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1 **How domestication alters fish phenotypes**

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13 **Running title:** Domestication affects fish phenotypes

14

15

16 **Abstract:**

17 Domestication can be defined as the adaptation of an animal to the human environment and

18 its constraints. Accumulating evidence strongly indicates that domestication plays essential

19 roles in modulating the phenotypes of teleosts, despite the scattered information. Animal

20 husbandry and molecular, physiological, and behavioural studies have identified a high

21 degree and complexity of biological changes induced by domestication. These phenotypic

22 modifications during domestication vary greatly amongst species and physiological function

23 (e.g. growth, reproduction, response to stress, and immunity), probably due to a variety of

24 intrinsic and extrinsic factors that can interfere with phenotypic changes. Indeed, much

25 information about domestication is lacking, which impedes the generalisation of our

26 understanding of the effects of domestication. This review gathers and clarifies the available

27 information about the main effects of fish domestication. We use a broad physiological

28 approach for understanding these biological consequences, from the genesis of domestication

29 (e.g. netting from the wild) to the ultimate step (controlled artificial selection). We also

30 suggest ways to predict the effects of domestication and to better understand the sources of

31 the biological changes.

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

33 **Introduction**

34

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

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

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

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

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

101

102 **1-Capture, transport (step 1), and acclimation (step 2)**

103

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

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

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

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

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

145

146 **2-First reproduction in captivity (step 3)**

147

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

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

175

176 **3-Adaptation and phenotypic changes (step 4)**

177

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

182

183 ***3-1-Growth, nutrition and flesh quality***

184

185 Controlled artificial selection for growth has greatly accelerated weight gains in fish,
186 especially salmonid fishes. Higher growth rates accompanied by higher conditions factors,
187 however, have also been observed in domesticated salmonids where artificial selection has
188 been poorly controlled (Table 1; Glover et al. 2009; Hedenskog, Petersson, and Järvi 2002;
189 Solberg et al. 2013; Tymchuk, Beckman, and Devlin 2009; Tymchuk and Devlin 2005).
190 Domestication without controlled artificial selection, though, is not necessarily linked to
191 increased growth (Brummett *et al.* 2004; Vandeputte *et al.* 2009). The physiological
192 mechanisms underlying this divergence between wild and domesticated fish, intentionally or
193 unintentionally selected, are poorly known. Differential levels of GH (Growth Hormone) or
194 IGF-1 (Insulin Growth Factor-1) may be physiological indicators of this salmonid response
195 (Fleming *et al.* 2002; Tymchuk *et al.* 2009). Contrasting nutritional behaviour may also
196 account for this response. Foraging activity is also modified during domestication, even
197 though it has only been demonstrated in a small range of fish species (Huntingford *et al.*
198 2012). Some species that have been more intensely domesticated, under controlled artificial
199 selection for growth or not, stay near the water surface rather near the bottom of the water
200 column (Reinhardt *et al.* 2001; Robison and Rowland 2005), which in turn improves their
201 feeding efficiency (Thodesen *et al.* 1999; Sánchez *et al.* 2012). Changes in social behaviour,
202 e.g. shoaling, would be an additional behavioural cause of the higher growth in domesticated
203 fish (Wright et al. 2006; Pasquet et al. 2019), potentially due to a higher homogeneity of age
204 and size in domesticated fish (Ruzzante and Doyle 1991, 1993). This change in the structure
205 of the social group may induce modifications of aggressiveness and hierarchy between

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

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

223

224 ***3-2-Reproductive function***

225

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

231 developmental period during which an individual first becomes capable of reproducing
232 sexually. Precocious puberty is a major problem in a wide range of farmed fishes, because
233 puberty adversely affects growth. For example, male sea bass under natural conditions in the
234 Mediterranean Sea reach sexual maturity at the age of two years. Early puberty under
235 intensive culturing conditions, however, affects 20–30% of one-year-old males in the
236 population (Felip *et al.* 2008). The increased growth in domesticated fish is probably one of
237 the major causes of early puberty in farmed species (Taranger *et al.* 2010). The quality and
238 timing of the stages of gametogenesis are very important for further spawning, fertilisation,
239 and embryonic development. Many reproductive traits in captivity are affected by natural
240 selection and/or uncontrolled artificial selection during domestication. Reproductive tactics
241 such as spawning frequency may be modified (Krejszeff *et al.* 2010), accompanied by
242 changes to the reproductive capacity of the progenitors, with modifications of their
243 physiological status (Dannewitz *et al.*, 2004; Krejszeff *et al.*, 2009).

244 These effects of domestication on fish reproduction, though, are quite controversial, which
245 questions the zootechnical assets to go deeper in the domestication by keeping the
246 domesticated broodstock to obtain the next offspring generations, rather than renewing the
247 broodstock at each generation by catching wild fish. Studies have reported a higher
248 reproductive capacity in domesticated than wild fish, e.g. cyprinid fishes whose ovulatory
249 response to hormonal treatments is higher in cultured fish (Krejszeff *et al.* 2009, 2010).

250 Reproductive capacity (spawning success and fecundity) in Nile tilapia (*Oreochromis*
251 *niloticus*) was higher in the most domesticated fish strain than in a strain collected from the
252 wild (Osure and Phelps 2006). Other recent studies did not find clear differences in the
253 reproductive features between wild and domesticated fish. Gonadogenesis in the Eurasian
254 perch and pikeperch (*Sander lucioperca*), was more precocious in populations that were more
255 domesticated (Khendek *et al.* 2017, 2018; De Almeida *et al.* 2019), but reproductive

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

269

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

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

293 ***3-3-Immunity and resistance to pathogens***

294

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

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

328

329 ***3-4-Response to stress***

330

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

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

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

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

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

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

415

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417

418

419 **4-Effect of the controlled artificial selection (step 5)**

420

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

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

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

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

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

458 Controlled artificial selection is usually driven by a single biological function (growth,
459 reproduction, or immunity), but the selection of strains with a higher growth potential may
460 indirectly contribute to altering the reproductive capacity of the broodstock. For example,
461 genetic correlations between growth and reproductive features in salmonids are associated
462 with these biological functions (O'Malley *et al.* 2003; Tentelier *et al.* 2016). The controlled
463 artificial selection for growth can decrease the proportion of mature male parrs (Harvey *et al.*
464 2018), and genetic interaction has been reported between body weight and early maturation of
465 female in Nile tilapia, suggesting that selection for larger body weight may lead to early
466 puberty in females (Longalong and Eknath 1995).

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

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

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

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

489 The aim of selection programmes is genetic progress and the preservation of genetic
490 diversity. These programmes, however, can have many consequences on genetic diversity
491 (Dupont-Nivet *et al.* 2006). Some programmes with high levels of inbreeding and in turn the
492 alteration of genetic diversity can strongly decrease zootechnical performance linked to
493 reproduction (Langen *et al.* 2017), resistance to pathogens and stressors (Smallbone *et al.*
494 2016), or even growth (Su *et al.* 1996), as demonstrated in a range of species. The
495 establishment of selection programmes based on the improvement of one biological trait
496 (typically growth) must thus consider the impact on genetic diversity.

497

498 **5-How to optimise studies of fish domestication**

499

500 ***5-1-Intrinsic factors influencing phenotypic responses to domestication***

501

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

506 has identified more than 34 200 species of fish, representing a potential large reservoir for
507 addressing questions of the effects of domestication. All of these species, however, are not
508 potentially amenable to domestication, as suggested by a functional approach (Lecocq et al.
509 2019). A range of criteria should also be considered to identify the best candidates, such as
510 their commercial interest, their cost of production relative to that generated from the captures
511 by conventional fisheries, their flesh quality for human consumption, their capacity to be
512 reared in captivity, and their advantages over species already farmed or domesticated. The
513 number of relevant species for addressing the question of domestication effects is thus much
514 more reduced. This may account for why broad comparisons of these effects between wild
515 and domesticated fish are difficult to discern from the literature, because extensive
516 bibliographical information is available for very few domesticated species, about 15
517 (Teletchea & Fontaine 2014). The conceptualisation of the consequences of fish
518 domestication thus requires choosing the best fish models to avoid confusion from the many
519 interspecific peculiarities and thus to straightforwardly demonstrate the main biological
520 guidelines driven by domestication. The choice of models may depend on factors at the
521 phylogenetic level by selecting species from different families. Species could also be selected
522 using aquacultural considerations based on a posteriori failures or successes throughout the
523 history of fish domestication. Species exhibiting contrasting phenotypes during domestication
524 (e.g. tilapia with decreased growth vs salmonids with increased growth) may be targets of
525 studies of comparative biology.

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

531 of a fish (e.g. growth and weight) influence its reproductive capacity (e.g. Marimuthu et al.
532 2009), so the modification of these factors in captive fish may bias the effects of
533 domestication. Most studies do not accurately document the characteristics of these intrinsic
534 factors, such as age, so evaluating their impact on the comparison of populations
535 differentiated by their advancement during domestication is difficult. Only a few studies have
536 determined if intrinsic factors interfere with the effects of domestication. A field experiment
537 comparing brown trout from wild-born parents and from seventh-generation hatchery stock
538 found that reproductive success was sex-dependent (Dannewitz *et al.* 2004).

539 The genetic background of populations is also relevant to the usual internal components
540 potentially affecting the effects of domestication. A close relationship between reproductive
541 failure and inbreeding has been identified in many captive fish. For example, genetic diversity
542 was substantially reduced in one generation in a captive population of Senegalese sole that
543 had problems spawning, demonstrating that the absence of genetic screening may lead to
544 serious disturbances during domestication (Porta *et al.* 2006). Genetic diversity also often
545 differs greatly between wild and domesticated populations (Ben Khadher *et al.* 2016).

546 Together with the close relationships between heterozygosity and some biological traits linked
547 to growth and reproduction (Lieutenant-Gosselin and Bernatchez 2006), we can assume that
548 phenotypic differences between populations at different stages of domestication may remain
549 unexplained due to the absence of clear information for the genetic features of the fish. The
550 traceability of broodstock is notably not always managed properly in the early generations of
551 uncontrolled artificial selection, because broodstocks are sometimes randomly chosen or are
552 too small for adequate mating, and crosses amongst siblings may have negative consequences
553 in future generations due to the effects of inbreeding. Scientific studies may even also suffer
554 from a lack of genetic analysis that could rule out genetic alterations during domestication as
555 the source of phenotypic differences.

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

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

573

574 ***5-2-Extrinsic factors influencing phenotypic responses to domestication***

575

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

581 influence all aspects of fish biology. The consequences of domestication on the same
582 population may thus vary under different environmental conditions during domestication,
583 notably if they are not compatible with the biological requirements of the species.
584 Even if most studies ensure that fish from different stages of domestication have always been
585 reared under the same environmental conditions after the initial stages of life, we cannot
586 exclude distinct conditions before or during an experiment. If these differential environmental
587 conditions differed before the experiment, they are not the effects of domestication but are the
588 effects of some events of the past that can later affect biological traits. For example, the
589 exposure of embryos to early stressful situations can lead to further alteration of juvenile
590 physiology (Cadiz *et al.* 2018). A comparison of populations with different histories before an
591 experiment led to specific responses to experimental treatments of reproductive control
592 (Khendek *et al.* 2018) but also of growth and behaviour (Jonsson and Jonsson 2014).
593 Attention in all cases should be paid to the description of these life paths in order to determine
594 if the effects of domestication are due to adaptation to rearing conditions or to previous life
595 events.

596 ***5-3-A multifactorial (and multitrait) approach for studying the effects of domestication***

597

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

606 humans, advancement of sexual maturation, attenuation of the activity of the HPI axis, and
607 alteration of neurotransmitter systems (Trut *et al.* 2009). All these phenotypic alterations may
608 be driven by epigenetic modulation and/or genetic selection and would be due to mild deficits
609 of neural-crest cells during embryonic development when migration defects are particularly
610 important (Pörtl and Jung 2017). Interestingly, most of these major traits belonging to
611 “domestication syndromes” in some mammals are those commonly altered during the
612 domestication of fish (e.g. reduced brain length, precocious puberty, decrease in frightening
613 behaviour, decrease in cortisolemia, modification of neurotransmitter level). Epimutations in
614 developmental genes during early stages of domestication have also been identified in farmed
615 European sea bass, some of which are associated with genes involved in developmental
616 processes that are expressed in embryonic structures, including the neural crest (Anastasiadi
617 and Piferrer 2019). Even if accepting some comparative parallels between piscine and
618 mammalian models is still premature, we cannot dismiss the idea that epigenetic mechanisms
619 could strongly affect phenotypes during fish domestication, as recently demonstrated in tilapia
620 (Podgorniak *et al.* 2019). These first indications may account for why such contrasted
621 procedures of domestication could lead to common physiological effects such as increased
622 growth or reduction of stress or modulation of immunological gene expression. Concurrently
623 studying the alteration of genomic, genetic, and epigenetic mechanisms during adaptation to
624 captivity therefore seems logical for identifying the molecular processes behind this evolution
625 and the causes of phenotypic changes. More generally, these intrinsic factors (gene expression
626 and genetic and epigenetic features) interact with extrinsic factors linked to domestication
627 (e.g. type of cages, temperature, and stressors) that increase the complexity of understanding
628 the evolution of phenotypes by domestication (Li and Leatherland 2013; Gavery and Roberts
629 2017; Nguyen *et al.* 2017). Future research should thus focus on understanding the

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

632

633 *5-4-A proposed experimental strategy for studying the effects of domestication*

634

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

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

661

662 **Conclusion**

663

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

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1093

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	(Doux fils, 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	(Cieśla <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	(Douxflis, Mandiki, <i>et al.</i> 2011)
<i>Perca fluviatilis</i>	F1 vs F5	Lower splenosomatic index in fish exposed to repeated hypoxia	(Douxflis <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	-	(Cieśla <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)	(Krišťan <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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