Fish domestication in aquaculture: reassessment and emerging questions

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Aquaculture, domestication, teleost fishes, diversification, sustainable development.

Abstract

Historically, aquatic products were derived from wild capture fishes. However, declining marine catches since the early 1990s, combined with an increasing demand for fish products, has created a strong impe-tus for aquaculture. By 2014, half of global seafood consumption originated from aquaculture. The rise of aquaculture production has relied mostly on the domestication of a growing number of teleost fishes. In total, 250 species belonging to 71 families have been farmed since 1950. Among the 250 species, 183 were still produced in 2009. This implies that 67 species had been farmed only for a short time (most often less than five years). Nearly 70% (n = 175) of the species farmed in 2009 were classified in the first three levels of domestication; the other 75 species reached levels 4 and 5, and might be considered as domesticated. The 35 species classified at level 5 belong to ten families, including Cyprinidae (n = 10), Salmonidae (n = 8), and Acipenseridae (n = 5). More than 90% of global production was based on only 20 species in 2009. This shows that aquaculture production is heavily skewed toward the farming of a few (often alien) species. Conversely, these data suggest that most domestication experiments have failed to reach significant volumes. However, a growing interest in promoting native species in aquaculture, particularly in South America, has resulted in significant changes. The strong development of alien and native aquaculture around the world, along with various supplementary hatchery stocking programmes, has resulted in billions of captive fish belonging to over 300 species being either accidentally or deliberately released into the wild each year. Yet, captive fish differ from their wild counterparts, and may develop phenotypes that are maladaptive in nature. Therefore, the release of hatchery-reared fish should be considered after other measures (e.g. limiting harvests, and habitat restoration or modification) have failed, and all efforts should be made to prevent farmed fish from escaping into the wild.

Introduction

Modern humans emerged about 200,000 years ago as hunters and gatherers (e.g. Vigne, 2011, 2015). The domestication of terrestrial plants and animals, ca. 12,000 years ago, were part of a major change in the way of life of an increasing number of human societies throughout the world a phenomenon known as Neolithisation (e.g. Childe, 1936; Vigne, 2011). Domestication allowed for a slow but drastic techno-economic shift from hunting and gathering to food production (e.g. Vigne, 2011). The vast majority of humans now depends on the tiny fraction of wild species that were domesticated (0.08% of known terrestrial plant species and 0.0002% of known terrestrial animal species) and progressively introduced to all populated continents (Diamond, 2002; Duarte et al., 2007). Croplands and pastures have now become the largest terrestrial biomes on the planet, occupying about 40% of the land surface; modern agriculture is acknowledged as the primary destructive force of terrestrial biodiversity (Foley et al., 2005; Teletchea, 2017).

The history of fish production is markedly different from that of terrestrial farming (Teletchea, 2015b). Historically, the majority of seafood products came from the capture of hundreds of wild animal species (fish and shellfish) in the oceans. Reported global marine capture fisheries increased from 1.5-2 million tons (mt) in 1850 to nearly 17 mt in 1950 (Garcia and Grainger, 2005). In the following decades, global captures continued to rise, reaching 80 mt in the mid-1980s (Fig. 1). However, this worldwide growth actually hid the collapse of numerous fish stocks (Froese et al., 2012), including the famous example of the Northern stocks of Atlantic cod Gadus morhua l., 1758 (Hutchings and Reynolds, 2004; Schrank and Roy, 2013) in the North-West Atlantic Ocean (Fig. 2A). These numerous collapses were masked, at least in volume, by the capture of new species (i) usually at lower trophic levels (Pauly et al., 1998), such as blue whiting Micromesistius poutassou (Risso, 1827) (Fig. 2B), (ii) at deeper waters (Morato et al., 2006), such as orange roughy Hoplostethus atlanticus Collett, 1889 (Fig. 2C), and (iii) farther offshore, especially in the South (Swartz et al., 2010), such as skipjack tuna Katsuwonus pela-mis (l., 1758) (Fig. 2D). However, global captures have been in decline since the end of the 1980s, as we have reached not only the upper limit of an increasing number of stocks (Froese et al., 2012), but also of the entire ocean (Pauly and Zeller, 2016). Consequently, global fisheries are generally considered to be in crisis (Pauly, 2009) and are unlikely to supply more seafood products than current rates of harvest, especially if management regimes remain the same (Costello et al., 2016). In addition, global fishing capacity should be reduced (Bell et al., 2017) to ensure a sustainable harvest, and to maintain biodiversity and ecosystem functions (Pauly et al., 2002).

The decrease of global marine fishery catches since the mid-1990s, combined with an increasing demand for fish products, both in developed and developing countries, has created a strong impetus for aquaculture, i.e. the farming of animals (and plants, not considered here) (Teletchea et al., 2016a). A result of this demand is that half of the global fish products that are destined for human consumption are farmed (FAO, 2016; Teletchea, 2016a). This also implies that fish species are today produced using a large diversity of methods that cannot be simply ascribed to wild capture or aquaculture (Klinger et al., 2013). Teletchea and Fontaine (2014) proposed a six-level classification system (Tab. I). This system uses the level of human control over the life cycle of species in captivity and independence from wild inputs to place a fishery on a continuum between wild capture (level 0) and aquacultural production based on genetically-modified individuals (level 5) (Teletchea, 2012, 2015b, 2016c; Teletchea and Fontaine, 2014).

The first goal of the present article is to build on the work of Teletchea and Fontaine (2014) to assess precisely which species have been farmed and domesticated since 1950. The second goal is to describe the extent to which fish domestication has followed the same path as the domestication of terrestrial species. Finally, because the relatively recent development of global aquaculture means that most aquaculture species are biologically similar to their wild ancestors, the third goal is to summarize the ways in which these species can interact with their wild counterparts.

Material and Methods.

1.1. Fish domestication: an overview since 1950

The rise of aquaculture production, particularly since the 1980s (Fig. 3), has relied mostly on the domestication of a growing number of teleost fishes (Fig. 4). This is true for the three main groups of fishes recognized by the FAO, i.e. a rise from 25 in 1950 to 106 in 2009 for freshwater species, from 6 to 24 for diadromous species, and from 2 to 53 for marine species (Fig. 4). In total, 250 species belonging to 71 families have been farmed in the past decades (Tab. II). Only four families (Cyprinidae, Sparidae, Cichlidae, and Salmonidae) displayed more than 10 farmed fish species since 1950, while nearly half (n = 30) had only one species. Among the 250 species listed in the FAO since 1950, 183 were still produced in 2009 (Tab. II). This implies that 67 species had been farmed for only a short time, most often less than five years (Teletchea and Fontaine, 2014). In other words, at least one-quarter of the domestication attempts of new fish species have failed, probably due to over-optimistic speculations about market demand, inadequate information about economic feasibility, and insufficient biological and technical knowledge (Jobling, 2010).

Nearly 70% (n = 175) of the species farmed in 2009 were classified in the first three levels of domestication (Tab. II), implying that their production still relied on wild inputs (Teletchea and Fontaine, 2014; Li and Ponzoni, 2015). Conversely, 75 species reached levels 4 and 5 (Tab. II), and might be considered as domesticated (Balon, 2004; Bilio, 2008; Vandeputte, 2009; Teletchea and Fontaine, 2014), with the use of selective improvement programs focusing mainly on growth performance, disease resistance, and meat quality traits, for some of them (Chavanne et al., 2016; Gjedrem and Rye, 2016; Nguyen, 2016; Janssen et al., 2017). The 35 species classified at level 5 belong to ten families: Cyprinidae (n = 10), Salmonidae (n = 8), Acipenseridae (n = 5), and seven others with a single species each (Tab. II).

Controlling the entire life cycle of a fish species in captivity (i.e. reaching at least level 4) is neither necessary nor sufficient to produce large quantities of meat (Ottolenghi et al., 2004). For instance, the Japanese amberjack Seriola quin-queradiata Temminck & Schlegel, 1845 totaled 155,247 tons despite being classified at level 2 (Fig. 5A). Conversely, the five sturgeon species ranked at level 5 had all a production lower than 250 tons (Teletchea and Fontaine, 2013, 2014). Nevertheless, the top 15 farmed species in 2009 (production higher than 450,000 tons) all reached levels 4 (n = 5) or 5 (n = 10), including species for which the onset of domestication is either centuries-old, such as common carp Cyprinus carpio l., 1758 (Fig. 5B) or Nile tilapia Oreochromis niloticus (l., 1758) (Fig. 5C), or a few decades-old, such as Atlantic salmon Salmo salar l., 1758 (Fig. 5D). Despite its recent domestication, Atlantic salmon was the first fish species to be subject to a systematic, family-based selective breeding program (Gjedrem, 2010), and today more than 12 generations have been consecutively bred in captivity for the oldest programs (Glover et al., 2017). In addition, it is the only species for which nearly 100% of global production is based on selectively bred stocks (Gjedrem, 2010). Inversely, it is estimated that about 10% of worldwide aquaculture production comes from domesticated and selectively bred farm stocks (Olesen et al., 2015; Gjedrem and Rye, 2016).

1.2. True species diversification of the aquaculture production?

Even though the domestication of probably hundreds of fish species have been attempted throughout the world since 1950, more than 90% of the global production was based on only 20 of them in 2009 (Fig. 6). This highlights that aquaculture production is heavily skewed toward the farming of a few species (Lazard and Levêque, 2009; Nguyen, 2016; Gjedrem and Rye, 2016), and that most domestication experiments have failed to reach significant volumes: 70 species had a production lower than 1000 tons in 2009. The 20 most-produced species worldwide belong to nine families, among which are Cyprinidae (n = 10), Cichlidae (n = 2), and Salmonidae (n = 2) (Tab. II). Among these 20 species, 16 live in freshwaters and four are diadromous. The top five species (production higher than 2.5 mt) are four cyprinids, grass carp Ctenopharyngodon idella (Valenciennes, 1844), silver carp Hypophthalmichthys molitrix (Valenciennes, 1844), common carp and bighead carp H. nobilis (Richardson, 1845), and one cichlid, Nile tilapia (Teletchea and Fontaine, 2014). For marine aquaculture only, the top ten farmed species totalled 86.5% of the global production identified at the species level (1,241,149 tons) in 2013 (Teletchea, 2015a). The production of the top three species, gilthead seabream Sparus aurata L., 1758, European sea bass Dicentrarchus labrax (L., 1758) and Japanese amberjack Seri-ola quinqueradiata reached 150,000 tons and represented together nearly 40% of this production (Teletchea, 2015a).

The main species for aquaculture production have been extensively introduced around the world, particularly in the past century (Casal, 2006; Shelton and Roth-bard, 2006; De Silva et al., 2009; Lazard and Levêque, 2009; Teletchea and Beisel, 2018). Five species have been introduced in more than 80 countries: common carp (n = 121 countries), grass carp (n = 92), rainbow trout Oncorhynchus mykiss (Walbaum, 1792) (n = 90), Mozambique tilapia Oreochromis mossambicus (Peters, 1852) (n = 90) and Nile tilapia (n = 85) (Casal, 2006). The bulk of aquaculture production relied on the farming of these few alien species in numerous countries; e.g. Indonesia (72% of total production is based on introduced species), or Philippines (77%) (Casal, 2006). In Europe, alien species (mostly rainbow trout, silver carp and common carp) accounted for two-thirds of inland production, reaching much higher proportions in Western regions: France (88%), Italy (93%), Denmark (93%), the British Isles (98%), and the Iberian Peninsula (99%) (Turchini and De Silva, 2008). In numerous areas, introduced species established self-sustaining, feral populations in the wild, which are nearly impossible to eradicate (Teletchea and Beisel, 2018). The possible direct and indirect adverse ecological and genetic impacts of alien species are considerable, and include, among others, hybridization, predation, competition, the extirpation of native species, the introduction of new pathogens and para-sites, habitat destruction, and food-web alteration (De Silva et al., 2009; Teletchea and Beisel, 2018). The introduction of alien species constitutes one of the major threats to global biodiversity (Teletchea and Beisel, 2018). Therefore, reducing the dependence on alien species, and thereby minimizing potential negative impacts on biodiversity, is increasingly perceived as an imperative for the development of sustainable aquaculture (De Silva et al., 2009).

In this context, there is a constant search for new native fish species to be farmed, while taking into account both the local environmental and socioeconomic conditions, and the link between the rearing system and species characteristics (Teletchea et al., 2009; Alvarez-Lajonchère and Ibarra-Castro, 2013). For instance, Alvarez-Lajonchère and Ibarra-Castro (2013) used a five-phase method to identify a handful of native, tropical marine fish species with the highest potential for aquaculture in tanks, ponds or cages. An example is Florida pompano Trachinotus carolinus (L., 1766), which is among the 2,175 fish species naturally occurring in the Western Caribbean Atlantic. In recent years, the resolve to promote native species in aquaculture has resulted in significant changes in various countries, particularly in South America (Ulrich, 2017; Valladao et al., 2018). Brazil, the second largest aquaculture producer in Latin America, went from having no native species farmed two decades ago to native species contributing nearly 40% of total aquaculture production (e.g. 540,442 tons in 2014) (Ulrich, 2017). This shift to an increasing share of native species is mainly due to the production of cachama Colossoma macropomum (Cuvier, 1816), which reached 186,029 tons in 2014 (Ulrich, 2017). Other native species, such as arapaima Arapaima gigas (Schinz, 1822), are also considered to have a high production potential (Ulrich, 2017).

In conclusion, the number of farmed species has strongly increased in the past decades, and will probably continue to do so in the coming decades; the contribution of native species to global aquaculture will perhaps improve, resulting in a more diversified and even production than today. Yet, demand will probably ensure that global production remains heavily skewed toward common aquaculture species. Common and novel species may still be introduced to promote aquaculture development as a means of food security, especially where native species suitable for aquaculture are rare, such as in small islands (De Silva et al., 2009).

1.3. Increasing interactions between wild and captive fish

Billions of captive fish belonging to over 300 species are either intentionally or unintentionally released into the wild each year (Grant et al., 2017). The deliberate release of hatchery-reared fish into natural habitats was one of the most common management practices on a large scale for more than 150 years. Such releases are a way to enhance, conserve or restore fisheries in both inland and coastal marine waters (Grant et al., 2017; Teletchea, 2017; Kitada, 2018). For marine fish only, a total of 187 species was released by 20 countries between 2011 and 2016 (Kitada, 2018). Accidental releases correspond to escapees from aquaculture facilities (Wringe et al., 2016). In Norway, where more than half of all farmed Atlantic salmon are produced globally, it is estimated that tens of millions of farmed salmon have escaped into the wild since the 1970s (Glover et al., 2017). In either case, the result is that an enormous number of captive fish are found in nature and subsequently in contact with wild fishes (Wringe et al., 2016). One of the main consequences of this contact is the potential for hybridization between hatchery-reared fish and their wild congeners, which can, in turn, leads to the introgression of hatchery genes (Kitada, 2018). For instance, half of the ~150 native Norwegian populations of Atlantic salmon that were tested showed evidence of introgression (0% to 47%) by farmed salmon escapees (Glover et al., 2017).

Recent analyses have demonstrated that exposure to captive conditions rapidity modify fish (Wringe et al., 2016). When comparing gene expression in the offspring of wild and first-generation hatchery rainbow trout reared in a common environment, Christie et al. (2016) found that more than 700 genes were differentially expressed between the two groups of offspring. These findings demonstrate that a single generation of domestication can translate into heritable differences in expression at hundreds of genes, mostly involved in wound healing, immunity and metabolism, which are probably due to adaptation to crowded conditions (Christie et al., 2016). Also, it is often noted that captive conditions (generally characterized by low habitat complexity, stable and abundant feed, consistent water velocity, and high density) result in the development of a similar, readily identifiable "cultured phenotype" that is characterized by shorter heads, upper jaws, and fins than those typical of their wild conspecifics (Wringe et al., 2016). In addition, species farmed for human consumption and in breeding programs (level 5) will progressively be strongly modified from their wild congeners because the goal is to promote "commodity traits", i.e. traits that culturists find desirable (Lorenzen et al., 2012; Teletchea, 2016b). Consequently, captive fish differ from their wild counterparts, and may develop phenotypes that are maladaptive in nature (Wringe et al., 2016). For instance, field experiments have demonstrated that the offsprings of farmed Atlantic salmon display lower lifetime fitness in natural conditions than wild salmon (Glover et al., 2017).

In conclusion, interactions between captive and wild conspecifics have tremendously increased in the past decades due to both deliberate and accidental releases. Yet, supplementation efforts may not always be necessary nor sufficient to enhance wild populations (Grant et al., 2017; Teletchea, 2017). The release of hatchery-reared fish should be considered as a last resort because of the high cost of implementation and the substantial ecological and genetic risks to wild populations (Grant et al., 2017). Instead, two other strategies should be considered first to rebuild depleted stocks: limiting harvests, and habitat restoration or modification (Grant et al., 2017; Teletchea, 2017). If hatchery-reared fish are to be used, then the best approach to promoted "wild-like types" (Lorenzen et al., 2012) is to farm individuals for the fewest number of generations in captivity, to use large brood stock sizes (Grant et al., 2017), and to modify hatchery environments to mimic key aspects of natural conditions, e.g. add shelters, use low densities (Johnsson et al., 2014). The escape of farmed fish into the wild is inevitable as long as facilities are not fully contained (Glover et al., 2017). Yet, all efforts should be made to prevent escapes because the recapture of escaped fish is broadly ineffective in marine habitats (Dempster et al., 2018). Dempster et al. (2018) suggested three approaches to reducing escapes: (i) protect populations of predatory fish around sea-cage farms because they prey upon smaller escapees; (ii) construct impact offset programs to target recapture in habitats where escapees can be efficiently caught; and (iii) ensure that technical standards are legislated so that fish farms invest in preventative technologies to minimize escapees. In Norway, following the implantation of new technical standards for the design, dimensioning, and operation of sea-cage farms, the total number of escaped Atlantic salmon declined by more than half between 2001-2006 and 2007-2011, despite the total number of salmon held in sea-cages increasing by > 50% (Dempster et al., 2018).

Table 1. Titre de la Table

Compound	TEF (WHO05)	Chemical characteristics			Transfer to milk		Transfer to hen eggs		Transfer to duck eggs
		Cln	Log Kow1	MW	TR2, % (n=8)	Level3	TR, % (n=4)	Level	TR4, % (n=1)
2,3,7,8-TCDD	1	4	6.6	322	34.0 ± 6.3	High	39.1 ± 12.6	High	2.0
1,2,3,7,8 -PeCDD	1	5	7.2	340	26.7 ± 7.1	High	35.8 ± 12.2	High	3.4
1,2,3,4,7,8-HxCDD	0.1	6	7.6	391	17.8 ± 8.0	Medium	43.3 ± 16.5	High	2.3
1,2,3,6,7,8-HxCDD	0.1	6	7.6	391	22.7 ± 7.1	Medium	40.6 ± 14.4	High	3.0
1,2,3,7,8,9-HxCDD	0.1	6	7.6	391	13.2 ± 3.4	Medium	29.1 ± 12.4	High	1.3
1,2,3,4,6,7,8-HpCDD	0.01	7	8.0	425	4.1 ± 1.3	Low	16.2 ± 6.2	Medium	1.1
OCDD	0.0003	8	8.4	460	1.2 ± 0.8	Low	6.8 ± 4.8	Low	1.0
2,3,7,8-TCDF	0.1	4	6.5	306	3.4 ± 2.9	Low	39.1 ± 16.8	High	6.4
1,2,3,7,8-PeCDF	0.03	5	7.0	340	4.9 ± 4.5	Low	38.0 ± 7.4	High	4.5
2,3,4,7,8-PeCDF	0.3	5	7.1	340	35.6 ± 14.8	High	40.0 ± 10.1	High	4.8
1,2,3,4,7,8-HxCDF	0.1	6	7.5	375	19.3 ± 8.9	Medium	39.8 ± 13.0	High	2.5
1,2,3,6,7,8-HxCDF	0.1	6	7.6	375	17.7 ± 6.0	Medium	37.3 ± 16.1	High	2.4
1,2,3,7,8,9-HxCDF	0.1	6	7.7	375	10.7 ± 7.0	Medium	25.6 ± 13.0	High	1.9
2,3,4,6,7,8-HxCDF	0.1	6	7.6	375	11.6 ± 8.7	Medium	23.0 ± 16.5	Medium	0.8
1,2,3,4,6,7,8-HpCDF	0.01	7	8.0	409	3.1 ± 1.1	Low	16.6 ± 10.7	Medium	0.7
1,2,3,4,7,8,9-HpCDF	0.01	7	8.2	409	4.6 ± 1.3	Low	17.8 ± 8.7	Medium	1.1
OCDF	0.0003	8	8.6	443	1.0 ± 1.3	Low	4.0 ± 2.5	Low	0.1

Bold mean integrated article in our dataset
1 Statement of steady state (SS) given by the authors or in brackets when statement was made by us.
2 TR- transfer rate, BCF – bioconcentration factor, BA- bioavailability, BTF- biotransfer factor. MISS – missing data. Values of the parameters taken from the authors or in brackets when re-calculated by us.
3 C – concentrations, Q-quantities where ✓ = given in the article; (✓) = Recalculated; ✗= not available
4 Compounds that below limit of quantification (LQ)
5 Decision of integration (✓) or not (✗) of the given study in our dataset.

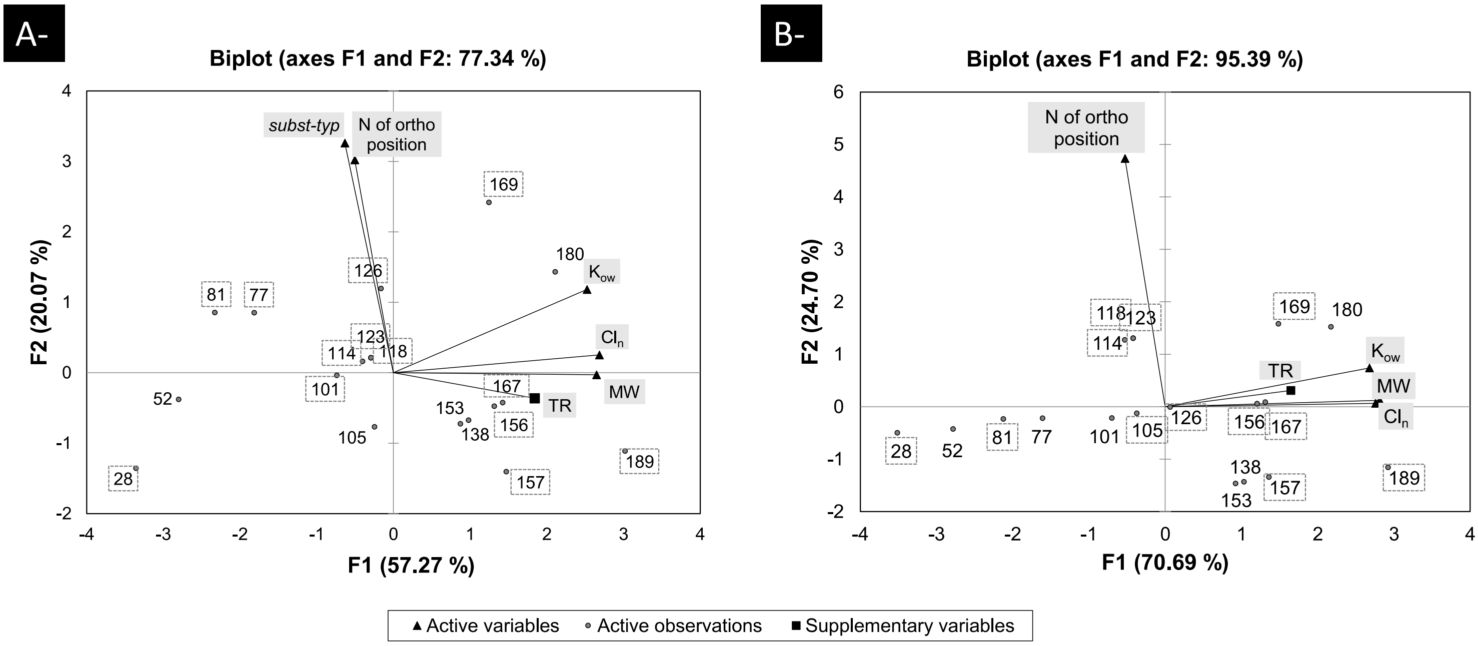

Figure 1. Titre du graphique

Indication: Numbers correspond to the PCB congeners. Framed congeners are dioxin-like PCBs. Bold numbers were congeners transferred at a high level ranking from 38 to 78% and from 30 to 80% respectively for milk and eggs.

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