How domestication alters fish phenotypes

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Abstract:

Domestication can be defined as the adaptation of an animal to the human environment and its constraints. Accumulating evidence strongly indicates that domestication plays essential roles in modulating the phenotypes of teleosts, despite the scattered information. Animal husbandry and molecular, physiological, and behavioural studies have identified a high degree and complexity of biological changes induced by domestication. These phenotypic modifications during domestication vary greatly amongst species and physiological function (e.g. growth, reproduction, response to stress, and immunity), probably due to a variety of intrinsic and extrinsic factors that can interfere with phenotypic changes. Indeed, much information about domestication is lacking, which impedes the generalisation of our understanding of the effects of domestication. This review gathers and clarifies the available information about the main effects of fish domestication. We use a broad physiological approach for understanding these biological consequences, from the genesis of domestication (e.g. netting from the wild) to the ultimate step (controlled artificial selection). We also suggest ways to predict the effects of domestication and to better understand the sources of the biological changes.

Keywords: domestication; fish; physiology; reproduction; stress; immunity

Introduction

The most recent FAO (Food and Agriculture Organization) reports found that captures from fisheries have been quite stable since the late 1980s, but aquaculture is still the key driver of the growing supply of fish for human consumption. The future of aquaculture will require the continuation of some economic models of sector development. Amongst these models, fish diversification is one way expected to support the growing aquacultural production, because this way of promoting aquaculture has many advantages at the social, ecological, and economic levels (Wellenreuther *et al.* 2019)(Fontaine *et al.* 2009). Diversification, however, requires the domestication of new species, which often faces serious bottlenecks linked to the lack of control of the life cycle. This strategy is thus not a priori the easiest, because the domestication of a new species is a long, difficult, and expensive process and is often conducted empirically (Teletchea and Fontaine 2014). Understanding and conceptualising the effects of domestication on fish phenotypes is of paramount importance for limiting failures of domestication.

Domestication is defined as the process by which a population of animals becomes adapted to humans and captive environments by one or more combinations of genetic modifications throughout generations and developmental events induced by the environment, recurring in each generation (Price 1999). Domestication at the individual or population level starts with the transfer of animals from the wild (F0 fish) to a captive environment where they are faced with a new living environment. Each history of domestication is unique, and the populations during domestication undergo a range of biological phenomena linked to human practices. These mechanisms contribute to genetic, genomic, and phenotypic changes of the animals. Some changes are not easily controlled by humans, such as inbreeding and genetic drift that

depend on the numbers of broodstock used in each generation. Natural selection in captivity promotes the survival of animals that are best adapted to the rearing environment and eliminates those unable to reproduce (Mignon-Grasteau *et al.* 2005). Multiple adaptive failures are common in the early generations due to a lack of human control of the capacity of some specimens to reproduce (unsuitable timing and egg and larval quality) or even to survive in captivity. Humans, however, can relax natural selection in captivity, which consists in reducing the selection pressure for some traits (e.g. breeding season, fish size, and fish feeding). Finally, artificial selection is the process by which we voluntarily select broodstock for a given objective of production (Mignon-Grasteau *et al.* 2005). The objective may be uncontrolled if the traceability and conditions of artificial selection are not fully monitored or may be considered as controlled if the objective is part of a rigorous genetic breeding programme tracked over several generations. Both types of selection (natural and artificial) may affect allelic frequencies or lead to mutations at some major loci (e.g. promoters) that may also affect the emergence of phenotypes (Wittkopp and Kalay 2011). These adaptive mechanisms are also linked with alterations of gene expression that are likely to modify fish phenotypes (Christie *et al.* 2016).

A theory of syndrome domestication has recently been proposed that accounts for such phenotypic changes in mammals (Wilkins *et al.* 2014). The theory suggests that some morphological, behavioural, and physiological alterations in domesticated animals may be due to mild deficits of neural-crest cells during embryonic development. Such deficiencies are proposed to be the sources of the modified morphological, behavioural, and physiological traits. Fish domestication, however, displays some specific characteristics compared to mammals, independent of these phenotypic changes. First, fish production benefits from a range of specific rearing systems, from production in ponds to intensive production in recirculated aquacultural systems (RASs), each offering one specific trajectory of

domestication (Fontaine & Teletchea 2019). Second, each trajectory offers the opportunity of many paths of domestication, which can be defined as the set of husbandry practices applied by the farmer (e.g. type of diets, fish density, temperature/lighting conditions) and the set of unpredictable events (climate, stressors, disease). This multiplicity of domestication paths is made possible by biological diversity, which is much higher in fish than mammals. Third, domestication is generally recent, with most captive species domesticated in recent decades (Teletchea and Fontaine 2014) and with numerous and rapid phenotypic changes even in the early generations. Fourth, bilateral flows are high between wild and captive individuals that could interfere with the progress of domestication, e.g. by the transfer of pathogens or the modification of genetic variability (Lorenzen *et al.* 2012). These peculiarities confer to fish the status of a relevant model for identifying the consequences of vertebrate domestication. Growing evidence suggests that domestication induces large changes at the ecological, behavioural, anatomical, and physiological levels, but some of these changes are controversial, depending on the species and especially on the biological function investigated. The aim of this review is first to clarify these equivocal effects along the successive steps of domestication that can strongly modify fish phenotypes or population structure and then to discuss how to develop new research strategies for exploring these effects in the future. We propose to break down the process of domestication into five main steps that greatly influence fish phenotype (Figure 1).

1-Capture, transport (step 1), and acclimation (step 2)

Transfer from the wild to rearing conditions is the first crucial step in the domestication of fish (Figure 1). Several manipulations (e.g. fishing, handling, and transport) occur during this stage that constitute mechanical, physicochemical, social, and sensory stressors likely to

disrupt many biological functions. The transport of fish is accompanied by severe modifications to water quality (e.g. acidification and increased concentrations of ammonia and carbon dioxide) and potentially mortality (Sampaio and Freire 2016). Strong stressors such as netting, exposure to air, handling, and transport can greatly perturb endocrine function, marked by increased releases of catecholamines and corticosteroids. These hormonal inductions are accompanied by physiological alterations such as demineralisation, immunological and haematological alterations, increased glycemia, and depressed production of sex steroids (Wedemeyer and Wydoski 2008; Cho *et al.* 2009; Nikoo and Falahatkar 2012), leading to well-known effects on fish biological functions. Most of these parameters return to resting levels in the surviving fish within 48-72 h after capture, indicating that the species can regain their physiological homeostasis within a relatively short time if the duration and intensity of the stresses linked to capture are mild. This period of allostatic load (physiological adjustment) that can be considered as the second step of domestication (Figure 1) corresponds to the period of acclimation (Segner *et al.* 2012) of the wild fish to the captive environment, where the fish are exposed to a multiplicity of cultured conditions (Lorenzen *et al.* 2012).

The success of acclimation is multifactorial in that it implies a complex response of the organism characterised by a way of life that differs greatly between the wild environmental conditions and those provided by the cultured system. Successful acclimation requires that all these environmental features of the rearing system (e.g. temperature, salinity, and ammonia concentration) be within the range of those compatible with the biological requirements of the species and the population (Ibarra-Zatarain *et al.* 2016). The capacity to acclimate thus depends on the level of divergence between the two environments but also on the characteristics of transition from the wild to captivity (e.g. acute vs progressive acclimation) and finally on the size and developmental stage of the fish caught in the wild (fertilised eggs

vs juveniles; e.g. (Okpala *et al.* 2017)). This challenge experienced by fish newly introduced to captivity may induce non-inherited changes in behaviour. This adopted behaviour is also vital, because the way the fish feed, compete or interfere with congeners or even to avoid potential predators are determinants of their survival (Huntingford *et al.* 2012). For example, feeding with artificial diets in RASs markedly modifies nutritional behaviour, notably for piscivorous fish species.

Increased growth becomes apparent within the first few weeks or months following the transfer to husbandry in response to safe rearing conditions (Lorenzen *et al.* 2012) and in case of adequate behaviour to eat and survive. The expenditure of energy is probably lower under *ad libitum* feeding than in the wild, allowing the animal to optimise growth. Fish growth is a main zootechnical endpoint in aquaculture, so positive modulation of growth is a positive effect of domestication from the human point of view. Other biological functions, though, may be altered in wild fish acclimated to captive conditions.

2-First reproduction in captivity (step 3)

Obtaining the first generation of captive fish from wild fish is the third step of domestication (Figure 1). This step allows the production of fry that have never experienced the wild and involves the initial mechanisms of adaption to the rearing conditions. The stages of gametogenesis in wild broodstock acclimated in farms may nevertheless not be fully completed in the rearing conditions, and these wild fish do not always successfully respond to the hormonal stimulations used for inducing gonadal maturation (Hassin *et al.* 1997; Krejszeff *et al.* 2009). This failure in reproductive control is not due to changes in genetic characteristics but to multiple differences in environmental and social factors between wild and cultured fish that disrupt hormonal control at the level of the hypothalamus-pituitary-

gonadal axis compared to the natural endocrine variations in the wild (Hassin *et al.* 1997). Changes in external factors such as temperature and/or photoperiod are important for driving the progress of gonadogenesis in temperate fish species (Wang *et al.* 2010), and the failure to mimic these environmental cues in husbandry may be the cause of poor reproductive performance. The accurate control of photothermal programmes is thus assumed to help increase the control of the stages of gametogenesis in wild fish dedicated to the renewal of broodstock populations. Even if acclimation is successful, chemical and physical stressors in captivity are additional external factors that may further disrupt the progress of the reproductive cycle in these F0 fish (Cleary *et al.* 2000). These stressors have well-known effects on reproductive success (Milla *et al.* 2009), but other sources of failure in mating programmes may be applied to broodstocks caught in nature. Indeed, reproductive defaults in wild broodstock are not necessarily due to defects in these environmental features but may also be due to the nutritional and energetic conditions provided by the systems of husbandry, as observed in wild cod (*Gadus morhua*) (Lambert *et al.* 2000). These eclectic causes of reproductive dysfunction indicate the importance of fully investigating and checking the suitability of the rearing conditions to the long-term survival of the wild fish. Step 3 of domestication, the success of obtaining a first generation in captivity (F1 fish), may remain illusory if these requirements are not fulfilled.

3-Adaptation and phenotypic changes (step 4)

After the first successful reproduction, the next generations in captivity further strengthen the progressive adaptation that leads to large phenotypic changes driven by natural selection and/or by uncontrolled artificial selection by fish producers. These changes can be considered as the fourth step of domestication (Figure 1).

3-1-Growth, nutrition and flesh quality

Controlled artificial selection for growth has greatly accelerated weight gains in fish, especially salmonid fishes. Higher growth rates accompanied by higher conditions factors, however, have also been observed in domesticated salmonids where artificial selection has been poorly controlled (Table 1; Glover et al. 2009; Hedenskog, Petersson, and Järvi 2002; Solberg et al. 2013; Tymchuk, Beckman, and Devlin 2009; Tymchuk and Devlin 2005). Domestication without controlled artificial selection, though, is not necessarily linked to increased growth (Brummett *et al.* 2004; Vandeputte *et al.* 2009). The physiological mechanisms underlying this divergence between wild and domesticated fish, intentionally or unintentionally selected, are poorly known. Differential levels of GH (Growth Hormone) or IGF-1 (Insulin Growth Factor-1) may be physiological indicators of this salmonid response (Fleming *et al.* 2002; Tymchuk *et al.* 2009). Contrasting nutritional behaviour may also account for this response. Foraging activity is also modified during domestication, even though it has only been demonstrated in a small range of fish species (Huntingford *et al.* 2012). Some species that have been more intensely domesticated, under controlled artificial selection for growth or not, stay near the water surface rather near the bottom of the water column (Reinhardt *et al.* 2001; Robison and Rowland 2005), which in turn improves their feeding efficiency (Thodesen *et al.* 1999; Sánchez *et al.* 2012). Changes in social behaviour, e.g. shoaling, would be an additional behavioural cause of the higher growth in domesticated fish (Wright et al. 2006; Pasquet et al. 2019), potentially due to a higher homogeneity of age and size in domesticated fish (Ruzzante and Doyle 1991, 1993). This change in the structure of the social group may induce modifications of aggressiveness and hierarchy between

individuals (Swain and Riddell 1990; Ruzzante and Doyle 1993; Lucas *et al.* 2004) that would alter feeding behaviour and may improve growth.

Differential diets and levels of growth are apparently accompanied by differential flesh quality between wild and farmed fish, as demonstrated by Eurasian perch (*Perca fluviatilis*) (Mairesse *et al.* 2007), salmon (*Salmo salar*) (Johnston *et al.* 2006), sea bass (*Dicentrarchus labrax*), and sea bream (*Sparus aurata*) (Grigorakis 2007). These differences are marked by higher lipid content and fillet firmness in domesticated fish, potentially due to higher collagen content (Johnston *et al.* 2006). Cultured sea bass also contain more fat than their wild counterparts (Fuentes *et al.* 2010), and even the lipid composition of muscle differs, with a higher content of monounsaturated fatty acids and lower contents of saturated and polyunsaturated fatty acids, except n-6 polyunsaturated fatty acids that are more abundant in farmed sea bass (Fuentes *et al.* 2010; Lenas *et al.* 2012). Finally, some amino acids that characterise the flavour of fish, such as glutamic acid, aspartic acid, alanine, and glycine, are more abundant in cultured sea bass. These differences, notably those in the lipid profile, however, may not be common in all domesticated species (Samy Yehya El-Zaeem 2012). The type of breeding system may also influence this divergence in the lipid profile between wild and domesticated fish (Mairesse *et al.* 2006).

3-2-Reproductive function

Some fish in each of the next generations (F1-FX) are used as broodstock to produce new offspring in captivity, which progressively leads to the fourth step of domestication, regardless of the quality of these successive reproductive periods, provided that the fingerlings are viable and able to become future broodstock in captive conditions. The possibility of mating requires the attainment of puberty, which is defined as the

developmental period during which an individual first becomes capable of reproducing sexually. Precocious puberty is a major problem in a wide range of farmed fishes, because puberty adversely affects growth. For example, male sea bass under natural conditions in the Mediterranean Sea reach sexual maturity at the age of two years. Early puberty under intensive culturing conditions, however, affects 20–30% of one-year-old males in the population (Felip *et al.* 2008). The increased growth in domesticated fish is probably one of the major causes of early puberty in farmed species (Taranger *et al.* 2010). The quality and timing of the stages of gametogenesis are very important for further spawning, fertilisation, and embryonic development. Many reproductive traits in captivity are affected by natural selection and/or uncontrolled artificial selection during domestication. Reproductive tactics such as spawning frequency may be modified (Krejszeff *et al.* 2010), accompanied by changes to the reproductive capacity of the progenitors, with modifications of their physiological status (Dannewitz *et al.*, 2004; Krejszeff *et al.*, 2009). These effects of domestication on fish reproduction, though, are quite controversial, which questions the zootechnical assets to go deeper in the domestication by keeping the domesticated broodstock to obtain the next offspring generations, rather than renewing the broodstock at each generation by catching wild fish. Studies have reported a higher reproductive capacity in domesticated than wild fish, e.g. cyprinid fishes whose ovulatory response to hormonal treatments is higher in cultured fish (Krejszeff *et al.* 2009, 2010). Reproductive capacity (spawning success and fecundity) in Nile tilapia (*Oreochromis niloticus*) was higher in the most domesticated fish strain than in a strain collected from the wild (Osure and Phelps 2006). Other recent studies did not find clear differences in the reproductive features between wild and domesticated fish. Gonadogenesis in the Eurasian perch and pikeperch (*Sander lucioperca*), was more precocious in populations that were more domesticated (Khendek *et al.* 2017, 2018; De Almeida *et al.* 2019), but reproductive

performance was generally better for the wild fish (Křišťan *et al.* 2012; Khendek *et al.* 2017). As another example, reproductive parameters and the biological quality of eggs in a farmed population were compared to those of the original wild population in brown trout (*Salmo trutta*). Except for egg diameter, the reproductive traits were similar in both populations (Randak *et al.* 2006). In contrast, most published data have indicated degraded reproductive performance of captive fish relative to less domesticated populations. Several features are common in captive fish, notably slower or blocked gametogenesis, lower levels of sex hormones, smaller and lighter eggs, and lower reproductive success (Table 2). Modifications of reproductive behaviour may also be a source of decreases in reproductive success. For example, the hierarchical position of captive male coho salmon (*Oncorhynchus kisutch*) during mating is lower relative to the wild broodstock, decreasing the reproductive success of wild males by 50% (Neff *et al.* 2015). Drawing bold conclusions about the effects of domestication on reproductive capacity may thus be premature.

Identifying the main causes of this divergence of reproductive success between wild and cultured strains is important. Published causes are rare, and tentative explanations can be quite speculative. One hypothesis is the deviation of fatty acid composition, storage, and metabolism, as reported for tabarana (*Salminus hilarii*) (Araújo *et al.* 2012), because the composition of fatty acids, notably unsaturated fatty acids, is a major determinant of the quality of fish eggs (Sorbera *et al.* 2001). The modification of genetic features during domestication is another putative source of differences between wild and domesticated fish. Genetic variability may decrease generation after generation, illustrated by decreased heterozygosity and allelic diversity (Sánchez *et al.* 2012). A decrease in this genetic diversity is often associated with changes in phenotypic characteristics (David 1999). Significant correlations between markers of heterozygosity and biological reproductive traits are good

indications that a decrease in genetic diversity can be linked to modifications in reproductive success (Lieutenant-Gosselin and Bernatchez 2006; Kalbe *et al.* 2009). Relying on the genetic diversity based on these data to identify the direction of the effects of domestication, however, is quite difficult, because the correlations between these genetic markers and the level of phenotypic reproductive performance are not clearly positive or negative. This divergence of reproductive success may also be due to putative differences in reproductive behaviour, but very few data support this premise. Human bias in the reproductive sequence of reared fish populations relative to the sequence in the wild is the most obvious cause, notably by removing the choice of sexual partners. Conversely, the reproductive behaviour of domesticated fish released in the wild causes relevant changes in some characteristics of the reproductive strategy (Pasquet 2019), which may also account for the modifications to mating performance during domestication.

3-3-Immunity and resistance to pathogens

Improvement of fish immunity is of primary importance to resist pathogenic invasion and to avoid disease proliferation in fish farms. Independently of artificial breeding programmes, taking into account the advancement of the domestication process to optimise the resistance to pathogens is not voluntary applied so far as there is little available information from the literature. Some indications, however, suggest that this strategy may be relevant to strengthening the immune potential of captive fish. One generation of domestication of the rainbow trout (*Oncorhynchus mykiss*), altered the expression of hundreds of genes, with gene ontology indicating that immunity over-represented some of the main gene classes in that list (Christie *et al.* 2016), as for the Australasian Snapper (*Chrysophrys auratus*) (Wellenreuther *et al.* 2019). The differential serum proteome between two generations of the Eurasian perch, displayed mainly immunological proteins, also suggesting that immunity is a primary target in

tissues or cellular fluids affected by domestication (Douxfls, Mandiki, *et al.* 2011; Douxfils, Mathieu, *et al.* 2011; Chen *et al.* 2017). The rationale to understand this differential expression of genes associated with immunology may depend on the environmental conditions of the domesticated fish, reared under crowded conditions where the cross-contamination of individuals with pathogens is favoured. Domestication would thus modify the fish transcriptome and proteome to allow adaptation to high densities in captivity. Changes in mRNA or protein levels, however, are not typically correlated with the level of protein activity (Greenbaum *et al.* 2003), because post-transcriptional and -translational modifications may ultimately affect the functionality of proteins. Studies of differential gene expression at transcript and protein levels thus cannot substitute for detailed functional analyses of candidate genes. These molecular studies generally do not validate a modified change in the immune response to pathogenic invasion. Whether or not domestication is linked to either immunostimulatory or immunosuppressive effects and in turn to conclusions about the usefulness of appealing to long-term adapted captive fish to further boost fish immunity is difficult to distinguish. To clarify, the comparative effect of bacterial challenges to fish mortality and immunity is a convenient tool for evaluating the positive benefits of domestication. Wild and domesticated strains of Atlantic salmon respond similarly to *Aeromonas salmonicida* (Glover *et al.* 2009), but levels of immunological parameters were higher in F4 than F1 perch after infection with *Aeromonas hydrophila* (Douxfls, Mandiki, *et al.* 2011). Definitively concluding that the effects of domestication improve fish immunity is thus currently too premature, but the first molecular results of the effect of domestication on cellular signalling pathways are very promising.

3-4-Response to stress

331 In addition to the immune response after pathogenic invasion, the ability of fish to cope with
332 aquacultural stressors is of paramount importance for the survival, growth, and reproductive
333 capacity of the fish. Fish possess anatomical, physiological, and behavioural strategies to
334 respond to stressors in aquacultural conditions. They display evidence of escape responses
335 associated with long-term memories of frightening events in captivity (Yue *et al.* 2004).
336 Specialised brain structures implied in the response to suffering and active nociceptors are
337 indications of a neurophysiological response to painful experiences (Sneddon *et al.* 2003).
338 The impacts of stressors due to husbandry on the level of stress or pain hormones, such as
339 catecholamines, corticosteroids, or opioids, indicate that domesticated fish are sensitive to
340 these stressors (e.g. (Øverli *et al.* 2001)). Interestingly, these behavioural and physiological
341 characteristics are affected by domestication.

342 The longer fish are domesticated, the lower their levels of stress hormones relative to wild
343 fish after exposure to acute or chronic stressors (Awata *et al.*, 2011; Douxfils *et al.*, 2011a;
344 Mazur and Iwama, 1993; Table 3). For example, wild trout have higher post-stress levels of
345 plasma glucose and DOPAC/DA than domesticated fish after exposure to a novel
346 environment or a predator (Lepage *et al.* 2000). These studies have unfortunately not linked
347 the anatomical, behavioural, or physiological alterations to identify relationships between the
348 progressive changes in the organs implied in the stress axis (brain, pituitary, and interrenal
349 cells), the modifications of hormones associated with stress, and the behavioural
350 consequences. Concluding whether this inhibition of the corticotropic axis is due to
351 hypoplasia of interrenal cells, a decrease in corticotropic enzymes or cortisol receptivity, or
352 even behavioural changes is thus difficult. How the effects of domestication on the
353 attenuation of these physiological indicators of stress can benefit the animals is also not clear.

354 At the behavioural level, domestication may reduce the responses to escape predation, as
355 demonstrated in a wide range of teleost species. Indeed, wild fish react to predators more

rapidly and intensively than domesticated fish, and this natural reaction attenuates over the first few generations of domestication (see (Pasquet 2019) for review). This effect of domestication is likely linked to physiological changes, where fish usually respond to stressors by altering physiological function in an attempt to reallocate energy for coping with stress (Schreck *et al.* 2001). The concept of coping style has emerged in recent decades, with personality and other new behavioural concepts such as “temperament” and “behavioural syndromes”. This new field of research has established links between behavioural and physiological indicators: “Coping refers to the individual’s behavioural and physiological efforts to manage (reduce, minimize, master, or tolerate) the internal and external demands of a situation that is appraised as stressful, and taxing or exceeding the individual’s resources” (Koolhaas *et al.* 1999). Coping styles in several domesticated freshwater and marine species of aquacultural importance have attracted great interest (Castanheira *et al.* 2017), such as the common carp (*Cyprinus carpio*), Nile tilapia, Atlantic salmon, Atlantic halibut (*Hippoglossus hippoglossus*), rainbow trout, sea bass, Senegalese sole (*Solea senegalensis*), and gilthead sea bass. These coping styles are consistent over time, so they are reliable for assessing individual fluctuations in response to stress. Two groups of animals are identified based on their coping styles: proactive and reactive animals. Proactive animals have a bolder, more aggressive and less flexible behavioural response to stress, with a lower physiological HPA reactivity (lower cortisol level), and reactive animals have opposite behavioural and physiological responses (Vindas *et al.* 2017).

Some recent experiments have demonstrated that the physiological response of domesticated fish to stressors is linked to coping style. The use of thermal gradients affects physiological and behavioural traits in Nile tilapia described as personality, and the proactive individuals preferred the higher temperatures that could be directly linked with their metabolism (Cerqueira *et al.* 2016). Styles of coping with stress in juveniles and breeders have been

characterised in Senegalese sole (Ibarra-Zatarain *et al.* 2016). Behavioural tests can differentiate between two groups of individuals: “fearfulness-reactive” and “active-exploration” individuals, which correspond to the defined proactive and reactive individuals with low and high levels of cortisol, respectively. Boldness, which is the propensity to take risks, is strongly linked to cortisol level in juvenile mullet (*Argyrosomus japonicus*) siblings (Raoult *et al.* 2012) after exposure to a stressor, with lower levels in bold individuals (proactive) in response to the stressor. Similar results have been reported for Senegalese sole (Silva *et al.* 2010), with proactive individuals having a shorter feeding latency (time to react to feed), longer duration of escape attempts from a net, and lower cortisol levels (before the stressful situation) than for reactive individuals, suggesting the existence of stress-coping styles in this species.

All these examples indicate that individual behavioural differences in a domesticated population in response to stressors are directly linked to the secretion of the stress hormone cortisol. The level of corticosteroids, however, is not the only indication of coping styles in fish. For example, domesticated fish approach a novel object more readily and take more risks, and these behavioural differences are often accompanied by physiological variations linked to cardiovascular activity (Pasquet 2019). These differences indicate that responses towards frightening stimuli are less intense in domesticated than wild fish and that these responses may be due to changes in physiological activity. A comparison between a wild-type and a domesticated strain of the fighting fish (*Betta splendens*), produced similar results, with the domesticated strain adopting a behavioural strategy of immobility during confinement, contrary to the wild fish (Verbeek *et al.* 2008). The domesticated individuals were predicted to exhibit a more proactive coping style characterised by a lower level of cortisol and a stronger sympathetic response (opercular beat rate) to non-social challenges (unfamiliar environment, spatial confinement).

We should, however, be cautious in evaluating if the effects of domestication on the inhibition of the corticotropic axis is always linked to behavioural changes. Some studies have reported changes in coping styles between wild and domesticated fish, but other studies prevent us from generalising this correlation between behavioural and physiological traits to all species and all stressors. For example, newly emerged fry of domesticated Atlantic salmon were tested for their behavioural responses to resume feeding after transfer to rearing in isolation. Bolder individuals adapted to the new situation more rapidly than shy individuals, and this difference remained after several months. Post-stress concentrations of cortisol, however, did not differ between the bold and shy individuals (Vaz-Serrano *et al.* 2011).

4-Effect of the controlled artificial selection (step 5)

Controlled artificial selection at the species level is part of the advanced stages of domestication (Teletchea and Fontaine 2014). Step 5 at the population and individual levels may also be considered as the ultimate degree of domestication (Figure 1) even if it can occur in parallel with stage 4, requiring that some former steps (at least steps 1-3) have been achieved. Step 5 is often used to optimise growth and relevant biological functions. One of the primary objectives of aquaculture is to produce the highest amount of piscine proteins while optimising food efficiency and flesh quality, so controlled artificial selection of growth has been the first goal of selection. Estimates of the heritability of traits associated with growth range from 0.10 to 0.60 (Priars and Smith 2010). This moderate to high heritability has been used to select for growth, which has increased weight or length relative to unselected fish (e.g.

(Vandeputte *et al.* 2009)). Reproductive capacity is not a usual target of controlled artificial selection in aquacultured fish, but markers of reproductive capacity are potentially relevant heritable traits that may be investigated to strengthen the reproductive performance of captive stocks (Trong *et al.* 2013a). Estimates of heritability, however, vary widely depending on the species and type of reproductive trait: puberty, fecundity, or traits associated with spawning (Trong *et al.* 2013a; b). The heritability of reproductive traits is generally similar to or slightly lower than the heritability of traits associated with growth (Friars and Smith 2010), but the little information available from the literature suggests that good progress may be expected by selecting for age at maturation or for gamete quality.

Controlled artificial selection of the immune response in the future could potentially improve the genetics of fish. Outbreaks of disease is an important bottleneck for the development of intensive aquaculture worldwide. The choice of selected lines with traits linked to the capacity to combat viral, bacterial, and parasitic diseases has been successful in a variety of species (Gjedrem 2012). A prerequisite is the availability of a sufficient proportion of highly heritable traits linked to immunity to target as an added protection against disease. Such heritability, however, is low to moderate (from 0.05 to 0.38) and is highly species-dependent, which renders this route of investigation unclear and requires selecting the best relevant traits (Mohanty *et al.* 2012; Evenhuis *et al.* 2015; Silva *et al.* 2019; Srisapoome *et al.* 2019). Identifying QTLs linked to immunological parameters, however, could be another way to implement such major traits in schemes of controlled artificial selection (Fraslin *et al.* 2018).

The selection of low-stress responders may be a good strategy to attenuate the impact of stress on growth, reproduction, or immune defence. Divergent lines have been selected based on the level of plasma cortisol following stress in rainbow trout (Pottinger *et al.* 1992). The heritability of the response of cortisol to stress varies strongly amongst species: 0.27-0.50 in rainbow trout, 0.60 in carp, but only 0.05 in Atlantic salmon and 0.08 in sea bass (Volckaert

et al. 2012). Interspecific differences, the type of stressor applied, and other methodological biases may account for these discrepancies.

Controlled artificial selection is usually driven by a single biological function (growth, reproduction, or immunity), but the selection of strains with a higher growth potential may indirectly contribute to altering the reproductive capacity of the broodstock. For example, genetic correlations between growth and reproductive features in salmonids are associated with these biological functions (O'Malley *et al.* 2003; Tentelier *et al.* 2016). The controlled artificial selection for growth can decrease the proportion of mature male parrs (Harvey *et al.* 2018), and genetic interaction has been reported between body weight and early maturation of female in Nile tilapia, suggesting that selection for larger body weight may lead to early puberty in females (Longalong and Eknath 1995).

Also, such selection for body size in salmon decreased anti-predatory behaviour (Johnsson *et al.* 2001) and the strength of the hypothalamus-pituitary-interrenal (HPI) axis, as discussed earlier, implying that the effect of domestication on the attenuation of stress may be due to genetic interactions with growth. This implication is supported by negative genetic interactions of cortisol level with body weight and standard body length that have been calculated for confined sea bass (Volckaert *et al.* 2012), suggesting that targeting genetic selection for aspects of both growth and stress is possible, at least in sea bass.

Immunity may also be a consequence of controlled artificial selection. For example, a study of the gill transcriptome of *S. salar* found a set of differently expressed genes between wild and domesticated fish selected for growth. Eight of these genes had adaptative and innate immune functions, indicating that immunity was one of the biological functions altered by domestication under controlled artificial selection (Debes *et al.* 2012).

In contrast to these growth×reproduction, growth×stress and growth×immunity genetic interactions, the response to stress was not correlated with reproductive capacity in rainbow

trout (Pottinger and Carrick 2000). If a genetic interaction is not generalisable to all species and all breeding programmes (Thoa *et al.* 2017), then controlled artificial selection for body size during domestication may inadvertently affect physiological traits and in turn induce unexpected consequences. The modification of fish behaviour during domestication that could also interfere with these other biological functions is another potential bias. In particular, the selection of some lineages of fish based on their potential for growth and development can influence other life traits, especially behavioural traits (Pasquet 2019). More generally, attention must be paid to the collateral effects of controlled artificial selection.

The aim of selection programmes is genetic progress and the preservation of genetic diversity. These programmes, however, can have many consequences on genetic diversity (Dupont-Nivet *et al.* 2006). Some programmes with high levels of inbreeding and in turn the alteration of genetic diversity can strongly decrease zootechnical performance linked to reproduction (Langen *et al.* 2017), resistance to pathogens and stressors (Smallbone *et al.* 2016), or even growth (Su *et al.* 1996), as demonstrated in a range of species. The establishment of selection programmes based on the improvement of one biological trait (typically growth) must thus consider the impact on genetic diversity.

5-How to optimise studies of fish domestication

5-1-Intrinsic factors influencing phenotypic responses to domestication

Interpreting the effects of domestication is complex, because multiple intrinsic factors can influence fish phenotypes at the various steps of domestication and are naturally linked to the advancement of domestication. Species is the most obvious factor. This review found large interspecific differences in response to the trajectories and paths of domestication. FishBase

has identified more than 34 200 species of fish, representing a potential large reservoir for addressing questions of the effects of domestication. All of these species, however, are not potentially amenable to domestication, as suggested by a functional approach (Lecocq et al. 2019). A range of criteria should also be considered to identify the best candidates, such as their commercial interest, their cost of production relative to that generated from the captures by conventional fisheries, their flesh quality for human consumption, their capacity to be reared in captivity, and their advantages over species already farmed or domesticated. The number of relevant species for addressing the question of domestication effects is thus much more reduced. This may account for why broad comparisons of these effects between wild and domesticated fish are difficult to discern from the literature, because extensive bibliographical information is available for very few domesticated species, about 15 (Teletchea & Fontaine 2014). The conceptualisation of the consequences of fish domestication thus requires choosing the best fish models to avoid confusion from the many interspecific peculiarities and thus to straightforwardly demonstrate the main biological guidelines driven by domestication. The choice of models may depend on factors at the phylogenetic level by selecting species from different families. Species could also be selected using aquacultural considerations based on a posteriori failures or successes throughout the history of fish domestication. Species exhibiting contrasting phenotypes during domestication (e.g. tilapia with decreased growth vs salmonids with increased growth) may be targets of studies of comparative biology.

Age and weight are other intrinsic factors that may be considered. Indeed, domestication generally influences growth, so comparing wild (F0) and domesticated fish with both the same age and weight is difficult (Table 4). Some intrinsic factors such as sex, weight, age, nutrition, and state of maturity are also determinants of immunological, reproductive, or growth functions (Duffy *et al.* 2003; Milla *et al.* 2009). For example, morphological features

of a fish (e.g. growth and weight) influence its reproductive capacity (e.g. Marimuthu et al. 2009), so the modification of these factors in captive fish may bias the effects of domestication. Most studies do not accurately document the characteristics of these intrinsic factors, such as age, so evaluating their impact on the comparison of populations differentiated by their advancement during domestication is difficult. Only a few studies have determined if intrinsic factors interfere with the effects of domestication. A field experiment comparing brown trout from wild-born parents and from seventh-generation hatchery stock found that reproductive success was sex-dependent (Dannewitz *et al.* 2004).

The genetic background of populations is also relevant to the usual internal components potentially affecting the effects of domestication. A close relationship between reproductive failure and inbreeding has been identified in many captive fish. For example, genetic diversity was substantially reduced in one generation in a captive population of Senegalese sole that had problems spawning, demonstrating that the absence of genetic screening may lead to serious disturbances during domestication (Porta *et al.* 2006). Genetic diversity also often differs greatly between wild and domesticated populations (Ben Khadher *et al.* 2016). Together with the close relationships between heterozygosity and some biological traits linked to growth and reproduction (Lieutenant-Gosselin and Bernatchez 2006), we can assume that phenotypic differences between populations at different stages of domestication may remain unexplained due to the absence of clear information for the genetic features of the fish. The traceability of broodstock is notably not always managed properly in the early generations of uncontrolled artificial selection, because broodstocks are sometimes randomly chosen or are too small for adequate mating, and crosses amongst siblings may have negative consequences in future generations due to the effects of inbreeding. Scientific studies may even also suffer from a lack of genetic analysis that could rule out genetic alterations during domestication as the source of phenotypic differences.

In addition to the lack of genetic information, defects of broodstock traceability can mask important information about the advancement of domestication. Domestication of a species or population, but even at the individual level, proceeds to a continuum starting from the capture of wild fish to the long-term adaptation to the captive system (Figure 1). Identifying the exact advancement of the animal or population along this continuum is therefore necessary. In particular, acclimation, which here refers to the period of allostatic load of a fish population after capture, must not be confounded with adaptation, defined as changes over several generations, to ensure that genes are passed on to the next generation (Flynn *et al.* 2014). Indeed, the mechanisms behind these processes differ greatly and can unfortunately notably superimpose when wild fish under acclimation are compared to fish that have spent generations in captivity.

Not all farms/studies have kept rigorous records of the number of generations in captivity, even for adapted fish, so the exact advancement of the captive fish during domestication is unknown, demonstrating why most studies do not specify the number of generations and features of mating (Table 4). In addition to this lack of traceability, the level of domestication is not homogenous amongst experiments, which causes further confusion for delineating the effects of domestication, as demonstrated for reproductive function.

5-2-Extrinsic factors influencing phenotypic responses to domestication

Extrinsic factors should also be taken into account for understanding responses to domestication. Environmental factors such as temperature, photoperiod, salinity, and water quality influence all biological functions, including reproduction, growth, immunity, and response to stress. Population factors (e.g. density, genetic origin, and sex ratios) should also be considered in the success or failure of the paths of domestication, because they also

influence all aspects of fish biology. The consequences of domestication on the same population may thus vary under different environmental conditions during domestication, notably if they are not compatible with the biological requirements of the species.

Even if most studies ensure that fish from different stages of domestication have always been reared under the same environmental conditions after the initial stages of life, we cannot exclude distinct conditions before or during an experiment. If these differential environmental conditions differed before the experiment, they are not the effects of domestication but are the effects of some events of the past that can later affect biological traits. For example, the exposure of embryos to early stressful situations can lead to further alteration of juvenile physiology (Cadiz *et al.* 2018). A comparison of populations with different histories before an experiment led to specific responses to experimental treatments of reproductive control (Khendek *et al.* 2018) but also of growth and behaviour (Jonsson and Jonsson 2014). Attention in all cases should be paid to the description of these life paths in order to determine if the effects of domestication are due to adaptation to rearing conditions or to previous life events.

5-3-A multifactorial (and multitrait) approach for studying the effects of domestication

The effects of domestication are the sum or the combined effects of many factors affecting fish traits at various levels. Marked genomic changes have been observed during the first generations of domestication, as described earlier (Christie *et al.* 2016). Also, the genetic changes are amongst the largest that may occur and alter the phenotypes of domesticated fish. Changes of traits during domestication in some mammals have been suspected to be due to epigenetic changes transmissible from one generation to the next. These traits encompass changes of morphological, physiological, and behavioural characteristics such as reduced cranial capacity and tooth size, partial depigmentation, decreased flight distance towards

humans, advancement of sexual maturation, attenuation of the activity of the HPI axis, and alteration of neurotransmitter systems (Trut *et al.* 2009). All these phenotypic alterations may be driven by epigenetic modulation and/or genetic selection and would be due to mild deficits of neural-crest cells during embryonic development when migration defects are particularly important (Pörtl and Jung 2017). Interestingly, most of these major traits belonging to “domestication syndromes” in some mammals are those commonly altered during the domestication of fish (e.g. reduced brain length, precocious puberty, decrease in frightening behaviour, decrease in cortisolemia, modification of neurotransmitter level). Epimutations in developmental genes during early stages of domestication have also been identified in farmed European sea bass, some of which are associated with genes involved in developmental processes that are expressed in embryonic structures, including the neural crest (Anastasiadi and Piferrer 2019). Even if accepting some comparative parallels between piscine and mammalian models is still premature, we cannot dismiss the idea that epigenetic mechanisms could strongly affect phenotypes during fish domestication, as recently demonstrated in tilapia (Podgorniak *et al.* 2019). These first indications may account for why such contrasted procedures of domestication could lead to common physiological effects such as increased growth or reduction of stress or modulation of immunological gene expression. Concurrently studying the alteration of genomic, genetic, and epigenetic mechanisms during adaptation to captivity therefore seems logical for identifying the molecular processes behind this evolution and the causes of phenotypic changes. More generally, these intrinsic factors (gene expression and genetic and epigenetic features) interact with extrinsic factors linked to domestication (e.g. type of cages, temperature, and stressors) that increase the complexity of understanding the evolution of phenotypes by domestication (Li and Leatherland 2013; Gavery and Roberts 2017; Nguyen *et al.* 2017). Future research should thus focus on understanding the

interactions of the environment with the epigenome, genetic characteristics, and epigenetic marks that could affect phenotypic expression.

5-4-A proposed experimental strategy for studying the effects of domestication

We propose the following practical guidelines based on these theoretical considerations to explore the effects of domestication on fish phenotypes. First, we suggest sampling wild fish and then producing successive generations in captivity while rigorously recording fish traceability. We recommend monitoring the level of environmental and populational characteristics and maintaining them as stable as possible to avoid the effects of external disturbances. Fish with equivalent characteristics (e.g. age, sex, reproductive stage) and already acclimated to their environment should be sampled in each generation. Morpho-anatomical and physiological analyses linked to the potential “vertebrate domestication syndrome” should be carried out on all generations, starting from wild fish sampled in their natural environment. These analyses would allow us to describe the phenotypic changes due to domestication. Omics technology (e.g. RNA-Seq or proteomics) or qPCR should be used to identify the molecular mechanisms within targeted organs (e.g. brain, head kidney, gonads) affected during domestication. An epigenetic analysis may be performed in parallel to link the changes in phenotype and gene expression with potential multigenerational epigenetic inheritance. Finally, a genetic analysis should be performed to estimate the putative loss of genetic variability in the generations of domestication. All data (anatomy, physiology, genetics, epigenetics, gene expression) should be gathered and examined using multifactorial statistical analysis to draw conclusions about the causes of phenotypic changes from generation to generation. These experiments must then be repeated in several species after the application of various domestication processes (range of trajectories and paths of

domestication). These experiments should include farmed species but should also include fish biological models (e.g. zebrafish) that exhibit a range of assets (e.g. short biological cycle) and for which extensive molecular information is available. If a homogenous interspecific response is obtained, we could conclude that a domestication syndrome exists in fish, which could be a future guide for predicting the effects of domestication and evaluating the advancement of domestication for a given fish population.

Conclusion

Domestication is a strong regulator of biological functions in fish. A wide variety of biological processes can be affected in a wide range of fish species or families. In particular, domestication increases fish growth, attenuates stress responses, and regulates immunological genes. The influence on reproduction, however, is quite variable. Caution, however, should be exercised when considering the intrinsic and extrinsic factors associated with fish and all biological processes as potential sources of these changes when standardising investigations and more thoroughly describing the phenotypes of domesticated fish.

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1094 Table 1: Main domestication effects on growth reported in teleost fish species

Species	Comparison	Effect of domestication	Reference
Negative effects on growth:			
<i>Oreochromis niloticus</i>	F0 vs domesticated	Decrease of growth rate in ponds	(Brummett <i>et al.</i> 2004)
Positive effects on growth:			
<i>Salmo salar</i>	F1 vs F7	Increase in weight, length, and condition factor after selection for growth, fillet quality, and late maturation	(Glover <i>et al.</i> 2009)
<i>Salmo salar</i>	F1 vs F10	Increase in weight and length after selection for growth, fillet quality, and late maturation	(Solberg <i>et al.</i> 2013)
<i>Salmo salar</i>	F1 vs F5	Increase in weight and condition factor after selection for growth rate	(Thodesen <i>et al.</i> 1999)
<i>Salmo salar</i>	F1 vs F5	Increase in weight, plasma GH content, and pituitary GH content after selection for growth	(Fleming <i>et al.</i> 2002)
<i>Salmo trutta</i>	F0 vs F6	Increase in growth rate at low fish densities after selection for growth	(Hedenskog <i>et al.</i> 2002)
<i>Oncorhynchus mykiss</i>	F1 vs domesticated	Increase in growth and length after controlled selection for growth	(Tymchuk and Devlin 2005)
<i>Oncorhynchus mykiss</i> and <i>Oncorhynchus kisutch</i>	F1 vs domesticated	Increase in growth and length after controlled selection for growth	(Tymchuk <i>et al.</i> 2009)
<i>Dicentrarchus labrax</i>	F1 vs F2	No difference in growth	(Vandeputte <i>et al.</i> 2009)
<i>Perca fluviatilis</i>	F0 vs F6	Increase in weight, length and growth rate in larvae	(Palińska-Żarska <i>et al.</i> 2020)
<i>Perca fluviatilis</i>	F0 vs F4	Increase in weight and growth rate	(Douxflis, Mandiki, <i>et al.</i> 2011)
<i>Sander lucioperca</i>	F0 vs F0 (reared in RAS)	Increase in growth rate	(Khendek <i>et al.</i> 2018)
<i>Chrysophrys auratus</i>	F0 vs F1	Increase in weight, length and growth rate at high temperature	(Wellenreuther <i>et al.</i> 2019)

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1106 Table 2: Main domestication effects on reproductive features reported in teleost fish species

Species	Comparison	Effect of domestication	Reference
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Negative effects on reproductive capacity:			
<i>Oreochromis niloticus</i>	F0 vs domesticated	Lower rates of ovulation and survival	(Osure and Phelps 2006)
<i>Seriola dumerili</i>	Wild F0 vs captive F0	Lower levels of GSI and sex steroids (T, E2) for both sexes, high levels of oocyte atresia and failed ovulation, blockage of spermatogenesis	(Zupa <i>et al.</i> 2017)
<i>Salminus hilarii</i>	F0 vs domesticated	Disruption of final oocyte meiotic maturation, ovulation blockage, decreases in FSH and LH gene expression	(Moreira <i>et al.</i> 2015)
<i>Trachurus japonicus</i>	Wild F0 vs captive F0	Lower GnRH1, FSH and LH gene expression and E2 levels, lower rates of gonadogenesis and oogenesis, ovulation blockage	(Imanaga <i>et al.</i> 2014)
<i>Thunnus thynnus</i>	Wild F0 vs captive F0	Delay in germinal-cell proliferation, increased apoptosis in testis, reduction of spermatozoan mobility	(Zupa <i>et al.</i> 2013)
<i>Salminus hilarii</i>	F1 vs domesticated	Lower rate of fertilisation, modification of oocyte lipid content	(Araújo <i>et al.</i> 2012)
<i>Salminus hilarii</i>	Wild F0 vs captive F0	Disruption of final oocyte maturation, blockage of spontaneous ovulation	(Honji <i>et al.</i> 2013)
<i>Perca fluviatilis</i>	F0 vs domesticated	Lower rates of ovulation and hatching	(Křišťan <i>et al.</i> 2012)
<i>Perca fluviatilis</i>	F1 vs domesticated	Lower egg and larval quality (egg survival, hatching rate, malformation rates)	(Khendek <i>et al.</i> 2017)
<i>Sander lucioperca</i>	F0 vs domesticated	Lower levels of GSI and sex hormones in females, slower oogenesis	(Khendek <i>et al.</i> 2018)
<i>Gadus morhua</i>	F0 vs domesticated	Lower rates of fertilisation and hatching, decreased larval resistance to high salinity	(Lanes <i>et al.</i> 2012)
<i>Gadus morhua</i>	F0 vs domesticated	Lower rates of fertilisation, hatching, and embryo survival	(Salze <i>et al.</i> 2005)
<i>Dicentrarchus labrax</i>	F0 vs F3	Lower rates of fertilisation and hatching, modification of lipid content in ova	(Crespel <i>et al.</i> 2008)
<i>Tinca tinca</i>	F0 vs domesticated	Lower ovulation rate and sperm motility	(Kujawa <i>et al.</i> 2011)
<i>Leuciscus cephalus</i>	F0 vs F2	Lower ovulation rate, oocyte weight, and larval size at hatching	(Krejszeff <i>et al.</i> 2010)
<i>Leuciscus idus</i>	F0 vs F4	Lower embryo survival in response to Ovopel treatment	(Krejszeff <i>et al.</i> 2009)
<i>Leuciscus idus</i>	F0 vs F1 vs F3	Lower ovulation rate after CPH treatment, positive correlation between level of domestication and latency time after treatment	(Cieřla <i>et al.</i> 2014)
<i>Solea senegalensis</i>	F0 vs F1	Absence of spontaneous ovulation and no fertilisation if spontaneous ovulation	(Guzmán <i>et al.</i> 2009)
<i>Solea solea</i>	F0 vs F2	Lower rates of fertilisation, hatching, and survival	(Lund <i>et al.</i> 2008)
<i>Salmo salar</i>	F0 vs F5	Lower ovulation rate and embryo survival	(Fleming <i>et al.</i> 1996)
Positive effects on reproductive capacity:			
<i>Salmo trutta</i>	F0 vs F7	Increase in sperm quality but no effect on females (wild environment)	(Dannewitz <i>et al.</i> 2004)
<i>Leuciscus cephalus</i>	F0 vs F2	Increase in annual spawn number	(Krejszeff <i>et al.</i> 2010)
<i>Leuciscus idus</i>	F0 vs F4	Increase in ovulation rate in response to Ovopel treatment	(Krejszeff <i>et al.</i> 2009)
<i>Barbus barbus</i>	F0 vs domesticated	Increase in rates of ovulation and embryo survival in response to Ovaprim treatment	(Targońska <i>et al.</i> 2011)
<i>Perca fluviatilis</i>	F0 vs domesticated	Increase in fertilisation rate, improvement of female survival rates after ovulation	(Křišťan <i>et al.</i> 2012)
<i>Perca fluviatilis</i>	F1 vs domesticated	Increase in levels of expression of GSI, GnRH, and gonadotropin genes during oogenesis	(Khendek <i>et al.</i> 2017)

1111 Table 3: Main domestication effects on stress reported in teleost fish species

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Species	Comparison	Effect of domestication	Reference
Positive effects on the stress response:			
<i>Plecoglossus altivelis</i>	F0 vs F4 vs F39	Lower serum cortisol concentrations in fish exposed for 3 h to water with 200 mg/l kaolin	(Awata <i>et al.</i> 2011)
<i>Perca fluviatilis</i>	F1 vs F4	Lower plasma cortisol in fish exposed to confinement and 15 min in anaesthetic bath	(Douxfls, Mandiki, <i>et al.</i> 2011)
<i>Perca fluviatilis</i>	F1 vs F5	Lower splenosomatic index in fish exposed to repeated hypoxia	(Douxfls <i>et al.</i> 2012)
<i>Oncorhynchus mykiss</i>	F0 vs domesticated	Lower levels of plasma glucose, brain DOPAC/DA, and brain 5-HIAA/5-HT	(Lepage <i>et al.</i> 2000)
<i>Melanoteania duboulayi</i>	F0 vs F15	Lower increase in cortisol content in fish confined in beaker for 30 min	(Zuberi <i>et al.</i> 2014)
<i>Oncorhynchus tshawytscha</i>	F0 vs F1	Lower increase in cortisol and haematocrit in fish exposed to density stressor	(Mazur and Iwama 1993)
<i>Betta splendens</i>	F0 vs domesticated	No elevation in release of water-borne cortisol in fish exposed to unfamiliar environment and spatial confinement	(Verbeek <i>et al.</i> 2008)
<i>Oncorhynchus mykiss</i>	F0 vs domesticated	Lower increase in plasma cortisol and glucose and lower decrease in plasma chloride in fish exposed to confinement in a net and to electroshock	(Woodward and Strange 2004)

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1126 Table 4: Some features of reproductive comparisons between wild and captive fish

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Species	Sex	Age	Weight	Comparison	Conditions of culture	Feeding	Reference
<i>Seriola dumerili</i>	Males and females	-	13-15 kg	Wild F0 vs captive F0	Sea cage	Prey fish and commercial diets	(Zupa <i>et al.</i> 2017)
<i>Salminus hilarii</i>	Females	-	843 (wild) vs 534 g (captive)	Wild F0 vs captive (ponds)	River (F0) vs pond	Commercial diet (captive fish)	(Moreira <i>et al.</i> 2015)
<i>Trachurus japonicus</i>	Males and females	-	307 (wild) vs 250 (captive)	Wild F0 vs captive F0	River (F0) vs cage (captive)	-	(Imanaga <i>et al.</i> 2014)
<i>Thunnus thynnus</i>	Males	-	? (wild) vs 40-70 kg (captive)	Wild F0 vs captive F0	Sea (F0) vs cage (captive)	-	(Zupa <i>et al.</i> 2013)
<i>Leuciscus idus</i>	Males and females	5-8 years	639-780 g	Wild F0 vs F1 vs F3	Wild vs semi-pond culture	-	(Cieřla <i>et al.</i> 2014)
<i>Salminus hilarii</i>	Females	-	570 g	Wild F0 vs captive F0	Ponds	Commercial diet	(Honji <i>et al.</i> 2013)
<i>Perca fluviatilis</i>	Females	3 years	146g (captive) vs 75 g (wild)	F0 vs domesticated	Pond-reared (F0) vs RAS (captive)	Commercial diet and forage fish (captive) vs forage fish (wild)	(Kriřtan <i>et al.</i> 2012)
<i>Salminus hilarii</i>	Females	3 years (dom.)	-	F1 vs domesticated	RAS	Commercial diet	(Araújo <i>et al.</i> 2012)
<i>Gadus morhua</i>	Males and Females	3 years (dom.)	2,7-2,9 kg	F0 vs domesticated	RAS	Unfed	(Lanes <i>et al.</i> 2012)
<i>Tinca tinca</i>	Males and Females	-	0.3-1.4 kg	F0 vs domesticated	Lake (F0) vs pond (captive)	Unfed	(Kujawa <i>et al.</i> 2011)

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1138 **Figure legend**

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1140 Fig. 1. Schematic representation of the main steps of the fish domestication processes that can
1141 alter the fish phenotypes. The dotted line in step 5 indicates that this step can start either
1142 synchronously or after step 4.

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