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Fish Domestication: An Overview

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Abstract

The first trials of fish farming date back about 3500 years. Yet, this is only in the 1980s that the exponential development of aquaculture occurred, driven by the strong demand for aquatic products, whereas global capture fisheries started decreasing. The strong increase of aquaculture production has relied chiefly on the domestication of an increasing number of fish species. Nevertheless, only a limited number has reached a high level of domestication. The aim of this chapter is to describe the domestication history of five of the main farmed fish species globally in which all have reached Level 5 and one example that has reached Level 2 only. These six species were chosen because enough scientific literature was available to describe their domestication history that allows illustrating both ancient and recent fish domestication.

Keywords: domestication level, wild, domesticated, fish species, aquaculture, diversification

1. Introduction

The first trials of fish farming date back about 3500 years [1, 2]. In Egypt, the earliest evidence of some kind of control of reproduction of the Nile tilapia (*Oreochromis niloticus*) in irrigation ponds is suggested about 1500 years BC on paintings and bas-reliefs found in Theban tombs [3, 4]. Nearly at the same period, the farming of the common carp (*Cyprinus carpio*) started in China, in link with irrigation of agriculture [1–3]. This is also in China that the first treatise ever written on aquaculture “Fish breeding” was published in 475 years BC by Fan Li [1, 5–7]. Few centuries later, the farming of three other carps started in China: the silver carp (*Hypophthalmichthys molitrix*), the bighead carp (*Hypophthalmichthys nobilis*) and the grass carp (*Ctenopharyngodon idella*). Also in Asia, the aquaculture in brackish water has arguably started in the fifteenth century with the farming of milkfish (*Chanos chanos*) in Java [6]. In Europe,

the farming of the common carp in freshwater ponds was already well developed during the Middle Ages [5, 8, 9]. The Italian “Vallicoltura” (farming in coastal lagoons and large open waterbodies of seabass, sea bream, eel, mullets, etc.) dates back to the fifteenth century, and the French trout culture started developing around the second half of the nineteenth century [9]. The rearing of oysters is also very ancient (dating back to 2500 years BC), either in Europe (particularly in Greece) or in Japan [9]. Nevertheless, other regions have a much more recent history of aquaculture. In North America, aquaculture started about 100 years ago [9]. In Africa, the aquaculture production dates back to the 1940s. In Australia, New-Zealand, and diverse Pacific Island states, the development of aquaculture is even more recent [9]. In conclusion, the rearing of aquatic animals is very old [10], particularly in Asia [11], even though the global increase is much more recent and has occurred mainly in the past three decades [4, 9, 11].

In 1950, global aquaculture production was almost negligible (about half a million tons), particularly in comparison to capture fisheries [9]. Up until the end of the 1970s, the production only slightly increased and represented at that time about 6% of the global production of aquatic products [2]. Yet, at the beginning of the 1980s, the improvements of rearing conditions, animal nutrition, larval rearing, and more recently genetics allowed strongly improving the production of an increasing number of species [9, 12, 13]. The exponential development of aquaculture during this period of time (**Figure 1**) was driven by the strong demand for aquatic products, whereas global capture fisheries started decreasing [14]. Between 1980 and 2010, global aquaculture production was multiplied by 12, with a mean annual increase of 8.8%, sometimes reaching more than 12% during certain years [9, 15]. During the 2000s, the aquaculture production has continued increasing [10, 16–18], but at a slower pace (6.8%) than in the 1980s (10.8%) and 1990s (9.5%) [19]. In 2014, aquaculture provided half of all aquatic products for human consumption [20], although this percentage was about 9% in 1980 [19]. More than 500 species and/or species groups had been farmed by 2014 (i.e., a sevenfold increase compared to 1950 [21]), including 362 finfishes, 140 molluscs, 62 crustaceans, and about 15 other aquatic animals [20]. The global aquaculture production (**Figure 1**) is dominated in 2016 by the farming of freshwater fish species (58%, i.e., 46.4 million tons) followed by the production of molluscs (21.4%), crustaceans (9.8%), diadromous fishes (6.2%), marine fishes (3.4%), and various aquatic animals (1.2%).

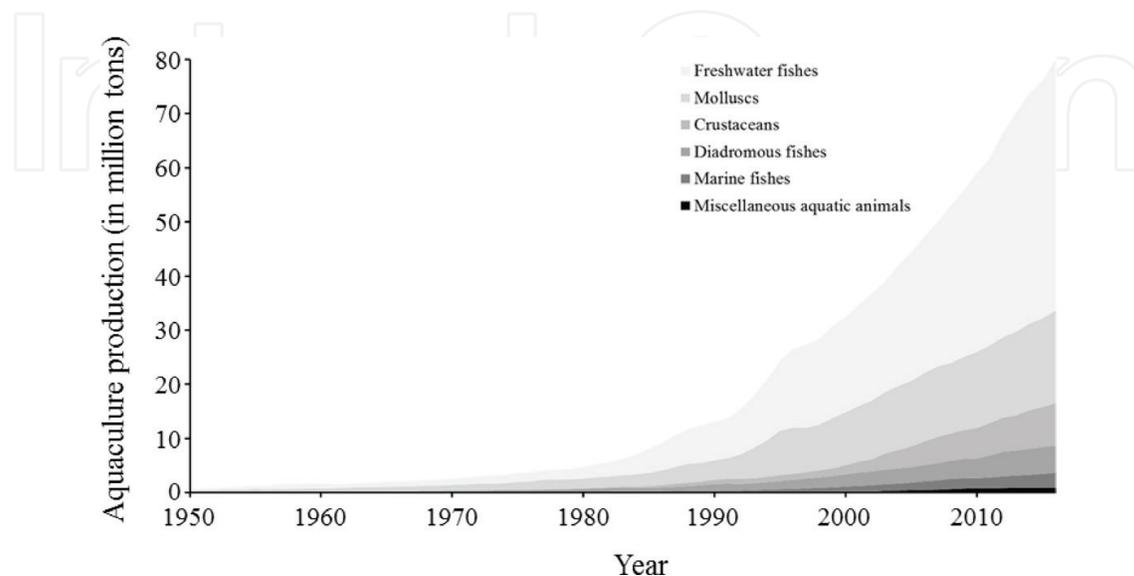


Figure 1. Global aquaculture production (excluding plants) from 1950 to 2016 (data from the FAO database).

Level	Definition	Top three families (number of species)
5	Selective breeding program is used focusing on specific goals	Cyprinidae (10), Salmonidae (8), Acipenseridae (5)
4	Entire life cycle closed in captivity without wild inputs	Cichlidae (6), Sparidae (5), Cyprinidae (4)
3	Entire life cycle closed in captivity with wild inputs	Sparidae (8), Cyprinidae (4), four families (3)
2	Part of the live cycle closed in captivity: several bottlenecks	Cyprinidae (9), Serranidae (5), Carangidae (4)
1	First trials of acclimatization to the captive environment	Cyprinidae (8), Siganidae (3), Sciaenidae (3)

Data from Teletchea and Fontaine [12].

Table 1. Domestication levels with their description and the list of the three leading families by levels in terms of number of species; the number of species by families by level is indicated in parentheses.

The aim of this chapter is to describe the domestication history of five of the main farmed fish species globally in which all have reached Level 5 and one example that has reached Level 2 only (**Table 1**). These six species were chosen because enough scientific literature was available to describe their domestication history that allows illustrating both ancient and recent fish domestication.

2. Domestication of freshwater fish species

2.1. The common carp (*Cyprinus carpio*)

The farming of the common carp, which started in China, is one of the most ancient with the tilapia farming, dating back at least 2500 years [5, 22]. During its long history of domestication, the common carp was profoundly modified by man, deliberately or not, resulting in several breeds with different body shapes, scales, colors, and performances [5, 23–25]. One of the most obvious changes is scales, whose shape and number strongly vary between the four main types of carps: scaled carp, line carp, mirror carp, and leather or naked carps [23–25]. Besides, the body has evolved from an elongated and torpedo shaped for wild individuals to become more laterally compressed and deep bodied [23]. The coloration is now also highly variable, including vivid pigmentations of white, red, black, yellow, blue, gold, and silver [5]. Most modifications of body shape, scalation, and color may have not appeared before the sixteenth century, even though it is possible that some might have existed before [5]. During the nineteenth century, a new trend developed, mainly in Japan [23], with the selection of colored carps [5, 22]. These new forms called “nishikigoi” or simply “Koi” were reproduced, selected, and auctioned for use as pets in small garden pools and many public waterbodies [5, 23]. This intensive selection and the commercial production of these various colored carps have only truly started in the 1950s [5]. Today, the Japanese recognize at least 13 basic color patterns, each with numerous varieties [5]. They would be today more than a hundred varieties of Koi [22], among which some specimens are the most expensive ornamental fish globally:

individual fish can reach a million dollars [23]. However, despite Koi (for the ornamental market), the bulk of global aquaculture production of the common carp for human consumption is based on unselected individuals [24–27]. Indeed, even though carps have undergone selective breeding, at least empirically, for centuries, a more rationale practice has nevertheless been used only at the beginning of the twentieth century [24–27].

During its long history of domestication, the common carp, whose natural range spreads from the Danube River (in Europe) to the Amur River (in China), was introduced in more than 120 countries; its current distribution is now almost global [5, 28–29]. In Europe, the common carp would be native from central regions (particularly the Danube delta), where its farming was started by the Romans about 2000 years ago [5]. During the Middle Ages, its farming spread to the entire European continent [5, 22, 25], particularly due to the development of fish farming in monasteries [5, 30]. In most countries where it was introduced, the common carp was naturalized, establishing self-sustaining populations, and qualified as feral, that is, farmed individuals returning to the wild [5, 23]. These feral populations are today found in hydrosystems of more than 90 countries globally [29], in Asia, Africa, North, Central and South America, Australia, and Oceania [31]. In Australia, for instance, the common carp is the largest freshwater fish introduced and now contributes more than 90% of fish biomass in many areas of south-east of Australia [31]. In Europe, feral populations, some of which could be centuries old, dominate most of drainage systems [22].

Today, the common carp is the third most important species in aquaculture production by volume with more than 4.1 million tons in 2014 (**Figure 2**). Its production was multiplied by more than 40 in the past decades (**Figure 2**). In 2000, it was produced in more than 80 countries, among which about 15 displayed a production higher than 10,000 tons [15, 22]. The rearing systems of the common carp are highly diversified: extensive monoculture in earthen ponds, with or without fertilization and/or additional feeding; intensive monoculture in small ponds, cages, or raceways; and integrated mono- or polyculture with other agricultural activities [32].

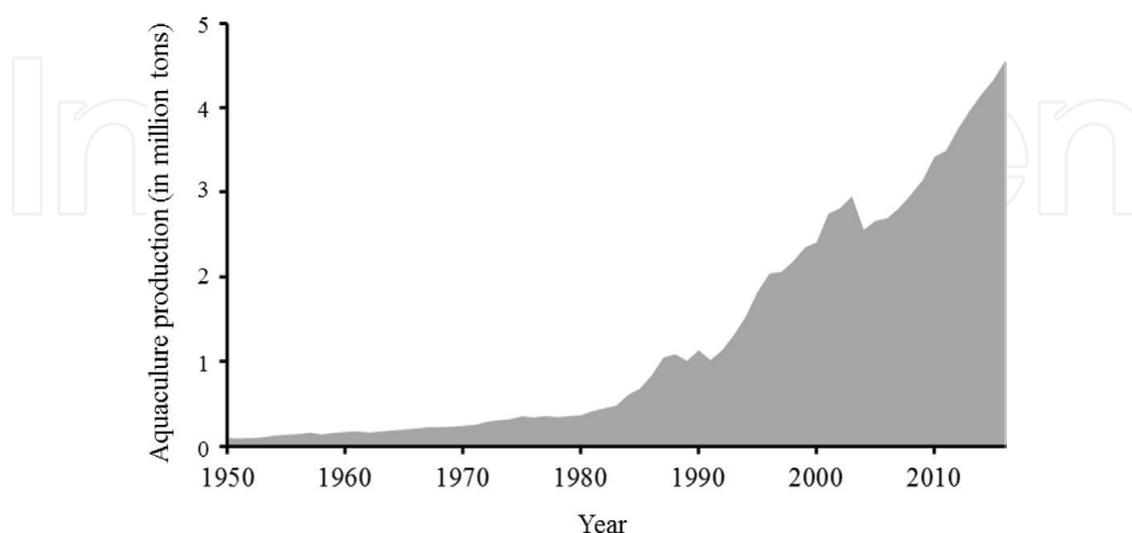


Figure 2. Global aquaculture production from 1950 to 2016 of the common carp *Cyprinus carpio* (data from the FAO database).

In Europe, the common carp is traditionally farmed in large ponds of one to several hundred hectares [32–34]. The degree of farming intensity ranges from highly extensive (low stocking densities with no additional feeding or fertilization) to relatively highly intensive (high density stocking, control of water quality, mechanical aeration, provision of complete feeds, etc.) [32]. In extensive systems, the common carp is the main species reared, sometimes associated with other cyprinids—the tench (*Tinca tinca*), the roach (*Rutilus rutilus*), the rudd (*Scardinius erythrophthalmus*)—and various piscivorous fish—the northern pike (*Esox lucius*), the Eurasian perch (*Perca fluviatilis*), the pikeperch (*Sander lucioperca*), or the Wels fish (*Silurus glanis*) [32, 33]. The main European producing countries are Russia, Ukraine, Czech Republic, Poland, Hungary, and Germany [22, 34]. In Japan and Southeast Asia, the traditional farming of the common carp is practiced in monoculture associated with agriculture (rice and cereals) or farming (duck) [32]. In both China and India, the common carp is traditionally reared in polyculture ponds in association with five or six species [32]: the silver carp (*Hypophthalmichthys molitrix*), the bighead carp (*Hypophthalmichthys nobilis*), the grass carp (*Ctenopharyngodon idella*), the mud carp (*Cirrhinus molitorella*), and the black carp (*Mylopharyngodon piceus*) [32]. This association allows obtaining much higher yields for the diverse farmed species [32].

In conclusion, the common carp is one of the first species to have been domesticated and has become the third leading farmed aquatic species and one of the most introduced worldwide [25–29]. Its biological characteristics (robustness, fast growth, easy propagation, omnivorous feeding regime, ability to readily accept pellets, resistance to disease, and tolerance to a wide range of climatic conditions [35]) make the common carp one of the most popular species [22] that succeeds to adapt to different geographic areas and rearing systems [32].

2.2. The Nile tilapia (*Oreochromis niloticus*)

The farming of the Nile tilapia is one of the most ancient in the world and dates back to the Egyptian antiquity, more than 3500 years ago [3]. Representations of farming are still visible today on the bas-reliefs of Theban tombs [3]. During the following centuries, the rearing systems and farmed tilapias had been slightly modified; thus, the global production remained very low, reaching only about 1500 tons in 1950 (**Figure 3**). However, during the second half of the last century, the production started increasing exponentially, notably from the end of the 1980s (**Figure 3**). The explosion of production is chiefly due to the control of the reproduction in captivity, thanks to the onset of monosex farming, including males only [15]. The farming of monosex male populations is today the rule (males displaying a much higher growth rate than females [36]), which is obtained by sex reversal induced by masculinizing hormones [36], hybridization, or both combined [15]. The production of sex reversal by hormonal treatment of fingerlings is now prohibited in fish destined to human consumption in Europe but is still authorized and largely used in the rest of the world [36]. The second method is the breeding with other species, such as the Mozambique tilapia (*Oreochromis mossambicus*) and the blue tilapia (*Oreochromis aureus*) [6]. In parallel to the sex reversal method, a selective breeding program was initiated at the end of the 1980s, in the Philippines, by an international research institute, among which Filipino and Norwegian researchers [36–38]. This program focused on growth and was called “Genetically Improved Farmed Tilapia” or GIFT [36–38]. In order to ensure a broad genetic variability, broodstock

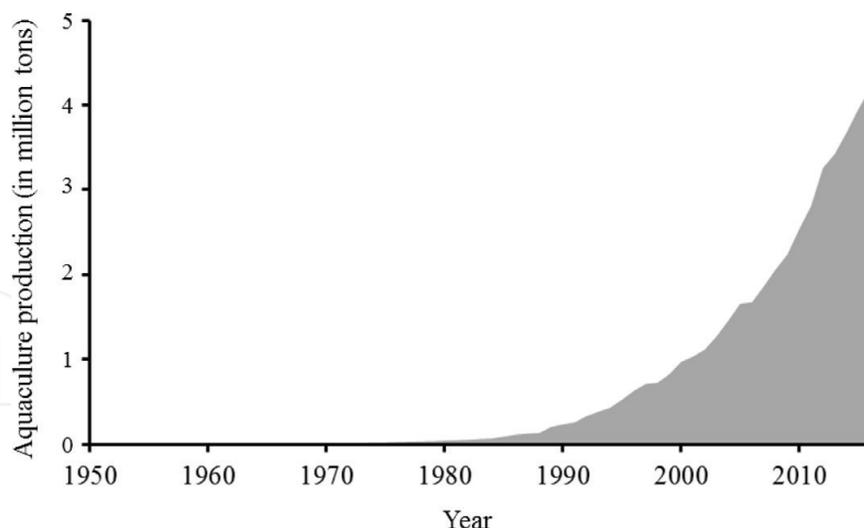


Figure 3. Global aquaculture production from 1950 to 2016 of the Nile tilapia *Oreochromis niloticus* (data from the FAO database).

were sampled from four strains of tilapias reared in the Philippines (Israel, Singapore, Taiwan, and Thailand stocks) as well as four wild populations imported from Africa (Egypt, Ghana, Kenya, and Senegal) [37]. Through five generations of selection, the cumulative gain for growth rate was 86%, corresponding to an average of 17% per generation [37]. At least 20 family-based breeding programs are now in operation globally, more than any other aquatic species [37]. The base populations in 10 of these 20 breeding programs come from the GIFT project, essentially breeders from the fifth generation of selection [37]. The GIFT and GIFT-derived strains are used in numerous farms throughout the world [39, 40]. They represented 80% of the total production of fingerlings in China, 75% in Thailand, and 40% in the Philippines [39]. Today, several species of tilapia are reared in the world, but the Nile tilapia remains by far the dominant species, with more than 80% of the total production, including those of the hybrids [36]. The two other species significantly produced are the Mozambique tilapia and the blue tilapia [36].

In parallel to its domestication, the Nile tilapia has progressively been introduced in numerous countries around the world, mainly during the years 1960–1980 [36]. It is now farmed in more than 100 countries, and its total production has reached more than 2.5 million tons in 2010 (**Figure 3**); this species ranked at the fifth place among the most produced aquatic species in the world in 2014 [38]. This represents a 60-fold increase of the production since 1980 [2, 36, 37]. According to some experts, tilapia has the potential to become the most important aquaculture species in the world in the coming years [37]. Besides, even though the tilapia is native from Africa, more than 70% of global production comes from Asia with more than 1 million tons from China only [9]. In Africa, the production is much lower (about 24%) and comes exclusively from Egypt with more than 550,000 in 2010 [9]. The rearing systems for tilapia are diverse: extensive or semi-intensive monoculture or polyculture in ponds, intensive monoculture in floating cages, in pens, in tanks, or in recirculated systems [9]. The extensive farming of tilapia in ponds is widespread in tropical zones and mostly destined to local consumption [36]. The intensive or hyper-intensive farming (high densities, selectively improved strains,

use of pellets) in tanks or floating cages in large lakes or reservoirs are practiced in several countries, such as China or Indonesia [36]. The farming in recirculated system has developed in temperate countries in order to produce tilapias all year long in controlled conditions, even though the production still remains low [9].

The tilapia, described as the aquatic chicken for its speedy and efficient growth, is often considered as a nearly perfect species for aquaculture [2]. Its biological characteristics are indeed particularly adapted to diverse rearing systems: high rusticity, spontaneous reproduction in captivity (multiple spawning), low-trophic level (phytoplankton and detritus), and extreme feeding plasticity [2, 29, 36]. Besides, the production costs are low, less than one dollar per kilo in subtropical and tropical countries that possess adequate temperature for its growth [36].

2.3. The rainbow trout (*Oncorhynchus mykiss*)

The farming of the rainbow trout started in the 1870s in California [41, 42]. Very rapidly, even though this species reproduces only once a year, the selective breeding in hatcheries and the control of the reproductive cycle using modifications of daylength duration allowed producing eggs virtually year round [41, 42]. In the same time, growth rate, disease resistance, and fecundity were all improved from the years 1930 to 1940, thanks to specific breeding programs [41, 42]. More recently, sterile triploid females were produced from thermal or pressure shock on eggs, leading to the farming of monosex females (which mature later than males and have much better flesh quality), which also ensure that if some fish escape from rearing systems into the wild, they will not be able to reproduce in natural conditions [42]. The rearing of triploid females is widely used in the world, notably in France [43].

In the following years after the onset of domestication, the rainbow trout was exported, in form of eggs, in other American States (Virginia, Michigan, notably), then to Japan, the United Kingdom, and Denmark [15, 41, 42, 44, 45]. During the twentieth century, its introduction was continued in numerous countries [15, 41, 42, 44–46] either for human consumption or for restocking of rivers and lakes for recreational fisheries (particularly in the USA, Europe, and Japan). Consequently, the rainbow trout is one of the most introduced fish species globally, being present in more than 90 countries [47]. The production of rainbow trout has strongly increased, particularly during the 1960s and 1970s [42], partly thanks to the development of new extruded pellets [42], from 4400 tons in 1950 to 145,124 tons in 1980, and continued increasing to reach 728,844 tons in 2010 (**Figure 4**). Today, the rainbow trout is produced in more than 70 countries globally [46, 47], among which 15 have a production higher than 15,000 tons [9]. In 2010, Europe was the leading producer of the rainbow trout with more than one-third of the production, followed by South America (mainly Chile), Asia (mainly Iran and Turkey), and Nord America (the United States) [15, 43, 46]. The production of the rainbow trout is consequently much more important in areas where it had been introduced than in its native range in North America (from Alaska to Mexico) [15, 43]. The rainbow is chiefly produced in intensive monoculture systems: individual ponds, concrete raceways, or other types of flow-through tanks (open systems) [18, 34, 42, 46], recirculated water systems, or floating cages either in freshwater or in marine waters [43, 46].

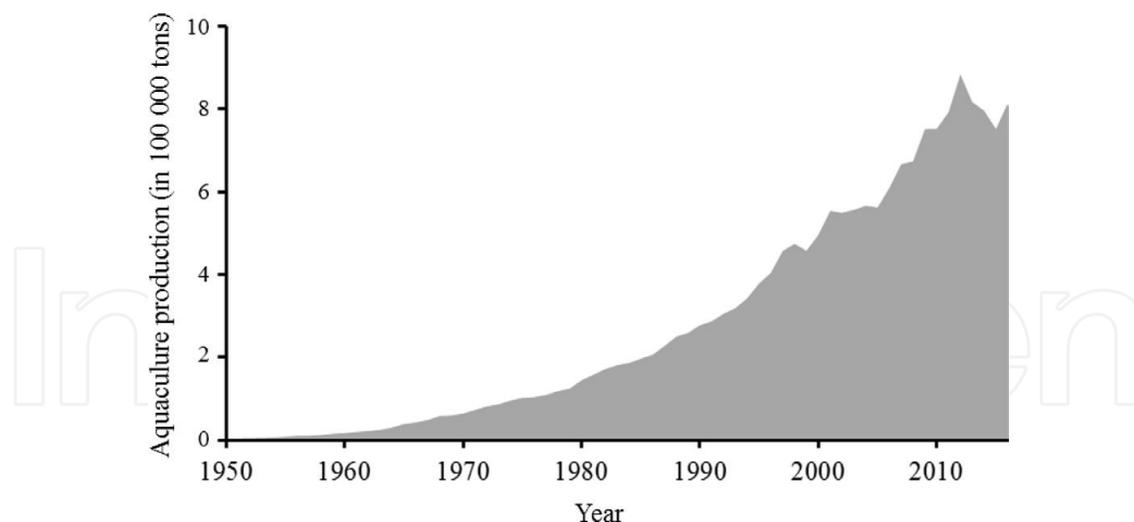


Figure 4. Global aquaculture production from 1950 to 2016 of rainbow trout *Oncorhynchus mykiss* (data from the FAO database).

The rainbow trout is one of the oldest fish in culture [41]. In Europe, up to 14 generations of selection have been performed in family selection and up to 20 in mass selection [44]. This is also the species for which the geographical area was the most increased following the numerous introductions in the past century. In 2014, the rainbow trout was the twelfth most produced aquatic species globally. Its biological characteristics (both sex mature in captivity, spawning is easy to obtain, eggs are relatively robust, fry are sufficiently developed at hatching to directly accept pellets, relatively large tolerance to both temperature and salinity) partly explain the success of its rearing throughout the world [41, 44, 47].

2.4. The striped catfish (*Pangasianodon hypophthalmus*)

The farming of the striped catfish, as well as a dozen of other fish species [48], is very ancient in the Mekong River, particularly in Vietnam, and, to a lesser extent, in Cambodia and Thailand [49]. Traditionally, the farming of the striped catfish relied on the capture of fry and juveniles in the wild, mainly in Cambodia [49], which was then farmed up to a sufficient size to be consumed by local populations [48, 50, 51]. Yet, the farming of striped catfish in Vietnam dramatically changed in the past decades [50], partly due to the ban, by the governments of Cambodia in 1994 and Vietnam in 2000, of the collection of wild fry and juveniles of all species in the natural environment [50], and partly thanks to the development, within the framework of a Franco-Vietnamese research program, of a reliable artificial propagation of two catfish species [49, 50, 51]. The control of reproduction in captivity was first developed for *Pangasius bocourti* [49] and then applied on the striped catfish [50], which allows securing the aquaculture production [49, 52]. In few years, several hundred hatcheries opened in the Mekong Delta allowing to provide all farms [49, 51], which rapidly became the leading farmed species in Vietnam [49]. The control of the reproductive cycle in captivity has changed the aquaculture of this species from being seen as an activity that overexploited natural resources to one that reduces pressure on wild populations [50]. Nevertheless, farming in both cages and pens in Cambodia, Laos, and, to a much lesser extent, Thailand still relies on the capture of juveniles in the wild [9].

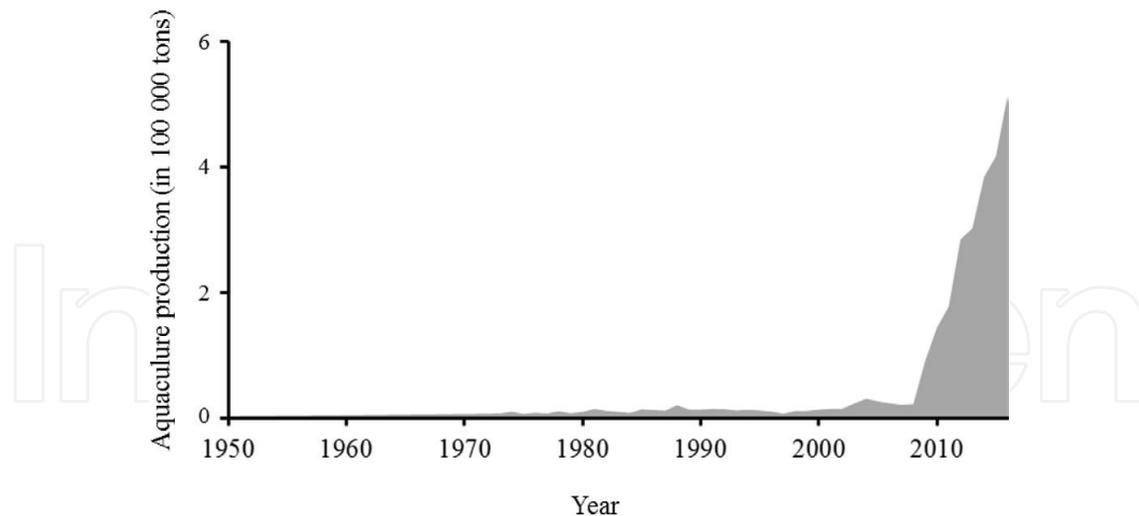


Figure 5. Global aquaculture production from 1950 to 2016 of the striped catfish *Pangasianodon hypophthalmus* (data from the FAO database).

The production of the striped catfish (**Figure 5**) was very low in the 1950s (few thousand tons) and strongly increased from the middle of 1990s [49], to reach more than 1.5 million tons in 2010, including its hybrids [48, 51]. The major part of the production is realized in its native area, i.e., the Mekong River [48, 53]. The Vietnam strongly dominates the production with more than 75% of the global volume, followed by Cambodia, Thailand, and Laos [49, 51]. This species was introduced in neighboring countries, notably in Indonesia, Bangladesh, and Malaysia that produced all together about 20% of the global volume [19, 48, 50]. Only in Vietnam, this species represents more than one third of the aquaculture production [51, 52]. More than 90% of the Vietnamese production of striped catfish is exported to a hundred of countries in the world [49–51, 53, 54]. In parallel to increase of the production, the rearing systems have also evolved [52]. Traditionally, the farming of striped catfish was realized in bamboo floating cages in rivers or reservoirs within which food was mainly constituted of domestic wastes or farming co-products, and in ponds, most often fertilized with organic effluents [49]. Today, most of the production is realized in ponds [52] using commercially made feed [49, 52]. The production could reach hundreds of tons (up to 1000 tons) by ha and year [49].

The striped catfish is without any doubt the aquatic species for which the production has increased the most during the past decade [52, 55]. The domestication of this species is still in its infancy, and genetic improvement programs have only recently started [50]. Because of its low-production cost, mainly due to its feeding regime, its rapid growth, along with high-rearing densities, and large volume, frozen striped catfish fillets have become extremely competitive on the international market [19]. In the early growth phases of the sector, it has to overcome trade embargoes, particularly link to the use of antibiotics; yet, recent studies have demonstrated that there is no food safety concern from either environmental or applied contaminant compounds in this species [49, 52, 56]. Currently, restrictions on the export of the striped catfish from Vietnam do not exist in most importing countries [52]. Catfish fillets are sold in more than 100 countries, among which the United States and more recently Europe (particularly in Eastern countries and Spain) and Asia (mostly Japan, Hong Kong, and Singapore) [19].

3. Domestication of diadromous and marine fish species

3.1. The Atlantic salmon (*Salmo salar*)

The farming of the Atlantic salmon started in the early nineteenth century in the United Kingdom in order to rebuild river populations for angling [9]. Nevertheless, this is only at the end of the 1960s that the farming in sea cages was used for the first time in Norway [57]. From the year 1970, the first ever family-based breeding program of the Atlantic salmon was initiated in Norway in a brand new research institute entitled AKVAFORSK [57, 58]. Even though the production of the Atlantic salmon was only 100 tons in Norway at this time, the equivalent of about 3.6 million US\$ was covered for two-thirds by the Norwegian government and the rest by industry (not working in the aquaculture field) and nongovernmental organizations [57]. In parallel, research programs were started to develop new dry pellet feed adapted to the Atlantic salmon, which were available from 1982 [57]. After about 40 years of farming, the time to produce a standard market-sized 4 kg fish has been halved, and while 3 kg of dry matter (in moist feed) was necessary to produce 1 kg of salmon in the beginning, this has also been reduced to 1.15 kg (dry pellets) [37]. Other traits were progressively added to the selection index such as age at sexual maturity, disease resistance, stress resistance, and quality of the flesh [10, 37, 57, 58]. From the early stages of the selective breeding programs, eggs and juveniles were sold to the industry resulting in that close to 100% of the production of the Atlantic salmon in Norway and in the rest of the world are now based on improved stocks [10, 57, 58]. Farmed salmon is regarded as one of the most domesticated fish species farmed for food, and one Norwegian strain has been exposed to ≥ 12 generations of domestication [59, 60].

In parallel to its domestication, the production was multiplied by 5000 (**Figure 6**) from 294 tons in 1970 to more than 1.4 million tons in 2010 [19, 61]. A dozen of countries currently

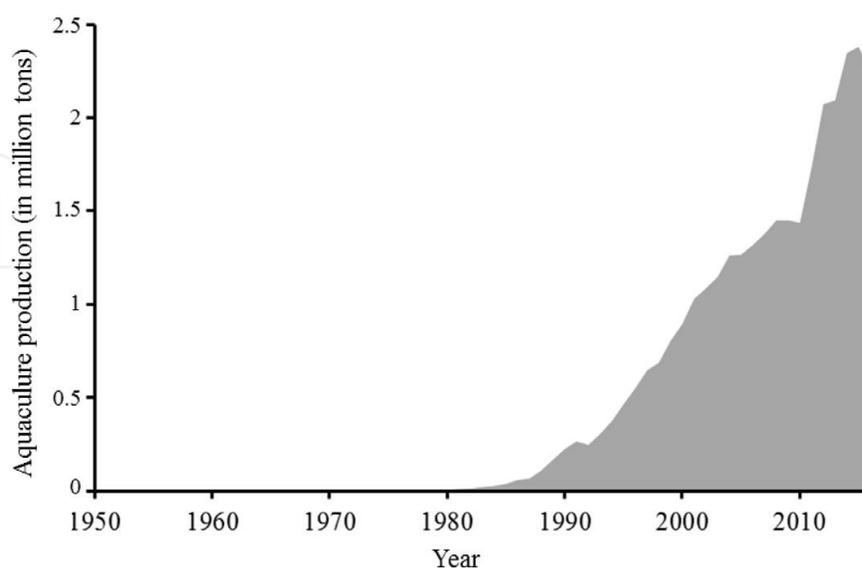


Figure 6. Global aquaculture production from 1950 to 2016 of the Atlantic salmon *Salmo salar* (data from the FAO database).

produce the Atlantic salmon, among which the four leading countries are Norway, Chile, the United Kingdom, and Canada [19, 47, 62]. In Norway and Chile (where this species was introduced), the farming of the Atlantic salmon has an enormous economic importance [63, 64]. In Norway, the farming of Atlantic salmon is the third largest industry after petroleum and mining [47]. In Chile, the exports of the Atlantic salmon represent about two-thirds of the total Chilean fisheries exports and became the third most important export commodity after copper and wood products [47]. Most part of the production (on-growing) is now performed in sea cages [19, 61], with hatcheries working with either flow-through or recirculating aquaculture systems [65].

The Atlantic salmon has evolved in few decades from a luxury item, which was consumed only at specific periods in the year (particularly at Christmas), to convenience products [9]. He has become in 2014 the ninth most produced aquatic products globally, with more than 2.3 million tons. The success of its farming in Norway (and in Chile) is mainly due to the presence of numerous suitable sites for its production, a dynamic research and industry as well as government support [9]. Besides, the Atlantic salmon displays several features (high growth in cages, flesh strongly appreciated by consumers, etc.) that contribute to its farming success [9]. In parallel, the capture by fisheries has strongly decreased from 118,000 tons in 1980 to 73,000 tons in 1990 to less than 40,000 ton in 2000 [47]. Today, almost 100% of the Atlantic salmon is coming from farming [47].

3.2. The European seabass (*Dicentrarchus labrax*)

The traditional farming of the European seabass in the Mediterranean Sea consisted of collecting juveniles in the wild and releasing them in semi-artificial coastal lagoons, such as “Vallicoltura” in Italy [66, 67]. Within these lagoons, seabass was reared extensively [68]. Nevertheless, from the year 1960, in the face of strong competition for wild juveniles between the on-growers and the decrease of natural resources [66], the first rearing trials were initiated in France and Italy [69]. In the middle of the 1980s, the development of reliable methods of reproduction techniques and husbandry methods allowed higher survival [68], and their diffusion rapidly led to the development of a true industry in several countries along the Mediterranean Sea [66, 68]. In the 1990s, the first breeding programs were initiated, first in France and Israel, then in Greece, Spain, and Italy, which allow obtaining the eighth generation of selection in the oldest program [67]. However, a large proportion of the broodstock used today is still coming from wild breeders or first-generation individuals [66, 69, 70].

The aquaculture production of seabass was almost inexistent in 1950 (**Figure 7**). With the control of the life cycle in captivity, the aquaculture production increased exponentially from the middle of 1980 to reach 134,711 tons in 2010 (**Figure 7**). In the same period of time, the capture by fisheries increased from 4460 tons in 1980 to 10,853 tons in 2010 [9]. Consequently, 9 of 10 seabasses consumed in the world are now farmed. The main producers are all located around the Mediterranean Sea: Turkey, Greece, Egypt, Spain, and Italy [9]. Most of the production (on-growing) is realized in sea cages, followed by tanks and lagoon [68].

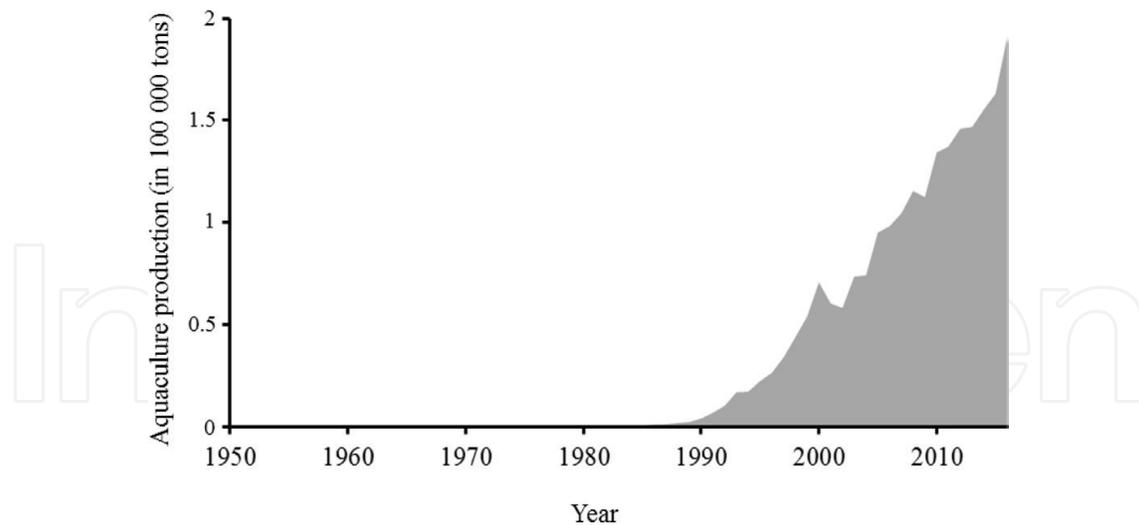


Figure 7. Global aquaculture production from 1950 to 2016 of the seabass *Dicentrarchus labrax* (data from the FAO database).

The seabass has become in less than three decades the second most produced fish species in the Mediterranean Sea, just after the sea bream *Sparus aurata* (whose production has followed a similar trend).

3.3. The Atlantic bluefin tuna (*Thunnus thynnus*)

The farming of the Atlantic bluefin tuna is recent [9]. The first trials of farming date back to the 1970s in Canada, Japan, and Australia [71]. Nevertheless, the aquaculture production truly started in the middle of the 1980s in the Mediterranean Sea, with the evolution of new techniques allowing to provide fish to fattening farms [71, 72]. Despite significant progress, notably thanks to the work of a consortium of European researchers, the reliable control of the life cycle of the Atlantic bluefin tuna in captivity was never reached [73, 74]. Consequently, this

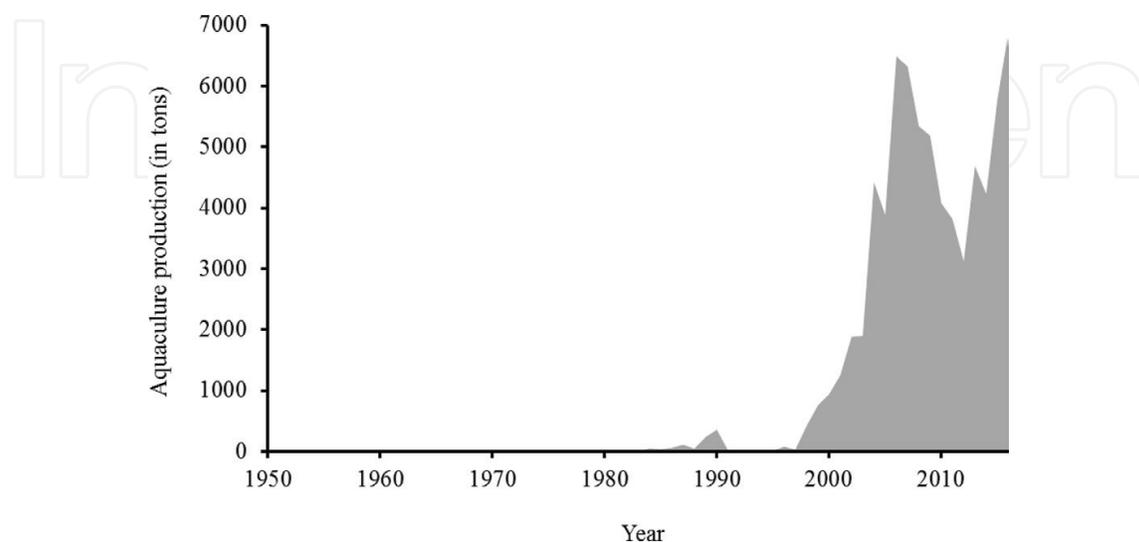


Figure 8. Global aquaculture production from 1950 to 2016 of the Atlantic bluefin tuna *Thunnus thynnus* (data from the FAO database).

industry is entirely based on the stocking of wild-caught specimens, which are reared in cages during a period varying from few months to 2 or 3 years [72–76].

Despite the lack of control of the full life cycle in captivity, the aquaculture production has evolved very quickly from the year 1990 to reach 4080 tons in 2010 (**Figure 8**). More than 10 countries around the Mediterranean Sea currently produce this species, that is, around 60–70 farms [72 - 74]. The leading producers are Croatia, Malta, Turkey, Spain, and Tunisia [77, 78]. The first kind of production, which dates back to the 1980s, is based on the capture of breeders, whose weight varies between 40 and 400 kg, during the migration season, most often close to the spawning areas [73]. Those large individuals are then transported at low speed (1–1.5 knots) over distances ranging from few to 100 km, which might sometimes take several weeks, before being transferred to very large sea cages [73, 79]. Within those very large rearing cages, which may reach 50–60 m of diameter (sometimes even larger than 100 m) and 20–35 m deep, fish are fattened during several months, time required to rebuild muscle fat content that confers to the high-quality flesh researched on the Japanese market of sushi and sashimi [71, 73, 76]. During the middle of 1990s, a second type of production was initiated and consists of capturing immature individuals (8–20 kg in body weight), which are then reared during about 2–3 years in smaller sea cages than for breeders (50–60 m of diameter for about 20 m deep) to get fish of 30–50 kg [73, 76]. This type of production is mainly developed in the Adriatic Sea, particularly in Croatia [71, 76]. In all rearing systems, tunas are most often feed small forage fishes, among which sardinella (*Sardinella aurita*), pilchard (*Sardina pilchardus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), chub mackerel (*Scomber japonicas*), horse mackerel (*Trachurus* sp.), bogue (*Boops boops*), and some cephalopods [71, 73, 75, 78, 79]. The feed conversion rates, which are estimated on a wet feed/wet tuna biomass, are most often high and vary between 10 and 20:1 [73, 78]. In other words, it requires 20 kg of forage fish to make 1 kg of tuna [73]. These feed conversion rates may be even beyond 40:1 for large specimens [73]. Two close relative species to the Atlantic bluefin tuna are also currently produced in other geographic areas using similar methods, namely the Northern Pacific bluefin tuna (*Thunnus orientalis*) in Mexico [78, 79] and the Southern bluefin tuna (*Thunnus maccoyii*) in Australia [80]. In 2002, Japanese scientists were able to obtain eggs and larvae of *T. orientalis* in an artificial setting; yet, there is not a broad knowledge of how to culture tuna in captive conditions, and much research is needed to consistently control the entire life cycle in captivity [78].

In conclusion, the aquaculture production of Atlantic bluefin tuna has strongly increased within the past two decades, mainly driven by the Japanese market [78], its high commercial value associated with its high growth (30 kg in 3 years) [73]. However, the production of this species is based on the capture of wild individuals in nature; thus, only a control of the entire life cycle could ensure the sustainability of the industry through a reduction in its reliance on wild stocks [72, 73, 80].

4. Conclusions

The strong increase of the aquaculture production since the early 1980s has relied chiefly on the domestication of an increasing number of fish species [12, 13, 81–85]. Nevertheless, only a limited number has reached a high level of domestication (**Table 1**), such as the rainbow trout,

the Nile tilapia, or the Atlantic salmon [83–85]. The 35 species classified at Level 5 [12] belong to 10 families, among which Cyprinidae ($n = 10$ species), Salmonidae ($n = 8$), and Acipenseridae ($n = 5$) [83]. For these species, the entire life cycle is controlled in captivity, and breeding programs have allowed improving, among others, growth, with average genetic gains comprised between 10 and 15% per generation [37, 58, 85–87]. Today, it is estimated that about 10% of the global production is based on improved individuals [37, 87–89]. Nevertheless, very often, even for the species that have reached Level 4 or 5 (**Table 1**), a significant part of global production is based on the introduction of wild individuals. Conversely to these few domesticated species, or more accurately domesticated populations, the majority of farmed fish species still rely on the regular inputs of wild individuals (**Table 1**); thus, there is no strong dichotomy within the same species between wild individuals (coming from fisheries) and farmed individuals (produced in aquaculture) [90–93]. Besides, for numerous species, aquaculture is not a true alternative to capture fisheries but rather a mean to produce wild individuals to a certain commercial size by strongly decreasing the high-mortality rate characteristics of wild populations [90, 94]. Most farmed fish are thus still relatively similar to their wild congeners [95, 96].

Even though the number of farmed aquatic species (including fish, molluscs, and crustaceans) has strongly increased from 1950 to 2010, from about 72 to more than 500 [19, 20], only few species ensure the bulk of the production today [30, 83, 97]. For fish only, 15 species ensure more than 85% of the global production in 2005 [30], despite the number of farmed species rose from 43 to 219 between 1950 and 2005 [97]. In 2009, this trend was confirmed with more than 90% of the global production relying on 20 species only [83]. Only in Europe, most of the aquaculture production is based on the rearing of 10 species only [34, 98]. For some species, which have a very high production today, their farming is quite recent, dating back only to two or three decades only, such as the striped catfish or the Atlantic salmon [30, 97]. Among the 33 species with more than 100,000 tons in 2005, about one-quarter was not produced 40 years ago [97], which illustrates that new species can contribute strongly to the global production [99–101]. Conversely, most farming trials of new species realized within the past decades, either failed or resulted in low production volumes, about tens of tons. This demonstrates how difficult it is to farm a new species, whose development depends on the interaction of various factors, among which biological (availability of wild individuals, ability to control the life cycle in captivity), economical (acceptability by consumers, competition with other animal products), and environmental ones (availability of suitable sites and water, competition with other resources) [12, 18, 84, 91]. More recently, it has also become evident that climate change, which may result, among others, in global warming, saline water intrusion, and ocean acidification, may affect aquaculture [102]. Therefore, aquaculture should use genetically improved and robust animals not suffering from inbreeding depression, resulting from well-managed selective breeding programs with proper inbreeding control and breeding goals [102]. The leading species for aquaculture production have been extensively introduced across the world, particularly in the past century, resulting in that the bulk of aquaculture production relied on the farming of these very few alien species in numerous countries [11, 15]. Yet, the contribution of native species to global aquaculture will perhaps improve resulting in a more diversified and even production than today [99–101]. At least the

intensity level of farming, from extensive to highly intensive, and industrialization are also very diverse [18]. From an activity mainly artisanal, aquaculture has evolved to include very large companies that export in numerous countries [17, 103]. According to FAO, the annual production by fish farmer also strongly varies from less than 1 ton in Indonesia to 4 tons in India, 7 tons in China, 35 tons in Chile, and 187 tons in Norway [19].

Conflict of interest

The author declares no conflict of interest.

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