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Unlocking the wild potential: integration of geographic differentiation in domestication processes to facilitate fish aquaculture diversification

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SUMMARY

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I would like to dedicate this PhD thesis to my grandpa. You could not see the end of it, but this work is for you…

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LIST OF ABBREVIATIONS

BAL: Lake Balaton

BOU: Lake Bourget

FAO: Food and Agriculture Organization the United Nations

GEN: Lake Geneva

HOH: Lake Hohen Sprenzer

ISO: Lake Iso-Valkjärvi

KIE: Lake Kierzlinskie

PU: Prospective Unit

RAS: Recirculated Aquaculture System

VAL: Lake Valkea-Mustajärvi

TIA: Traits of Interest for Aquaculture

LIST OF SPECIES MENTIONED IN THE MANUSCRIPT

Kingdom	**Class / Clade**	**Order**	**Family**	**Species**
Plantae	Angiosperms	Poales	Poaceae	*Triticum dicoccoides*
				Hordeum vulgare
				Oryza sativa
				Hordeum spontaneum
		Malpighiales	Euphorbiaceae	*Ricinodendron heudelotii*
			Irvingiaceae	*Irvingia gabonensis*
		Santalales	Santalaceae	*Santalum austrocaledonicum*
		Malvales	Malvaceae	*Adansonia digitata*
		Sapindales	Anacardiaceae	*Sclerocarya birrea*
		Fabales	Fabaceae	*Phaseolus vulgaris*
		Solanales	Solanaceae	*Capsicum annuum*
Animalia	Insecta	Hymenoptera	Formicidae	*Atta* sp.
			Apidae	*Bombus terrestris*
				Apis mellifera
	Branchiopoda	Anostraca	Artemiidae	*Artemia* sp.
	Mammalia	Carnivora	Canidae	*Vulpes vulpes fulvus*
				Canis lupus
		Primates	Hominidae	*Homo sapiens*
	Actinopterygii	Cichliformes	Cichlidae	*Oreochromis niloticus*
		Cypriniformes	Cyprinidae	*Cyprinus carpio*
				Coptodon guineensis
		Pleuronectiformes	Pleuronectidae	*Hippoglossus hippoglossus*
			Soleidae	*Solea senegalensis*
		Gadiformes	Gadidae	*Gadus morhua*
		Perciforms	Sciaenidae	*Argyrosomus regius*
			Percidae	*Sander lucioperca*
				Perca flavescens
				Perca fluviatilis
				Perca schrenkii
			Moronidae	*Dicentrarchus labrax*
			Pomacentridae	*Amphiprion melanopus*
			Anarhichadidae	*Anarhichas lupus*
			Sparidae	*Diplodus puntazzo*
		Anguilliformes	Anguillidae	*Anguilla anguilla*
		Salmoniformes	Salmonidae	*Salmo salar*
				Salmo trutta
				Oncorhynchus mykiss
				Oncorhynchus tshawytscha
				Oncorhynchus keta
				Oncorhynchus clarkii
		Acipenseriformes	Acipenseridae	*Acipenser ruthenus*
				Acipenser gueldenstaedtii
				Acipenser stellatus
				Acipenser baerii
				Acipenser persicus
				Huso huso
		Scombriformes	Scombridae	*Thunnus thynnus*

CONTEXT

CONTEXT: Domestication and intraspecific differentiation

1. Domestication: definition(s) and process

1.1 Definition(s)

The domestication of organisms is one of the most essential developments in human history and it has triggered major changes leading to mankind's current state. Across the literature, domestication is seen as a relationship, often mutualistic, between humans and plant or animal populations. Even though some authors use the domestication term to describe non-human interactions (e.g. fungus growing ants [Insecta, Hymenoptera, Formicidae, *Atta sp.*]; Mueller et al. 1998), the term in this work is used within an anthropocentric context. Domestication is still a widely debated concept given the wide range of alternate definitions referenced in literature (**Table 1**). This results from (i) disagreements regarding on which actor of the relationship the emphasis should be placed (i.e. human and/or animal/plant involved in the domestication process), (ii) its complexity due to the involvement of both biological and social notions, and (iii) the narrowing of some definitions to a particular species/species group (Russell 2002; Zeder 2015). For this work, domestication is defined as the process in which a wild population is bred in a human-controlled environment and this population evolves across generations from its wild ancestor, in ways making it more useful to humans who increasingly control their reproduction and food supply (Lecocq 2019). This definition is integrative and allows to combine concepts from different previous definitions. The human control on the culture environment can be more or less important (e.g. weaker control in extensive production systems such as open ponds or ranching; stronger control in intensive production systems such as indoor recirculating aquaculture systems or factory farms). Domestication is not performed on all populations of a species but rather on specific population(s) of a given species.

1.2 Domestication steps

Domestication is a difficult, long, and continuous process which can be divided in five steps (**Table 2**; called "domestication levels"), depending on the degree of control over the life cycle and the level of gene flow with wild conspecifics (Teletchea and Fontaine 2014; Lecocq

2019). This classification has been initially developed for fishes (Teletchea and Fontaine 2014) but has been further applied to other taxa (Lecocq 2019).

Table 1: Examples of alternate domestication definitions referenced in literature.

Source	Domestication definition
Price (1984)	« Process by which a population of animals becomes adapted to man and to the captive environment by genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation »
Diamond (1997a)	« Domestication involves wild animals' being transformed into something more useful to humans »
Weisdorf (2005)	« Unintentional process by which human intervention, selection and replanting (i.e., environmental manipulation) eventually gave rise to strains of plants and animals that depended upon human assistance for their survival and upon which humans in turn depended sustenance »
Bilio (2007)	« Gradual adaptation of an organism to living conditions that are determined by some form of human intervention »
Driscoll et al. (2009)	« Permanent genetic modification of a bred lineage that leads to, among other things, a heritable predisposition toward human association »
Zeder (2012a)	« Sustained multi-generational mutualistic relationship in which humans assume some significant level of control over the reproduction and care of a plant/animal in order to secure a more predictable supply of a resource of interest and through which the plant/animal is able to increase its reproductive success over individuals not participating in this relationship »
Jensen and Wright (2014)	« Process whereby populations of animals change genetically and phenotypically in response to the selection pressure associated with a life under human supervision »
Zeder (2015)	« A coevolutionary, mutualistic relationship between domesticators and domesticates »
Lecocq (2019)	« Process in which populations are bred in man-controlled environment and modified across succeeding generations from their wild ancestors in ways making them more useful to humans who control, increasingly during the process, their reproduction and food supply »

The first step corresponds to the acclimatization process, when a wild population is transferred from the wild to a human-controlled environment. The next domestication steps are defined by an increasing human-control over the life cycle and a decrease of the use of wild counterparts to replenish farmed stocks. In this way, step two refers to the stage in which a part of the life cycle is controlled but there are still major bottlenecks preventing the completion of the life cycle; step three corresponds to the full completion of the life cycle but wild individuals are still collected in the wild to supply farmed stocks; and finally step four refers to when the entire life cycle is closed in captivity without further input from wild captures. The last stage of domestication (step five) corresponds to the development of selective breeding (or artificial selection) programs, which aim at intentionally modifying organisms based on desirable traits (Vaughan et al. 2007; Teletchea and Fontaine 2014). Domestication is therefore a continuum and populations can move forward or backward along the process.

Table 2: Domestication levels according to Teletchea and Fontaine (2014).

Domestication level	Description
1	"First trials of acclimatization to the culture environment"
2	"Part of the life cycle is completed in captivity, but several important bottlenecks still exist in others (e.g. reproduction, larval rearing)"
3	"The entire life cycle is closed in captivity but with wild inputs"
4	"The entire life cycle is closed in captivity without wild input, but no selective breeding programs is used"
5	"Selective breeding programs"

2. Historical context of domestication

During the Upper Paleolithic era, modern humans (Mammalia, Primates, Hominidae, *Homo sapiens*) were composed by hunter-gatherer communities. The primary subsistence strategy was relying on hunting, fishing, and gathering (Diamond 1997b). The premises of domestication of animal and plant populations started at least 15 000 years ago with the domestication of wolf populations, which correspond to the ancestors of modern dog (Mammalia, Carnivora, Canidae, *Canis lupus*) population(s) (Braastad and Bakken 2002). Nevertheless, it is later, during the Neolithic period, that human lifestyle radically changed with the rise of agriculture and the shift from the hunter-gatherer lifestyle to farmers (Vigne 2011). The oldest traces of agriculture activity were found in the Fertile Crescent about 10 000 years ago, notably through the culture of vegetal species, which resulted from the sowing of these species (Diamond 1997a; Lev-Yadun et al. 2000). Hunter-gatherers initiated the domestication of numerous cereals, such as wheat (Angiosperms, Poales, Poaceae, *Triticum* sp.) and barley (Angiosperms, Poales, Poaceae, *Hordeum spontaneum*) in the Middle East, as well several other annual plants (Diamond 1997a 2012). Domestication of animal populations, particularly terrestrial mammals which are essential in modern agriculture, overall developed later (Bruford et al. 2003; Vigne 2011). Through time, sedentary farmer societies replaced hunter-gatherers' societies, independently in several geographic locations. This transition is referred as the Neolithic revolution (Diamond 2002).

The transition to the farming lifestyle has provided a selective advantage to humans, notably through the food resource securing, which allowed them to progressively disseminate their lifestyle (but see also some negative consequences such as health decline or increased spread of pathogens; Latham 2013). As a point of comparison, half of a hectare of land culture can nourish ten to 100 times more individuals than hunter-gatherers (Diamond 1997). Therefore, the Neolithic revolution corresponds to a major turning point in human history and led to deep shifts in the evolution, ecology, and demography of humans (e.g. human settlement, diversification of techniques, outbreak of structured human societies; Vigne 2011; Gepts et al. 2012). The triggering factors which lead human populations to abandon the hunter-gatherer lifestyle to start agriculture are still under investigation but several (sometimes complementary) hypotheses have been raised (e.g. population growth and resource decline, climate, social changes; Price 1995; Gupta 2004; Vigne 2011).

So far, examples of domestication for food purposes have been highlighted. However, it must also be underlined that food provisioning was not the only benefit from domestication. Indeed, populations which were domesticated have also been used for other purposes: protection, basic materials, transport, and later on as biological control agents, laboratory models, for entertainment, or for ornamental purposes (Diamond 1997a, 2002; Price 1999, 2002; Driscoll et al. 2009; Santana et al. 2010; Moorhead and Zeng 2010; Lecocq 2019). In addition, these domestication purposes are not independent since some conspecific populations have been used for different outputs (e.g. wool production and meat).

Humans have domesticated/attempted to domesticate numerous terrestrial species populations (Diamond 2002), in several instances without an initial intentional action to domesticate. Different domestication pathways have been suggested (Zeder 2012b; Larson and Fuller 2014): (i) the commensal pathway for which there is no initial intention to domesticate but in which wild populations got benefits from staying in the human niche (e.g. dog domestication; Larson and Fuller 2014), (ii) the prey pathway in which the initial motivation is not domestication but food provisioning (perhaps because of local stocks depletion of hunted preys) and in which hunting strategies evolved over time to game management/keeping strategies and later on to herd-management strategies (e.g. large terrestrial mammals domestication, Zeder 2012a), and (iii) the direct pathway when there is a deliberate domestication initiated by humans towards a wild population which is the most common pathway for modern populations under domestication (e.g. golden hamsters, fish species, most insects; Fritzsche et al. 2006; Teletchea and Fontaine 2014; Lecocq 2019). However, these pathways are not independent, and domestication can result from the involvement of several pathways (Larson and Fuller 2014). In the frame of this work, the focus was placed on the direct pathway, more particularly for food provisioning purposes.

Overall, domestication efforts for food purposes have been focused on populations from a few species (Gepts et al. 2012). Indeed, four cereal crops (rice, maize, potatoes, and wheat) provide around two-thirds of total human needs (Troell et al. 2014). Similarly, land agriculture rests on solely five major species which display a very high breed diversity (Diamond 2002; Teletchea 2012). Overall, modern human diet is based on a few species (0.08% of terrestrial plants and 0.0001% of animal terrestrial species described nowadays), which were domesticated these last 12 000 years (Diamond 2002; Duarte et al. 2007) and terrestrial species are nowadays considered for domestication for other purposes than food provisioning. On the contrary, in aquaculture (i.e. production of aquatic species), domestication processes started overall recently and numerous species have been/are considered for the food market. Yet, the aquaculture production still relies on a low number of species (see Introduction).

3. Domestication: a long and difficult process

Domestication is long and difficult and often results in unfruitful attempts (Diamond 2002; Teletchea and Fontaine 2014; Metian et al. 2019). Domestication attempts and subsequent production can fail due to technical limitations, socio-economic constraints, or intrinsic species features (i.e. single feature or quantifiable measurement of an organism; Liao and Huang 2000; Diamond 2002; Driscoll et al. 2009). Analyzing previous success-stories or failures, several features can be highlighted as limiting or facilitating the domestication process and subsequent production (see **Table 3** for animal species). These features include both intrinsic biological traits (essential for domestication) and socio-economic characteristics (relevant for production). In this way, for instance, low growth rate, high aggressiveness, poor market value, and low disease resistance characterize poor candidates for animal domestication and subsequent production (**Table 3**) while numerous species fruitfully domesticated and produced present the opposite characteristics. In addition, depending on the domestication system, the importance of some of these characteristics is going to vary. For instance, sensitivity to environmental changes is essential in outdoor culture (Ficke et al. 2007; Altieri et al. 2015) while the tolerance to conspecifics is important in intensive production (Bouissou and Boissy 2005; Jobling 2010). This implies that not all species are suitable to start new domestication processes in every human-controlled environment.

Table 3: Characteristics which can facilitate or limit the animal population domestication and subsequent production (according to Webber and Riordan 1976; Tennessen and Hudson 1981; Liao and Huang 2000; Diamond 2002; Price 2002; Driscoll et al. 2009; Jobling 2010; Zeder 2012a).

Characteristic type	Facilitating	Limiting
Behavior	Absence of aggressiveness	Aggressive disposition
	High tolerance of high densities in intensive conditions	Low tolerance to high densities in intensive conditions
	Solicits attention	Avoids attentions/independent
	Dominance hierarchy	Territoriality
	Large gregarious groups	Structure in small groups or solitary lifestyle
	Male social group affiliation	Males in separate groups
	Persistent groups	Open membership
	Males dominant over females	Females dominant or males appease females
	Easy divestiture of young	Difficult divestiture of young
	Limited agility	Highly agile/difficult to contain
	Non shelter seeking	Shelter seeking
	Implosive herd reaction to threat	Explosive herd reaction
	Exploits anthropic environments	Avoids anthropic environments
Growth	High growth rate	Low growth rate
	High food conversion efficiency/ratio	Low food conversion efficiency/ratio
Nutrition	Diet easily supplied by humans / Generalist herbivorous feeder or omnivore	Diet not easily supplied by humans / Specialist or carnivore
Development	Precocial young	Altricial young
	High survival rate	Low survival rate
Reproduction	Short birth spacing	Long birth spacing
	Reproduction in captivity	Reluctance to breed in captivity
	Polygamous/Promiscuous mating	Pair bonding prior to mating
	Males initiate	Females initiate
	Movement or posture mating cues	Color or morphological mating cues
Physiology	No tendency to panic in enclosures or when facing predators	Tendency to panic in enclosures or when facing predators
	Low sensitivity to environmental changes	High sensitivity to environmental changes
	High disease resistance	High sensitivity to diseases
	Wide environmental tolerance	Narrow environmental tolerance
Socio-economical characteristics	High yield per unit/volume	Low yield
	High sale value	Low sale value
	Established appeal	Unknown
	Alternative processing techniques and products	No alterative techniques
	Useful by-products	No exploitable by-products
	No legal restrictions	Legal restrictions
	Indigenous species	Exogenous species
	Large source of foundation stock	Limited source of foundation stock
Distribution	Small home range	Large home range

Many domestication processes still rely on trial and error approaches, which are time and money consuming. Therefore, there is a need to rationalize new domestication processes. Yet, the analysis of these favoring/limiting characteristics can be useful to point out poor and good candidates for domestication and subsequent production and avoid those expressing numerous limiting characteristics which would lead to potentially unfruitful domestication attempts. In this perspective, several methods have been developed at the inter-specific level to identify candidate species with high agriculture/aquaculture potential (i.e. quantification of how much the expression of all key traits [biological and socio-economical]/functions is favorable for domestication and subsequent production). For instance, DeHaan et al. (2016) developed a pipeline approach for grain crop domestication. This approach relies on the fact that wild crops have traits limiting their domestication and/or production while others have characteristics making them easier/faster to domesticate and produce (e.g. easiness to harvest, high yield, high nutrition and quality attributes). The approach focuses on screening the biodiversity and identifying among all wild candidates the species with the highest potential(s) for agriculture. However, these approaches neglect a part of the wild biodiversity which could facilitate the domestication and subsequent production of new candidate species: the wild geographic differentiation.

4. Geographic differentiation: its potential usefulness for domestication and production

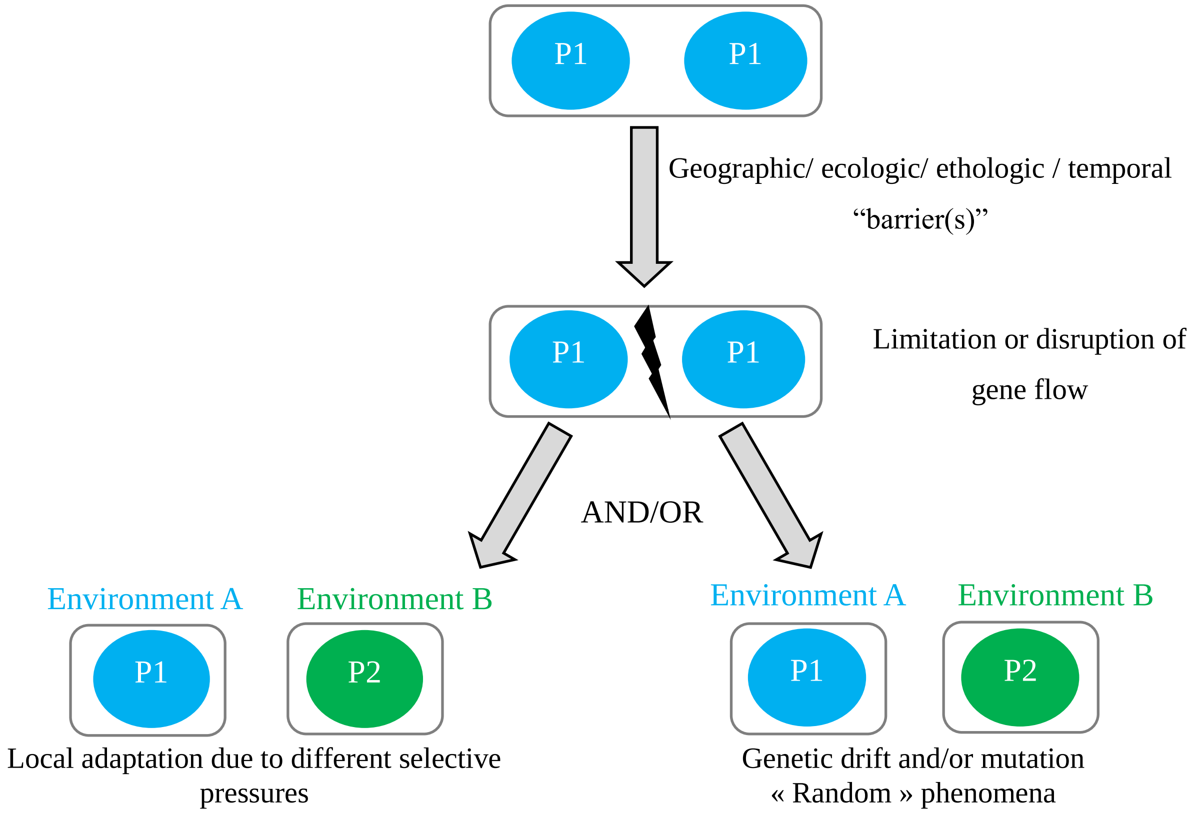
4.1 What is geographic differentiation?

Except for clonal species, all conspecific individuals are genetically and phenotypically unique. Intraspecific differentiation corresponds to the differentiation found either within-populations (at the individual level) or between conspecific populations (inter-populational level). A large part of the wild intraspecific differentiation is linked with the geographic origin of populations: this refers to the geographic differentiation, which is considered here as the differentiation between allopatric (i.e. geographically distinct) conspecific populations (Mayr 1942, 1963). Geographic variation has been investigated for a wide range of taxa (Mayr 1963). Indeed, it is well known in the wild for plants (Li et al. 1998; Więski and Pennings 2014), fishes (Blanck and Lamouroux 2007; Yeates-Burghart et al. 2009), insects (Araki et al. 2009; Chen and Kang 2009), reptiles (Sperry et al. 2010; Du et al. 2014), mammals (Pitman and Ensor 2003; Delarue et al. 2009), and birds (Tremblay and Cherel 2003; Mainwaring et al. 2012).

Geographic differentiation: how?

Geographic differentiation is shaped by inter-population divergence processes, resulting from distinct demographic histories, random genetic drift, and/or local adaptations (**Box 1**; Mayr 1963; Avise 2000; Hewitt 2001). Past demographic events (e.g. distribution range shifts triggered by climate cycles; Bernatchez and Wilson 1998; Hewitt 2004b) and barriers (e.g. geographic, climatic, behavioral, temporal) are important factors shaping geographic differentiation. Indeed, they can limit/prevent gene flow between gene pools. The limitation of gene flow and differences in selective pressure regimes can lead to genetic divergence between these gene pools though random processes (i.e. genetic drift, random mutations) and/or local adaptations (i.e. process increasing the frequency of traits which favor fitness in a given environment, Carvalho 1993; Mayr 1963; Losos and Ricklefs 2009). Local adaptation can shape population specificities in numerous traits, including key features for domestication and commercial production. Geographic differentiation can ultimately lead to allopatric speciation in the absence of gene flow.

Box 1: Examples highlighting processes leading to geographic differentiation in key trait(s)



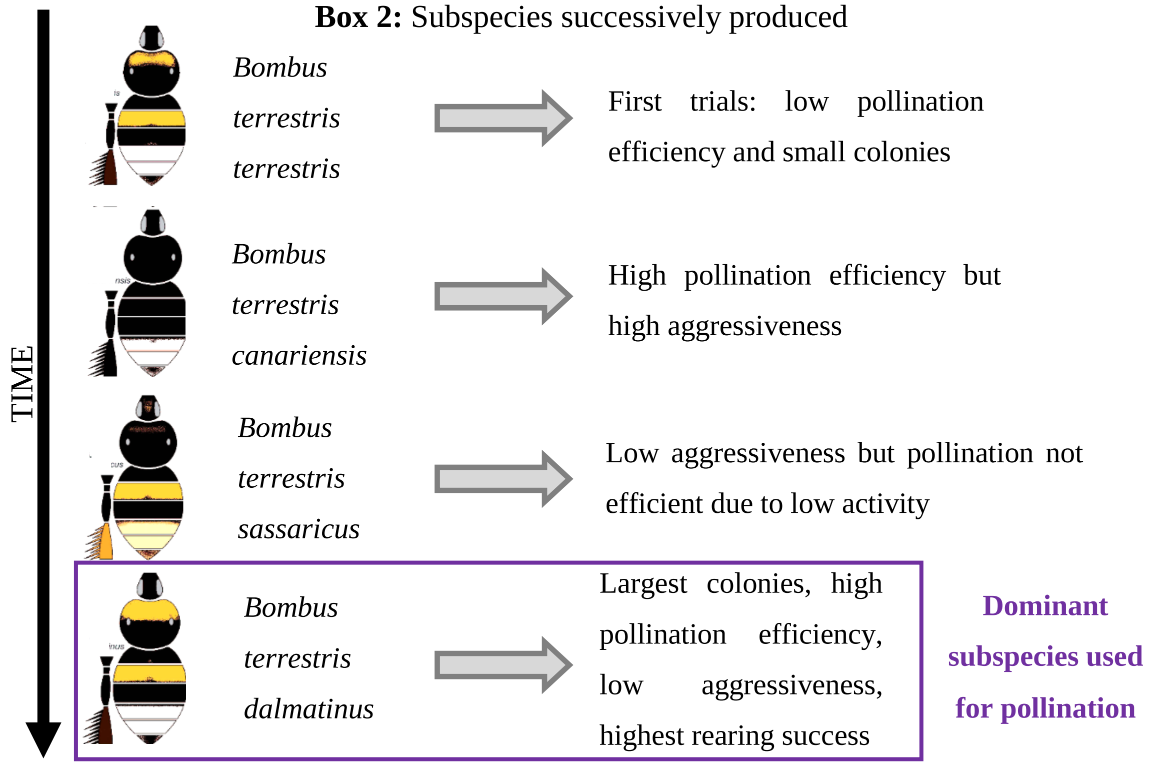
Two alternate non-exclusive processes shaping geographic differentiation between two gene pools are exemplified: (i) local adaptation and (ii) divergences through random processes (genetic drift and mutation). P1 and P2 correspond to alternative phenotypes. Phenotypic differentiation can implicate both genetic and epigenetic factors.

4.2 Why can geographic differentiation facilitate domestication?

Any trait, morphological, physiological, behavioral, or ecological may vary geographically (Mayr 1963; Foster 1999). However, interestingly, geographic differentiation was highlighted in the literature for several characteristics which can facilitate or limit domestication and subsequent production (**Table 3**). For instance, a wild geographic differentiation was highlighted for growth rate (e.g. Chauvaud et al. 2012), aggressiveness (e.g. Wiltenmuth and Nishikawa 1998), sensitivity to environmental changes (e.g. Räsänen et al. 2003), reproductive behavior (e.g. Herring and Verrell 1996), food consumption (e.g. Lindgren and Laurila 2005), disease resistance (e.g. Owen-Ashley et al. 2008), or survival rate (e.g. Blanchette et al. 2002). This highlights that there could be an interest in considering wild geographic differentiation in order to find wild populations which could facilitate domestication and subsequent production, as suggested recently for seaweed culture (Valero et al. 2017). Indeed, picking in the wild phenotypes which present multiple favoring and few limiting characteristics would optimize chances of success for a given domestication trial.

A few success stories have shown that considering population specificities can lead to fruitful domestication and production. For instance, the buff-tailed bumblebee (Insecta, Hymenoptera, Apidae, *Bombus terrestris*) provides a good example of the successful use of wild geographic differentiation in a domestication/production process. This bumblebee is used for greenhouse pollination (Velthuis and van Doorn 2006) and displays a large geographic differentiation in several commercially important traits involved in its ability to be industrially produced and pollinate crops (Velthuis and van Doorn 2006; Kwon 2008; Lecocq et al. 2016b, a). At the beginning of the buff-tailed bumblebee production, European breeders tried to successively rear several wild subspecies (Velthuis and van Doorn 2006). Within a fairly short time, one subspecies proved to have superior characteristics for commercial use (i.e. largest colonies, high pollination efficiency, low aggressiveness; **Box 2**). This subspecies allowed to develop a fruitful production (Lecocq et al. 2016b). Even though domestication was already initiated and production running, this example shows how the consideration of wild geographic differentiation helped to facilitate domestication and production.

Box 2: Subspecies successively produced



Bombus terrestris terrestris → First trials: low pollination efficiency and small colonies

Bombus terrestris canariensis → High pollination efficiency but high aggressiveness

Bombus terrestris sassaricus → Low aggressiveness but pollination not efficient due to low activity

Bombus terrestris dalmatinus → Largest colonies, high pollination efficiency, low aggressiveness, highest rearing success

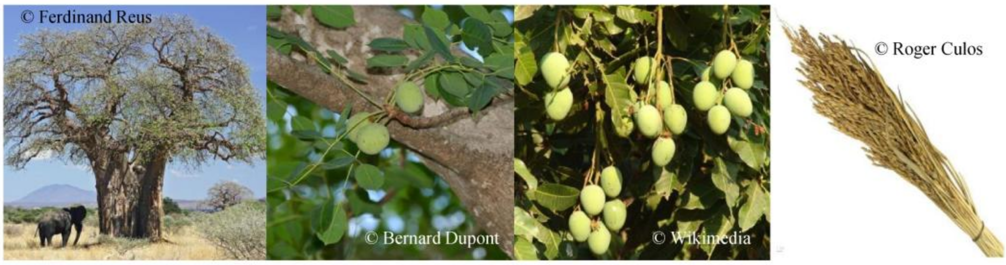
Dominant subspecies used for pollination

Bumblebee images from Rasmont et al. (2008)

At more advanced stages of domestication, geographic differentiation was considered for the European honeybee (Insecta, Hymenoptera, Apidae, *Apis mellifera*) production since non-African populations presented characteristics facilitating beekeeping (e.g. survival in temperate regions, low aggressiveness; Lecocq 2019). Other examples can be found in land agriculture (**Box 3**). Indeed, geographic differentiation in commercially important traits (e.g. fruit mass, flesh depth, tree height, flesh fibrosity) was investigated between wild allopatric populations in the "ideotype" research for new tree domestication programs (Leakey et al. 2012). This was performed for several species, such as *Ricinodendron heudelotii* (Angiosperms, Malpighiales, Euphorbiaceae; Mpeck et al. 2003), *Santalum austrocaledonicum* (Angiosperms, Santalales, Santalaceae; Page et al. 2010), *Adansonia digitata* (Angiosperms, Malvales, Malvaceae ; Jensen et al. 2011), *Sclerocarya birrea* (Angiosperms, Sapindales, Anacardiaceae ; Leakey et al. 2005a, b), and *Irvingia gabonensis* (Angiosperms, Malpighiales, Irvingiaceae; Ladipo et al. 1996; Atangana et al. 2001). Similarly, geographic differentiation was also highlighted and used to develop vegetable culture (e.g. Angiosperms, Solanales, Solanaceae, *Capsicum annuum*; Ben Mansour-Gueddes et al. 2010). Finally, geographic differentiation is strongly suspected to have contributed to the successful cultivation of several cereals. Evidence of multiple domestications of conspecific allopatric populations, afterwards used to develop several strains at advanced domestication levels, was shown for several species such as *Oryza sativa* (Angiosperms, Poales, Poaceae; Sweeney and McCouch 2007), *Hordeum vulgare* (Angiosperms, Poales, Poaceae; Morrell and Clegg 2007; Saisho and Purugganan 2007), and *Phaseolus vulgaris* (Angiosperms, Fabales, Fabaceae; Chacón S et al. 2005).

Box 3: Illustration of species mentioned for geographic differentiation

Bombus terrestris *Apis mellifera* *Ricinodendron heudelotii*



Adansonia digitata *Sclerocarya birrea* *Irvingia gabonensis* *Oryza sativa*

Santalum austrocaledonicum *Capsicum annuum* *Phaseolus vulgaris* *Hordeum vulgare*

4.3 How to integrate geographic differentiation in domestication processes?

The success-stories presented demonstrate that considering geographic differentiation can unlock the potential contained in the wild biodiversity and pave the way to the domestication and production of new species populations. However, culture systems are very diverse, and domestication can occur in a culture system which can be quite different from wild conditions. Yet, the variance of a phenotype is the result of both genetic and environmental factors (Falconer and Mackay 1996; Zamudio et al. 2016). Therefore, phenotypic differentiation observed in the wild between allopatric populations can result from (i) genetic divergence and local adaptation (or random processes), (ii) environmentally-induced phenotypic plasticity (i.e. “ability of a single genotype to exhibit a range of different phenotypes in response to variation in the environment”; Forsman 2015), or (iii) a combination of both factors (DeWitt and Scheiner 2004; Merilä and Hendry 2014). This implies that phenotypic differentiation observed in the wild between allopatric populations might not be preserved in culture systems. Therefore, only genetically based differentiations are of interest for production which makes the detection of *a priori* favorable phenotypes directly in the wild unlikely.

The assessment of genetically based phenotypic differentiation in key traits between allopatric populations requires performing common-garden experiments. The common-garden experiment consists in applying the same environmental conditions to populations in order to study the genetic basis of traits without the confounding effects of the wild environment (de Villemereuil et al. 2016). Indeed, this experimental set up allows to minimize potential effects of environmentally induced-phenotypic plasticity (West-Eberhard 2003). Yet, it is not pragmatic and ultimately feasible to sample and evaluate all populations across a species distribution range. Moreover, conspecific populations are not all divergent from each other, making such assessments uselessly time and money consuming. However, it is not optimal to test random populations or sampling populations over a small part of the distribution range of a particular species. Indeed, this strategy could lead to miss out the potential expressed by populations not sampled. Therefore, an efficient and pragmatic approach requires the development of a standardized method to integrate geographic differentiation in domestication processes.

Take-home message

Domestication is here considered as the process in which a wild population is bred in a human-controlled environment and this population evolves across generations from its wild ancestor, in ways making it more useful to humans who increasingly control their reproduction and food supply. Beginning during the late Pleistocene, domestication is one of the most important developments in human history and deeply impacted human civilizations. Domestication attempts are still occurring nowadays, but failures are reported due to technical limitations, socio-economic limitations, or species-intrinsic features. Several traits were identified as limiting or facilitating domestication and subsequent production, showing that the ability to be successfully domesticated/produced varies between species. Approaches were developed to identify species of interest, but they do not consider an essential part of the wild biodiversity: the geographic differentiation. Geographic differentiation is well-known in the wild, including for traits identified as facilitation/limiting domestication and production. Some success-stories show how its consideration can lead to successful domestication/production. However, it is not possible to identify directly in the wild *a priori* favorable phenotypes. Therefore, there is a need to develop a standardized and pragmatic method in order up to integrate geographic differentiation in domestication processes.

INTRODUCTION

INTRODUCTION- Domestication and aquaculture: interest to integrate geographic differentiation

1. Aquaculture: definition and farming systems

Aquaculture is the farming of aquatic organisms through several alternative practices. Aquaculture systems are very diverse and there are numerous ways to classify production systems depending on the culture structure (e.g. sea cage, land-based tank), water exchange (e.g. recirculated, open), the farming method (e.g. monoculture/polyculture), or the intensity of production. This latter is commonly used to classify aquaculture systems and depends on several criteria such as food input, density of fish, or water renewal (Mozes et al. 2011; Lekang 2013). Extensive systems are usually characterized by low densities of individuals (i.e. low production per unit volume), minimal input of artificial substances in the system, low investment, low technological level, as well as a low human intervention. Aquaculture in ponds might be the best example to illustrate extensive systems. On the contrary, intensive production usually involves a much higher production per unit volume, higher costs, a strong human intervention, and a high control of rearing parameters. The recirculating aquaculture system (RAS) is an intensive system which is increasingly used nowadays in the aquaculture sector. A third system type exists which is an intermediate of the first two systems: the semi-intensive system. This represents for instance a system in which the fry production is intensive, but the on-growing is performed in an extensive system (Lekang 2013).

What is a recirculating aquaculture system?

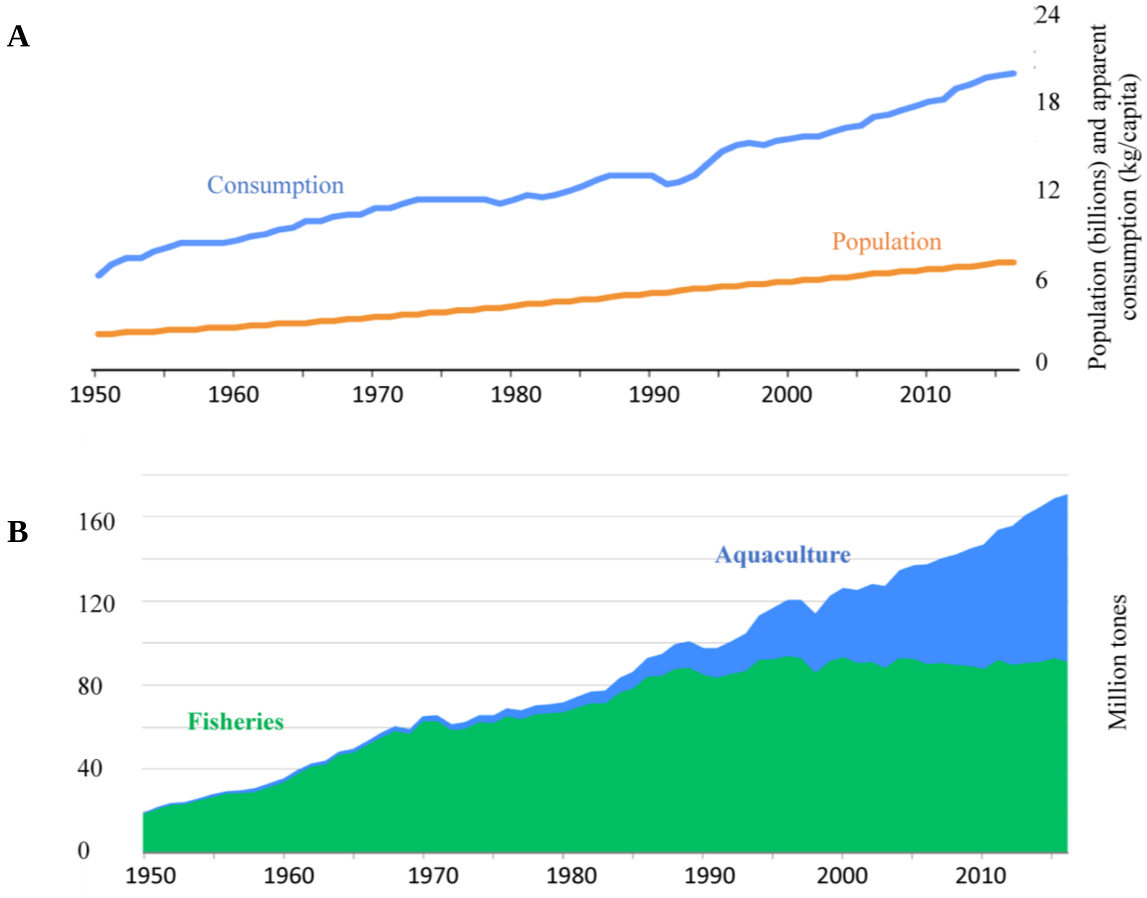
A recirculating aquaculture system is an intensive fish production technology which aims at reusing the culture water through series of water treatment steps to depurate the water. This system is therefore a closed circuit and works using mechanical and biological filters. The system produces waste products (e.g. solid particles, ammonium) which are either removed or converted to non-toxic products. It is currently widely used in the aquaculture sector. Its advantages are a fully controlled environment, a low use of water, an efficient land and energy uses, disease control, and an ease to manipulate fish.

Ebeling and Timmons (2012); Espinal and Matulić (2019)

2. Aquaculture: a fast-growing food production sector

Nowadays, aquatic products represent a major part of the human diet (FAO 2018; Pradeepkiran 2019). Until the 1950s, most of the human consumption of aquatic products was supplied by fisheries (FAO 2018). With the increasing human population and the associated rising demand for aquatic products (**Figure 1A**), fisheries output increased but wild stocks are limited. Fisheries production stagnating through time, there was a shift to target species further from coastlines and deeper in the ocean. However, nowadays, a large part of exploited wild fish stocks is considered as fully exploited or over-exploited (Watson and Pauly 2001; Pauly et al. 2003; FAO 2018). In addition, some fishery techniques are not considered as sustainable and are condemned by international organizations (Myers and Worm 2003; Pauly et al. 2003; Roberts 2002). Fisheries are therefore no longer enough to keep supplying aquatic products to humanity. Shortly after the beginning of the stagnation in fisheries, aquaculture got developed in order to keep supplying the increasing demand in aquatic products (**Figure 1B**).

Figure 1: **A**. World population and fish apparent consumption. **B**. World fisheries and aquaculture production between 1950 and 2016. Adapted from FAO (2018).



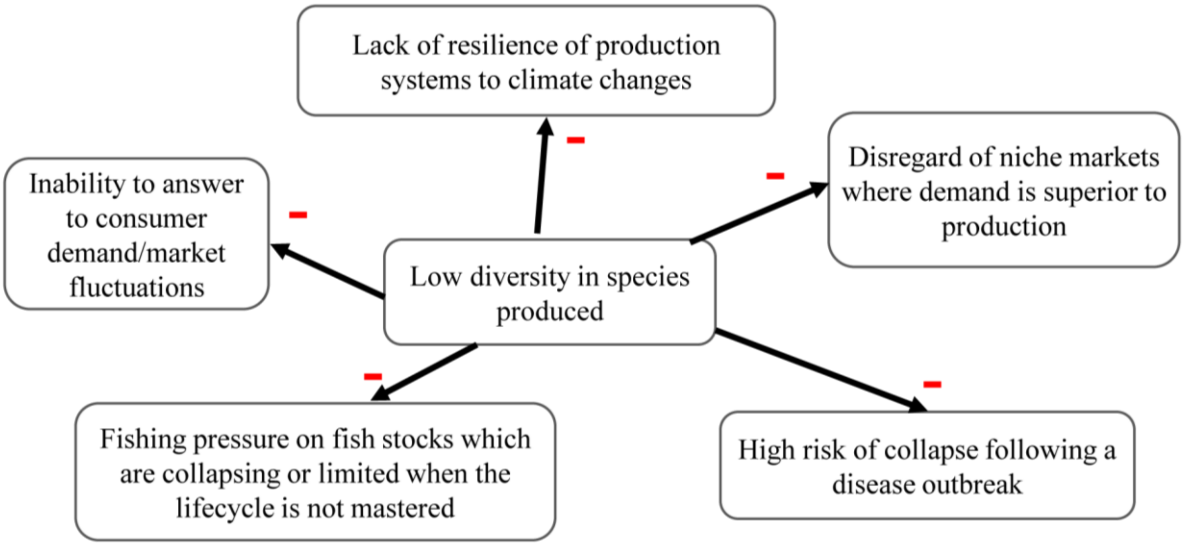
Aquaculture is considered as the fastest-growing food production sector in the world and now provides more than 50 % of the aquatic products consumed worldwide (Subasinghe et al. 2009; FAO 2018). The rapid growth of aquaculture presents several benefits, including the potential to (i) provide year-round incomes for farmers and fish supplies, (ii) reduce fishing pressure on wild stocks, and (iii) provide ecosystem services (e.g. bioremediation, wastewater treatment, enhancing depleted wild stocks; Klinger and Naylor 2012; Troell et al. 2014). In this work, the focus was set on the production of fish species. The global average per capita supply of fish increased substantially these last fifty years and fish and shellfish account now for 6.5 % of total global protein consumption (Troell et al. 2014).

3. A will for sustainability: towards production diversification.

Aquaculture has become increasingly popular over the years (Froehlich et al. 2017) but remains criticized because of its potential unsustainable development and its negative environmental impacts (Fontaine et al. 2009; Martinez-Porchas and Martinez-Cordova 2012; Christou et al. 2013; Diana et al. 2013). These negative impacts include the destruction of habitats, the introduction of invasive species, a stress on freshwaters resources, an increased pressure on wild stocks when the life cycle is not fostered or in order to produce aquaculture feeds (i.e. fish meal and fish oil), enhanced disease/parasite transmission to wild populations, and pollution of ecosystems (Naylor et al. 2005; Silva et al. 2009; Klinger and Naylor 2012; Troell et al. 2014; FAO 2018).

The low species diversity that contributes to production is one of the main issues hampering the sustainability of the aquaculture sector. Indeed, although numerous species are farmed (i.e. 212 in 2017; Metian et al. 2019), a low number of species contribute significantly to the global production in terms of value and volume (Teletchea 2015; FAO 2018). In this way, 85% of the global fish aquaculture production relies on only 15 species (Lazard 2013). This is notably due to the fact that the production of many fish species (i) was abandoned after one or several trials due to zootechnical or economic issues or (ii) remains marginal when compared to the global volume of production (Teletchea and Fontaine 2014; Metian et al. 2019). The low species diversity contributing to production triggers numerous socio-economic and environmental issues (**Box 4**; Fauconneau 2004; Naylor and Burke 2005; Asche et al. 2009; Fontaine et al. 2009; Silva et al. 2009; FAO 2018). First of all, low species diversity triggers a low resilience of aquaculture to face environmental changes or consumer demand/market fluctuations (Fontaine et al. 2009; Troell et al. 2014; FAO 2018). This is particularly concerning given the predicted impact of climate change on aquaculture production (Cochrane et al. 2009). Moreover, when the life cycle is not closed, it can generate fishing pressure on species which wild stocks are limited or collapsing (Fontaine et al. 2009). There is also a high risk of market collapse in the scenario of a disease outbreak as experienced by the salmon farming industry in Chile in 2005 due to an outbreak of infectious salmon anemia (Godoy et al. 2008; Asche et al. 2009). Finally, a production model based on a few species neglects some parts of the market such as niche markets for which production is still inferior to the demand and where the development potential is high (Fontaine et al. 2009)

Box 4: Negative consequences triggered by the low species diversity in aquaculture production



Nowadays, there is a will to develop a more sustainable aquaculture industry to ensure food security and cope with ongoing and future environmental changes. Several scenarios are currently prospected to promote the sustainability of the aquaculture sector. One potential way, promoted by the European commission and the FAO, relies on diversification. Several diversification strategies are advocated (Harvey et al. 2017): (i) increasing the number of farmed species, (ii) increasing the evenness (i.e. contribution of each species to overall production) of farmed species, (iii) increasing the diversity within currently farmed species (i.e. strain diversity), and (iv) increasing the diversity of farming systems (e.g. integrated multitrophic aquaculture, aquaponics). Therefore, the production diversification is notably possible through new fish species domestication (Muir 2005; Fontaine et al. 2009; Subasinghe et al. 2009; Spanish Ministry of Environmental and Affairs 2010; FAO 2018; Metian et al. 2019).

4. Particularities of teleost species domestication

Contrary to land species, domestication of fish species is significantly more recent and wild populations commonly co-exist with farmed populations (Liao and Huang 2000; Teletchea 2018). The time lag of 8 000 years between terrestrial agriculture and aquaculture can be partly explained by the fact that wild aquatic resources and fisheries used to be sufficient to supply the demand for fish products and because of technical challenges to rear aquatic species. However, a few species started to be considered for domestication a long time ago. Evidences of fish culture trials date back about 3 500 years (Nash 2011). Traces of Nile tilapia (Actinopterygii, Cichliformes, Cichlidae, *Oreochromis niloticus*) and common carp (Actinopterygii, Cypriniformes, Cyprinidae, *Cyprinus carpio*) cultures have been reported, notably in South-east Asia (Harache 2002; Balon 2004; Jobling 2010; Nash 2011; **Table 4**). Although some other carp and salmonid species populations were also domesticated during the Middle Ages by monks in European monasteries, domestication processes only noticeably multiplied recently, notably since the 1960s (Jobling 2010). The will to diversify the production, facilitated by scientific and technological advances, has led to multiple domestication trials of new species (Jobling 2010; Teletchea and Fontaine 2014).

Starting the domestication of a new fish species implies to select a candidate which (i) meets an unsatisfied human demand, need, or interest (e.g. Norway tried to diversify its production through halibut [Actinopterygii, Pleuronectiformes, Pleuronectidae, *Hippoglossus sp.*] and Atlantic cod [Actinopterygii, Gadiformes, Gadidae, *Gadus morhua*] production, but both species were out-competed by their wild fisheries; Harvey et al. 2017), and (ii) has a potentially viable production, for instance though a potential occupation of different market segments than currently produced species (e.g. niche markets). Yet, domestication and subsequent production of new species populations are difficult process and can fail because of socio-economic criteria (e.g. over-estimation of future markets, under-estimation of costs, price elasticity) but also because of biological features (e.g. **Table 4**; Liao and Huang 2000; Jobling 2010; Le François et al. 2010; Teletchea and Fontaine 2014; Harvey et al. 2017). It is hard to estimate the failure rate of aquaculture domestication/production attempts, but some insights can be given from species which were previously identified as candidates of interest. For example, Abellán and Basurco (1999) suggested 25 Mediterranean marine fish with high potential for aquaculture but only eight were subsequently farmed (Harvey et al. 2017). In the same way, among the top ten species identified by Lal and Pickering (2012) for inland aquaculture in the Pacific Islands, only two are currently farmed (Harvey et al. 2017).

However, the reasons explaining domestication failures, whether socio-economic or biological, remain often blurry. An additional insight can be seen in the large number of species populations which remain between the first and third levels of domestication due to major bottlenecks preventing the closure of the life cycle or production-related issues (Teletchea and Fontaine 2014).

As mentioned previously, there are some characteristics (biological and socio-economic) which can limit or facilitate domestication and subsequent production. Numerous of these characteristics apply to fish domestication (see examples in **Table 4**). This allowed developing methods to identify fish species of interest for aquaculture production diversification (e.g. Matthews and Samuel 1992; Brummett 1996; Abellán and Basurco 1999; Quéméner et al. 2002; Suquet 2010; Lal and Pickering 2012; Alvarez-Lajonchère and Ibarra-Castro 2013). In the same way, a project aiming at diversifying European production (DIVERSIFY project, https://www.diversifyfish.eu/) identified six promising species based on both biologic and socio-economic criteria. Yet, some candidate species highlighted by these various articles/project present several bottlenecks which are limiting domestication and subsequent production, such as variable growth rates in meager (Actinopterygii, Perciformes, Sciaenidae, *Argyrosomus regius*; Campoverde et al. 2017), low larval survival rates in pikeperch (Actinopterygii, Perciformes, Percidae, *Sander lucioperca*; Colchen et al. 2019), reproduction bottlenecks for the European eel (Actinopterygii, Anguilliformes, Anguillidae, *Anguilla anguilla*; Tomkiewicz et al. 2012), or variable egg quality in halibut (Actinopterygii, Pleuronectiformes, Pleuronectidae, *Hippoglossus hippoglossus*; Mommens et al. 2010).

Methods aiming at identifying candidate species at the interspecific level often do not sufficiently consider geographic differentiation. Yet, geographic differentiation could potentially help to facilitate domestication of new species and potentially overcome bottlenecks linked to domestication (e.g. survival rate) and/or production (e.g. quality product traits) for species at incipient stages of domestication.

Table 4: Examples of characteristics which favor fish domestication and production (Liao and Huang 2000; Diamond 2002; Jobling 2010; Teletchea and Fontaine 2014), associated to examples of wild geographic differentiation for these characteristics.

Favoring characteristics	**Examples of wild geographic differentiation**
Large gregarious groups	Magurran and Seghers (1991); Wark et al. (2011)
Tolerance to conspecifics / Lack of aggressiveness	Huntingford (1982); Herczeg et al. (2009); Pereira et al. (2017)
High food conversion ratio / consumption rate	Present and Conover (1992); Jonassen et al. (2000)
High growth potential	Chavarie et al. (2010); Rypel (2012)
High survival rate	Heibo et al. (2005); Blanck and Lamouroux (2007)
Positive physical appearance (color, shape, flavor)	O'Reilly and Horn (2004); Schultz et al. (2007)
Resistance to stress and diseases	Imsland et al. (2002); Fangue et al. (2006)
Short birth spacing	Blanck and Lamouroux (2007); Gortázar et al. (2007)

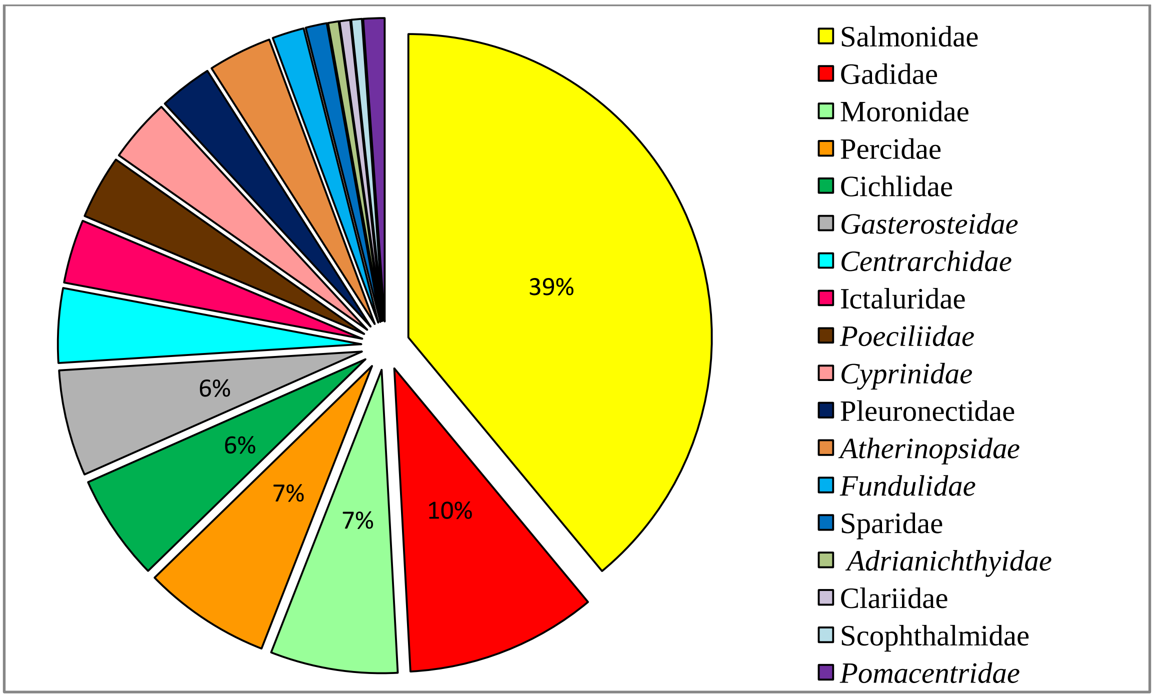
5. Geographic differentiation in aquaculture standardized conditions

Wild fish allopatric populations experience diverse selective pressures and spatio-temporal changes in biotic and/or abiotic parameters. One could expect to see adaptations to local conditions in these populations (Mayr 1963). These local adaptations could have triggered changes in key traits for aquaculture. A geographic differentiation was shown in the wild for a wide range of traits, such as age at sexual maturity or fecundity (Houde 1989; Conover 1992; Fleming 1996; Blanck and Lamouroux 2007), including several domestication/production-favoring characteristics (see examples in **Table 4**). Yet, as mentioned previously, only wild genetically based differences are of interest for aquaculture. Several studies highlighted the loss of inter-populational trait divergences in a common-garden environment due to the fact that environmental factors (i.e. phenotypic plasticity; Pigliucci et al. 2006; Kelly et al. 2012) outweighed any genetic contributions: e.g. for *Cyprinus carpio* (Vandeputte et al. 2002), *Gadus morhua* (Godø and Moksness 1987), or *Perca flavescens* (Actinopterygii, Perciformes, Percidae ; Rosburg 2017). Therefore, the detection of *a priori* favoring phenotypes in the wild remains unreliable without comparison of performances in a standardized environment corresponding to the culture system.

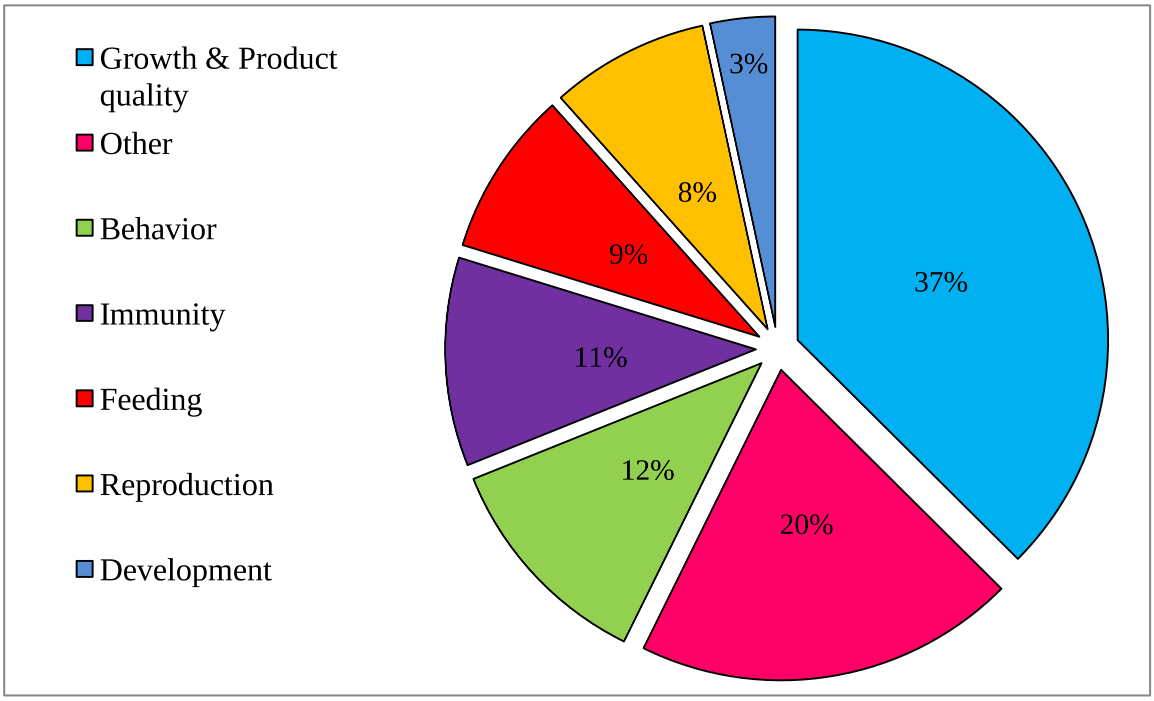
In order to evaluate the knowledge acquired on geographic differentiation in teleost species (i.e. when comparing allopatric populations in a standardized environment), studies investigating geographic differentiation in a common-garden environment were reviewed (on-going review during the course of this work using Google scholar, ScienceDirect, and PubMed). The various terms used at the intraspecific level made this synthesis difficult and several key words were used, such as "geographic origin", "strain", "population", “latitude”, "common-garden", "intraspecific, "population origin", "stock", “race”, “form”, and “variety”. Only studies highlighting inter-populational differences in a common-garden experiment are presented here (n=177; **Annex 1**, **Figure 2**). 60 % of these studies compared populations during the first generations (F0, which corresponds to wild individuals placed in a controlled environment, or F1, descendants of wild individuals), 22 % compared allopatric populations at more advanced stages (F2 [individuals from the second generation] or more), and 18 % compared allopatric populations presenting different domestication stages (F0/F1 compared to more advanced stages). Only studies for which the geographic origin of farmed stocks was certain (i.e. for at least two populations: studies comparing populations at advanced stages with geographic origins uncertain for all populations were excluded) and unique (i.e. studies comparing solely strains originating from a mix of different wild populations were also excluded) were considered. Caution must be paid to studies comparing populations at advanced stages of domestication since geographic origin is not the only differentiation driver (i.e. domestication effect; Rocha De Almeida et al. 2019). However, general trends were the same when analyzing domestication stage groups separately or together. In the same way, studies evaluating species with other interests than food production were included, but general trends remain the same when only considering species useful for human consumption. All traits studied were classified in different biological functions: growth and product quality (e.g. growth rate), development (e.g. deformity rate), reproduction (e.g. age at sexual maturity), immunity (e.g. sensibility to pathogens), feeding (e.g. feed conversion ratio), behavior (e.g. aggressive rate), and other transversal traits not belonging to a particular biological function (e.g. survival rate, resistance to stress).

Figure 2: Families and biological functions/other traits studied in articles included in the geographic differentiation review in controlled conditions (N=177).

a) Families. Only percentages higher than 5% are indicated. In italic are indicated studied families with a majority of species having an interest for environmental studies, angling, and/or aquarium trade, rather than aquaculture production for human consumption.



b) Biological functions/Other traits (transversal traits).



It should be noted that a large part of these studies focused on Salmonidae (Actinopterygii, Salmoniformes; 39 %; **Figure 2a**), followed by Gadidae (Actinopterygii, Gadiformes; 10 %). This could be expected given the major importance of Salmonidae in worldwide aquaculture (FAO 2018) and the consideration of intraspecific variability in the salmon domestication programs (see further). Looking closer at which biological functions were investigated, 39 % of these studies investigated growth and product quality traits (**Figure 2b**; among which 28 % focused exclusively on growth traits and 24 % on growth and other transversal traits [mostly survival rate]). This is not surprising since growth is the premium criterion considered for domestication processes (e.g. Eknath et al. 1993; Rye et al. 2010; Gjedrem 2012). Indeed, domestication processes, including selective breeding programs, often focused, at least in the first steps, on growth characteristics since growth is considered as the most important socio-economic criterion (Eknath et al. 1993; Gjedrem 2005a). However, geographic differentiation was also highlighted for all other biological functions/other traits (**Figure 2b**) and for a diverse range of traits of interest for aquaculture (**Table 5**).

Table 5: Examples of the main traits/parameters investigated in the geographic differentiation studies referenced.

Biological function/Other traits	**Main traits/Parameters investigated**
Growth & product quality	Length, weight, growth heterogeneity, body shape, color, fillet yield, lipid content/fatty acid content, protein content, slaughter weight, liver weight, gutter weight, biomass gain
Development	Cleavage status, swim bladder inflation rate, deformity rate, sex ratio
Behavior	Boldness, shoaling, aggressiveness (sometimes more specifically cannibalism rate), activity, anti-predator behavior, foraging, courtship activeness in males
Immunity	Susceptibility to various diseases/parasites
Feeding	Food intake, feed conversion efficiency, feed conversion ratio, yolk sac utilization, total digestibility, relative nitrogen digestibility, passage time, digestion rate
Other	Survival rate, metabolic rate, ATPase activity, thermal tolerance, tolerance to low ammonia and low oxygen, saltwater/freshwater tolerance stress response and recovery
Reproduction	Gonadosomatic index, fertilization rate, egg diameter/length/weight, hatching rate, fecundity, age/size at sexual maturation, spawning time, spawning rate, ovulation success

6. How can geographic differentiation be useful for fish domestication?

Even though geographic differentiation was shown for a wide range of taxa and for many key traits for domestication and aquaculture production (**Table 5**), it has been overall poorly considered when starting new domestication processes. It is hard to determine why geographic differentiation was poorly exploited when starting to domesticate new candidate species. It could be partly because when a new domestication process starts, the founder stock used often corresponds to the neighboring wild population(s) or the population(s) already used by other fish farms. Moreover, there is poor traceability in aquaculture about geographic origin of founder populations which might lead to an under-estimation of the use of geographic differentiation. A last hypothesis is that geographic differentiation is globally considered later in the domestication process, for selective breeding programs (stage five of the domestication process; Teletchea and Fontaine 2014).

A few success stories show the interest of using geographic differentiation at more advanced stages of domestication (i.e. selective breeding programs). The most striking example is the Atlantic salmon (Actinopterygii, Salmoniformes, Salmonidae, *Salmo salar*) domestication. A family breeding program started in the 1970's in Norway which aimed at improving the Atlantic salmon production. Eggs were sampled from 40 Norwegian rivers and one Swedish and performances were evaluated in several marine farms (Gjedrem et al. 1991; Gjedrem 2010, 2012). Several traits were studied and allowed to highlight a differentiation between allopatric populations for several commercially important traits (**Table 6**), even though the global between-population variation was low (< 10 %) compared to the within-population variability (Gjedrem et al. 1991; Gjøen and Bentsen 1997). This research program led to a fruitful development of the Atlantic salmon industry (Gjøen and Bentsen 1997; Gjedrem 2010, 2012). In the 1990's, a selective breeding program also started for Nile tilapia (*Oreochromis niloticus*). It aimed at evaluating performances of four farmed populations (originating from different geographic locations) and four African wild populations. Differences were highlighted between populations for survival and growth (Eknath et al. 1993). The use of a base population, constituted by broodstock selected from all purebred (i.e. crosses between individuals from the same population) and crossbred (i.e. crosses between several populations) groups, allowed to greatly develop Nile tilapia production leading to a worldwide impact on aquaculture (Gjedrem 2012). Other examples at smaller scales can be found in literature, such as Guinean tilapia (Actinopterygii, Perciformes, Cichlidae, *Coptodon guineensis*) production in Ghana (Agyakwah 2004; Falk et al. 2004) and European seabass

(Actinopterygii, Perciformes, Moronidae, *Dicentrarchus labrax*) production in Israel (Gorshkov et al. 2004). These examples refer to species for which the life cycle was closed and production well established (i.e. advanced stages of domestication, at least for several populations). Yet, the consideration of geographic differentiation could be useful to facilitate domestication of new candidate species. It could also be useful for species at incipient domestication levels which present major bottlenecks impeding domestication (e.g. low fertility, low survival rate), such as species populations remaining in the first levels of domestication according to Teletchea and Fontaine (2014).

Table 6: Examples of studies highlighting trait differentiation between *Salmo salar* allopatric populations. *Remark: These studies did not all perform an evaluation on all 41 populations but rather on a subset of populations.*

Article	Trait(s)
Gjedrem and Aulstad (1974)	Resistance to vibrio disease of salmon parr
Kanis et al. (1976)	Mortality for eggs and fingerlings
Terje et al. (1977)	Percentage of salmon smoltifying at one year old
Refstie and Steine (1978)	Body weight after 190 days
Gunnes and Gjedrem (1978)	Body growth (weight and length) after two years at sea
Gjerde and Refstie (1984)	Egg diameter, body weight, survival, percentage of fish expected to spawn by the following spawning season
Gjerde and Gjedrem (1984)	Ungutted and gutted body weight, body length, dressing percentage, meatiness, flesh color, liver color, and percentage of fish expected to spawn by the following spawning season

The consideration of geographic differentiation could not solely be useful to facilitate domestication of new candidate species in the current diversification context. Indeed, in addition of enhancing diversity within animal production systems to increase resilience to climatic or economic hazards, there are several other challenges to promote sustainable production systems such as (i) improving animal welfare (“state of the individual as it copes with the environment”; Ashley 2007; Browman et al. 2019; Saraiva et al. 2019), (ii) developing alternative aquaculture systems (e.g. integrated multi-trophic aquaculture [“cultivation of aquaculture species with other extractive aquaculture”]; Dumont et al. 2013, 2014; Thomas et al. 2014), (iii) producing robust animals (i.e. animals able to “survive, reproduce, and maintain production in a wide variety of environmental conditions”; Knap 2005; Dumont et al. 2014), and (iv) decreasing the reliance on fish meal and fish oil in aquafeeds as these ingredients come from capture fisheries through the development of a plant-based diet aquaculture (Naylor et al. 2009; Rey-Valette 2014). All these challenges aiming at developing a more sustainable aquaculture imply that new domestication programs might need to be developed. This is true for new candidate species but also for currently produced species. Indeed, current farmed stocks might not be adequate for new purposes such as developing production in new aquaculture systems or finding phenotypes which are interesting for polyculture or plant-based diet. In addition, given the diversity of environments and aquaculture systems, it is highly plausible that one biological unit will not be suitable for all purposes. The best population for a particular aquaculture system might not be the best for another system. Therefore, the consideration of geographic differentiation could be helpful to (i) facilitate domestication of new candidate species or species at the beginning of the domestication process which face major bottlenecks/production issues and (ii) answer to current and future challenges.

7. How to integrate geographic differentiation in fish domestication and production processes

The success-story examples highlight the potential usefulness of considering geographic differentiation in aquaculture domestication processes. However, there is no standardized methodology available to consider geographic differentiation when starting domestication and production of new fish species. Indeed, looking back at the Atlantic salmon success-story, the sampling design focused on a small part of the native distribution range (which might explain the low between-population variance). Applying such a strategy could lead to miss out the potential contained in non-sampled populations. Yet, once again, it is not feasible to consider all populations across the distribution range. This underlines the importance of developing a pragmatic and standardized approach to domesticate new candidates while considering geographic differentiation.

In addition, as mentioned previously, domestication trials, as well as selective breeding programs, often focus in the first steps on growth rate. Yet, a successful domestication and production requires the favorable expression of traits involved in several biological functions: a population can be domesticated if it can reproduce (reproductive and behavior functions), grow (growth, behavior, and development functions), feed (nutrition and behavior functions), and overcome stresses (e.g. resistance to diseases, immune, and behavior functions). Therefore, a multi-function and multi-trait approach is required to evaluate the aquaculture potential at the intraspecific level. A careful assessment needs to be led regarding which traits should be considered in the aquaculture potential assessment.

Considering that domestication of fish species is quite recent and the will to diversify production, there is an opportunity to standardize new domestication processes. This work hereby promotes that the potential contained in the wild should be assessed to facilitate domestication and subsequent production of new species. The domestication process could begin using the wild intraspecific unit(s) presenting the highest aquaculture potential in standardized conditions. Assuming that key traits are at least partially genetically coded, this would allow starting new domestication processes with the best biological unit(s) available in the wild and increase chances of domestication success.

Take-home message

Aquaculture is the fastest-growing food production sector in the world and domestication of aquatic species is quite recent. Nowadays, there is a will to diversify the production, notably through new species domestication. However, domestication and subsequent production of a new population is difficult and can fail. New species domestication trials could be facilitated by considering geographic differentiation. Even though geographic differentiation has been poorly considered at the beginning of the domestication process, a few success stories at more advanced domestication stages highlight its usefulness. Moreover, a geographic differentiation has been shown in literature for a wide range of species and for diverse key traits in standardized conditions (i.e. domestication system). Assuming differentiation in performances are, at least partly, genetically coded, it could allow beginning new domestication trials with the best unit available in the wild. However, a methodology to consider geographic differentiation in new domestication processes needs to be developed.

OBJECTIVES

AND

HYPOTHESES

OBJECTIVES AND HYPOTHESES

The major aims of this PhD work were:

A1- Demonstrating the usefulness of geographic differentiation for domestication of a targeted species.

A2- Conceptualizing and applying a standardized and pragmatic method aiming at integrating geographic differentiation in domestication processes.

We implemented this method on a species used as a test-case: the European perch (Actinopterygii, Perciforms, Percidae, *Perca fluviatilis*). We hypothesized that:

H1: There is a geographic differentiation in *Perca fluviatilis* for key traits.

H2: There are units with high potential for aquaculture within species.

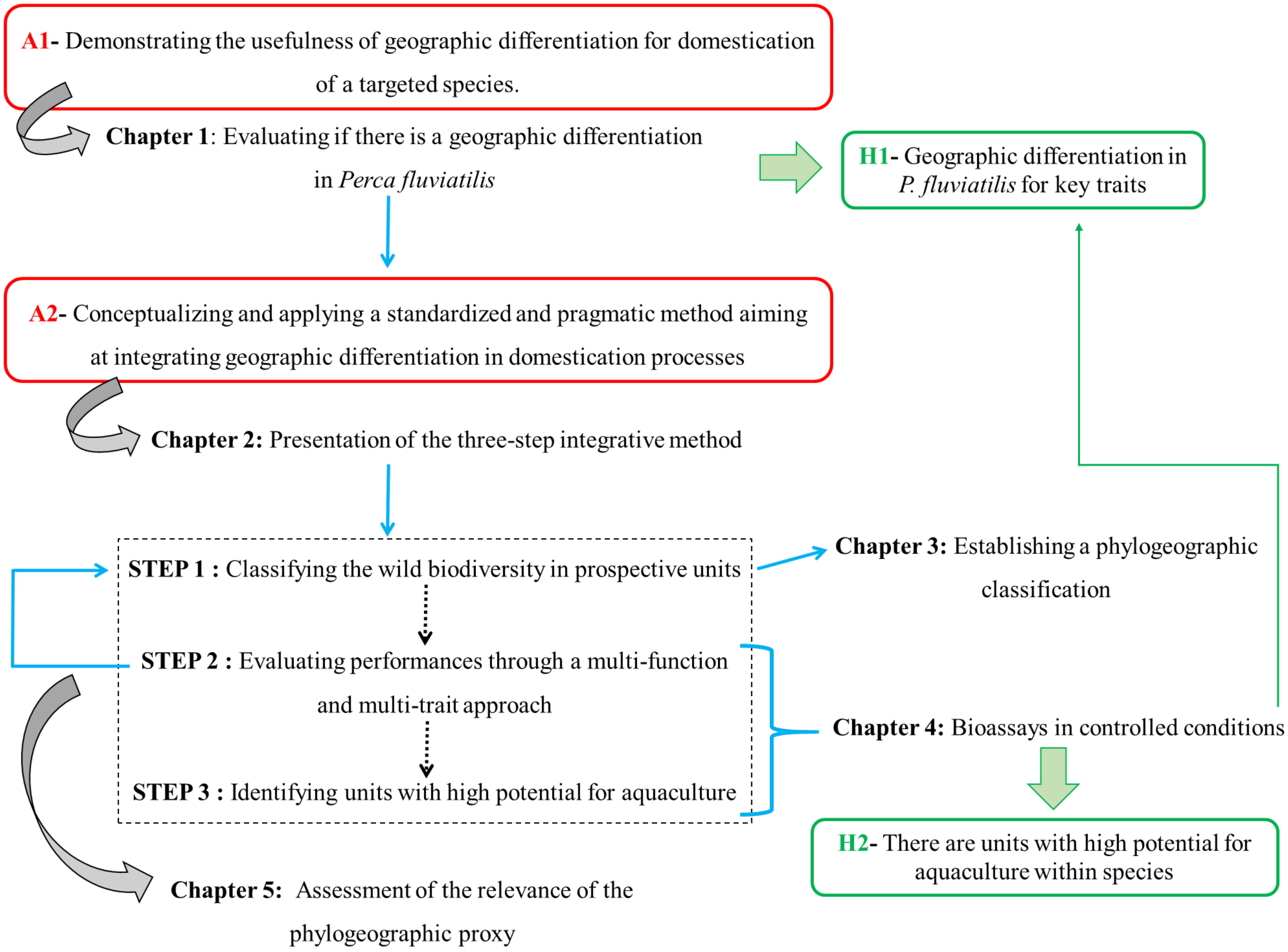
In order to answer to the first **aim A1**, the **chapter 1** is focused on demonstrating that *Perca fluviatilis* geographic differentiation can be useful for domestication and subsequent production (validation of **H1**).

The **chapter 2** aimed at conceptualizing a method to integrate geographic differentiation in domestication processes in order to facilitate new species domestication and production (**aim A2**). This method consists of three steps: (i) classifying wild populations into prospective units (i.e. groups of differentiated conspecific and allopatric populations) which are likely divergent for key traits in aquaculture, (ii) evaluating the performance of the different prospective units in culture conditions, and (iii) identifying the prospective unit with the highest potential for aquaculture. The next two chapters aimed at applying the method on *Perca fluviatilis* first life-stages.

The first step is illustrated in **chapter 3**. This chapter aims at classifying wild populations in prospective units in order to restrict the number of populations to study in the step 2 (**aim A2**). As mentioned earlier, it is not feasible and pragmatic to compare all populations across a species distribution range. One way to limit the range of possibilities relies on the use of a classification method which would assemble populations that are likely undifferentiated and highlight population groups which are likely differentiated in key traits. One could expect that the use of already available classifications (e.g. subspecies, management units, evolutionarily significant units; Frankham et al. 2004; Haig et al. 2006) could be a solution but these classifications (i) were not available for European perch and (ii) have been criticized because the choice of definition criteria is debated (Ryman et al. 1995; Fraser and Bernatchez 2001; Phillimore and Owens 2006; Braby et al. 2012). Therefore, a classification needed to be established for *P. fluviatilis.* We needed to select a proxy which could (i) highlight prospective units which likely display different abilities to be domesticated and fruitfully produced and (ii) be easily assessed at large scale. As a first approach, we chose to perform a phylogeographic classification. Indeed, population groups having different/independent demographic histories and/or potential local adaptations are likely to present divergences in key traits. Therefore, we used genetic differentiation in neutral markers (i.e. theoretically not submitted to selection and not influencing fitness) as a proxy to highlight population groups with potential divergences in key traits (as previously suggested in Pouyaud and François 1995).

Once intraspecific classification is established, the different PUs must be evaluated in the same environment (i.e. common garden experiment) with rearing conditions being as close as possible to the domestication system used for production. The **chapter 4** illustrates the second and third steps of the integrative approach (**aim A2**). This chapter is aimed at (i) evaluating differentiation in performances of populations representative of the different prospective units in standardized conditions (**aim A1**, validation of **H1)**, (ii) demonstrating the usefulness of the multi-function and multi-trait approach since growth is not the only important trait for production, and (iii) elaborating an aquaculture potential index to take into account the variable importance levels of traits studied according to the opinion of stakeholders. This index allows making a consensus between all trait results to facilitate the identification of units with high potential for aquaculture (verification of **H2**).

Finally, the relevance of the genetic classification assessed in the third chapter can be questioned. In **chapter 5**, we assessed the relevance of three alternative proxies (i.e. genetic, habitat, and hydrologic/geographic proxies) to highlight inter-populational divergences in key traits for larviculture in *P. fluviatilis*. This chapter corresponds to a retro-evaluation of the relevance of the proxy used in the third chapter.



A1- Demonstrating the usefulness of geographic differentiation for domestication of a targeted species.

Chapter 1: Evaluating if there is a geographic differentiation in *Perca fluviatilis*

H1- Geographic differentiation in *P. fluviatilis* for key traits

A2- Conceptualizing and applying a standardized and pragmatic method aiming at integrating geographic differentiation in domestication processes

Chapter 2: Presentation of the three-step integrative method

STEP 1 : Classifying the wild biodiversity in prospective units

STEP 2 : Evaluating performances through a multi-function and multi-trait approach

STEP 3 : Identifying units with high potential for aquaculture

Chapter 3: Establishing a phylogeographic classification

Chapter 4: Bioassays in controlled conditions

H2- There are units with high potential for aquaculture within species

Chapter 5: Assessment of the relevance of the phylogeographic proxy

SPECIES USED
AS A TEST CASE

SPECIES USED AS A TEST CASE

1. *Classification*

Perca fluviatilis belongs to the Actinopterygii class, Perciformes order, and Percidae family. This family is thought to have diverged 66-65 million years ago and contains 11 genera and between 266 and 275 species (Stepien and Haponski 2015). The genus *Perca* appeared about 19,8 million years ago during Miocene and comprises three monophyletic and morphologically similar species: two species native to Eurasia, the European perch (*P. fluviatilis* Linnaeus 1758*)* and the Balkhash perch (*P. schrenkii* Kessler 1874), and one species in North America, the yellow perch (*P. flavescens* Mitchill 1814) (Couture and Pyle 2015; Stepien and Haponski 2015).

2. *European perch distribution*

The European perch (**Figure 3**) is a temperate species which is widespread across Eurasia (**Figure 4**) due its strong tolerance to temperature and salinity variations (Kottelat et al. 2007). It can be found from the United Kingdom to Siberia in a diverse range of habitats such as rivers, lakes, estuaries, or ponds, from eutrophic to oligotrophic waters (Collette et al. 1977; Stepien and Haponski 2015). This species was also introduced across Eurasia, for instance in Italy, Spain, and, Ireland, but also in other continents such as Australia and Africa (Kottelat et al. 2007; Kestemont et al. 2015a).

Figure 3: European perch (*Perca fluviatilis*). Credit: A) Yannick Ledoré, B) Sascha Antipine, C) Roland Roesch

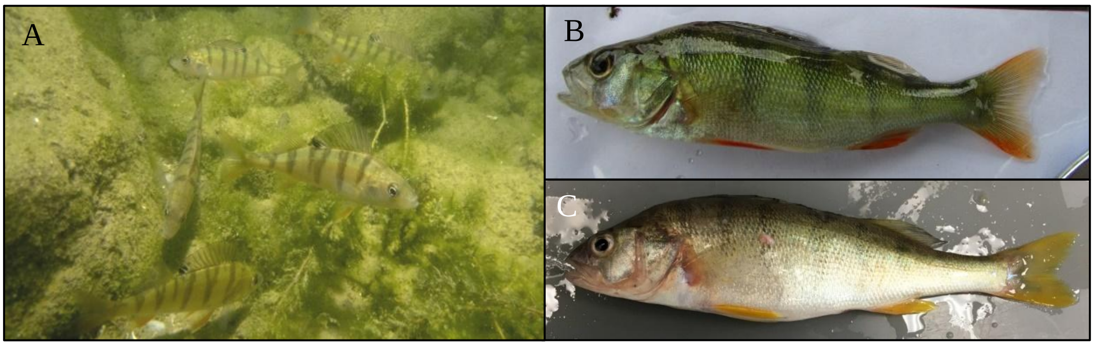
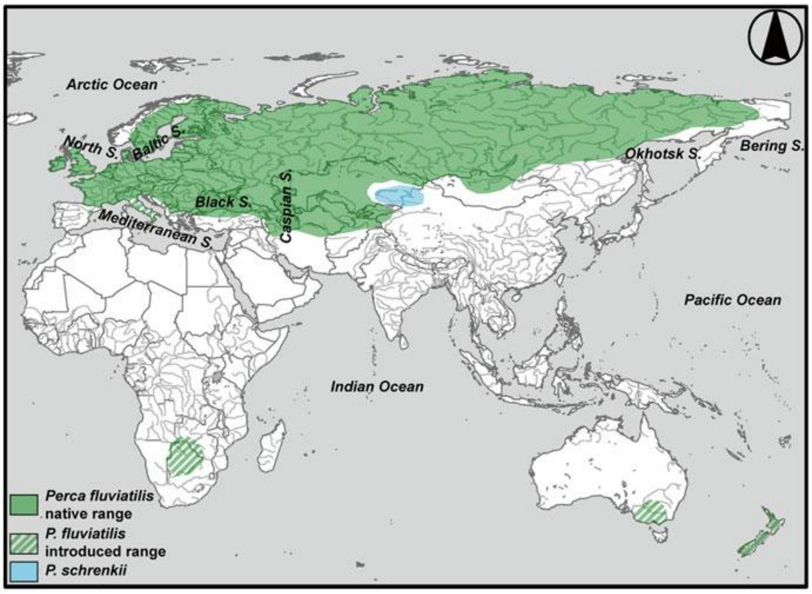


Figure 4: Native distribution range (in green) and introduction zones (in dashed green) of the European perch (*Perca fluviatilis*). From Stepien and Haponski (2015).



3. *Biology of wild European perch*

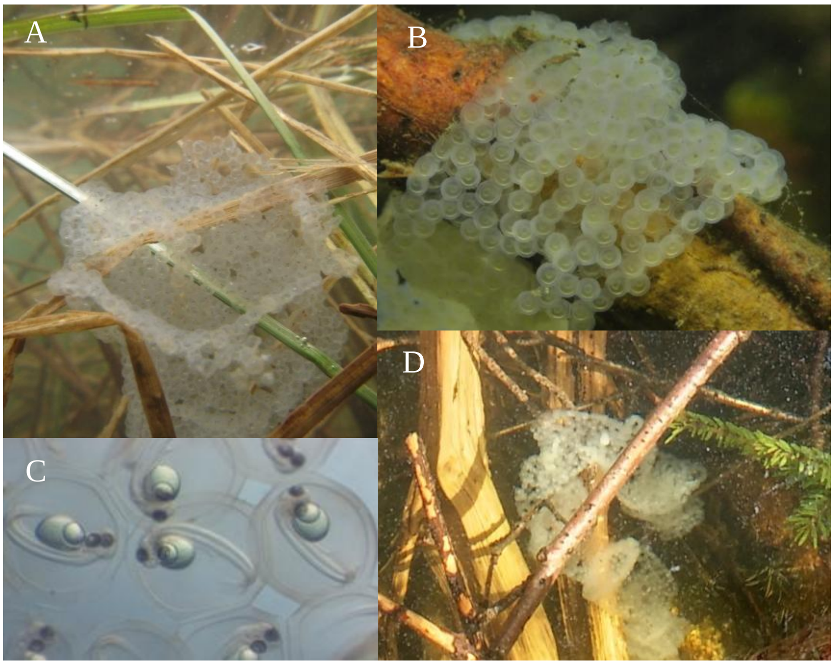
European perch feeding regime varies through ontogeny depending on size and foraging habitat: from zooplanktivory when larvae occupy the water column in the pelagic zone, to benthivory (mostly macroinvertebrates) in the littoral zone and later piscivory in both pelagic and littoral zones (Feiner and Höök 2015; Magnhagen 2015). Individuals are overall opportunistic (Feiner and Höök 2015). European perch is considered as a social fish, but inter-individual interactions also depend on ontogeny (among other related factors such as predation pressure; Vainikka et al. 2005; Magnhagen 2015). Indeed, in general, larvae are found in large shoals, the number of individuals in the shoal tends to decrease with size, and some adults can even be solitary (Magnhagen 2015).

The European perch is an early spring spawner without parental care (Teletchea et al. 2009). A homing behavior was described (Järv 2000) even though the dispersion distance of European perch remains under investigation. Sexual maturation for reproduction requires low temperatures and is overall more precocious in males (late 1st year-2nd year) than females (late 2nd year to 4th year; Kottelat et al. 2007; Abdulfatah et al. 2011). When females are mature, the spawning is triggered by a set of endogenous and exogenous mechanisms, notably through temperature and photoperiod changes (Abdulfatah 2010; Feiner and Höök 2015). The spawning occurs once a year, between February and June given the strong latitudinal variation (Kottelat et al. 2007; **Table 7**), with southern populations spawning generally earlier than northern populations (Feiner and Höök 2015). Eggs are grouped in clusters -commonly named egg ribbons- which are found lying over submerged substrates (**Figure 5**). Each mature female spawns all its eggs in a single egg ribbon and eggs are fertilized externally by one or, more frequently, several males (Bruslé and Quignard 2001; Kottelat et al. 2007; Couture and Pyle 2015). A relationship was suggested between the ribbon size and the female size (Craig 1974; Dubois et al. 1996; Schaerlinger and Żarski 2015), but this is not verified everywhere (Dalimier et al. 1982).

Table 7: Examples of variation of the spawning period and temperature at spawning between allopatric populations of European perch. Adapted from Fontaine et al. (2015). *NR: Not Reported*.

Location	Spawning period	Temperature at spawning (°C)	Source
Mirgenbach reservoir, France	Late February / Mid-April	12-14	Flesch (1994)
Lake Agios Vasilios, Greece	Mid-March / Early April	8	Papageorgiou (1977)
Slapton Ley, England	Mid-March / Early May	8-14	Craig (1974)
Lindre pond, France	Mid-April	14-15	Sulistyo et al. (2000)
Reservoir Ivan'kovo, Russia	April / May	7-15	Makarova (1973)
Lake Varese, Italy	April / May	14	Ceccuzzi et al. (2011)
Forsmark and Oskarshamn basins, Sweden	Early April / Late June	7-24	Sandström et al. (1997)
Stour river, England	Late April / Early May	NR	Mann (1978)
Lakes Kord and Davan, Scotland	Late April / Mid-May	9-11	Treasurer (1983)
Lake Zürich, Switzerland	Late April / Mid-May	8-15	Zeh et al. (1989)
Trent and Warwickshire Avon rivers, England	Late April / Mid-May	NR	Nunn et al. (2007)
Lake Geneva France	Late April / Early June	8-16	Gillet and Dubois (2007)
La Gombe, Belgium	Late April / Mid-June	8.5-13.5	Dalimier et al. (1982)
Lake Leven, Scotland	Late April / Mid-June	9-11.5	Jones (1982)
Mozhaisky and Uchinsky reservoirs, Russia	May	5-10	Spanovskaya and Grygorash (1977)
Lakes Pieni Lehmälampi, Iso Valkjärvi, Vähä Valkjärvi, Tammelan Kaitajärvi, Valkea Mustajärvi, Finland	Early May / Early June	6 - 11	Rask et al. (1990)
Lakes Molnbyggen and Djursjön, Sweden	Mid-May	10-13	Noaksson et al. (2004)
Lake Windermere, England	Mid-May / Mid-June	9-18	Guma'a (1978)
Lake Saarlampi, Finland	Mid-May / Late May	12-14	Urho (1996)

Figure 5: European perch egg ribbons. Credit: A) and B) Yannick Ledoré; C) Daniel Zarski; D) Lola Toomey



4. *European perch domestication and production*

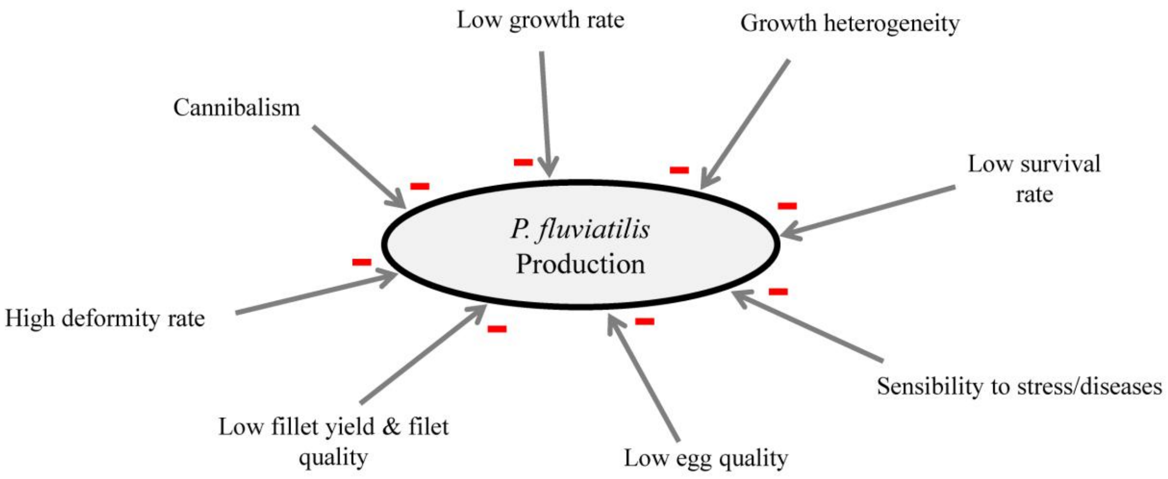
4.1 Interest for continental aquaculture diversification

Diversification is particularly important in Europe in order to decrease the dependency of the European market from seafood imports (Direction générale de l’énergie et du climat 2014; FAO 2018). Production diversification could be facilitated by the consideration of some microterritories which display a strong link between the territory history/traditions, a specific landscape (e.g. pond, lake), and human populations (Fontaine 2004; Fontaine and Teletchea 2019). Indeed, cultural traditions can be seen, associated with a consumption of specific products (e.g. smoked eel in the Netherlands, fried cyprinids in Luxembourg), which allows to foresee production development in these specific regions. European perch is one of these niche products presenting a demand in Alpine areas (Switzerland, Italy, and France), Benelux, and Scandinavia. The European perch presents a strong socio-economic interest for fisheries, recreational fishing, and aquaculture (Stepien and Haponski 2015; Policar et al. 2019).

4.2 Domestication and bottlenecks

The European perch domestication process started in the 1990s and has been suggested as one of the most interesting species for European inland aquaculture development while considering other economic sectors already running (i.e. no competition involved). Given the variability of quality of individuals from fisheries and the will to have products available all year round, perch aquaculture production was promoted as the path to follow (Fontaine 2004; Watson 2008). After production trials in ponds, cages, and RAS, the latter was highlighted as the best production system for this species, for instance due to nanism issues in ponds and sensibility to water quality variations and diseases (Fontaine and Teletchea 2019 and references therein). Most of the production nowadays is performed in RAS even though other culture systems are explored such as mesocosm methods to produce juveniles (e.g. perch production in Ireland; Kestemont et al. 2015b; Policar et al. 2019). To date, between 500 and 1 000 tons of perch are produced per year in RAS (Fontaine and Teletchea 2019), including 100 tons in France, and production remains inferior to the demand. Regarding the consumption market, this fish is consumed at different sizes and in various forms (e.g. wholefish, fillet; Fontaine 2004). However, despite all the research efforts to improve perch production (e.g. reproduction [Abdulfatah 2010; Castets 2011], larval rearing [Mélard et al. 1996; Kestemont et al. 2003], feeding and growth [Fiogbé et al. 1996; Fontaine et al. 1997; Fiogbé and Kestemont 2003]), there are still many bottlenecks limiting its production and up-scaling (**Figure 6**; Fontaine 2004; Kestemont et al. 2015a; Fontaine and Teletchea 2019; Policar et al. 2019). Therefore, there is a need to improve the domestication and production of this species.

Figure 6: Major bottlenecks limiting *Perca fluviatilis* production.



4.3 The European perch production cycle

There are several stages in *P. fluviatilis* production:

- Reproductive phase: During the breeding period, the reproductive cycle is divided in three steps: primary growth (from the beginning of gametogenesis up to the cortical alveoli stage), secondary growth (early and late vitellogenesis), and final oocyte maturation. Egg ribbons are then stripped manually, and external fertilization is performed by collecting sperm from males (Fontaine et al. 2015; Żarski et al. 2017).

- Hatchery-Nursery: The embryonic period lasts between fertilization and first oral feeding. It can be sub-divided in several periods (i.e. cell cleavage, gastrulation, organogenesis; see details in the development table developed by Alix et al. 2015) which involve visual, musculoskeletal, nervous, digestive, and circulation systems. After hatching, the embryo obtains resources from its vitellin bag (i.e. endogenous feeding) which resorbs. The first oral feeding (i.e. consumption of live prey such as *Artemia sp.* [Branchiopoda, Anostraca, Artemiidae]) corresponds to the embryonic-to-larval transition (Alix et al. 2015). The larval period starts with exogenous feeding. During that period, larvae inflate their swim bladder by going to the surface and gulping air, cannibalism behavior onsets from 11 days post-hatching, and individuals switch from live prey feeding to inert diet during the weaning period (Baras 2013; Kestemont et al. 2015b; Kupren et al. 2019). The transition between larvae and juveniles is not clear, usually juveniles are considered as such once they attain the same morphology as adults (i.e. end of metamorphosis; Urho 2002; Schaerlinger and Żarski 2015; Kupren et al. 2019).

- On-growing phase: All anatomic structures are developed. This phase consists of growing fish until market size. The difference between a juvenile and an adult usually just relies on the ability to start a reproductive cycle (i.e. sexual maturity). At the end of this phase, individuals are harvested for the market or kept as broodstock.

In this PhD work, it was not possible to work on the whole life cycle since it takes about 2.5 years to perform a full cycle (egg to egg). Therefore, the focus was set on fist life stages, more particularly larval stages from one to 60 days post-hatching, since: (i) the experimental length was appropriate for the PhD project, (ii) many bottlenecks are tied to this life stage (e.g. mortalities due to cannibalism, high deformity rate, low survival rate), and (iii) it is easier to collect and acclimatize wild egg ribbons than to catch and transport juveniles or adults to the culture system.

5. *Perca fluviatilis* and the three-step integrative approach

5.1 Geographic differentiation

A geographic differentiation in European perch was already highlighted in the wild between allopatric populations, for instance regarding color (Pimakhin 2012), growth rate, size at maturity (Rask 1983; Heibo and Vøllestad 2002; Heibo et al. 2005; Heibo and Magnhagen 2005), filet quality (Mairesse et al. 2006), activity patterns (Jacobsen et al. 2015), and boldness (Magnhagen 2006; Magnhagen and Borcherding 2008; Hellström and Magnhagen 2011). Geographic differentiation has also been highlighted for several key traits in aquaculture conditions, including traits which were shown as limiting/facilitating factors for domestication and subsequent production (**Table 8**). However, these studies were performed on a limited number of traits, mostly related to growth and survival. Therefore, geographic differentiation in aquaculture conditions remains to be assessed for traits linked to other biological functions.

Table 8: Studies highlighting *Perca fluviatilis* geographic differentiation in aquaculture conditions. *Remark: Only traits for which a geographic differentiation was shown are reported here.* Rivers, lakes, brackish waters, and ponds are indicated by R, L, B, and P, respectively.

Study	Populations studied	Life stage	Traits investigated
Mandiki et al. (2004)	Four populations from Italy (L), northwest France (P), southeast France (P), Belgium (R)	Larvae	Survival, body weight, specific growth rate
	Three populations from Belgium (R), Finland (B), Poland (L)	Small juveniles	Survival, cannibalism rate, body weight, specific growth rate, feed efficiency
	Three populations from Belgium (R), Finland (B), Poland (L)	Large juveniles	Body weight, specific growth rate, feed efficiency, feed consumption
Pimakhin and Zak (2014)	21 populations from Poland (R and L), Czech Republic (R), Germany (L), Bulgaria (L), Finland (L), Slovakia (L)	Larvae & juveniles (14 to 56 days post-hatching)	Swim bladder inflation, weight
Vanina et al. (2019a)	Three populations from Czech Republic (P), Slovakia (R), and Poland (L)	Larvae & juveniles (31-115 days post-hatching)	Body weight, specific growth rate, mortality rate, growth heterogeneity
Vanina et al. (2019b)	Seven populations: Finland (L), Poland (L and B), Czech Republic (P), Slovakia (L and R)	Larvae (three to 24 days post-hatching)	Survival rate of embryos, egg diameter, body weight, total length, specific growth rate

5.2 What did we know about European perch phylogeography?

Box 4: The usefulness of phylogeography

The current distribution of species is the result of past and current events (Taberlet 1998; Avise 2000, 2009; Hewitt 2004a,b). Therefore, the current geographic differentiation patterns must be studied considering historical forces (e.g. bottlenecks, migrations, vicariance). Phylogeography consists of studying the distribution of lineages through genetic inter-individual variations and has been particularly investigated for European species (Avise et al. 1987; Avise 2000; Hewitt 2004b). It relies on the use of neutral genes since they are not submitted to selection and depend on the demographic history of the population they belong to (*Note: excluding random phenomena such as genetic drift and mutation*). It is useful to study the recent history of populations, particularly since the last glaciations. Indeed, climatic shifts during the Quaternary led to cycles of contraction and expansion of species ranges which shaped the current genetic diversity and differentiation patterns (Andersen and Borns 1994; Hewitt 2000, 2004a). During glaciations, some populations survived in more favorable areas called refugia, in which genetic differentiations accumulated across time. When ice retreated, they could recolonize empty niches, often implicating a loss of genetic diversity because of multiple founder events (Hewitt 1996, 1999; Stewart et al. 2010). Once established in a territory, new migrants might have had to compete with local populations, which likely favored the persistence of genetic specificities inherited from post-glacial recolonizations (Hewitt 1999). The existence of several refugia often promoted the emergence of genetically differentiated lineages (Avise 2000; Hewitt 2004b). On the contrary, populations originating from recent divergence events are characterized by a lesser important differentiation degree in neutral markers.

Overall, the phylogeographic approach allows highlighting genetically differentiated groups of populations which present different demographic histories. These groups are likely to present divergences in key traits due to local adaptation or random processes (e.g. genetic drift).

Box 5: How to perform a phylogeographic study? (1/2)

Several steps are needed to perform a phylogeographic study:

(A) Sampling across the distribution range in order to consider the different lineages potentially originating from different refugia. The sampling size relies on a compromise between the extent of distribution, the markers' polymorphism degree, and the budget.

(B) Choice of genetic markers: Mitochondrial markers are usually used in phylogeographic studies due to (Avise 2000; Zhang and Hewitt 2003; Makhrov and Bolotov 2006; Costedoat and Gilles 2009; Bowen et al. 2014) : (i) their high mutation rate and their lower effective population size (one-quarter that of nuclear genes) which maximize chances to detect differentiation without an extensive sampling effort, (ii) their low rate of recombination (i.e. genetic material exchange between different organisms) which leads to the assumption that all sites have the same genealogical history, (iii) their high prevalence in cells which makes them easier to amplify, and (iv) their haplotypic status which facilitates their sequencing (but see rare cases of heteroplasmy [i.e. presence of more than one type of organellar genome within a cell/individual], including for *Perca fluviatilis;* Nesbø et al. 1998a). In this work, we chose to use four mitochondrial markers which are widely used in freshwater teleost studies: cytochrome b (e.g. Houdt et al. 2003; Culling et al. 2005), D-loop (e.g. Weiss et al. 2002), 16S rRNA (e.g. Costedoat et al. 2006), and cytochrome oxidase I (e.g. Nwani et al. 2011). However, mitochondrial markers present some disadvantages because (i) they are maternally inherited and therefore biased to female-mediated processes (e.g. not reflecting potential differential dispersions between males and females; Prugnolle & De Meeus, 2002; Toews & Brelsford, 2012) and (ii) nuclear introgressions can trigger technical issues (Bruford et al. 2003; Ballard and Rand 2005; Larson and Burger 2013). Because of these limitations, the use of mitochondrial markers should be coupled with nuclear markers (Nichols 2001; Ballard and Whitlock 2004; Costedoat and Gilles 2009). However, the study of nuclear markers is more complicated given their low mutation rate and because it requires cloning before sequencing to separate alleles from heterozygous individuals. Yet, the use of microsatellite markers (i.e. repetitive nucleotidic motifs of one to six base pairs) provides an interesting alternative coupled with mitochondrial markers (Beheregaray 2008). Microsatellites have been widely used in teleost genetic studies (Makhrov and Bolotov 2006). They are supposedly neutral, biparentally inherited, highly polymorph, spread across the genome, and very useful to characterize genetic diversity (Zhang and Hewitt 2003; Arif and Khan 2009).

Box 5: How to perform a phylogeographic study ? (2/2)

However, microsatellites also present some disadvantages such as homoplasy (i.e. similarities in fragment length which are not inherited from a common ancestor but linked to changes in adjacent areas such as flanking regions), high development costs, or mutation rate which varies considerably between organisms (Zhang and Hewitt 2003; Miah et al. 2013; Abdurakhmonov 2016). The combination of these two markers could therefore help to elucidate more accurately the phylogeographic structure.

(C) Acquisition of data: Obtaining sequences (or scores for microsatellites) requires DNA extraction, amplification of sequences through polymerase reaction chain with chosen primers, and Sanger sequencing (or genotyping in the case of microsatellites).

(D) Data analysis:

- Polymorphism: The analysis of polymorphism relies on the calculation of haplotypic or allelic diversity (i.e. variant forms of a gene).
- Phylogeographic structure: When there is a polymorphism, it is possible to evaluate the distribution of genetic variance between populations through an Analysis of MOlecular VAriance (AMOVA), which gives the percentage of variance existing between population groups, within population groups, and within populations (Excoffier et al. 1992). The AMOVA takes into account haplotype sequences and nucleotidic distances between haplotypes. It allows to calculate a F_{ST} value (which varies between 0 [no genetic differentiation] and 1 [no gene flow, strong genetic structure]) and a non-parametric permutation test allows to calculate the significativity (p-value) associated to each structure level. However, this analysis requires defining groups according to a chosen *a priori*. The Spatial Analysis of MOlecular Variance (SAMOVA) is based on the AMOVA but allows to define groups of populations which are geographically homogenous and genetically differentiated (Dupanloup et al. 2002). This procedure maximizes genetic differentiation between groups and minimizes differentiation within groups. Regarding microsatellite analyses, several approaches can be used but the most common method is the Bayesian clustering method implemented in STRUCTURE (Pritchard et al. 2000). It is aimed at identifying population clusters respecting Hardy-Weinberg and linkage equilibriums. Further methods (e.g. ΔK method; Evanno et al. 2005) allow to identify the optimal number of clusters. The STRUCTURE method estimates allelic frequencies in each cluster and cluster memberships of each population/individual.

The phylogeography of *P. fluviatilis* was previously investigated in Nesbø et al. (1999). In this study, 55 European populations and one Siberian were studied using the mitochondrial D-loop and 35 populations were studied using three Random Amplification of Polymorphic DNA (RAPD). This work allowed highlighting four main groups (**Figure 7**): a southern European group (including Greek and southern Danubian populations), a western European group, an eastern European group which includes the Siberian populations, and a Norwegian group (which includes populations from northern Norway and western side of Oslofjord). However, further investigations are required since (i) the former phylogeographic study was based on a small part of the mitochondrial genome, (ii) RAPD markers have been since shown as limited and replaced by more powerful markers such as microsatellites (Sunnucks 2000; Arif and Khan 2009), and (iii) other studies were performed but investigated specific geographic areas (**Table 9**) and some discrepancies exists in conclusions between studies. Therefore, due to limitations and discrepancies between conclusions, the phylogeographic structure of European perch needed to be further studied.

Figure 7: Mitochondrial D-loop haplotype distribution of *Perca fluviatilis* in Europe. The colors of the diagrams correspond to the first clade level identified in Nesbø et al. (1999). Numbers correspond to populations studied (the Siberian population is not represented here). The white regions correspond to the areas which were glaciated during the last glaciations. From Nesbø et al. (1999).

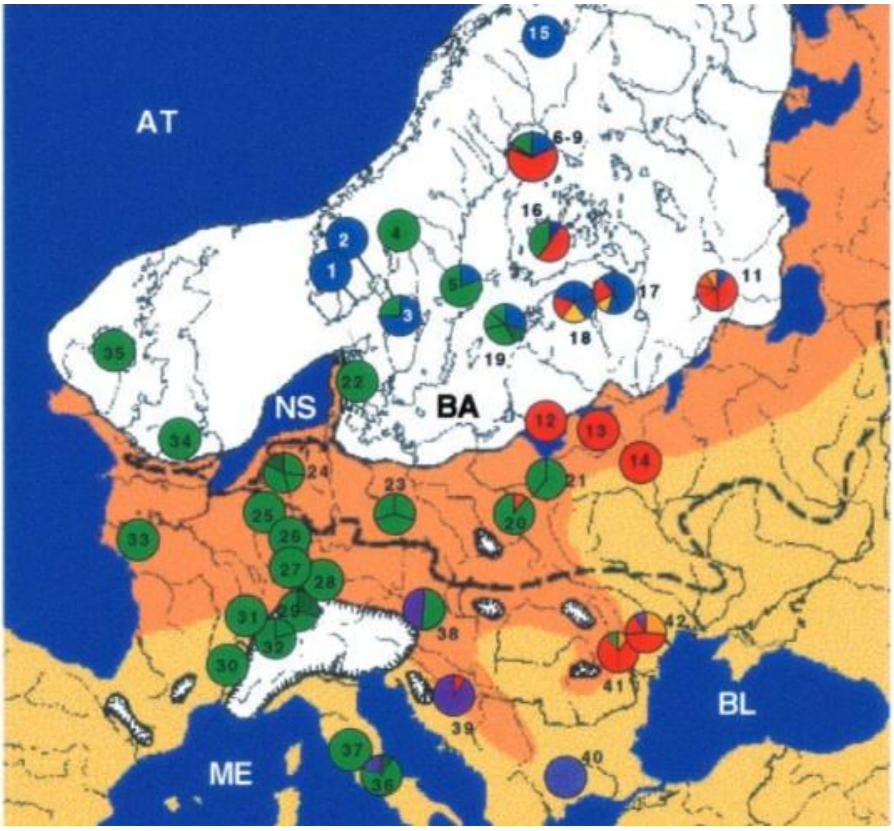


Table 9: Previous studies having investigated *Perca fluviatilis* genetic differentiation

Article	Sampling site(s)	Genetic structure?	Marker(s)
Gerlach et al. (2001)	Lake Constance (Germany)	Two populations differentiated	Microsatellites
Heldstab and Katoh (1995)		Differentiated from lakes Zürich, Geneva, and Maggiore	Allozymes *
Behrmann-Godel et al. (2004)		No differentiation within Lake Constance or with the Rhine river. Differentiation between Lake Constance and Rhine river with lakes Walensee and Zürich	Mitochondrial D-loop
Behrmann-Godel et al. (2006)		Differentiation between kin shoals	Microsatellites
Ben Khadher et al. (2015)	Lake Geneva (Switzerland)	No differentiation	Microsatellites
Ben Khadher et al. (2019)	Lakes Geneva (Switzerland) & Neufchâtel (France)	Differentiation between the two lakes	Microsatellites
Gyllensten et al. (1985)	Five brackish water areas and eight freshwater areas (Ireland, Scotland, Sweden, Finland)	No differentiation	Allozymes
Bergek and Björklund (2009)	Baltic Sea (Sweden)	Strong differentiation	Microsatellites
Olsson et al. (2011)		Differentiation between central Baltic and Bothnia gulf	Microsatellites
Bergek et al. (2010)		Differentiation along an environmental gradient	Microsatellites
Demandt (2010)	Biotest basin (Sweden)	Differentiation	Microsatellites
Bergek and Björklund (2007); Bergek and Olsson (2009)	Lake Erken (Sweden)	Differentiation	Microsatellites
Faulks et al. (2015)	Lakes Bysjön, Dagarn, Fiolen, Stora Envättern, & Stensjön (Sweden)	Within each lake, differentiation between pelagic and littoral populations	AFLP **
Nesbø et al. (1998a)	Lake Anjersjön, Bothnia Gulf, Rovagen peninsula, Ängeran river (Sweden)	Differentiation	Mitochondrial D-loop and AFLP
Refseth et al. (1998)	Baltic sea & Scandinavian peninsula (Norway, Sweden)	Differentiation	Mitochondrial and minisatellites ***
Sruoga et al. (2008)	Baltic sea & Curonian Lagoon (Lithuania)	No differentiation	Microsatellites
Butkauskas et al. (2012)	Lakes Drūkšiai, Plateliai, Metelys, & Nemunas and Neris rivers (Lithuania)	Lake Drūkšiai differentiated from other populations	Mitochondrial D-loop
Ragauskas et al. (2020)	19 Baltic sea populations (Lithuania, Latvia, and Belarus)	Four groups genetically differentiated	Mitochondrial D-loop
Kokina et al. (2018)	Lakes Kala & Babites (Latvia)	Low genetic differentiation	Microsatellites

Pukk et al. (2016)	Baltic sea (Estonia)	Differentiation between blackish zones (Baltic) and freshwater waters (Lake Peipus)	Microsatellites
Bodaly et al. (1989)	Lake Windermere (UK)	Differentiation	Enzymes
Yang et al. (2012)	Eight sites on Irtse River (China)	Differentiation	Microsatellites
Mankiewicz-Boczek et al. (2013)	Sulejów, Próba, & Jeziorsko reservoirs (Poland)	No differentiation	Mitochondrial D-loop and cytochrome b
Christensen et al. (2016)	Fjord Præstø, Lake Sjælsø, & harbor Ishøj (Denmark)	Mix of haplotypes from Central and Western Europe and Baltic sea relatively to Nesbø et al. (1999)	Mitochondrial D-loop
Kalous et al. (2017)	Římov Reservoir (Czech Republic)	No differentiation	Cytochrome b and microsatellites
Vanina et al. (2019a)	Lake Stary Dwór (Poland), Nové Hrady pond (Czech Republic), River Váh (Slovakia)	Genetic differentiation between the Polish populations and the two other populations	Mitochondrial D-loop, cytochrome b, 16S, and COI
Vanina et al. (2019b)	Lakes Valkea- Kotinen & Majajärvi (Finland), Lake Stary Dwór & Wiślany Lagoon (Poland), Nové Hrady Pond (Czech Republic), Váh river & Liptovská Mara Reservoir (Slovakia)	Strong genetic differentiation	Mitochondrial D-loop, cytochrome b, 16S, and COI

* *Variant forms of an enzyme coded by different alleles at the same locus.* ** *Amplified Fragment-Length Polymorphisms (digestion of DNA by restriction enzymes).* *** *Similar to microsatellites, repetition of DNA motifs ranging from 10–60 base pairs*

5.3 Which domestication system for the second step of the approach?

As mentioned earlier, RAS is the most widespread culture system used for European perch production. Although this species started to be domesticated in the 1990s, there is still no consensus about the rearing conditions which should be used (diverse rearing conditions in the literature; **Table 10**), which makes comparisons between studies difficult (Palińska-Żarska et al. 2019, 2020). In 2017, before performing the second step of the integrative approach, we performed a survey regarding rearing conditions for European perch production and got answers from three perch farms. The number of answers was low but even with three farms we could state a high variability of rearing conditions (e.g. feeding protocol, tank shape and color, photoperiod) between farms. Therefore, the rearing conditions were based on a compromise between the literature, the survey results, and our own knowledge of European perch production techniques (**Table 11**). Most of the rearing conditions used are recognized as optimal for Percid larval culture (Policar et al. 2019 and references within).

Table 10: Example of rearing conditions used in literature for European perch larviculture. *Dph: days-post hatching; NA: not available*

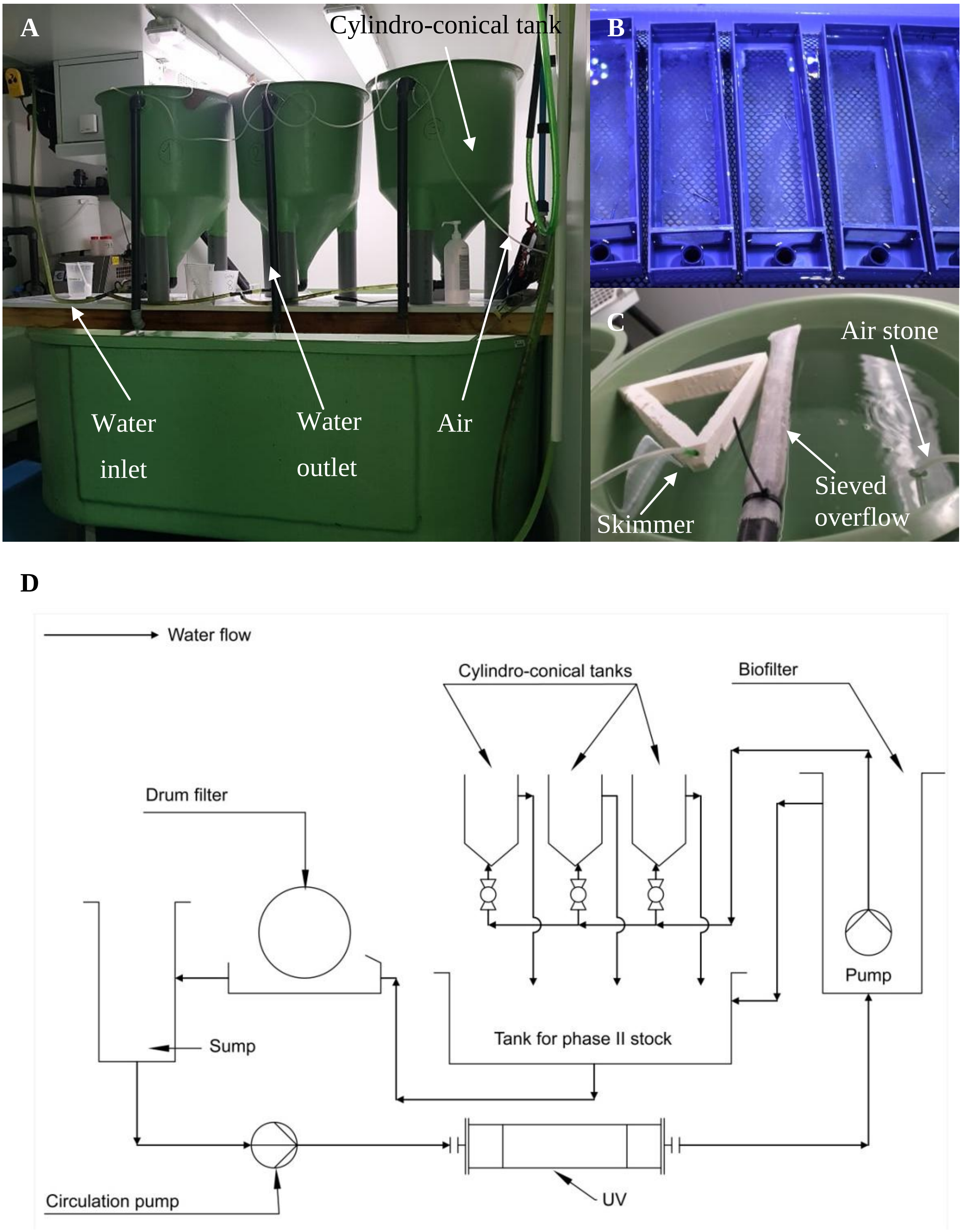
Article	Age	Tank shape	Inner tank color	Tank volume	Water renewal rate	Density (larvae/L)	Temperature (°C)	Photoperiod (L:D)	Luminosity (lx)	Feeding protocol
Tamazouzt et al. (2000)	1 to 15 dph	Cylindro-conical	Black, light grey, dark grey, white	100 L	20 % /day	10	19,7 - 21,6	14:10	250, 400, and 800	1 to 3 dph: zooplankton. 4 dph: dry feed, 6 times/day
Kestemont et al. (2003)	1 to 21 dph	Rectangular or cylindro-conical	NA	25-100 L	NA	10, 32, or 100	17, 20, or 23	8:16, 12:12, 16:8, or 24:0	5, 30, 90, or 400	*Artemia* between 3 and 21 dph, weaning for seven days. Different feeding ratios: 1%, 5%, 10%, 20% biomass/day
	22 to 44 dph	Rectangular or cylindro-conical	NA	25-100 L	NA	1, 3.2, or 10	23	8:16, 12:12, 16:8, or 24:0	5, 30, 90, or 400	Different weaning strategies: 100:0, 99/1, 95/5 (dry feed/*Artemia*).
Babiak et al. (2004)	1 to 84 dph	NA	NA	60 L, then 120 L after 50 dph	NA	20 - 40 or 200	Incubation: 13, after 1 dph: 17.6	NA	NA	*Artemia* nauplii between 9am and 7pm, weaning from 14 pdh, dry feed exclusively after 37 dph
Jentoft et al. (2006)	1 to 35 dph	Rectangular	Black or grey	100 L	1 L/min	23	Incubation at 11.1, then 16	24:0	100-150	*Artemia* for four weeks then weaning
Król et al. (2015)	10 to 87 dph	NA	NA	1000 L for hatching then 30L at 10 dph	NA	50	Incubation at 17, then 22	16:8	NA	*Artemia* between 4 and 11 dph (6 times a day), then weaning, and dry feed exclusively after 22 dph (5 times a day)
Król et al. (2019)	1 to 33 dph	NA	NA	500 L	NA	NA	Incubation at 14, before hatching 17, then rise to 21	16:8	75	From 5 to 15dph *Artemia* and fry feed6 times a day. Then only dry feed.
Palińska-Żarska et al. (2019)	1 to 20 dph	NA	White / Black	50 L	NA	60 / 500	Incubation at 14, then 15 / 20 / or 25	24:0	100 during incubation, then 1500	*Artemia* two times a day from 5 dph
Vanina et al. (2019b)	1 to 24 dph	Rectangular	Light grey	200 L until 3 dph then 60 L	1 L/min	67 after 3dph	Incubation at 17, then 23	12:12	200-250	*Artemia* from 3 dph, weaning between 21 and 24 dph

In this work, two independent experimental phases were performed in the bioassay studies: phase I from hatching until the end of weaning (i.e. transition from live feed to inert pellets; 26 days post-hatching, dph) and phase II from 27 dph until the end of nursery, at 60 dph. The larval period was split in two phases in order to ensure availability of larvae across the whole larval period since there is a very high mortality rate during first-life stages. All experiments were conducted in cylindro-conical tanks (three cylindro-conical tanks per population corresponding to three replicates; **Figure 8**).

Table 11: Rearing parameters used for the bioassays.

	Incubation	**Phase I: 1 dph to 26 dph**	**Phase II: 27 dph to 60 dph**
Experimental structure	Incubators (110x64x186 cm) containing nine racks each (45x7x12 cm)	Green (RGB: 137, 172, 118) internal-wall 71 L cylindro-conical tanks	Green (RGB: 137, 172, 118) internal-wall 71 L cylindro-conical tanks
Flow renewal	4 $m^3.h^{-1}$	1dph to 15 dph: 25 $\%.h^{-1}$ 16 dph to 26 dph: 50 $\%.h^{-1}$	75 $\%.h^{-1}$
Temperature	13 °C	13 to 20 °C	20 °C
Photoperiod	12:12	12:12	12:12
Density	1-4 ribbon(s) / crate	50 larvae / L	19 larvae / L
Light intensity at water surface	400 lx	400 lx	80 lx
Feeding	-	*Artemia* nauplii from 3 dph, seven times / day (8.30 am to 5.30 pm) From 16 dph: weaning for nine days (25% decrease of *Artemia* every three days, increase of dry feed in the same proportions) Dry feed: BioMar, 300 µm until 21 dph, then 500 µm	Dry feed, seven times a day (8.30 am to 5.30 pm). BioMar 500 µm, then 700 µm at 44 dph until 60 dph

Figure 8: Rearing system. **A.** Experiment set up for each population with three cylindro-conical tanks. **B.** Hatchery table with racks. **C.** Top of the cylindro-conical tank. **D.** Drawing detailing the experimental set up and the water flow. Credit: L. Toomey.



Overall, why choosing the European perch as a study model?

+ Interest in facilitating this species domestication and production which are hampered by numerous bottlenecks

+ High socio-economic interest and at intermediate stage (i.e. level four) in the domestication process

+ Geographic differentiation known for several key traits in the wild and in aquaculture conditions

+ Our knowledge on this fish and rearing techniques

+ Large geographic distribution which favors chances to observe local adaptations

+ Eggs assembled in ribbons which makes the collection of biological material easier

+ Large collaborative network available for sampling purposes

CHAPTER 1

CHAPTER 1: *When behavioral geographic differentiation matters: inter-populational comparison of aggressiveness and group structure in the European perch*

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- *Specific Goal*: Demonstrating that there is a geographic differentiation in *Perca fluviatilis* for other key traits than growth and developmental traits.

The first chapter of this thesis is aimed at evaluating if *P. fluviatilis* displays geographic differentiation for key traits in aquaculture conditions. Geographic differentiation had already been highlighted for several key traits, mostly related to growth and survival. Yet, behavioral traits are essential to study since they can facilitate or limit domestication and production (Liao and Huang 2000; Jobling 2010), but geographic differentiation was only shown previously in *P. fluviatilis* for cannibalism rate (Mandiki et al. 2004). Therefore, this chapter focused on three behavioral parameters of interest for aquaculture: group structure, aggressive interaction rate, and activity. Tolerance to conspecifics in intensive rearing conditions is an essential parameter for production. Focusing domestication on populations which present an aggregative, homogenous, and cohesive group structure would be favoring welfare (Kristiansen et al. 2004). Moreover, aggressive interactions can lead to negative consequences in fish culture (e.g. mortalities, stress, immune suppression; Damsgård and Huntingford 2012). Finally, activity is also an important trait to consider since it contributes to the total energetic budget of individuals (Boisclair and Leggett 1989). This chapter brings another line of evidence that geographic differentiation can be helpful to facilitate domestication and production of *P. fluviatilis*. Taking into account results from previous studies and results from this chapter, geographic differentiation exists for several key traits and highlights the interest of using this species to develop and apply the three-step integrative approach.

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

Short title: Behavioral geographic differentiation in *Perca fluviatilis*

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ABSTRACT

Domestication is still a long and difficult process and it is particularly impacted by species behavioral 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, behavioral domestication predispositions could change at the intraspecific level. Here, we investigate three essential behavioral 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 - behavior - cannibalism - intraspecific differentiation - larvae - *Perca fluviatilis* - social structure

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, 2019). 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 favoring 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 behavioral 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 behavioral 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 favoring 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 behaviors (Damsgård and Huntingford 2012), such as attacks or bites, leading in some cases to cannibalism (Baras 2013). These aggressive behaviors 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.

Behavioral intraspecific differentiation and its potential for selection of founder populations have been poorly investigated to date. However, intraspecific differences in aggressive behavior (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 behaviors (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 behavioral intraspecific differentiation could allow improving aquaculture for species for which production is still limited by behavioral bottlenecks.

The European perch, *Perca fluviatilis* L., is one of the fish species involved in the European aquaculture diversification (Kestemont et al 2015a). Its long standing socio-economic interest (high market value and recreational interest) led to the development of its aquaculture in the 90’s (Kestemont and Mélard 2000; Kestemont et al. 2015a). However, its production is still limited due to several bottlenecks including some aspects related to fish behavior such as aggressiveness and high cannibalism and subsequent mortalities (Kestemont et al. 2015a). However, geographic differentiation has been previously observed for some of problematic behavioral 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 behavioral 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. 2015a), 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 (110x64x186cm; one incubator per population), containing nine racks each (45x7x12cm), at 13°C. Each incubator had its own temperature control and recirculated water (flow rate of $4m^3.h^{-1}$) system and water was UV sterilised. Oxygen rate ($10.5 \pm 0.2mg.L^{-1}$) 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 $0.05mg.L^{-1}$) and nitrite concentrations were monitored three times a week until hatching (lower than $0.01mg.L^{-1}$). 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 71L cylindro-conical tanks (three replicates per population; recirculated aquaculture system (RAS)) at a density of $50 larvae.L^{-1}$. Temperature was gradually increased during two weeks to 20°C, photoperiod was 12L:12D and light intensity was 400lx. Larvae were fed with newly hatched *Artemia* naupli (Sep-Art, INVE) every 1h30 from 3 dph until weaning. At 16 dph, *Artemia* ration was decreased by 25% every three days and dry feed ration (BioMar, 300µm until 21 dph, then 500µm) was increased by the same ratio. After 25 dph, larvae were only fed with dry feed *ad libitum* (BioMar 500µm, then 700µm 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 2m^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 ± 2.3mg.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 were 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 two 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 two days; see appendix 1) with an 80lx 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 1.5cm 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 10lx 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 30min acclimatisation, individuals were filmed for 30min using camcorders (Sony, Handycam, DCR-SR72E) located 50cm above the arena. The three arenas were filmed simultaneously and the order of replicates tested was randomly assessed. After 1h, 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 ± 0.55mm, 12.90 ± 0.62mm, and 13.87 ± 0.26mm. 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 ± 1.67mm, 26.28 ± 1.99mm, and 22.97 ± 1.08mm (no statistical difference between populations for the two experiments; experiment I: F=0.712, df=2, *P*=0.528; 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 five minutes. Coordinates of each individual were noted for each image and then distance swam was calculated every second during the five seconds 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 5.30pm 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 five-minute acclimatisation to the presence of the observer and five minutes of focal sampling (Colchen et al. 2019). Daily observations were carried out between 8.30am and 10am from 10 dph until the end of experiment I (26 dph). For experiment II, observations were carried out every three days (see 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 were randomly assigned. Several aggressive behaviors 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).

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 Animal Care Committee of Lorraine (CELMA n°66) and the Ministry of Higher Education, Research, and Innovation (APAFIS13368-2018020511226118).

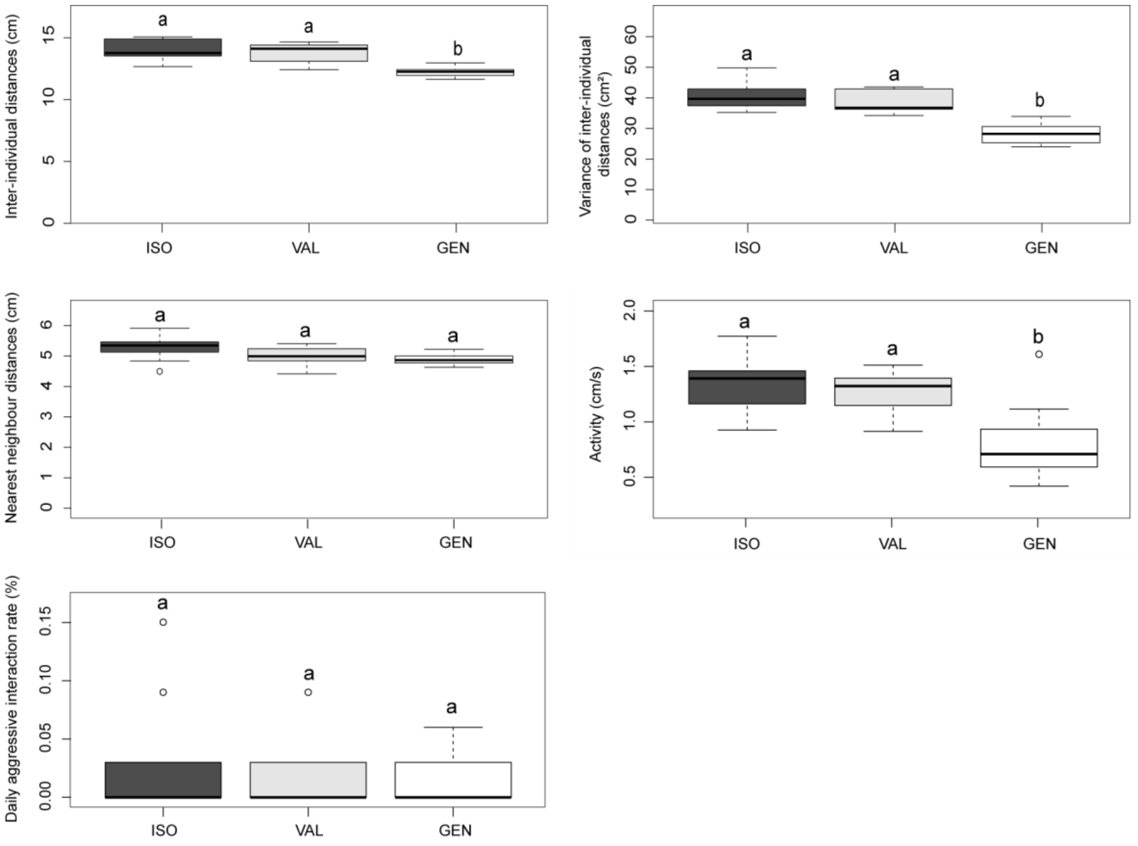
RESULTS

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**).

Fig. 1: Boxplots 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.



Experiment II (45-46 dph)

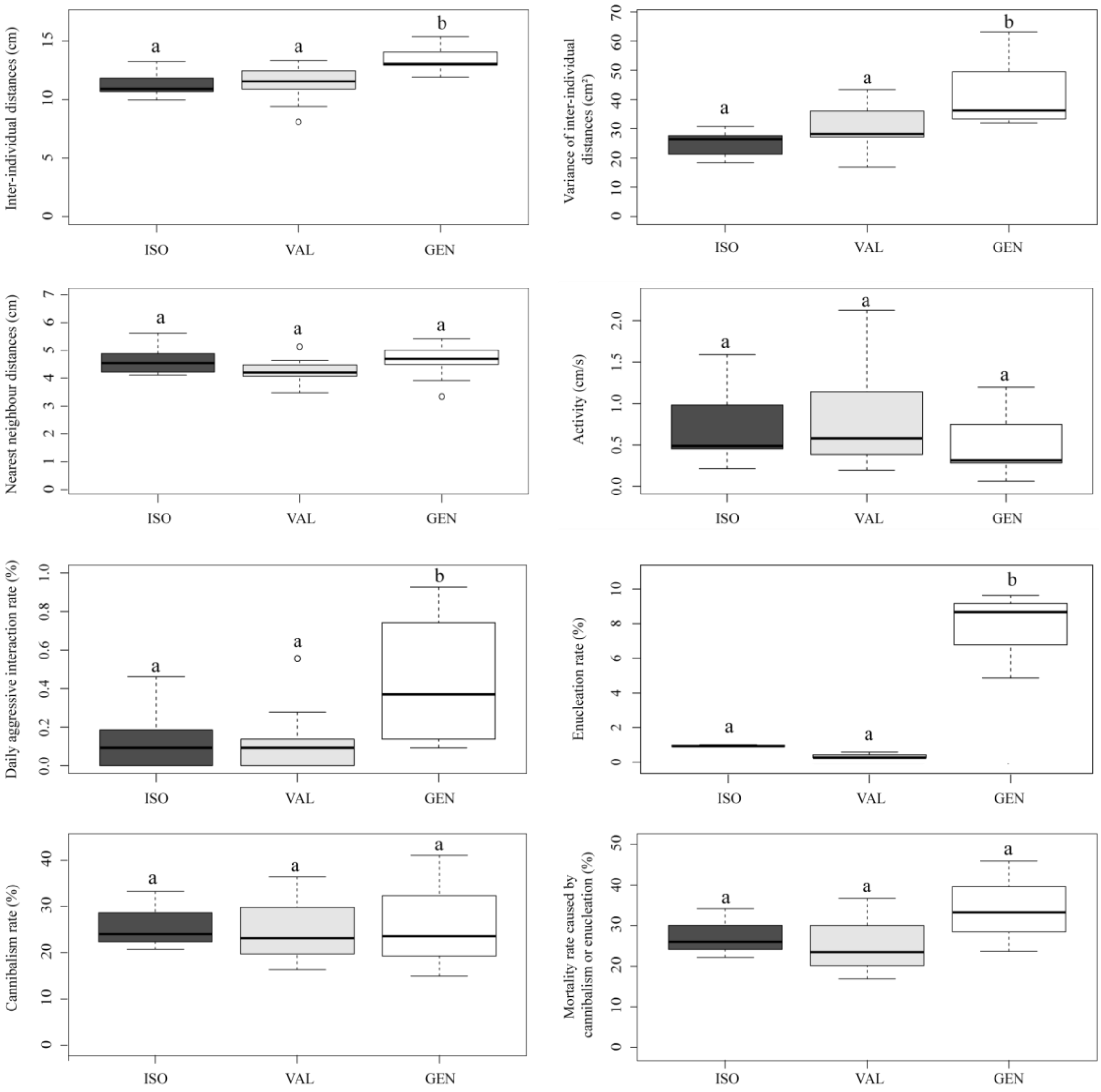
Inter-individual distances (F=7.8, df=2, *P*<0.05) and variance of inter-individual distances (F=9.9, df=2, *P*<0.05) are significantly higher for GEN compared to VAL and ISO (**Fig. 2**). There is no statistical difference between ISO and VAL. There is no statistical difference between populations for 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 behaviors 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. 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**).

Fig.2: Boxplots 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 interactions 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.



DISCUSSION

Inter-populational differentiation in behavioral 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 behavior 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 behavioral differentiations at two ages are limited.

Intraspecific differentiation in group structure and aggressive behaviors 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 intra-cohort 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 behavioral differences can be shaped by genetic differentiation, by phenotypic plasticity, or by their combination.

On the one hand, the observed inter-populational behavioral 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 behavioral 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* prevent 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 behavioral differentiations between populations (DeWitt and Scheiner, 2004) with behavior reflecting the strategy adopted under the influence of environmental factors. This was suggested as the driving factor for cannibalism in *P. fluviatilis* (Król 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 minimized 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; Król et al. 2015).

Overall, we cannot assess the importance of genetic differentiation, phenotypic plasticity, and specific development rates in population-specific behavior. Behavioral 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 behavior cannot be ruled out as it was previously suggested as an important factor for the behavioral 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 behavior.

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

For each population, we observe a behavioral 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-dependant 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 behavior differentiation: a way to improve aquaculture production?

The variability occurring in behavior at the intraspecific level offers the opportunity to select fishes whose behaviors 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 population 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 behavioral traits are modified by this process (Kohane and Parsons 1988). Yet, taking into account behavioral intraspecific differentiation would allow starting domestication program on populations presenting the best behavioral pre-disposition.

Selecting best populations for aquaculture production cannot be made through only behavioral 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-traits approach rather than a single-trait decision framework.

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CONFLICT OF INTEREST AND ETHICAL STATEMENT

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

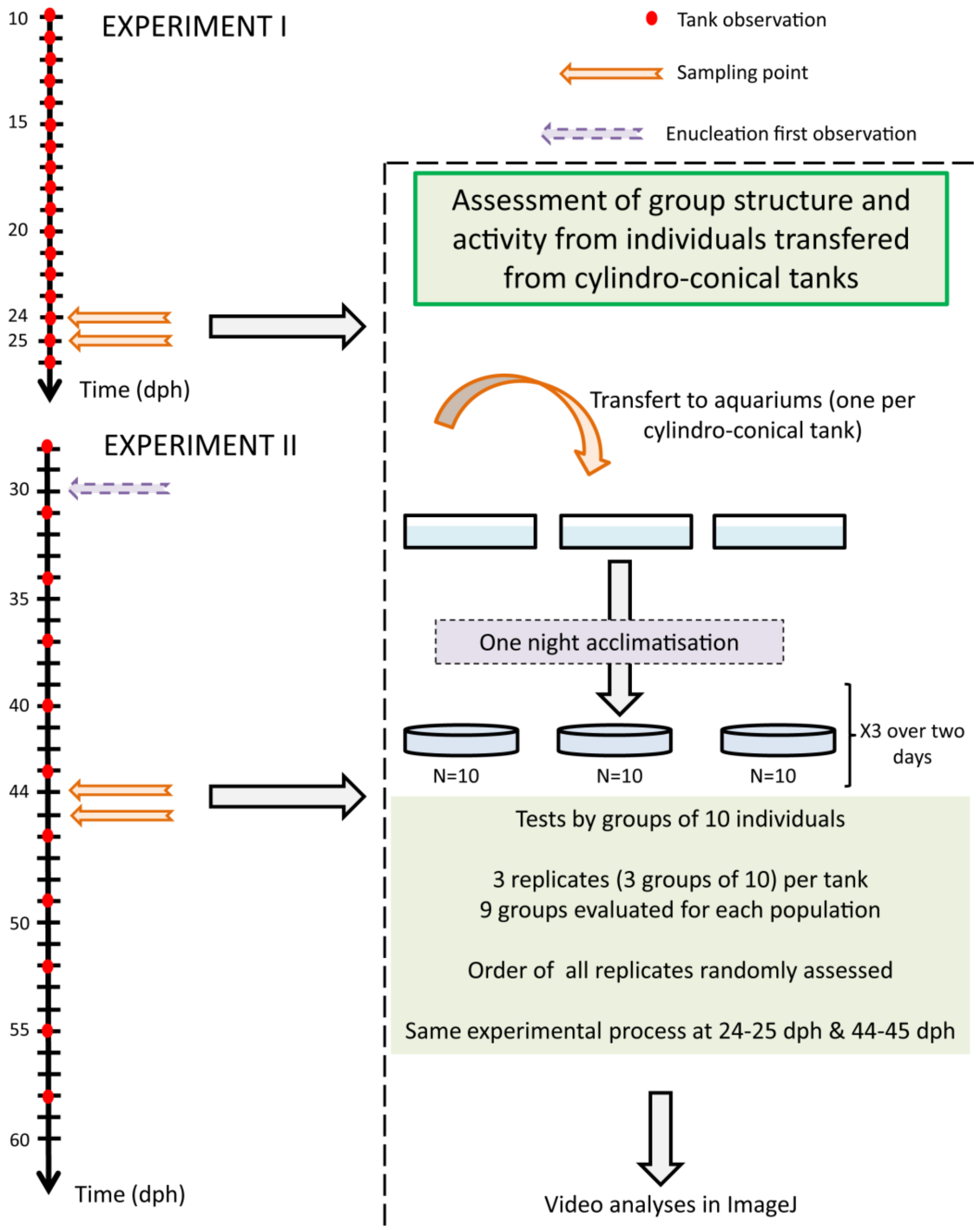
VAL: Lake Valkea-Müstajärvi

ISO: Lake Iso-Valkjärvi

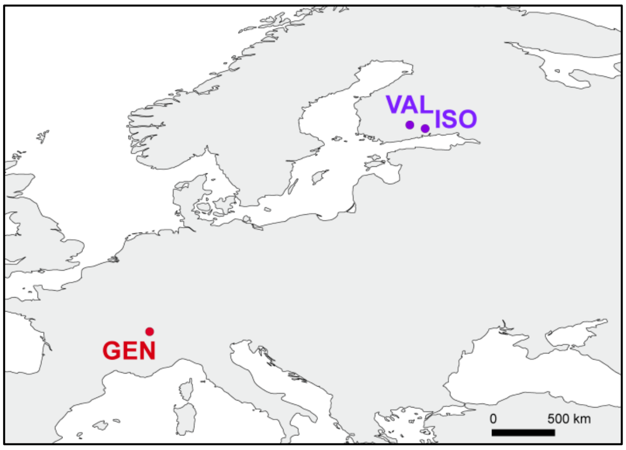
RAS: Recirculated Aquaculture System

APPENDIX

Appendix 1: Material and methods workflow.



TAKE HOME MESSAGE



GEN: Lake Geneva
ISO : Lake Iso-Valkjärvi
VAL : Lake Valkea-Mustajärvi

➢ Activity : No inter-populational differences

➢ Aggressive interactions :

GEN > **ISO – VAL**

\- ⟶ + *Interest for aquaculture*

➢ Group structure :

ISO – VAL > **GEN**

\+ ⟶ - *Interest for aquaculture*

- We demonstrated a geographic differentiation for aggressive interactions and group structure between three allopatric larval populations of *Perca fluviatilis*.

- The differentiation in behavioral parameters is lower between the two Finnish populations (VAL and ISO) than when compared to Lake Geneva.

- These results highlight the potential usefulness of considering geographic differentiation for *P. fluviatilis* domestication and production.

CHAPTER 2

CHAPTER 2: Unlocking the intraspecific aquaculture potential from the wild biodiversity to facilitate aquaculture development

In press in *Reviews in Aquaculture in 2020*

- *Specific Goal*: Conceptualizing a method to integrate geographic differentiation in domestication processes in order to facilitate new species domestication and production.

One way to facilitate the domestication and production of new species may consist in considering wild geographic differentiation. This chapter is aimed at finding a way to integrate geographic differentiation in domestication processes. This chapter proposes a standardized conceptual approach to achieve this objective. This approach relies on three steps: (i) classifying wild populations of a species of concern in prospective units which are likely divergent for key traits in aquaculture, (ii) comparing performances of these prospective units through a multi-function and multi-trait approach in a common garden experiment (i.e. in an environment corresponding to the culture system), and (iii) calculating an aquaculture potential index to identify units of high potential for aquaculture within species to start new domestication processes. One challenge of this chapter was also to define what can be considered as key traits for domestication and subsequent production. Key traits were classified in four categories.

Unlocking the intraspecific aquaculture potential from the wild biodiversity to facilitate aquaculture development

Short title: Aquaculture potentials within species

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ABSTRACT

Domestication of new candidate species remains a long and difficult process often resulting in unfruitful attempts. Early steps in most domestication programs often consider species as a unity, disregarding a part of the biodiversity: the wild intraspecific geographic differentiation. Yet, this differentiation can shape local specificities, which could lead to different domestication predisposition or socio-economic attractiveness between populations. Therefore, considering this population-specific potential could facilitate domestication and subsequent production of new candidate species. Here, we propose a three-step integrative approach to standardize and facilitate new domestication attempts by taking advantage of wild geographic differentiation. The step 1 consists in classifying the wild biodiversity to identify prospective units (i.e. groups of differentiated allopatric populations). The step 2 allows comparing performances of these units in standardized conditions (i.e. rearing system) through a multi-function and multi-trait assessment. Finally, the step 3 highlights units with higher aquaculture potentials through the calculation of an aquaculture potential score. This approach, here applied to fish culture for human consumption, also aims at being extended to other taxa (e.g. crustaceans, molluscs) and other production goals.

Keywords: Domestication, Fish culture, Intraspecific differentiation, Multi-function, Multi-trait, Sustainability

CONTEXT

Aquaculture is the farming of aquatic organisms through several alternative practices (i.e. monoculture/polyculture, outdoor/indoor, flow through systems/recirculated systems, and extensive/intensive). Since the 1960s, aquaculture production has rapidly expanded and exponentially grown worldwide as far as to provide more than 50% of the world's aquatic food consumption nowadays (FAO 2018). This development has been triggered by the need to meet the increasing human demand for aquatic products since wild fisheries catches are no longer sufficient (Watson and Pauly 2001; Froese et al. 2012). Nevertheless, aquaculture is often criticized due to its negative environmental impacts and its potential unsustainable development (Martinez-Porchas and Martinez-Cordova 2012; Christou et al. 2013; Diana et al. 2013). The low species diversity which contributes to worldwide aquaculture production is one of the main causes of these issues. Indeed, although numerous species have been farmed, the production of most of these species (i) was quickly abandoned due to zootechnical or economic problems or (ii) remains marginal when compared to the total volume of aquaculture production (Teletchea and Fontaine 2014; Metian et al. 2019). Thereby, 85% of the current world fish production relies on about fifteen species (Lazard 2013). Such production model based on few species, jeopardizes (i) local native fish fauna by increasing interspecific competition in the wild (Garibaldi and Bartley 1998; Silva et al. 2009) or triggering pathogen spillover (Martinez-Porchas and Martinez-Cordova 2012) when accidental introductions or invasions by the alien farmed species happen, (ii) human food security since the heavy dependence on few species puts at risk aquaculture production (e.g. if an epizootic outbreak happens in farmed species, see for instance Godoy et al. 2008), and (iii) economic prospect since poorly diversified production limits the adaptive potential of aquaculture to face environment/consumer demand changes (Fontaine 2009; Metian et al. 2019). In face of such threats, international organizations (e.g. the Food and Agriculture Organization of the United Nations) are strongly advocating for diversification in regard to species while strengthening well-established species (FAO 2018; Metian et al. 2019). Indeed, species diversification appears as one way to improve the sustainability of the aquaculture sector and promote its resilience, particularly through the production of new species occupying other market segments, for instance niche markets (Liao and Huang 2000; Muir 2005; Fontaine et al. 2009; FAO 2018; Metian et al. 2019). This political will has triggered the development of new species production (e.g. DIVERSIFY project [https://www.diversifyfish.eu/], Aruho et al. 2018; Mitra et al. 2018).

One of the biggest challenges in aquaculture diversification is the required domestication of wild taxa (Liao and Huang 2000; Harache 2002; Fontaine et al. 2009). Domestication is the process in which some populations are bred in a human-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 2019). This is a stepwise process (i.e. the domestication levels *sensu* Teletchea and Fontaine 2014) ranging from the first trials of acclimatization (level one) in the culture environment to the life cycle completion in captivity (levels three and four) and, eventually, to the selective breeding program setting up (level five). It is a long and tough process and attempts are often unfruitful (Teletchea and Fontaine 2014). Indeed, previous domestication attempts on new species show that such tries often lasted only a few years before being abandoned (Teletchea and Fontaine 2014; Metian et al. 2019). Furthermore, even when the life cycle is completed in captivity, major bottlenecks can still remain, impeding domestication continuation and production development (Teletchea and Fontaine 2014). Such failures and issues result from the inability of domestication programs to meet challenges of initiating domestication process (i.e. acclimatization), completing lifecycle, and overcoming major bottlenecks (i.e. very low survival rate) due to technical limitations, economic constraints, or some intrinsic species traits (i.e. single feature or quantifiable measurement of an organism; Jobling 2010). These latter are for instance low growth rate, sensitivity to disturbances or diseases, or high aggressiveness, which characterize poor candidates for domestication (Liao and Huang 2000; Jobling 2010). In contrast, most of already domesticated and fruitfully produced species display the opposite expression pattern for these traits (Diamond 2002). Other intrinsic features can also be important in some particular human-controlled environments such as the ability to tolerate high rearing densities in intensive culture (Jobling 2010) or the resistance to environmental disturbances occurring in outdoor aquaculture (Ficke et al. 2007). This means that some species might be suitable for a particular rearing system but would poorly perform in another. Overall, a successful domestication requires the favorable expression of traits involved in several biological functions or intrinsic characteristics (i.e. trait not associated to a specific biological function) of the targeted species. Indeed, a group of individuals can be domesticated if it can reproduce (reproductive and behavior functions), grow (growth, development, and behavior functions), feed (nutrition and behavior functions), and overcome stresses (e.g. resistance to diseases, immune, and behavior functions) in a particular controlled environment. Besides these traits, the costly domestication process of a wild taxon cannot be achieved without stakeholders' support and/or interest (Suquet 2010), highlighting the importance of considering other traits involved in the socio-economic context (e.g. product quality traits). Overall, all of these factors shape the so called aquaculture potential: a quantification of how much expression of all key traits/functions (biological and socio-economic traits) is favorable for domestication and subsequent production. Therefore, the aquaculture potential assessment requires a multi-function and a multi-trait evaluation. Beside the species intrinsic aquaculture potential, domestication of a taxon is unlikely if the human needs that it could meet are already addressed (e.g. by other currently domesticated species [Le François et al. 2010] or when capture fisheries already fulfil consumer demand for a particular species, e.g. Otterå 2004).

The differential species suitability for domestication programs places a premium on the development of an approach to find relevant candidates in the wild biodiversity. High-throughput screening of the wild biodiversity has recently been proposed as a solution to highlight such species in crops by testing many wild candidate taxa (DeHaan et al. 2016). These candidates are tested across several steps including a first step of screening wild species to identify candidates of interest through an evaluation of traits linked to several biological functions (e.g. growth rate, yield, suitability for special diets; DeHaan et al. 2016). Similar approaches, although less developed, are also available for fishes and consider wild fish biological characteristics as well as socio-economic traits in the evaluation process (e.g. Le François et al. 2002; Quéméner et al. 2002). Nevertheless, such approaches often consider species as a unity and disregard wild inter-populational geographic differentiation (*sensu* divergence between allopatric groups of conspecifics; Mayr 1963) and its consequences on aquaculture potential.

WILD INTRASPECIFIC DIFFERENTIATION: AN ASSET FOR FISH FARMING?

Inter-populational geographic differentiation is a common phenomenon in fish species (see Bernatchez and Wilson 1998; Costedoat and Gilles 2009) which could be important for new domestication programs. Indeed, allopatric populations can undergo specific demographic histories as well as geographic and ecologic isolation triggering (i) gene flow disruption or limitation and subsequently genetic divergence and (ii) local adaptations to different selection regimes (Mayr 1963; Avise 2000). Ultimately, this shapes local specificities in genetic, morphology, physiology, behavior, and/or ecology which could impact the aquaculture potential and economic attractiveness of each wild population (e.g. for non-fish species in Lecocq et al. 2016a,b).

In non-fish species, geographic differentiation of important traits for domestication and production is known for several wild species of interest such as plants (e.g. Ben Mansour-Gueddes et al. 2010; Healey 2016) and fungi (e.g. Liti et al. 2009; Warringer et al. 2011). Moreover, a few previous success stories show that the best candidates to start new species production are not a particular species but rather one or some particular groups of populations within the species of concern for a particular culture system. The bumblebee production industry provides one remarkable example where population-specificity inclusion through multi-trait evaluation in domestication programs fostered a fruitful economic development (Velthuis and van Doorn 2006; Lecocq et al. 2016a,b). One species, the buff-tailed bumblebee (*Bombus terrestris*) displays significant differentiation in key traits for bombiculture (i.e. foraging efficiency, behavior, colony size, diapause condition, and phenology) between allopatric groups of populations corresponding to subspecies (reviewed in Lecocq et al. 2016b). In the early years of production, European bumblebee breeders tried to domesticate several subspecies (Velthuis and van Doorn 2006). Within a fairly short amount of time, one of these subspecies proved to have superior characteristics from a commercial point of view and has become the dominant taxa in the bumblebee production industry (Lecocq et al. 2016b).

In fish production, geographic differentiation has been poorly considered at the beginning of new wild fish domestication trials. However, the few examples involve some of the most successful fish productions. In the 1970s, 41 wild Scandinavian salmon (*Salmo salar*) populations were bred in a standardized production environment to evaluate their performances (Gjedrem et al. 1991). This work considered, on different year classes, several desirable traits (e.g. growth, age at sexual maturity, furunculosis resistance, filet color) in order to identify the best populations to be used for production (which greatly improved salmon production, Gunnes and Gjedrem 1978, Gjedrem et al. 1991; Gjedrem 2010, 2012). Later, in the 1990s, four Middle Eastern and Asian farmed populations along with four wild allopatric African populations of Nile tilapia (*Oreochromis niloticus*) were crossbred to produce fish stocks (Eknath et al. 1993; Gjedrem 2012). Among these fish, best breeders (i.e. with highest growth rate) were selected to develop the genetically improved farmed tilapia strain that grows up to 85% faster than the earlier farmed fish stocks and is now disseminated across the world (Gjedrem 2012).

Conversely to the bumblebee example, the Scandinavian salmon and Nile tilapia cases only show how the geographic differentiation can be useful for advanced fish domestication programs. Here, we argue that fish domestication programs could take advantage of geographic differentiation to initiate or to continue the earlier levels of the domestication process (i.e. levels from one to three, and possibly four, see levels in Teletchea and Fontaine 2014). Indeed, non-domesticated or species at incipient domestication levels display, when bred in captive conditions, differentiation for several traits impacting the aquaculture potential such as features related to growth (e.g. Vanina et al. 2019a), nutrition (e.g. Jonassen et al. 2000), reproduction (e.g. Kokita 2004), aggressiveness (e.g. Toomey et al. 2019), immunity (e.g. Glover et al. 2003), and stress sensibility (e.g. Delabbio et al. 1990). Therefore, considering wild geographic differentiation when starting new fish domestication programs could unlock population-specific potential included in the wild intraspecific biodiversity.

Besides the obvious choice of populations with the highest aquaculture potential to start domestication programs, differentiated populations can display specificities that could allow overcoming current bottlenecks in species at intermediate domestication levels (i.e. level four; e.g. the aquaculture of *Perca fluviatilis*, a species facing strong bottlenecks in its development due to a low larval survival rate and high deformity rate; Fontaine and Teletchea 2019). In such species, assessment of wild population aquaculture potential could pave the way to improve current fish stock or even restart an improved domestication process with better populations if no alternatives can be considered.

Since considering wild geographic differentiation could facilitate aquaculture diversification process, it raises the question how its integration in domestication programs should be achieved. Indeed, this integration cannot be based on very long-term or unrationalized experiments otherwise using wild geographic differentiation for domestication programs would be poorly justified. Therefore, we here propose a conceptual approach to facilitate the integration of geographic differentiation in new candidate species domestication processes.

HOW TO TAKE INTO ACCOUNT WILD GEOGRAPHIC DIFFERENTIATION: A THREE-STEP INTEGRATIVE APPROACH

The aim of this work is to propose a new standardized and rationalized three-step integrative approach to integrate wild intraspecific differentiation in new domestication programs through a multi-function and multi-trait assessment. This approach aims at facilitating domestication of new wild fish candidates or species at incipient domestication levels facing major bottlenecks in the domestication process and/or production-related issues. It aims at, successively, classifying, evaluating, and identifying best population group(s) in the context of new domestication trials (**Fig. 1**).

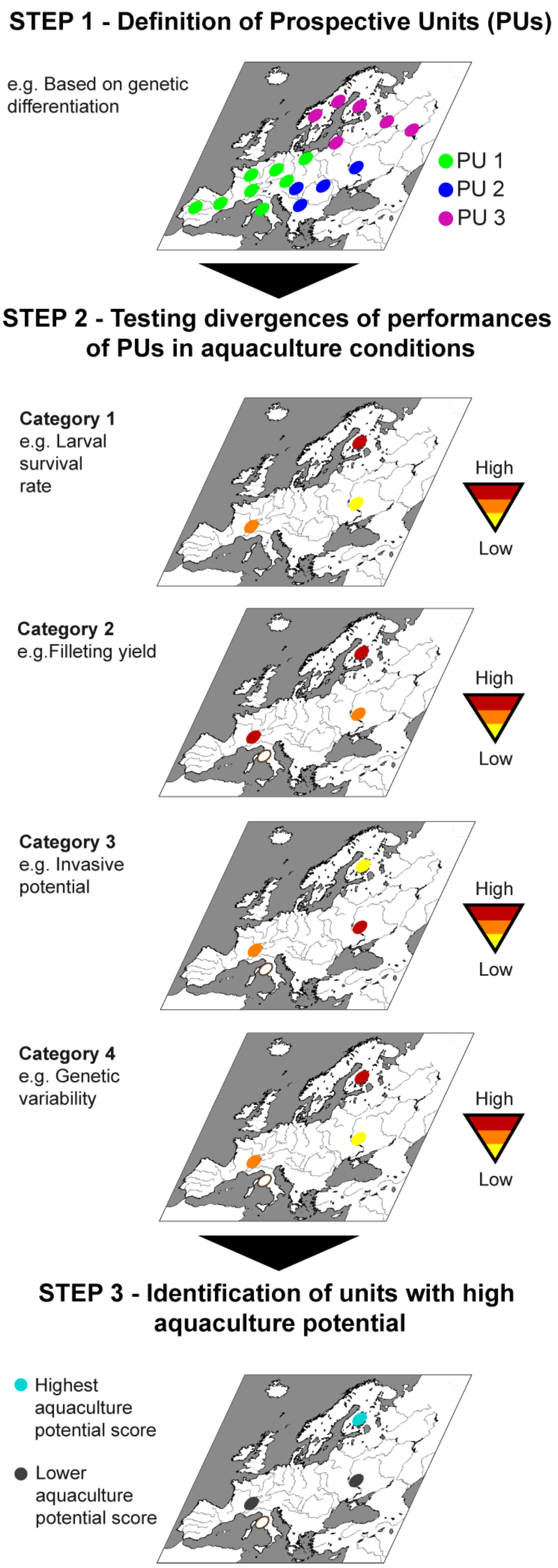

Figure 1: Overview of the three-step integrative approach. The step 1 highlights the different prospective units (PU). A population representative of the prospective unit is sampled between steps 1 and 2. Category 1 includes biological traits measured on a group of individuals of the target prospective unit which reflect the fitness (i.e. ability to survive, grow and reproduce) in captive conditions. Category 2 includes biological traits which are specifically relevant to a particular production system (e.g. RAS, pond, raceway) and/or a specific production goal (e.g. fillet, whole fish sale). Category 3 includes biological traits linked to the interaction between the group of individuals and the rearing system which could impact surrounding environments. Category 4 includes biological traits relative to future major challenges and disturbances. In order to simplify the figure, only one trait is represented for each category in the step 2.

Step 1 - Classification of the wild intraspecific biodiversity

Evaluating the potential for aquaculture of all wild populations of a particular species would be time/money-consuming and is, ultimately, not achievable in practice. Moreover, such comprehensive evaluation would be inaccurate because all conspecific populations are not genetically and phenotypically divergent (Mayr 1963; Hewitt 2000).

However, comparing randomly chosen wild populations is not an efficient solution to this issue because the best population(s) for aquaculture purpose could be missed out. An efficient rationalization relies on the development of a classification system that can identify population groups that have different/independent demographic histories and/or potential local adaptations, making divergences in aquaculture potentials likely. Therefore, such a classification should be based on proxies reflecting evolutionary histories and/or local adaptations of the different population groups. Three different proxies can be used: (i) phenotype, (ii) habitat, and (iii) genetic information.

Phenotype, especially morphological characteristics (e.g. color patterns, shape), is the earliest, the easiest, and the most commonly used information to classify biological units (Strauss and Bond 1990; Haig et al. 2006; Craig et al. 2017). It has been widely used to define subspecies (Mayr 1963; Haig et al. 2006) which can be an efficient classification strategy to split population groups with different aquaculture potentials (e.g. for fish species, Pivnička 1970; Karakousis et al. 1991; Kalayci et al. 2018). Other phenotypic information such as reproductive or behavior traits could be used but, to our knowledge, they have not been applied in fish species to classify at the intraspecific level. Nevertheless, phenotypic traits can be unreliable since there can be a part of subjectivity when defining and interpreting character states (Padial et al. 2010) and it often requires extensive investigation of inter-individual variability (Haig et al. 2006). Moreover, some phenotypic traits can be plastic and might not reflect population-specific histories or local adaptations (Vogler and Desalle 1994; Joyce et al. 2009). These concerns have led to criticisms regarding the relevance and the efficiency of phenotype-based intraspecific classifications (e.g. Mallet 2001; Patten 2010). Although phenotype information could still be useful under the condition that trait variations are indicative of underlying genetic divergences (e.g. morphology in brown trout [*Salmo trutta*]*;* Pakkasmaa and Piironen 2001; Kalayci et al. 2018), such classifications must be applied prudently.

Habitat information (biotic and/or abiotic factors) has rarely been used to classify conspecific populations (but see e.g. the distinction between habitats, such as rivers or lakes, contributed to define intraspecific units in *S. trutta*, Blanc et al. 1971; Guyomard 1989). Yet, one could expect that populations living in different biotic/abiotic conditions can display different demographic histories or local adaptations (Avise 2000). Therefore, a relevant approach to classify populations before evaluating their aquaculture potential could simply consist of developing a classification based on habitat differentiations (e.g. different biogeographic regions, distinct hydrographic basins, different water parameters). However, establishing if different habitats can lead to differential evolutionary paths between allopatric populations is still hard to achieve due to the potential non-congruence with population-specific histories and/or local adaptations. Moreover, there is a part of subjectivity when selecting criteria to detect habitat specificity. Therefore, these limitations make this classification approach unpractical to date for fishes.

Genetic information has been increasingly taken into account to investigate intraspecific differentiation (Frankham et al. 2004; Padial et al. 2010). The phylogeography-based classification appears as one of the most suitable strategies to achieve an *a priori* classification. Phylogeography aims at identifying groups of genetically differentiated populations which underwent specific demographic histories (Avise 2000) and could have acquired, through local adaptations, some phenotypic specificities. Moreover, information about phylogeographic structure is already available for many fish species (Bernatchez and Wilson 1998; Costedoat and Gilles 2009). In the context of our three-step approach, genetic proxies allow maximizing chances of detecting populations with different potentials for aquaculture that can be conserved in production environments. Indeed, domesticated fishes will often be produced in a culture environment which can be quite different from their native habitat. Therefore, only genetic-based divergences are of interest while differentiations triggered by phenotypic plasticity (i.e. the ability of a genotype to vary in phenotype depending on environmental conditions; Pigliucci et al. 2006) processes would be useless. However, special attention should be paid to the limitations of the genetic approach. On the one hand, an approach using only few arbitrarily picked genetic pieces of evidence could result in an insufficient resolution to detect populations with different potentials for aquaculture because phenotypic or ecologic differentiations are not always being represented by many genetic differences, making their detection unlikely when using a small part of the genome (Arif and Khan 2009; Cruaud et al. 2014; Patwardhan et al. 2014). This places a premium on using large genome parts or highly variable DNA sequences. On the other hand, a high resolution genetic-based classification could fail because of absence of interpopulational variation of the potential for aquaculture despite different evolutionary histories revealed by genetic markers. Using sequences of genes involved in traits impacting the potential for aquaculture could be an efficient solution. Unfortunately, such an approach remains unfeasible to date because (i) most traits are under polygenic control, (ii) the genetic basis of variation in traits is often very complex, and (iii) quantitative trait loci are mostly studied for a few major aquaculture species (Falconer and Mackay 1996; Yue 2014; Abdelrahman et al. 2017; Robledo et al. 2018). Therefore, the risk of using a classification which might not lead to the identification of inter-populational divergences cannot be ruled out to date but several studies already highlighted a congruence between genetic differentiation in neutral markers and phenotypic differentiation in controlled conditions (e.g. Rosauer *et al*. 2011; Vanina *et al*. 2019a).

Overall, special attention should be paid to the *a priori* classification used, and advantages/disadvantages of each proxy should be assessed for each target species through co-working with systematicians, phylogeographers, and ecologists. The resulting classification allows identifying the different prospective units (i.e. groups of allopatric populations differentiated) that will be evaluated in the step 2.

Step 2 - Evaluating keys traits of the aquaculture potential

The step 2 aims at comparing the performances of prospective units in fish farming conditions through an integrative (i.e. multi-function and multi-trait) assessment. For a wild species for which even acclimatization has not been tried before, it implies to first design a culture system that most likely will be suitable for the targeted species and stakeholders. Such a system can be defined by applying farming conditions used for phylogenetically closely related or ecologically similar fish species that are already produced in captivity or using knowledge from habitat conditions experienced by wild populations (Liao and Huang 2000; Teletchea et al. 2009). For fish species for which incipient production already exists, the current aquaculture conditions should be used. Choosing the aquaculture system (i.e. domestication system) in which wild populations will be assessed is an important preliminary step. Indeed, expression of traits shaping the aquaculture potential can change according to the environment (e.g. Rowland et al. 2004). A relevant aquaculture potential assessment should be thus obtained through bioassays in a human-controlled environment as close as possible to the targeted production system (e.g. cages, flow-through system, indoor Recirculated Aquaculture System [RAS], ponds). This means that all prospective units should be evaluated in a common-garden experiment in which the rearing system is similar to future rearing conditions. Therefore, this evaluation might have to be performed again if another rearing system is considered (i.e. the results from a RAS assessment might not be useful for pond production).

Special attention should be paid to which set of individuals is needed for the aquaculture potential assessment. Two alternative solutions can be used: (i) broodstock sampling or (ii) early-life stage collection. One could consider that it is necessary to sample wild broodstock to produce captive-born offspring that will be evaluated. This requires respecting good rearing practices in stock constitution such as using a sufficient number of individuals in order to avoid inbreeding issues (relatively to the minimal effective size; Duncan et al. 2013). However, sampling broodstock could be difficult for some species because tolerance to transport and acclimatization varies between fish taxa depending on the life stage considered (Berka 1986; Omeji et al. 2017, e.g. for *Perca fluviatilis*, early life stages (i.e. eggs, juveniles) remain the preferred wild biological material transported by fish farmers given the high adult mortalities subsequent to transport). This implies that the sampling material choice can be species-dependent. Therefore, for some species, early life stages could be sampled as initial biological material when accessible, but the phenotypic plasticity impact might be more substantial. Beside the choice of life stage to be sampled, it should be noted that, although the step 1 aims at defining groups with similar demographic histories and/or potential local adaptations and, thus, similar aquaculture potentials, different populations from the same prospective unit could display different performances. Indeed, temporary specific environmental disturbances affecting some populations of the same prospective units (e.g. unusual regional food shortage, disease outbreak, or local pollution events) can impact evaluated traits (e.g. Scott and Sloman 2004; Claireaux et al. 2013). In such case, the initial state of the sampled population impacts results obtained in controlled conditions (e.g. 100% mortality if presence of Perhabdovirus in Percids; Bigarré et al. 2017; Rupp et al. 2019). Consequently, a reliable evaluation of prospective unit aquaculture potential could include an assessment of the initial state of wild sampled populations through, for instance, toxicological (e.g. Tabari et al. 2010) and veterinary tests (e.g. Talbi et al. 2011; Bigarré et al. 2017) as well as a check-up of the quality of breeders (e.g. lipid content in oocytes; Dhurmeea et al. 2018). Unfortunately, some of such tests are still unavailable (e.g. unavailability/lack of efficiency of some disease detection methods) or unfeasible at large scale. Therefore, two strategies could be used: (i) sampling the same wild populations at different years and repeating independently the step 2 and/or (ii) avoiding sampling populations occurring in areas where unusual events have been recently recorded (e.g. recent chemical pollution). Because the former strategy would increase the workload, we regard this strategy as poorly implementable and recommend the latter.

The suitability of traits chosen for the evaluation is based on the relevance of the trait (i.e. integrative traits, important to measure and relevant regarding welfare and ethics) and its accessibility (i.e. trait measurable at large scale but not necessarily evaluated yet in routine because of the lack of proper method). A literature overview of such traits for fishes (e.g. Lensi 1995; Liao and Huang 2000; Quéméner et al. 2002; Otton 2004; Teletchea et al. 2009; Jobling 2010; Le François et al. 2010) allowed us to select a first set of traits which are overall relevant for teleosts (**Table 1**). This selection has been further reinforced by a survey conducted among Percids and Sturgeons producers. These two species groups were chosen since they include species with recent domestication processes and with different production outputs (see **Annex S1**). The ongoing production of these species allows having an overview on traits which turned out to be essential for production. We asked farmers (ongoing production of one or both species groups) in this survey to give their opinion on the different traits selected and to suggest additional relevant traits to be considered (see details and results in **Annex S1** and **Fig. S1**). For all traits involved in the aquaculture potential assessment, there is a performance expected by stakeholders (e.g. growth: expected high growth rate; deformity: low deformity rate). Traits chosen were classified in four categories (**Table 1**) corresponding to the different aspects which need to be considered when starting a new domestication process.

The first category is characterized by all biological traits measured on a group of individuals of the target prospective unit which reflect the fitness (i.e. ability to survive, grow, and reproduce) in captive conditions (**Table 1**). This category is common to all rearing systems (e.g. on-growing survival rate important in all production systems when on-growing is part of the production outlet). It includes traits linked to the different steps of a production cycle (reproduction, larviculture, on-growing) but also to the different biological functions (reproduction, growth, nutrition, and behavior).

The second category is characterized by all biological traits which are specifically relevant to a production system (e.g. RAS, ponds, floating cages) and/or a specific production goal (e.g. fillet, whole fish sale). It includes traits (i) involved in responses to breeding-environment-specific stresses (e.g. antipredator behavior is relevant in ponds [Huntingford et al. 2012] while resistance to handling is important in intensive monoculture in RAS, Milla et al. 2010) and (ii) related to the production target (e.g. filleting yield for the food consumption output). Here, we consider as examples two different scenarios with a common outlet (consumption market) but different rearing systems commonly used in aquaculture: RAS and ponds (**Table 1**).

Table 1: **Set of traits considered in the integrative approach in the context of monoculture in RAS and ponds for the consumption market**. Category 1 includes biological traits measured on a group of individuals of the target prospective unit which reflect the fitness (i.e. ability to survive, grow and reproduce) in captive conditions. Category 2 includes biological traits which are specifically relevant to a production system (e.g. RAS, pond, raceway) and/or a specific production goal (e.g. fillet, whole fish sale). Category 3 includes biological traits linked to the interaction between the group of individuals and the rearing system, which could impact surrounding environments. Category 4 includes biological traits relative to future major challenges and disturbances. Traits in italic correspond to traits less important according to Percid and Sturgeon farmers (less than 50% of opinions considering the trait as quite important or important for at least one or both species groups).

Category	Sub-category	Trait group	Trait
Category 1	Reproduction	Breeders	Breeder survival rate Age and size at sexual maturity Fecundity
		Gametes	*Volume of sperm* Number of oocytes *Number of spermatozoids*
		Fertilized eggs	Survival rate Egg diameter Malformation rate Fertilization rate Hatching rate
		Spawning	Spawning timing Spawning duration
	Larviculture	Growth	Growth rate *Growth heterogeneity*
		Nutrition	Volume of the yolk sac Larvae size at hatching Timing for the exogenous feeding transition
		Development	Swim bladder inflation rate Deformity rate Survival rate
		Aggressive behavior	*Cannibalism rate* *Age at cannibalism onset* *Size at cannibalism onset*
	On-growing	Growth	Growth rate Growth heterogeneity
		Development	*Sex-ratio* Survival rate
		Nutrition	Food conversion ratio
Category 2	Intensive monoculture in RAS -	Traits involved in response to captive environment pressures	Resistance to sub-lethal stress and diseases/parasites which are expectable in RAS environment

	consumption market		(e.g, handling) Acceptance of artificial diet (weaning) *Group structure* *Activity (i.e. individuals more or less active)* Water volume occupation
		Traits important for output quality	Filleting yield *Condition factor* Body shape Organoleptic characteristics Nutritional value
	Extensive monoculture in ponds - consumption market	Traits involved in response to captive environment pressures	Resistance to sub-lethal stress and diseases/parasites which are expectable in the pond environment (e.g, physico-chemical changes, transport) *Antipredator behavior (e.g. birds, parasites)*
		Traits important for output quality	Filleting yield *Condition factor* Body shape Nutritional value
Category 3		Invasive risk	*Invasive potential*
		Pathogen spillover risk to wild populations	*Pathogen load*
		Risks of genetic homogenization and outbreeding	*Genetic divergence between farmed and neighboring wild populations*
Category 4		Maintenance of fish performances in the future	Robustness (including adaptive potential to ongoing climate change) *Future invasive potential in the climate change prospect*
		Future selective breeding programs	Genetic variability (fish individual specificities)
		Ability to face new stakeholder requirements/expectations	Acceptance of alternative feeds

The third category includes all biological traits linked to the interaction between the group of individuals and the environment of the rearing system, which could impact the surrounding environments (e.g. invasive potential, pathogen load, competition; **Table 1**). In all rearing systems, there are risks of escapees (particularly relevant in outdoor culture, yet risks cannot be ruled out in indoor aquaculture; Summerfelt and Vinci 2009). These escapees can trigger negative impacts which vary according to the identity of populations bred (i.e. local population, non-native population introduced in a species native area or in a new area out of the geographic species native range): (i) invasive risk (estimated by the invasive potential; Kolar 2004; Naylor et al. 2005), (ii) introduction of pathogens (evaluated through the pathogen load; Naylor et al. 2005), (iii) genetic introgression/homogenization or outbreeding with local wild populations (see for example Fraser et al. 2008; Bolstad et al. 2017; Wringe et al. 2018), and (iv) competition risk between domesticated and wild populations (there is no assessment protocol available for fishes [but see for other vertebrates e.g. Polo-Cavia et al. 2009]; therefore, we ruled out this last risk from the aquaculture potential evaluation).

The last category is characterized by all biological traits relative to future major challenges and disturbances. A literature overview allows identifying four main challenges. First, there are high stakes to domesticate robust individuals. Here, we describe robustness as the ability of individuals to express their production potential in a wide range of environment changes (e.g. climatic changes, feeding shifts, disease outbreaks; based on Knap 2005). This includes adaptive potential to future climate change (i.e. large-scale changes predicted related to temperature, winds, and acidification) since it will provide novel challenges (Cochrane et al. 2009), especially in outdoor aquaculture (e.g. ability to survive in aquaculture conditions despite more frequent severe weather events). Second, it is also important to consider the future invasive potential, taking into account predicted climate changes, since invasive potential is partially shaped by climatic requirements. Third, the maintenance of genetic variability during domestication has been pointed out as a major feature to promote a sustainable development of aquaculture (Liao and Huang 2000). While stock management aiming at limiting inbreeding has been proposed, the selection of units with sufficiently high genetic variability increases chances to have individual specificities of interest for future selective breeding programs (e.g. rare genes counter-selected in the wild but presenting an advantage in rearing systems; Vandeputte and Launey 2004). Finally, one major challenge relies on the acceptance of alternative aquafeeds (i.e. less rich in fish oil and fish meal) such as plant-based feeds (Naylor et al. 2009). Indeed, due to wild resources limitation, it is essential to shift towards alternative feedstuffs in order to promote sustainability of aquaculture and an inter-individual variability in the ability to adapt to vegetal-based diets was already assessed for some species (e.g. Burel 2017).

Step 3 - Identification of units with high aquaculture potential

The step 3 aims at identifying units with high aquaculture potential through the establishment of an integrative decisional framework.

According to our survey, traits are perceived differently among fish farmers and are not given the same level of importance (see in **Table 1**; **Fig. S1**). For instance, growth rate during on-growing is globally considered as very important for both Percids and Sturgeons while group structure (i.e. structure of a group of individuals created by relationships between several individuals; Hinde 1976) is evaluated as less important for both species. In addition, the importance of traits also varies between species groups, production systems, and production goals (**Fig. S1**). For instance, sex ratio is considered as quite important or important by 71.4% of Sturgeon farmers but only by 14.6% of Percid farmers. Therefore, in order to identify units with high aquaculture potential, it is necessary to adjust the importance of different traits through weighting coefficients. Moreover, some traits are so important (e.g. major bottlenecks preventing the completion of the life cycle) that when a minimum threshold of their required expression is not met in a unit, this latter is regarded to be void of aquaculture potential. For instance, a paltry survival or fecundity rate observed in a unit will impede further domestication programs (e.g. inability for males to fertilize eggs due to the absence of courtship behavior in Senegalese sole [*Solea senegalensis*]; Guzmán et al. 2008; Morais et al. 2016). Nevertheless, special attention should be paid to the definition of minimum required expression threshold needed for a trait. Indeed, although some trait expressions can constitute a major bottleneck in future production, they might not fully prevent domestication/production or depress profitability (as observed in sturgeon aquaculture where the species high socio-economic value offset its low growing out potential and late sexual maturation). Moreover, some bottlenecks could be overcome through other alternatives such as technological improvements. Therefore, we advocate that minimum expression thresholds should be defined only for characteristics which are not surmountable at the time of the evaluation and completely prevent domestication/production.

The assessment of weighting coefficients (0 to 100; adapted from Quéméner et al. 2002; similarly to breeding goals index but for which each trait is weighted according to its socio-economic value; Chavanne et al. 2016), as well as minimal expression thresholds, to all traits needs to be performed by a panel which includes all potential interested parties. These latter include fish farmers, scientists, environmental managers, and other socio-economic stakeholders. Since this approach targets species which are new candidates for domestication, stakeholders can take decisions using (i) literature, (ii) knowledge from ongoing domestication trials and farming experiences, and/or (iii) on extrapolations from closely related species when no rearing experience is available. The weight coefficient and minimal expression threshold attribution can be done through a consensus for each trait performed by all stakeholders (e.g. mean of the weights attributed by all stakeholders or using Quaker-based or spokescouncil models; Roy and Bouyssou 1993; Hartnett 2011). These weighting coefficients and minimal expression thresholds need to be evaluated for each new domestication attempt since they can vary between species targeted and through time depending on stakeholders' expectations.

Besides trait weighting, it is unlikely that a prospective unit has the best performances for all criteria. It is more likely that a unit displays the best performance for a specific trait (e.g. best growth rate) but the worst for another (e.g. lowest larval survival rate). Therefore, an indicator is required in order to make a synthesis at the multi-function and multi-trait levels to identify units with high aquaculture potential. Some methods and associated scores were suggested at the interspecific level in order to identify good candidate species (e.g. method used in Quéméner et al. 2002; Le François et al. 2010; Suquet 2010; Alvarez-Lajonchère and Ibarra-Castro 2013; at the intraspecific level Toomey et al. *under review*). These scoring methods, or other indexes available in literature (e.g. similarly to the selection index, Gjedrem 2005a), could be used to evaluate the aquaculture potential at the intraspecific level.

WHAT ARE THE LIMITATIONS OF THE APPROACH?

Overall, three limitations should be stated: (i) methodological limitations, (ii) pragmatic concerns, and (iii) legal regulation context.

Methodological limitations

A first limitation can be dreaded if translocations of the targeted species happen concurrently with the evaluation by three-step approach. If they occur between the steps one and two of the approach, the classification step would be irrelevant for next steps of the approach. Moreover, if they happen after the selection of units with high potential for aquaculture, future population resampling in the wild could lead to the establishment of fish stock with specificities different from those expected according to the previous three-step assessment. Even species that are not currently produced can undergo such a phenomenon because they can be the focus of recreational activities (e.g. angling), triggering the risk of introduction of exogenous individuals. Nevertheless, fish translocations are increasingly monitored due to international and local regulations, minimizing the potential negative impacts of this limitation.

Another limitation concerns step 2's experiment. It aims at (i) minimizing expression of aquaculture potential divergences driven by phenotypic plasticity due to specific wild environmental pressures and (ii) allowing observation of those shaped by genetic-based differentiations. Nevertheless, some observed prospective unit performances could not be genetically based and, thus, not be conserved in the next farmed generations. Indeed, even in a common-garden design, population-specific phenotypes can be consequences of past environmental pressures triggering phenotypic plasticity, including epigenetics effects (Massicotte and Angers 2012; Schlichting and Wund 2014) as well as transgenerational effects (Mousseau and Fox 1998; Youngson and Whitelaw 2008). Such phenomena cannot be ruled out since step 2's assessment in based on individuals which (i) parents lived in the wild at least some part of their life or (ii) lived in the wild if eggs are sampled (see step 2's sampling strategies). One solution to minimize this limitation consists in assessing performances over several generations. However, such a solution could be difficult to operationalize for taxa with long lifecycles. Indeed, multi-generations assessment and late sexual maturation species evaluation will increase the workload, the cost, and the length of the approach. However, overall, the use of a common-garden set up allows minimizing the impact of phenotypic plasticity.

Pragmatic concerns

Our approach can be seen as heavy-going. However, any domestication trials are still time and money consuming. Our approach aims to balance the complexity of multi-trait assessment over several prospective units (though the step 1's classification allows restricting the range of possibilities regarding biological units to compare) by choosing the best part of the wild biodiversity. Indeed, gains of highlighting populations with the highest aquaculture potential can provide important benefits for fish production (see for instance for *Perca fluviatilis,* Mandiki et al. 2004; Toomey et al. 2019; Vanina et al. 2019a). However, consequent investment may not be operated for each new candidate. One way to decrease investments could consist of extrapolating the knowledge or the results obtained for some species to others in order to minimize the extent of evaluation for new species. Especially, population classification of a species (step 1 when based on genetic differentiation) could be inferred from commonly observed phylogeographic patterns of other co-distributed taxa (e.g. rather than based on a new genetic assessment across the species range (e.g. Danubian regions often host fish populations with genetic specificities and therefore could be considered as a relevant place for step 2's sampling). Indeed, an overview of already known phylogeographic structures (e.g. Bernatchez and Wilson 1998; Costedoat and Gilles 2009; Hickerson et al. 2010) allows identifying general phylogeographic patterns in fishes. This means that one could assume that population(s) from a region could be genetically distinct since populations of other taxa display genetic specificities. Therefore, such populations should be evaluated in the step 2.

Legal regulation context

One limitation could be related to national and international regulations regarding the biological material sampling or importation. Indeed, such regulations should be considered before step 2 since it would be a waste of time and energy to perform an assessment on wild populations that could not be imported or sampled to create fish stocks for future production.

WHEN IS THIS APPROACH APPLICABLE?

The three-step approach is designed to help stakeholders to facilitate domestication programs of new species or species at incipient domestication levels (i.e. from level one to three of the domestication process; Teletchea and Fontaine 2014). At these levels, domestication programs are commonly facing major bottlenecks in domestication and/or production (e.g. *Anguilla anguilla*; Tomkiewicz *et al*. 2012). Focusing domestication efforts on the units with the highest aquaculture potential could allow overcoming or minimizing such bottlenecks. Moreover, the approach allows considering all traits important for aquaculture (i.e. multi-trait assessment) from the outset of the domestication programs and thus most likely facilitating future production development.

One could expect that the three-step approach is a less efficient alternative than selective breeding methods that allow improving fish stocks at individual/family levels (Lind et al. 2012). However, selective breeding methods are poorly implementable when only a part of the lifecycle is performed in captivity (i.e. capture-based productions) or when significant number of wild individuals must still be integrated in farmed fish stocks. Under these circumstances corresponding to the early levels of domestication, the three-step approach can be seen as a way to move forward in the domestication process and to design the best fish stocks before potentially handing over to selective breeding programs in the further levels of domestication (i.e. levels four and five). Therefore, the three-step integrative approach and selective breeding methods should be seen as complementary rather than opposite and could eventually be used successively along the domestication process. We argue that selective breeding programs should be favored at intermediate stages of domestication (i.e. level four) when the differentiation within population is higher than the inter-populational differentiation (Quillet et al. 2007) or when the genetic gain prediction for one generation of individual selection is higher or equal to the between-population differentiation (Vandeputte et al. 2014). Nevertheless, future studies are needed to assess to feasibility of the three-step approach in the real world production by evaluating costs, gains, and human and technological means. More specifically, cost and benefit comparison with selective breeding programs are needed to assess the complementarity of the two approaches and the relevance of the three-step method. However, cost and benefit analyses are performed for selective breeding programs (e.g. Janssen et al. 2018), but they are not available for the three-step approach since we propose here a new methodology which remains to be tested.

The three-step integrative approach aims to be a model approach applicable to all new candidate species, including non-fish taxa (e.g. for shrimp stripes, Wenger 2012; U.S. Fish and Wildlife Service 2017) provided that the set of traits is adjusted for the target taxon group (e.g. swim bladder inflation or cannibalism rates are not relevant for molluscs while success of successive metamorphoses are). However, as stated previously, the trait choice must also be adjusted according to (i) production goals, (ii) production method, and (iii) technologic advances. First, the approach can be applied to restocking or ornamental market provided that further relevant traits are integrated in category two. For instance, in the case of ornamental aquaculture, external color needs to be considered while resistance to wild pathogens are particularly relevant for restocking programs. Second, the approach adjustment is also necessary when considering some production methods such as polyculture for which traits related to interspecific interactions should be considered. Third, the trait list can also be updated through time as technologic development and new challenges arise (e.g. sperm long-term storage techniques would allow to improve fertilization issues, making fertilization rate less important for the aquaculture potential score; e.g. Alavi et al. 2015; Policar et al. 2019).

WHAT’S NEXT?

Once the multi-stage aquaculture potential assessment approach is performed, questions can be raised when planning future production. An overview of previous studies which used wild intraspecific differentiation at advanced stages of domestication, show that two alternative paradigms to exploit geographic differentiation can be considered (Gjedrem 1985, 2005a): (i) crossing the best prospective units (i.e. crossbreeding) or (ii) concentrating on the best unit to develop production (i.e. purebreeding). On the one hand, crossbreeding aims at exploiting hybrid vigor, or heterosis, which is characterized by offspring performing better than parents for one or several traits. This strategy was explored for several species such *O. niloticus* (Eknath et al. 1993; Gjedrem 2012) or the rainbow trout (*Oncorhynchus mykiss*; Ayles and Baker 1983). However, no heterosis effect was found for some species when crossing several wild populations such as *S. salar* (Gjerde and Refstie 1984). This strategy appears as interesting (i) when the aquaculture potential is not that different between prospective units and if an heterosis effect is demonstrated or (ii) when planning selective breeding programs to ensure a large genetic basis. On the other hand, purebreeding, implying a continuous genetic improvement within a biological unit(s) over a long period of time, was also widely used in terrestrial livestock species as well as for fishes (Gjedrem et al. 1991; Gjedrem and Baranski 2009; Gjedrem 2010, 2012). This strategy has been pointed out as particularly efficient when one biological unit presents overall better performances than other units (Gjedrem 1985, 2005a). Indeed, purebreeding has been recommended in breeding programs when there is additive genetic variation while crossbreeding has been suggested if the magnitude of hybrid vigor is larger than the expected genetic gain though a purebreeding program (Gjedrem 1985, 2005a).Whether or not crossing prospective units depends on breeding goals and genetic variation of traits of interest and is beyond the three-step integrative approach which is the first step before potential future breeding programs.

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APPENDICES

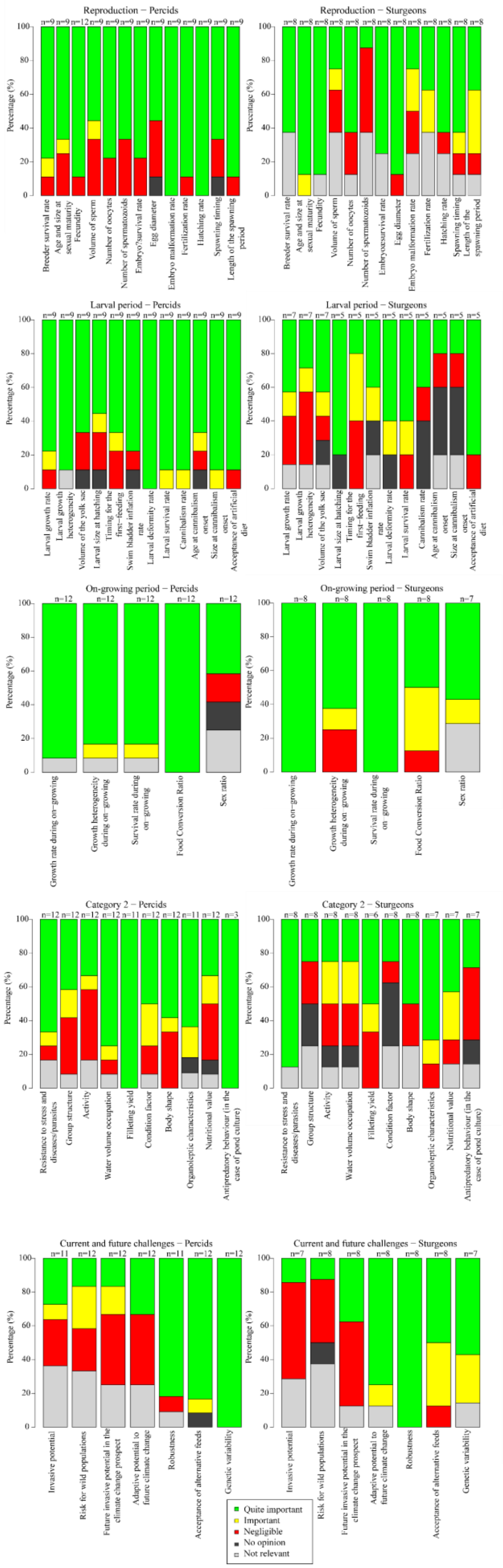
Annex S1: Context of the survey

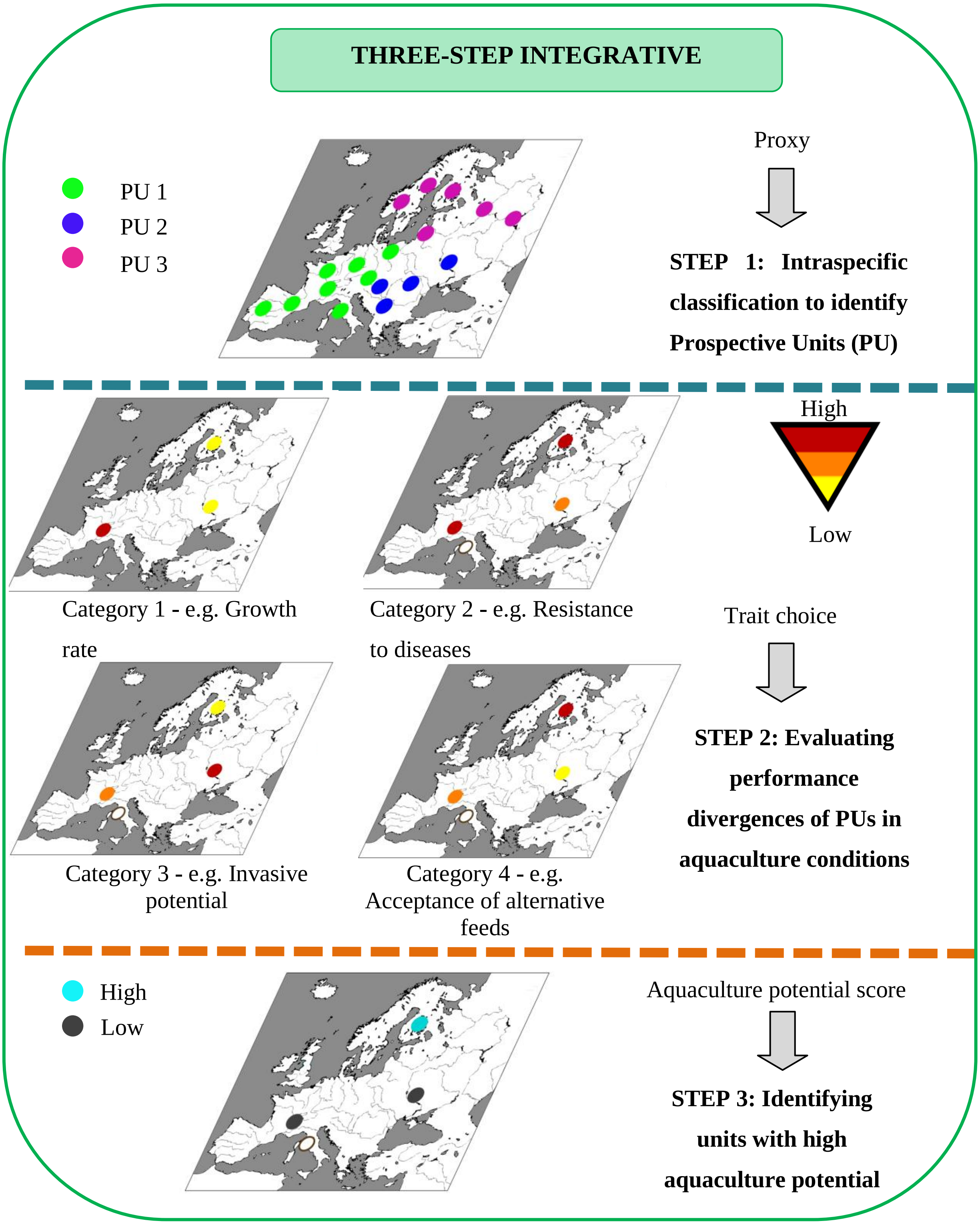
The survey focused on two different scenarios targeting species at the beginning of the domestication process and with a high socio-economic interest. The first scenario focused on European production of Percids, taking as an example the European Perch (*Perca fluviatilis*) and the pikeperch (*Sander lucioperca*). These two species are among the most promising species to boost European inland aquaculture (Fontaine 2004; Fontaine *et al.* 2009; Kestemont *et al.* 2015a) due to their high socio-economic interest (high market value and recreational interest; Kestemont & Mélard 2000; Kestemont *et al.* 2015a). They are at their nascent stage of production and geographic differentiation has already been demonstrated for European perch (e.g. Mandiki *et al.* 2004; Toomey *et al.* 2019). Percids farming still presents several bottlenecks related for instance to high growth heterogeneity and subsequent cannibalism, low survival rate, or low egg quality (Kestemont *et al.* 2015a). Therefore, there is a strong interest in improving these species' productions. The second scenario consisted in investigating Sturgeons production (*Acipenser ruthenus*, *Acipenser gueldenstaedtii*, *Acipenser stellatus*, *Acipenser baerii*, *Acipenser persicus*, Hybrid bester, and *Huso huso*) for consumption in Europe. Substantial progress in rearing techniques in the 1980s allowed developing a fruitful sector for meat and caviar production (Bronzi *et al.* 1999; Williot 2009). The market will most likely extend (Williot 2009), triggering an interest in improving Sturgeon domestication processes. This survey being focused on biological traits, stakeholders involved in the environmental and economic sectors were not consulted in this preliminary investigation.

The survey was led between February and March 2019. For Percids, between nine and 12 answers were taken into account (variable numbers depending on production goals and production systems of the different farms; e.g. no answers for the larval period when larviculture is not performed in the farm, see **Fig. S1** for details), except for anti-predatory behavior for which only three answers were considered since only three farms used outdoor systems. Most of the fish farms use indoor RAS (91.6% [n=11 farms]), 25.0% [n=3 fish farms] use outdoor RAS, and two fish farmers use both systems. The fish farms produce fillets (75%, n=9 fish farms), fingerlings (75%, n=9 farms), and/or wholefish for consumption (33.33% of the farms, n=4 fish farms). Nine farms have more than one production goal. Concerning Sturgeons, between five and eight answers were considered for each trait depending on production goals and rearing systems of the different fish farms (see **Fig. S1** for details). Most of the fish farmers use several rearing systems, including flow-through systems

(75% n=6 fish farms), 50% using indoor RAS (n=4), 25% using outdoor RAS (n=4), and 25% using ponds (n=2). Regarding production goals, fish farms produce caviar (75%, n=6), juveniles (37.5%, n=3), fillets (50%, n=4), individuals for restocking (12.5%, n=1), and/or wholefish for consumption (62.5%, n=5). One farm produces Percids and Sturgeons.

Figure S1: Barplots representing the estimation of importance (in %) for all traits included in the survey for Percids (*Perca fluviatilis* and *Sander lucioperca*; graphs on the left column) and Sturgeons (*Acipenser ruthenus, Acipenser gueldenstaedtii, Acipenser stellatus, Acipenser baerii, Acipenser persicus, Hybrid Bester,* and *Huso Huso*; graphs on the right column). Barplots represent different group of traits: reproduction period, larval period, on-growing period, traits relative to category 2 [i.e. biological traits which relevance vary according to production systems and production goals], and traits linked to current and future challenges (categories 3 [i.e. biological traits linked to the interaction between the group of individuals and the rearing system, which could impact surrounding environments] and 4 [i.e. biological traits relative to future major challenges and disturbances]). Colors correspond to the different degrees of importance: (i) light grey when the trait was not considered as relevant (even though part of the production goal), (ii) dark grey when the fish farmer has no opinion on the importance, (iii) red when the trait was estimated as negligible, (iv) yellow when the trait was considered as important, and (v) green when the trait was considered as quite important. The number above each trait bar indicates the number of farmers which gave their opinion on this particular trait.


Reproduction – Percids
Reproduction – Sturgeons
Percentage (%)
Breeder survival rate
Age and size at sexual maturity
Fecundity
Volume of sperm
Number of oocytes
Number of spermatozoids
Embryo?survival rate
Egg diameter
Embryo malformation rate
Fertilization rate
Hatching rate
Spawning timing
Length of the spawning period
Larval period – Percids
Larval period – Sturgeons
Larval growth rate
Larval growth heterogeneity
Volume of the yolk sac
Larval size at hatching
Timing for the first–feeding
Swim bladder inflation rate
Larval deformity rate
Larval survival rate
Cannibalism rate
Age at cannibalism onset
Size at cannibalism onset
Acceptance of artificial diet
On-growing period – Percids
On-growing period – Sturgeons
Growth rate during on–growing
Growth heterogeneity during on–growing
Survival rate during on–growing
Food Conversion Ratio
Sex ratio
Category 2 – Percids
Category 2 – Sturgeons
Resistance to stress and diseases/parasites
Group structure
Activity
Water volume occupation
Filleting yield
Condition factor
Body shape
Organoleptic characteristics
Nutritional value
Antipredatory behaviour (in the case of pond culture)
Current and future challenges – Percids
Current and future challenges – Sturgeons
Invasive potential
Risk for wild populations
Future invasive potential in the climate change prospect
Adaptive potential to future climate change
Robustness
Acceptance of alternative feeds
Genetic variability
🟩 Quite important
🟨 Important
🟥 Negligible
■ No opinion
□ Not relevant


THREE-STEP INTEGRATIVE
PU 1
PU 2
PU 3
Proxy
STEP 1: Intraspecific classification to identify Prospective Units (PU)
High
Low
Category 1 - e.g. Growth rate
Category 2 - e.g. Resistance to diseases
Trait choice
Category 3 - e.g. Invasive potential
Category 4 - e.g. Acceptance of alternative feeds
STEP 2: Evaluating performance divergences of PUs in aquaculture conditions
High
Low
Aquaculture potential score
STEP 3: Identifying units with high aquaculture potential

CHAPTER 3

CHAPTER 3: *Getting off on the right foot: integration of spatial distribution of genetic variability for aquaculture development and regulations, the European perch case*

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- *Specific Goal*: Classifying wild populations in groups genetically differentiated in order to restrict the number of populations to study in the step 2. The classification aims at maximizing inter-group differentiation and minimizing intra-group differentiation.

This chapter corresponds to the first step of the integrative method: the establishment of an intraspecific classification to identify prospective units (i.e. groups of conspecific and allopatric populations which are differentiated). As a first approach, we chose to perform a phylogeographic study. Indeed, population groups having different/independent demographic histories and/or potential local adaptations are likely to present divergences in key traits. Therefore, we used genetic differentiation in neutral markers (i.e. not submitted to selection and not influencing fitness) as a proxy to highlight population groups with potential divergences in key traits. We had already shown in a study, performed in collaboration with some Czech colleagues from the University of South Bohemia, a link between genetic differentiation and a few key trait differentiations for three European perch populations (Vanina et al. 2019a).

This chapter aimed at establishing an intraspecific classification but also aimed at considering the use of this classification for conservation purposes. Indeed, when the production and subsequent trade begin, translocations of individuals within and outside the species range lead to many conservation concerns such as outbreeding, genetic homogenization, or competition risks threatening the wild population(s) of produced/managed species. Although these challenges and issues have been reported many times (i.e. in vertebrates and invertebrates, in aquatic and terrestrial taxa), species conservation concerns and translocation regulations often begin to be considered when issues are observed. Indeed, lessons from the past are poorly taken into account when a species is becoming of interest for humans although they should be considered to avoid common issues. One way to overcome these challenges consists of integrating the knowledge of spatial genetic variability patterns in conservation and management strategies of species.

In this chapter, we proposed to consider intraspecific genetic variability for the ongoing development of *Perca fluviatilis* production. The aquaculture of this fish species is still at the nascent stage. Therefore, it is a good opportunity to provide (i) guidelines for conservation and efficient regulations of the movements of the species within its natural range and (ii) a genetically-based population structure which is the first step before the bioassays (i.e. step two of the integrative approach).

Getting off on the right foot: Integration of spatial distribution of genetic variability for aquaculture development and regulations, the European perch case

Short title: Integration of spatial distribution of genetic variability

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ABSTRACT

Knowledge of spatial genetic variability patterns allows improving conservation actions, translocation regulations, and farming productivity. However, these genetic variability patterns are often considered after issues are observed, long after the beginning of production. By taking into account lessons from other species, we investigate the genetic variability of *Perca fluviatilis*, a species at a nascent stage of production. The genetic variability has been previously studied but, due to discrepancies between conclusions and methodological limits, the spatial distribution of genetic variability in *P. fluviatilis* has not been demonstrated conclusively. Here, we characterize the genetic variability across 84 West-Palaearctic sampling sites using mitochondrial and microsatellite markers. We aim to provide (i) a genetically-based population structure that could act as an impetus for further production improvement and (ii) guidelines for translocation regulations. Our analyses show an uneven distribution of genetic variability. Based on inter-populational genetic differentiation, we identify five large geographic scale clusters which are further divided into several subgroups. Local genetic diversity mapping highlights a spatial pattern with several hotspots, which has serious implications in the development of appropriate regulations of translocations. Moreover, we here report an association between genetic differentiations and previously reported zootechnical performances. We ultimately propose guidelines for further investigations of population-specific performances in aquaculture and potentially efficient regulations for policy-makers.

Keywords: Geographic differentiation - Genetic diversity - *Perca fluviatilis* - Management – Production

INTRODUCTION

During the Quaternary, most inland species went through several climatic cycles (Andersen and Borns 1994). The alternation of Ice Ages and interglacial periods resulted in range shifts which depended on eco-climatic requirements and tolerances of taxa. Temperate-adapted taxa underwent range shrinking during Ice Ages and distribution expansions to at least portions of their initial distribution range during interglacial periods (Avise 2000; Hewitt 2004a; Stewart et al. 2010), while cold-adapted taxa went through the opposite pattern (Fedorov et al. 2008; Magnuson et al. 1979; Martinet et al. 2018; Quinzin et al. 2017). Such movements have shaped the current distribution and genetic variability patterns of species (Hewitt, 2004b; Stewart et al. 2010). First, the distribution of many species was fragmented into different isolated refugia during range shrinking times (Avise 2000; Hewitt 2004b). This led to a decrease of gene flow between populations and, potentially, to geographic genetic differentiations (Hewitt 2000; Stewart et al. 2010). Second, post-glacial re-colonizations of non-refuge areas led to a loss of genetic diversity through founder events occurring at the expanding front while ancestral genetic diversity was often maintained in refuge regions (Avise 2000; Hewitt 2004b). Finally, the mixing of individuals from different refugia in newly colonized areas created regions of high genetic diversity (i.e. suture zones; Avise 2000; Hewitt 2004b). Moreover, species intrinsic features (e.g. limited dispersal, (partial) post-zygotic reproduction isolation) can also contribute to shape local genetic specificities of populations (Behrmann-Godel 2004; Lecocq et al. 2017, 2018). This has resulted in an uneven distribution of the genetic variability (i.e. genetic diversity and genetic differentiation) across species ranges (Avise 2000; Hewitt 2004b).

Meeting human nutritional needs has often required the domestication (*sensu* Lecocq 2019) and trade of wild animal species (Salo et al. 2014; Teletchea and Fontaine 2014; Velthuis and van Doorn 2006). However, this development is characterized by challenges which can impede the sustainability of animal production. Successfully domesticating a novel species is a long-term and difficult task since it implies mastering species life cycle in a human-controlled environment (see production development pathways in Teletchea and Fontaine 2014). Furthermore, translocation of individuals within and outside the species native range can occur when the production and subsequent trade begin. This can lead to many conservation concerns (e.g. biological invasion, pathogen spillover, genetic homogenization; Lecocq et al. 2016a; Mack et al. 2000; Perrings et al. 2010). Knowledge of spatial genetic variability patterns provides key information to enhance animal production development as well as to mitigate its potential negative impacts on wild populations (Danancher and Garcia-Vazquez 2011).

For animal producers, understanding spatial patterns of genetic variability is potentially valuable in order to optimize the exploitation of a particular species in controlled conditions. Indeed, genetically differentiated populations underwent specific evolutionary histories and could have acquired phenotypic specificities (i.e. geographic differentiation; Blanck and Lamouroux 2007; Forschler and Kalko 2007; Youngson et al. 2003) through genetic adaptations to local environments (Losos and Ricklefs 2009). Some of these specificities (i.e. characteristics which are particular to a specific population) can concern biological traits of interest for production, trade, and profit (e.g. improved provision of ecosystem services, higher resilience, higher acceptability by stakeholders; Imsland et al. 2002; Janhunen et al. 2009; Lecocq et al. 2016a, 2016b; Stort 1974). This leads to different potentials between populations for production. Ultimately, considering these population potentials can foster successful animal production development (e.g. Velthuis and van Doorn 2006).

Globalization of species production and trade (for agriculture, pets, model organisms for scientific purposes, game, restocking, or biological control agents) leads to translocations that can threaten local species and population(s). While risks related to invasions of non-native species have been widely studied (Mooney and Cleland 2001; Simberloff et al. 2013), translocations within the distribution range of a particular species have received far less attention (Lecocq et al. 2016a). Yet, they have been shown in some cases to be more detrimental (Buoro et al. 2016). Translocations of genetically differentiated individuals within a species range can lead to outbreeding, genetic homogenization, or competition issues threatening genetic intraspecific variability (Champagnon et al. 2012; Cross 2000; Danancher and Garcia-Vazquez 2011; Rhymer and Simberloff 1996). This genetic variability (i.e. the combination of local genetic diversity and inter-population genetic differentiation) is seen as one of the key factors to species conservation and survival (Booy et al. 2000; Frankham et al. 2010). Indeed, local genetic diversity and inter-populational genetic differentiation contribute to the species ability to adapt to future challenges (Laikre et al. 2005; Sgrò et al. 2011) and to global biodiversity that maximizes species long-term survival chances (Conner and Hartl 2004; Lecocq et al. 2015; Phillimore and Owens 2006), respectively. Therefore, preserving genetic variability is an important focus in conservation programs (Laikre et al. 2005; Mankiewicz-Boczek et al. 2013; Sgrò et al. 2011). Given the important advantages of many produced/traded species for human livelihood, health, or economy, a complete interdiction of translocations is not feasible. Therefore, pragmatic translocation regulations are needed. Finding spatial patterns of genetic variability allows developing relevant regulations to preserve population specificities and guidelines for translocations (e.g. Lecocq et al. 2016a, 2015).

Despite their potentially valuable integration in incipient species domestication and trade, intraspecific genetic variability patterns often begin to be considered long after the beginning of production (Fleming et al. 2000; Lecocq et al. 2016a; Lemer and Planes 2012). Indeed, new candidate species often start to be produced without due consideration to issues already encountered with other fish species when spatial patterns of intraspecific variability when not considered early in the domestication process (Fleming et al. 2000; Lemer and Planes 2012; McGinnity et al. 2003). In this study, we focus our attention on the European perch (*Perca fluviatilis* L.), an inland fish species at a nascent stage of its aquaculture production. *Perca fluviatilis* is a temperate freshwater and brackish water fish species distributed across the Palaearctic realm (except in most of the Mediterranean Sea coast regions; Stepien and Haponski 2015). This species, traditionally used in both commercial and recreational fisheries, is the focus of an increasing interest in aquaculture since the 90s in western Europe (Fontaine 2004; Kestemont et al. 2015a; Kestemont and Mélard 2000). Although several major bottlenecks are still observed in aquaculture (Kestemont et al. 2015a; Policar et al. 2019), further development of *P. fluviatilis* production can be expected because this species has an increasingly impressive market potential (i.e. current production is largely inferior to European demand; Kestemont et al. 2015a). Since the species displays a significant invasive potential (Kestemont et al. 2015a) as well as documented intraspecific genetic (e.g. Bergek and Björklund 2009; Nesbø et al. 1999) and phenotypic (Blanck and Lamouroux 2007; Pimakhin 2012; Roch et al. 2015) differentiations, it is likely that (i) production potential may vary between populations and (ii) unregulated translocations could lead to dramatic consequences. This suggests that production and translocations of the European perch should be optimized and regulated, respectively, at the nascent stage of its production.

The demographic history of the European perch was investigated in previous studies. However, most of these studies focused on limited geographic areas (e.g. Bergek and Björklund 2009; Butkauskas et al. 2012). Only one study investigated the species genetic variability at large geographic scale and identified four genetic groups and three refugia (suggesting a plausible fourth one, not contributing to re-colonization) during the last glacial maximum (25,000 to 15,000 before present; Nesbø et al. 1999). However, tremendous developments in analytical and statistical approaches occurred since these previous publications. The former large-scale phylogeographic study (Nesbø et al. 1999) was only based on a small part of the mitochondrial genome as well as a few Random Amplification of Polymorphic DNA (RAPD) markers but limitations of such approaches have now been highlighted. First, phylogeographic and population genetic studies based on only a small part of genome, in this case mitochondrial genome, remain controversial because (i) the part of genome analyzed is often chosen arbitrarily (Cruaud et al. 2014) and (ii) population differentiations are not always characterized by the accumulation of many genetic differences, making their detection by using small genome part unlikely (Arif and Khan 2009; Patwardhan et al. 2014). Second, multilocus nuclear markers such as RAPD markers have been replaced by more powerful multi-allelic markers such as microsatellites because RAPD approach presents a low reproducibility and a limited usefulness for meta-analysis (Arif and Khan 2009; Sunnucks 2000). Beside potential limitations due to the state of scientific and technical knowledge at the time of previous investigations, an overview of phylogeographic studies investigating specific geographic areas shows discrepancies in conclusions (see for instance Gyllensten et al. 1985 and Olsson et al. 2011). Therefore, due to analytical limitations and discrepancies between conclusions, previous studies have not demonstrated conclusively the spatial distribution of genetic variability in *P. fluviatilis*.

In the present study, we establish the spatial genetic variability patterns and the population structure of the European perch through the analysis of four mitochondrial regions and eight nuclear microsatellite markers. By considering these spatial patterns, we aim to provide (i) a genetically-based population structure that could act as an impetus for further improvement of *P. fluviatilis* production and (ii) guidelines for efficient regulations of the species translocations within its natural range to preserve wild intraspecific variability.

MATERIAL AND METHODS

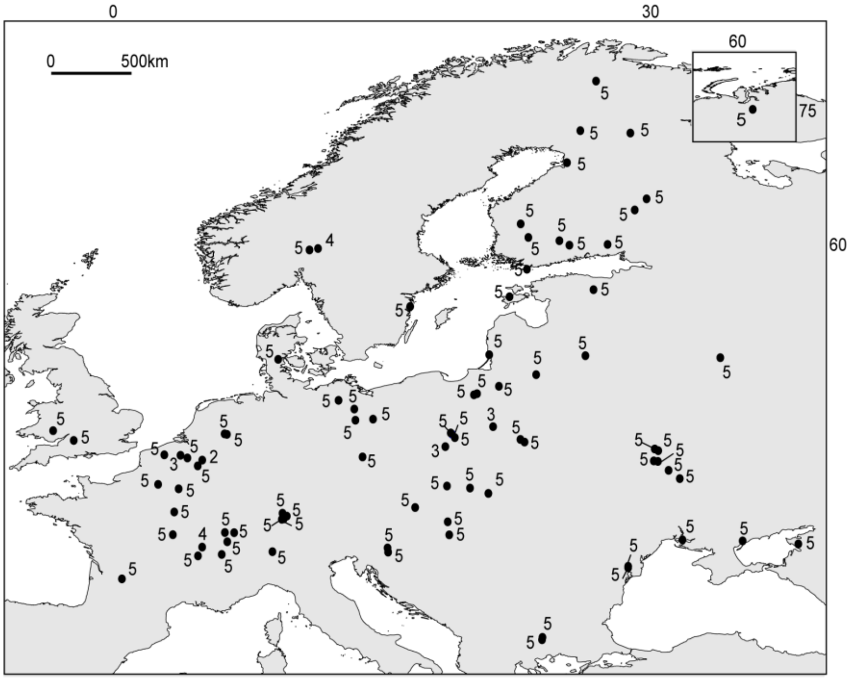
1. *Sampling*

We collected 409 European perch tissue samples from 84 sampling sites (five individuals per sampling site, except for six sites for which less individuals were collected) from different drainage basins (estuaries, rivers, and lakes) across the species native range in western Eurasia and Siberia (**Table S1**, **Fig. 1**, and **Fig. S1**). Sample providers dissected a small piece of caudal or dorsal fins or scales from field captured individuals. Samples were stored in 99% ethanol at – 20 °C. We included samples of *P. schrenkii* Kessler 1874 (seven samples from two sites, **Table S1**) and *P. flavescens* Mitchill 1814 (sequences from GenBank), the two sister species of *P. fluviatilis*, as outgroups for mitochondrial analyses. All samples were collected respecting both European and national sampling regulations. We isolated genomic DNA using DNeasy® Blood and Tissue kit (QIAGEN France SAS®) (18-h incubation in proteinase K at 56 °C). Voucher specimens used in molecular investigations were deposited at the University of Lorraine (Nancy, France).

2. *Genetic analyses*

We selected four mitochondrial regions, commonly used to evaluate phylogeographic patterns of fish species (Costedoat and Gilles 2009; Makhrov and Bolotov 2006): cytochrome b (Cytb), D-loop or control region (D-loop), 16S rRNA (16S), and cytochrome oxidase I (COI). Polymerase chain reaction amplifications of Cytb, D-loop, 16S, and COI were carried out using primers L14724F / H15918R (Song et al. 1998), HV2 / CSBD (Nesbø et al. 1998a), 16Sar / 16Sbr (Palumbi et al. 1991), and jgLCO1490 / jgHCO2198 (Geller et al. 2013), respectively. The reaction components were 10 pmol primers, PPP MasterMix (Top Bio®), DNA (100 - 200 ng/µL), and water. An initial step of five minutes at 95 °C was followed by 38 cycles of denaturation at 94 °C for 40 s, 50 s at annealing temperature (55.8 °C for 16S, 49 °C for COI, 55 °C for Cytb and D-loop), and one minute extension at 72 °C, and a 10 min final extension at 72 °C. We purified PCR products with E.Z.N.A.® Gel Extraction Kit (Omega Bio-tek®) and single read sequencing was performed by Macrogen Europe (Amsterdam, Netherlands) on a 3730XL (Applied Biosystems) using primers H15918R, CSBD, 16Sbr, and jgLCO1490. We edited sequences of mitochondrial markers using CodonCode Aligner 7.1.2 (CodonCode Corporation, Dedham, Massachusetts, USA). The *P. fluviatilis* origin of each sequence was checked in NCBI using BLAST (Zhang et al. 2000). We aligned all sequences using MAFFT (default parameters; Katoh et al. 2019). Translation to proteins for partial COI and Cytb sequences was performed in Mesquite using vertebrate mitochondrial code. We deposited sequences in GenBank (GenBank accession numbers: MG969725 to MG969793; **Table S1**). Mitochondrial regions were ultimately concatenated into a single alignment for the different analyses using Mesquite 3.20 (Maddison and Maddison 2001).

Figure 1: Sampling map for *Perca fluviatilis*. Sampling sites are represented by black circles and juxtaposed numbers indicate the number of individuals sampled at each site.



We selected eight microsatellite markers previously used for *P. fluviatilis* (Ben Khadher et al. 2015): PflaL1, PflaL2, PflaL4, PflaL6 (developed in *Perca flavescens*; Leclerc et al. 2000), SviL7 (developed in *Stizostedion vitreum*; Wirth et al. 1999), SVi17 (developed in *Stizostedion vitreum*; Borer et al. 1999), YP60, and YP111 (developed in *Perca flavescens*; Li et al. 2007). We performed amplifications through the use of two multiplexes using fluorescently labelled primers. A first multiplex (A) contained PflaL2 (FAM), PflaL4 (PET), SviL7 (VIC), Svi17 (FAM), and YP111 (PET). The second multiplex (B) contained YP60 (FAM), PflaL1 (VIC), and PflaL6 (FAM). Polymerase chain reaction was carried out using Multiplex TEMPase 2X MasterMix (VWR®), 10 pmol fluorescent primer mix, water, and DNA (100 - 200 ng/µL). PCR conditions for multiplex A were: 95 °C for five minutes, 28 cycles at 95 °C for 30 s, 55 °C for 90 s, and 72 °C for 30 s, and a final extension of 45 s at 60 °C. For multiplex B, PCR conditions were: 95 °C for five minutes, six cycles at 95 °C for 30 s, 48 °C for 90 s, and 72 °C for 30 s, 22 cycles at 95 °C for 30 s, 50 °C for 90 s, and 72 °C for 30 s, and a final extension at 60 °C for 45 s. We diluted PCR products (1:151) with deionised water and added Hi-Di™ Formamide (Applied Biosystems®) and GeneScan™ 600 LIZ® Size Standard (Applied Biosystems®). We performed fragment analysis on a 3500 Genetic Analyser (Applied Biosystems HITACHI®). We scored alleles in Geneious 11.0.2 (Kearse et al. 2012).

3. *Spatial distribution of genetic variability*

Analyses hereby presented were performed on the concatenated mitochondrial alignment (but see **Table S2** and **Fig S2** for locus specific results). We calculated haplotype diversities and nucleotide diversities (Nei and Li 1979) in DnaSP (Librado and Rozas 2009). We constructed haplotype networks using the median-joining algorithm (Bandelt et al. 1999) implemented in Network 5.0.0.1 (available at http://www.fluxus-engineering.com/sharenet.htm), treating insertion-deletion (indel) events as a fifth state.

We performed phylogenetic analyses using maximum likelihood (ML) and Bayesian (BA) methods. We partitioned coding genes, COI and Cytb, by base position (1^{st}, 2^{nd} and 3^{rd}) to identify the best-fitting substitution model with jModeltest 2.1.10 (Darriba et al. 2012) with the Akaike information criteria corrected for small sample sizes. Best models are reported in **Table S3**. We conducted BA in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Selected models unimplemented in MrBayes were replaced by the closest overparameterized model available (Huelsenbeck and Rannala 2004). All analyses were performed on concatenated and individual markers. We ran five independent analyses in MrBayes (20 million generations) and the first 380,000 generations were discarded as burn-in. We performed ML analyses in Garli 2.0 (Zwickl 2006). We carried out five independent runs and evaluated statistical confidence in nodes using 1,000 non-parametric bootstrap replicates.

In addition, we generated maps displaying the geographic distribution of local genetic diversity. For this purpose, we first used a sliding window approach to estimate the nucleotide diversity π (Nei and Li 1979) associated with each cell of a template raster grid covering the study area (spatial resolution: 12.5 arcmin). This method attributes, to each grid cell, a value of nucleotide diversity estimated from sequences sampled within a circle centered on the considered cell. Nucleotide diversity is corrected for unequal sample size and is based on both allelic frequencies and genetic distances between sequences, which are complementary aspects when studying distribution of genetic variability. The sliding window is implemented in a R script available with the toolbox SPADS (Dellicour and Mardulyn 2014). We tested several values for the radius r (25, 50, 100, and 200 km) used to define the sliding window. Several radius values were tested in order to evaluate the impact of the sliding window extent on the genetic diversity distribution. Starting from the raster files obtained by the sliding window approach, we then performed an inverse distance interpolation with the R function "GDivPAL" also available with the toolbox SPADS (distance weighting parameter a = 5). As a third step, we drew a convex hull around fictive circles of 100 km radius centered on sampling locations for each generated interpolation surface in order to define the different "study areas" by cropping the surfaces and thus avoiding excessive extrapolation. Only results with a radius of 50 km are presented and maps with other radius are available in **Fig. S3**. The use of the sliding window approach allows to avoid the arbitrary "population" delimitation and to minimize the effect of small sampling sizes (Lecocq et al. 2018). Indeed, through this approach, the genetic diversity is estimated within a circle radius. For a particular location, the genetic diversity can thus be estimated from a large number of individuals even though few individuals were sampled per site (except in the case of isolated sampling sites).

For the microsatellite dataset, potential errors (allelic dropouts, stuttering, and null alleles) were assessed using the MICRO-CHECKER software (Van Oosterhout et al. 2004). We conducted a factorial correspondence analysis (FCA) as implemented in the program GENETIX 4.02 (Belkhir et al. 2004) in order to get a graphical representation of genetic variation among individuals. We estimated global locus genetic diversity through the computation of two coefficients in HP-RARE 1.1 program (Kalinowski 2005): number of alleles per locus (A) and allelic richness (Ar). Number of private alleles was assessed in GenAIEx 6.5 (Peakall and Smouse 2006) and observed (Ho) and expected (He) heterozygosities were calculated in GENETIX. As for the analysis of mitochondrial sequences, we generated a map representing the geographic distribution of genetic variability. For this purpose, we estimated and averaged the Bray-Curtis dissimilarity (Bray and Curtis 1957) within a sliding window using the same interpolation protocol detailed above for mitochondrial sequences.

4. Population structure

For mitochondrial sequences, we first assessed population structure by estimating Φ_{ST} statistic on sampling sites through an Analysis of MOlecular VAriance (AMOVA; i.e. when considering only one group of sampling sites; Excoffier et al. 1992) performed in Arlequin 3.5 (Excoffier and Lischer 2010) with 10,000 permutations. We then used SPADS to estimate the phylogeographic structure as measured by $N_{ST} - G_{ST}$ (Pons and Petit 1996), and its statistical significance was tested by recalculating them with 10,000 random permutations of haplotypes in the original data sets. As the global Φ_{ST} estimate was significant, patterns of genetic variation were assessed by Spatial Analysis of MOlecular VAriance (SAMOVA; K=2 to K=10; 10,000 iterations, ten repetitions; Dupanloup et al. 2002) as implemented in SPADS.

The SAMOVA algorithm assigns sampling sites to groups (or "clusters") based on geographic vicinity and sequence similarity. The number of clusters reflecting the most-likely genetic structure was chosen based on the maximized among-group variation (Φ_{CT}). Among the ten repetitions performed for a given K (number of clusters) to identify, we systematically kept the run associated with the highest value of Φ_{CT}.

For microsatellites data, we first assessed global differentiation by estimating F_{ST} statistic on sampling sites (i.e. when considering only one group of sampling sites) through an AMOVA performed in Arlequin 3.5 (Excoffier and Lischer 2010) with 10,000 permutations. Genetic population structure was assessed with the Bayesian clustering method implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000) that aims to identify population clusters respecting Hardy-Weinberg and linkage equilibriums. We performed ten independent STRUCTURE runs for each tested value of K ranging from one to 50. Each run was made of 10 million Markov chain Monte Carlo iterations, discarding the first one million iterations as burn-in. We used the model with correlated allele frequencies and assuming admixture. The most probable K was identified based on the consensus of the ΔK method (Evanno et al. 2005) and of log-likelihood values associated with each K ("log(P(K)) method") using STRUCTURE HARVESTER 0.9.94 (Earl and VonHoldt, 2012). We conducted another analysis with the most probable K using the software CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) to calculate individual ancestry values (one Q-value per cluster) averaged over ten runs using the "Greedy" algorithm.

RESULTS

1. *Sequence and microsatellite variation*

The concatenated mitochondrial alignment resulted in 1,893 aligned nucleotides: 541 base pairs (bp) from 16S (10 variable sites), 641 bp from COI (23 variable sites), 399 bp from Cytb (18 variable sites), and 312 bp from D-Loop (seven variable sites; see descriptive indicators in **Table S2**). Our median-joining network results showed a star-like structure with one dominating haplotype surrounded by several haplotypes (distant from the main haplotype by one or two mutations) as well as other less frequent haplotypes (**Fig. 2A**). For the microsatellite dataset based on eight markers, there was no significant evidence for the presence of scoring errors across populations. Number of alleles varied from 14 (Yp111) to 40 (Svi17) between loci across samples and descriptive indicators are available in **Table S4**.

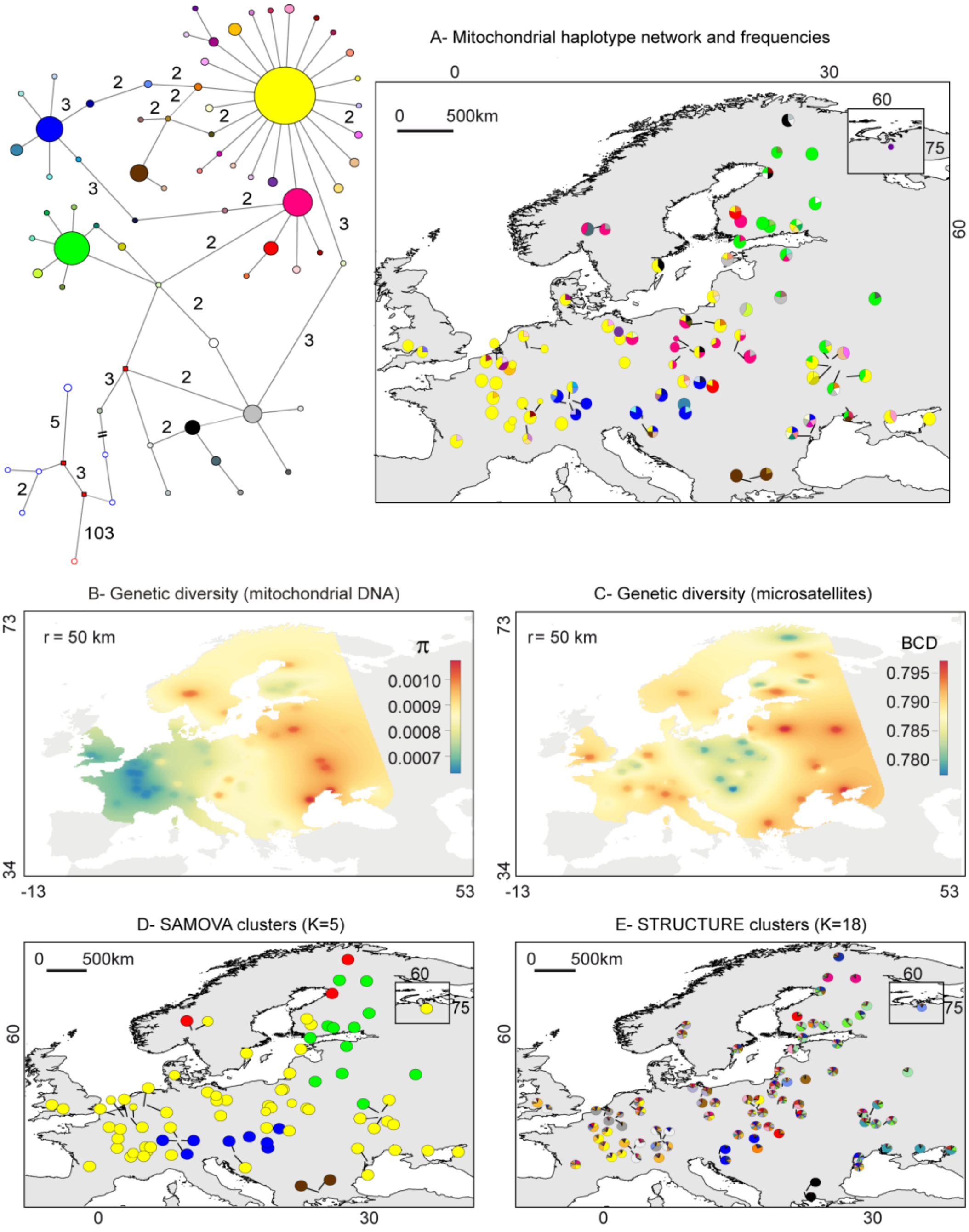
2. *Geographic distribution of genetic variability*

Overall, our median-joining network (64 different haplotypes) based on mitochondrial concatenated alignment supported the geographic genetic differentiation between five major groups of haplotypes (**Fig. 2A**): (i) the current European Plain (i.e. ranges from the Pyrenees Mountains across northern Europe to the Ural Mountains in Russia), (ii) the Danube drainage system and Alpine Foreland (i.e. from Lake Constance in the west to Linz in the east), (iii) the Balkans, (iv) western and northern Fennoscandia, and (v) eastern Europe (i.e. between 20°E and 40°E and between 45°N and 70°N). ML and BA phylogenetic analyses led to similar tree topologies, thus here we present only results obtained with the concatenated matrix with Bayesian analyses. The overall geographic pattern for each marker is similar to network analyses, except for the delineation between western and northern Fennoscandia and eastern Europe (**Fig. S4**). However, there was no lineage sorting within *P. fluviatilis* and intraspecific lineages were not well supported (**Fig. S4**). Nonetheless, with all markers and different analyses, Danube individuals formed a monophyletic group. Regarding microsatellites, the FCA showed that Balkans, Danube and Alpine Foreland tended to be slightly separated from other sampling sites (**Fig. S5**).

Mapping of local genetic diversity based on mitochondrial sequences and microsatellites showed that this genetic diversity was unevenly distributed (**Fig. 2B-C**). The mitochondrial nucleotide diversity was higher in Fennoscandia, surrounding the Danube and along an eastern diagonal (i.e. from Baltic countries to the north of the Black Sea; **Fig. 2B**). On the contrary, lower diversity was highlighted in western Europe. Genetic diversity estimated with microsatellites was quite homogeneous across the sampling range with lower genetic diversity spots in western and central Europe as well as in southern and northern Finland (**Fig. 2C**).

Figure 2: Mitochondrial haplotype network, distribution of genetic diversity and population structure of *Perca fluviatilis*. (A) Mitochondrial median-joining haplotype network and spatial distribution of haplotype frequencies based on the concatenated alignment. In the network, each haplotype is represented by a circle, circle sizes are relative to haplotype frequencies and numbers correspond to the number of mutations that differentiates haplotypes (absence of number corresponding to a single mutation). Red squares on lines represent undetected/extinct intermediate haplotype states. Black circles correspond to *P. fluviatilis* sequences, empty red circles to *Perca flavescens* sequences, and empty blue circles to *Perca schrenkii* sequences. The adjacent map reports the haplotype frequencies in each sampling site and corresponding pie chart colors refer to the corresponding haplotype color of the network. Pie chart sizes are relative to the number of individuals

analysed for each sampling site. (B) Interpolation of genetic diversity (nucleotide diversity π) estimated with the concatenated alignment of mitochondrial sequences (r =50 km). (C) Interpolation of genetic diversity (Bray-Curtis dissimilarity “BCD”) estimated with the eight microsatellite markers (r = 50 km). (D) Results of genetic clustering based on the concatenated alignment of mitochondrial sequences (spatial analysis of molecular variance). (E) Results of genetic clustering based on microsatellites (STRUCTURE). For clustering analyses (D-E), we only report the clusters identified for the best-supported partition, i.e. K = 5 clusters for SAMOVA (based on the concatenated mitochondrial sequences alignment) and K = 18 clusters for STRUCTURE (based on microsatellites). On these maps, pie charts sizes indicate the number of samples collected from a sampling site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).



3. *Population structure*

Geographic structuring was significantly supported by analysis of AMOVA which indicated a differentiation over all sampling sites (Φ_{ST} = 0.58, p-value < 0.05). We also found a significant phylogeographic signal (N_{ST} - G_{ST} = 0.14, p-value < 0.05). In SAMOVA, Φ_{CT} decreased until K = 6 clusters before increasing with higher number of clusters, levelling out at K = 8 (Φ_{CT} = 0.64, Φ_{ST} = 0.70, Φ_{SC} = 0.17; **Table S5**). Two levels of structure were distinguished to fit our results: K = 2 and K = 5. At K = 2, the clustering split sampling locations belonging to the Danube drainage basin along with one sampling location of the Alpine Foreland *versus* all other sampling locations. With increasing number of clusters, the clustering split sampling locations from the (i) Balkans, (ii) eastern Europe, (iii) western and northern Fennoscandia, and (iv) the European Plain. Above K = 5, additional clusters corresponded to single sampling sites which made little biological sense. Therefore, structure at K = 5 (Φ_{CT} = 0.63, Φ_{ST} = 0.70, Φ_{SC} = 0.19) was considered (**Fig. 2D**). The K = 5 geographic clusters were congruent with results obtained in haplotype networks.

Overall AMOVA based on microsatellites revealed a significant genetic differentiation (F_{ST}=0.21, p-value < 0.05). STRUCTURE analyses based on this dataset identified a best supported value for K = 18 clusters (**Fig. S6**). Overall, these 18 clusters were consistent with SAMOVA clusters identified with mitochondrial sequences since they appeared as subdivisions of the five SAMOVA clusters: (i) European Plain cluster is subdivided into eleven subgroups, (ii) western and northern Fennoscandia cluster matches with microsatellite subgroups except for the Norwegian sampling site, (iii) eastern Europe cluster is split into three subgroups, (iv) Danube cluster is divided into two subgroups, and (v) Balkans cluster is identical to the mitochondrial one. There were few mismatches with mitochondrial clusters (i.e. in the border areas in southern Fennoscandia, north of the Danube, and in eastern Europe; **Fig. 2E**).

DISCUSSION

Although similar sampling size is used in several other phylogeographic studies (e.g. Fontanella et al. 2008; Lougheed et al. 2013; for fishes: Cook et al. 2017; Santos et al. 2009), our results for regions associated with lower sampling effort (i.e. Scandinavia, South-East Europe, and Russia) should be considered with caution. Indeed, lower sampling efforts could impact the accuracy of genetic diversity estimates or the relevance of population structure analysis. Therefore, we cannot rule out potential artefactual conclusions in these areas.

However, we argue that the observed global phylogeographic patterns are likely since a previous study with higher sampling effort in these areas obtained similar results (Nesbø et al. 1999; i.e. specific haplotypes[s] in Scandinavia and southern Europe corresponding to haplotypes found in this study).

1. *Spatial distribution of genetic variability in Perca fluviatilis*

Mitochondrial DNA-based analyses show an uneven distribution of the genetic variability (**Fig. 2A-B**). The observed strong genetic structure between populations (**Fig. 2A**) shapes five major clusters occurring in different geographic regions of the *P. fluviatilis* range (**Fig. 2D**): (i) the European Plain, (ii) west-northern Fennoscandia, (iii) eastern Europe, (iv) the Danube and the Alpine Foreland (hereafter called Danube), and (v) the Balkans. Mapping of spatial distribution of genetic diversity shows some hotspots across the species range (**Fig. 2B**): (i) in the eastern diagonal which reflects the suture zone between the European Plain and eastern Europe clusters, (ii) in northern Finland where west-northern Fennoscandia and eastern Europe clusters co-occur, and (iii) in the Alpine Foreland, north of the Danube basin, and in Slovenia where European Plain and Danube clusters meet. Microsatellites-based analyses highlight a similar uneven distribution of the genetic variability. Although more genetic diversity hotspots occur in western Europe, the population structure is overall a subdivision of mitochondrial clusters (**Fig. 2C-D**). Microsatellites-based results should be carefully considered since they are based on a limited sampling size but their congruence with mitochondrial DNA-based analyses tends to support their relevance (**Fig. 2**). The differences between the two types of genetic information are most likely due to nuclear genome specificities in effective population size and mutation rates (Arif and Khan 2009; Johnson et al. 2003; Selkoe and Toonen 2006) that increase the variability of microsatellite dataset making short-range differentiation more likely (as observed in other species; e.g. Wirth and Bernatchez 2001).

The geographic pattern of genetic variability identified in the present study slightly differs from previous studies on the European perch (e.g. Christensen et al. 2016; Nesbø et al. 1999). Firstly, we detect genetic difference between populations from Danube region and from south-east Europe, which belong to different clusters, while previous studies regarded them as a single unit (Nesbø et al. 1999). Secondly, we highlight the larger geographic range of the European Plain cluster in south-east Europe and Siberia which were previously assigned to the eastern Europe group (Nesbø et al. 1999). These differences are most likely due to the use of different sampling efforts and genetic information. Indeed, current analyses are based on sampling including more populations from Danube and Black Sea regions along with a larger amount of genetic information (i.e. compared to Nesbø et al. 1999).

Observed geographic pattern of genetic variability is similar to other European freshwater species (e.g. Durand et al. 1999; Gum et al. 2005; Østbye et al. 2005). However, *P. fluviatilis* displays high genetic variability in eastern Europe, Fennoscandia, and central Europe while most European freshwater fish species have their genetic variability hotspots in southern Europe (e.g. Durand et al. 1999; Gum et al. 2005 but see Kotlík and Berrebi 2001).

2. *Potential shaping factors of the geographic patterns of genetic variability*

The observed genetic variability pattern of the European perch can be poorly explained by current barriers to gene flow (e.g. drainage basins, seas). Therefore, we argue that this pattern and large scale population structure have been most likely shaped by past biogeographic events as for other species (e.g. Costedoat and Gilles 2009; Hewitt 2004b, 2001). We suggest that *P. fluviatilis* survived to the last Ice-Age in at least three main refugia (i.e. regions currently displaying strong genetic specificities and higher genetic variability; **Fig. 2A-B**): (i) in the west of the European Plain (between 5°E and 20°E), (ii) in the north-east of the European Plain (potentially located in a large ice dammed lake east of the north European ice sheet; Mangerud et al. 2004; Maslenikova and Mangerud 2001), and (iii) in the upper part of the Danube drainage basin (i.e. west of 20°E). Two other areas may also have acted as refugia: the Balkans and the west-northern Fennoscandia since they host endemic haplotypes. However, the low genetic variability and the lack of sufficient amount of samples from the above areas makes difficult to assess if these regions (i) were refugia in which repeated or protracted bottleneck events decreased the local genetic diversity (Avise 2000; Petit et al. 2003) or (ii) were secondarily colonized from one of the three main refugia and then underwent local genetic differentiation (Kotlík and Berrebi 2001). Additional sampling from eastern drainages and western Fennoscandia are needed to test these hypotheses.

The sub-structuring of mitochondrial DNA-based clusters detected by the microsatellite analyses and previous studies (e.g. Bergek and Björklund 2009; Butkauskas et al. 2012; Olsson et al. 2011) is most likely due to local differentiation phenomena fostered by species intrinsic features. First, the species natal homing behavior reduces gene flow between populations leading to local genetic structuring (Järv 2000). Second, species short migration distances (from one to 20 km; Stepien et al. 2015; Zamora and Moreno-Amich 2002) can further increase the structuring at local geographic scale by decreasing gene flow between adjacent populations. Third, selective disadvantage of foreign individuals due to local environmental conditions and (partial) post-zygotic reproduction isolation between allopatric populations observed in *P. fluviatilis* (Behrmann-Godel 2004; Behrmann-Godel et al. 2006, 2004; Behrmann-Godel and Gerlach 2008) can limit gene flow and shape genetic differentiation between neighboring populations.

3. *Considering spatial patterns of genetic variability for Perca fluviatilis aquaculture: Towards an improved production?*

Improving *P. fluviatilis* aquaculture is a major challenge for fish farmers since they are facing several bottlenecks which are limiting *P. fluviatilis* economic development such as low survival and growth rates, high growth heterogeneity, cannibalism, or low egg quality (Kestemont et al. 2015a). Moreover, genetic diversity is also a limiting factor in breeding programs since it can lead to inbreeding depression (Mignon-Grasteau et al. 2005). One solution to overcome current issues consists in (i) sampling individuals to create fish farmers stocks in genetic diversity hotspots and (ii) taking into account variation of zootechnical traits between geographically distinct populations of the European perch. Indeed, this latter could be potentially relevant since variations in traits related to growth (e.g. growth rate, growth heterogeneity rate), development (e.g. swim bladder inflation rate, survival rate), organoleptic characteristics (e.g. color, filet quality), and behavior (cannibalism rate, group structure) have been highlighted in *P. fluviatilis* (Mairesse et al. 2006; Mandiki et al. 2004; Mélard et al. 2003; Pimakhin et al. 2015; Pimakhin and Zak 2014, Toomey et al. 2019, Vanina et al. 2019a). Moreover, differences in growth and survival rates between several populations (i.e. Belgian, Finnish, French, and Italian; Mandiki et al. 2004) correspond to genetically differentiated groups in our analyses (**Fig. 2**). In the same way, aggressiveness and group structure differ between two Finnish populations and Geneva Lake which belong to different genetic groups (Toomey et al. 2019). Therefore, we suggest that investigations of populations from different genetic groups could allow highlighting populations with divergent performances for aquaculture.

4. *Implications and future guidelines for conservation, management, and production of the European perch*

For the time being, the European perch does not seem to be threatened by potential issues that could modify its geographic genetic variability pattern. Indeed, *P. fluviatilis* (i) is not a threatened species (Freyhof and Kottelat 2008), (ii) has a quite large ecological niche (Kestemont et al. 2015a), (iii) has presumably undergone few within-range translocations (often unintentional; but it can constitute up to 11.6% of unintentionally stocked fishes when stocking material is produced in Polish carp ponds, Kaczkowsk 2006), (iv) is not presumably the subject of restocking programs, and (v) has low dispersion potential (Stepien et al. 2015; Zamora and Moreno-Amich 2002). However, the ongoing development of its aquaculture could change this situation (Fontaine 2004; Kestemont et al. 2015a; Kestemont and Mélard 2000). Consequently, we argue that production, trade, and translocations of the European perch should be regulated at the nascent stage of the production (see also Allendorf 1991) in order to avoid detrimental problems observed for other fish species (e.g. Fleming et al. 2000; Lemer and Planes 2012; McGinnity et al. 2003).

In this perspective, prohibition of all importations of wild *P. fluviatilis* to lands inhabited by distinct genetic populations should be promoted to hamper potential genetic homogenization as well as risks of competition with local populations from the translocation of non-native populations performing better (see for example Michener 1975; Vehanen et al. 2009). Moreover, characterizations of current *P. fluviatilis* farmed stocks have shown specificities compared to wild populations in the neighboring areas of production facilities (Ben Khadher et al. 2016). This means that escapees from fish farms could lead to genetic introgression and, potentially, fitness decrease in the wild (i.e. hybrid offspring from wild and domestic parents are often less adapted to local environment; Besnier et al. 2015; Bolstad et al. 2017; Tufto 2017). One could expect that using local populations or at least populations belonging to the same genetic group could avoid further issues (Youngson et al. 2003). However, captive breeding leads rapidly to genetic changes through adaptation to captive environment (Williams and Hoffman 2009). Therefore, regulations aiming at limiting gene flow from fish farms should be strongly encouraged, even in indoor aquaculture for which risks cannot be excluded (Summerfelt and Vinci 2009).

5. *Further prospects*

The European perch aquaculture is currently at the beginning of its development and we consider that it is a good opportunity to (i) carefully plan future production and translocation management strategies and (ii) investigate genetic units ‘intraspecific differentiation of zootechnical traits to improve production. In order to promote a better management strategy, it could also be useful to delineate evolutionarily significant units (Moritz 1994), widely used in conservation and fisheries management, by considering other lines of evidence such as phenotypic traits. Here applied to *P. fluviatilis*, the provision of guidelines through the consideration of spatial patterns of genetic variability could be applied to other socioeconomically interesting species exhibiting intraspecific geographic differentiation.

SUPPORTING INFORMATION

Table S1: *Perca fluviatilis* sampling sites.

This table is too large to be included in the manuscript. It is available at: https://www.sciencedirect.com/science/article/abs/pii/S0044848618323640

Table S2: Descriptive indicators for each locus and for the concatenated alignment of *Perca fluviatilis*. G_{ST}, N_{ST} and Φ_{ST} correspond to genetic differentiation metrics (see the text for further details). (*) refers to p-values < 0.05.

Locus	16S	COI	CytB	D-Loop	Concatenated matrix
Sequence length (bp)	541	641	399	312	1893
Number of variable sites	10	23	18	7	58
Number of haplotypes	11	22	16	7	64
Haplotype diversity	0.32	0.73	0.59	0.40	0.83
Nucleotide diversity	0.00048	0.0030	0.0023	0.0025	0.0021
G_{ST}	0.56 *	0.57 *	0.53 *	0.49 *	0.43 *
N_{ST}	0.61 *	0.62 *	0.42 *	0.62 *	0.58 *
N_{ST} - G_{ST}	0.05 *	0.04 *	-0.10	0.13 *	0.14 *
Global Φ_{ST} for K=1	0.60 *	0.63 *	0.43 *	0.62 *	0.58 *

G_{ST}, N_{ST} and Φ_{ST} correspond to genetic differentiation metrics (see the text for further details). (*) refers to p-values < 0.05.

Table S3: Best-fitting substitution models identified with jModeltest for the different genes and the concatenated mitochondrial alignment of *Perca fluviatilis*. Locus corresponds to the gene or the concatenated matrix according to codon position for coding genes (COI and Cytb). Best fitting model corresponds to the model found using jModeltest with the Akaike information criteria corrected for small sample sizes. MrBayes substitution model corresponds to the closest over-parameterized model available.

Locus	Best fitting model	MrBayes substitution model
16S	K80	-
COI 1st	GTR	-
COI 2nd	TVM	GTR
COI 3rd	TIM1+G	GTR+G
Cytb 1st	TVM+I	GTR+I
Cytb 2nd	TrN+I	GTR+I
Cytb 3rd	GTR	-
D-Loop	TIM1+I	GTR+I
Concatenated matrix	TPM3uf+I+G	GTR+I+G

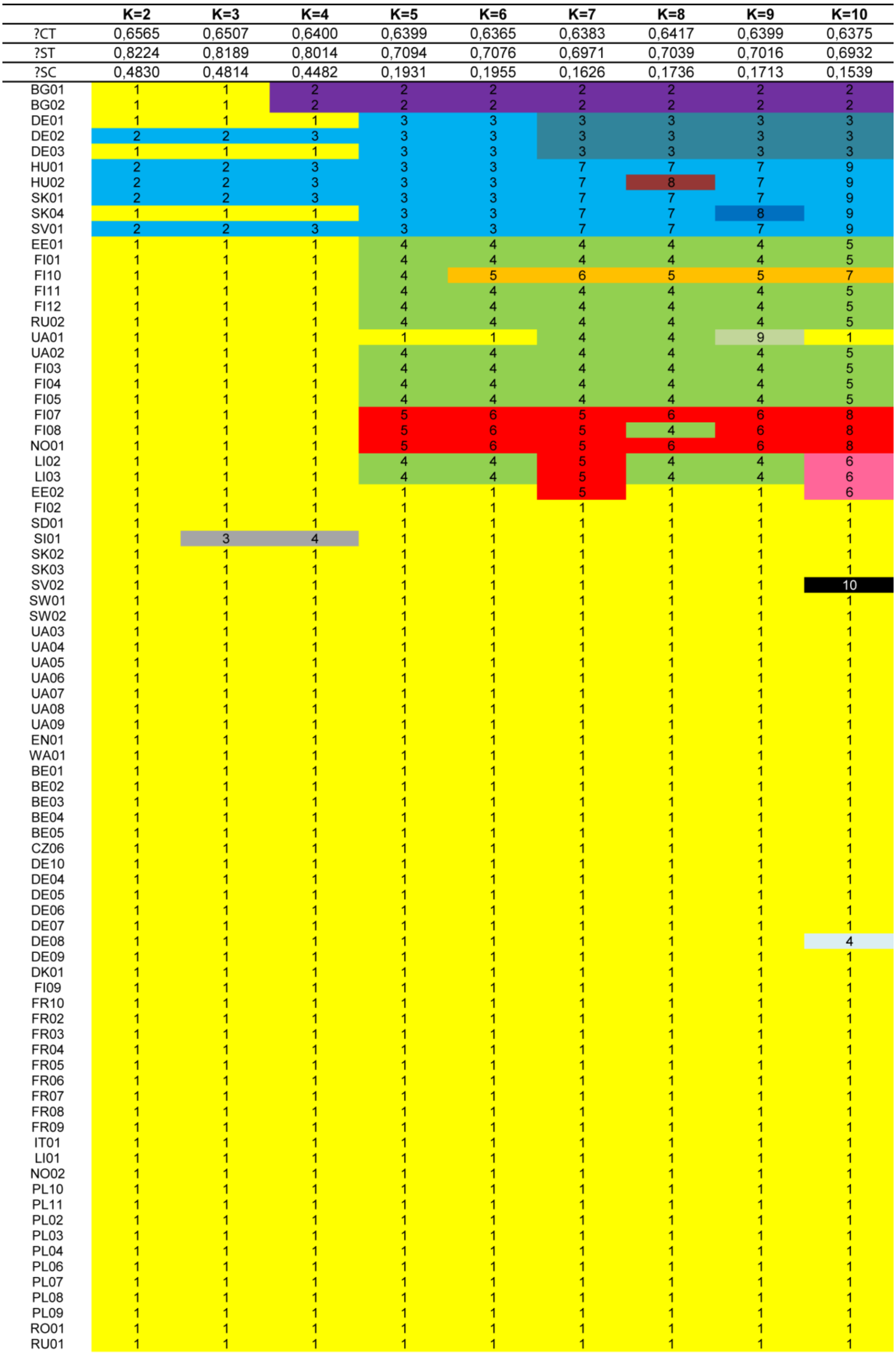
Locus corresponds to the gene or the concatenated matrix according to codon position for coding genes (COI and Cytb). Best fitting model corresponds to the model found using jModeltest with the Akaike information criteria corrected for small sample sizes. MrBayes substitution model corresponds to the closest over-parameterized model available.

Table S4: Properties of the eight microsatellite loci of *Perca fluviatilis* used in this study. A: number of alleles per locus; Ar: allelic richness, Ho and He: observed and expected (He) heterozygosities.

	Svi17	PflaL2	SviL7	PflaL4	YP111	PflaL6	YP60	PflaL1	Total over loci and populations
A	40	35	28	22	14	18	19	23	-
Ar	4.06	4.39	3.87	4.01	2.67	2.72	3.87	3.52	-
Ho	0.563	0.701	0.467	0.535	0.557	0.577	0.618	0.534	0.569
He	0.657	0.668	0.630	0.653	0.500	0.476	0.627	0.611	0.603

A: number of alleles per locus; Ar: allelic richness, Ho and He: observed and expected (He) heterozygosities.

Table S5: Spatial analysis of molecular variance (SAMOVA) based on the concatenated mitochondrial alignment (16S, COI, D-loop and Cytb) for *Perca fluviatilis*. Analyses were performed for K values ranging from one to 10 with 10,000 iterations and 10 repetitions. For each K, the best run was selected based on its associated Φ_{CT} (see the text for further details). Colors and numbers indicate the SAMOVA clusters identified for each sampling location for a given value of K.



	K=2	K=3	K=4	K=5	K=6	K=7	K=8	K=9	K=10
?CT	0,6565	0,6507	0,6400	0,6399	0,6365	0,6383	0,6417	0,6399	0,6375
?ST	0,8224	0,8189	0,8014	0,7094	0,7076	0,6971	0,7039	0,7016	0,6932
?SC	0,4830	0,4814	0,4482	0,1931	0,1955	0,1626	0,1736	0,1713	0,1539
BG01	1	1	2	2	2	2	2	2	2
BG02	1	1	2	2	2	2	2	2	2
DE01	1	1	1	3	3	3	3	3	3
DE02	2	2	3	3	3	3	3	3	3
DE03	1	1	1	3	3	3	3	3	3
HU01	2	2	3	3	3	7	7	7	9
HU02	2	2	3	3	3	7	8	7	9
SK01	2	2	3	3	3	7	7	7	9
SK04	1	1	1	3	3	7	7	8	9
SV01	2	2	3	3	3	7	7	7	9
EE01	1	1	1	4	4	4	4	4	5
FI01	1	1	1	4	4	4	4	4	5
FI10	1	1	1	4	5	6	5	5	7
FI11	1	1	1	4	4	4	4	4	5
FI12	1	1	1	4	4	4	4	4	5
RU02	1	1	1	4	4	4	4	4	5
UA01	1	1	1	1	1	4	4	9	1
UA02	1	1	1	4	4	4	4	4	5
FI03	1	1	1	4	4	4	4	4	5
FI04	1	1	1	4	4	4	4	4	5
FI05	1	1	1	4	4	4	4	4	5
FI07	1	1	1	5	6	5	6	6	8
FI08	1	1	1	5	6	5	4	6	8
NO01	1	1	1	5	6	5	6	6	8
LI02	1	1	1	4	4	5	4	4	6
LI03	1	1	1	4	4	5	4	4	6
EE02	1	1	1	1	1	5	1	1	6
FI02	1	1	1	1	1	1	1	1	1
SD01	1	1	1	1	1	1	1	1	1
SI01	1	3	4	1	1	1	1	1	1
SK02	1	1	1	1	1	1	1	1	1
SK03	1	1	1	1	1	1	1	1	1
SV02	1	1	1	1	1	1	1	1	10
SW01	1	1	1	1	1	1	1	1	1
SW02	1	1	1	1	1	1	1	1	1
UA03	1	1	1	1	1	1	1	1	1
UA04	1	1	1	1	1	1	1	1	1
UA05	1	1	1	1	1	1	1	1	1
UA06	1	1	1	1	1	1	1	1	1
UA07	1	1	1	1	1	1	1	1	1
UA08	1	1	1	1	1	1	1	1	1
UA09	1	1	1	1	1	1	1	1	1
EN01	1	1	1	1	1	1	1	1	1
WA01	1	1	1	1	1	1	1	1	1
BE01	1	1	1	1	1	1	1	1	1
BE02	1	1	1	1	1	1	1	1	1
BE03	1	1	1	1	1	1	1	1	1
BE04	1	1	1	1	1	1	1	1	1
BE05	1	1	1	1	1	1	1	1	1
CZ06	1	1	1	1	1	1	1	1	1
DE10	1	1	1	1	1	1	1	1	1
DE04	1	1	1	1	1	1	1	1	1
DE05	1	1	1	1	1	1	1	1	1
DE06	1	1	1	1	1	1	1	1	1
DE07	1	1	1	1	1	1	1	1	1
DE08	1	1	1	1	1	1	1	1	4
DE09	1	1	1	1	1	1	1	1	1
DK01	1	1	1	1	1	1	1	1	1
FI09	1	1	1	1	1	1	1	1	1
FR10	1	1	1	1	1	1	1	1	1
FR02	1	1	1	1	1	1	1	1	1
FR03	1	1	1	1	1	1	1	1	1
FR04	1	1	1	1	1	1	1	1	1
FR05	1	1	1	1	1	1	1	1	1
FR06	1	1	1	1	1	1	1	1	1
FR07	1	1	1	1	1	1	1	1	1
FR08	1	1	1	1	1	1	1	1	1
FR09	1	1	1	1	1	1	1	1	1
IT01	1	1	1	1	1	1	1	1	1
LI01	1	1	1	1	1	1	1	1	1
NO02	1	1	1	1	1	1	1	1	1
PL10	1	1	1	1	1	1	1	1	1
PL11	1	1	1	1	1	1	1	1	1
PL02	1	1	1	1	1	1	1	1	1
PL03	1	1	1	1	1	1	1	1	1
PL04	1	1	1	1	1	1	1	1	1
PL06	1	1	1	1	1	1	1	1	1
PL07	1	1	1	1	1	1	1	1	1
PL08	1	1	1	1	1	1	1	1	1
PL09	1	1	1	1	1	1	1	1	1
RO01	1	1	1	1	1	1	1	1	1
RU01	1	1	1	1	1	1	1	1	1

Figure S1: Sampling map for *Perca fluviatilis*. Sampling sites are represented by blue circles and juxtaposed population names refer to Table S1.

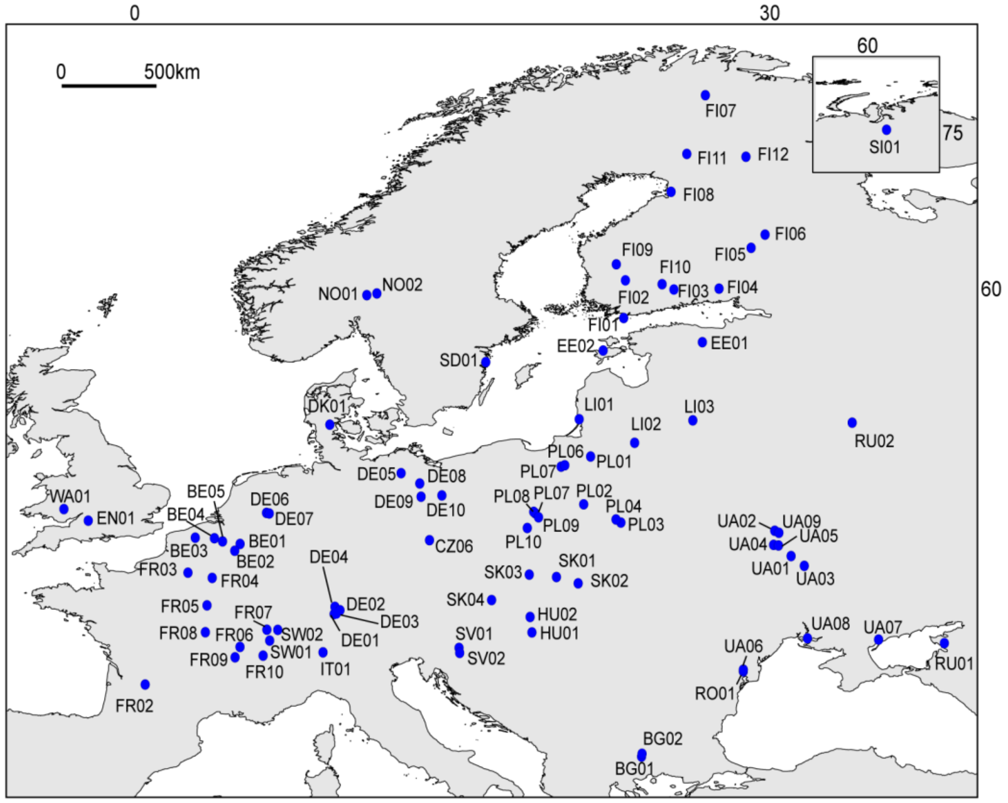


Figure S2: **Mitochondrial haplotype networks for each distinct locus as well as for the concatenated alignment of *Perca fluviatilis*.** For each mitochondrial locus as well as for the concatenated alignment, we report the median-joining network and the spatial distribution of haplotypes, i.e. pie charts indicating the haplotypes frequencies identified in each sampling site. In the network, each haplotype is represented by a circle and circle sizes are relative to haplotype frequencies. The number attributed to the line separating two haplotypes represents the number of mutations that differentiates these haplotypes (absence of number corresponding to a single mutation). Red squares on lines represent undetected/extinct intermediate haplotype states. Black circles correspond to *P. fluviatilis* sequences, empty red circles to *P. flavescens* sequences, and empty blue circles to *P. schrenkii* sequences. Each map reports haplotype frequencies in each sampling sites and colors refer to the corresponding haplotype color of the network. Pie chart sizes are relative to the number of individuals analyzed for each sampling site.

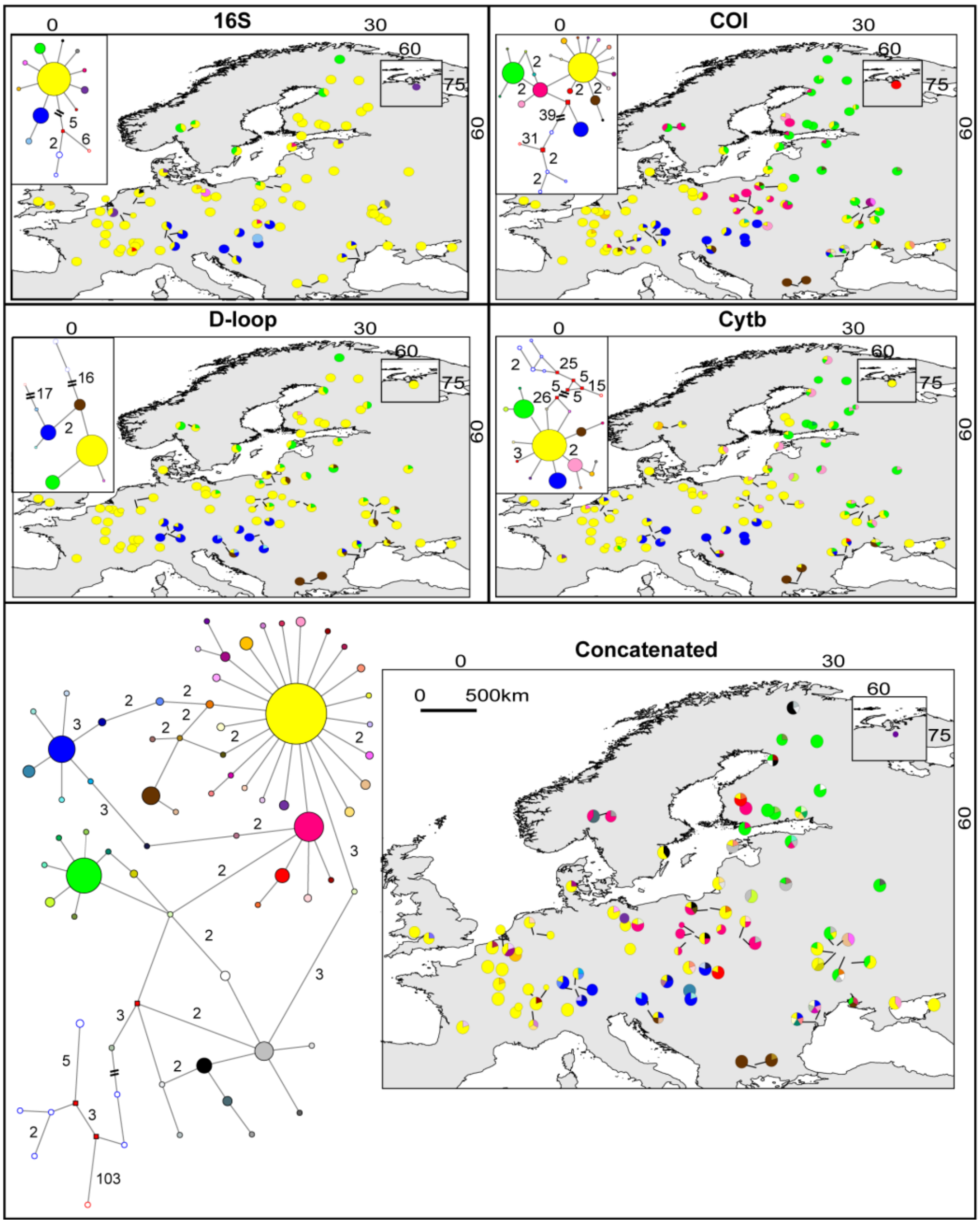


Figure S3 Interpolation of genetic diversity of *Perca fluviatilis* estimated with the concatenated alignment of mitochondrial sequences (nucleotide diversity π) or with the eight microsatellite markers (Bray-Curtis dissimilarity "BCD") (see the text for further details on the interpolation procedure) for several radius (25, 100, and 200 km).

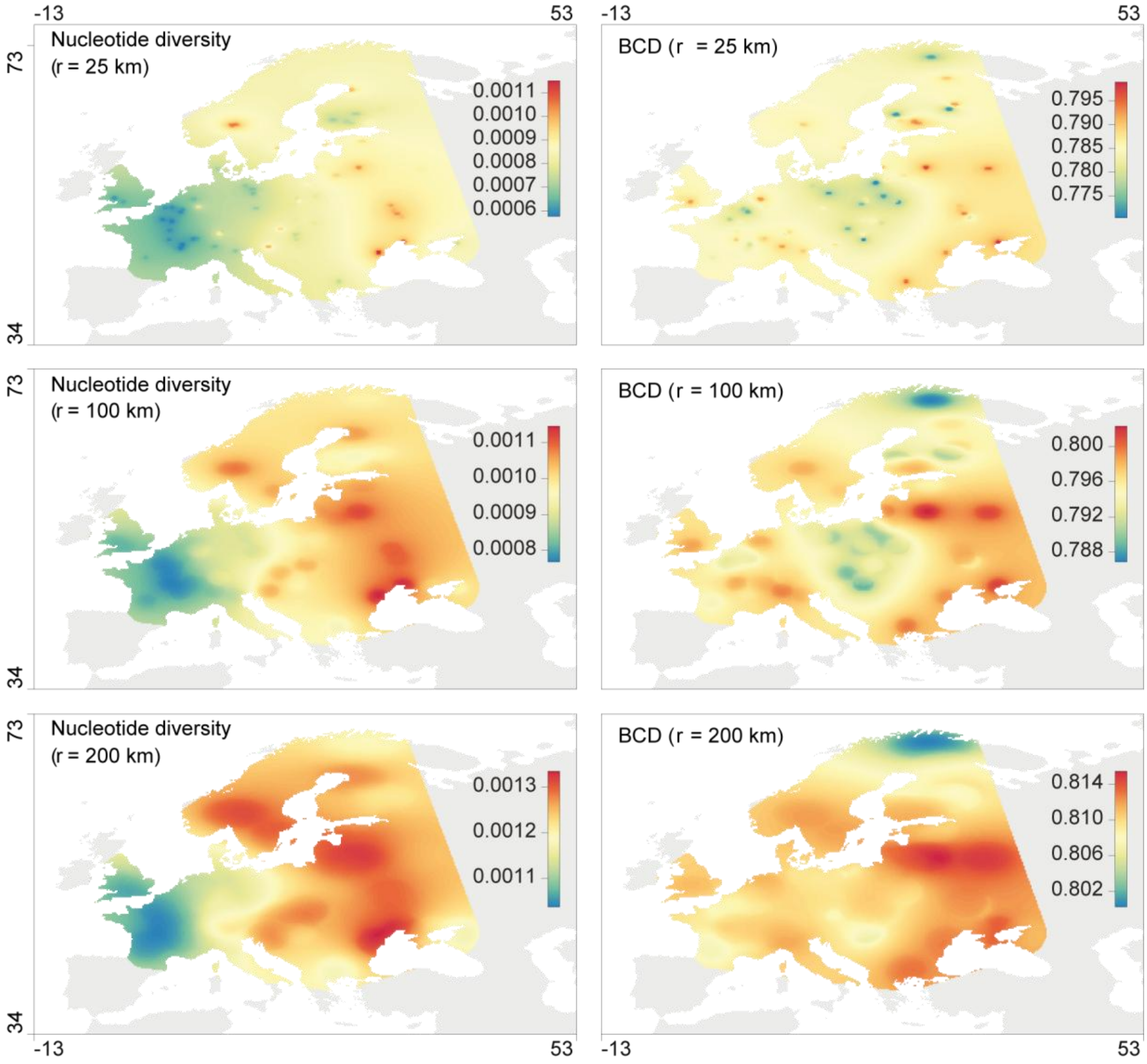


Figure S4: **Majority-rule consensus of the trees sampled by the Bayesian analysis performed on the concatenated molecular data matrix (COI, Cytb, D-loop and 16S) of *Perca fluviatilis*.** Values above branches are Bayesian posterior probabilities/Maximum likehood bootstrap values (only values > 0.5/50 are shown). Posterior probabilities and bootstrap values inferior to 0.95 or 95, respectively, are considered as poorly supported. Color labels of branches refer to geographic areas: yellow for the European Plain Europe, green for Northern and Eastern Europe, brown for the Balkans, and blue for the Danube. *P. schrenkii* and *P. flavescens* were used as outgroups to root the trees. Available at: https://www.sciencedirect.com/science/article/abs/pii/S0044848618323640

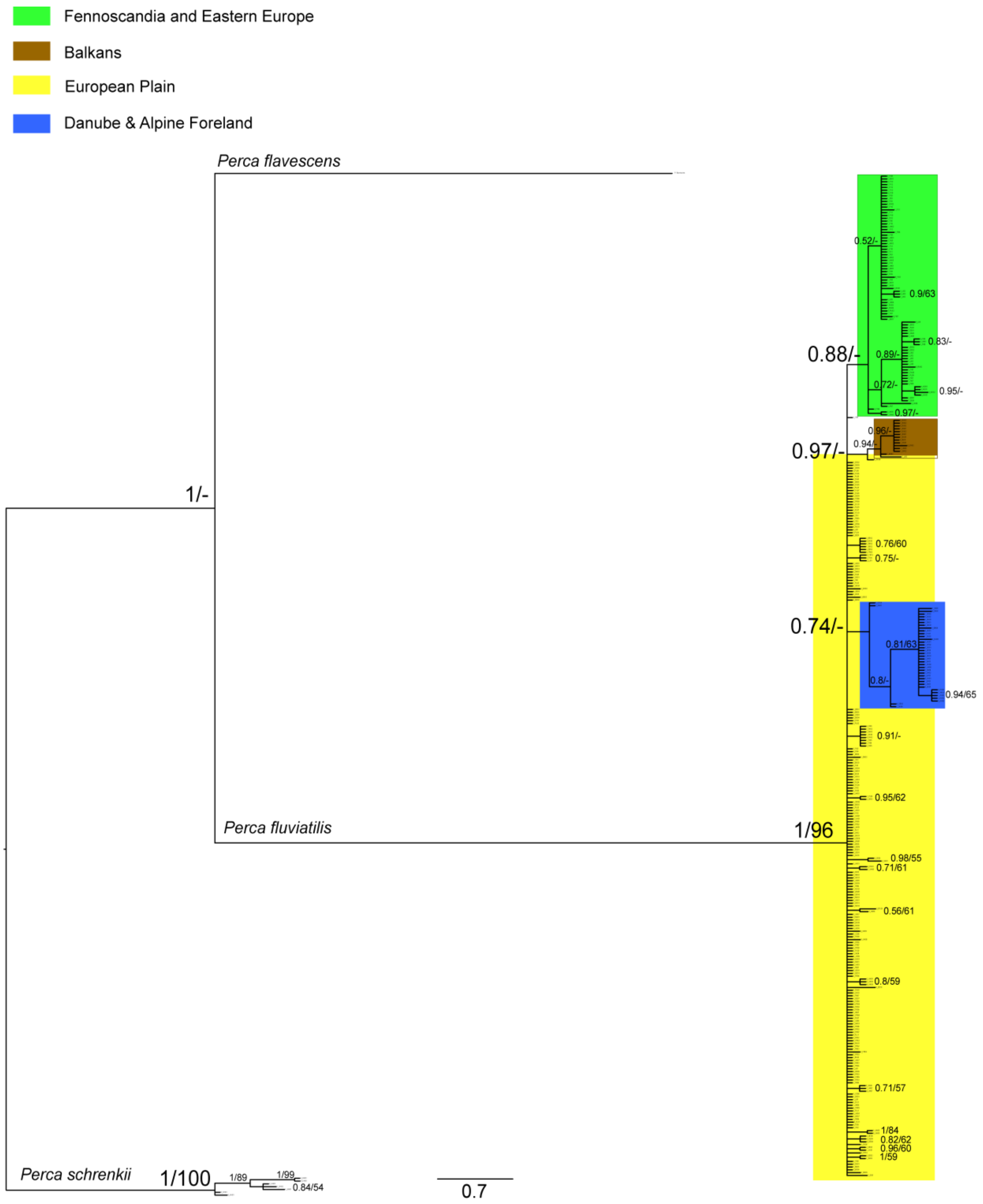


Figure S5: Factorial correspondence analysis based on eight microsatellites loci in the European perch (*Perca fluviatilis*). Each square represents a distinct sampling location. Sampling locations from the Balkans, the Danube drainage, and the Alpine Foreland are colored in red, blue, and green, respectively.

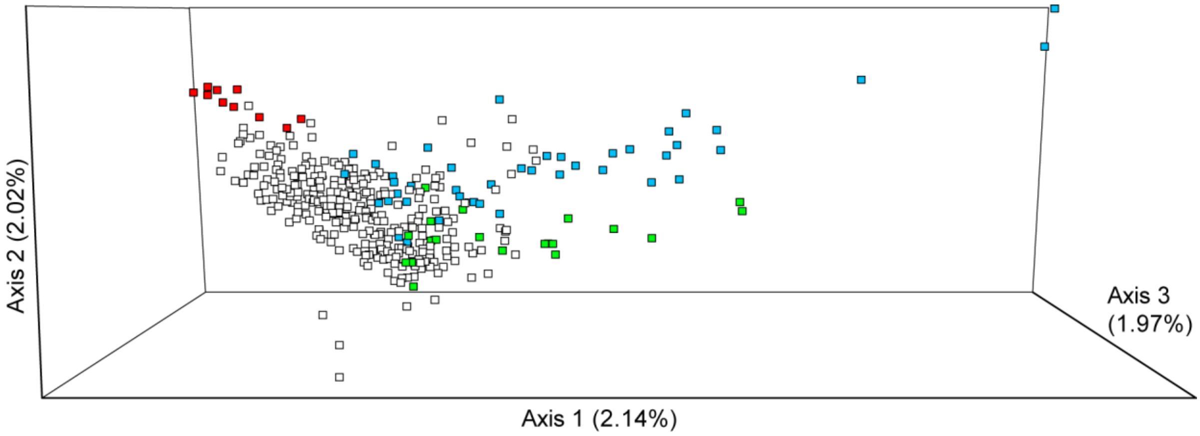
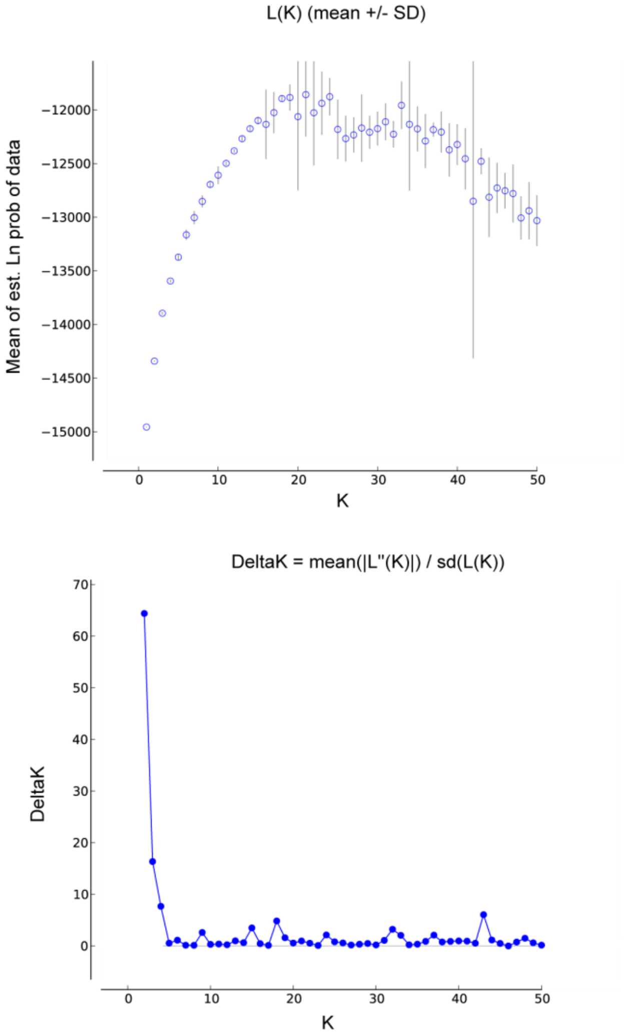


Figure S6: **STRUCTURE HARVESTER results using ΔK method of Evanno et al. (2005) and of log-likelihood values associated with each K ("log(P(K)) method") for *Perca fluviatilis***



DECLARATIONS

8.1 Ethics approval and consent to participate

Sample providers complied with institutional, national, and international guidelines and regulations as well as Nagoya protocol to obtain our fish clip samples. No ethic committee approval was necessary for the collection of fish clips. All fish treatments used for sampling were in accordance with the guidelines of the European Directive (2010/63/EU) on the protection of animals used for scientific purposes (and the French Animal Care Guidelines). In addition, *P. fluviatilis* is neither an endangered species nor a species at risk of Extinction according to the IUCN (Red List category: Least Concern).

8.2 Competing interests

Declarations of interest: none

8.3 Funding

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8.4 Author Contributions

LT, PF, and TL designed the study. LT, TV, JP, ZK, JK, PF, and TL contributed to the collection of fin samples. LT, TV, and MB contributed to laboratory analyses. LT, TV, SD, PF, FT, and TL analyzed and interpreted the results. All authors participated to manuscript writing. All authors read and approved the final manuscript.

8.5 Availability of data and materials

Mitochondrial sequences are available in GenBank (accession numbers: MG969725 to MG969793).

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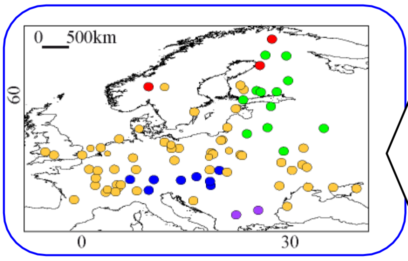
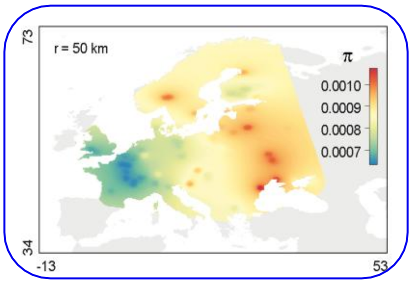
TAKE HOME MESSAGE

Genetic variability mapping



5 mitochondrial clusters further subdivided with microsatellites

European Plain
Danube & Alpine Foreland
Northern and Eastern Fennoscandia
Eastern Europe
Balkans

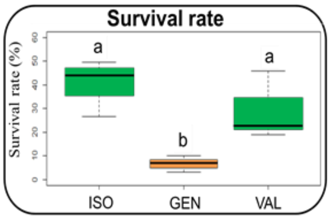


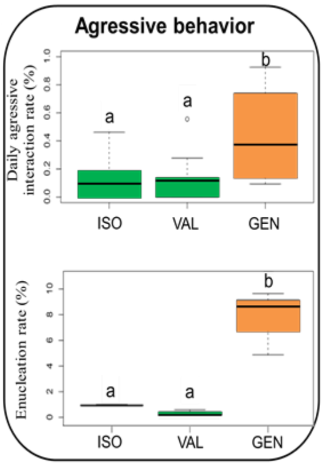
Uneven distribution of genetic variability

Translocation regulations

- Within-range translocations will most likely increase with production intensification and subsequent trade.
- Prohibition of all imports of wild *P. fluviatilis* to lands inhabited by distinct genetic populations should be promoted to prevent genetic homogenization, outbreeding and competition with wild conspecifics.
- Current farmed stocks have genetic specificities compared to wild populations in the neighboring areas of production facilities. Therefore, limiting gene flow from fish farms should be strongly encouraged.

WHAT ABOUT GEOGRAPHIC DIFFERENTIATION HIGHLIGHTED IN THE FIRST CHAPTER?





- Considering spatial patterns of genetic variability is potentially valuable to foster successful animal domestication/production
- Similarities between genetic differentiation (clusters identified) and zootechnical performances with two Finnish populations (Lakes Valkea-Mustajärvi VAL & Iso-Valkjärvi ISO) and one French population (Lake Geneva GEN) studied in the first chapter

CHAPTER 4

CHAPTER 4: When the simple way fails: comparison of single- and multi-trait approaches to identify best wild candidates for aquaculture

Under review in *Scientific Reports*

- *Specific Goal*: In a common-garden experiment, only genetically based differences are expressed. This step aims at (i) evaluating differentiation in performances of populations representative of the different prospective units (PU) in standardized conditions, (ii) demonstrating the usefulness of the multi-function and multi-trait approach since growth is not the only important trait for production, and (iii) elaborating an aquaculture potential index to take into account the variable importance levels of traits studied according to the opinion of stakeholders. This index allows making a consensus between all trait results to identify the PU with the highest aquaculture potential.

This chapter illustrates steps two and three of the integrative approach. Once the intraspecific classification is established, the different PUs must be evaluated in the same environment with rearing conditions being as close as possible to the domestication system used for production (i.e. common-garden experiment). All PUs were compared in the same domestication environment (same as chapter 1). We hypothesized that divergences in key traits would be sufficiently important to find differences in aquaculture potential between PUs.

Which populations?

In the previous chapter, five PUs were identified. Of these, three were compared: the European Plain, Danube, and Eastern Europe. One population was sampled per unit. In addition, in order to verify that the differentiation intra-PU was lower than the differentiation between PUs, an additional population was sampled for the Eastern European group.

Which traits?

This step required choosing the traits which needed to be evaluated. The focus was placed on traits desired for a successful culture of larvae, namely:

- Growth performance: Growth rate is the main trait of interest when starting a new domestication process (Kestemont et al. 2015a). However, growth rate is more important during on growing than in larviculture. Larval size at hatching is also an important criterion since can influence resistance to starvation (Teletchea and Fontaine 2010). During larval stages, it is essential for a farmer to limit growth heterogeneity and, in consequence, reduce time-consuming size sorting to limit aggressive interactions between individuals (Fontaine and Le Bail 2004; Kestemont et al. 2015a).

- Feed intake capacity: This implies to have in the first stages a sufficiently big yolk sac to survive before exogenous feeding (Teletchea and Fontaine 2010). Then, further survival relies on the ability to feed on *Artemia* and then later on dry feeds (Kestemont et al. 2015a; Król and Zieliński 2015).

- Survival rate: Low survival rate is one of the major bottlenecks in perch larviculture. In addition, aggressive interactions can greatly impact productivity (Kestemont et al. 2015a; Naumowicz et al. 2017). These aggressive interactions include notably enucleation (which can be particularly important in European perch; Jourdan 1999) and cannibalism. This latter can be of two types: type I (i.e. when prey is captured tail-first and that ingestion is partial) and type II (when the prey is captured head-first and that the ingestion is total; Baras 2013). Cannibalism-induced losses can be important, up to more than 50% of the initial stock density (Baras et al. 2003; Baras 2013; Kestemont et al. 2015a; Król et al. 2015).

- Shoaling behavior: Intensive production implies high rearing densities. Therefore, tolerance to conspecifics is essential (Kristiansen et al. 2004) and a cohesive group structure (relatively to inter-individual distances) is advantageous.

- Activity: This trait is also important since it contributes to the total energetic budget (Boisclair and Leggett 1989) and less active individuals could contribute to decrease potential aggressive interactions.

- Incidence of deformities and swim bladder inflation: Swim bladder inflation is a crucial process (Policar et al. 2019). Individuals which do not inflate their swim bladder often develop skeletal deformities and display lower growth and survival rates than individuals with inflated swim bladder (Jacquemond 2004; Kestemont et al. 2015a). Deformity rate is also essential for production since it hampers survival (Kestemont et al. 2015a; Alix et al. 2017).

All these parameters (except for enucleation which is specific to the studied model) were previously listed in the second chapter.

When the simple way fails: comparison of single- and multi-trait approaches to identify best wild candidates for aquaculture

Short running title: Single- *vs* multi-trait approaches in aquaculture

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ABSTRACT

In agriculture, diversifying production implies picking up, in the wild biodiversity, species or populations that can be domesticated and fruitfully produced. Two alternative approaches are available to highlight wild candidate(s) with high interest for aquaculture: the single-trait (i.e. considering a single phenotypic trait and, thus, a single biological function) and multi-trait (i.e. considering multiple phenotypic traits involved in several biological functions) approaches. Although the former is the traditional and the simplest method, the latter could be theoretically more efficient. However, an explicit comparison of advantages and pitfalls between these approaches is lacking to date in aquaculture. Here, we compared the two approaches to highlight best candidate(s) between four wild allopatric populations of *Perca fluviatilis* in standardized aquaculture conditions. Our results showed that the single-trait approach can (i) miss key divergences between populations and (ii) highlight different best candidate(s) depending on the trait considered. In contrast, the multi-trait approach allowed identifying the population with the highest domestication potential[1] thanks to several congruent lines of evidence. Nevertheless, such an integrative assessment is achieved with a far more time-consuming and expensive study. Therefore, improvements and rationalizations will be needed to make the multi-trait approach a promising way in the aquaculture development.

Key words: Multi-criterion approach, Trait, Intraspecific variability, Geographic origin, Domestication, Aquaculture

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[1] "Domestication potential" and "Aquaculture potential" must be considered as synonyms. The co-use of the two names in this Ph-D thesis manuscript reflects the ongoing development of the index. We kept the name used in the submitted version for each article, but the names will be homogenized during the reviewing process as "Aquaculture potential"

INTRODUCTION

The emergence of agriculture is one of the most important evolutions in human history. It was enabled by wild species domestication (Diamond 2002). Domestication is the process in which groups of individuals are bred in a human-controlled environment and modified across succeeding generations from their wild ancestors, in ways these become more useful to humans who increasingly control their food supply and reproduction (Lecocq 2019). This process ranges from the first trials of acclimatization to the setting up of selective breeding programs (Teletchea and Fontaine 2014). The main wave of domestication for fishes only started at the beginning of the 20th century to develop aquaculture (i.e. the farming of aquatic organisms), notably to mitigate provisioning service disruptions due to fishery collapse (Teletchea and Fontaine 2014; FAO 2018). Aquaculture is the fastest-growing food production sector in the world and now provides about 50% of the world's aquatic food consumption (FAO 2018). However, the aquaculture development has been criticized, notably because of its negative consequences on environments and its potential unsustainable development (Fontaine et al. 2009; Christou et al. 2013; Teletchea and Fontaine 2014). Despite the numerous attempts to domesticate new fish species, one of the main weaknesses of today’s aquaculture is its low species diversity (i.e. 85% of world fish production relies on about fifteen species; Lazard 2013). Indeed, this latter threatens (i) wild native fauna (e.g. biological invasions, pathogen spill over; Naylor et al. 2005; Silva et al. 2009; Martinez-Porchas and Martinez-Cordova 2012), (ii) food security (e.g. epizooty hazard; Godoy et al. 2008), and (iii) economic prospect (e.g. low adaptive potential to face environment/market fluctuations; Fontaine et al. 2009). This alarming situation has triggered a new trend in aquaculture development: the production diversification to enhance the sustainability of the sector (Fontaine et al. 2009; FAO 2018).

Promoting species production diversification is not an easy task since it implies domesticating and commercially producing new species. This often fails due to either technical limitations, economic constraints, or intrinsic species features (Liao and Huang 2000; Jobling 2010; Teletchea and Fontaine 2014; see also for non-fish species: Diamond 2002; Driscoll et al. 2009; DeHaan et al. 2016). These latter features are, for instance, low growth rate, high aggressiveness level, or low tolerance to high rearing densities, which are seen as impeding traits to start fruitful species production (Liao and Huang 2000; Quéméner et al. 2002; Jobling 2010). On the opposite, the ability to grow, feed, reproduce, and tolerate conspecifics and aquaculture-induced stress facilitates domestication (Driscoll et al. 2009; Jobling 2010). This means that the predisposition to be successfully domesticated and produced is species-dependent (Jobling 2010). Furthermore, these features could also vary at the intraspecific level, especially due to geographic differentiation (e.g. Purchase and Brown 2000; Toomey et al. 2019). Indeed, this differentiation between geographically distant conspecific populations (Mayr 1963), triggered by distinct demographic histories and local adaptations, can shape population specificities in key features for domesticating and commercially producing fishes (e.g. growth and development; Marcil et al. 2006; Vanina et al. 2019a). Therefore, taking into account geographic differentiation could facilitate new species domestication (Toomey et al. 2019; Vanina et al. 2019a).

Evaluating the ability of a species/population to be successfully domesticated and commercially produced requires an initial assessment of its expression of key trait(s). Looking back at past domestication programs, two alternative paradigms can be used to identify species or population(s) of interest for further production development: the (i) single-trait and (ii) multi-trait approaches.

The single-trait assessment is the traditional approach which consists of studying a single phenotypic trait, and consequently a single biological function, to highlight population(s) with desirable expression of the trait for further production development. This approach has been widely applied at the beginning or at advanced stages of the domestication process in agriculture of animals (e.g. Eknath et al. 1993; Rauw et al. 1998; Pryce et al. 2004; Gjedrem 2005a; Chavanne et al. 2016; Dugatkin 2018; see also for plants: Chabriat and Sarazin 2010). Single-trait assessments often focus on an easily measurable trait which expression is involved in the domestication process and/or production profitability. Most of the time, growth rate is considered as a premium criterion (Gjedrem 2005a, 2012). This was for instance the case with Nile tilapia (*Oreochromis niloticus*), which domestication programs initially focused on the growth rate (Eknath et al. 1993; see for other species: Nguyen and Ponzoni 2006; Rye et al. 2010; Gjedrem 2012). However, other traits are sometimes considered. For example, the beginning of the silver fox (*Vulpes vulpes fulvus*) domestication programs focused on tameness (Trut 1999; Dugatkin 2018), which facilitates the domestication process (Diamond 2002; Jobling 2010). In the same way, selective breeding programs in land agriculture have often focused on fertility (Pryce et al. 2004). Therefore, alternative choices of traits could be considered to perform the single-trait approach.

The multi-trait approach has recently been raised as an alternative method to the single-trait assessment. It has been suggested as a promising way to overcome domestication bottlenecks (e.g. Gjedrem 2005a; Miglior et al. 2005; Chavanne et al. 2016; Lachambre et al. 2017). It assumes that a successful domestication process requires the favorable expression of several traits involved in various biological functions. Indeed, it is possible to successfully domesticate a population if it can reproduce, feed, grow, and overcome stresses in a human-controlled environment (Gjedrem 2005a; Miglior et al. 2005). First applied in land agriculture (e.g. Miglior et al. 2005), this approach is now promoted in fish aquaculture, especially at advanced stages of domestication (Gjedrem 2005a, 2012; Chavanne et al. 2016). At these advanced stages, growth performance, morphology, disease resistance, flesh quality traits, age at sexual maturation, and feed efficiency have been considered (Gjedrem 2005a; Chavanne et al. 2016). However, it is still poorly considered at the beginning of the domestication processes (i.e. first trials of acclimatization of new candidates) even though a few examples exist (population [Gjedrem 2010] or species selections [Alvarez-Lajonchère and Ibarra-Castro 2013]).

Although the multi-trait approach is the focus of an increasing research, an explicit assessment of its advantages and its pitfalls has not been performed to date. Indeed, no comparison between single-trait and multi-trait approaches to highlight best wild populations for fish aquaculture is currently available. Here, we compare the potential interest for aquaculture of four wild allopatric populations of a test-case species, the European perch (*Perca fluviatilis*), during the larval period using the two different paradigms. We hypothesize that these two approaches lead to divergent conclusions.

RESULTS

We studied four wild lakes (**Appendix S1**): Valkea-Müstajärvi (VAL), Iso-Valkjärvi (ISO), Geneva (GEN), and Balaton (BAL). We compared populations at the larval stage based on 12 traits involved in growth, development, nutrition, and behavior (**Fig. 1-2**). These traits can impact the ability to be domesticated and fruitfully produced in aquaculture. For the single-trait approach, we considered all possibilities of initial trait choice. This means that we performed independent assessments of aquaculture interest based on each trait independently. For the multi-trait approach, we achieved an integrative assessment by using a domestication potential index (**Table 1**; **Appendix S2**) to reach a consensus between results observed for all traits considered. The calculation of the domestication potential score was possible thanks to a survey addressed to perch farmers, which allowed to assign to each trait an average weighting coefficient (i.e. level of importance according to perch farmers). Correlations between traits were evaluated in order to determine if there were redundant traits in the multi-trait assessment. All details are in the Material and Methods section.

Figure 1. Barplots representing results obtained for traits studied in phase I for which a statistically significant difference was found between populations (n = 3 per population except for activity and inter-individual distances for which n=9). Different letters indicate significant differences between populations (p-value<0.05) using post-hoc tests. The arrow represents how the expression of each trait should vary to meet stakeholder demands.

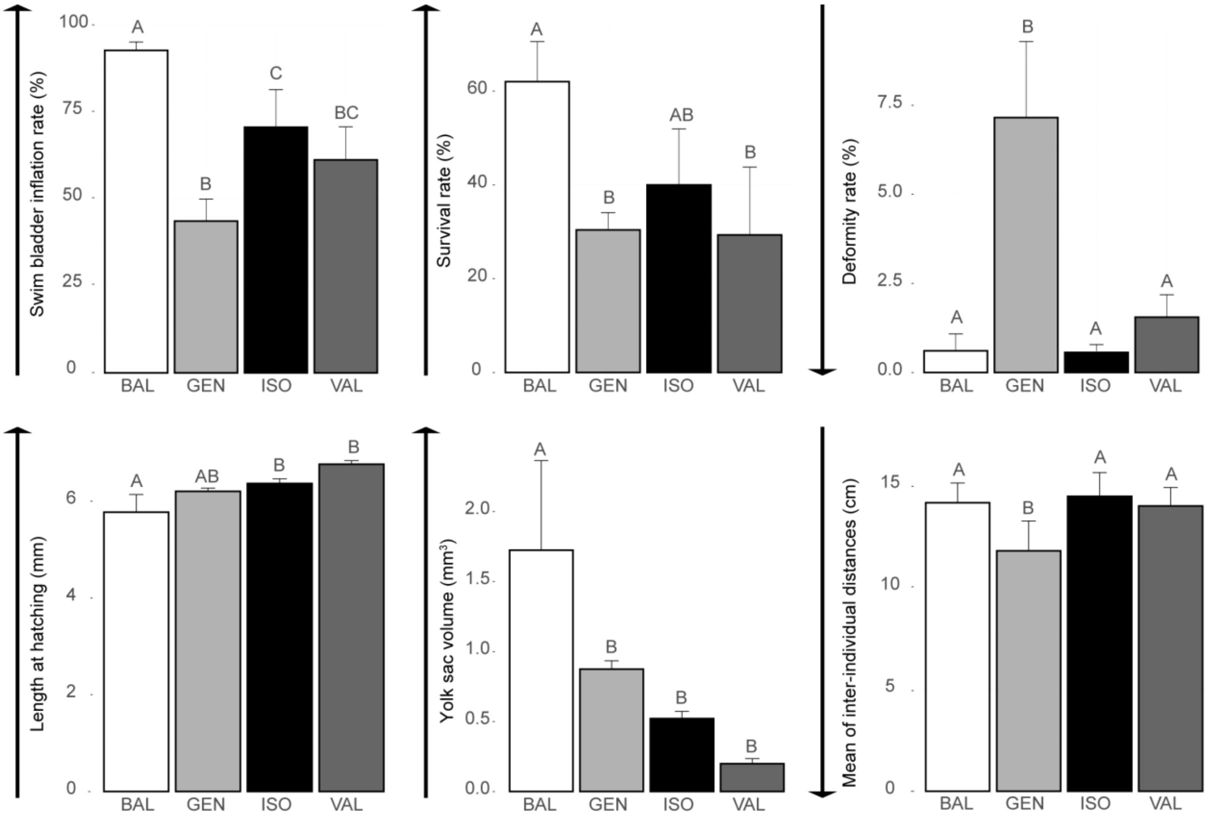

Figure 2. Barplots representing results obtained for traits studied in phase II for which a statistically significant difference was found between populations (n = 3 per population except for activity and inter-individual distances for which n=9). Different letters indicate significant differences between populations (p-value< 0.05) using post hoc tests. The arrow represents how the expression of each trait should vary to meet stakeholder demands.

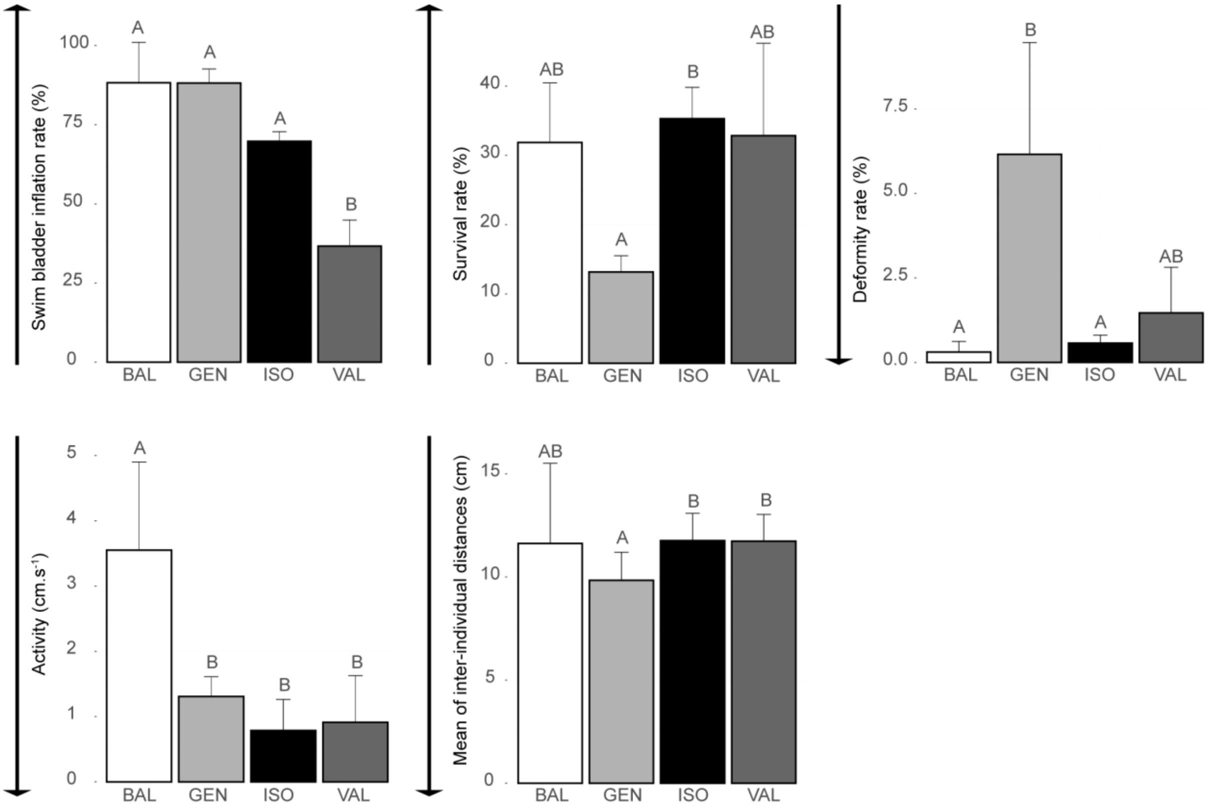

Table 1. Domestication potential score obtained for the four *Perca fluviatilis* wild populations in the multi-trait analysis. ISO : Lake Iso-Valkjärvi, VAL : Lake Valkea-Müstajärvi, GEN : Lake Geneva, BAL : Lake Balaton.

	ISO	VAL	GEN	BAL
Domestication potential score	378,98	350,89	346,67	571,66
Domestication potential rank	2	3	4	1

Inter-populational differences in phase I

No statistical difference between populations was found for final length heterogeneity ($F_{(3,8;\text{ where 3 corresponds to the first degree of liberty [number of populations-1] and 8 to the second degree of liberty [total number of replicates-number of populations])}}$=1.27, p-value=0.35) and activity ($F_{(3,32)}$=2.79, p-value=0.06).

A significant statistical difference between populations was found for the swim bladder inflation rate ($F_{(3,8)}$=19.79, p-value=4.65x10^{-4}), survival rate ($F_{(3,8)}$=7.29, p-value=0.019), deformity rate ($F_{(3,8)}$=22.88, p-value=2.80x10^{-4}), length at hatching ($F_{(3,8)}$=12.45, p-value=2.87x10^{-3}), yolk sac volume ($F_{(3,8)}$=10.85, p-value=2.21x10^{-3}), and for the mean of inter-individual distances ($F_{(3,32)}$=10.22, p-value=7.12x10^{-5}) (**Fig. 1**). The **figure 1** summarizes which population(s) tend to display the most desirable expression value for each trait.

Inter-populational differences in phase II

No statistical difference between populations was found for specific growth rate in length ($F_{(3,8)}$=2.20, p-value=0.17) and weight ($F_{(3,8)}$=3.06, p-value=0.09), in final growth heterogeneity for length ($F_{(3,8)}$=1.26, p-value=0.35) and weight ($F_{(3,8)}$=0.49, p-value=0.70), and aggressiveness ($F_{(3,8)}$=2.58, p-value=0.15).

A statistically significant difference was found between populations (**Fig. 2**) for swim bladder inflation rate ($F_{(3,8)}$=22.97, p-value=1.36x10^{-4}), survival rate ($F_{(3,8)}$=4.60, p-value=0.040), deformity rate ($F_{(3,8)}$=6.95, p-value=0.013), activity ($F_{(3,32)}$=15.77, p-value=1.79x10^{-6}), and the mean of inter-individual distances (K=8.25, df=3, p-value=0.041) (**Fig. 2**). The **figure 2** summarizes which population(s) tend to display the most desirable expression value for each trait.

Evaluation of the population interest for domestication

Regarding the single-trait approach, populations' interests for aquaculture differed depending on the trait initially chosen and were not consistent across experimental phases. Indeed, the best population is not the same depending on which trait is considered to perform the single-trait analysis (**Fig. 1-2**). For instance, when considering only growth rate, it did not allow identifying a differentiation in the interest for domestication between populations. On the contrary, when considering deformity rate, GEN appeared as the least suitable population in both phases. In the same way, when considering swim bladder inflation rate, BAL presented the highest interest for domestication in phase I but that would hide the fact that this population presented in phase II the highest activity rate (**Fig. 1-2**). Regarding the multi-trait approach, it highlighted that the population with the highest domestication potential score is BAL, followed by ISO, VAL, and GEN (**Table 1**; **Appendix S2**).

Phenotypic correlations

Very few correlations were highlighted: 14 pairs of traits were positively correlated (p-value<0.05), 13 pairs were negatively correlated (p-value<0.05), and 144 pairs were not significantly correlated (**Appendix S3**).

DISCUSSION

Our results were based on a common garden experiment which allows investigating the genetic basis of phenotypic differences (i.e. heritable divergences) between populations (Hutchings 2011). Therefore, it is an efficient way to compare larviculture performances between several wild populations. However, some limitations must be underlined. Indeed, evaluations were based on individuals originating from eggs collected from the wild. Therefore, we cannot completely rule out that some of the observed trait expressions had been shaped by phenotypic plasticity (i.e. the ability of a genotype to display several phenotypes when exposed to different environments; Pigliucci et al. 2006) or transgenerational effects (Youngson and Whitelaw 2008). Therefore, aquaculture performances of the four studied European perch populations should be considered with caution by fish farmers. Nevertheless, we argue that we minimized these potential biases thanks to our common-garden environment. Moreover, if such limitations ever impact our results, they would affect both the single-trait and the multi-trait approaches. Finally, this study aimed at comparing the two approaches rather than highlighting the best biological unit for larviculture within *P. fluviatilis*. Further comparisons between populations over the entire lifecycle using the multi-trait approach would allow identifying within species the best unit to further develop *P. fluviatilis* production.

When the simple way fails

Our study shows that the alternative single-trait and multi-trait approaches can lead to divergent results when highlighting the best population(s) for aquaculture purpose.

Overall, we detect three main limitations of the single-trait approach. First, considering a single trait can lead to miss the potential available in the wild biodiversity if the targeted trait does not vary between studied populations. This is particularly noticeable for the growth rate (no significant differentiation between populations despite a differential length at hatching; **Fig. 1**), which has traditionally been the most considered trait when assessing performances in aquaculture (Eknath et al. 1993; Gjedrem 2005a; Rye et al. 2010). In the worst-case scenario, this would lead to start a production with a suboptimal population that will have to be improved through costly and difficult selective breeding programs while better candidates were available in the wild. Second, the identification of populations with the highest interest for aquaculture can vary depending on the trait picked for evaluation. For instance, the observed differentiations for survival and deformity rates allow identifying best population(s) for aquaculture but do not converge to highlight the same best population(s) (**Fig. 2**). Furthermore, some of the conclusions obtained by the alternative tested single-trait approaches are completely contradictory (e.g. deformity rate would highlight Lake Balaton as the one of the best populations while if activity is considered, it would qualify this population as the least suitable; **Fig. 1-2**). This places a premium on the definition of the most important trait for fish production although this is still unachievable information due to divergent opinions between fish farmers and the numerous traits evaluated as very important (e.g. **Appendix S2**). Third, the choice of a population based on a single trait, and consequently a single biological function, can lead to start fish domestication/production with a population displaying deleterious expression of other key traits. Indeed, since traits are linked in complex ways, selection of only one trait will inevitable be associated with the indirect selection of other traits (i.e. through linkage and/or pleiotropy; Akdemir et al. 2019), including undesirable characteristics (Falconer and Mackay 1996; Grandin 1998). Eventually, this leads to deleterious impacts of the species production (Nguyen and Ponzoni 2006). This last limit is a well-known fact in land species domestication history (but see for aquaculture negative genetic correlations, e.g. Yáñez et al. 2016). For instance, continuous selection towards milk yield and growth led respectively to a decrease of (i) fertility in dairy cow (Pryce et al. 2004) and (ii) reproductive and immune performances in broilers (Rauw et al. 1998). In the same way, artificial selection in domestic turkeys for large breast size has led to the artificial insemination of females due to the inability of males to copulate naturally (Price 1999). Similarly, the focus on taming at the beginning of the domestication process of the silver fox (*Vulpes vulpes fulvus*) led to morphological changes disadvantageous for the pelt market (Dugatkin 2018).

More is more but it is more complicated too

Multi-trait approach allows overcoming the single-trait method limitations. Indeed, investigating several traits minimizes the risk of missing valuable populational specificities or choosing a population with hidden undesirable characteristics. Therefore, the nascent promotion of multi-trait approach in land and aquatic agriculture development (Gjedrem 2005a; Akdemir et al. 2019) is a timely and welcomed trend. Moreover, it provides a more efficient and realistic assessment to start new domestication processes and to increase the sector sustainability since they both involve several biological functions that could be studied only through the consideration of many traits. Indeed, as mentioned before, the domestication itself involves several biological functions such as growth, nutrition, behavior, and reproduction. Moreover, the willingness to develop a more sustainable aquaculture production implies for instance to study traits involved in robustness (e.g. resistance to thermal changes, vulnerability to new pathogens/parasites) and nutrition (e.g. ability to grow with a plant-based diet) (FAO 2018). However, beyond the bright sides of multi-trait approach, three main limitations could make its implementation difficult.

First, the most obvious pragmatic issue is that workload and cost associated with this approach are much more substantial than with the single-trait approach. Nevertheless, the complexity of multi-trait assessment should be seen as balanced by choosing the best part of the wild biodiversity before starting large-scale domestication programs which are far more expensive and time-consuming. Second, methodological limitations could impede the relevance of the multi-trait and multi-function approach. Indeed, the lack of efficient methods to measure some traits (e.g. assessment of traits involved in the nutrition function such as food conversion ratio requiring complex protocol, Gjedrem and Baranski 2009) and the increased risk of errors when working on multiple traits could lead to false decisions when choosing candidates for domestication/production. Finally, working with multiple traits implies using a method to make a consensus between results obtained for individual traits. Here, we proposed a scoring method in order to highlight within species a biological unit of interest. This method presents the inconvenience of not highlighting deltas of difference between populations since ranks are used to classify populations (see Material and Methods section for calculation details; **Appendix S2**). However, it allows putting all traits at the same level and then uses weighting coefficient to take into account trait importance divergences according to fish farmers. Other alternative methods could have been used but, nowadays, there is no consensus about which method should be favored (e.g. using the majority rule: the best population is the one which is ranked first for a majority number of traits; it would also highlight Lake Balaton as the best population but does not take into account divergent levels of importance of the traits; **Appendix S2**).

How to facilitate the multi-trait approach?

Although research advances are making (i) fish trait information available or (ii) trait analysis methods easier and cheaper, reckless integration of many traits in the multi-trait approach could make the previously cited limitations worsen. Therefore, this places a premium on restricting the assessment framework to a limited set of relevant traits. Such an optimization could be achieved through (i) socio-economical/biological considerations and (ii) trait correlation assessments. First, only traits which are relevant for domestication and/or production need to be considered. Such a finite list of relevant traits can be achieved through stakeholder involvement in the assessment framework design. Here, for instance we only considered traits that were regarded as relevant by the majority of questioned fish farmers (**Appendix S2**), considering only biological functions which are relevant for the studied life-stage. Second, some traits could be removed from the assessment framework by considering phenotypic correlations between traits (assuming phenotypic correlations are a good proxy for genetic correlations; Cheverud 1988; Roff 1996). Indeed, when such correlations are observed (e.g. feed efficiency improvement when growth rate considered [Kause et al. 2006; Chavanne et al. 2016], aggressiveness decrease when growth rate considered [Johnsson et al. 1996]), one could expect that by focusing on a few traits, it is possible to take into account expressions of other correlated traits. However, in our study, we highlighted only few correlations including biological non-relevant relationships (e.g. positive correlation between length at hatching and activity in phase II). Therefore, this suggests that considering trait correlations may not be helpful, at least in some cases, to restrict the evaluation to a handful of traits.

CONCLUSION

Our results highlighted that the single-trait approach can (i) miss key divergences between the populations and (ii) highlight different best candidate(s). Conversely, the multi-trait approach, which includes several key traits for larviculture, allowed identifying the population with the highest domestication potential thanks to several congruent lines of evidence. Nevertheless, this approach is more complex and requires making consensus between trait results. However, despite these limitations, it appears as the most suitable approach to highlight within species populations with higher domestication potential.

MATERIAL AND METHODS

Test-case species

Perca fluviatilis (Actinopterygii, Percidae) is a common widely spread Eurasian species living in freshwater and brackish habitats (Kestemont et al. 2015a). Its economic (high market value) and recreational (i.e. fishing) interests have led to the development of its RAS (i.e. recirculating aquaculture systems) farming since the 1990's (Kestemont et al. 2015a). *Perca fluviatilis* is among the most interesting species for the development of inland aquaculture in Europe (Kestemont et al. 2015a). However, despite its economic potential, the production is still limited. This is mainly due to major bottlenecks, especially in first-life stages, such as low growth rate, low survival rate, and high cannibalism rate (Kestemont et al. 2015a). This highlights the potential interest of re-starting new domestication programs. An intraspecific differentiation was already highlighted for this species in standardized conditions (e.g. growth [Mandiki et al. 2004; Vanina et al. 2019a], behavior [Toomey et al. 2019], development [Pimakhin and Zak 2014]).

Biological material collection and pre-experiment rearing conditions

Population sampling and rearing conditions were adapted from Toomey et al. (2019). Egg ribbons (one ribbon corresponding to one female) were obtained during the May 2018 and May 2019 spawning seasons from four lakes (**Appendix S1**): Valkea-Müstajärvi (VAL; 2018; Finland; 61°13'08"N, 25°07'05"E), Iso-Valkjärvi (ISO; 2018; Finland; 60°57'21"N, 26°13'3"E), Geneva (GEN; 2019; France; 46°22′7.20"N, 6°27′14.73"E), and Balaton (BAL ; 2019 ; Hungary ; 46°54’23.375"N, 18°2’43.119"E). We chose these populations since a phenotypic differentiation is known between the Finnish and Geneva populations (Toomey et al. 2019) while genetic specificities of central Europe populations have been already observed (Nesbø et al. 1999; Vanina et al. 2019b). After transportation, 13 to 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) at 13 °C in incubators (110x64x186cm; one incubator per population) containing nine racks each (45x7x12cm). Each incubator had its own temperature control and recirculated water system (flow rate of $4m^3.h^{-1}$). Water was UV-sterilized. Temperature (13.0 ± 0.4 °C) and oxygen rate (10.0 ± 0.5 $mg.L^{-1}$) were checked daily while pH (8.0 ± 0.2) was monitored three times a week (± standard error). Ammonium and nitrite concentrations (lower than 0.05 $mg.L^{-}$

^{1}) were measured three times a week until hatching. Light intensity was 400 lx at the water surface. Photoperiod was 12L:12D (12 hours of light and 12 hours of darkness).

Experimental rearing protocol

Two independent experimental phases were performed: phase I from hatching until the end of weaning (i.e. transition from live feed to inert pellets; 26 days post-hatching, dph) and phase II from 27 dph until the end of nursery, at 60 dph. The larval period was split in two phases in order to ensure availability of larvae across the whole larval period since there is a very high mortality rate during first-life stages. Because wild egg ribbons are not available the same time for all populations (i.e. asynchronous spawning seasons) and in order to prevent potential pathogen transmission, all populations were reared in independent structures. Since there are increasing concerns about the epizootic disease Perhabdovirus in Europe (Kestemont et al. 2015a), all populations were tested for the occurrence of this virus (*Laboratoire Département d'Analyses du Jura*, Poligny, France). All results were negative to the presence of the Perhabdovirus.

Regarding phase I, larvae from the different egg ribbons of each population were mixed after hatching and transferred to three green (RGB: 137, 172, 118) internal-wall 71 L cylindro-conical tanks (three replicates per population; RAS) at a density of 50 larvae.L^{-1}. Photoperiod was 12L:12D (simulation of dawn and dusk for 30 min) and light intensity was 400 lx at the water surface. Temperature was gradually increased during the first two weeks to 20 °C (one °C.day^{-1}). Larvae were hand-fed with newly hatched *Artemia* nauplii (Sep-Art, INVE; seven times a day, every 1h30 from 8.30 am to 5.30 pm) from three days post-hatching until at 16 dph, which corresponds to the beginning of the weaning (i.e. transition from live feed to inert dry artificial diet) period. At 16 dph, *Artemia* ration was decreased by 25 % every three 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 fed with dry feed *ad libitum* (BioMar 500 µm, then 700 µm at 44 dph until 60 dph). At 26 dph, the larvae left in the cylindro-conical tanks were removed in order to start phase II.

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

During the two phases, oxygen concentration (8.5 ± 2.3 mg.L^{-1}) and temperature (20.0 ± 0.6°C) were checked daily in all tanks (± standard error). Ammonium and nitrite concentrations (means inferior to 0.05 mg.L^{-1}) and pH (7.7 ± 0.6 mg.L^{-1}) were monitored three times a week (± standard error). Tanks were cleaned daily after first feeding and dead individuals were removed every morning.

Larviculture performance assessment

A trait is considered in this study at the replicate level. Each trait value is obtained from the mean of individual values.

Survival and development traits

Survival rate is one of the key traits contributing to the success of larviculture production (Kestemont et al. 2015a; Conceicao and Tandler 2018). Because of fast decomposition of dead larvae, it was not possible to count dead larvae during the first five days post-hatching. Consequently, the daily count of dead larvae was only performed in phase II. Therefore, survival rate in phase I was calculated for each cylindro-conical tank thanks to the final count of larvae using the following formula: Nf*100/(Ni-Ns), where Nf is the final number of fish counted at the end of phase I, Ni the initial number of fish, and Ns the number of fish sampled along the phase (i.e. for behavior experiments, see below). For phase II, the Bergot survival rate (Bergot et al. 1986) was used since it takes into account the number of fish removed for sampling and the daily mortality. Two traits related to the development of individuals and essential for larviculture were considered (Kestemont et al. 2015a): swim bladder inflation rate and deformity rate. Swim bladder inflation rate was estimated at the end of each experimental phase (following the protocol used in Jacquemond 2004; 20 g.L^{-1} of sea salt and 70 mg.L^{-1} of MS-222): 100 * (SB+/Nf) with SB+ the number of larvae with swim bladder and Nf the final number of larvae. Deformity rate was estimated in the final counting of each experimental phase using the following formula: 100*(Nm/Nf) with Nm the number of deformed larvae (only visible column deformities) and Nf the final number of larvae counted. Finally, the volume of the yolk sac was also evaluated at one day post-hatching since it reflects the quantity of nutritional reserves available before exogenous feeding (Kestemont et al. 2015a). It is calculated using the following formula: $\pi/6 * YSL*YSH^2$, where YSL is the length of the yolk sac and YSH the height of the yolk sac (Bagarinao 1986).

Behavioral traits

The ability of a biological unit to be efficiently produced in intensive conditions (i.e. intensive farming is an increasing trend in the aquaculture development) also depends on (i) inter-individual relationships, (ii) inter-individual distances, and (iii) activity (Toomey et al. 2019). Indeed, tolerance to conspecifics in a restricted area is essential for production since it can impact individual welfare (Huntingford 2004). Highlighting populations which present a cohesive group structure would be advantageous. Nevertheless, living in group is not costless because it can trigger aggressive behaviors which can lead to uneven competition for food, mortalities, stress, or immune suppression (Toomey et al. 2019). Therefore, both inter-individual distances and inter-individual interactions need to be considered. Finally, activity is also important since it contributes to the total energetic budget (Toomey et al. 2019). Furthermore, less active individuals could contribute to decrease the occurrence of inter-individual contacts and subsequent potential aggressive interactions.

Regarding aggressive interaction quantification, aggressiveness was calculated for phase II using the formula : $100*(Ni-(Nf+Nd+Ns)+Nc)/(Nf-Ns)$ with Ni the initial number of larvae, Nf the final number of larvae, Nd the sum of dead larvae counted daily, Ns the number of sampled larvae, and Nc the number of truncated or enucleated (enucleation being a specific indicator of aggressiveness in perch; Toomey et al. 2019) larvae among the dead ones (not possible in phase I since it was not possible to count dead larvae during the first five days post-hatching due to fast decomposition; in addition, no truncated or enucleated individuals were recorded for phase I).

Regarding the evaluation of inter-individual distances and activity, the detailed protocol is available in Toomey et al. (2019). Briefly, for each population, three replicates for each cylindro-conical tank were performed (nine replicates per population) over two days for phase I (25 and 26 dph) and phase II (44 and 45 dph). For each population, 90 individuals (n=30 per cylindro-conical tank, 10 individuals per replicate) were sampled and transferred to three aquaria (58 L; light intensity of 80 lx light intensity, 20 °C). After one night of acclimatization, populations were tested per groups of ten individuals in circular arenas (30 cm diameter, 1.5 cm of water depth, 10 lx) to study inter-individual distances and activity (Toomey et al. 2019). After 30 min acclimatization, individuals were filmed for 30 min. After the experiment, individuals were euthanized (overdose of MS-222) and kept in formalin 4% for later length measurements. Larvae tested in the circular arenas from ISO, VAL, BAL, and

GEN were respectively 14.05 ± 0.55 mm, 12.90 ± 0.62 mm, 10.62 ± 0.47 mm, and 11.81 ± 1.01 mm during phase I and 26.74 ± 1.67 mm, 26.28 ± 1.99 mm, 19.24 ± 1.22 mm, and 12.26 ± 0.45 mm during phase II (± standard error). Analyses were performed using the ImageJ software. Images were extracted from videos at five-minute interval (six images per video). For each image, coordinates of individuals were noted using the middle point between the eyes. The mean of inter-individual distances was evaluated per replicate. It corresponds to the mean of distances between a focal fish and all the other fish of the group and it is an indicator of the group cohesion. Detailed calculation is available in Colchen et al. (2016). Activity was analyzed in ImageJ. Every five minutes, one image per second was extracted for six consecutive seconds. For each image, coordinates of each individual were noted. This allowed calculating distance swam every second during the five seconds. The mean allowed obtaining for each individual the mean distance swam per second. From these values, we were able to calculate an average activity per replicate.

Growth traits

Growth traits are important in larviculture production, more particularly the length at hatching, specific growth rate, and growth heterogeneity (Kestemont et al. 2015a). To evaluate these traits, 30 larvae per population (i.e. ten larvae per cylindro-conical tank) were sampled the first and last days of each experimental phase, euthanized with an overdose of MS-222, and kept in formalin 4 %. For phases I and II, larvae were measured using ImageJ (± 0.01 mm). For phase II, larvae were also individually weighted (± 0.1 mg; not possible in phase I due to the imprecision of measure at one day post-hatching). Since specific growth rate (SGR) is a trait of interest at the end of larviculture, it was calculated only in phase II using the following formula: $SGR=100*(\ln(Xf)-\ln(Xi))*\Delta T^{-1}$ where Xi and Xf are respectively the average initial and final weight/length and ΔT the duration of phase II. Final growth heterogeneity was calculated for both phases in the following way: CV_{Xf} / CV_{Xi} in which CV is the coefficient of variation (100* standard deviation/mean) and Xi and Xf the initial and final weight/length, respectively.

Statistical analyses

All statistical analyses were performed in R 3.0.3 to assess if there were statistical differences ($p\text{-value}<0.05$) in traits between populations. To test the normality of distribution, a Shapiro-Wilk test was used. Homogeneity of variances was tested using the Levene test (R-package *lawstat*). When assumptions were not met, data was log-transformed. Then, in order to check if the cylindro-conical tank had no influence on our results, Corrected Akaike Information Criterion (AICc; R-package *qpcR*) were used to compare linear mixed models (biological traits as fixed factors and cylindro-conical tanks as random factor; R-package *lmer*) and linear model (biological traits as fixed factors, no random factor). For most factors, there was no influence of the cylindro-conical tank on the model. Therefore, one-way analyses of variance (ANOVA F test) followed by Tukey post hoc tests were used to evaluate differences between populations. When the effect of the cylindro-conical tank was significant, the ANOVA was performed on the linear mixed model and estimated marginal means were calculated (R-package *emmeans*). When assumptions were not respected despite log-transformation (only for inter-individual distances in phase II), Kruskal-Wallis H test was used followed by Dunn post-hoc test (R-package *PMCMR*). All post-hoc results were corrected relatively to the number of comparisons using Benjamini-Hochberg procedure. In order to improve the multi-trait approach, we assessed if there were redundant traits in the assessment. To do so, Pearson’s correlation coefficients between traits were calculated (except for correlations with inter-individual distances in phase II for which Spearman’s correlation coefficients were calculated).

Evaluation of the population interest for domestication with the two approaches

Regarding the single trait analysis, growth rate is the most often considered trait in domestication programs. However, in this study, we considered all possibilities of initial trait choice and analyzed results for all alternative cases. This means that we obtained independent assessments of aquaculture interest based on each trait independently. Providing a statistical difference is observed, we considered as the best population(s), the one (those) which displayed the most desirable expression (from a fish farmer point of view, Kestemont et al. 2015a). The expression value considered is the mean obtained over the three replicates.

In the multi-trait approach, an integrative decision framework is necessary in order to make a consensus between the different traits. Indeed, it is unlikely that a population has the best performances for all criteria. It is more likely that a unit displays the best performance for a specific trait (e.g. best growth rate) but the worst for another (e.g. lowest larval survival rate). Therefore, an indicator is required in order to make a synthesis at the multi-function and multi-trait levels to identify units with high domestication potential. Some methods and associated scores were suggested at the interspecific level in order to identify good candidate species (see for instance method used in Quéméner et al. 2002; Alvarez-Lajonchère and

Ibarra-Castro 2013). However, previous scoring methods integrate some traits for which intraspecific variability is unlikely (e.g. presence of bones in Quéméner et al. 2002) or do not include all traits considered here in the multi-function and multi-trait approach. Therefore, we propose a domestication potential score that aims at making a synthesis at the multi-trait level. The first step of this score calculation consists in ranking populations according to their performance for each trait (average rank per trait obtained from the mean of all replicate ranks; **Appendix S2**) when a statistical difference between populations was highlighted. Then, since all traits do not present the same level of importance for production according to fish farmers (which was confirmed in a survey we led before this work; see **Appendix S2**), it is necessary to adjust the importance given to each trait through the use of weighting coefficients (between zero and 100; adapted from Quéméner et al. 2002, similarly to breeding goals index but for which each trait is weighted according to its socio-economic value, Chavanne et al. 2016). Thanks to the survey addressed to perch farmers, we were able to assign to each trait an average weighting coefficient (**Appendix S2**). For each trait, we then divided the average weighting coefficient attributed by fish farmers by the rank of the population (**Appendix S2**). When traits were evaluated over two phases, they were considered as two separate traits in the calculation of the domestication potential score. Once this ratio is attributed to each trait, the sum of all ratios allows calculating the domestication potential score for each population (**Appendix S2**). Overall, the domestication potential score (ranging from 0 to ∞) is defined as:

$$\text{Domestication potential score} = \sum_{i=1}^{n}\left(\frac{\text{Weighting coefficient(i)}}{\text{Rank(i)}}\right)$$

Where: n corresponds to the number of traits, *i*=1 the first trait evaluated, *i* the trait considered, *n* = the last trait considered, and the weighting coefficient corresponds to the weight attributed to each trait by perch farmers and the rank corresponds to the rank attributed to the population for each trait.

The population with the highest score is the population with the highest potential for domestication.

Compliance with ethical standards

All along this experiment, individuals were handled as little as possible. All procedures used in the experiment were in accordance with national and international guidelines for protection of animal welfare (Directive 2010/63/EU). This study was conducted with the approval Animal Care Committee of Lorraine (CELMA n°66) and the French Ministry of Higher Education, Research, and Innovation (APAFIS13368-2018020511226118, APAFIS17164-2018101812118180).

CONFLICT OF INTEREST

The author(s) declare no competing interests.

DATA AVAILABILITY

All data generated or analyzed during this study are included in this article (and its Supplementary Information files).

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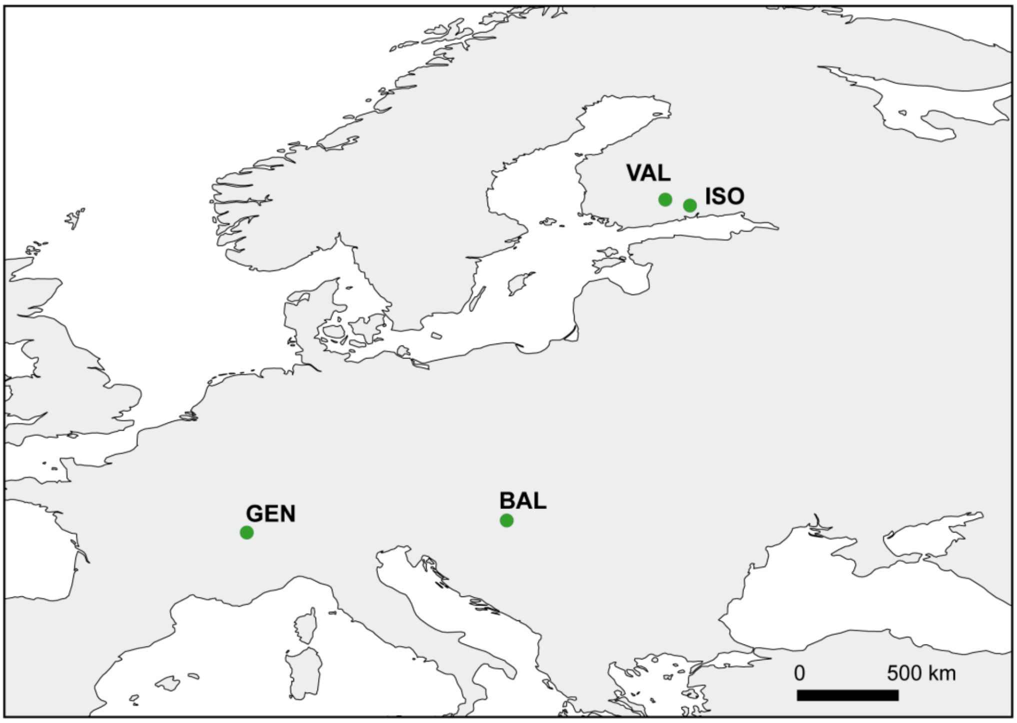
AUTHOR CONTRIBUTION

PF, TL, AP, and LT conceived and designed the experiment. All authors performed the experiment and/or analyzed data. TL, PF, and LT wrote the manuscript and all authors contributed to the final version.

SUPPLEMENTARY MATERIAL

Appendix S1*:* Map representing the four wild *Perca fluviatilis* populations sampled. VAL: Valkea-Müstajärvi, ISO : Iso-Valkjärvi, GEN : Geneva, and BAL: Balaton.



Appendix S2: A survey was performed between February and March 2019. Nine Percid farmers working with perch larviculture were questioned. We asked them to give their opinion on the importance of different traits involved in larval stages (from "not important" to "very important"). A weight coefficient was attributed to each opinion category: 0 for "not important", 25 for "slightly important", 50 for "Important", 75 for "Fairly important", and 100 for "very important". The first step consists in calculating an average weight coefficient for each trait taking into account farmers' opinions (step A). Then, for each replicate, populations are ranked per trait when a significant statistical differentiation was highlighted (p-value<0.05; Step B). This allows calculating an average rank per population and per trait (Step B). Finally, a score per trait and per population is calculated by dividing the average weighting coefficient by the average rank (Step C). The sum of all these scores allows calculating for each population a domestication potential score.

Step A

Trait weight	Not important		Slightly Important		Important		Fairly important		Very important		Weight coefficient sum	Total number of answers	Average weight coefficient
	Number of answers	Weight coefficient	Number of answers	Weight coefficient	Number of answers	Weight coefficient	Number of answers	Weight coefficient	Number of answers	Weight coefficient			
Trait / value attributed		0		25		50		75		100			
Larval growth rate	0	0	1	25	1	50	3	225	4	400	700	9	77,78
Larval growth heterogeneity	0	0	0	0	0	0	0	0	8	800	800	8	100,00
Volume of the yolk sac	0	0	2	50	0	0	1	75	5	500	625	8	78,13
Larval size at hatching	1	0	1	25	1	50	1	75	4	400	550	8	68,75
Swim bladder inflation rate	1	0	0	0	0	0	2	150	5	500	650	8	81,25
Larval deformity rate	0	0	0	0	0	0	1	75	8	800	875	9	97,22
Larval survival rate	0	0	0	0	1	50	2	150	6	600	800	9	88,89
Aggressiveness	0	0	0	0	1	50	2	150	6	600	800	9	88,89
Group structure (ability for shoaling, gregariousness)	2	0	2	50	1	50	3	225	1	100	425	9	47,22
Activity (i.e., fish more or less active)	0	0	3	75	1	50	2	150	1	100	375	7	53,57

Step B

		Replicate 1				Replicate 2				Replicate 3				Average rank			
Phase	Rank	ISO	VAL	GEN	BAL	ISO	VAL	GEN	BAL	ISO	VAL	GEN	BAL	ISO	VAL	GEN	BAL
II	Larval growth rate - Weight	No significant differentiation															
II	Larval growth rate - Length	No significant differentiation															
I	Larval growth heterogeneity - length	No significant differentiation															
II	Larval growth heterogeneity - length & weight	No significant differentiation															
I	Volume of the yolk sac	3	4	2	1	3	4	2	1	3	4	2	1	3,00	4,00	2,00	1,00
I	Larval size at hatching	3	1	2	4	2	1	3	4	2	1	3	4	2,33	1,00	2,67	4,00
I	Swim bladder inflation rate	3	2	4	1	2	3	4	1	3	2	4	1	2,67	2,33	4,00	1,00
II	Swim bladder inflation rate	3	4	2	1	3	4	1	2	3	4	2	1	3,00	4,00	1,67	1,33
I	Larval deformity rate	1	3	4	2	1	3	4	2	2	3	4	1	1,33	3,00	4,00	1,67
II	Larval deformity rate	2	3	4	1	3	2	4	1	2	3	4	1	2,33	2,67	4,00	1,00
I	Larval survival rate	3	4	2	1	2	3	4	1	2	4	3	1	2,33	3,67	3,00	1,00
II	Bergot Larval survival rate	1	3	4	2	2	1	4	3	3	2	4	1	2,00	2,00	4,00	2,00
II	Aggressiveness	No significant differentiation															
I	Inter-individual distances	4	2	1	3	3	2	1	4	4	2	1	3	3,67	2,00	1,00	3,33
II	Inter-individual distances	2	3	1	4	3	4	1	2	4	3	1	2	3,00	3,33	1,00	2,67
I	Activity (i.e., fish more or less active)	No significant differentiation															
II	Activity (i.e., fish more or less active)	2	1	3	4	1	2	3	4	1	2	3	4	1,33	1,67	3,00	4,00

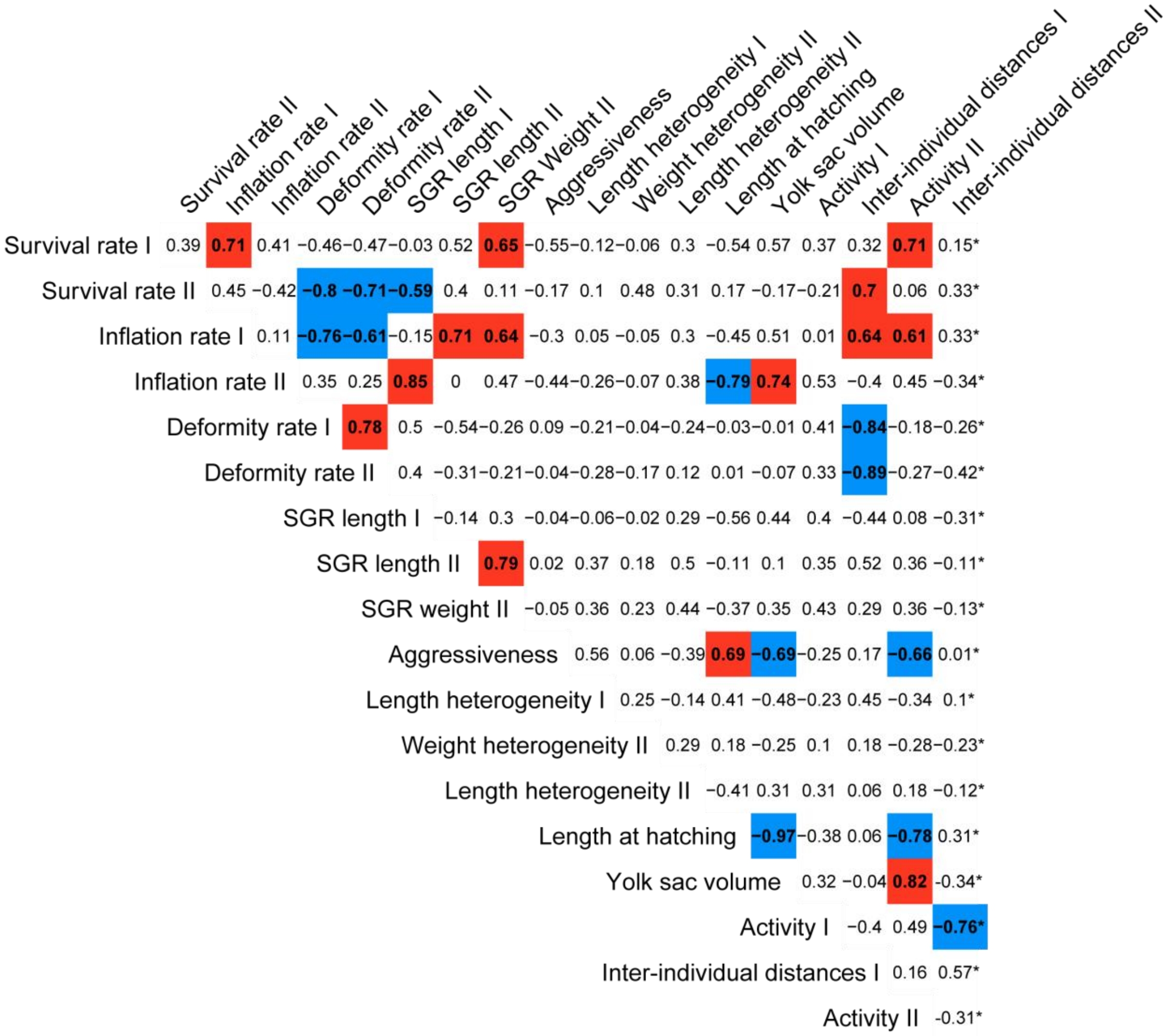
Step C

Phase	Trait	Trait weight	ISO rank	VAL rank	GEN rank	BAL rank	Score per trait - ISO	Score per trait - VAL	Score per trait - GEN	Score per trait - BAL
II	Larval growth rate - Weight	77,78								
II	Larval growth rate - Length	77,78								
I	Larval growth heterogeneity - length	100,00								
II	Larval growth heterogeneity - length & weight	100,00								
I	Volume of the yolk sac	78,13	3,00	4,00	2,00	1,00	26,04	19,53	39,06	78,13
I	Larval size at hatching	68,75	2,33	1,00	2,67	4,00	29,46	68,75	25,78	17,19
I	Swim bladder inflation rate	81,25	2,67	2,33	4,00	1,00	30,47	34,82	20,31	81,25
II	Swim bladder inflation rate	81,25	3,00	4,00	1,67	1,33	27,08	20,31	48,75	60,94
I	Larval deformity rate	97,22	1,33	3,00	4,00	1,67	72,92	32,41	24,31	58,33
II	Larval deformity rate	97,22	2,33	2,67	4,00	1,00	41,67	36,46	24,31	97,22
I	Larval survival rate	88,89	2,33	3,67	3,00	1,00	38,10	24,24	29,63	88,89
II	Bergot Larval survival rate	88,89	2,00	2,00	4,00	2,00	44,44	44,44	22,22	44,44
II	Aggressiveness	88,89								
I	Inter-individual distances	47,22	3,67	2,00	1,00	3,33	12,88	23,61	47,22	14,17
II	Inter-individual distances	47,22	3,00	3,33	1,00	2,67	15,74	14,17	47,22	17,71
I	Activity (i.e., fish more or less active)	53,57								
II	Activity (i.e., fish more or less active)	53,57	1,33	1,67	3,00	4,00	40,18	32,14	17,86	13,39

DOMESTICATION POTENTIAL SCORE

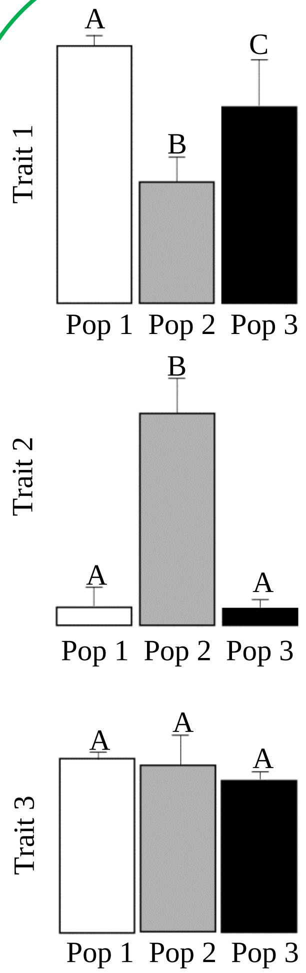
	ISO	VAL	GEN	BAL
FINAL SCORE	378,98	350,89	346,67	571,66
FINAL RANK	2	3	4	1

Appendix S3*:* Correlation matrix between all traits (I relative to phase I and II referring to phase II) based on Pearson's correlation coefficients (between -1 and 1; except for comparisons with an asterisk (*) for which Spearman's correlation coefficients were used). Correlation values are indicated for each test and statistically significant correlations (p-value<0.05) are highlighted in bold. The color corresponds to the value of the correlation coefficient (red for positive coefficients, blue for negative coefficients).



	Survival rate II	Inflation rate I	Inflation rate II	Deformity rate I	Deformity rate II	SGR length I	SGR length II	SGR Weight II	Aggressiveness	Length heterogeneity I	Weight heterogeneity II	Length heterogeneity II	Length at hatching	Yolk sac volume	Activity I	Inter-individual distances I	Activity II	Inter-individual distances II
Survival rate I	0.39	**0.71**	0.41	−0.46	−0.47	−0.03	0.52	**0.65**	−0.55	−0.12	−0.06	0.3	−0.54	0.57	0.37	0.32	**0.71**	0.15*
Survival rate II		0.45	−0.42	**−0.8**	**−0.71**	**−0.59**	0.4	0.11	−0.17	0.1	0.48	0.31	0.17	−0.17	−0.21	**0.7**	0.06	0.33*
Inflation rate I			0.11	**−0.76**	**−0.61**	−0.15	**0.71**	**0.64**	−0.3	0.05	−0.05	0.3	−0.45	0.51	0.01	**0.64**	**0.61**	0.33*
Inflation rate II				0.35	0.25	**0.85**	0	0.47	−0.44	−0.26	−0.07	0.38	**−0.79**	**0.74**	0.53	−0.4	0.45	−0.34*
Deformity rate I					**0.78**	0.5	−0.54	−0.26	0.09	−0.21	−0.04	−0.24	−0.03	−0.01	0.41	**−0.84**	−0.18	−0.26*
Deformity rate II						0.4	−0.31	−0.21	−0.04	−0.28	−0.17	0.12	0.01	−0.07	0.33	**−0.89**	−0.27	−0.42*
SGR length I							−0.14	0.3	−0.04	−0.06	−0.02	0.29	−0.56	0.44	0.4	−0.44	0.08	−0.31*
SGR length II								**0.79**	0.02	0.37	0.18	0.5	−0.11	0.1	0.35	0.52	0.36	−0.11*
SGR weight II									−0.05	0.36	0.23	0.44	−0.37	0.35	0.43	0.29	0.36	−0.13*
Aggressiveness										0.56	0.06	−0.39	**0.69**	**−0.69**	−0.25	0.17	**−0.66**	0.01*
Length heterogeneity I											0.25	−0.14	0.41	−0.48	−0.23	0.45	−0.34	0.1*
Weight heterogeneity II												0.29	0.18	−0.25	0.1	0.18	−0.28	−0.23*
Length heterogeneity II													−0.41	0.31	0.31	0.06	0.18	−0.12*
Length at hatching														**−0.97**	−0.38	0.06	**−0.78**	0.31*
Yolk sac volume															0.32	−0.04	**0.82**	-0.34*
Activity I																−0.4	0.49	**−0.76***
Inter-individual distances I																	0.16	0.57*
Activity II																		-0.31*

TAKE HOME MESSAGE



Pop : Population
Different letters indicate statistically significant differences between populations

SINGLE-TRAIT

Choice of one key trait

▽

e.g. Trait 1: Pop 1 > Pop 3 > Pop 2

+ Simplest method

− Divergent conclusions depending on the trait considered
e.g. Trait 2: Pop 2 > Pops 1 & 3

− Can miss key divergences between populations e.g. Trait 3

MULTI-TRAIT

Weighting of the traits + Ranking

▽

Domestication potential score

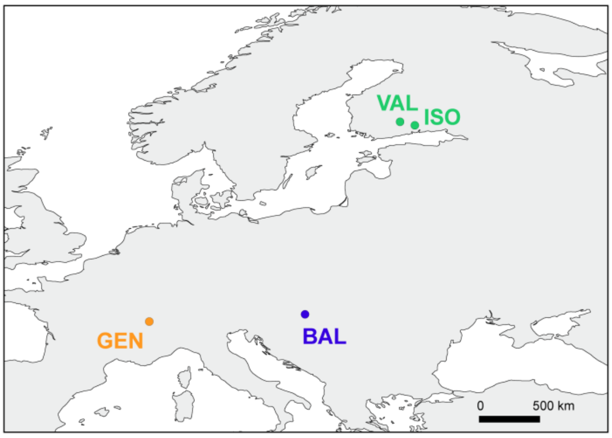
▽

Final rank: Pop 2 > Pop 1 > Pop 3

+ Consensus between several lines of evidence

− Time and money consuming

WHAT ABOUT GEOGRAPHIC DIFFERENTIATION?



PU
European Plain Danube Eastern Europe

Aquaculture potential score:

BAL > ISO > VAL > GEN

Danube > Eastern > European Plain

✓ Differential aquaculture potentials between populations & PU

✓ VAL and ISO belong to the same PU and present similar performances

CHAPTER 5

CHAPTER 5: *Split it up and see: Using proxies to highlight divergent inter-populational performances in aquaculture standardized conditions*

Under review in *Scientific Reports*

- *Specific goal:* Assessing if the use of the genetic proxy was the most relevant proxy regarding the larval performance results.

Highlighting the best candidates to start domestication and subsequent production relies on difficult and time-consuming bioassays. Since it is not feasible to compare performances of all populations across a species distribution range, we used in previous steps a genetic proxy to group populations. The results obtained in the first and fourth chapters are congruent with the classification established in the third chapter. Indeed, differentiation for key traits was observed between populations belonging to different PUs. In addition, differentiation is overall stronger between populations belonging to different PUs than between the two Finnish populations which belong to the same PU. However, the verification that the intra-PU differentiation was lower than the inter-PU differentiation was only performed with two populations. Therefore, the relevance of the genetic classification can be questioned.

In this chapter, we assessed the relevance of three alternative proxies (i.e. genetic, habitat, and hydrologic/geographic proxies) to highlight inter-populational divergences in key traits for larviculture in *P. fluviatilis*. In order to evaluate the relevance of these three proxies, we used larval performance results obtained on seven populations of *P. fluviatilis*. This higher number of populations allowed to (i) better consider the geographic differentiation and potential intra-PU differentiation and (ii) integrate populations geographically/hydrologically distant and potentially presenting different selective pressure regimes.

CHAPTER 5

Split it up and see: Using proxies to highlight divergent inter-populational performances in aquaculture standardized conditions

Short running title: Proxies of phenotypic divergence

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ABSTRACT

Considering wild inter-populational phenotypic differentiation can facilitate domestication and subsequent production of new species. Indeed, populations can present phenotypic specificities which can be of interest for domestication. Starting new domestication processes with the best population(s) available in the wild would optimize chances of success in a breeding environment. However, comparing all populations across a species range to identify populations exhibiting trait expressions interesting for domestication (i.e. key traits) is not feasible. Therefore, proxies highlighting inter-populational divergences in key traits are needed. Here, we assessed the relevance of three alternative proxies of inter-populational divergences in key traits for aquaculture: (i) genetic distance, (ii) habitat divergence, and (iii) geographic/hydrologic distances. We performed this evaluation on seven allopatric populations of the European perch (*Perca fluviatilis*) for which divergences in key traits had been already shown. Our results revealed differences in the correlation degree between the alternative proxy-based and key trait-based distance matrices, with the genetic proxy being correlated to the highest number of key traits. However, no proxy was correlated to all inter-populational divergences in key traits. Consequently, we suggest using a multi-proxy assessment along with a prioritization of populations that should be further investigated to detect divergences for their key trait expressions.

Keywords: Proxy, Distance, Aquaculture, Domestication, *Perca fluviatilis*

INTRODUCTION

Inter-populational differentiation (i.e. differentiation between allopatric, peripatric, or parapatric conspecific populations; e.g. see in fishes [Blanck and Lamouroux 2007] and insects [Lecocq et al. 2015]) can result from specific demographic history, limited gene flow, random genetic drift, and/or local adaptations (Mayr 1963; Avise 2000). Often considered in evolutionary and conservation biology (Frankham et al. 2010), analyzing and exploiting inter-populational phenotypic differentiation is also of crucial interest for agriculture development. Indeed, populations can present divergent expressions of key traits (i.e. phenotypic traits which are important for domestication and subsequent production; e.g. for fishes; Alvarez-Lajonchère and Ibarra-Castro 2013). Therefore, considering population specificities could allow identifying population(s) presenting different domestication potentials (i.e. most interesting expression of key traits). This could ultimately facilitate domestication (Lecocq 2019) programs of a new species and its subsequent production. Several success-stories have highlighted the interest of considering inter-populational specificities. For instance, the buff-tailed bumblebee (*Bombus terrestris*), which has been domesticated to act as pollinator in greenhouses, displays phenotypic differentiations between allopatric wild populations for traits impacting its ability to be industrially produced and to pollinate valuable crops (Velthuis and van Doorn 2006). At the beginning of its production, bumblebee breeders tried to rear several wild populations (Velthuis and van Doorn 2006) and, eventually, identified one with superior characteristics, triggering a flourishing development of the bumblebee production industry (Lecocq et al. 2016b). Similarly, the development of the Atlantic salmon (*Salmo salar*) industry was facilitated by reaping the benefits from inter-populational differentiation. Indeed, initial comparisons of several key traits for fish farmers (e.g. growth rate, disease resistance) between wild populations allowed identifying those with higher performances which were then used as cornerstone fish stock of salmon production (Gunnes and Gjedrem 1978; Gjedrem 2010). Beside new domestication instances, wild intraspecific differentiation can also be used to enhance old-established species farming, because introduction of adaptive traits (i.e. genomic introgression) from wild populations can lead to phenotypic novelty in produced stocks (Warschefsky et al. 2014).

Given the potential benefits of considering inter-populational phenotypic differentiation in domestication/farming programs, there is a premium on highlighting wild populations with divergences in key traits. This requires population assessments that can only be achieved through bioassays in which expressions of key traits are evaluated in a common experimental environment (i.e. common garden) close to future farming conditions. Indeed, similar assessments *in natura* would be doubtful because (i) some traits cannot be characterized during fieldworks due to technical reasons, and/or (ii) trait expression is the result of both genetic and environmental factors. The latter point is the main issue because phenotypic plasticity (*sensu* Pigliucci et al. 2006) can shape observed divergences between wild populations. However, such divergences would be useless for domestication programs because they will not be (i) observed in *ex-situ* farming and (ii) conserved in future production environment. Only genetic differentiations are of interest for domestication because production occurs in a system that is often quite different from the wild environment. The common-garden experiment is an efficient way to assess such differentiations. Indeed, it can highlight inter-populational divergences with a genetic basis (Hutchings 2011). However, it is not feasible to evaluate trait expressions in experimental conditions for all populations inhabiting the species distribution range. Moreover, from a phenotypic perspective, populations are not all notably divergent from each other, making comprehensive assessments uselessly time/money consuming. One solution relies on limiting potential comparisons before performing bioassays by (i) gathering populations that are likely undifferentiated, or (ii) highlighting population groups that most likely display specificities or, at least, divergences in key traits.

Already available intraspecific taxonomic classifications like subspecies (Mayr 1942; historically widely defined, e.g. Haig et al. 2006; Braby et al. 2012) could provide the needed population shorting (i.e. inter-populational differentiation of key traits in *B. terrestris* matches with the subspecies; Lecocq et al. 2016b). However, these taxonomic statuses have been fiercely criticized because (i) their relevance for systematics and (ii) criteria that should be considered for their definitions are doubtful (Phillimore and Owens 2006; Braby et al. 2012). This has triggered a trend to eliminate the trinomial designation in several species groups (e.g. Mulcahy 2008; Torstrom et al. 2014). In conservation biology, evolutionarily significant units, management units, distinct population segments, or designatable units, have been proposed to complement existing taxonomy and/or to go beyond systematists' feud (Frankham et al. 2004; May et al. 2011; Mee et al. 2015). However, their interpretations and definition criteria vary among species and scientists (e.g. Ryman et al. 1995; Fraser and Bernatchez 2001). Overall, debates and lack of consensus in systematics, evolutionary biology, and biological conservation make a ready-to-use population shorting approach unavailable for species domestication/production programs. Moreover, such classifications can highlight populations that are diagnosably distinct from other conspecific population groups but cannot detect the clines of variation that could lead to inter-populational divergences for key trait without clear geographic boundaries (e.g. Heibo et al. 2005; Blanck and Lamouroux 2007). Yet, such divergences could be useful for domestication programs. Therefore, there is a need to establish which approach(es) could be used to efficiently highlight populations that most likely display divergences in key traits prior to their assessment by bioassays. This would ultimately allow selecting wild populations which need to be evaluated in aquaculture conditions to determine which ones are the most interesting for further domestication and production.

We here propose to explore a new approach based on proxies that (i) diverge concomitantly with key traits and (ii) can be easily studied at large-scale. It is obvious that the best proxy should consist in using genes under selection and coding for key production traits. However, most phenotypic traits are under polygenic control and research identifying quantitative trait loci is still underway (Yue 2014; Robledo et al. 2018; but see for instance research on *Salmo salar*; e.g. Besnier et al. 2015). Therefore, alternative proxies of phenotypic differentiation are needed. A first alternative proxy consists in using neutral genes (i.e. locus that does not influence fitness). Indeed, divergences in such genes is widely used to highlight population groups which underwent divergent demographic histories (Avise 2000). Such groups could have acquired some phenotypic specificities, including in key traits for production (e.g. Lecocq et al. 2016a; Vanina et al. 2019a). Genetic differentiation in neutral markers has previously been suggested as, at least partially, indicative of differentiation in genes coding for quantitative loci (Merilä and Crnokrak 2001, but see opposite opinion in Holderegger et al. 2006). Therefore, neutral loci-based genetic distance could be a relevant proxy to discriminate populations that are most likely different in their key traits. A second alternative proxy is based on the degree of divergence of a phenotypic trait (Haig et al. 2006; Craig et al. 2017; e.g. behavioral, eco-chemical, or morphological features). Such features can be used to evaluate phenotypic distance that could be linked to genetic divergence (Karakousis et al. 1991; Joyce et al. 2009) and, therefore, potentially highlight divergences in key traits. A third alternative proxy relies on using the degree of habitat divergence to maximize the detection of population groups with different key trait expressions. Indeed, populations inhabiting different environments may be phenotypically divergent (Carvalho 1993) because resulting distinct selective pressures act as driving forces for phenotypic differentiation, notably through genetic-based local adaptations (Schluter 2001; Nakazato et al. 2008) that could impact key trait expression. Finally, a fourth alternative could be to consider spatial distance as a relevant proxy. Indeed, given the limited dispersal ability, individuals that are far apart tend to be genetically more divergent than individuals that are spatially close (Meirmans 2012). Overall, all these alternative strategies could provide a solution to highlight wild population groups with divergences in key traits for species production. However, the relevance of these alternative proxies is still unsettled because there is no comparison of their efficiency to discriminate populations.

Here, we aim to compare the relevance of different proxies to highlight inter-populational divergences in the expression of traits of interest for aquaculture (TIA) among populations. First, we evaluate TIA expressions in several fish populations. Second, we perform a retro-evaluation of the different proxies on the same fish populations. Finally, we compare the degrees of correlation between alternative proxy-based and TIA-based distance matrices. As a test case, we study a part of the life cycle (larval stage) of seven allopatric populations of the European perch (*Perca fluviatilis*).

MATERIAL AND METHODS

Species and traits studied

The European perch (*Perca fluviatilis*) is a freshwater species which is widespread across a diverse range of habitats in Eurasia (Stepien and Haponski 2015). This species started to be produced in the 1990's, mostly in intensive recirculated aquaculture systems (RAS), and presents a high socio-economic value (i.e. food market, recreational interest; Fontaine 2004). A geographic differentiation was already shown for *P. fluviatilis* in standardized conditions for TIA related to growth (e.g. Vanina et al. 2019a), development (e.g. Pimakhin and Zak 2014), and behavior (e.g. Toomey et al. 2019).

We evaluated a set of TIA which is related to several biological functions: growth, development, nutrition, and behavior. Growth traits (e.g. growth rate, final growth heterogeneity, initial and final lengths) are widely studied because they are very important for perch larviculture (Kestemont et al. 2015a). Development and nutrition traits (e.g. survival rate, deformity rate, swim bladder inflation rate, yolk sac volume) were also considered because they impact individual fitness and, consequently, larviculture success (Woolley and Qin 2010; Boglione et al. 2013). Finally, behavioral traits were also included in this study since the ability to be successfully produced in intensive conditions depends on aggressiveness (Kestemont et al. 2003), inter-individual distances (Toomey et al. 2019), and activity (Boisclair and Leggett 1989).

TIA evaluation in aquaculture standardized conditions

All procedures used in this study were in accordance with national and international guidelines for protection of animal welfare (Directive 2010/63/EU). This study was conducted with the approval Animal Care Committee of Lorraine (CELMA n°66) and the French Ministry of Higher Education, Research, and Innovation (APAFIS13368-2018020511226118, APAFIS17164-2018101812118180).

Biological material sampling and aquaculture rearing conditions were adapted from Toomey et al. (2019). Egg ribbons were collected during the spawning seasons across two years (May 2018 and April-May 2019). Seven lakes were sampled (**Supplementary Fig. S1**) : Valkea-Müstajärvi (VAL; 2018, Finland; 61°13'08"N, 25°07'05"E), Iso-Valkjärvi (ISO; 2018, Finland; 60°57'21"N, 26°13'3"E), Kierzlinskie (KIE; 2019, Poland; 53°47′54″N, 20°44′45″E), Geneva (GEN; 2019, France; 46°22′7.20"N, 6°27′14.73"E), Bourget (BOU; 2019, France; 45°44’12.469”N, 5°52’1.617”E), Hohen Sprenzer (HOH; 2019, Germany; 53°55’10.369"N, 12°13’6.005"E), and Balaton (BAL; 2019, Hungary ; 46°54’23.375"N, 18°2’43.119"E). After transportation, 13 to 32 ribbons were incubated at 13 °C at 400 lx (for incubation details, see Toomey et al., 2019). Temperature (13.0 °C ± 0.5 °C) and oxygen rate (9.8 ± 0.7 mg.L^{-1}) were monitored every day. Ammonium and nitrite concentrations (lower than 0.05 mg.L^{-1}) as well as pH (8.0 ± 0.3) were checked three times a week until hatching.

The experiment, performed in a RAS, started at one day post-hatching (dph) until the end of weaning, at 26 dph. For each population, after hatching, larvae from the different egg ribbons were mixed and transferred to three green (RGB: 137, 172, 118) internal-wall cylindro-conical tanks (three replicates per population) at a density of 50 larvae.L^{-1} at our experimental platform of aquaculture (Unit of Animal Research and Functionality of Animal Products, University of Lorraine, Vandœuvre-lès-Nancy, France). Temperature was gradually raised to 20 °C (1 °C rise per day). Photoperiod was 12L:12D and light intensity stayed constant during the lighting period at 400 lx at the water surface (with simulation of dawn and dusk for 30 min). Larvae were hand-fed from three days post-hatching, seven times a day, during the illuminated period, every 1h30, with newly hatched *Artemia* nauplii (Sep-Art, INVE). At 16 dph, weaning started: *Artemia* ration was diminished by 25% every three days while ration of dry feed (BioMar [Nersac, France], 300 µm until 21 dph, then 500 µm) was increased in the same proportions. After 25 dph, larvae were only fed with dry feed. Tanks were cleaned daily after first-feeding and dead larvae were removed and counted. Oxygen (8.6 ± 1.4 $mg.L^{-1}$) and temperature (20.0 °C ± 0.4 °C) were checked daily. Nitrite and ammonium concentrations (inferior to 0.1 $mg.L^{-1}$), as well as pH (7.8 ± 0.4 $mg.L^{-1}$), were monitored three times a week. At the end of the experiment, larvae left in each tank were counted and sorted according to the presence/absence of swim bladder inflation (following protocol used in (Henderson-Arzapalo et al. 1992); 20 $g.L^{-1}$ of sea salt and 70 $mg.L^{-1}$ of MS-222) and skeletal deformities.

Survival rate was calculated using the following formula : Nf*100/(Ni-Ns), in which Nf is the final number of larvae counted at the end of experiment, Ni the initial number of individuals, and Ns the number of larvae sampled along the experiment (i.e. sampling for behavior experiments, see below). In order to evaluation growth traits, 30 larvae per population (i.e. ten larvae per cylindro-conical) were sampled the first and last days of the experiment. After sampling, larvae were euthanized with an overdose of MS-222 and preserved in formalin 4%. Individuals were measured for total length in ImageJ (Schneider et al. 2012) (± 0.01 mm). Specific growth rate (SGR) was calculated using the following formula: $SGR=100*(\ln(Lf)-\ln(Li))*\Delta T^{-1}$ where Li and Lf are respectively the initial and final length and ΔT the length of experiment. Final growth heterogeneity was calculated in the following way: CV_{Lf} / CV_{Li} where CV is the coefficient of variation (100* standard deviation/mean) and Li and Lf the initial and final length, respectively. Swim bladder inflation rate was calculated in the following way: 100 * (SB+/Nf) with SB+ the number of larvae with swim bladder and Nf the final number of larvae. Deformity rate was evaluated using the following formula: 100*(Nm/Nf) with Nm the number of deformed larvae (visible skeletal deformities) and Nf the final number of larvae. Aggressiveness, including enucleation which is a specific aggressive behavior in *P. fluviatilis* (Jourdan et al. 2000), was evaluated based on the daily examination of dead larvae using the following formula: (Ne + Nt) / Nd where Ne is the number of enucleated larvae, Nt the number of truncated larvae (cannibalism type I; Baras 2013), and Nd the number of dead larvae counted between five and 26 dph (not possible to count dead larvae the first five days but aggressive interactions are reported to start at later stages; Baras et al. 2003; Kestemont et al. 2015a).

The protocol to evaluate inter-individual distances (Buske and Gerlai 2011a) and activity is adapted from Colchen et al. (2016) and Toomey et al. (2019). All methods were performed in accordance with the relevant guidelines and regulations. In a nutshell, each population was evaluated at 25 and 26 dph. For each population, 90 larvae (i.e. 30 larvae per cylindro-conical tank) were sampled the day before the experiment and transferred to aquaria (58 L; 80 lx) at 20 °C. After one night of acclimatization, populations were tested by groups of ten larvae which were placed in circular arenas (10 lx, 30 cm diameter, 1.5 cm of water depth) and filmed (three arenas tested simultaneously; three replicates per cylindro-conical tank, nine replicates per population). After 30 min acclimatization, the following 30 min were used to evaluate activity and inter-individual distances. At the end of the experiment, larvae were euthanized with an overdose of MS-222 for further length measurements. Mean total lengths of larvae tested from VAL, ISO, KIE, GEN, BOU, HOH, and BAL were respectively 12.90 ± 0.62 mm, 14.05 ± 0.55 mm, 10.90 ± 0,73 mm, 11.81 ± 1.01 mm, 11.77 ± 0.48 mm, 11.35 ± 0.72 mm, and 10.62 ± 0.47 mm. Images were extracted from videos every five minutes (six images per video) to evaluated inter-individual distances (i.e. mean of distances between a focal individual and all the other individuals of the group; group cohesion indicator; Buske and Gerlai 2011a). Analyses were made in ImageJ (Schneider et al. 2012). For each image, coordinates of each individual (using the middle point between the eyes) were noted. This allowed measuring distances between a given individual and the other individuals of the group and these distances were averaged to obtain one value per individual. The mean of values of all group members were averaged per image and the mean between all image values allowed getting a mean value of inter-individual distances per replicate (Colchen et al. 2016). Regarding activity, one image per second was extracted for six consecutive seconds every five minutes. Distance swam every second for five seconds was calculated and the mean allowed obtaining the distance swam per second for each individual. The mean between individual values allowed getting an activity for each image series. The mean between image series allowed calculating the activity per replicate.

Distance matrix for the different proxies

In the present study, we did not use any phenotypic proxy because morphological and/or behavioral information was not available for all wild perch populations. Moreover, we did not estimate such a proxy on larvae reared in the bioassays because these phenotypic traits can be strongly influenced by the environment (e.g. Svanbäck and Eklöv 2006). Therefore, we only evaluated three proxies: (i) genetic distance, (ii) habitat divergence, and (iii) geographic/hydrologic distance.

Genetic distance proxy

The genetic assessment of the seven populations was performed on 10 individuals per population collected randomly at the end of the experiment. Larvae were stored in 99% ethanol at -20 °C until analyses. Samples were sent to Genoscreen (Lille, France) for DNA isolation, marker amplification, and Sanger sequencing. Three mitochondrial regions were studied (D-loop of control region, cytochrome b, and 16S rRNA; see references for primers in Toomey et al. 2020) following the protocol available in Toomey et al. (2020). Both strands of each PCR product were sequenced. Consensus sequences of mitochondrial regions were computed and edited using CodonCode Aligner 7.1.2 (CodonCode Corporation, Dedham, Massachusetts, USA). There was no uncertainty in the consensus sequences. The *P. fluviatilis* origin of each sequence was verified using BLAST (Zhang et al. 2000). Sequence alignment was performed in MAFFT (default parameters; Katoh et al. 2019). Translation to proteins for Cytb was performed in Mesquite 3.20 (Maddison and Maddison 2001). A tandemly repeated array was identified in D-loop (previously reported in previous *P. fluviatilis* studies; Nesbø et al. 1998a) and mutations in the repeated array were coded as a single mutational step for further analyses. Mitochondrial markers were concatenated within a single alignment for further analyses using Mesquite. Haplotype sequences were deposited in GenBank (GenBank accession numbers: MN939382 to MN939395). Genetic distances between populations were calculated in R using ϕ_{ST} distance (Excoffier et al. 1992) in SPADS (Dellicour and Mardulyn 2014).

Habitat divergence proxy

We used 19 bioclimatic data (BIO1 to BIO19) as well as annual mean solar radiation (kJ.m^{-2}.day^{-1}), annual mean wind speed (m.s^{-1}), and annual mean water vapor pressure (kPa) from WorldClim Version2 to assess sampling place environments. We considered these abiotic environmental parameters (at the sampling location) recorded between 1970 and 2000 at a resolution of 10 arc-minutes (Fick and Hijmans 2017). We also used four additional variables: lake area (km^2), catchment area (km^2), average and maximum depths (m), and altitude (m). All variables were standardized to zero mean and unit variance due to their different scales of measurement (package "vegan"). A principal component analysis was performed (**Supplementary Fig. S2**; packages "MASS" and "factoextra") using the Kaiser-Guttman rule to determine the number of axes to retain (here the first four axes representing 98.0 % of the variance). Coordinates for each population replicate were extracted from the first four axes and a distance matrix using the Bray-Curtis distance method was calculated (R package "vegan").

Geographic and hydrologic distance proxies

Geographic distance matrix was set through the calculation of the great-circle distances (i.e. shortest distance over the earth's surface) according to the « Vincenty (ellipsoid) » method (Vincenty 1975) implemented in the R package "geosphere*"*. Because this geographic distance is a priori not relevant for fish species, we also estimated an hydrologic distance using an algorithm based on circuit theory and implemented in the program Circuitscape (Shah and Mcrae 2008). Rivers and lakes shapefiles were respectively extracted from the Catchment Characterization and Modelling river and catchment database v2 (Vogt et al. 2007) and HydroSHEDS (Lehner et al. 2008) and from Natural Earth (www.naturalearthdata.com) databases, and jointly rasterized on a geo-referenced grid with a resolution of 0.5 arcmin. Specifically, we assigned a value of "1" to terrestrial raster cells that were not crossed by a river or occupied by a lake and a value of "100" for terrestrial raster cells crossed by a river or occupied by a lake. We then used the program Circuitscape (Shah and Mcrae 2008) to compute the pairwise electric resistance between all pairs of populations and this, by treating the resulting raster as a conductance grid. One of the advantages of the Circuitscape algorithm is that it takes into account the contribution of several potential pathways to compute pairwise distances (resistances) between locations. We used these pairwise electric resistances as an estimation of pairwise hydrologic distances between populations.

Relevance of the different proxies

In order to create a trait-by-trait distance matrix, we first checked the statistical differentiation (p-value<0.05) of phenotypic traits between populations: we tested normality of distribution and homogeneity of variances using a Shapiro-Wilk test and a Levene test, respectively (R package "lawstat"). When assumptions were not respected, data were log-transformed. To check the influence of the cylindro-conical tank on results, we compared linear (phenotypic traits as fixed factors, no random factor) and linear mixed models (cylindro-conical tanks as random factor and phenotypic traits as fixed factors; R package "lmer") using the corrected Akaike Information Criterion (AICc; R package "qpcR"). For most traits, there was no significant influence of the cylindro-conical tank on the model. Therefore, we used one-way analyses of variance (ANOVA F-test), followed by Tukey *post hoc* tests (R package "stats"), to evaluate differences between populations. When the effect of the cylindro-conical tank was significant, we performed the ANOVA on the linear mixed model and estimated marginal means were calculated (R package "emmeans"). Regarding aggressive rate and activity, assumptions were not met despite log-transformation. Thus, Kruskal-Wallis H tests and Dunn *post hoc* test (R package "PMCMR") were used. Traits presenting no significant differentiation between populations were excluded from further analyses.

A trait-by-trait distance matrix was created using the Euclidean method (R package "vegan", three replicates per population). All distance matrices are available in Figshare (doi: 10.6084/m9.figshare.11407128). We performed multivariate analyses using multi-regression on distance matrices (1000 permutations) coupled with commonality analyses (further referred as "MRDM-CA") using R packages "ecodist" and "yhat". For these analyses, all proxy-based distance matrices were preliminary standardized. The multi-regression on distance matrices (MRDM) analysis allows estimating the Pearson correlation coefficient r (i.e. direct effect of the proxy on the response variable, irrespectively from the influence of other proxies) and beta weights (i.e total effect of the proxy on the response variable, taking into account the contribution of other proxies). The commonality analysis (CA) is a detailed variance-partitioning procedure which allows taking into consideration collinearity between proxies (Prunier et al. 2015). This analysis estimates the unique ("U"; amount of variance in the TIA accounted for by each single proxy) and common ("C"; variance jointly explained by several proxies) contributions of each proxy. After the first round of MRDM-CA, total suppressors were identified and discarded because they can be responsible for artefactual relationships among variables. This can allow purifying the relationships between the remaining proxies and the response variable (i.e. in our case the TIA-based distance matrices; Prunier et al. 2015). Successive MRDM-CA were performed until all suppressors were removed. A proxy was considered as a total suppressor when unique contribution is counter-balanced by its (negative) common contribution (classical suppression) and/or when regression and correlation coefficients are of opposite signs (cross-over suppression; Prunier et al. 2015; Dellicour et al. 2017). In addition, we investigated correlations between trait-based and proxy-based distance matrices using Mantel tests in R (R package "vegan"; 9,999 permutations). Four Mantel tests were performed for each TIA: (i) ϕ_{ST} genetic distance *vs* TIA-based distance matrix, (ii) habitat divergence *vs* TIA-based distance matrix, (iii) geographic distance *vs* TIA-based distance matrix, and (iv) hydrologic distance *vs* TIA-based distance matrix.

RESULTS

TIA evaluation in aquaculture standardized conditions

There was no statistically significant difference between populations for aggressive rate (K=8.85, df=6, p-value=0.18) and length heterogeneity ($F_{(6,14)}$; where 6 corresponds to the first degree of liberty [number of populations-1] and 14 to the second degree of liberty [total number of replicates-number of populations]=0.86, p-value=0.55).

A significant statistical differentiation between populations was found for survival rate ($F_{(6,14)}$=9.45, p-value=$5.75x10^{-4}$), swim bladder inflation rate ($F_{(6,14)}$=22.73, p-value=$6.79x10^{-6}$), deformity rate ($F_{(6,14)}$=11.29, p-value=$1.12x10^{-4}$), specific growth rate ($F_{(6,14)}$=8.64, p-value=$4.69x10^{-4}$), length at hatching ($F_{(6,14)}$=17.33, p-value=$2.85x10^{-5}$), final length ($F_{(6,14)}$=8.35, p-value=$5.58x10^{-4}$), yolk sac volume ($F_{(6,14)}$=32.95, p-value=$1.77x10^{-7}$), activity (K=20.24, df=6, p-value=0.003), and inter-individual distances ($F_{(6,56)}$=5.59, p-value=$1.35x10^{-4}$). All inter-populational comparisons are available in **Supplementary Figure S3**.

Correlation degrees of the different proxies with the TIA-based matrices

The series of successive MRDM-CA allowed identifying several suppressors. Therefore, some TIAs are only correlated with a single proxy remaining after suppressors' removal (**Table 1**). Overall, MRDM-CA results indicate that significant global MRDM R^2 are relatively high (>10%), and that all TIA are associated with a positive and significant correlation with a unique proxy-based matrix (when considering only proxies for which the CA unique contribution U > 5 %), except for final length which is not correlated with any proxy (**Table 1**). The geographic distance proxy is not correlated with any TIA-based distance matrix while the genetic distance proxy is the one which is correlated to the highest number of TIA-based distances matrices. However, none of the proxy is showing a systematic significant contribution with all TIA. Considering genetic, habitat, and hydrologic distance proxies, all TIA are correlated with at least one of the proxies, except for final length (**Table 1**). Regarding Mantel tests, results are available in **Supplementary Table S1** and are globally congruent with MRDM-CA analyses. Overall, for each TIA, the proxy which was the most correlated in the Mantel test is the one which is significant in the MRDM-CA analysis.

Table 1: Multi-regression (MRDM) and commonality analyses (CA) results after having successively removed all suppressors (Supplementary Table S1). Analyses were performed between each TIA-based distance matrix (response variable) and all proxy-based (genetic distance, habitat divergence, geographic distance and hydrologic distance proxies) distance matrices. With: Pearson's correlation coefficient (r), β weights (β), and unique (U) and common (C) contributions of proxies to the variance of the response variable. (*) indicates significant R^2 associated with a p-value<0.05 (after Benjamini-Hochberg correction).

TIA	R^2 MRDM	CA				
		Proxy	r	β	U	C
Survival rate	0.432*	Genetic	0.505	0.874	-	-
Swim bladder inflation rate	0.399*	Genetic	0.631	0.638	-	-
Deformity rate	0.223*	Geographic	0.350	0.030	0	0.122
		Genetic	0.193	0.038	0.001	0.036
		Habitat	0.469	0.437	0.101	0.120
Specific growth rate	0.121*	Hydrologic	0.237	0.712	-	-
Initial length	0.224*	Genetic	0.472	0.500	-	-
Final length	0.023	Hydrologic	0.089	0.031	0.001	0.007
		Habitat	0.108	0.088	0.005	0.007
Yolk sac volume	0.235*	Hydrologic	0.315	0.948	-	-
Activity	0.121*	Habitat	0.215	0.415	-	-
Inter-individual distances	0.199*	Geographic	0.348	0.069	0.001	0.120
		Hydrologic	0.366	0.009	0	0.134
		Genetic	0.407	0.319	0.057	0.109
		Habitat	0.295	0.141	0.010	0.077

DISCUSSION

Assessment of TIA expression differentiation

Because we used a common garden experiment, we assumed that observed differentiations in the TIA expression have a genetic basis and are not due to phenotypic plasticity. Nevertheless, we used individuals sampled at the egg stage in the wild. Therefore, we cannot rule out that a part of TIA expression divergences is shaped by transgenerational effects or phenotypic plasticity (Pigliucci et al. 2006; Youngson and Whitelaw 2008). However, we argue that our experimental design has minimized as far as possible such potential biases. Another potential bias relies on the variable number of egg ribbons used between populations which could have influenced TIA results. However, we minimized the female specificity bias by taking a large number of egg ribbons for each population.

One proxy is not enough

We showed that no single proxy-based distance matrix is correlated with all TIA-based distance matrices. We found four significant correlations for genetic distance and two significant correlations for hydrologic distance and habitat divergence when we compared them with TIA-based distance matrices (**Table 1**). We also observed that each TIA is only significantly correlated with one proxy (**Table 1**).

Since inter-populational divergences can be shaped by (i) gene flow disruption/limitation and/or (ii) local adaptation to specific selective pressures, we were expecting that the assessments based on alternative proxies could lead to different results. Indeed, relationships between these two divergence-triggering factors and the alternative proxy-based distance matrices are different.

Although larger spatial disjunction (using geographic or hydrologic distance) increases the likelihood to reinforce these divergence-triggering factors (e.g. Wright 1943), inter-populational differentiation can happen between adjacent populations, for instance due to a strong ecological barrier (e.g. for *Perca fluviatilis*: Bergek and Björklund 2007) or behavioral processes (e.g. natal homing behavior; Carvalho 1993). Detections of such differentiations at small geographic scale are thus unlikely with spatial disjunction *a priori* (e.g. divergent results between hydrologic and survival rate distance with ISO, KIE, and BAL, see Figshare doi: 10.6084/m9.figshare.11407128).

The habitat divergence proxy can theoretically overcome limitations of spatial disjunction proxies because it could highlight specific selective pressures at any geographic scale and, thus, inter-populational divergences (e.g. Jørgensen et al. 2005; Langerhans et al. 2007). Nevertheless, we observed only few significant correlations between TIA and habitat divergence. This can be explained because the habitat divergence proxy assessment most likely fails to highlight populations undergoing different selective pressures. First, the selection of relevant variables involved in local selective pressure is still hard to achieve. Indeed, the importance of environmental variables on population evolution is species-specific (and unsettled for *P. fluviatilis*) and cannot be known without long and difficult bioassays (e.g. Chabot and Claireaux 2008). Second, relevant environmental data on freshwater ecosystems are unevenly available for the different regions of the world. For instance, in our study, the worldwide databases of freshwater environmental variables (e.g. Domisch et al. 2015) do not cover the whole studied sampling area. This led us to use terrestrial data in order to extrapolate aquatic environment characteristics (see similar strategy in Knouft and Anthony 2016; Sherwood et al. 2018), although it could potentially blur studied lake specificities. Optimally, analyses should be performed using data specific to lakes (e.g. lake physico-chemical parameters, feeding base) to improve the use of this proxy but the unavailability of sufficient data limits this strategy. Beside these difficulties, the habitat divergence proxy assessment can fail because extensive gene flow from adjacent regions can limit local adaptations (Carvalho 1993) and, thus, minimize TIA expression divergences, even if specific environmental pressure occurs locally.

One could expect that the genetic distance proxy would be the most efficient to highlight populations with divergent TIA expressions. Indeed, it could detect populations with genetic divergences due to gene flow limitation/disruption triggered by spatial/hydrologic distance (i.e. isolation by distance), geographic barriers (i.e. geographic isolation), ecological barriers, or behavioral specificity (e.g. natal homing behavior). However, our results highlight that not all TIA are correlated with the genetic distance proxy. Moreover, some traits which are not correlated with the genetic distance proxy are correlated with another proxy. To explain the absence of correlation of some TIA with the genetic distance proxy, it could be hypothesized that populations could have diverged recently, implying that few divergences in neutral markers had time to appear (Arif and Khan 2009; Cruaud et al. 2014).

How to better catch the divergence: a multi-proxy strategy

Because there is no proxy-based distance correlated with all TIA-based distances, highlighting populations that likely display TIA expression divergences should be based on the use of several proxies. Genetic distance and habitat divergence proxies are theoretically complementary to maximize the detection of such populations. On the one hand, the genetic distance proxy is relevant to highlight divergence by distance or populations with divergent demographic histories while the habitat divergence proxy can reflect local adaptations which are not (already) visible in neutral markers. On the other hand, populations occurring in similar habitats can display phenotypic divergences, including in TIA. Thus, the use of these two proxies allows taking into consideration both gene flow disruption/limitation and local adaptation to specific selective pressures. However, these proxies can be sometimes misleading due to their intrinsic limitations (see before), particularly the habitat divergence proxy (unless performing the analysis with more relevant lake variables). One way to mitigate their limitations relies on the combination of these two proxies with the hydrologic distance proxy (according to our results, the geographic distance proxy can be beneficially replaced by hydrologic distance proxy, which is more relevant for aquatic species and is the only one correlated to some TIA-based distance matrices). The hydrologic distance proxy could be correlated with both phenotypic differentiation by distance and local adaptations between distant populations. Moreover, the hydrologic distance proxy is correlated in our study with two TIA which are not correlated neither with genetic distance or habitat divergence proxies. Even though its calculation might be time and system memory-consuming, it requires no specific information except for geographic coordinates which makes it simple and useable in all scenarios. Here, we promote the use of a multi-proxy approach to pinpoint a population or population group to be assessed for TIA expression divergences. Another potential alternative would rely on ranking the TIA since not all TIA have the same importance to stakeholders. This strategy would consist in choosing the proxy which is correlated to the most important TIA (e.g. growth rate and survival rate; Kestemont et al. 2015a). However, this strategy is not optimal since a successful domestication process requires the favorable expression of several traits involved in various biological functions.

Regarding the multi-proxy strategy, it is likely that the different proxies drive to divergent conclusions regarding which populations should be considered. Moreover, all populations cannot be evaluated in bioassays if many populations are considered and if they are all somewhat divergent for one or more proxies. Indeed, the potential over-estimation of populations or population groups that could be potentially TIA-divergent (Padial et al. 2010) is the main pitfall of multi-proxy based assessment. Therefore, prioritization procedures should be developed. For instance, a ranking of population/population group pairs according to their degree of divergences in each proxy could be performed. Then, bioassay effort could be focused on the most distant pair(s) for each proxy considered, as well as eventually population pair(s) which are distant across all proxies (e.g. high average rank across proxies) could be a solution. It would maximize the probability to highlight population with TIA expression divergences. The number of pairs that will be effectively evaluated in bioassays will depend on availability of experimental facilities as well as financial and human means.

Nevertheless, any alternative assessment approach should be tested on other species in order to extend its relevance at global scale.

DATA AVAILABILITY

All proxy-based matrices are available in Figshare (doi: 10.6084/m9.figshare.11407128 / https://figshare.com/s/1067e47637c5572caaf7). All haplotype sequences are available in Genbank (MN939382 to MN939395).

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AUTHOR CONTRIBUTIONS

TL, PF, and LT designed the study. LT, PF, TL, AK, DZ, FB contributed to the collection of egg samples. SD and LT performed the analyses. TL and LT interpreted results and wrote the manuscript. All authors read and approved the final manuscript.

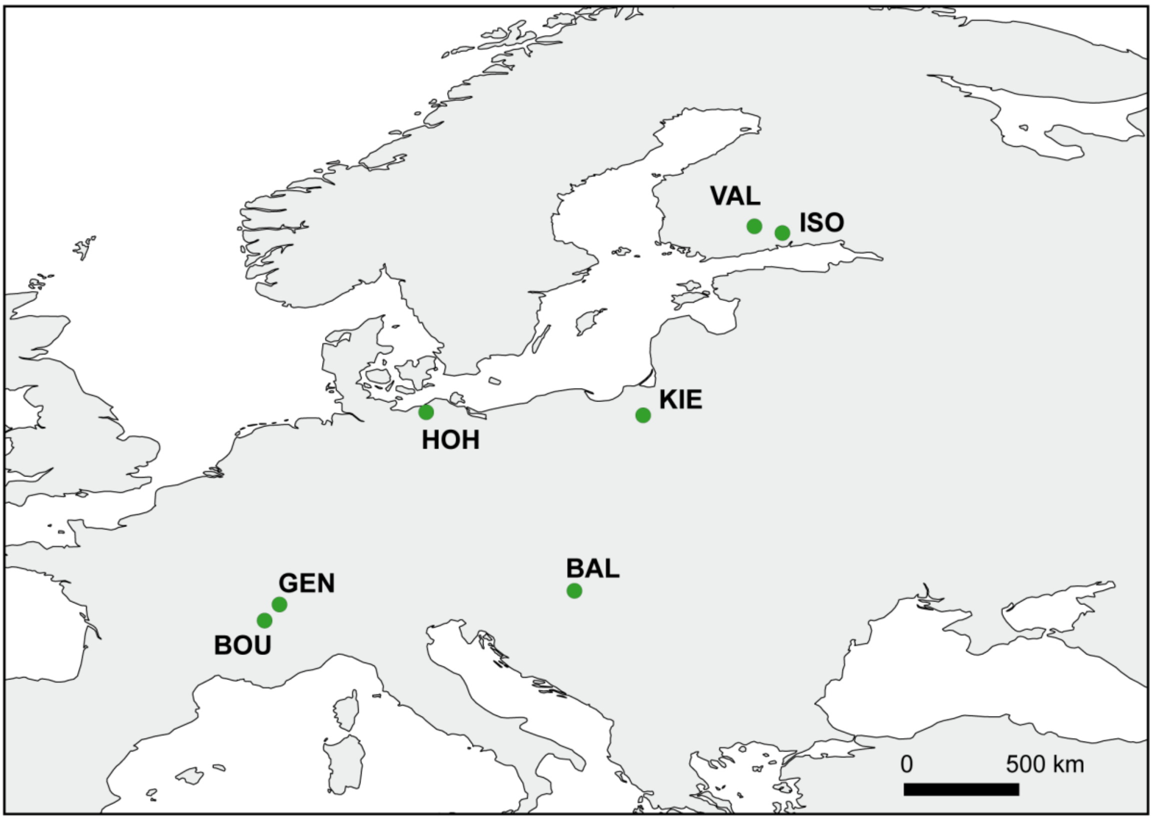
ADDITIONAL INFORMATION

Conflict of interest

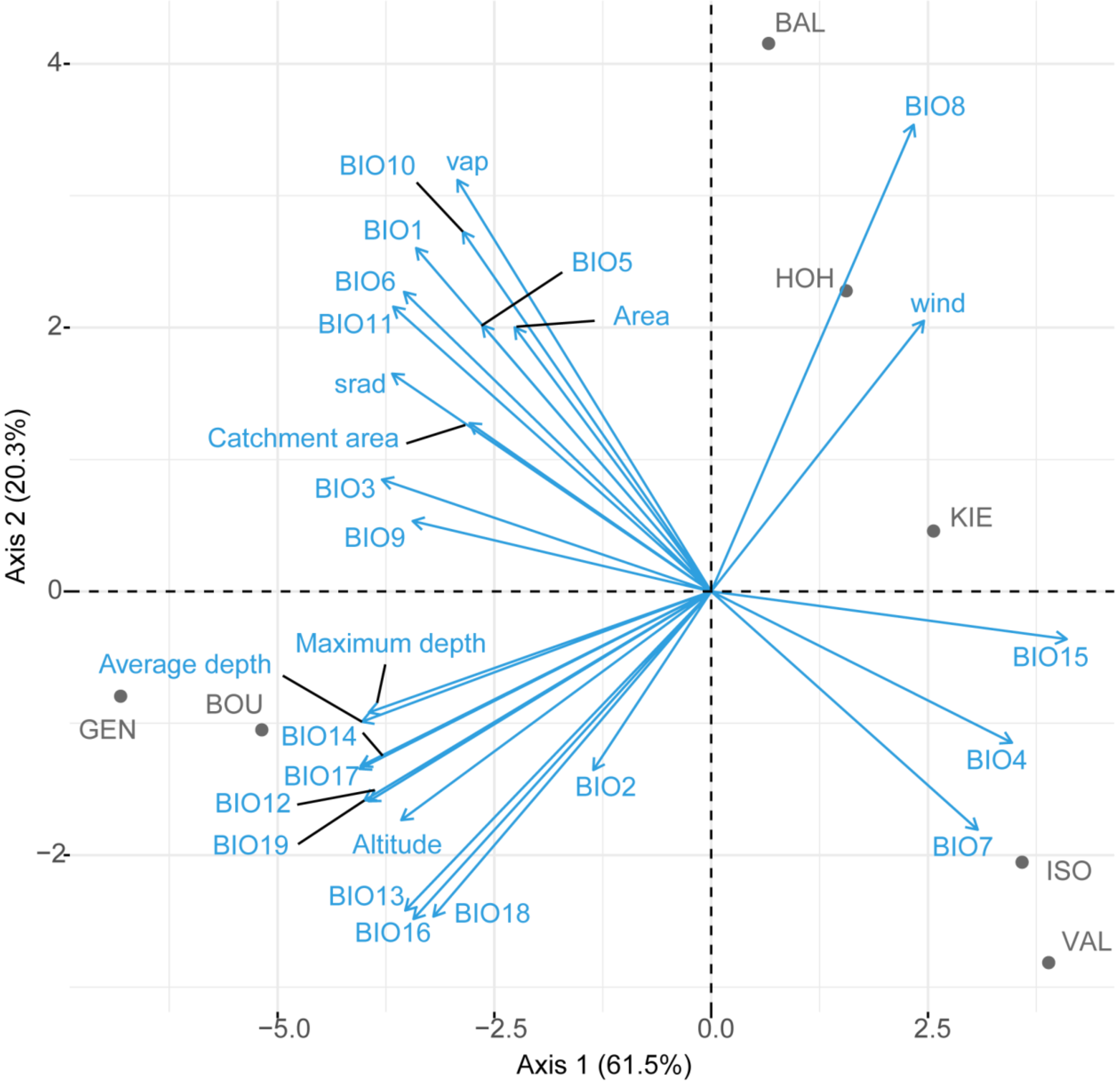
The author(s) declare no competing interests.

Supplementary data

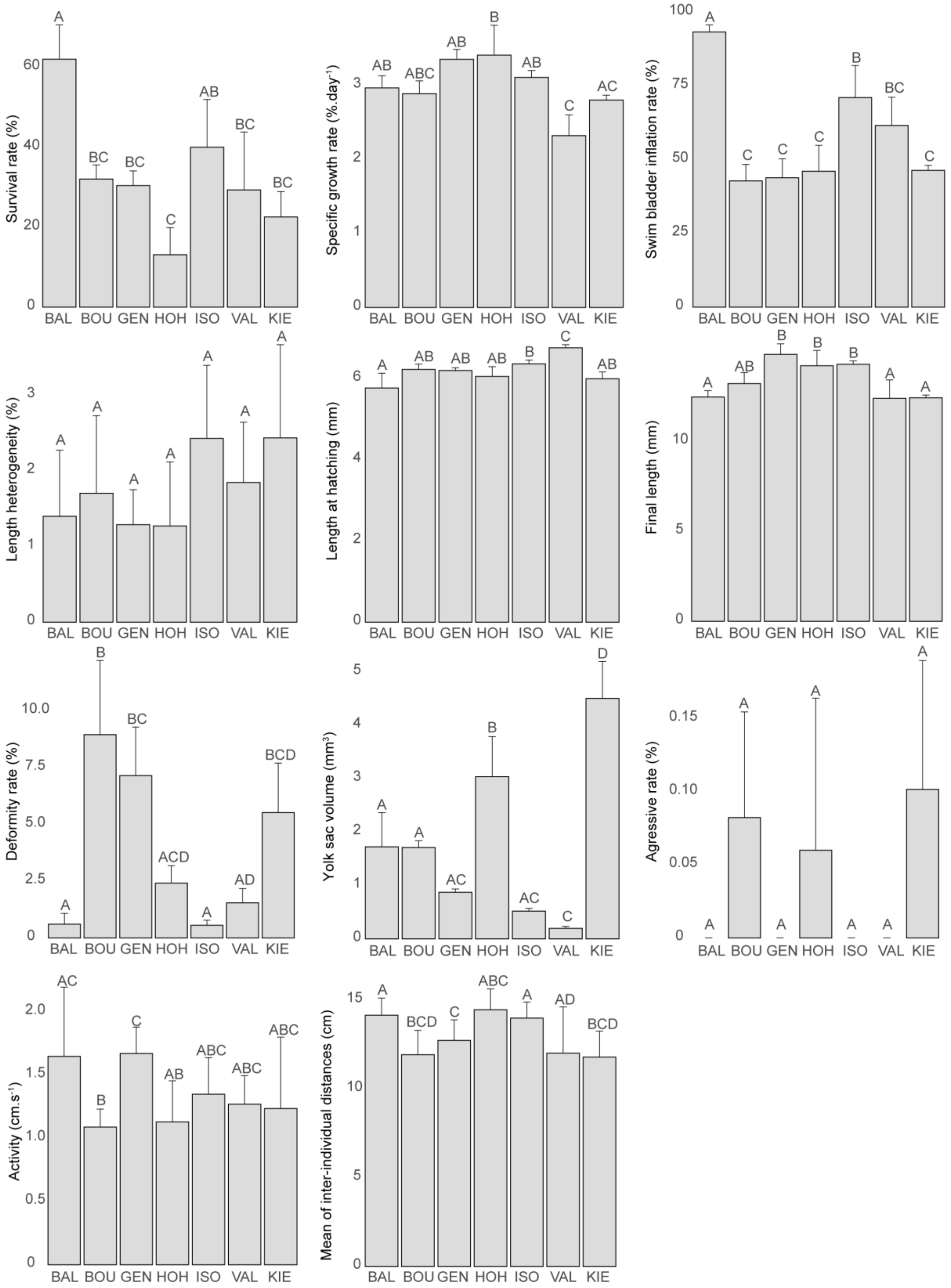
Supplementary Fig. S1: Map representing the seven wild *Perca fluviatilis* populations sampled. VAL: Valkea-Müstajärvi, ISO: Iso-Valkjärvi, KIE: Kierzlinskie, GEN: Geneva, BOU: Bourget, HOH: Hohen Sprenzer, and BAL: Balaton.



Supplementary Fig. S2: Principal component analysis biplot representing environmental variables (in blue) and populations (dots in grey) using the first two axes. Populations: BAL: Balaton, VAL: Valkea-Müstajärvi, ISO: Iso-Valkjärvi, KIE: Kierzlinskie, GEN: Geneva, BOU: Bourget, HOH: Hohen Sprenzer. BIO1 to BIO19 correspond to the bioclimatic variables from Worldclim. Vap, wind, and srad correspond to water vapor pressure, wind speed, and solar radiation, respectively.



Supplementary Fig. S3: Barplots representing results obtained for all traits studied (n = 3 per population, except for activity and inter-individual distances for which n=9). Different letters indicate significant differences between populations (p-value<0.05) using post-hoc tests.

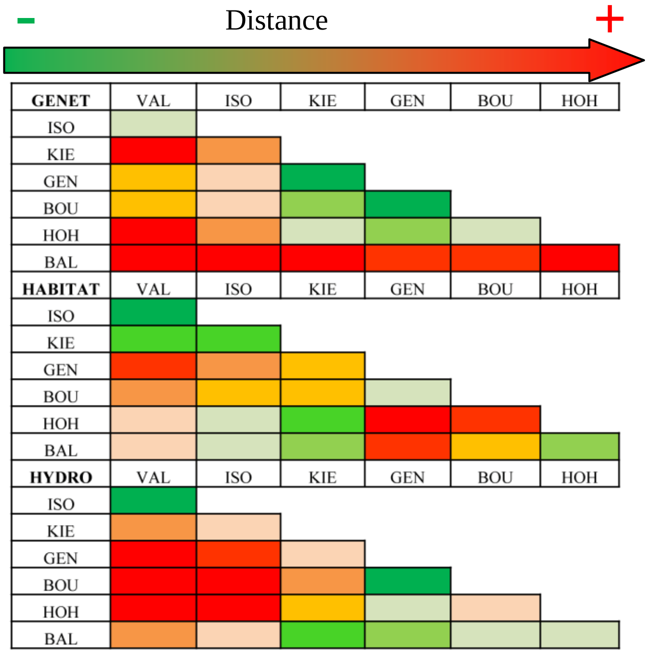


Supplementary Table S1: Correlation results between proxy-based (geographic, hydrologic, genetic, and habitat proxies) and TIA-based distance matrices with r the Mantel correlation value and its associated p-value (significant r (p-value<0.05) are indicated in bold).

TIA	Mantel test (r) results			
	Geographic distance proxy	Hydrologic distance proxy	Genetic distance proxy	Habitat divergence proxy
Survival rate	r=0.035 (p-value=0.260)	r=0.042 (p-value=0.222)	**r=0.505** (p-value= 1x10^{-4})	r=-0.082 (p-value=0.183)
Swim bladder inflation rate	**r= 0.199** (p-value=0.017)	**r=0.142** (p-value=0.037)	**r=0.631** (p-value= 1x10^{-4})	**r=0.182** (p-value=0.043)
Deformity rate	**r=0.350** (p-value=0.001)	**r=0.286** (p-value=0.001)	**r=0.193** (p-value=0.034)	**r=0.469** (p-value=6x10^{-4})
Specific growth rate	r=0.077 (p-value=0.114)	**r=0.237** (p-value=0.002)	r=0.133 (p-value=0.110)	r=0.070 (p-value=0.237)
Initial length	**r=0.223** (p-value=0.004)	**r=0.244** (p-value=0.001)	**r=0.472** (p-value=1x10^{-4})	r=0.020 (p-value=0.399)
Final length	r=0.038 (p-value=0.212)	r=0.086 (p-value=0.102)	r=0.039 (p-value=0.294)	r=0.108 (p-value=0.110)
Yolk sac volume	r=0.099 (p-value=0.075)	**r=0.315** (p-value=0.001)	**r=0.217** (p-value=0.024)	r=0.005 (p-value=0.424)
Activity	r=0.034 (p-value=0.255)	r=-0.053 (p-value=0.792)	r=0.016 (p-value=0.381)	**r=0.215** (p-value=0.028)
Inter-individual distances	**r=0.348** (p-value=0.002)	**r=0.366** (p-value=5x10^{-4})	**r=0.407** (p-value=1x10^{-4})	**r=0.295** (p-value=0.003)

TAKE-HOME MESSAGE

Key trait	Best proxy
Survival rate	Genetic
Swim bladder inflation rate	Genetic
Deformity rate	Habitat
Specific growth rate	Hydrologic
Initial length	Genetic
Final length	-
Yolk sac volume	Hydrologic
Activity	Habitat
Inter-individual distances	Genetic



- ✓ The genetic proxy is the one which is correlated to the highest number of key traits

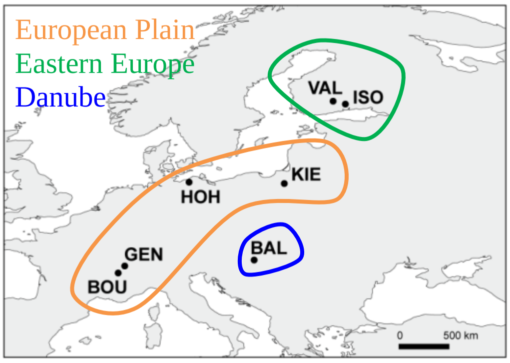
➡ Initial proxy choice in this work was not bad

BUT

➡ No proxy was correlated to all inter-populational divergences in key traits

Multi-proxy approach

WHAT ABOUT AQUACULTURE POTENTIAL WITH THE INITIAL CLASSIFICATION ?



Aquaculture potential (1 to 26 dph)

BAL > ISO > HOH > VAL > KIE > BOU > GEN

Globally:

Danube > Eastern Europe > European Plain

BUT this tends to confirm that the genetic proxy is not sufficient (but low difference in potential between ISO and HOH)

DISCUSSION

DISCUSSION

A. Experimental biases, traits studied, and applications of the three-step method for *P. fluviatilis* larviculture

Several potential experimental biases can be identified in the methodologies used to assess the intraspecific classification and evaluate performances. Experimental biases and potential alternative methods/improvements are discussed in this section. Applications of the three-step method for European perch larviculture are also discussed at the end of this section.

1. Sampling for the phylogeographic structure assessment

The phylogeographic structure could only be studied in western Eurasia, in addition of one location from Siberia. Therefore, samples were missing from the Eastern range of distribution where some specificities could eventually be seen. A more extensive sampling could be performed in Eastern Eurasia but the collection and transportation of biological material in these regions is more challenging.

The sampling size in some regions was low (e.g. Scandinavia, south-east Europe; Russia), especially for estimating genetic diversity. Yet, this sampling size has already been used in previous phylogeographic studies (e.g. Fontanella et al. 2008; Cook et al. 2017). Moreover, results are congruent in these regions with Nesbø et al. (1999) and a sliding window approach was used to evaluate local genetic diversity, which allowed us to minimize the effect of small sampling sizes. Indeed, this approach does not use the arbitrary "population" delimitation since the genetic diversity is estimated within a circular sliding window and is corrected for unequal sampling size. Except for remote sampling sites, this approach allowed minimizing the effect of small sampling sizes.

2. Bioassay experimental biases and potential improvements

2.1 Stock constitution for bioassays

Variation among families within a population can be almost as high as variation between populations (Gunnes and Gjedrem 1978). In addition, intrapopulation genetic variability might contain sub-optimal adapted genotypes (Carvalho 1993). Therefore, an optimal approach would rely on sampling broodstock and simultaneously rear separate family lines for each prospective unit. This would allow quantifying intra-population differentiation *vs* inter-population differentiation and to verify the potential maternal effects on offspring performance (e.g. as performed for instance in Glover et al. 2003). Maternal effects, due to differences between female states (e.g. age, feeding regime, and nutritional reserves, stress), can have an impact on the fitness of the offspring. They have already been shown for many species such as *P. flavescens* (Heyer et al. 2001), *Oncorhynchus tshawytscha* (Actinopterygii, Salmoniformes, Salmonidae; Heath et al. 1999), or *Amphiprion melanopus* (Actinopterygii, Perciformes, Pomacentridae; Green and McCormick 2005). However, rearing several family lines and several populations is ultimately not pragmatic and feasible (i.e. it requires to significantly increase the workload). An alternative consists in performing factorial mating (crossing all males and females) which allows estimating maternal effects, but this is a costly approach (Dupont-Nivet et al. 2002). As an alternative, in this work, individuals originating from 13 to 32 egg ribbons were used (**Table 12**). It can be argued that the higher the number of egg ribbons is, the more the intra-population variability was considered, and the more maternal effects were minimized. However, an uncertainty remains regarding the true contribution of each female to the experimental larval population. Indeed, larvae were mixed after hatching to constitute experimental groups from the pool of larvae, but strong mortalities occurred in the first days post-hatching and during the transition between endogenous and exogenous feeding. It cannot be assessed that all ribbons contributed to the larvae which survived. This would require genotyping both parents and offspring and performing parental assessment (as made in Borrell et al. 2008; Król et al. 2015), which was not possible in this study, having no family background information about the broodstock. In addition, regarding sampling, egg ribbons should be ideally collected at several spawning locations within a site to avoid sampling uniquely siblings, but this was not possible for all populations in this work. Despite these biases, the demonstration of inter-populational differentiation is more robust when using a high number of ribbons since it allows (i) taking into account intra-population variability, (ii) limiting the risk of sampling only sub-optimal phenotypes or siblings, and (iii) limiting the female specificity bias.

The variable number of ribbons between populations (**Table 12**) could have influenced the results. Yet, this step was not possible to standardize because of the (i) uncertainty of the number of ribbons which could be collected before the sampling season, (ii) the temporal shift between spawning seasons which made adjustments between populations impossible, and (iii) the size of the ribbons which were smaller for northern populations implying a higher number of ribbons required to have a sufficient number of larvae. However, no consistency was found between the number of ribbons and performances (e.g. the highest number of ribbons does not correspond to the population performing the best). Therefore, the variable number of ribbons does not seem to have significantly influenced results.

Table 12: Summary of sampling, transport, and incubation of egg ribbons for the different populations. Development stages refer to Alix et al. (2015). O1: first phase of organogenesis (from the first cell differentiation to the first heart beatings; 2-4 days post-fertilization); O2: second phase of organogenesis (from the first heart beatings to the differentiation of the organs associated to the digestive system; 4-7 days post-fertilization).

Lake	Country	Sampling year	Time between sampling and incubation	Transport mode	Development stage at arrival	Number of ribbons used
Valkea-Müstajärvi	Finland	2018	23h	Plane + car	Early O2	19
Iso-Valkjärvi	Finland	2018	25h	Plane + car	Early O2	19
Geneva	France	2019	14h	Car	Early O1	15
Bourget	France	2019	7h	Car	Late O2	16
Hohen Sprenzer	Germany	2019	20h	Car	Mid O2	20
Kierzlinskie	Poland	2019	15h30	Car	Late O1	32
Balaton	Hungary	2019	14h30	Car	Early O2	13

Ribbons of very bad quality (i.e. fragmented egg ribbon, low egg survival at eyed-stage; Schaerlinger and Żarski 2015) or unsynchronized (with the majority of other egg ribbons) in terms of embryo development (according to the development table in Alix et al. 2015) were excluded from the experiment during the incubation phase. However, this might not be sufficient to standardize the use of initial biological material. In order to ensure the homogeneity of this incubation phase, the initial state of eggs could be checked using biochemical parameters (e.g. fatty acid composition) to correctly assess egg quality. However, relevant indicators of perch egg quality are still debated (Schaerlinger and Żarski 2015). A study suggested a relationship between the perch female length and the egg and fry quality (Olin et al. 2012). However, this relationship was demonstrated in one specific lake and we did not have information about females since the relationship between female length and egg ribbons width is not valid in all lakes (Gillet et al. 1995; Huss et al. 2007; Olin et al. 2012).

Finally, egg ribbons were only sampled from lakes in this study. Indeed, it was easier to collect biological material from lakes compared to rivers and more importantly the lake morphotype is the one required by consumers. Yet, populations from rivers and estuaries might have shown different performances. However, (i) environmental conditions between lakes are also quite different and (ii) according to the phylogeographic study, populations belonging to different habitats (lakes, rivers, estuaries) are present within a same PU. Yet, it would be interesting to sample egg ribbons from rivers and brackish waters to assess the importance of local factors such as water velocity or salinity. However, this would imply working at smaller scale than the one used in this work.

2.2 Differential pre-experimental conditions

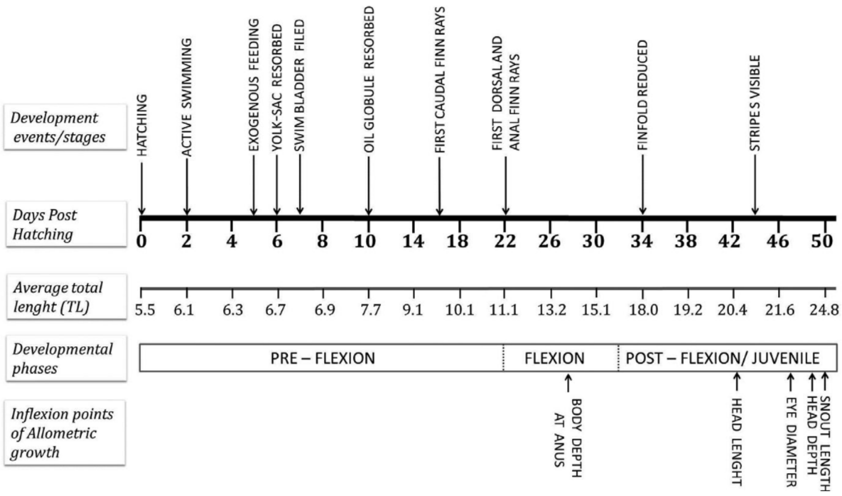
Another possible limitation might have been the transport time which was different between populations and could have triggered negative effects (**Table 12**). However, the longest transportation time (Finnish populations) does not correspond to the population with the lowest performance. In addition, all ribbons were transported before the eyed stage which is the most sensitive stage. Thus, the impact of transport seems minimal in our experiment.

2.3 Potential bias in the experimental set up

In order to highlight genetically-based differentiations, common garden experiments are required. However, it was not possible to perform a “true” common-garden experiment (i.e. larvae from the different populations in the same tank) since (i) it is not possible to tag newly hatched larvae and (ii) there is a temporal shift in the spawning seasons and therefore, at a given date, larvae from different populations had different age and length. Thus, a part of the variability between populations could be due to micro-variations between tanks (Sae-Lim et al. 2016). However, three replicates were performed for each population which allowed limiting this bias and the cylindro-conical tank was included as a random effect in statistical analyses.

Another potential bias corresponds to the comparison of populations relatively to the age post-hatching. Indeed, all parameters were evaluated after important production stages (weaning, end of larviculture) at precise dates post-hatching. However, different populations might present different developmental speeds (i.e. intraspecific heterochrony; Kawajiri et al. 2009; De Jong et al. 2009). By the time of the experiment, a development table was only available from fertilization until exogenous feeding (Alix et al. 2015). However, another development table was published in 2019 and covers larval and juvenile stages (Kupren et al. 2019). This development table (**Figure 9**) could help in the future to better standardize experiments and to compare populations at development stages rather than specific days post-hatching. Through the analysis of pictures taken at different time steps for the different populations, the shift of development could be tested. Indeed, at given post-hatching ages, inter-population differences in yolk sac resorption, fin development, fin rays apparition, or swim bladder inflation would confirm/refute developmental shifts.

Figure 9: Major developmental events of *Perca fluviatilis* during larval and juvenile stages according to Kupren et al. (2019).



Finally, because of differences in spawning season timing, trials did not occur at the same time between perch populations. However, same exact protocols were used between populations and trials overlapped between all populations within each year. The differential years of experiment could have influenced results, but the exact same protocol was used between 2018 and 2019.

3. *Which implications for European perch larviculture?*

Reminder of work hypotheses

H1: There is a geographic differentiation in *Perca fluviatilis* for key traits.

H2: There are units with high potential for aquaculture within species.

We validated that geographic differentiation exists in European perch for many key traits (**chapters one, four, and five**), both at population and PU levels (**Table 13**; validation of hypothesis **H1**). These results can be useful for European perch larviculture, particularly considering key traits for which the difference delta is quite high between populations/PU such as for survival rate, swim bladder inflation rate, deformity rate, or final weight (**Table 13**). Differentiation in European perch key traits was already previously shown for several key traits (Mandiki et al. 2004; Pimakhin and Zak 2014; Vanina et al. 2019a, b), but the differences in age post-hatching evaluations and rearing conditions makes comparisons with our results difficult.

The **fourth chapter** allowed validating the hypothesis **H2** since there are divergent potentials for aquaculture (here limited to larviculture) between prospective units. Considering all results across the different chapters, Lake Balaton/Danube group was shown as the population/PU with the highest aquaculture potential. Unfortunately, Lake Balaton was the only population representative of the Danube group. Therefore, it was not possible to verify the within-Danube group differentiation. The lowest potential for aquaculture was highlighted for Lake Geneva at the population level. This is consistent with a hypothesis raised by Ben Khadher (2015). In European perch farmed stocks studied, Lake Geneva individuals were supposedly at the origin of the founder stocks (Ben Khadher et al. 2016). Yet, they were poorly represented in farmed stocks, in which several probable introductions of individuals from different geographic origins occurred. Authors suggested as a plausible explanation a poor performance of individuals from Lake Geneva in aquaculture conditions compared to other allopatric populations (Ben Khadher et al. 2016). Differences in performances could have substantial impacts for perch farms. Considering a specific example with survival rate which is a major bottleneck in Percid larviculture (Policar et al. 2019), there is a high differentiation between Lakes Geneva and Balaton. On the base of price quotations, selling cost of European perch larvae at 3g is about 10-30 cents per larvae. Looking at results obtained at the end of phase I (phase with the highest mortalities), there is a loss of about 212 euros per replicate worth of sale for Lake Geneva compared to Lake Balaton (not considering variable costs). Rearing more larvae (in the limit of the company capacities) is going to increase variable costs (e.g. feed) but fixed costs will be the same (e.g. equipment, oxygen, salaries). The larvae are less than 3g at 26 dph but this still gives an idea about the impact of survival differences on farm revenues. Improving survival could allow decreasing the overall production cost. This estimation is made for rearing densities used in this work, but fish farmers use higher densities and larger tanks. Therefore, there can be a substantial financial impact in the choice of the founder population. Overall, these results are first insights which could be helpful for *P. fluviatilis* larviculture, but these results are specific to our RAS system.

Traits relevant for European perch larviculture were evaluated but some traits listed in the second chapter were not included in the following chapters. Firstly, regarding the category 1, timing for exogenous feeding was not evaluated since the feeding protocol was the same for all populations (i.e. fixed domestication system). Other traits were not included because of method evaluation limitations. In this way, age/size at cannibalism onset were not included in the fourth and fifth chapters. We did get this information for five populations but it relied on daily 10-minute observations, which triggered several biases: (i) observers were different between 2018 and 2019, (ii) observations were made after first feeding but cannibalism might occur at other moments through the day, and (iii) the presence of the observer might disturb the behavior of larvae. We suggest that a new protocol should be developed to evaluate this trait (e.g. camera above the tank with a lower water depth). However, the global aggressiveness rate, which includes cannibalism rate (I and II) and enucleation, was assessed which allowed to evaluate mortalities potentially due to aggressiveness. This also illustrates the global difficulty tied to the life-stage studied. Working on larvae is not easy because of the small size (**Figure 10**) of individuals and makes the evaluation of some traits difficult. For instance, respecting precise initial densities and following daily mortalities requires counting individuals and because larvae are small, some errors in counting are inevitable. However, these biases are the same for all populations.

Figure 10: Larva from Lake Geneva at 21 days post-hatching.

The rest of the life cycle needs to be performed in order to evaluate other traits from category one (see **Table 1** in the second chapter). Moreover, the evaluation over the full life cycle is required to assess if the best populations/PU for larviculture are also the best for on growing and reproduction. Regarding category 2, related to larviculture, the acceptance of artificial diets and the resistance to sub-lethal stress were not evaluated directly, but survival rate is an integrative trait which, among other factors, reflects mortality subsequent to non–acceptance of dry feed and stress. Yet, an experiment to specifically evaluate resistance to stress (see for instance protocol in Colson et al. 2015) and diseases (e.g. protocol in Giri et al. 2013) would allow to better evaluate the aquaculture potential. Traits relative to categories three and four still need to be evaluated and require the development of specific methodologies such as the acceptance of alternative feeds (e.g. Fountoulaki et al. 2009; Gisbert et al. 2016; see first experiment on *P. fluviatilis* juveniles with linseed oil replacement : Geay et al. 2015a; Geay et al. 2015b), which is partly determined by genetic components (Blonk and Komen 2015).

Table 13: Univariate statistics results on differentiation between populations and prospective units (PU) for the different traits studied. ☑ indicates a statistically significant differentiation (p-value<0.05), a cross (x) indicates a lack of statistically significant differentiation (p-value>0.05). Diff corresponds to differentiation. Mean value corresponds the mean across all populations/PUs, minimum to the lowest value, maximum to the maximal value.

Phase	Biological function	Trait	Populational level		PU level	
			Diff ?	Mean value (Minimum-Maximum)	Diff ?	Mean value (Minimum-Maximum)
I		All traits combined	☑	-	☑	-
	Growth	SGR length	☑	2.98 %.day^{-1} (2.32-3.41)	x	2.93 %.day^{-1} (2.72-3.11)
		Initial length	☑	6.20 mm (5.77-6.76)	☑	6.15 mm (5.77-6.56)
		Final length	☑	13.40 mm (12.39-14.83)	x	13.16 mm (12.47-13.67)
		Final length heterogeneity	x	1.77 % (1.27-2.44)	x	1.74 % (1.40-2.14)
	Other	Survival rate	☑	32.77 % (13.11-62)	☑	40.39 % (24.53-62)
	Development	Deformity rate	☑	3.82 % (0.56-8.96)	☑	2.56 % (0.60-6.01)
		Swim bladder inflation rate	☑	57.87 % (42.81-93.29)	☑	68.14 % (44.79-93.29)
	Nutrition	Yolk sac volume	☑	1.79 mm^3 (0.20-4.50)	☑	1.45 mm^3 (0.36-2.53)
	Behavior	Global aggressive rate	x	0.03 % (0-0.10)	x	0.02 % (0-0.06)
		Activity	☑	1.33 cm.s^{-1} (1.09-1.70)	☑	1.41 cm.s^{-1} (1.26-1.65)
		Inter-individual distances	☑	12.99 cm (11.71-14.48)	☑	13.49 cm (12.09-14.24)
II		All traits combined	☑	-	☑	-
	Growth	SGR length	x	3.05 %.day^{-1} (2.71-3.30)	x	3.09 %.day^{-1} (2.94-3.30)
		SGR weight	x	10.14 %.day^{-1} (8.89-11.15)	x	10.31 %.day^{-1} (9.75-11.14)
		Initial length	☑	12.85 mm (10.88-14.74)	☑	12.94 mm (11.02-14.70)
		Final length	☑	33.20 mm (25.93-33.80)	☑	33.63 mm (27.47-37.65)
		Initial weight	☑	17.90 mg (10.20-28.52)	☑	12.84 mg (11.02-14.90)
		Final weight	☑	396.90 mg (203.77-584.66)	☑	409.09 mg (239-518.25)
		Final length heterogeneity	x	1.51 % (1.04-1.82)	x	1.54 % (1.37-1.67)
		Final weight heterogeneity	x	0.86 % (0.73-1.16)	x	0.84 % (0.73-0.95)
	Other	Survival rate	☑	26.27 % (13.17-35.30)	☑	27.20 % (15.68-34.07)
	Development	Deformity rate	☑	1.87 % (0.31-6.16)	x	1.61 % (0.31-3.50)
		Swim bladder inflation rate	☑	75.64 % (36.66-95.35)	☑	77.74 % (53.22-91.75)
	Behavior	Global aggressive rate	x	19.58 % (10.92-26.36)	x	18.14 % (10.96-25.87)
		Activity	☑	1.60 cm.s^{-1} (0.74-3.38)	☑*(n=4)*	1.85 cm.s^{-1} (0.83-3.38)
		Inter-individual distances	☑	11.56 cm (10.12-12.53)	☑ *(n=4)*	11.47 cm (10.12-12.53)

Take home message

There are several experimental biases which can potentially influence results obtained on *P. fluviatilis* first life stages. However, numerous of theses biases are inevitable and were minimized as much as possible. Some alternative solutions were proposed in this section, but the pragmatism of the methods used for each step of the integrative approach remains a priority. Despite these experimental biases, a geographic differentiation was highlighted for numerous key traits for larviculture at the population and PU levels for *P. fluviatilis* first life stages. This is translated by differential potentials for aquaculture. Therefore, the two initial hypotheses of this work were validated. This work is a first step towards a facilitation of domestication and subsequent production of *P. fluviatilis* through the consideration of geographic differentiation. Further studied are needed to assess performances over the full life cycle and for traits belonging to other categories.

B. The three-step integrative method: limits of the approach and potential improvements

1. *Step 1: Classification*

1.1 Establishing a phylogeographic classification

This first step is essential and is aimed at classifying wild populations in order to (i) restrict the range of possibilities and (ii) identify biological units which are likely to present differentiations in key traits for domestication and production. We relied for this first step on a phylogeographic classification based on neutral markers since there can be a congruence in the wild between phenotypic differentiation and phylogeographic structure due to long periods of neutral and selective evolution of lineages (Zhao et al. 2008; Zamudio et al. 2016). Indeed, groups of populations presenting divergent demographic histories could have acquired, notably through local adaptations or random phenomena, some phenotypic specificities. In this way, populations inhabiting divergent environments and/or exchanging few or no migrants (i.e. low gene flow) may differ genetically and display phenotypic differences due to local selective pressures (Mayr 1963; Carvalho 1993; Kawecki and Ebert 2004; Zamudio et al. 2016). The degree of genetic differentiation depends on population history (range expansion, founder effect, secondary contact), population size, time since divergence, and gene flow (Hauser and Carvalho 2008). Using mitochondrial markers, we provided a large-scale genetic structure. Congruent results were observed with microsatellites at smaller-scale with a subdivision of the main prospective units, despite the low number of samples used for this marker type. The genetic differentiation can be high at even smaller scales, such as within the course of a river or within a lake, since differentiations in life-history and habitats can be strong (e.g. Behrmann-Godel et al. 2004; Vähä et al. 2007; Bergek et al. 2010; Hughes et al. 2012). However, this study is aimed at being pragmatic and at highlighting a large-scale genetic structure. By considering the mitochondrial genetic structure, we increased chances of detecting differentiations in key traits which can be preserved across generations. The establishment of such a classification is an undeniable advantage since it is not possible to compare all wild populations in the second step and comparing random populations is not an optimal approach.

1.2 Limitations of the phylogeographic classification

Establishing a phylogeographic classification might be easier for freshwater fishes due to the presence of physical barriers compared to marine fishes where genetic differentiations are often lower because of greater dispersal (Carvalho 1993; Ward 2006; Hauser and Carvalho 2008; Nielsen et al. 2009). For instance, identifying a large-scale genetic structure might be challenging for the European eel (*Anguilla anguilla* L.) because of a low genetic differentiation highlighted at smaller geographic scales (Hoffmann et al. 2001; Dannewitz et al. 2005; Palm et al. 2009; Ragauskas et al. 2014). However, a strong genetic structure was highlighted for plenty of other species (e.g. Durand et al. 1999; Kotlík and Berrebi 2001; Van Houdt et al. 2003; Gum et al. 2005; Østbye et al. 2005; Seifertová et al. 2011; Salmenkova 2011; Jamaluddin et al. 2019). Therefore, the difficulty of this first step is species dependent and since phylogeographic studies are widely performed (Zamudio et al. 2016), the classification might be available in literature when considering a new candidate species, providing that this classification was established based on a multi-marker approach and at large-scale. However, genetic techniques evolving fast, it might drive phylogeographic structures previously established to be quickly obsolete.

The usefulness of the phylogeographic classification might be limited for species for which translocations are performed at the time of the three-step evaluation. Indeed, some new candidate species for domestication could have an interest for recreational fisheries or could be submitted to enhancement programs to restore natural stocks (for conservation or exploitation purposes). In these scenarios, there might be introduction of exogenous individuals in some targeted sampling sites between the first and second steps. This leads to the risk to sample for bioassays individuals which are not representative of the prospective unit. In addition, if translocations are performed after the three-step approach, it can be an issue when constituting a stock using the results of the three-step method. Indeed, when targeting a unit with high potential for aquaculture, there is a risk of sampling fish which will display different specificities than those highlighted during the three-step assessment. Therefore, sites in which translocations are performed at the time of the evaluation or after should be avoided for the sampling step of bioassays or farm stock constitution. Finally, translocations can have greater impacts when performed widely across the distribution range. Indeed, in extreme cases, it could also present the establishment of an intraspecific classification because of a genetic homogenization across the distribution range (Ryman et al. 1995; Champagnon et al. 2012). In this extreme case, applying the three-step approach would be limited.

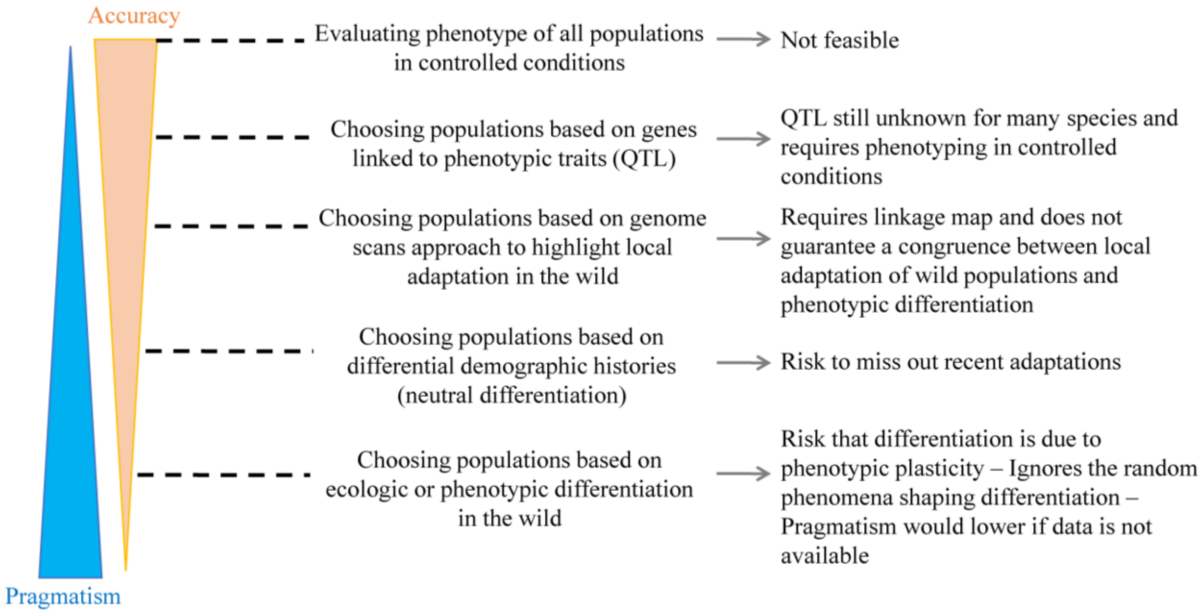
The fifth chapter highlighted that the genetic proxy does not allow reflecting differentiation for all key traits. The use of neutral markers has been hypothesized as the main explanation about the lack of correlation between some trait distance matrices and the genetic distance matrix. Even though genetic differentiation can occur quickly (i.e. decades) when selective pressures and/or genetic drift are strong, recent adaptations might not be visible in neutral markers (Ballentine and Greenberg 2010; Zamudio et al. 2016). Therefore, neutral divergence can be a poor predictor of adaptive trait variation (Leinonen et al. 2008).

1.3 Genetic alternatives to the phylogeographic proxy?

One could state that genetic differentiation could have been replaced by genetic heterozygosity. Indeed, a relationship was suggested between the level of heterozygosity and fitness (e.g. Koehn and Gaffney 1984; Hayes et al. 2006). However, this relationship varies among and within species and many studies show the absence of a correlation (Appleyard et al. 2001; Wang et al. 2002 and references within). Although there is an overall agreement that inbreeding can lead to a decrease in biological performance (but see potential increase of natural selection effectiveness [i.e. genetic purging]; García-Dorado 2015) under culture conditions, no correlation can be made between genetic heterozygosity and performance (Wang et al. 2002; Vandeputte and Launey 2004).

The use of adaptive markers could be an interesting alternative since they can provide better estimates of differentiation caused by ecological gradients (Conner and Hartl 2004; Holderegger et al. 2006). Approaches have been developed to infer the genetic basis of adaptive phenotypic divergence between populations using multilocus mapping approaches such as quantitative trait loci (QTL) mapping (Erickson et al. 2004; Storz 2005). However, this approach requires comparisons of populations in controlled conditions to identify adequate QTL and genetic underpinnings of many quantitative traits are still unknown (Holderegger et al. 2006; Merilä and Hendry 2014). An alternative approach to detect locus-specific signature of directional selection without screening phenotypic variation relies on genome scans approaches (Storz 2005). Indeed, using a large number of genetic markers, adaptive population divergence can be demonstrated through the identification of outlier loci (i.e. loci subjected to directional selection; Storz 2005; Nielsen et al. 2009). This approach was already used in fish to detect local adaptation (e.g. Meier et al. 2011; Lowry et al. 2017) and could help to pinpoint which populations could have undergone local adaptation. However, this approach requires that a high-density genetic map is available, which is not the case for many fish species (but see Qiu et al. (2018) and references within). Moreover, the loci relevance to demonstrate adaptive phenotypic change remains often uncertain (Storz 2005; Merilä and Hendry 2014). These alternative approaches could help to identify biological units of interest, but they are costly and therefore, they are not suitable to develop a pragmatic method (**Figure 11**). In addition, even though neutral markers are less accurate to highlight differentiations triggered by ecological gradients, they can also reflect differentiations triggered by random processes, which is not the case with adaptive markers.

Figure 11: Comparison of different methods which could be used to classify populations according to their accuracy (i.e. in highlighting populations presenting divergences in key traits) and their feasibility (i.e. pragmatism).



Take home message

The use of neutral genetic differentiation to highlight population groups with potential divergences in key traits presents some limits. However, alternative strategies also present some limits and/or are difficult to apply. Therefore, overall, the use of neutral markers for the phylogeographic classification appears as a good compromise between the ability to highlight phenotypic divergences and the pragmatism of the approach.

1.4 Towards a single or a multi-proxy step 1?

1.4.1 Was the genetic proxy the right one?

The relevance of the genetic proxy was only checked on phase I (1 dph to 26 dph; fifth chapter). Therefore, to check the consistency of conclusions, I performed the same analysis (MRDM+CA and Mantel tests) using available data for phase II (27 dph to 60 dph) regarding seven key traits on five populations[2] (GEN, KIE, ISO, VAL, BAL). There is no inter-populational differentiation for specific growth rate (length and weight), final growth heterogeneity (length and weight), and aggressive interaction rate, which were therefore not included in this analysis. The MRDM-CA results (**Table 14**) point to a similar conclusion than the fifth chapter: no proxy-based distance matrix is correlated to all key trait distance matrices. However, it also shows that among alternative proxies, the genetic proxy is the most relevant since it is correlated to all key traits except for deformity rate.

Table 14: Summary of MRDM-CA and Mantel results for phase II. Best proxies correspond to proxies with a unique contribution > 1%. * indicates a significant R^2 (p-value<0.05).

Key trait	R^2 MRDM	Best proxy(ies) according to the MRDM-CA	Proxies correlated using Mantel tests
Deformity rate	0.473*	Habitat	Hydrological + Habitat + Geographic
Survival rate	0.252*	Genetic	All
Swim bladder inflation rate	0.377*	Hydrological + Genetic	Hydrological + Habitat + Genetic
Initial length	0.647*	Hydrological + Genetic	All
Initial weight	0.515*	Hydrological + Genetic	All
Final length	0.447*	Hydrological + Habitat + Genetic	All
Final weight	0.338*	Hydrological + Genetic	All

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[2] *Data was added from a fifth population [KIE], which is not included in the fourth chapter. These results still need to integrate behavioral traits (i.e. inter-individual distances and activity) for which phase II raw data still needs to be analyzed).*

1.4.2 *Two alternative strategies possible*

Given that the genetic proxy is not correlated to all key traits, two alternative approaches were suggested in the fifth chapter.

The first one consists of selecting the proxy which is correlated with the most important key-traits according to fish farmers/stakeholders. Using the survey from the fourth chapter, we can see that this strategy is limited in our case since the two most important traits are correlated to two different proxies (**Table 15**). For instance, only considering the habitat distance proxy would lead to an under-estimation of differentiation in key traits. However, a pragmatic alternative would be to use only the genetic proxy, as performed in this work. Indeed, when considering both phases and ignoring the collinearity between proxies (i.e. focusing on Mantel test results), the genetic proxy is correlated with 12 trait-based distance matrices out of 15 and with correlation values overall higher than other proxies (higher than the hydrologic proxy correlated to 13 trait-based distance matrices). Moreover, when performing a multivariate statistical analysis to check the overall differentiation between prospective units considering all traits simultaneously, there is a differentiation between all prospective units for phase I (perMANOVA: DF=2, F=19.28, p-value<0.001) and between the European Plain *vs* Danube-Eastern Europe for phase II (perMANOVA: DF=2, F=17.62, p-value<0.001). Therefore, the use of the genetic proxy is useful for highlighting major differences between prospective units. The usefulness of using neutral genetic differentiation to highlight divergences in key traits was previously demonstrated in *P. fluviatilis* (Vanina et al. 2019a) and *P. flavescens* (Rosauer et al. 2011).

Table 15: Summary of MRDM-CA and Mantel results for phase I associated to the weight coefficients obtained in the fourth chapter.

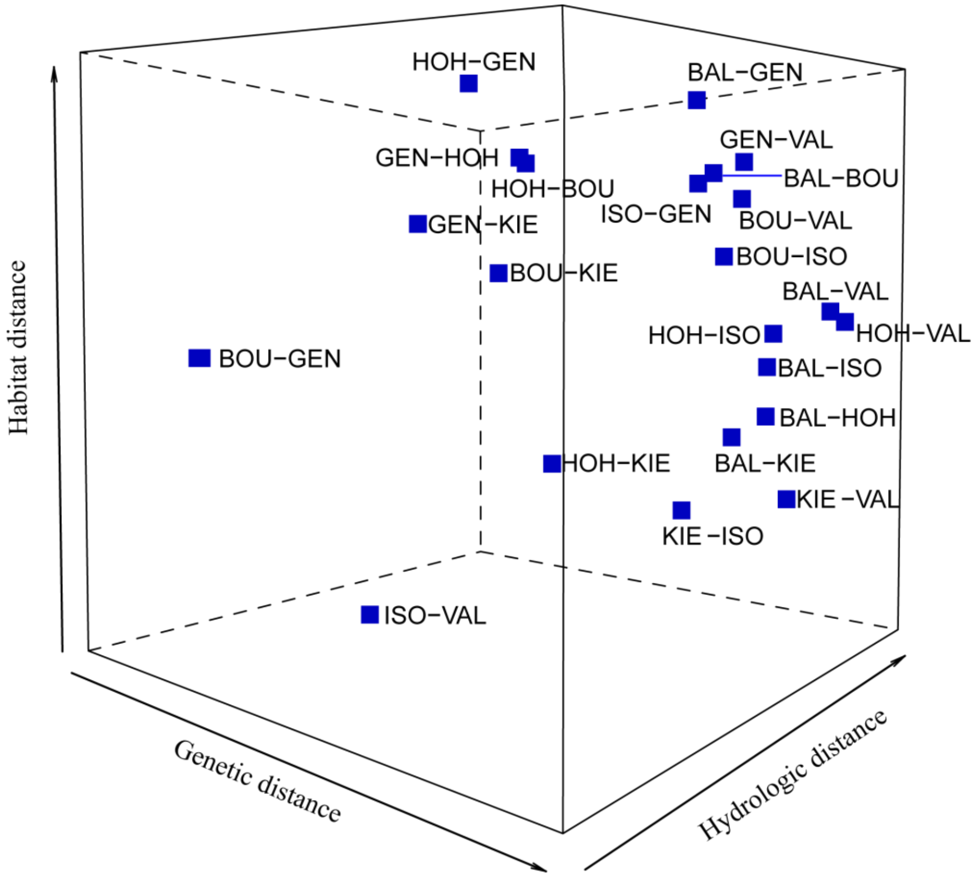
Key trait	Best proxy according to MRDM-CA	Proxies correlated in Mantel test	Survey weight coefficient (0-100)
Deformity rate	Habitat	All	97.22
Survival rate	Genetic	Genetic	88.89
Swim bladder inflation rate	Genetic	All	81.25
Yolk sac volume	Hydrological	Hydrological + Genetic	78.13
Specific growth rate	Hydrological	Hydrological	77.78
Initial length	Genetic	Geographic + Hydrological + Genetic	68.75
Activity	Habitat	Habitat	53.57
Inter-individual distances	Genetic	All	47.22

The second strategy promoted the use of a multi-proxy strategy which would allow improving the single-proxy approach used in this work. However, a multi-proxy classification might be hard to achieve because of limitations of each proxy in the frame of a classification (which can also prevent their use in the single-proxy approach). Indeed, establishing a multi-proxy classification would imply (i) the occurrence of 'breaks' in the genetic differentiation which are required to highlight a genetic structure (e.g. genetic differentiation by distance would prevent the establishment of a classification), (ii) to determine arbitrary values to create a classification based on hydrologic distance or the use of arbitrary notions such as hydrographic basins (without considering connections via artificial canals), and (iii) to have significant divergences in ecosystems to be able to perform a habitat classification. Moreover, it is difficult to make a consensus between alternate classifications. It could be performed through clustering analyses and a consensus between the different proxy-based clusters, but this strategy remains sub-optimal. Overall, establishing a classification in step 1 might therefore not be the most optimal approach.

1.4.3 An alternative to the classification approach?

As an alternative, working with distances rather than differentiations would allow overcoming difficulties of establishing a classification. This alternate strategy is based on the ranking and prioritization of populations (the biological unit is the population rather than the prospective unit). It consists of simultaneously testing populations across the distribution range for genetic, habitat, and hydrological distances (i.e. the consideration of these three proxies allows to cover correlations with all key traits distance matrices). With this approach, population pairs which are the most distant (for the three proxies) would be considered for further steps (**Figure 12**). Although considering populations genetically, hydrologically, and environmentally distant may seem obvious, this step is essential to avoid the random sampling of populations. The number of population pairs considered for the bioassays mainly depends on the capacities of the fish farm/research structure where the step 2 is performed. If the upper capacity is to study two populations, then the two populations which are the most distant across all proxies should be considered (in **figure 12** that could correspond to BAL and GEN).

Figure 12: Figure illustrating the prioritization of populations for phase I. Pairwise comparisons of populations are plotted (blue squares) according to three proxies (genetic, hydrologic, and habitat distances).



Take home message

Overall, establishing an intraspecific classification, either single- or multi-proxy, remains limited since it implies potential arbitrary choices to delineate groups. The single proxy classification worked rather well in this work, but an alternative strategy is proposed here: prioritizing population pairs using several proxies, rather than classifying. This allows to overcome limits tied to the classification and could simplify the first step of the approach.

2. *Step 2: Comparing performances in a common-garden environment*

2.1 Limits of the step 2

The second step of the integrative approach is probably the most work-intensive step since rearing several populations and evaluating their performance over the full life cycle is challenging and time-consuming. The use of a multi-function and multi-trait approach increases the workload of this step. However, as shown in the fourth chapter, the single-strait approach is limited and might lead to erroneous conclusions. The multi-trait evaluation is necessary to estimate the potential for aquaculture correctly. This underlines the importance of the first step to limit the number of populations which need to be compared during bioassays.

The common-garden set up allows to state that differences observed between populations are genetically based. However, egg ribbons were spawned in the wild and therefore experienced the environment effect before being transferred to the experimental structures. Differences seen between populations can thus be attributed to (i) phenotypic plasticity, including parental effects mentioned earlier and epigenetic effects and (ii) genetically based differences. The effect of phenotypic plasticity could have been limited through the sampling of broodstock to produce offspring in controlled conditions. However, for *Perca fluviatilis*, as well as for many other species, first life stages are the preferred wild biological material for fish farmers since mortality rates following transport and acclimatization are high for adults. Moreover, transgenerational effects can still impact the descendants from wild-caught breeders (Youngson and Whitelaw 2008; Bhandari et al. 2015). Therefore, phenotypic plasticity impacts cannot be ruled out when applying the three-step approach, but these latter are limited thanks to the use of a common-garden experiment, even though adaptive epigenetic changes (i.e. heritable; e.g. linked to DNA methylation or histone modifications) could also be of interest, similarly to genetically-based divergences, since they have the potential to influence fitness (Klironomos et al. 2013).

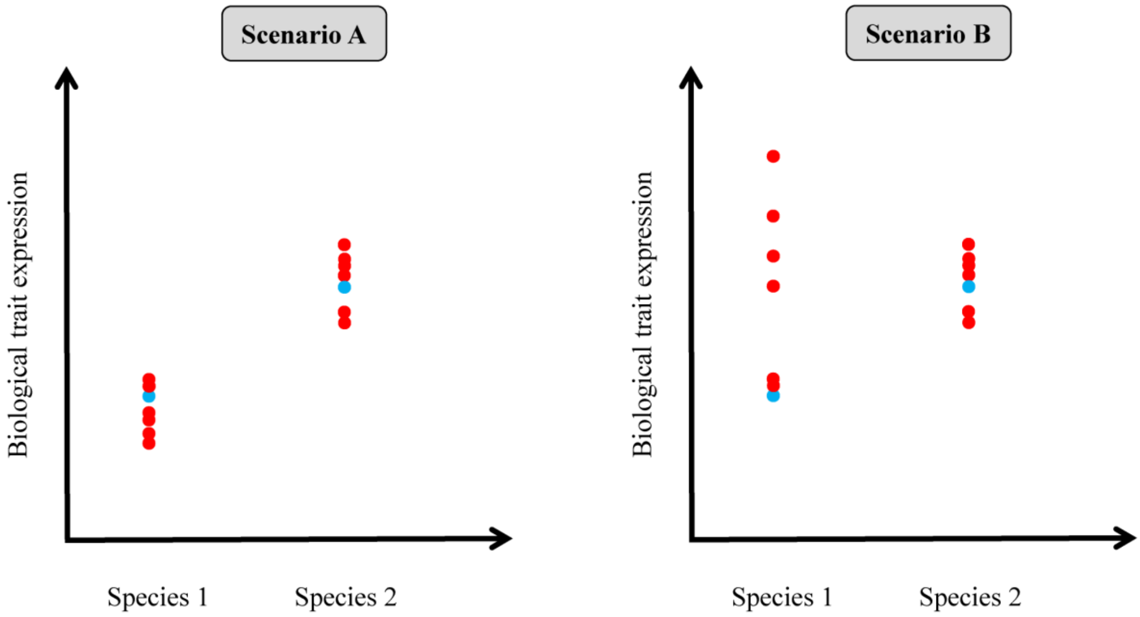
A (partial) genetic basis (i.e. heritability = fraction of the phenotype variation which can be explained by variation in genotype) was already assessed in other species for several key traits (e.g. McKay and Gjerde 1986; Afonso et al. 2000; Gjedrem and Olesen 2005; Friars and Smith 2010; Wang et al. 2010; Ødegård et al. 2011; Blonk and Komen 2015; García-Celdrán et al. 2015; Kristjánsson and Arnason 2016). Therefore, we can expect that at least a part of these differentiations would be transmitted to following generations, but this still requires further studies. One way to verify that the observed inter-populational differentiations are genetically based would be to continue the experiment for the full life cycle and to verify on the F1 (first generation born in captive conditions) that the same differentiations are observed. However, the impact of domestication can occur even after only one generation in the culture environment (see further; Christie et al. 2016). Another solution would be to repeat the performance assessment of wild populations the following year to evaluate the genetic basis of phenotypic differentiation.

One could state that a particular population/PU may perform better than others in the experimental system because it is better adapted to these conditions (e.g. rearing conditions closer to their wild habitat). For instance, as these populations come from different geographic locations, it is likely that their optimal rearing temperatures differ due to local adaptation, although the thermo-tolerance of European perch is quite high. However, this is a concept proof study aiming at highlighting differentiations in key traits for a particular rearing system. Varying both factors (biological unit [population or PU] and different rearing systems) would be interesting to assess the interaction between genetic and environment variances but it was not the purpose of this work.

2.2 Implications regarding the inter-specific candidate evaluation?

In the introduction of this work, some methods used at the interspecific level to highlight candidate species of interest based on socio-economic and biological criteria were presented (**Tables 3 and 4)**. Geographic differentiation was highlighted for several key traits and this calls these methods into question. Indeed, the question can be raised regarding the differentiation between species *vs* the differentiation within species. A good candidate species could be missed if the evaluation at the inter-specific level is only performed on one population (wild or in controlled conditions) to assess the potential of this particular species. In the **figure 13**, I suggest two scenarios. The first scenario would lead to the identification of species 2 as the best candidate species for domestication. Species 1 would not be considered for further domestication trials. In scenario 2, the same conclusion would be drawn. Yet, if geographic differentiation had been taken into account, species 1 would not have been excluded from further evaluation since some populations present a high expression of this key trait. Therefore, the best method would be to evaluate from the beginning geographic differentiation of all species of interest for aquaculture (i.e. species meeting an unsatisfied human demand, need, or interest and has a high socio-economic value). However, this might not be feasible/pragmatic for all new candidate species since it requires time and money. Therefore, caution should be paid regarding biological characteristics when ranking candidate species for interest for domestication and production (e.g. by putting more weight to socio-economic criteria than biological criteria). It should be known that a good candidate species could be missed and exclusion of candidate species from the evaluation process should not be based solely on biological characteristics, even though the interspecific differentiation can be expected to be overall higher than the intraspecific differentiation.

Figure 13: Hypothetical scenarios regarding the expression of a key trait considered as a facilitating characteristic for domestication/production. Two species are screened, and one population is considered (in blue) for the assessment. In red are represented other conspecific populations' expressions which are not considered in the evaluation process. The two scenarios would lead to consider species 2 as more suitable for domestication/production than species 1.



3 *Step 3: Identifying units with the highest aquaculture potential*

This step requires attributing a weighting coefficient to each trait. Indeed, not all traits are equally important to stakeholders as confirmed by the survey led in the fourth chapter. In our survey, only fish farmers were questioned (12 farms). It would be interesting to include in the survey all stakeholders involved in the industry (e.g. scientists, environmental managers, and socio-economic actors), even though this complicates the weight assessment (i.e. consensus between stakeholders). This weighting step is species dependent, or even species group dependent since some convergences exist. That implicates that a survey will be needed for each new species/species group. Not all traits being equally heritable, one could state that more weight should be put for traits with higher heritability. However, this seems difficult since this approach targets new candidates for domestication (i.e. heritabilities unknown) and traits' heritabilities can be highly variable between species (Gjedrem and Olesen 2005; Blonk and Komen 2015).

All traits do not drive to the same conclusions regarding the biological unit with the highest potential for aquaculture as highlighted in the fourth chapter. This implies that there is no "ideal" prospective unit/population presenting all best performances for all traits (as suggested previously when comparing allopatric populations for European sea bass; Vandeputte et al. 2014). Therefore, the use of an aquaculture potential index was proposed in the fourth chapter to simplify the interpretation of conclusions. Such index implies to attribute a weighting coefficient to each trait and to rank populations. However, ranking populations can be problematic when considering statistical differentiations. Indeed, in a simple case with three populations A, B, and C for a given trait: A has a significantly higher expression than B, C is not statistically different from A and B, with higher values considered as beneficial for domestication. In this example: A is ranked first, B ranked second, but no rank can be attributed to C. An average rank is not optimal for C since it is not different neither from A nor B. Therefore, an aquaculture potential index was proposed in which a mean rank (average of the ranks from the three replicates) is attributed to each biological unit based on the raw values of key trait expressions (**Figure 14A**). However, there is a risk that the aquaculture potential index score may not well appreciate the true differences between populations. For instance, different biological units may have very close phenotypic performances for the highest weighting traits but very different for the lowest weighting traits. With the ranking approach, units with the highest ranks for the most important traits will be favored although their performance values on these main traits may not be very different from the other units while the main differences may be observed on the secondary traits.

An alternative index could be used and consists of using directly trait values rather than ranks to take into account deltas of differences between populations. Since value ranges are different among traits, this approach requires standardizing data (centering and scaling: mean of zero and standard deviation of one). The new formula considering phenotypic standardized values is inspired from the selective index using in quantitative genetics (Moreira et al. 2019; **Figure 14B**). Attention should be paid to the trait expression expected. For instance, while for most traits the highest value is the most interesting (e.g. growth rate, survival rate), for some other traits the lowest values are of higher interest (e.g. activity, inter-individual distances, deformity rate). Therefore, for these traits, for which the lowest values are of interest, the standardized values should be multiplied by "-1". In formula B, just like formula A, the higher the score is, the more interesting the biological unit is for domestication. Testing formula B on data used for the fourth chapter, the same conclusions are reached but the formula B presents the advantage of better taking into account the deltas of differences between biological units (**Table 16**).

Figure 14: A. Aquaculture potential index formula using the ranking method. **B.** Aquaculture potential index formula using the standardized values of traits.

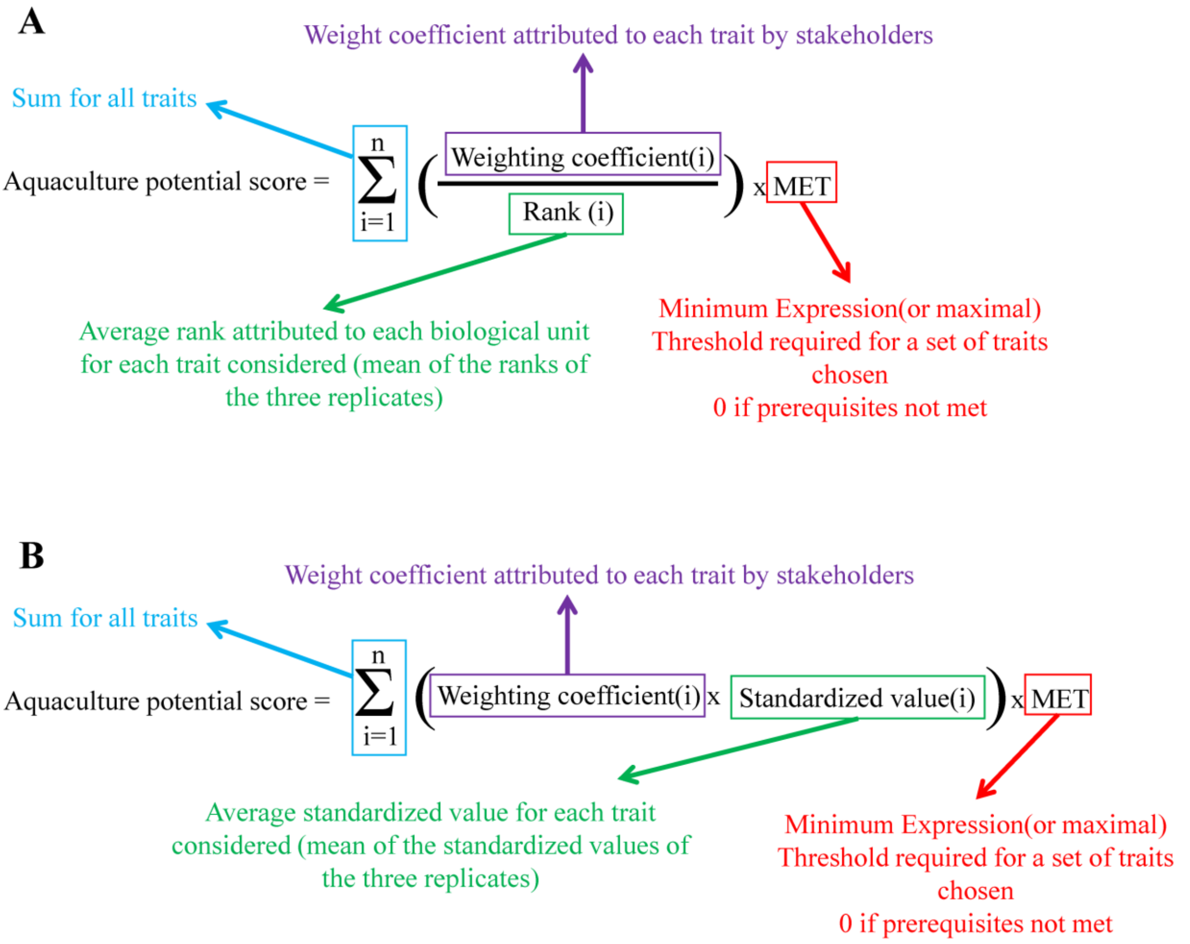


Table 16: Calculation of the aquaculture potential score using formulas A and B and data from the fourth chapter.

Population	**Formula A**		**Formula B**	
	Aquaculture potential score	**Interest for domestication**	**Aquaculture potential score**	**Interest for domestication**
ISO	378.98	+	151.14	+
VAL	350.89	-	-98.44	-
BAL	571.66	++	306.85	++
GEN	346.67	--	-359.55	--

Take home message

The three-step method presents some limits, but some are inevitable, and some improvement could overcome the others. However, there is no other standardized method available to date to integrate geographic differentiation in domestication processes. Therefore, given the interest of considering geographic differentiation and despite its limits, this approach could be greatly useful to facilitate domestication of new species. Ultimately, this evaluation needs to be performed in a commercial farm to test the method and compare with strategies currently led when starting a new species domestication (i.e. often sampling random or geographically close wild populations). This would allow validating conclusions drawn and ensure technological transfer.

C. Applicability of the method

1. *Repeatability*

As mentioned earlier in this discussion, results obtained could be (partly?) due to non-adaptive epigenetic and/or transgenerational effects which could impede the repeatability of results. The repeatability of results needs to be assessed through the repetition of the experiment and the evaluation of the inter-year variability of performances. In addition, studying additional populations for the Eastern and Danube groups would allow re-enforcing the verification that the differentiation within-PU is lower than the differentiation between-PU.

The results obtained are only valid for the rearing system used. Indeed, we did not assess in this study if there was a genotype x environment interaction (Falconer and Mackay 1996; Sae-Lim et al. 2016). The presence of such interaction implies that the best biological unit for our rearing system may not be as interesting in different rearing conditions (i.e. genotype presenting different phenotypes in different rearing environments). Therefore, it could prevent the election of a specific PU/population as the best universal biological unit. Yet, given the diversity of aquaculture systems and the will to develop production in diverse systems, it is a factor which would need to be evaluated. The genotype x environment interaction is a factor regularly evaluated in selective breeding programs and has already been studied for several traits and species (e.g. Gunnes and Gjedrem 1978; Ayles and Baker 1983; Saillant et al. 2006; Domingos et al. 2013; Turra et al. 2016; Srimai et al. 2019; Li et al. 2019). However, in this approach, it is not realistic to include this assessment since it requires larger investments and much higher operating costs. It could be checked later when there is a will to develop production in a new rearing environment.

2. *Feasibility*

2.1 First and second steps of the integrative method

In the first step, proxies can be evaluated relatively easily (providing the availability of relevant data for the habitat differentiation proxy). However, the genetic assessment could be more challenging. The genetic evaluation requires expertise and equipment for DNA extraction, amplification, and sequencing, as well as data analyses. However, with the fast development of genetic techniques and the appraisal of new markers, genetic analyses costs are decreasing (Schlötterer 2004; Martinsohn et al. 2018). In addition, the genetic assessment effort may be shared by stakeholders and/or outsourced. In any case, the transfer and implementation of such approach in commercial practices will likely need a collaborative effort between the industry and scientists.

The second step is a trial and error approach which will be invariably resource-consuming. This step would need to be performed in any case when starting domestication of a new species population, but testing several biological units requires higher investments. However, the first step restricts possibilities regarding the number of biological units to compare. Even though rearing several biological units across a life cycle is challenging, this step is essential since it is not possible to extrapolate from phenotypic differentiation observed in the wild. When working on a new species, one difficulty might also be found in the choice of the domestication system. Rearing conditions can be chosen from the knowledge of wild conditions and first trials could be performed to set the domestication environment. It is also possible to get some insights from ecologically related species in order to start rearing trials (Teletchea et al. 2009). In addition, one fact that could limit the feasibility of step 2 is the ability to measure accurately some phenotypic traits. Indeed, some traits can be hard to measure accurately (e.g. feed efficiency; de Verdal et al. 2018) but this is relative to the set of traits chosen before performing bioassays. Finally, as demonstrated in the fourth chapter, some correlations exist between traits. These correlations could help to decrease the number of traits studied and simplify the evaluation of performances. Some correlations are obvious (such as between length and weight which was shown for other species, e.g. Nousias et al. 2020) but others make little biological sense (e.g. correlation between length at hatching and activity). Overall, this could allow simplifying the set of traits for both phases, but this is specific to our dataset since correlations between traits can vary between species (e.g. Gjedrem and Olesen 2005).

Take home message

Overall, in order to apply this three-step approach, stakeholders need to (i) be convinced of the potential advantages to start new domestication processes considering geographic differentiation, (ii) obtain technical expertise, and (iii) commit resources at the beginning of the domestication process. This last point might be the most plausible impediment as investing in the domestication/production of a new species is financially risky.

2.2 Additional filters before bioassays?

The ability to survive in culture conditions is a prerequisite for domestication that might or might not be shared by different biological units. Therefore, an improvement of the method could rely on the *a priori* selection (i.e. before bioassays) of biological units that have this ability. This filtering step could allow limiting the trial and error approach through the evaluation of the suitability of aquaculture conditions for biological units through predictive models (using species distribution models based on occurrence and environmental data). Beside intrinsic factors which are evaluated in bioassays (e.g. ability to live in high densities), this suitability depends on the similarity between the wild and the culture ecological niches. This similarity is likely when the culture environment is within the species natural environment (e.g. outdoor aquaculture), but artificial environments (e.g. RAS) can be quite different from the wild, making suitability of culture environment unsettled. The suitability of each biological unit could be evaluated through ecological niche modeling approaches (May et al. 2011; Lecocq et al. 2019). This approach requires delimitating which environmental factors shape ecological niches. This task is challenging since assessing shaping factors is not easy (see the fifth chapter) and these shaping factors can be different between wild and artificial niches. Therefore, only relevant parameters in the artificial indoor environment need to be considered (e.g. temperature, pH, alkalinity, water velocity). Yet, as mentioned in the fifth chapter, this data is not always available for wild populations. Providing data is available, the suitability between the wild and artificial niches of each biological unit could be assessed using the Hutchinson's hypervolume (Hutchinson 1957). The overlap between niches could be quantified (with the bias of using realized niche and not fundamental niche). However, this approach does not allow to take into account tolerance abilities of the different biological units. With our species of concern, it could be expected that all RAS systems could be suitable to all populations since Percids are quite tolerant to abiotic variations (Kestemont et al. 2015a), but this strategy could for instance be useful for species with stenotopic [i.e. tolerate to a small range of environmental conditions] populations.

In the aquaculture potential score index, there is a minimum threshold expression factor. Minimum expression thresholds correspond to characteristics which prevent domestication/production, and which are not surmountable at the time of the evaluation. These species-dependent characteristics could include prerequisites which can be used as filters before bioassays. For example, for *Perca fluviatilis*, the absence of Perhabdovirus, - a viral pathogen of importance in percid culture- (Bigarré et al. 2017; Rupp et al. 2019) can be considered as a prerequisite. The definition of these prerequisites constitutes an additional filter before bioassays.

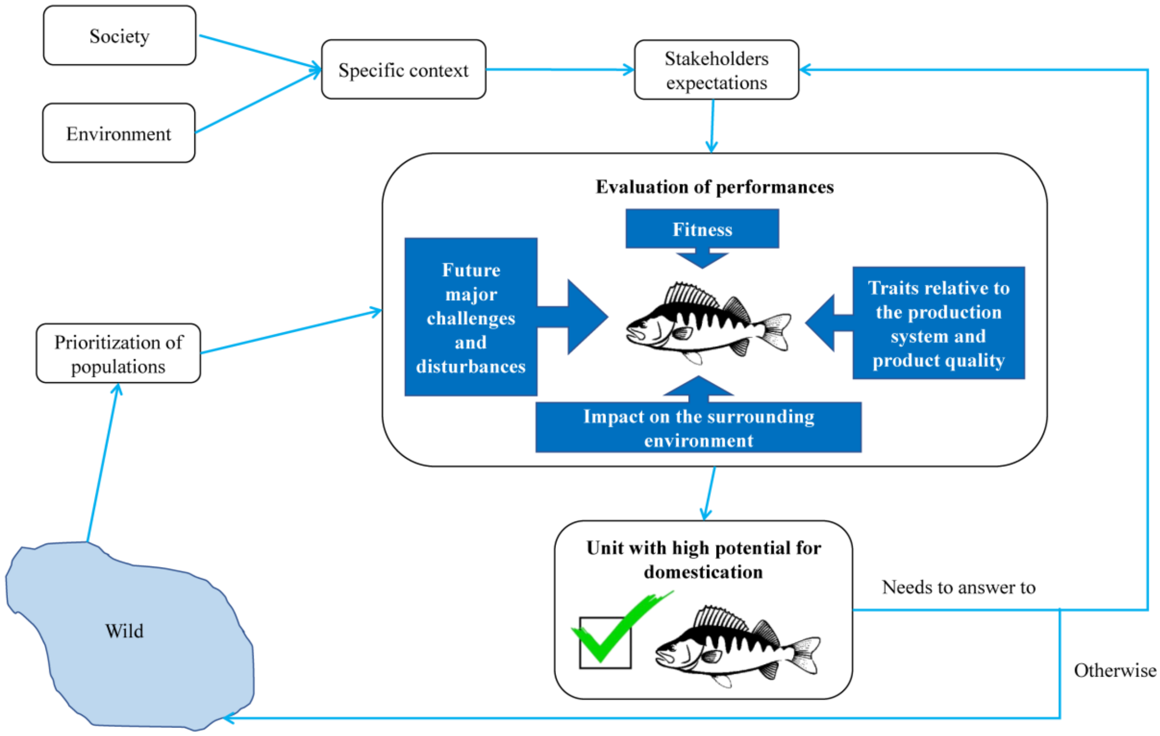
3. *Guidelines*

Starting domestication with a stock originating from one wild population requires sampling a sufficient number of individuals to (i) avoid future inbreeding issues, (ii) have a representative sampling of the natural population, and (iii) have a sufficient genetic variability for potential future selective breeding programs (Vandeputte and Launey 2004; Blonk and Komen 2015). Spreading the sampling across the sampling season and/or across several years can be a solution to avoid sampling a minimal fraction of the total variability (Chevassus 1989). Genetic variability was not considered here as a prerequisite. Indeed, a lower genetic diversity increases chances to sample kin individuals, increasing risks to have deleterious allele expression and inbreeding issues. However, it is also possible to sample closely related individuals when considering a population with a higher genetic variability. Therefore, it is all a matter of good practice in stock constitution to have a sufficient effective size (Lorenzen et al. 2012). Moreover, temporary disturbances (e.g. disease, unusual food shortage, pollution) can affect performances of sampled individuals. Therefore, the occurrence of unusual events should be verified before the sampling step.

The restrictions regarding sampling and transporting biological material should also be considered when choosing biological units which need to be evaluated in the second step. Indeed, when sampling biological material is limited or difficult in administrative terms, then populations concerned should be excluded from the assessment. In addition, attention should be paid to the Nagoya Protocol on “access to genetic resources and the fair and equitable sharing of benefits arising from their utilization to the convention on biological diversity”. This international agreement implies that if the genetic resources of a specific country is exploited then benefits should be shared with this country (monetary or not [e.g. royalties] and sharing of research results). Regarding national rules, even if sampling restrictions are limited to national populations, this approach is still useful in countries with environmental gradients since differential potentials for aquaculture are likely. Finally, since wild ecosystems already support fishing pressure, aquaculture should not increase this pressure. Therefore, the sourcing of individuals for farmed stock should ideally be performed in a sustainable manner. Moreover, wild stocks from declining/endangered populations should not be used when extensive sampling is planned to provide several farms (except for recovery purposes; Simard et al. 2008). Yet, producing a particular population could allow decreasing fishing pressure in this site. Therefore, populations which are decreasing because of fishing pressure should not be automatically excluded from the assessment. Overall, the choice of targeted populations depends on several factors such as sampling effort, future uses of wild resources, regulations, and wild population effective site.

Finally, this approach gives an overview of the potential contained in the wild biodiversity at a given time. Therefore, the evaluation is context-dependent and might need to be performed again if the context evolves (e.g. different fish farmers expectations, consumer preference changes [e.g. product quality, age at sexual maturation (Gjedrem 2010)], environmental changes; **Figure 15**).

Figure 15 : Conceptual figure showing the dependency of the identification of units with high aquaculture potential to the specific context (stakeholders' expectations and environmental changes).



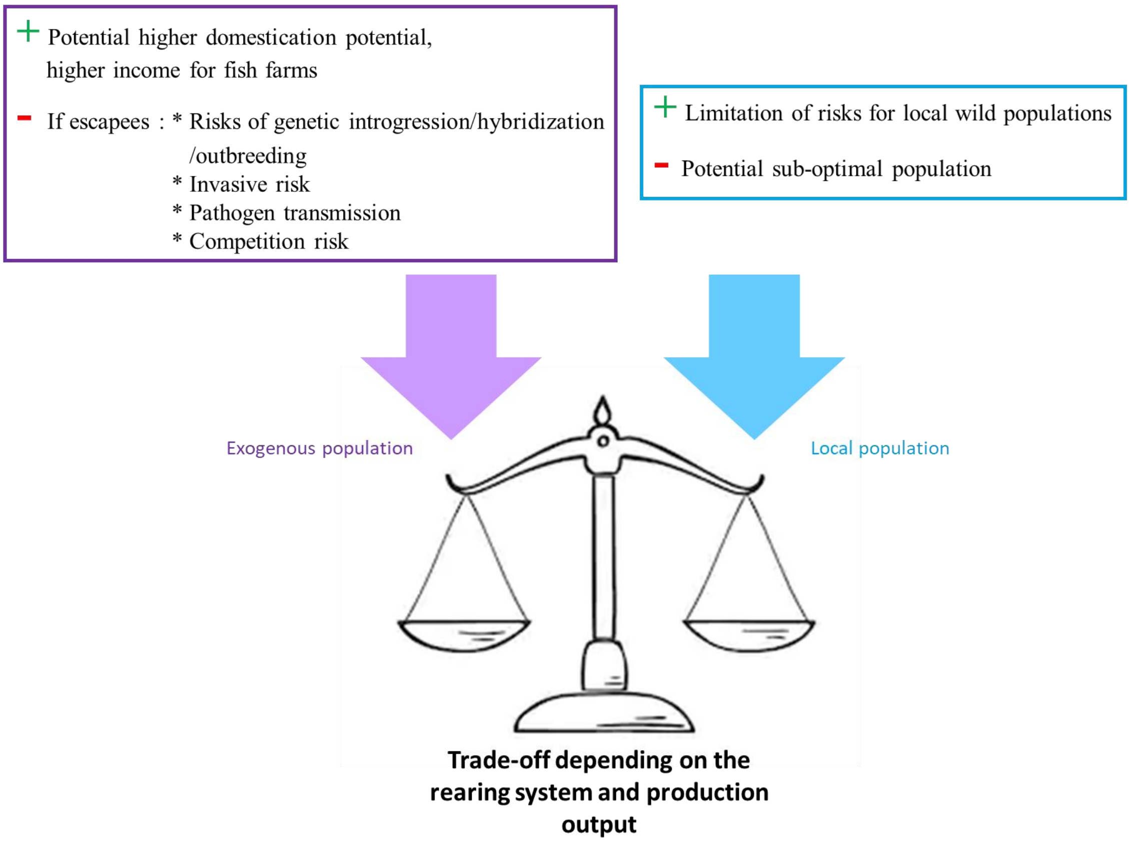
4. *A trade-off between advantages and risks*

On the one hand, attention should also be paid to the environmental risks of using non-local populations. Indeed, there are risks of escapees of individuals, particularly in outdoor aquaculture but risks cannot be ruled out in indoor aquaculture (Summerfelt and Vinci 2009). These escapees can trigger negative consequences on the genetic integrity and fitness of locally adapted populations, for instance through genetic homogenization/introgression, competition for resources, or pathogen introduction (Ryman et al. 1995; Laikre et al. 2005; Weir and Grant 2005; Marra 2005; Svåsand et al. 2007; Danancher and Garcia-Vazquez 2011; Arechavala-Lopez et al. 2013, 2018). The fitness of escaped individuals is often lower than wild conspecifics (but see Dannewitz et al. 2004), implying that few escaped individuals will breed successfully, but risks are not null when the number of escapees is high (Muir 2005). The negative impacts on wild populations are particularly well known in Salmonids (Hansen and Loeschcke 1994; Fleming et al. 2000; McGinnity et al. 2003; Naylor et al. 2005; Bekkevold et al. 2006; Hutchings and Fraser 2008; Bolstad et al. 2017; Wringe et al. 2018). These risks could lead to the promotion of the use of local population for domestication. Indeed, even if modifications are induced by the domestication environment (see further), it is mostly going to consist of modifications in allele frequencies and selection of variants already existing in the wild. In the same way, risks regarding pathogen load and invasive risk will be lesser compared to exogenous populations.

On the other hand, benefits of using exogenous populations should also be considered in the equation. Indeed, local populations might not be optimal for domestication. Taking as an example our results on *Perca fluviatilis* larviculture, local French fish farms used originally individuals originating from alpine lakes, including Lake Geneva (Ben Khadher et al. 2016). Yet, we showed that for the larval period, this population presents the lowest aquaculture potential score. On the contrary, the Lake Balaton presents the highest aquaculture potential score and is genetically very distant from populations belonging to the European Plain group. Overall, production efficiency is one of the major bottlenecks limiting the expansion of the sector. Improving zootechnical performances appears as an efficient solution to reduce production costs (Policar et al. 2019).

The decision on which population should be used for aquaculture is therefore a matter of compromise between risks (for the wild biodiversity) and benefits (degree of performance differentiation; **Figure 16**). This trade-off is going to be culture system dependent. Indeed, risks are much higher in outdoor aquaculture and less important in indoor aquaculture. For outdoor aquaculture, the use of local populations, adapted to their specific region, makes more sense than importing new populations from distant geographical regions which might not be suitable for local conditions. The decision is also dependent on the domestication goal. Indeed, if the purpose is restocking, risks are much higher than production for market purposes. The decision resulting from this trade-off must be based on a consensus between the different stakeholders. In the case of rearing exogenous populations, several measures should be followed (Simard et al. 2008): (i) rearing systems must be designed to minimize the escape risk and (ii) research on potential impact of escaped fish should be performed.

Figure 16: Conceptual figure regarding the trade-off between risks and advantages in the choice of the founding population(s)



5. *Usefulness*

In order to improve domestication and subsequent production of new candidate species, most of the efforts are currently put into improving the rearing system through the evaluation of variable abiotic conditions and technological improvements (see for Percids references in Policar et al. 2019). However, a complementary approach consists of focusing on the most interesting biological unit.

5.1 Which species/populations?

The three-step integrative approach could be useful in several instances:

(i) New candidate species for diversification of the production: This is the main target of the three-step method. When new candidate species of interest are identified at the inter-specific level (e.g. high market potential), the consideration of geographic differentiation can be helpful to facilitate domestication and subsequent production. The geographic differentiation trials could be performed (i) after first rearing trials with one population (with the risk of using an unsuitable population for the trial) or (ii) from the beginning of the domestication process, using knowledge on ecologically close species (Teletchea et al. 2009) or wild environment to choose rearing conditions. If first trials are performed with a random population and are successful, the three-step approach is not very advantageous. On the opposite, if first rearing trials with a random population are unsuccessful, then the consideration of geographic differentiation could be useful to increase chances of success rather than abandoning the domestication trial. The time to develop new species production could be reduced which is important since time and cost to develop new species is one of the diversification limitations (Muir 2005). Performing first trials with one population seems likely since testing from the beginning different biological units might be too resource-consuming. However, ideally, geographic differentiation should be considered from the beginning of the domestication process to optimize chances of success.

(ii) Species populations already on the domestication pathway but for which domestication/production is limited because of major bottlenecks. The approach appears particularly useful for species populations which remain in the domestication process at stage two (i.e. when a part of the life cycle is completed but several bottlenecks exist in other parts; e.g. *Thunnus thynnus* [Actinopterygii, Scombriformes, Scombridae], *Anguilla Anguilla*; Teletchea and Fontaine 2014). It appears also useful for species which production cannot increase due to diverse biological/socio-economic issues. This is the case of *Perca fluviatilis* which was used as a test case and for which bottlenecks hamper production. Overall, the three-step approach could be useful for species which are at incipient domestication stages (first three levels), or eventually intermediate stages (i.e. level four), and/or for which there is a need to improve domestication/production.

(iii) Species populations already farmed but for which there is a will to develop production in a new domestication system or for which there is a new demand market: even for species populations which are considered as advanced in the domestication process, there might be new market/societal demands which require starting new domestication processes. Indeed, the will for robust (i.e. “able to grow and keep functioning in the presence of environmental variation”) and adaptive (i.e. “able to change in response to gradual changes in mean of environmental cues") animals (Vandeputte et al. 2009; Sae-Lim et al. 2017), fish meal/oil substitution (Naylor et al. 2009; Bostock et al. 2010; Osmond and Colombo 2019), and welfare and health management (Bostock et al. 2010) might trigger the need to domesticate new populations. Current farmed stocks might not be appropriate for all new societal/market demands. In addition, because of the diversity of rearing system and the potential genotype x environment interaction, the best-performing unit in one rearing system might not be the best in another environment triggering a re-ranking of biological units according to the rearing system considered. In the presence of such interaction which has been demonstrated for several species and key traits (Sae-Lim et al. 2016), the three-step approach could be performed when considering a new domestication system.

(iv) Further production improvement could be achieved by considering wild genetic resources for selective breeding programs. Introduction of adaptive traits (i.e. genomic introgression) from wild populations allows to obtain phenotypic novelty in produced stocks when this phenotype is absent from the farmed stock (Gjedrem 2012; Warschefsky et al. 2014). Potential genetic gains from wild relatives through hybridization have been particularly investigated in crops (Maxted and Kell 2009; Warschefsky et al. 2014; Dempewolf et al. 2017; Mammadov et al. 2018; Janzen et al. 2019). For instance, the occurrence of beneficial mutations in wild emmer wheat (*Triticum dicoccoides*) populations (Fu et al. 2019) opens the door to crossbreeding with produced crops in order to obtain climate resilient varieties.

(v) Restocking/Enhancement purposes: the use of geographic differentiation appears less useful when considering enhancement (i.e. increase of natural stocks to enable larger catches) and restocking (i.e. restoration of depleted stocks) of wild populations. Indeed, in these cases local populations should be favored to avoid issues raised in the previous section (e.g. genetic homogenization/introgression, competition; Ward 2006; Laikre et al. 2010). However, in the case of local populations collapsing or closed areas (i.e. no contact with other water bodies), the three-step integrative approach could be used.

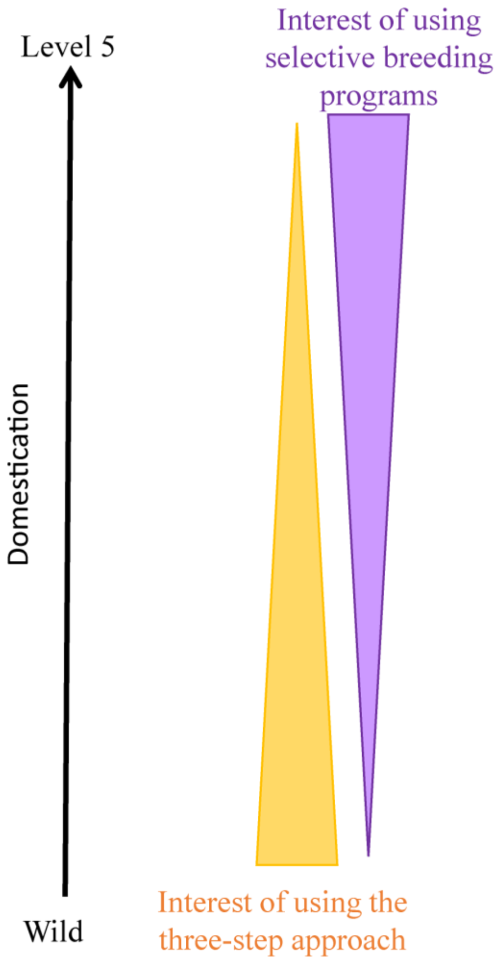
This work can be considered as a steppingstone for further research about the integration of geographic differentiation in domestication process and aquaculture development. The approach, here applied to a freshwater fish species, aims to be extended to other species, particularly marine species presenting bottlenecks such as Atlantic halibut (*Hippoglossus hippoglossus*), wolf-fish (Actinopterygii, Perciformes, Anarhichadidae, *Anarhichas lupus*), and various bream (e.g. *Diplodus puntazzo* [Actinopterygii, Perciformes, Sparidae]), which have been a target for diversification research because of their high sale value (Muir 2005). A geographic differentiation was already highlighted for instance for Atlantic halibut (e.g. Jonassen et al. 2000; Imsland et al. 2002, 2007). However, ultimately the approach aims at being extended to other species groups such as mollusks or arthropods (e.g. shrimp farmed stocks were derived from various geographic locations even though no comparison of performances was performed; Benzie 2009; see also geographic differentiation found for *Octopus vulgaris*, a candidate species for marine aquaculture diversification which production is hampered because of high larval mortalities, Garrido et al. 2017).

5.2 What about selective breeding programs?

Selective breeding programs have been led for various species such as Salmonids, sea bass and sea bream, tilapia, and shrimps (Muir 2005; Gjedrem et al. 2012). Even though the geographic sampling has been previously used in selective breeding programs, the purpose was to sample a sufficient genetic variation to ensure long-term genetic response in breeding programs (Hayes et al. 2006) rather than exploiting directly geographic differentiation to start a new domestication process or overcome bottlenecks limiting domestication/production at early domestication stages. Selective breeding programs are considered as long-term investments (baseline breeding program profitable after 5 years; Janssen et al. 2018) but gains obtained over generations of selection can be very high (e.g. +113% in growth rate over five generations in *S. salar*; Gjedrem et al. 2012). The usefulness of selective breeding programs is undeniable to improve farmed stocks (Haffray et al. 2004; Vandeputte et al. 2009; Chavanne et al. 2016). However, farmed stocks are still today based in majority on genetically unimproved stocks (Gjedrem 2005b).

The three-step approach appears as complementary rather than opposite to selective breeding programs. The principle underlying the three-step approach is overall not very different from selective breeding methods, such as mass selection or family-based programs. Indeed, the need and challenge to phenotype individuals is needed in both approaches, even though advanced selective breeding programs allow working at different scales (i.e. family, individual) with potential control of crosses between breeders and pedigree assessment through genotyping (Lind et al. 2012). Compared to selective breeding programs, the three-step integrative approach works at a different scale (i.e. population level) and presents potentially the risk of narrowing the genetic variability by focusing on a single biological unit. However, the prevention of inbreeding remains a management caution and rely on good practices in constituting the founder stock (i.e. sufficient number of breeders; Vandeputte and Launey 2004).

Figure 17: Comparison of the usefulness of the three-step integrative approach and selective breeding programs



Choosing the most suitable populations before starting a selective breeding program was previously highlighted as important to spare generations of within-strain selection (Ponzoni et al. 2013), as suggested for instance in European sea bass (Vandeputte et al. 2014, 2019). The three-step approach appears particularly useful for species which are at the beginning of the domestication process (i.e. first three stages according to Teletchea and Fontaine 2009) and which are facing major bottlenecks preventing successful domestication and/or production. In this way, selective breeding methods are poorly implementable when only a part of the life cycle is performed in captivity (i.e. capture-based productions). For species well advanced in the domestication process, selective breeding programs might be favored (**Figure 17**) rather than starting the process all over again from wild populations. Indeed, there is a high risk of pathogen transmission when introducing wild individuals in farmed stocks (Blonk and Komen 2015). Moreover, farmed populations (i.e. advanced in the domestication process) were shown to often present better performances than wild individuals (e.g. Fleming et al. 2000; Glover et al. 2009; Douxfils et al. 2011b; Lorenzen et al. 2012), even though this is not true for all traits and all species (e.g. Mayer et al. 2011; Khendek et al. 2017; Saraiva et al. 2019; Pasquet 2019). Therefore, using wild individuals could potentially erase all gains obtained from successive generations in the rearing environment (Blonk and Komen 2015). Finally, selective breeding programs are particularly interesting when the differentiation within population is higher than the differentiation between populations (Withler and Evelyn 1990; Quillet et al. 2007) or when the genetic gain prediction for one generation of individual selection is higher or equal to the between-population differentiation (see for instance Vandeputte et al. 2014 in which one generation of mass selection is sufficient to equal the magnitude of inter-populational difference). Selective breeding programs could potentially be used after the three-step integrative approach, providing that the genetic variability is sufficient for selection (Vandeputte and Launey 2004).

6. *Extrapolation to other species?*

Consequent investment may not be operated for each new candidate given the risks of failure when starting domestication of a new species or when facing major bottlenecks. One way to decrease investments could rely on the extrapolation of knowledge acquired on a particular species to another.

Some approaches were developed at the inter-specific level to establish some functional classifications (i.e. clustering biological units displaying similar life histories) between wild species (e.g. Balon 1975; Teletchea et al. 2009). These approaches based on functional traits were chosen rather than phylogeographic classifications since highly divergent taxa sometimes exhibit biological trait convergences due to the adaptive status of traits (Winemiller 1989). The aim of these approaches is to extrapolate knowledge among species belonging to the same cluster (Teletchea et al. 2009). However, the use of such an approach appears unlikely at the intraspecific level. Indeed, performances observed in the second step are species- and eventually system- specific. Results could probably not be extended to other species, but this remains to be verified. Therefore, until specific experiments are performed to answer this question, the performance evaluation in the second step appears inevitable for all new candidate species.

The first step could eventually be skipped. Indeed, biogeographic convergences could allow extending conclusions of the first step using already available phylogeographic studies. Indeed, there are some general phylogeographic patterns in co-distributed fishes with common specificities across species (Bernatchez and Wilson 1998; Costedoat and Gilles 2009; Hickerson et al. 2010; Bowen et al. 2016; Zamudio et al. 2016). This means that a particular population/groups of populations could be genetically distinct since other taxa display genetic specificities in this area. However, even though this can be helpful for freshwater fishes with common phylogeographic patterns, it might be more difficult to apply with marine species. Moreover, the existence of common areas with genetic specificities across co-distributed species is not guaranteeing to find specificities for a target species. Indeed, the genetic structure can vary quite a lot, even between closely-related species (e.g. large differences in genetic differentiation between *Oncorhynchus keta* [Actinopterygii, Salmoniformes, Salmonidae], *Oncorhynchus clarkii clarkia* [Actinopterygii, Salmoniformes, Salmonidae], and *Oncorhynchus mykiss* [Actinopterygii, Salmoniformes, Salmonidae]; Chevassus 1989), making difficult the extrapolation of the first step conclusions.

Overall, the extrapolation of conclusions is unlikely, and the approach should therefore be applied in priority to species with a very high economic interest and facing major bottlenecks. As mentioned earlier, regarding the extrapolation between rearing systems, this does not appear as possible if there is a significant interaction between genotype and environment.

7. *What is next?*

7.1 Domestication: a continuum of modifications

The three-step integrative method aims at identifying biological units of interest at the beginning of the domestication/production process. However, how will performances of these units change along domestication?

The domestication environment is often quite different from the wild environment, particularly in indoor culture. Therefore, this implies that there is a new set of selective pressures that will change gene frequencies. The transfer from the wild to breeding systems happens in concomitance with (Price 1999; Vandeputte and Launey 2004; Mignon-Grasteau et al. 2005; Groeneveld et al. 2010; Gering et al. 2019):

(i) Non-controlled processes such as inbreeding (i.e. mating between closely-genetically individuals which leads to a decrease of fitness and a genetic diversity loss) and random genetic drift (i.e. change in allele frequency(ies) in a population due to chance/sampling error).

(ii) Semi-controlled processes which are the relaxation of natural selection (i.e. reduction of the selective pressure on traits which are essential in the wild but not in captivity) and natural selection in captivity (i.e. selection of individuals with higher fitness in captivity).

(iii) Controlled processes which correspond to artificial selection programs (i.e. process in which breeders consciously select for or against particular traits).

Therefore, the domestication process leads to some phenotypic and genetic changes (Price 1999; Balon 2004; Driscoll et al. 2009), including potential epigenetic modifications (Feeney et al. 2014). Domestication consequences are sometimes visible as early as in the first generation (Vandeputte and Prunet 2002; Dunham 2011; Christie et al. 2016; Roussel et al. 2019). Morphological, physiological, and behavioral changes through the domestication process refer to the "domestication syndrome" (Olsen and Wendel 2013; Larson and Fuller 2014; Wilkins et al. 2014). For instance, phenotypic changes attributed to domestication have been highlighted for growth (Clutton-Brock 1999; Tymchuk and Devlin 2005; Glover et al. 2009), reproductive traits (Schütz et al. 2002; Osure and Phelps 2006; Krejszeff et al. 2009; Khendek et al. 2017; Rocha De Almeida et al. 2019), immune parameters (Douxfils et al. 2014; Christie et al. 2016), stress response (Mazur and Iwama 1993; Douxfils et al. 2011a), or behavior (Ruzzante 1994; Price 2002; Huntingford 2004; Pasquet 2019). Features of the domestication syndrome are not universal, but some common features can be seen across taxa. Research aiming at determining the origin of this domestication syndrome remains ongoing. However, in vertebrates, one major hypothesis raised in the literature relies on neural crest cells (Wilkins et al. 2014; Sánchez-Villagra et al. 2016). These cells appear during embryogenesis at the dorsal edge of the neural tube. Along development, they migrate ventrally throughout the body and are the precursors of several tissues and cell types (e.g. adrenal medulla, external ears, odontoblasts). The initial selection for tameness at the beginning of the domestication process could lead to a reduction of the number of neural crest cells at final sites, which triggers unselected morphological changes (Wilkins et al. 2014; Sánchez-Villagra et al. 2016). However, neural crest cell might only be part of the explanation and studies still need to be performed to validate this hypothesis across taxa.

These numerous changes imply that differentiation in performances between allopatric populations/PUs might not be preserved through generations. However, this approach aims at starting with the best biological unit available in the wild. Therefore, even though modifications occur through domestication, the use of a particular population will allow to start domestication/production with higher chances of success and/or to overcome major bottlenecks in domestication/production.

7.2 What to do with units with high potential for aquaculture?

If several biological units of interest are identified or if all biological units are at the same level of interest (i.e. same aquaculture potential), we can wonder what the strategy to adopt is. On the one hand, the focus could be set on a particular unit or some units could be reared separately (similarly to purebreeding in selective breeding programs). This would allow keeping the specificities of populations. However, this strategy was said to be more efficient when one biological unit presents significantly better performances than others (Gjedrem 2005b). On the other hand, crosses could be made between biological units, which are particularly interesting if there is heterosis (i.e. hybrid vigor). Heterosis has already been highlighted for several species such as Nile tilapia or rainbow trout (Ayles and Baker 1983; Gjedrem 2012). However, crossing genetically differentiated stocks for aquaculture production is delicate since the optimum for heterosis (i.e. hybrid vigor) is just beyond the one where fitness decreases. Indeed, interbreeding between populations which are genetically distinct can lead to outbreeding depression and a reduction of fitness (except in the case of heterosis). Yet, this strategy could be wished if there is a will to create a common founder stock for production and that fish farmers expectations are divergent (“consensus” unit creation).

7.3 Assessing the geographic differentiation causes?

Identifying shaping factors structuring genetic and phenotypic differentiations has been a wide topic of research in evolutionary biology. Natural selection exerts a pressure towards genotypes which favor fitness in a given environment (Ward 2006). Adaptive differentiation can result from barriers to gene flow and/or environmental differences (Heibo et al. 2005; Rundle and Nosil 2005; Hauser and Carvalho 2008). Local adaptation results from a balance between the homogenizing effect of gene flow and the divergence force of natural selection [i.e. phenotypic differentiation resulting from a genetic composition modification triggered by selective pressures] (Garant et al. 2007; Hauser and Carvalho 2008; Zamudio et al. 2016). Local adaptation can be prevented (i.e. non adaptive or maladaptive genetic changes) by high gene flow, high genetic drift in small populations, or if genetic variability is not sufficient (i.e. adaptive potential not sufficient to reach optimal adaptation) (Kawecki and Ebert 2004; Merilä and Hendry 2014; Faulks et al. 2015). The stability of selective pressures influences the strategy of populations. Indeed, when selective pressures are stable through time, disruptive selection favors specific genotypes. On the opposite, when selective pressures are variable, phenotypic plasticity is favored (alternative phenotypes preserved through generations). Phenotypic changes can therefore be plastic or genetic, and these two processes are not exclusive (Faulks et al. 2015). Indeed, phenotypic plasticity is often seen as a step in the phenotypic evolution which leads to the evolution of a canalized phenotype when selective pressures are not variable. This is referred as genetic assimilation (i.e. trait becomes ‘fixed’ in a population; West-Eberhard 2003; Pigliucci et al. 2006; Aubret and Shine 2009; Ehrenreich and Pfennig 2016).

Wild breeders have undergone generations of selection in their wild environment. Therefore, selective pressures are undoubtedly different between biological units. The identification of selective pressure leading to local adaptation is not easy (Merilä and Hendry 2014) but several factors were suggested for a few key traits such as temperature, heterogenous and fluctuating environments, predation pressure, resources availability and diversity, or population density (Foster 1999; Schluter 2000; Heibo et al. 2005; Rundle and Nosil 2005; Marcil et al. 2006; Olsson et al. 2007; Valente et al. 2013; Rosburg 2017; Gering et al. 2019). Intra- and interspecific competitions are also known factors leading to genetic variation and phenotypic differentiation (Faulks et al. 2015). One way to demonstrate local adaptation is the use of reciprocal transplants in the wild, by transplanting populations between wild habitats (Kawecki and Ebert 2004; Merilä and Hendry 2014). For instance, a transplant experiment of guppies *Poecillia reticulata* highlighted adaptation to predation on guppy behavior (schooling) and morphology (Magurran and Seghers 1991; Carvalho 1993). However, even though previously used (e.g. Magurran et al. 1995; Declerck et al. 2001), these approaches are nowadays often impossible due to legal, pragmatic, and ethical reasons (Kawecki and Ebert 2004). An alternative approach could rely on experimental evolution studies. It consists in exposing populations to different selective pressure under controlled conditions (Kawecki et al. 2012; Merilä and Hendry 2014). Laboratory natural selection experiments have been performed by fixing the environmental driver(s) causing selection to quantify genetically-based phenotypic changes (Bennett et al. 1990; Sunday et al. 2014; see examples in Kawecki et al. 2012). However, these experiments are hardly feasible except for species with very short generation times (e.g. bacteria, drosophila) and a rigorous control of experimental conditions is required. An alternative could consist in establishing correlations between phenotypic differentiation seen in a common-garden experiment (due to genetic differentiation and/or adaptive epigenetic changes) and potential selective pressure in the wild as a first approximation even though this hypothesizes that current selective pressures are the ones determining phenotypic differentiation (and not past selective pressures).

LIST OF PUBLICATIONS

Articles published or submitted

- **Toomey L**, Fontaine P, Lecocq T (2020) Unlocking the intraspecific aquaculture potential from the wild biodiversity to facilitate aquaculture development. Reviews in Aquaculture. *In press*.

- **Toomey L**, Dellicour S, Vanina T, Pegg J, Kaczkowski Z, Kouřil J, Teletchea F, Fontaine P, Bláha M, Lecocq T (2020) Getting off on the right foot: integration of spatial distribution of genetic variability for aquaculture development and regulations, the European perch case. Aquaculture 521: 734981. doi: 10.1016/j.aquaculture.2020.734981

- **Toomey L**, Bláha M, Mauduit E, Vanina T, Baratcabal M, Ledoré Y, Vesala S, Fontaine P, Pasquet A, Lecocq T (2019) When behavioral geographic differentiation matters: inter-populational comparison of aggressiveness and group structure in the European perch. Aquaculture International 27: 1177–1191. doi: 10.1007/s10499-019-00458-3

- Vanina T, Gebauer R, **Toomey L**, Stejskal V, Rutegwa M, Kouril 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. doi: 10.1016/j.aquaculture.2018.12.071

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- Rocha de Almeida T, Alix M, Le Cam A, Klopp C, Montfort J, **Toomey L**, Ledoré Y, Bobe J, Chardard D, Schaerlinger B, Fontaine P (2019) Domestication may affect the maternal mRNA profile in unfertilized eggs, potentially impacting the embryonic development of Eurasian perch (*Perca fluviatilis*). PLoS One, 14(12): e0226878. doi: 10.1371/journal.pone.0226878

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- **Toomey L**, Dellicour S, Zarski D, Buhrke F, Fontaine P, Lecocq T. Split it up and see: intraspecific proxies highlighting divergent performances in aquaculture standardized conditions. Scientific reports. *Under review.*

Oral communications

- **Toomey L**, Fontaine P, Lecocq T. Integration of spatial distribution of genetic variability for aquaculture regulations and development, the European perch case. *Frontiers in Marine Science.* Conference Abstract: XVI European Congress of Ichthyology. September 2nd-6th, 2019. Lausanne, Switzerland.

- **Toomey L**, Lecocq T, Fontaine P. Vers une perciculture plus durable et mieux intégrée aux territoires: Intégration de la différenciation intraspécifique dans les programs de domestication. Séminaire SIReNa - Science et Territoire: vers une nouvelle économie. February 7th, 2019. Nancy, France.

- **Toomey L**, Teletchea F, Fontaine P, Lecocq T. Improving *Perca fluviatilis* aquaculture by considering population-specific performances in recirculating aquaculture system. European Aquaculture Society - AQUA2018. August 25th-31st, 2018. Montpellier, France.

- Lecocq T, **Toomey L**, Fontaine P. Defining units with high potential for aquaculture within species - Towards an integration of intraspecific differentiation in fish domestication programs. European Aquaculture Society - AQUA2018. August 25th-31st, 2018. Montpellier, France.

- Rocha De Almeida T, Alix M, Schaerlinger B, Le cam A, Montfort J, **Toomey**, L Bobe J, Chardard D, Fontaine P. A transcriptomic comparison suggests an influence of the domestication process on egg quality in Eurasian perch (*Perca fluviatilis*).

11th symposium on reproductive physiology of fish. June 3rd-8th, 2018. Manaus, Brazil.

Poster communications

- **Toomey L**, Pasquet A, Teletchea F, Fontaine P, Lecocq T. Getting off the right foot: integration of spatial distribution of genetic variability for aquaculture development and regulations, the European perch case. 9th Biennial Conference of the International Biogeography Society. January 8th-12th, 2019. Malaga, Spain.

- **Toomey L**, Aubin J, Benard A, Fontaine P, Jaeger C, Lecocq T, Ledoré Y, Nahon S, Pasquet A, Puillet L, Thomas M, Wilfart A. De l'étude de la biodiversité à la determination des meilleures populations et associations d'espèces. Nouvelles approches méthodologiques pour des systèmes piscicoles plus durables. Séminaire Défis Scientifiques, Département Physiologie Animale et Système d'Elevage, INRA. November 6th-7th, 2019. Rennes, France.

- **Toomey L**, Lecocq T, Teletchea F, Fontaine P. Integrating intraspecific differentiation in fish domestication programs: definition of units with high potential for aquaculture for European perch, *Perca fluviatilis*. Doctoral school in science and engineering for "Resources, Processes, Products and Environment" Seminar. February 2nd, 2017. Vandoeuvre-Lès-Nancy, France.

- Lecocq T, **Toomey L**, Teletchea F, Fontaine P. Defining units with high potential for aquaculture (UHPA) within species: towards an integration of intraspecific differentiation in fish domestication programs. 23rd Congress of Zoology. December 16-17th, 2016. Antwerp, Belgium.

OTHER ACTIVITIES DURING THE PhD

- **Teaching experience:** I got the opportunity during my PhD to teach bachelor students (first to third year bachelor). During the first two years, I contributed to teach practical classes in zoology (total of 86h over the two years). This experienced allowed me to improve my presentation skills and to acquire competences in educational methods. In order to start my fourth PhD year, I started a part-time teaching contract (October 2019 - to date) which allowed me to diversify my teaching topics (zoology, evolutionary biology, functional diversity, behavioral ecology; 132 hours).

- **Mentoring experience**: I supervised 13 students between 2018 and 2019, from third year bachelor to second year Master students. This experience improved my supervision skills and rigor in explaining and planning experiments.

- **Representing experience**: I was a student representative at the Scientific Pole A2F “Agronomy, Agrifood, Forests” between 2016 and 2018. This experience allowed me to obtain a better understanding of how the academic system works, research recruitment, and grant application processes.

RÉSUMÉ SUBSTANTIEL EN FRANCAIS

La demande en protéines aquatiques ne cesse d'augmenter au niveau mondial dû à l'augmentation de la population et de la consommation en produits aquatiques. Historiquement, la pêche permettait de subvenir à cette demande croissante. Cependant, depuis la fin des années 1980, les captures de la pêche stagnent, voire diminuent. La pêche n'était donc plus suffisante pour répondre à la demande. L'aquaculture s'est alors développée et c'est un des secteurs alimentaires qui a connu une des croissances les plus rapides de ces dernières décennies. Actuellement, l'aquaculture fournit plus de la moitié des produits aquatiques qui sont consommés au niveau mondial. Toutefois, la production aquacole se base à l'heure actuelle sur peu d'espèces. En effet, 85% de la production aquacole repose sur seulement 15 espèces. Cela pose plusieurs problèmes, socio-économiques et environnementaux, qui se traduisent par une faible résilience du secteur aquacole. De nos jours, il existe une volonté de développer une aquaculture plus durable. L'une des voies prometteuses pour promouvoir la durabilité du secteur de l'aquaculture repose sur la diversification de la production, notamment par la domestication et la production de nouvelles espèces.

La domestication correspond au processus par lequel des populations sont élevées et reproduites dans un environnement contrôlé par l'Homme et modifiées au fil des générations par rapport à leurs ancêtres sauvages dans un objectif de les rendre plus utiles pour l'Homme qui contrôle durant l'ensemble du processus leur reproduction et leurs apports alimentaires. Contrairement aux espèces terrestres, la domestication des espèces aquatiques est beaucoup plus récente et la volonté de diversification de la production mène à de nombreux essais de domestication de nouvelles espèces. Cependant, la domestication et la production de nouvelles espèces sont des processus longs et difficiles qui peuvent échouer en raison de défis techniques, de limitations socio-économiques ou de caractéristiques propres aux espèces. L'identification de ces caractéristiques (biologiques et socio-économiques) a permis de développer des approches pour sélectionner de nouvelles espèces candidates à la domestication. Cependant, ces approches ne prennent pas en compte le fait que certaines de ces caractéristiques peuvent également varier au niveau intraspécifique. En effet, la différenciation géographique (différenciation entre populations conspécifiques allopatriques) peut façonner des spécificités génétiques, phénotypiques et écologiques, ce qui pourrait entraîner des prédispositions différentielles à la domestication ou différents attraits socio-économiques entre populations allopatriques.

Une différenciation géographique a déjà été démontrée entre populations allopatriques sauvages pour des traits clés (par exemple : taux de croissance, taux de survie, taux d'agressivité) et pour de nombreux taxons. Par conséquent, le choix d'une ou de plusieurs populations sauvages présentant un potentiel élevé pour l'aquaculture (c'est-à-dire présentant une expression intéressante des traits clés) pourrait permettre de faciliter la domestication et la production de nouvelles espèces.

Toutefois, les spécificités observées dans le milieu sauvage pourraient ne pas être conservées dans les conditions d'élevage. En effet, l'expression des traits pourrait changer dans l'environnement d'élevage car ces traits, comme tout trait phénotypique, sont façonnés par la divergence génétique et l'environnement. Or, les conditions environnementales en milieu d'élevage peuvent être très différentes du milieu sauvage, particulièrement dans des systèmes d'élevage intensifs. Par conséquent, seules les différenciations phénotypiques qui sont façonnées par des divergences génétiques présentent un intérêt pour la domestication. Afin d'évaluer la différenciation d'expression de traits entre populations allopatriques, des expériences en *common-garden* (« jardin-commun ») sont donc nécessaires, qui permettent la comparaison de populations dans un même environnement d'élevage. En effet, comparer les populations dans le même environnement permet d'éliminer les effets dus à l'environnement. En conséquence, une différenciation d'expression de traits en *common garden* sera attribuée à des différenciations génétiques. Néanmoins, (i) il n'est pas possible en pratique de comparer l'ensemble des populations d'une espèce à travers son aire de répartition géographique et (ii) la sélection aléatoire de populations pour des expériences *common garden* pourrait mener à ne pas évaluer des populations qui présentent un fort potentiel pour l'aquaculture. De plus, l'attention est souvent portée sur un seul trait biologique (souvent le taux de croissance et/ou la qualité du produit) ou une fonction biologique précise lors du processus de domestication. Or, la capacité à être domestiqué et produit dépend d'un ensemble de traits liés à plusieurs fonctions biologiques (ex : croissance, développement, reproduction, immunité, comportement). Il est donc nécessaire de définir un ensemble de traits clés qu'il est nécessaire d'évaluer pour étudier le potentiel pour l'aquaculture (potentiel d'une population à être domestiquée et produite avec succès) à l'échelle intraspécifique. Par conséquent, le développement d'une méthodologie est nécessaire pour prendre en compte la différenciation géographique dans la domestication de nouvelles espèces. Cette méthodologie se veut pragmatique et générique pour être applicable à tout nouveau processus de domestication.

Cette thèse vise à :

(i) Evaluer si la différenciation géographique peut être utile dans la domestication/production de nouvelles espèces chez une espèce cible.

(ii) Conceptualiser et mettre en application une méthode pragmatique et standardisée pour intégrer la différenciation géographique dans les processus de domestication.

L'approche développée a été testée sur une espèce d'intérêt pour la diversification de l'aquaculture continentale: la perche européenne (*Perca fluviatilis*) et les premiers stades de vie (nurserie).

Le premier chapitre de la thèse vise à évaluer si *P. fluviatilis* présente une différenciation géographique pour des traits clés pour l'aquaculture. Une différenciation géographique a été précédemment mise en évidence pour des traits liés à la croissance et à la survie. Toutefois, la domestication est également influencée par d'autres traits, comme des traits comportementaux. Ce chapitre est donc axé sur des traits comportementaux des larves et nous avons démontré l'existence d'une différenciation géographique pour les interactions agressives et la structure de groupe entre trois populations allopatriques de *P. fluviatilis*. Ces résultats ont mis en évidence l'utilité de considérer la différenciation géographique pour la domestication/production de la perche commune.

Le deuxième chapitre vise à conceptualiser l'approche intégrative pour considérer la différenciation géographique dans le processus de domestication. Ce chapitre présente dans un premier temps le contexte lié à la diversification et la domestication de nouvelles espèces ainsi que l'intérêt de prendre en compte la différenciation géographique. Puis, la méthode proposée est présentée. Elle se compose de trois étapes : (i) la classification des populations sauvages en unités prospectives (c'est-à-dire en groupes de populations différenciées) qui présentent des chances d'être divergentes pour des traits clés en aquaculture, (ii) l'évaluation des performances des différentes unités prospectives dans des conditions d'élevage standardisées (*common garden*) à travers une approche multi-fonction et multi-trait, et (iii) l'identification d'une (des) unité(s) prospective(s) ayant le plus grand potentiel pour l'aquaculture à travers la pondération des différents traits et l'utilisation d'un score qui permet la synthèse des résultats obtenus dans l'approche multi-trait. Les chapitres suivants ont permis de mettre en application cette méthode sur les premiers stades de vie de *P. fluviatilis*.

Le troisième chapitre vise à établir une classification intraspécifique de *P. fluviatilis* (c'est-à-dire une classification des populations sauvages en unités prospectives). Comme première approche, nous avons choisi de réaliser une étude phylogéographique puisque des groupes de populations ayant des histoires démographiques divergentes sont susceptibles d'avoir acquis certaines spécificités phénotypiques, notamment par des processus d'adaptation locale. Ces groupes de populations pourraient présenter des potentiels divergents pour l'aquaculture. A travers le séquençage de quatre marqueurs mitochondriaux, nous avons identifié cinq unités prospectives: Plaine européenne, Danube, nord et est de la Fennoscandie, Europe de l'Est et Balkans. Cette classification est corroborée par l'utilisation de marqueurs microsatellites qui mène à une subdivision de ces cinq unités prospectives. En plus de présenter une classification intraspécifique, ces résultats ont été utilisés pour suggérer des pistes pour la conservation et la gestion des populations sauvages. Enfin, des similarités entre différenciation génétique et différenciation comportementale (chapitre 1) ont pu être mises en évidence.

Le quatrième chapitre vise à évaluer les performances de trois des cinq unités prospectives pour les premiers stades de vie de *P. fluviatilis* dans des conditions d'élevage standardisées (*common garden*). Quatre populations allopatriques ont été étudiées, dont deux appartenant à la même unité prospective. Ce chapitre vise à comparer l'utilité des approches mono-trait et multi-trait pour identifier les unités à fort potentiel aquacole. Nos résultats ont montré que l'approche mono-trait peut (i) mener à négliger des différenciations inter-populationnelles pour d'autres traits que celui considéré et (ii) mettre en évidence différentes populations d'intérêt en fonction du trait considéré. En revanche, l'approche multi-trait permet d'établir un consensus entre tous les traits et d'identifier la population ayant le plus fort potentiel aquacole grâce à l'élaboration d'un score de potentiel aquacole. Outre l'intérêt de l'approche multi-trait, ce chapitre a également permis de mettre en évidence (i) une forte différenciation géographique entre populations/unités prospectives, (ii) une similarité des performances de deux populations appartenant à la même unité prospective (différenciation intra-unité), et (iii) des convergences entre différenciation génétique et différenciation géographique.

Le cinquième chapitre vise à évaluer si le proxy génétique utilisé pour la première étape de la classification était la bonne approche. Nous avons évalué la pertinence de trois proxies alternatifs pour mettre en évidence les divergences inter-populationnelles pour des traits clés pour la larviculture : (i) la distance génétique, (ii) la divergence des habitats et (iii) les distances géographiques/hydrologiques. Cette étude a été effectuée à partir des résultats acquis sur les performances de sept populations allopatriques de perche commune. Nos résultats ont révélé des différences dans le degré de corrélation entre les matrices de distance basées sur les proxies alternatifs et les matrices de distance basées sur les traits clés. La distance génétique est le proxy corrélé au plus grand nombre de traits clés. Cependant, aucun proxy n'est corrélé à toutes les matrices de distance des différents traits. Par conséquent, nous suggérons comme méthode alternative pour la première étape d’utiliser une approche multi-proxy associée à une hiérarchisation des populations. La hiérarchisation des populations permettra d’identifier les unités biologiques qu’il faut considérer pour la deuxième étape de l’approche intégrative.

Dans la discussion, les biais expérimentaux, les limites et les améliorations potentielles sont passées en revue pour chaque étape de la méthode intégrative ainsi que les implications pour la larviculture de perche commune. En effet, la population du lac Balaton présente le potentiel pour l’aquaculture le plus élevé mais ces résultats sont néanmoins spécifiques au système d’élevage utilisé. Dans un deuxième temps, l'applicabilité de la méthode est discutée en termes de répétabilité, faisabilité et généricité. Les facteurs de risque et les précautions à prendre sont également abordés ainsi que les différents scenarios d’applicabilité de la méthode. Enfin, dans une dernière partie sont abordées les différentes perspectives quant au devenir des unités biologiques utilisées ainsi qu’une éventuelle détermination de l’origine des différenciations géographiques démontrées dans cette thèse.

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ANNEX 1: List of studies included in the geographic differentiation review.

Article	DOI / web link (when symposium paper or no DOI)
Abdel-Tawwab 2004	6th International Symposium on Tilapia in Aquaculturehttps://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&cad=rja&uact=8&ved=2ahUKEwiugoqb_OnnAhVM0uAKHf_2DVMQFjAAegQIBBAB&url=https%3A%2F%2Fag.arizona.edu%2Fazaqua%2Fista%2Fista6%2Fista6web%2Fpdf%2F510.pdf&usg=AOvVaw2VSpkFvbdgWuqDmWKnj9I1
Adams et al. 2016	10.1111/jfb.12855
Arendt and Wilson 1999	10.1890/0012-9658(1999)080[2793:CSFRGI]2.0.CO;2
Ayles and Baker 1983	10.1016/0044-8486(83)90407-6
Baker, 1983	http://hdl.handle.net/1993/29195
Bakke et al. 1990	10.1111/j.1095-8649.1990.tb05890.x
Bakke et al. 1990	0022-1 112/90/010577+ I1 $03.00/0
Bakker and Feuth-de Bruijn 1988	10.1016/S0003-3472(88)80233-1
Beacham and Evelyn 1992	10.1577/1548-8667(1992)004<0153:PAGVIR>2.3.CO;2
Beacham and Evelyn 1992	10.1577/1548-8667(1992)004<0168:PVIROP>2.3.CO;2
Bell 2005	10.1111/j.1420-9101.2004.00817.x
Bentsen et al. 1998	10.1016/S0044-8486(97)00230-5
Bernard et al. 2018	10.1016/j.ygcen.2018.01.004
Billerbeck et al. 1997	10.1139/f97-084
Billerbeck et al. 2000	10.1007/PL00008848
Borown et al. 2002	10.1300/J028v12n01_02
Bower et al. 1995	10.1577/1548-8667(1995)007<0185:GVIRTT>2.3.CO;2
Brown et al. 1998	10.1577/1548-8659(1998)127<0598:VILGRA>2.0.CO;2
Bruneaux et al. 2014	10.1002/jez.1889
Bryden et al. 2004	10.1016/j.aquaculture.2004.01.027
Buchanan et al. 1983	10.1577/1548-8659(1983)112<541:RSOFSO>2.0.CO;2
Bui et al. 2017	10.1111/jfd.12707
Burns et al. 2009	10.1111/j.1095-8649.2009.02314.
Chappell 1979	PhD thesis – Results reported in https://www.springer.com/gp/book/9781475713787
Cheng et al. 1987	.10.1016/0044-8486(87)90215-8
Clugston, 1964	10.1577/1548-8659(1964)93[146:GOTFLB]2.0.CO;2
Conover and Present, 1990	10.1007/BF00317554
Conover et al. 1997	10.1139/f97-147
Costa et al. 2010	10.1111/j.1095-8312.2010.01512.x
Curry Woods III 2001	10.1016/S0044-8486(01)00783-9
Da Costa 1998	Conference proceeding: https://www.documentation.ird.fr/hor/fdi:010015293
Dalgaard et al. 2004	10.1577/H03-004.1
DeLabbio et al. 1990	10.1016/0044-8486(90)90025-I
Dingemanse et al. 2007	10.1111/j.1365-2656.2007.01284.x

Dunham and Smitherman, 1981	10.1577/1548-8659(1981)43[63:girtwf]2.0.co;2
Dunham and Smitherman, 1983	10.1016/0044-8486(83)90389-7
Dunham et al. 1983	10.1577/1548-8659(1983)112<436:RPOCAP>2.0.CO;2
Eknath et al. 1993	10.1016/0044-8486(93)90035-W
Elghobashy et al. 2000	http://kenanaonline.com/users/MarineAquacultu/posts/518647
Fangue et al. 2006	10.1242/jeb.02260
Feminella and Matthews 1984	10.1111/j.1095-8649.1984.tb04892.x
Fields et al. 1987	10.1577/1548-8659(1987)116<856:cactmo>2.0.co;2
Flick and Webster 1964	10.1577/1548-8659(1964)93[58:CFYSAP]2.0.CO;2
Fraser et al. 2007	https://www.jstor.org/stable/40213003
Fullerton et al. 2000	10.1577/1548-8659(2000)129<0001:OGASOL>2.0.CO;2
Galarowicz and Wahl 2003	10.1577/1548-8659(2003)132<0425:DIGCAM>2.0.CO;2
Garcia et al. 2014	Workshop article : https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=11&ved=2ahUKEwj6k7C4g-rnAhWP3oUKHRqrAdAQFjAKegQIBRAB&url=http%3A%2F%2Frepositorio.upct.es%2Fbitstream%2F10317%2F4565%2F1%2Fego.pdf&usg=AOvVaw210DRBNkcIBUKGBw5J-kP0
García-Celdrán et al. 2015	10.1016/j.aquaculture.2015.04.006
Giles and Huntingford 1984	10.1016/S0003-3472(84)80346-2
Gilles et al. 1998	Proceeding paper : https://www.semanticscholar.org/paper/Comparison-of-brackish-water-growth-performances-of-Gilles-Amon-Kothias/f3bcc4e91f81374cc277afc4a9732d8907e3217d
Gjedrem and Aulstad 1974	10.1016/0044-8486(74)90098-2
Gjerde and Refstie 1984	10.1016/0301-6226(84)90061-7
Glover et al. 2001	10.1111/j.1095-8649.2001.tb00216.x
Glover et al. 2003	10.1016/S1054-3139(03)00088-2
Glover et al. 2003	10.1016/S1054-3139(03)00088-2
Glover et al. 2004	10.1016/S0044-8486(03)00454-X
Gorshkov et al. 2004	10.1111/j.1439-0426.2004.00513.x
Guinand et al. 2017	10.1002/ece3.2832
Gunnes and Gjedrem 1978	10.1016/0044-8486(78)90069-8
Hamzah et al. 2008	Congress proceeding : https://www.researchgate.net/publication/237721139_Performance_and_survival_of_three_red_tilapia_strains_Oreochromis_spp_in_pond_environment_in_Kedah_state_Malaysia
Hemmingsen et al. 1986	10.1577/1548-8659(1986)115<492:SOPFCA>2.0.CO;2
Herczeg et al. 2009	10.1016/j.anbehav.2008.10.023
Hershberger 1978	10.1111/j.1749-7345.1978.tb00239.x
Hjort and Schreck 1982	https://spo.nmfs.noaa.gov/content/phenotypic-differences-among-stocks-hatchery-and-wild-coho-salmon-oncorhynchus-kisutch
Huizinga et al. 2009	10.1111/j.1420-9101.2009.01799.x
Hunt von Herbing and Boutilier 1996	10.1007/BF00351042

Hunt von Herbing et al. 1996	10.1007/BF00351041
Huntingford 1982	10.1016/S0003-3472(82)80165-6
Imsland et al. 2000	10.1111/j.1749-7345.2000.tb00880.x
Imsland et al. 2000	10.1006/jfbi.2000.1384
Imsland et al. 2002	10.1016/S0044-8486(01)00656-1
Imsland et al. 2007	10.1111/j.1749-7345.2000.tb00880.x
Iwama et al. 1992	Congress proceeding : https://www.researchgate.net/publication/263580540_The_effect_of_stock_and_rearing_history_on_the_stress_response_in_juvenile_coho_salmon_Oncorhynchus_kisutch
Jacobs et al. 1999	10.1016/S0044-8486(98)00485-2
Janhunen et al. 2009	10.1111/j.1600-0633.2008.00329.x
Jayaprakas et al. 1988	Conf proceedings https://books.google.fr/books?hl=fr&lr=&id=k6UTNUgLXMIC&oi=fnd&pg=PA197&dq=Growth+of+two+strains+of+Oreochromis%E2%80%83niloticus+and+their+F1,+F2,+and+backcross+hybrids&ots=BWnybKHXsZ&sig=2_D4J_1C996jo0H5kUxpNerrzk0#v=onepage&q&f=false
Jennings and Philipp 1992	10.1007%2FBF00001892
Jonassen et al. 2000	10.1111/j.1095-8649.2000.tb02106.x
Kanis et al. 1976	10.1016/0044-8486(76)90088-0
Kenter et al. 2018	10.1016/j.aquaculture.2018.04.017
Khanh Doan et al. 2017	10.1016/j.aquaculture.2017.05.011
Khater and Smitherman 1988	Conference proceeding: https://books.google.fr/books?hl=fr&lr=&id=k6UTNUgLXMIC&oi=fnd&pg=PA215&dq=Cold+tolerance+and+growth+of+three+strains+of+Oreochromis%E2%80%83niloticus&ots=BWnybKG2w_&sig=m5ru7yetvlH4cCazUlO-Ms0k6lA#v=onepage&q=Cold%20tolerance%20and%20growth%20of%20three%20strains%20of%20Oreochromis%E2%80%83niloticus&f=false
Kincaid et al. 1994	10.1577/1548-8640(1994)056<0111:HPOSAS>2.3.CO;2
Kohler et al. 2001	10.1016/S0044-8486(01)00784-0
Kokita 2003	10.1007/s00227-003-1104-x
Kokita 2004	10.1007/s10641-003-0304-z
Lahti et al. 2001	10.1006/anbe.2001.1821
Lahti et al. 2002	10.1046/j.1365-2435.2002.00618.x
Langson et al. 2001	10.1006/fsim.2001.0354
Larsen et al. 2012	10.1007/s10528-011-9490-0
Leithner and Wanzenböck 2015	10.5539/jas.v7n5p28
Linder et al. 1983	10.1111/j.1365-2109.1991.tb00502.x
Ljubobratovic et al. 2015	Conference proceeding: https://www.researchgate.net/publication/318038168_Intensive_rearing_perfomance_of_three_pikeperch_Sander_lucioperca_fingerlings_populations_from_Hungary
Lucas et al. 2004	10.1023/B:BEGE.0000017879.68818.21
MacLean et al. 1981	10.1139/f81-217

Magnhagen 2006	10.1007/s00442-005-0302-2
Magurran and Pitcher 1987	10.1098/rspb.1987.0004
Magurran and Seghers 1991	10.1163/156853991X00292
Magurran and Seghers 1990	10.1016/S0003-3472(05)80524-X
Magurran 1986	10.1007/BF00300641
Magurran 1990	10.1016/S0003-3472(05)80947-9
Mairesse et al. 2005	PhD thesis: http://www.theses.fr/fr/2005INPL115N
Mandiki et al. 2004	10.1016/S0044-8486(03)00359-4
Marcil et al. 2006	10.1111/j.1095-8312.2006.00656.x
McCauley,1958	10.1139/z58-059
McGeer et al. 1991	10.1139/f91-208
Morkramer et al. 1985	10.1016/0044-8486(85)90229-7
Naevdal et al. 1978	10.1139/f78-021
Näslund and Henricson 1996	10.1111/j.1365-2109.1996.tb01240.x
Nelson et al. 1994	10.1086/physzool.67.2.30163852
Nelson et al. 1996	https://www.jstor.org/stable/30163852
Nicieza et al. 1994a	10.1139/z94-213
Nicieza et al. 1994b	10.1007/BF00627736
Nicieza et al. 1995	http://www.jstor.org/stable/2390008
Otterå et al. 2006	10.1016/j.icesjms.2005.11.004
Otterå et al. 2012	10.1093/icesjms/fss135
Otterlei et al. 1999	10.1139/f99-168
Overtuf et al. 2003	10.1016/S0044-8486(02)00014-5
Pakkasmaa and Piironen 2001a	10.1oos/bij1.2000.0488
Pakkasmaa and Piironen 2001b	10.1111/j.1095-8312.2001.tb01313.x
Persson et al. 2013	10.1016/j.toxicon.2013.08.066
Philipp and Whitt 1991	10.1577/1548-8659(1991)120<0058:SAGONF>2.3.CO;2
Piironen et al. 2013	10.5735/086.050.0101
Pimakhin and Zak 2014	Congress proceeding: https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&cad=rja&uact=8&ved=2ahUKEwit3piNiOrnAhVK1hoKHa2YAJsQFjAAegQIBhAB&url=https%3A%2F%2Fwww.researchgate.net%2Fpublication%2F269337454_Effect_of_Body_Size_on_Swim_Bladder_Inflation_in_Intensively_Cultured_Eurasian_Perch_Larvae_from_Different_Locations&usg=AOvVaw1iLD4mk5QFCFpLbE0rAqXK
Plumb et al. 1975	10.1577/1548-8659(1975)104<140:CCVEWD>2.0.CO;2
Present and Conover 1992	10.2307/2389767
Purcell et al. 2008	10.1577/H08-028.1
Purchase and Brown 2000	10.1139/f00-204
Purchase and Brown 2001	10.1111/j.1095-8649.2001.tb00497.x
Puvanendran and Brown 1998	10.3354/meps167207
Refstie and Steine 1978	10.1016/0044-8486(78)90096-0
Refstie et al. 1977	10.1016/0044-8486(77)90004-7
Reinitz et al. 1978	10.1577/1548-8659(1978)40[21:DPOFSO]2.0.CO;2
Rennert et al. 2003	10.1046/j.1439-0426.2003.00464.x

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ABSTRACT

Unlocking the wild potential: integration of geographic differentiation in domestication processes to facilitate fish aquaculture diversification

Nowadays, there is a will to develop a more sustainable aquaculture. One of the ways supported to promote the sustainability of the aquaculture sector relies on the production diversification, notably through the domestication and production of new species. However, domestication is a long and difficult process which can fail due to technical challenges, socio-economic limitations, or inadequate biological features of the species of interest. Yet, some of these biological features can also vary at the intraspecific level, between allopatric populations. Indeed, geographic differentiation can shape genetic, phenotypic, and ecologic specificities, which could lead to unique domestication predisposition or socio-economic attractiveness among allopatric populations. Therefore, choosing wild populations exhibiting a high potential for aquaculture (i.e. presenting interesting expression of key traits) could facilitate the domestication and production of new species. This PhD work was aimed at (i) assessing if geographic differentiation could be useful in domestication/production of a targeted species and (ii) developing and applying an integrative method to integrate geographic differentiation in domestication programs. The approach developed was tested on a species of interest for inland aquaculture diversification, the European perch (*Perca fluviatilis*), and targeted first life stages. The method consists of three steps: (i) classifying wild populations into prospective units (i.e. groups of populations differentiated) which are likely divergent for key traits in aquaculture, (ii) evaluating the performance of the different prospective units in standardized culture conditions through a multi-function and multi-trait approach, and (iii) identifying the prospective unit with the highest potential for aquaculture. The first step allowed identifying five prospective units: the European Plain, Danube, Northern and Eastern Fennoscandia, Eastern Europe, and the Balkans units. The second step highlighted a geographic differentiation in key traits for aquaculture in *P. fluviatilis*. The third step allowed identifying differential potentials for aquaculture between prospective units. Despite some limitations, this three-step approach could allow facilitating domestication of new species or species at incipient stages of domestication which face major bottlenecks in domestication and/or production.

Keywords: Intraspecific, Domestication, Aquaculture, Potential, Multi-trait, Sustainability

Déverrouiller le potentiel sauvage: Intégration de la différenciation géographique dans les processus de domestication pour faciliter la diversification piscicole

De nos jours, il existe une volonté de développer une aquaculture plus durable. L'une des voies prometteuses pour promouvoir la durabilité du secteur de l'aquaculture repose sur la diversification de la production, notamment par la domestication et la production de nouvelles espèces. Cependant, la domestication est un processus long et difficile qui peut échouer en raison de défis techniques, de limitations socio-économiques ou de caractéristiques biologiques inadaptées des espèces. Toutefois, certaines de ces caractéristiques biologiques peuvent varier au niveau intraspécifique, entre populations allopatriques. En effet, la différenciation géographique peut façonner des spécificités génétiques, phénotypiques et écologiques qui pourraient entraîner des différences de prédisposition à la domestication ou d’attraits socio-économiques entre populations allopatriques. Par conséquent, le choix de populations sauvages présentant un potentiel élevé pour l'aquaculture (c'est-à-dire présentant une expression intéressante de traits clés) pourrait faciliter la domestication et la production de nouvelles espèces. Ce travail de thèse visait à (i) évaluer si la différenciation géographique pouvait être utile dans la domestication et production d’une espèce cible et (ii) développer et mettre à l’épreuve une méthode intégrative pour considérer la différenciation géographique dans les programmes de domestication. L'approche développée a été testée sur une espèce d'intérêt pour la diversification de l'aquaculture continentale, la perche européenne (*Perca fluviatilis*), et a ciblé les premiers stades de vie (nurserie). La méthode comprend trois étapes: (i) la classification des populations sauvages en unités prospectives (c'est-à-dire en groupes de populations différenciées) qui sont susceptibles de présenter des divergences pour des traits clés, (ii) l'évaluation des performances des différentes unités prospectives dans des conditions d'élevage standardisées par une approche multi-fonction et multi-trait, et (iii) l'identification de l'unité prospective ayant le plus fort potentiel pour l'aquaculture. La première étape a permis d'identifier cinq unités prospectives: Plaine européenne, Danube, nord et est de la Fennoscandie, Europe de l’est et Balkans. La deuxième étape a mis en évidence une différenciation géographique pour des traits clés pour l'aquaculture de *P. fluviatilis*. La troisième étape a permis de mettre en évidence des différences de potentiel aquacole entre des unités prospectives. Malgré certaines limites, cette approche en trois étapes pourrait permettre de faciliter la domestication de nouvelles espèces ou d’espèces au début du processus de domestication qui sont confrontées à d'importants goulots d'étranglement en matière de domestication et/ou de production.

Mots clés : Intraspécifique, Domestication, Aquaculture, Potentiel, Multi-trait, Durabilité