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Review

The effect of geographical origin of perch (*Perca fluviatilis* L. 1758) populations on growth rates under natural and aquaculture conditions: a review

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Summary

Wild Eurasian perch populations (Perca fluviatilis L.) are characterized by annual fluctuations in abundance as a result of environmental and intra-specific interactions. Variations in these interactions may be the source of differences in the characteristics of perch originating from different geographic regions. Perch abundances are higher in northern biotopes than in the south, although climate conditions in the latter would seem to be more conducive to perch growth. Research conducted on the growth of wild Eurasian perch strains from various regions of Europe reared in recirculating aquaculture systems (RAS) revealed differences among strains in body weight, survival, morphometric parameters, and other biological characteristics such as growth rate and feeding. Knowledge of survival and growth differences among perch strains is necessary as a tool for improvement of perch culture. Identification of the strain best adapted to RAS is the first step in a stock selection program.

Introduction

Commercial aquaculture has shown strong growth, increasing at an average annual 6.3% rate of production from 34.6 million tonnes (t) in 2001 to 59.9 million t in 2010 (faostat.fao.org). In 2010, the top ten producers of farmed aquatic species were developing countries such as China, India, Vietnam, and Indonesia, which contributed 87% of world production by weight. The net fishery exports of developing countries were significantly higher than other agricultural commodities including rice, coffee, and tea. World aquaculture production in 2010 comprised 56.4% freshwater fishes, of which carp accounted for 71.9% of the total production by quantity (FAO, 2012a). In 2010, the Eurasian perch was the most harvested species of Percidae. Europe is the main producer of Eurasian perch, at 68.1% of a total production of 20 150 t. Countries with the major catches of Eurasian perch were the Russian Federation (11 351 t) and Finland (6 252 t) (FAO, 2012b). Within the EU, the countries with the major imports of perch of European origin are Switzerland and France, and the main consumption market is Switzerland. The EU market for perch is still under supplied (Watson, 2008).

The intensive culture of Eurasian perch is an expanding branch of commercial fish farming in Europe. Perch fillets are characterized by a high protein content of 18.5 g (20.1 g in cultivated perch) per 100 g of edible portion (Jankowska et al., 2007; Skurikhin and Tutelian, 2007).

A slow growth rate is the major limiting factor in the commercial culture of Eurasian perch. With cage rearing under a natural temperature regime, in Belgium more than 800 days are required to obtain fish of minimum market size. Growth rate heterogeneity is another challenge to perch rearing, with some fish growing at double the rate of others (Rougeot et al., 2008b). The production of 80–100 g fish that were reared from larvae under optimal conditions of water quality, feeding, and nutrition in a recirculating aquaculture system (RAS) and saleable on the Swiss market can be accomplished in a single year (Mélard et al., 1996a,b,c). Therefore use of RAS is optimal for intensive culture from a biological point of view.

Perch growth rate and sexual development differ with geographical region, being affected by climatic conditions and availability of food (Tyutyunov et al., 1993; Popova et al., 1997; Craig, 2000). Currently, perch larvae are mainly obtained from controlled reproduction of wild broodstock without being able to perform any genetic selection that could perhaps result in improved survival and growth performances under culture conditions (Mandiki et al., 2004b). The climate and differences in available forage can be the sources of variation in the biological characteristics of perch originating from different geographical regions.

The aims of this review were to summarize the literature on the biology of wild perch populations of varying geographical origin, and to evaluate their suitability for intensive culture in intensive RAS.

Historical background of Perca species taxonomy

The first scientific description of Eurasian perch was in 1730 by Peter Artedi, who defined the basic morphology after

studying perch from Swedish lakes. In 1758, Carl Linnaeus named it *Perca fluviatilis* after a description based on Artedi's research (Semenov, 2005). In 1820, a detailed study of perch conducted by French scientists Georges Cuvier and Achille Valenciennes defined the basic features of a typical perch, determined the number of scales, described the structure of the skeleton and the internal organs on the basis of measurements of perch from French ponds (Semenov, 2005).

Attempts were periodically made to categorize specific populations of perch into separate species. In 1761, Jacob Christian Schaeffer identified perch from the Danube River as a separate species, *Perca vulgaris*; in his view, local perch differed by having a deeper body with a roach back and a higher first dorsal fin (Kottelat, 1997). In 1828, Georges Cuvier identified *Perca italica*. In 1854, Laurence Theodor Gronow identified *Perca helvetica* (Kottelat, 1997). These species were later recognized as *Perca fluviatilis*. At the beginning of the 20th century the focus of study moved from perch distribution and habitat to its morphology. Variations of *Perca fluviatilis* were detailed by the Russian ichthyologist, Vyacheslav Pokrovsky (1951), who also developed a system of fish biometrics.

Due to the wide ecological and geographical distribution of perch, selected ecological forms were formerly separated and identified as subspecies or races. In 1837, Heckel identified a separate subspecies, Perca fluviatilis nigrescens. In 1893, Smith identified three subspecies of perch: Perca fluviatilis aurea, Perca fluviatilis gibba, and Perca fluviatilis maculata. In 1924, Karaman described one population as a subspecies entitled Perca fluviatilis macedonica. In 1933, Berg described Perca fluviatilis phragmiteti. In 1951, Pokrovsky identified coastal perch to be a slow growing form and a separate subspecies, Perca fluviatilis gracilis. Dianov (1955) identified the perch from Lake Zaysan as Perca fluviatilis zaissanica. Svetovidov and Dorofeeva (1936) described perch from the Kolyma River as Perca fluviatilis intermedius. These subtypes have all been invalidated; in the global electronic data bank of fishes the www.FishBase.org includes all of these subspecies and races under the general scientific species name of Perca fluviatilis Linnaeus, 1758; the differences in growth rates are mainly based on local feeding characteristics of perch and the environmental conditions in different locations (Baranov, 2007).

Three species of *Perca* are currently recognized and which are similar: *Perca fluviatilis* Linnaeus 1758 (Eurasian or European perch), *Perca flavescens* (Mitchill, 1814) (yellow perch) and *Perca schrenkii* Kessler, 1874 (Balkhush perch). To date, *Perca fluviatilis* is one of the few species in which systematics, morphology, early stages of development, growth, and ecology are well studied (Voskoboynikova, 2006).

Biology and growth characteristics of Eurasian perch under natural conditions

Eurasian perch is widespread in Eurasian rivers and lakes and some brackish waters. Perch are not present in the Pyrenees or Apennine peninsula, northern England, the freshwater systems along the coast of Norway, the mountainous regions of the Caucasus and Central Asia, southern Mongolia, and the Far East from the basin of the Amur River onward with Kamchatka and Chukotka, or in Siberia, north of 70°N (Berg, 1949; Lugovaya, 1988; Craig, 2000). Paleontological data indicate that perch previously inhabited the Amur River (Yakovlev, 1961). Perch have been introduced into continents and countries including Australia, New Zealand, South Africa, and the Azore Islands (Thorpe, 1977).

Natural populations of perch differ widely with respect to life history, habitat, diet, and growth rate. Even within a single body of water, two or three different forms or ecological races of perch may occur (Tyutyunov et al., 1993; Popova et al., 1997; Craig, 2000; Romare, 2000; Fedorovykh, 2012). In contrast to other predatory fish, perch growth is slow. Perch initially feed on plankton and later move to predation, often not until age-2 (Baranovskiy and Sokolov, 2010). If zooplankton density in the littoral zone in late summer is low, the young-of-the-year perch begin to feed earlier on macroinvertebrates (Persson et al., 2000). Later, individual fish may change from benthivory to piscivory. This niche shift is accompanied by an increase in the growth rate. If the shift does not occur, usually in the second year of life, the perch then remain small (Byström et al., 1998). Thus, under natural conditions, there are two forms of perch: small or dwarf, and large.

In 1930, Sviderskaya identified small and large perch forms in Lake Ubinskoye (Novosibirsk, Russia) (Berg, 1949). In 1951, a small, slow-growing form of Eurasian perch was described incorrectly by Pokrovsky (1951) as a separate subspecies *Perca fluviatilis gracilis*, also classified as *Perca fluviatilis var. macrophthalma* and *Perca fluviatilis var. maculate*. Popova et al. (1997) identified distinctive features of small perch, which included smaller body size, eye size, and fin length, the presence of a dark spot on the caudal fin, shorter distance between the dorsal fins, and an elongated body shape.

Pavlov (2005) also described a dwarf form having a shorter head with a wider forehead, smaller eye diameter, shorter lower jaw, lower height of dorsal fin, longer caudal peduncle, and greater ante-anal distance.

Both forms of perch live together at an early age, with no differences in diet. Beeck et al. (2002) showed that the initially unimodal cohort of 0 + perch in a eutrophic gravel pit gradually broadened and became bimodal in mid-summer. Fish of the larger, piscivorous cohort grew more rapidly. Van Densen et al. (1996), based on the analyses of perch from three lakes in the Netherlands, hypothesized that differential growth within cohorts is more prominent in systems with a strong discontinuity in the size distribution of potential food items.

The study focus of polymorphisms has been on morphology, but the differential use of food resources could influence other phenotypic traits such as digestion characteristics (Beeck et al., 2002).

Eurasian perch juveniles of both forms have a short digestive tract (Dgebuadze, 1993). Their main food is plankton, which is easily digested and absorbed and never fills the gut to capacity. Fast-growing predatory perch have a large stomach and long gut. The stomach is filled quickly and digestion is almost complete; the breakdown of the food bolus occurs only in the stomach. Fast-growing Eurasian perch have a less developed stomach and longer gut, because they feed on fish and invertebrates with a chitinous shell, which are poorly digested (Dgebuadze, 1993; Olsson et al., 2007; Fedorovykh, 2012; Shatunovskiy and Ruban, 2013). Although stomach content analyses have revealed that the large-size cohort was at least temporarily piscivorous while the small-size cohort fed on zooplankton, the possibility that other food sources were utilized cannot be ruled out (Beeck et al., 2002).

Growth rates for certain age-classes of Eurasian perch under natural conditions

The Eurasian perch growth rate can vary greatly with geographical location (Table 1) and is primarily affected by climatic characteristics and the supply of available food that allows the move to predation (Popova et al., 1997; Craig, 2000; Čech et al., 2004).

In general, perch growth rate is low. Perch grow to 5 cm in total length (TL) in the first year and up to 20 cm in 6 years in small ponds as well as in reservoirs with a meager food supply. In large lakes, reservoirs, and estuaries of large rivers, perch TL may reach 12 cm in the first year, and in 5 years may reach TL 35 cm (Reshetnikov et al., 2003; Voskoboynikov, 2006). Average TL is 20–35 cm up to a maximum 51 cm TL. Mean body weight is 0.3–2 kg up to a maximum 5 kg. Growth rate peaks in late spring and summer. The minimum growth rate, or even a cessation of growth, is observed in the late autumn and in winter. The optimum water temperature for perch growth is 23°C (Craig, 2000; Reshetnikov et al., 2003).

Eurasian perch grow more rapidly in the southern hemisphere than in most bodies of water in the northern hemisphere. As New Zealand's winters are milder and of shorter duration than those of many northern hemisphere countries, perch in New Zealand are probably capable of more rapid growth, experiencing lower associated overwinter mortality (Closs et al., 2003).

In the European areas of Russia, perch grow more slowly in waterbodies of Karelia and the Kola Peninsula and in Lake Peipus and the Ivankovo Reservoir (frost-free period approx. 100 days), and most rapidly in the Volga River delta and the lower reaches of the Dnieper River (frost-free period approx. 250 days) (Popova et al., 1997; Ponomarev and Fedorovykh, 2006). Since the length of the growing period in natural bodies of water increases from north to south, the food resources that determine the growth and development of perch and its phenotypic traits also increase (Vinogradov, 2009).

Phylogenetic analyses by Nesbø et al. (1999) of 55 Eurasian perch populations and one Siberian population suggested that the present Eurasian perch populations in western and northern Europe colonized the region from three main refuge areas located in southeastern, northeastern, and western Europe. Mandiki et al. (2004a) reported that Eurasian perch abundance levels are higher in northern than in southern biotopes, although climatic conditions in the latter would seem to be more conducive to Eurasian perch growth.

		Age of fish	T							
Habitat	Year of study	1^+	2+	3+	4+	5+	+9	7+	8+	+6
L. Kamennoye, Karelia, Russia (Semenov, 2005) L. Il'men, Russia (Semenov, 2005) Volga River (delta), Russia (Semenov, 2005) Kuibyshev Res., Russia (Semenov, 2005) L. Chany, Russia (Gold, 1967) L. Zaysan, Kazakhstan (Gold, 1967) L. Khubsugul, Mongolia (Dulmaa, 1999) L. Pounui, New Zealand (Jellyman, 1980) Res. Lipno, Czech Republic (Baruš et al., 1995) Res. Kimov, Czech Republic (Baruš et al., 1995) Vistula River, Poland (Szczyglinska, 1983)	1986 1975, 1983 1965 1965 2003 1960 1980 1974–1975 1974–1975 1974–1980	7/5 - 111/26 7/15 11.0/18 5:9/- 6.1/-	$\begin{array}{c} 11/18\\ 11/23\\ 17/115\\ 10/32\\ 13/41\\ 9/11\\ -\\ 15.0/47\\ 8.3/-\\ 9.7/-\\ 9.7/-\\ 9.0/-\end{array}$	13/30 14/56 21/184 13/47 15/62 17/56 17.5/83 9.7/- 12.9/- 11.8/-	15/52 17/104 24/188 16/77 17/87 21/107 20.7/121 20.3/114 11.1/- 16.1/- 14.2/-	19/123 20/166 18/102 20/159 20/157 20.1157 23.1/175 12.4/- 16.3/- 16.3/-	19/126 23/252 20/173 20/173 24/241 30/450 22.6/168 13.8/- 23.0/- 18.6/-	21/162 25/344 25/344 21/250 25/297 33/580 33/580 25.8/- 25.8/- 25.8/-	22/201 28/451 24/340 28/460 27/2296 15.8/- 15.8/- 24.0/-	23/205 29/581 28/395 31/475 39/1132 29/390
L. Karhujärvi, Southern Finland (Rask, 1984) L. Nimetön, Southern Finland (Rask, 1984)	1983 1983	6.4/- 5.7/-	9.7/- 9.8/-	$\frac{11.6}{12.5}$	12.8/- 15.2/-	13.3/- 16.7/-	13.7/- 17.8/-	14.1/- -	1 1	1 1

Average age-related size of Eurasian perch, Perca fluviatilis [total length (cm)/weight (g)] in various locations

Table 1

Several years of perch monitoring in Lake Volkerak in the Netherlands did not reveal a correlation between the growth rate of perch fingerlings and water temperature. The growth rate was found to be positively associated with the age of onset of piscivory (Gold, 1967; Wang and Eckmann, 1994; Mélard et al., 1996a; Van Densen et al., 1996; Popova et al., 1997; Akin, 2002).

The growth rate and population structure of Eurasian perch can vary significantly according to environmental conditions within a body of water in different years (Popova et al., 1997; Baranov, 2007). A seasonal variation in growth has been reported with an increasing temperature and day length, mainly in April through July (Rask, 1984; Staffan, 2004; Ceccuzzi et al., 2011). This growth variation indicates that juvenile perch possess an endogenous rhythm that can act without external cues (Staffan, 2004). In late autumn, perch migrate to deep, cool water for over-wintering (Wang and Eckmann, 1994; Craig, 2000; Rougeot et al., 2008a). During winter, feed intake and growth are low, and metabolic rates are reduced to a greater extent than would be expected at low temperatures (Strand, 2009).

In the Volga delta, the highest growth rates of perch were observed in the 1950s. This period was characterized by a high abundance of juvenile catadromous fish. In the 1970s, after a substantial depletion of those numbers, the perch growth rate also decreased (Popova et al., 1997).

When there are wide differences in recruitment among years, relative year-class annual growth can be determined from the opercula. Sarvala and Helminen (1996) assessed year-class growth variation of perch in Lake Pyhäjärvi (Finland) from 1989 to 1995, and found the year class of 1988, and possibly 1992, to show higher growth rates. The results of the Sarvala and Helminen study showed a positive correlation between perch year-class size and summer temperature.

Temperature exerts a direct physiological influence on metabolism and growth, but it also has indirect effects on growth via food resources (Sarvala and Helminen, 1996; Popova et al., 1997).

Rask (1984) studied the reproduction, growth, and food resources of a perch population with a focus on pH conditions in a small, extremely humic forest lake and found increased growth under low pH conditions. This may be due to the absence of competition for food and related to decreased fish species diversity and decreased fish population in acidic lakes.

Optimum growth for Eurasian perch was at the lowest salinities, 0 and 4 ppt. Even small increases in salinity have been shown to be detrimental to perch growth. At 10 ppt salinity, body weight was reduced by about 50% (Overton et al., 2008). Other research has shown that hatching success was similar in freshwater and in brackish water, irrespective of female origin (Tibblin et al., 2012; Skovrind et al., 2013).

The survival of yolk-sac and free swimming fry was significantly reduced in brackish water, independent of whether the fish was of migratory or brackish resident origin (Tibblin et al., 2012).

Under natural conditions Eurasian perch display sexual dimorphism, with females growing 20% faster and reaching a larger size than males (Rougeot et al., 2002). The sex-deter-

mining mechanism in perch is not yet described (Zelenkov, 1981; Malison et al., 1988). This sex-related dimorphic growth appears in early life stages (± 110 mm length) and is correlated with the onset of vitellogenesis and spermatogenesis (Craig, 2000).

Popova et al. (1997) suggested that the development of large and small forms of perch is more commonly a typically female characteristic. It was also demonstrated that the slowgrowing females exhibited a delay in the development of germ cells, and that spawning did not occur annually.

Culture of Eurasian perch and their growth in RAS conditions Advantages in the intensive culture of the Eurasian perch

Use of RAS has become increasingly common in intensive aquaculture, replacing the traditional method of growing fish in ponds. Fish are reared indoors in high density tanks with a controlled environment. Fresh water is added to the tanks only to replenish that lost through splashing, evaporation, and flushing out waste materials (Helfrich and Libey, 1990).

The intensive culture of Eurasian perch in RAS has many advantages, including stable conditions, ability to rear fry produced by out-of-season spawning, more predictable production of juveniles, and easier monitoring and control of cannibalism compared to culture in ponds and mesocosms (Kucharczyk et al., 1998; Kouřil and Hamácková, 2000; Kestemont and Baras, 2001; Babiak et al., 2004).

Limiting factors of intensive culture of the Eurasian perch

As in wild natural conditions, intensive culture has factors limiting the growth and development of perch. The survival and growth rate of juveniles is reduced, and the fish size heterogeneity is high compared with other species of fish in intensive culture (Mélard et al., 1996a). Eurasian perch produce small larvae compared to other species, necessitating production of live feed, which can be costly and time consuming. The larvae are initially fragile and prone to problems such as failure to inflate the swimbladder (Jacquemond, 2004), and cannibalism can develop, particularly during adaptation to pellet feeds (Mélard et al., 1996a; Baras et al., 2003; Overton and Paulsen, 2005). Despite the availability of high quality feeds for small larvae mainly formulated for marine species, the food acceptance, growth, and survival of perch fed formulated diets as a starter food are still highly variable and unsatisfactory (Kestemont and Baras, 2001).

Growth characteristics among populations of Eurasian perch in intensive conditions

As under natural conditions, growth and feed intake of Eurasian perch in culture is regulated by a variety of abiotic and biotic factors, for example, temperature and light, as well as size of the fish and social interactions (Kestemont and Baras, 2001).

Feed intake and growth rate in fish will increase as temperature increases to the species optimum, and subsequently decrease when the temperature is further increased and approaches the upper thermal tolerance limit (Wootton, 60

1998). The decrease in appetite at high temperatures has been attributed to limitations in the capacity of the respiratory and circulatory systems to deliver oxygen to the tissues under conditions of very high oxygen demand. Furthermore, the reduction in growth rate is related to an increase in maintenance energy cost as the temperature increases (Jobling, 2003). In conditions of intensive aquaculture, the feed intake and growth of perch is affected by the lighting conditions and tank wall color. In such conditions perch juveniles prefer white and light grey tanks (Strand, 2009). On the other hand, in perch larvae two contradictory recommendations are in the literature for black tanks (Jentoft et al., 2006) and for light grey and white tanks (Tamazouzt et al., 2000).

Perch growth in RAS systems is also affected by the level of animal breeding care, as was demonstrated in an experiment that showed a poor growth rate in disturbed fish (Strand, 2009). This was probably related to a higher sensitivity of perch to stress (Jentoft et al., 2005).

The study of the perch growth rate reared in RAS showed that at a stable water temperature of 17°C for the first year of life, the perch will reach a weight of approx. 110 g compared to 160 g at 24°C. As in natural conditions, adult female perch grow faster than males. At earlier stages males have a greater length and body weight compared to females. Females in older age groups are larger than males (Mairesse et al., 2005; Mélard et al., 2004; Gillet and Dubois, 2007).

It is important to note that growth rates of wild populations of perch of varying geographical origins show significant differences in growth rate when reared in RAS (Mandiki et al., 2004a; Rougeot et al., 2008a). Considering that perch colonized southern and northern regions of Europe via different routes, it may be assumed that wild perch populations from southern Europe are genetically distinct from those in northern areas (Nesbø et al., 1999). In research conducted by Mélard et al. (2004) on growth of several Eurasian perch wild strains originating from different regions of Europe reared in RAS at 23°C, suggested marked differences among strains. At day 200 of rearing from larvae, body weight of Belgian strains was 56% greater than in those of southwest France; in northeast France strains, the body weight was 76% greater than in those from northern Italy. Except in geographical origin, Schaerlinger et al. (2012) found other intrinsic factors such as effect of the breeders' weight and domestication, which strongly influences the spawning date and reproductive influences.

Mandiki et al. (2004b) studied androgen and estrogen mediation of sex-related growth differences. Survival, gonadosomatic index, and hepatosomatic index were not affected by steroid treatments. Relative food intake, feed efficiency, and specific growth rate were found to be higher in females than in males. They reported evidence that methyltestosterone could affect sex-related growth dimorphism by decreasing food intake and feed efficiency in Eurasian perch. Estrogens have been shown to affect sex-related dimorphic growth in juvenile Eurasian perch, being stimulatory in females but passive in males. Estradiol action on the growth process is still unclear. Estrogens may act directly by stimulating anabolic processes such as protein synthesis (Mandiki et al., 2004c). Another important consideration in the intensive culture of the Eurasian perch is the quality of the cultured fish populations. Mairesse et al. (2005) characterized quality descriptors of wild Eurasian perch, taking into account spatial and temporal variability to evaluate quality of reared perch compared to wild perch. Cultured perch were shown to possess morphology similar to wild perch, irrespective of the rearing system. On the other hand, there are differences between wild and cultured perch, mainly in the fatty acids profile, texture, and flesh color (Jankowska et al., 2007, 2010; Stejskal et al., 2011).

Conclusions

Inter- and intra-population ecological differences are highly dependent on biotic factors (i.e. predation risk, resource availability, and competition). Spatial and temporal variations in food intake efficiency, resistance to disease, and stress factors all affect growth in RAS.

These findings highlight the importance of evaluating growth and food consumption of the different Eurasian perch stocks. Such evaluation is a necessary tool for genetic selection for improving performance in perch aquaculture.

Techniques based on genetic characteristics including strain selection, domestication, all-female populations, and hybridization have been developed to improve the growth rate of Eurasian perch in culture conditions (Rougeot et al., 2008a; Stejskal et al., 2009).

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