary, substantial progress has been made in some fields, e.g., domestication process and identifying broodstock effects on reproductive performance, whereas others have not received sufficient attention yet. Several aspects, mainly the directed selection of breeders, but also genetic effects, cross-breeding of spawners, the identification of reliable predictive biomarkers for gamete quality, nutrition, and further optimization of photothermal protocols, are still in need of research since reproductive performance often remains highly variable and—to a certain extent—unreliable to date. Furthermore, concepts, such as species-specific, functional broodstock diets, and mainly potential interactions, especially regarding broodstock effects, e.g., effects of stress, rearing environment and maternal characteristics on egg quality and subsequent larval performance, have been suggested as lacking supportive experimental data. Conclusively, it might be too early to describe the status of broodstock management in freshwater percids as having reached a stage of fine-tuning or domestication.

When analyzing the existing literature and research approaches, one cannot but notice two general trends, competing or complementing each other. A focus on RAS-based production can be observed in Western and Central Europe, while pond-based rearing of percids dominates toward the east. In addition to culture techniques, broodstock operations most often differ in terms of the use of hormonal agents, which are mainly being applied in Eastern Europe. Such diversity is undoubtedly beneficial. However, the different foci complicate the identification of general patterns and might result in the fragmentation or loss of information. In many aspects of broodstock management, only the surface is touched so far. Researchers should be aware of these trends and always consider the transfer and comparison of results between these regional groups when discussing observations. For example, what are the desirable characteristics for broodstock fish in ponds and RAS? Are they the same or do they—more likely—differ? Possibly, differing culture techniques may serve an entirely different purpose and market segment in the future and therefore require a different set of traits and research approaches. It might be hypothesized that larvae hatched and juveniles reared in ponds are more suited for stocking of ponds and open water bodies, while specimen being produced and recruited in RAS are more suitable for intense cultivation in a confined

environment. For now, this remains purely speculative and careful attention should be paid to avoid misinterpretation of results and obstruction of future system-adapted broodstock recruitment and domestication approaches.

Controlled reproduction

Controlled reproduction can be defined as a technical process intended to acquire high quality larvae at a defined point in time from breeder fish undergoing a natural maturation process (Żarski et al. 2017c). Profound understanding of gamete biology of percids is required in order to harmonize both processes, which have been extensively described by Alavi et al. (2015), Schaeerlinger and Żarski (2015) and Żarski et al. (2015a).

For intensive percid aquaculture purposes, wild (Żarski et al. 2013), pond-cultured (Křišťan et al. 2013), and domesticated, fully grown in RAS (Zakęś et al. 2013) fish are typically spawned. Within the commonly accessible literature, the first two groups of fish were predominately used during research and development operations aiming to elaborate effective reproductive protocols (Żarski et al. 2015a). This stems from the fact that very few fully functional domesticated broodstock were available for research and relatively little research activities were visible from industry. In this review, endocrine regulation of reproduction in percids will be intentionally omitted as this has already been described in detail by Żarski et al. (2015a). In effect, this section summarizes the most important and recent technological aspects of controlled reproduction of percid fishes developed and practiced in Europe and outlines further prospects and challenges.

One of the biggest bottlenecks in controlled reproduction of percids is the prediction of the moment of ovulation. Percids are known for spontaneous, unassisted release of eggs into the tank following ovulation (Żarski et al. 2015a). This creates a problem for efficient reproduction since the eggs lose fertilizing capacity within minutes following contact with water (Żarski et al. 2012a; Kristan et al. 2018). However, time of ovulation in percids may be currently predicted only when hormonal stimulation of final oocyte maturation process is applied and the maturation stage of each specimen is monitored following injection (Żarski et al. 2011, 2012b). In both, perch and pikeperch, the maturation stages are currently recognized on the basis of a six-stage classification (Żarski et al. 2011; 2012c). The relevance of the application of different hormonal preparations in percids has been extensively described by Żarski et al. (2015a). However, further optimization of this technique is in progress (Żarski et al. 2019). Most recently, an intensive study has been carried out on the potential implementation of dopamine antagonists in pikeperch, potentially improving hormonal treatments with the application of gonadoliblerine analogs (Żarski et al. 2015a). However, this study has revealed that the dopamine-effect following hormonal stimulation can be totally omitted as application of several different dopamine antagonists did not improve the spawning performance in this species (Roche et al. 2018). This is a very important finding indicating that whenever gonadoliblerine analogs are considered to be used in controlled reproduction of percids, they should not be administered together with dopamine antagonists, as it is the case in other freshwater species (Kucharczyk et al. 2008).

Furthermore, considerable differences in latency time following hormonal stimulation in RAS-grown pikeperch were recorded (Żarski et al. 2019). It was found, that despite fish being grown in the same system and originating from the same stock, latency time of fish injected at stage I varied between 100 and 150 h. This phenomenon has not been observed in either wild

or pond-reared pikeperch suggesting that there are several different, still unknown, processes involved conditioning responsiveness of domesticated fish to hormonal treatment. However, the time of response was also suggested to be a potential trait for selection since the same fish were exhibiting early responsiveness to hormones over three subsequent years. These findings shed light on the problem of individual differences in response to reproductive protocols, probably arising from natural genetic variation and the effect of individual physiological stimuli. Further research is needed in order to understand this phenomenon and to bring this knowledge in commercial application.

Acquiring males' sperm for *in vitro* fertilization in percids is usually a minor problem during the spawning season. However, in RAS-grown stocks, this can be an issue when females are ready to be stimulated and spawned. As a consequence, in farm conditions, it is very convenient to hormonally induce spermiation before stripping eggs. Żarski et al. (2017b) found that regardless of the type of hormonal preparation (hCG or GnRH α), in wild Eurasian perch treated in advance of the spawning season, the latency time between the hormonal injection and collection of sufficient quantities of high quality sperm is a minimum of 4 days and that the sperm retains its quality until a minimum of day 8 following the injection. Interestingly, the application of sGnRH α prolonged the positive effect on sperm quality for two more days compared to hCG. So far, there is no specific study clarifying the protocol of induction of spermiation in pikeperch. However, transferability of other specific protocols from perch to pikeperch allows—with high probability—to presume that such a latency time can also be recommended for pikeperch.

Collection of sperm usually does not create a problem in percids. However, it has recently been reported that there is a considerable risk of urine contamination during regular stripping (into the syringe) in pikeperch (Sarosiek et al. 2016). Similar phenomenon was reported for Eurasian perch by Król et al. (2018), who described a negative effect of urine contamination on sperm motility in additional detail. Therefore the practice of controlled reproduction of percids using a catheter for sperm collection is highly recommended (Sarosiek et al. 2016). This facilitates the collection of higher initial sperm quality and prevents pre-activation of the spermatozoa, otherwise leading to continuous decrement of sperm quality over time.

One of the main challenges in controlled reproduction of percids is the evaluation of egg quality. Different quality indices, typically used in controlled reproduction, have been extensively reviewed by Schaerlinger and Żarski (2015). Different aspects of egg quality evaluation in Eurasian perch were also described by Żarski et al. (2017c). As previously mentioned, there have been several studies devoted to elaborate objective egg quality indices, where FA profiling (Ljubobratović et al. 2017b; Żarski et al. 2017c) and other molecular markers (such as antioxidant capacity and DNA fragmentation; Schaefer et al. 2016a) were assessed without significant success. Evaluation of the developmental competence of the eggs following *in vitro* fertilization remains the only tool in use at present. Alix (2016) indicated that such an evaluation of egg quality cannot be objectively made by using only one parameter. Instead, it was proposed that the most objective evaluation of developmental competence is to analyze fertilization rate after mid blastula transition (Alix et al. 2015) along with hatching rate and the deformity rate of larvae. These three indices can provide conclusive information not only about the ability of the eggs to be fertilized, but also whether it can be developed into a normal embryo, being the commonly accepted definition of egg quality introduced by Bobe and Labbé (2010). Of course, the evaluation of all three indices is highly laborious and requires specific protocols to be developed at the fish farm. It should be pointed out that objective indices of egg quality in a long-term perspective may be very useful for commercial

production. Detailed record of the performance of broodstock over generations may allow the development of efficient selective breeding strategies and increase the efficiency of the entire production. Therefore, the development of specific quality markers of percid eggs remains one of the biggest challenges.

Along with the development of the production technology, new challenges arose. Sperm of percid, whenever stripped with catheter and without urine, can be stored under chilled conditions (i.e., at circa 4 °C) for a few hours without negative effect on their quality (up to 4 h in Eurasian perch; Król et al. 2018). Of course, whenever the sperm is obtained by a regular stripping (without catheterization), the storage time is very hard to predict as it depends on the level of urine contamination. Nonetheless, up to 10% of urine contamination, the sperm can be stored at about 4 °C for 1–2 h (Król et al. 2018). This was also confirmed by Schaefer et al. (2016b) in pikeperch who reported that sperm stripped in a typical way (into a dry syringe by massage of the abdomen) can be stored undiluted for about 1 h without significant degradation. The same authors, however, have suggested that the sperm of pikeperch can be more efficiently stored whenever samples obtained from different males are not pooled, as lowered quality sperm can negatively influence sperm of higher quality. Therefore, whenever sperm needs to be stored under chilled conditions, samples obtained from each male should be kept separately. This is especially important during longer storage periods as it is already known that sperm of Eurasian perch, whenever diluted in a specifically developed artificial medium, can be effectively stored for up to 1 week (Sarosiek et al. 2014). This, along with further progress on percid, could potentially increase the effectiveness of fertilization procedures and facilitate hatchery operations. However, this requires first specific research on the impact of such long storage times to the fertilizing ability of such a sperm, as well as larval performance of the obtained offspring.

Short-term storage of the eggs has been studied in both—Eurasian perch and pikeperch. Those studies have revealed that perch eggs can be stored for a longer time (up to 12 h at 4 °C) (Samarin et al. 2017) than those of pikeperch (after 12 h of storage at 4 °C resulted in an average of 80% decrease in fertilization and hatching; Samarin et al. 2019). It should be pointed out that the effectiveness of short-term storage of the eggs is inversely correlated with temperature and 4 °C can be recommended, whenever this is needed to be applied in the hatchery. There is still, however, a lack of information on how long the eggs of pikeperch can be stored under hatchery conditions without negative effects on their quality, as well as the relation between the egg quality and maximum time of effective storage. Therefore, further research on short-term storage of percid eggs would help to improve controlled reproduction practices.

Fertilized eggs of Eurasian perch do not require further treatment except the provisioning of suitable conditions allowing effective incubation. Egg ribbons, being specific cylindro-conical jelly-like structures (Formicki et al. 2009), with eggs being located within, need to be placed in incubators in a way that each egg is exposed to oxygenated water. On the contrary, effective incubation of pikeperch eggs requires specific procedures eliminating adhesive properties of eggs (Żarski et al. 2015b). Debate on the most suitable method for removal of adhesive properties of eggs of pikeperch has been conducted for already more than a decade (Kucharczyk et al. 2007; Zakęś and Demska-Zakęś 2009). A significant improvement has been made following the study of Żarski et al. (2015b) who reported that any kind of egg treatment is more effective when applied minimum 30-min post-activation, which corresponds with the end of the swelling period (water-hardening) of the eggs (Żarski et al. 2012b). Since then, several authors have verified this hypothesis and considerable improvements have been achieved. For instance, Ljubobratović et al. (2017b) reported that in some specific conditions,

difficulties in hatching of the larvae can be observed whenever eggs were treated with tannic acid, which has not been observed by Źarski et al. (2015b). This highlighted the potential application of alcalase for removing the adhesive layer of the eggs (Kristan et al. 2016), which has already been reported to allow larvae to hatch without any disturbance (Ljubobratović et al. 2017b). However, the most recent study has indicated that application of alcalase for egg treatment in pikeperch is speeding up the hatching process leading to lowered larval performance (Ljubobratović et al. 2018). This was most probably caused by the premature exposure of the larvae to an “unfavorable” outer environment. Therefore, from the perspective of egg treatment in pikeperch, the most “safe” method of egg treatment is to use a bath of milk and later treat with kaolin (clay) preventing the eggs adhesiveness (Ljubobratović et al. 2018). This procedure—although effective—is time consuming (it still lasts at least 30 min) and does not allow observation of embryonic development inside the egg (kaolin particles adhere to the eggs shell covering it tightly) and ploidy manipulation. Therefore, further improvement of this procedure is still needed to decrease labor requirement and to simplify the entire process.

A high number of scientific articles published within the last 5 years on the topic of controlled reproduction clearly indicate that there is still an urgent need to optimize this short, but very important production step. Keeping in mind that the spawning operation of percids usually takes a few days, it would be highly beneficial for the farmers to find out whether already hormonally stimulated and entirely striped males can still produce sperm following the repeated procedure of stimulation and sperm collection. Also, potential consequences of such a treatment to fish and sperm quality should be revealed. This is especially important from the perspective of future selective breeding procedures, where few targeted males would have to be used several times during the spawning operation. Besides, future research priorities should include evaluation of processes of excessive *in vivo* aging of sperm following hormonal stimulation from the perspective of its suitability for fertilization and, consequently, production of the larvae. However, it should be also highlighted that for the last 5 years, huge improvement has been observed in cryopreservation of sperm of percids, with strong focus on the possible commercialization of this technology (Bernáth et al. 2015a, b, 2016; Judycka et al. 2019). This underlines the future importance of application of a more advanced biotechnological approach allowing facilitation of husbandry protocols, selective breeding, and gene banking of valuable strains and/or populations. Consequently, in the area of controlled reproduction of percids, more precise, predictable, and effective methods are yet to be developed, which are the next steps toward sustainable expansion of this sector.

Larval and early juvenile culture

Percid larval culture is—due to biological properties of both species (cf. below)—relatively complicated and expensive, demands good skills, experience, and equipment, is time and labor consuming, and is still not efficient (Steenfeldt 2015). The main bottlenecks of the larval culture phase are low survival rates, fluctuating quality of cultured larvae, and early juvenile stages of both species. Larval and early juvenile culture must be continuously improved with balanced nutrition and husbandry with the aim of significantly increasing fish survival and eliminating cannibalism, swim bladder inflation failure, and deformity rates enabling good development and rapid growth of the following culture stages (Kestemont et al. 2015; Kestemont and Henrotte 2015; Steenfeldt 2015).

Quality of larvae and the whole process of larval culture is already pre-determined to some extent by egg traits as shown by Schaefer et al. (2019). Pikeperch and perch larvae exhibit a very small body size at hatch and a comparatively little mouth gap with primitive digestive tract lacking a functional stomach (Hamza et al. 2015; Kestemont and Henrotte 2015; Xu et al. 2017). These factors influence several traits, such as acceptable initial feeding in terms of size and nutritional composition (Kestemont et al. 1996; Ostaszewska et al. 2005; Hamza et al. 2015), swim bladder inflation, growth, development, cannibalism, and hence, survival rates.

Ontogenetic development and growth rate of larvae is highly dependent on water temperatures and currently a low temperature (16–20 °C) is recommended at the beginning of the culture process for a prolonged course of larval development (Steenfeldt 2015; Yanes-Roca et al. 2018; Blecha et al. 2019). Absorption of yolk-sac and oil globule were observed at 11 and 14 days post-hatching (DPH), respectively, in pikeperch (Xu et al. 2017), which is consistent with perch (Kestemont et al. 1996; Hamza et al. 2015). The beginning of the first exogenous feeding takes place at 2–3 DPH and 5–8 DPH in perch and pikeperch, respectively.

Larvae of both species have a reduced ability to digest their first feed. Therefore, live feed organisms of acceptable size are essential as first exogenous feed for larvae of perch and pikeperch (Kestemont and Henrotte 2015). In ponds, natural first feed include rotifers, nauplii of copepods, and cladoceran species (Peterka et al. 2003). In intensive perch and pikeperch larval culture, smaller strains of brine shrimp (*Artemia salina* or *Artemia* sp.) nauplii (420–480 µm) have been widely used as the first feed (Kestemont and Henrotte 2015). However, the use of even smaller rotifers (around 280 µm) (species *Brachionus plicatilis* or *B. calyciflorus*) for larvae of both species during the first days of exogenous feeding (maximum till 12–17 DPH) can significantly increase their growth, survival (up to 50–80% at 17 DPH), feed consumption, and FA composition and development (Kestemont et al. 1996; Yanes-Roca et al. 2018). Mentioned positive effects of live feed in larval performance are provided by FA such as LA (linoleic acid), ALA (α-Linolenic acid), and DHA. After the mentioned period, rotifers must be replaced by *Artemia* nauplii and later by starter feeds during the weaning process because rotifers are too small and become nutritional limiting for fast growing larvae (Yanes-Roca et al. 2018).

Ljubobratović et al. (2015) tried to improve the weaning process in pikeperch larval culture with a short 4-day co-feeding period (from 15–19 DPH) and with supplemental feeding (starter application with *Artemia* feeding as last feed each day) during 4 days (15–19 DPH) and 7 days (15–22 DPH) without any positive effect on larval efficiency. Generally, co-feeding (*Artemia* nauplii + starter feed) from 12–15 DPH with a duration of 7 days till 19–22 DPH is the most effective weaning technique currently used in both species (Kestemont et al. 1996, 2007; Zakeš 2012; Kestemont and Henrotte 2015). Composition of starter feeds must be optimized for the intensive culture of percid larvae allowing for shortening the period utilizing live feed. This requires the development of highly digestible feeds, which could be applied as early as just a few days after the beginning of exogenous feeding (Kestemont and Henrotte 2015). Level of phospholipids (at least 8.2% w.w. level) and supplementation of docosahexaenoic (1.004% DM DHA) and eicosapentaenoic (0.169% DM EPA) acids in starters can increase growth, improve digestive enzyme activity, and reduce anomalies in pikeperch larvae (Lund et al. 2018). Król and Zakeš (2016) tested supplementation of artificial starters with crystalline L-tryptophan (TRP with doses from 5–20 g TRP kg⁻¹) during 28 days intensive culture of pikeperch larvae (age 15 DPH). This study showed that TRP can increase serotonin level in the body tissue, slightly decrease both types of cannibalism but does not affect survival and growth rates and feeding behavior, which were previously positively affected in early juvenile stages of other fish species (Winberg et al. 2001; Hseu et al. 2003; Höglund et al. 2005; Wolkers et al. 2014).

Cannibalism of percid fish is a regulatory factor on population size in different ecosystems (Frankiewicz et al. 1999), which has a negative effect on culture efficiency and profitability mainly in larvae and early juvenile stages (Kestemont et al. 2015). Cannibalism caused by or facilitated by growth heterogeneity of cultured population can be reduced in larval culture by the stocking of same sized and aged larvae (Żarski et al. 2015a), adequate feed size (Kestemont and Henrotte 2015), higher density of live feed, and lower temperature (Mélard et al. 1996) and later in early juvenile stages by size sorting (Król et al. 2019; Szczepkowski et al. 2011). The positive phototactic behavior of pikeperch larvae between 10 and 22 DPH can be used for a self-grading mechanism decreasing larval growth heterogeneity and size variability. However, this technique is completely insufficient from 28 DPH (Tielmann et al. 2016). Two types of cannibalism occur in percid fish, type I when prey is captured by tail first from 11 till 16–18 DPH with low impact on overall survival rate and type II starts when growth and size heterogeneity is developed in population and prey is captured by head first. Type II has higher impact on survival up to 50% of total mortality and can be mainly reduced by size sorting (Baras et al. 2003; Kestemont et al. 2015). In total, 60% of prey is caught by tail-first ingestions between 14 and 48 DPH but after 48 DPH, head-first ingestions are increased in cannibalism behavior of intensively cultured pikeperch (Colchen et al. 2019). Król et al. (2015) did not find any effect of all-female and mixed-sex populations in full sibling and half-sibling version on cannibalism, survival and growth rates of perch larvae, and early juvenile stage during 77 days intensive culture; however, maternal effect on the rate of cannibalism type I was found by these authors. Toomey et al. (2019) found different behavior and interactions of cultured perch larvae and early juvenile stages from three different geographic populations (two Finnish and one Swiss) with the conclusion that more homogeneous and cohesive population structure was found in both Finnish compared to Swiss populations. Cannibalism remains one of the most important negative factors which can significantly decrease survival, efficiency, and profitability of cultured early stages of percid fish. Husbandry, feeding protocol, and later size sorting must be optimized according to the current conditions with the aim of decreasing cannibalism level. This is essential to ensure that larval and early juvenile culture of percid fish is effective.

Swimbladder inflation is the next important factor affecting efficiency of percid larval culture not only under intensive (Steenfeldt 2015) but also under pond (Blecha et al. 2019) or lake conditions (Egloff 1996). The period when the swim bladder is inflated in perch and pikeperch is dependent on water temperature and ongoing from 5 to 14 DPH under 17–20 °C (Demska-Zakeś et al. 2003; Ott et al. 2012; Blecha et al. 2019). Rate of swim bladder inflation is also highly affected by other environmental conditions such as water surface, depth, salinity, turbidity, light intensity, photoperiod, and even tank color under controlled conditions (Steenfeldt 2015; Palińska-Żarska et al. 2019) and presence of littoral vegetation, water depth, and surface area under pond conditions (Blecha et al. 2019).

Inter- and intra-individual variability of growth and feed consumption was observed by Schaefer et al. (2017) in pikeperch early life stages in an effort to understand the reasons for different growth rate under identical cultured conditions. These authors found that different levels of feed consumption among cultured larvae are the main reason for their different growth and individuals can compensate for initial size differences.

Increased water salinity of around 2–4 ppt is commonly used in pikeperch larval culture where marine (euhaline) rotifers are used as the first live feed because increased salinity providing higher survival and mobility of applied rotifers and better utilization by pikeperch larvae (Yanes-Roca et al. 2018; Imentai et al. 2019). Lund et al. (2019) tested the effect of

different salinities on pikeperch larvae physiology, growth, and survival during their culture till 30 DPH. Authors did not find any effect of higher salinity (10 ppt) on growth and survival of larvae and no clear effect on larval digestive enzymatic activity. However, this study showed that higher salinity can have an effect on endocrine hormonal prostaglandin production, occurrence of endochondral bones anomalies, and lipid and FA metabolism in larvae.

In summary, optimal conditions for effective percid larval culture providing high quality early juveniles with fluctuating survival around 20–80% (Kestemont et al. 2015; Kestemont and Henrotte 2015; Yanes-Roca et al. 2018) are initial stocking density 20–100 larvae per L (Steenfeldt 2015; Tielmann et al. 2017; Yanes-Roca et al. 2018), water temperature 15–20 °C (Steenfeldt 2015; Yanes-Roca et al. 2018), increased salinity up to 3–10 ppt (Yanes-Roca et al. 2018; Lund et al. 2019), light regime 24L:0D or 12–16L:8–12D with intensity of 50–140 or 500–1000 lux (Steenfeldt 2015; Tielmann et al. 2017; Palińska-Żarska et al. 2019), cylindrical and conical tanks with black or dark walls (Steenfeldt 2015; Palińska-Żarska et al. 2019), water level 900–2000 mm (Steenfeldt 2015; Blecha et al. 2019), oxygen saturation 80–100% (Yanes-Roca et al. 2018; Palińska-Żarska et al. 2019), water exchange 25–50% per hour, use of surface skimmer or trapping of surface films (Steenfeldt 2015), and live feed such as rotifers (till 10–12 DPH), and *Artemia* nauplii (till 19 – 22 DPH) also combined with improved and better balanced starter feeds (Król and Zakęś 2016; Lund et al. 2018) as co-feeding during weaning technique (Kestemont et al. 2015; Kestemont and Henrotte 2015; Yanes-Roca et al. 2018). However, survival rates and quality of produced early juvenile stages as final product of this culture phase are fluctuating and commercial production can be negatively affected by lower larval and early juvenile efficiency in terms of following fish production and profitability. Therefore, larval and early juvenile culture must be continuously optimized by different husbandry protocols eliminating the aforementioned negative production factors and applying cost efficient and widely available first live feed as well as easily digestible starter feeds in both percid species.

Juvenile and nursery culture

In total, five different production systems are commonly being used for perch and pikeperch juvenile production and the ongrowing phase: pond monoculture, mesocosm systems, pond in pond systems, combination of pond and intensive RAS culture, and exclusive intensive culture in RAS (Kestemont et al. 2008, 2015; Steenfeldt et al. 2015; Policar et al. 2015, 2016a, b). Optimal husbandry protocols and nutritional optimizations were tested, described, and have been used with the aim to create adequate conditions providing high and stable growth, survival, feed conversion rates, and welfare of fish with good profitability. Stable, effective, and profitable production with utilization of alternative feed raw materials, i.e., with higher plant or insect composition as a replacement for fish meal, was identified as main bottlenecks of this phase in both percid species. From 2015, several innovations were applied including new technological innovations of commercial aquaculture and production-related systems for percid juveniles and ongrowing which have tried to solve identified bottlenecks.

In Europe, there has been the development of technology using a tandem pond-RAS production culture for juveniles of both percid species. This technology is often used in countries with large pond areas to provide high quality fish in a profitable manner (Policar et al. 2015, 2016a b). Härkönen et al. (2017) and Lepič et al. (2017) tested tutor fish (brown trout *Salmo trutta* and vimba bream *Vimba vimba*) for more effective (survival 73–94%) and

easier adaptation of perch and pikeperch to dry feed and RAS conditions, respectively. This technique can be applied but its process is technically complicated and does not provide any higher survival of adapted fish compared to commonly adapted perch (survival 95%) and pikeperch (survival 78%) according to Policar et al. (2015, 2016a, b). However, the adaptation of pond-cultured pikeperch juveniles can be effectively improved by supplementing vitamin C-enriched live feed (mainly frozen chironomids) fed during adaptation phase (Ljubobratović et al. 2016). Molnár et al. (2018) observed three different groups of pond-cultured pikeperch juveniles which can be adapted to artificial feed with different speed: early weaners need 7 days for adaptation, normal weaners (with 14-day adaptation), and late weaners (with 21-day adaptation). Early weaners are considered as the most appropriate fish for aquaculture with fast growth, although these fish can be less bold and competitive. The character of these fish can eliminate growth heterogeneity, subsequent decreasing growth, production, and survival in further culture (Policar et al. 2015; Mélard et al. 1995). Ljubobratović et al. (2018) compared the adaptation of two pond-culture populations of pikeperch juveniles originated from RAS and pond-cultured broodstock and found that juveniles from RAS broodstock had lower adaptation success to artificial feed. However, after the adaptation, they had higher growth rate during intensive culture. These authors recommended the use of RAS-cultured broodstock exclusively for juvenile production under RAS conditions. On the other hand, Blecha et al. (2016b) found that pikeperch juveniles produced by pond-RAS tandem (BW 21–24 g) can be successfully used as suitable stocking material for pond culture and even after 178 days of pond culture can be easily readapted back to RAS conditions.

Intensive juvenile and nursery culture of perch and pikeperch under RAS conditions is more and more applied in Western and Northern Europe (e.g., Ireland, France, Switzerland, Netherlands, Germany, Denmark, Sweden, Austria) (Policar et al. 2013, 2015; Steinfeldt et al. 2015). For this kind of percid culture, optimal abiotic and biotic factors, husbandry practices, and nutrition were investigated and have been applied as follows: water temperature 20–27 °C (Geay and Kestemont 2015; Kestemont and Henrotte 2015; Kestemont et al. 2015; Policar et al. 2015; Steinfeldt 2015; Swirplies et al. 2019), black walls of circular tanks, light regime 12L:12D or 16L:8D with intensity 200–1100 lx for perch (Policar et al. 2015) and 8L:16D or 14L:10D or 24L:0D with intensity of 10–100 lx for pikeperch (Kowalska et al. 2015; Policar et al. 2016a, b; Jarmolowicz et al. 2018; Baekelandt et al. 2018; Steinberg et al. 2018a), water quality: salinity under 4 ppt, ammonia below 0.3 mg NH₃-N L⁻¹ and nitrite below 0.5 mg NO₂-N L⁻¹, oxygen saturation of more than 60% for perch (Policar et al. 2015) and around 100% for pikeperch (Policar et al. 2016a, b; Jarmolowicz et al. 2018), and disturbance (cleaning tanks, size sorting, etc.) reduced to a minimum supported by the notion that low frequency does not have any negative effect on production and optimal fish density for 10 g fish 10–20 kg m⁻³, for 100–150 g fish 60–70 kg m⁻³ (Policar et al. 2015; Zakeš 2012). Artificial diets in version of floating and sinking pellets contain the following nutrients: 43–50% of protein, 13–18% of lipid, 10–15% of carbohydrate supporting very good growth performance when feed is applied continuously or three times per day (Geay and Kestemont 2015; Wysujack and Drahotta 2017; Baekelandt et al. 2018). Daily feeding rates are decreasing with increasing fish body weight (BW) from 5–10% of BW day⁻¹ in 1–5 g fish to 1–5% of BW day⁻¹ in 5–150 g fish (Geay and Kestemont 2015). Different bioactive substances such as brewer's yeast, yeast *Saccharomyces cerevisiae* extract, levamisole in combination with vegetable oils, probiotic *Enterococcus faecium* have been tested and successfully used in intensive pikeperch aquaculture to increase juvenile growth, immunological and physiological response, and disease resistance by Kowalska et al. (2015), Faeed et al. (2016) and Jarmolowicz et al. (2018).

Rożyński et al. (2017) and Zakeš et al. (2015, 2019) described that surgically implanted, tissue adhesive telemetry transmitters tags, passive integrated transponder (PIT), coded-wire tags (CWT), and visible implant elastomer tags (VIE) can be successfully used for the tagging of pikeperch juveniles with different BW (2.5–170 g) without any negative effect on growth and survival with fully healed wounds after 14 days post-application. Mentioned tagging methods can be effectively used during percid aquaculture for example for individuals or groups of fish during a selective breeding program and the culture of selected or genetically defined broodstock (Frederick et al. 2015; Blonk and Komen 2015).

A lot of mentioned factors, husbandry practices, and nutritional protocols were tested and have been optimized. However, the commercial percid sector still has issues with relatively high production costs for stable and high quality juvenile and production of ongrowing fish which are needed for a stable and demanding market. New culture systems with lower energy, feed, and labor demand must be found and tested for future progress. Improved and efficient economical profitability which is the main bottleneck for further large-scale percid production must be achieved to improve growth, immunology, feed conservation, and prevention of mass mortalities as well as decrease of production cost.

Grow-out culture

The description of husbandry and production systems of the final grow-out phase of both species is partly mentioned by Geay and Kestemont (2015), Policar et al. (2015), and Steinfeldt et al. (2015). Large-scale and year-round stable grow-out culture of both species has been performed exclusively under RAS conditions in Denmark, Switzerland, Germany, Netherlands, Ireland, France, and others (Steenfeldt et al. 2015). Stable, high-quality, and profitable production with low production costs will only be realized in adequately designed and operated RAS, providing optimized water and stable-quality and pathogen-free bacterial communities.

Optimal temperature, light regime, and husbandry practices are similar to ongrowing phase with maximal final density of 70–80 kg m⁻³ (Zakeš 2012; Policar et al. 2015; Steinberg et al. 2017, 2018a,b). Due to the high fish density and sensitivity of percids to low water quality, highly effective RAS technology is required. Water quality parameters of effective grow-out pikeperch culture should not exceed the following threshold ranges: 45.2–69.9 mg L⁻¹ NO₃-N, 0.51–1.03 mg L⁻¹ NO₂-N, 7.1–9.7 mg L⁻¹ CO₂, 5.6–14.5 mg L⁻¹ TSS (total suspended solids), 14.6–29.6 mg L⁻¹ TOC (total organic carbon), and 33.6–51.6 mg L⁻¹ TC (total carbon) (Steinberg et al. 2018a). Different water exchange rates during the start-up of RAS affected with protein productive value and feed loading in the system has a direct effect on pikeperch performance and health. Low salinity level (3‰ using NaCl) can help to reduce nitrite toxicity during the start-up phase of grow-out pikeperch culture (Steinberg et al. 2018a). Steinberg et al. (2017) found that higher levels of carbon dioxide (15–30 mg CO₂ L⁻¹) decreases growth and oxygen consumption rate, hematocrit, and metabolic oxygen consumption. Market-sized pikeperch can survive carbon dioxide concentrations up to 30 mg L⁻¹ when other water parameters are within the optimal level, but lower CO₂ levels in the range of 7–10 mg L⁻¹ are recommended (Steinberg et al. 2018a). Lower salinity up to 4 ppt is recommended in grow-out culture of percid fish as an effective treatment against bacterial and fungal break out (Policar et al. 2015).

Formulated diets used in the grow-out phase are very similar to feed used in the nursery phase. Both floating and sinking pellets with optimal sizes 5.0–10.3 mm or 1.5–2.7% of total length of cultured fish or 15–27.6% of their mouth gape of pikeperch (Mattila and Koskela 2018) are applied three times or continuously per day. Formulated feed can often cause higher deposition of visceral fat in body captivity and macroscopically visible lipid deposition in the spleen without any negative effect on growth, morphological indexes, and survival in perch (Stejskal et al. 2016). Varju et al. (2018) tested the effect of 3 and 6 weeks of starvation on body weight, antioxidant defense, and lipid peroxidation of 732 g commercial-sized pikeperch within intensive culture. Results showed that starvation process has only negative effect on significantly decreased body weight, lipid peroxidation processes, and glutathione concentration and glutathione-peroxidase activity in liver compared to normally fed fish.

A stable and high-quality marketable production of percid fish under optimum conditions with low mortality, rapid growth, good feed conversion, and reduced production costs is a continuing bottleneck for further progress of this sector.

Improvement of growth and production

Relatively slow specific growth, low production rate, and high growth heterogeneity are major limits and a production bottleneck for profitable intensive percid production in all live stages. Therefore, different techniques based on genetic strain selection (Pimakhin et al. 2015; Vanina et al. 2019), selective breeding program, genetically defined broodstock (Blonk and Komen 2015, Frederick et al. 2015), sex and ploidy manipulation (Rougeot 2015; Blecha et al. 2016c), and use of exact embryonic development for micromanipulation of primordial germ cells (PGC) with aim to produce germline chimera (Güralp et al. 2016, 2017a,b) have been currently developed with the aim to increase efficiency of percid production with decreasing production cost and effort.

Pimakhin et al. (2015) summarized the phenotypic variations of performance in wild perch populations under different culture conditions with an emphasis on utilizing this knowledge to increase perch aquaculture efficiency. Vanina et al. (2019) used genetic differentiation of three European wild perch populations which were cultured under standardized conditions with the aim of comparing aquaculture performance. This study showed the highest aquaculture performance differences between genetically distant populations. Lower differences were found in allopatric genetically similar populations. Selective breeding programs should be established according to instructions of Blonk and Komen (2015) with the aim to increase percid performance and finally decrease production cost. In this case, controlled selection and domestication process of percid fish will continue with the aim to keep genetic diversity, control inbreeding rate, maintain healthy populations, and select fish according to selective criteria such as reproduction ability under controlled conditions, rapid growth, and better feeding efficiency. Production of all-female perch populations with use of sex-reversed male breeders were developed, tested, and summarized by Rougeot (2015) with 30% improved growth and resultant marketable sized fish after 280 days of culture. The same authors published only the first attempts related to sex manipulation in pikeperch without any exact effect for improvement of commercial production. Triploidization of perch for following culture with the aim of producing sterile fish and to avoid the negative effects of gonadal development on growth, survival, and flesh quality in marketable fish was also summarized by Rougeot (2015). Triploidization process in perch was optimized by Rougeot et al. (2003) and Rougeot and Méléard (2008) which recommend to apply heat shock of 30 °C at 5–7 min post-

egg fertilization for 10–20 min as the best treatment as for production of 93–100% triploid population with survival rate 45%. However, any production perch farm in Europe does not use this technique for commercial production, yet. Ploidy manipulation based on heat shock (29 and 31 °C) was tested in pikeperch by Blecha et al. (2016c) who induced a 100% triploid population with heat shock (31 °C) beginning 1 min post-egg fertilization and lasting 20 or 40 min. However, this induction of triploid pikeperch population caused very low hatching rate (2.3–3.1%) and future research is required to improve this techniques for commercial using.

All the mentioned techniques are considered as potential tools for future improvement of percid aquaculture and production as these methods have already been successfully applied in the salmon aquaculture industry resulting in increased profitability of this sector. However, the application and use of these techniques in percid aquaculture need further research activities, closed and effective cooperation between RTD and production parties, and good and stable support with the aim to optimize and establish effective protocols for commercial use. Generally, development of each technique is expensive and time and labor consuming. The future will show if some techniques will be successfully developed and commercially utilized but any quick process cannot be predicted in this field.

Conclusion

Assessing the progress achieved in the individual sectors since the publication of the last major review of scientific literature back in 2015, it can be concluded that percid aquaculture in Europe is moving away from candidacy status to becoming an established European freshwater aquaculture sector. There are still however major bottlenecks to be tackled ranging from broodstock management to grow-out optimization. Until these remaining roadblocks are solved, caution should be exercised in avoiding a segregation of the sector since regional differences can be observed and a substantial gap between scientific knowledge and industrial implementation exists. Recent progress achieved by the formation of professional networks of percid experts and cooperation of academic and industry partners from all over Europe has proven the validity of this cooperative approach to development. Overall, high variability continues to be a bottleneck toward moving past the candidate status and efforts should continue to be focused on accomplishing a more stabilized production.

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Compliance with ethical standards

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

Ethics statement This article does not contain any studies with animals performed by any of the authors.

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