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Article

Domestication of Marine Fish Species: Update and Perspectives

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Abstract: Domestication is a long and endless process during which animals become, generations after generations, more adapted to both captive conditions and humans. Compared to land animals, domestication of fish species has started recently. This implies that most farmed marine fish species have only changed slightly from their wild counterparts, and production is based partly or completely on wild inputs. In the past decades, global marine fish production has increased tremendously, particularly since the 1990s, to reach more than 2.2 million tons in 2013. Among the 100 marine fish species listed in the FAO's database in 2013, 35 are no longer produced, and only six have a production higher than 100,000 tons. The top ten farmed marine species accounted for nearly 90% of global production. The future growth and sustainability of mariculture will depend partly on our ability to domesticate (*i.e.*, control the life cycle in captivity) of both currently farmed and new species.

Keywords: domestication level; wild; domesticated; marine fish species; capture-based aquaculture; bottlenecks

1. Introduction

Domestication is a long and endless process during which animals become, generations after generations, more adapted to both captive conditions and humans [1–3]. Therefore, domestication should not be confused with taming, which is conditioned behavioral modification of wild-born animals [3,4].

During domestication, captive animals are progressively modified from their wild ancestors and at a certain moment are considered domesticated. Nevertheless, it is difficult to determine when captive animals have become domesticated, and such a decision is subjective and arbitrary [1]. According to most authors, a domesticated animal is bred in captivity and thereby modified from its wild ancestors in ways making it more useful to humans who control its reproduction and its food supply [4–6].

Domestication on land started about 12,000 years ago [4]. Over millennia, animal populations were modified by humans and changes in behavior, physiology and morphology occurred [6,7]. At the beginning of the twentieth century, modern breeding programs were initiated leading to dramatic changes in productivity, e.g., increase laying rate for laying hens or improved feed conservation ratio, meat yield and growth rate in broiler chickens [2,8,9]. As a result, thousands of genetically distinct livestock breeds have been created, and there is an apparent dichotomy between domesticated species and their wild congeners, which have sometimes gone extinct [6,10,11].

Compared to the domestication of land animals, the domestication of aquatic animals is a recent phenomenon [5]. Except for few species, such as the common carp (*Cyprinus carpio*) and the goldfish (*Carassius auratus*), the bulk of farming has started in the past century [5,12,13]. Most fish species farmed today are not much different from their wild conspecifics [9,10,13–15]. It is estimated that 90% of the global aquaculture industry is based on wild, undomesticated or non-selectively bred stocks [2,16]. Conversely, less than 10% of aquaculture production comes from selectively bred farm stocks [2]. The Atlantic salmon (*Salmo salar*) is an outlier, as almost 100% of the total production is based on selectively bred stocks [8,16]. Consequently, depending on the species considered, the control over aquaculture production can vary from managing only a portion of the life cycle to managing the complete life cycle in captivity [11,14,17–20]. In order to better describe the various fish production strategies, Teletchea and Fontaine [20] proposed a new classification based on the level of human control over the life cycle of farmed species and independence from wild inputs. This classification comprises five levels of domestication with one being the least domesticated to five being the most domesticated. Among the 250 species recorded in the Food and Agriculture Organization (FAO) database in 2009, 39 belong to level 1 (first trials of acclimatization to the culture environment), 75 to the level 2 (part of the life cycle closed in captivity, also known as capture-based aquaculture), 61 to the level 3 (entire life cycle closed in captivity with wild inputs), 45 to the level 4 (entire life cycle closed in captivity without wild inputs) and 30 to the level 5 (selective breeding programs are used focusing on specific goals) [20].

The main goal of the present study is to analyze the evolution of the aquaculture production of marine fish species since 1950, while updating the number of species per domestication level since 2009.

2. Materials and Methods

The central source of data about the world's fisheries and aquaculture operations is the United Nation's Food and Agriculture Organization (FAO). With fisheries catch and aquaculture production data going back to 1950, the FAO's database is an invaluable source of temporal information about the quantity, value, and geographic location of global seafood production [19]. Nevertheless, concerns have been raised in the past two decades about the quality of the data, mainly due a lack of clarity and transparency in terms of what is and is not being reported as "aquaculture", if reported at all [19,21].

However, a full discussion of these concerns lay outside the scope of this paper (instead, see [19,22]). In the present study, I choose to focus on marine fish species, thus excluding diadromous species, such as Atlantic salmon [23]. The domestication level for all marine fish species listed in the FAO in 2013 (n = 100 species) was determined based on [20] for species already in the database in 2009 (n = 87), and on the literature for "new" species (n = 17). Group of species were excluded.

3. Results

3.1. Evolution of Global Marine Fish Aquaculture Production

Global marine fish production increased slightly from 1950 up to the beginning of the 1970s. Then, the production increased steadily up to the 1990s; thereafter, it rose tremendously (Figure 1). However, more than half of the production is not identified at the species level in the FAO database (Figure 1). One group called "Marine fish nei (not elsewhere included)" totaled 621,275 tons, which is more than one-quarter of the global production in 2013.

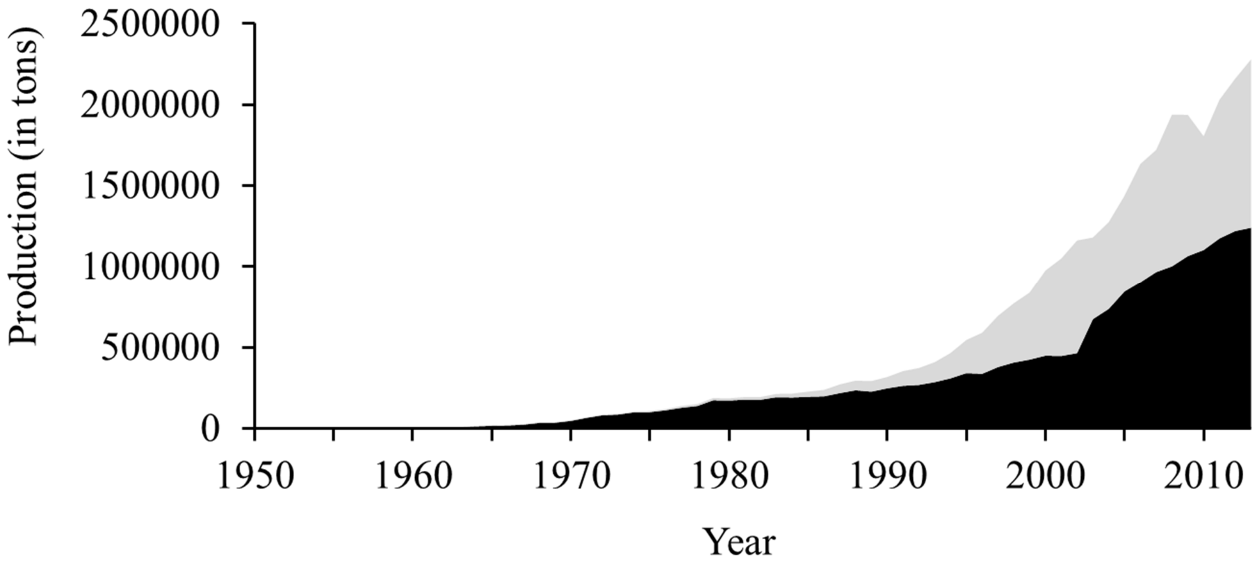

Figure 1. Evolution of global aquaculture production of marine fish species. Group of species, not identified at the species level (**upper** part, in grey), identified at the species level (**lower** part, in black).

In 2013, global marine fish production reached more than 2.2 million tons (Figure 1), which represents about half the production of diadromous fish and about 6% of freshwater fish production (Figure 2). This implies that despite its strong increase, marine fish aquaculture remains small compared to non-marine fish production.

Marine fish are mainly produced in Asia (83.1%), followed by Europe (9.2%) and Africa (7.1%) (Figure 3a). Asia is also the main producer of diadromous fish (39.0%); yet the production is more evenly distributed in the world, with Europe (37.8%) and the Americas (21.9%) (Figure 3b). For freshwater fish, almost the entire production (93.8%) is realized in Asia (Figure 3c).

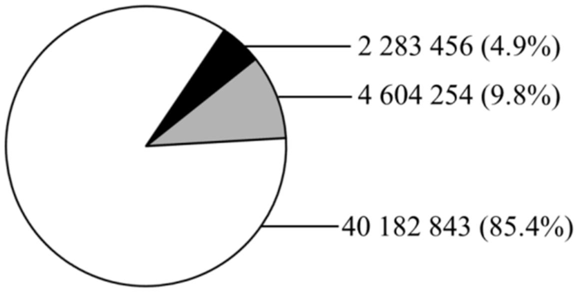

Figure 2. Comparison of the aquaculture production of marine fish species (**black**) with those of diadromous (**grey**) and freshwater (**white**) species in 2013. The first number is the total production followed by the percentage in parentheses.

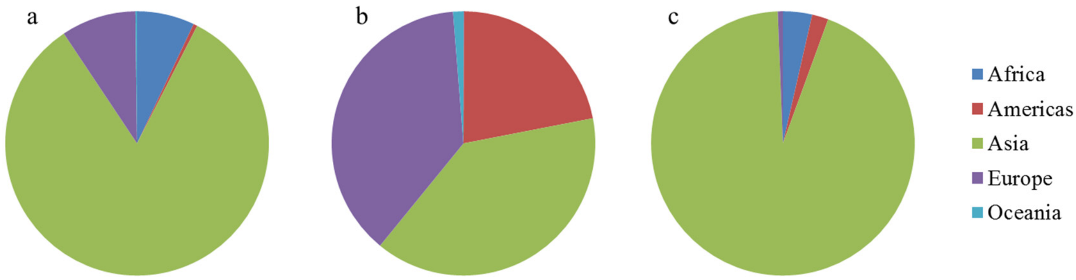

Figure 3. Main aquaculture regions of fish species in 2013: (**a**) marine fish species; (**b**) diadromous fish species; and (**c**) freshwater fish species.

3.2. Evolution of the Number of Farmed and Domesticated Fish Species

The number of farmed species has strongly increased in the past decades to reach 65 in 2013 (Figure 4). Since the mid-1990s, the number has doubled, despite slight decreases in 1997, 1998, 2006, 2007, 2009, 2011 and 2012.

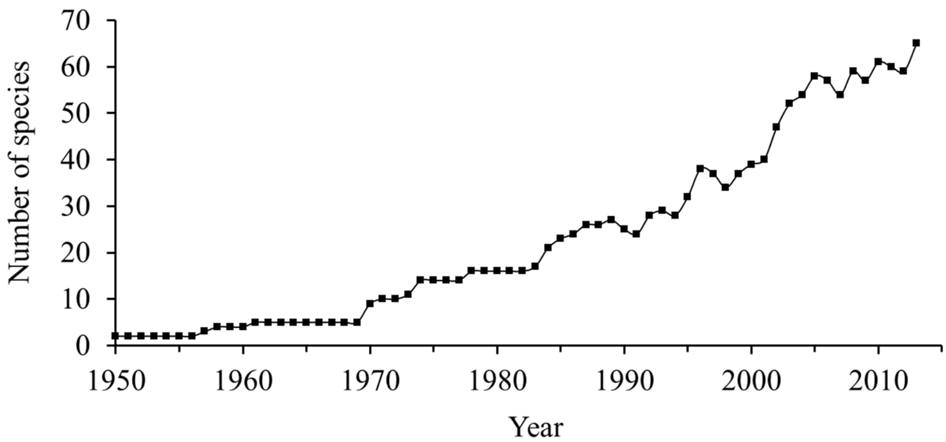

Figure 4. Evolution of the number of marine fish species farmed per year.

The comparison between 2009 and 2013 showed that 87 species were listed in 2009 and 100 in 2013. Four species listed in 2009 are no longer present in 2013, the striped weakfish (*Cynoscion striatus*), the eastern pomfred (*Schuettea scalaripinnis*), the streamerish (*Agrostichthys parkeri*) and the rice-paddy eel (*Pisodonophis boro*). Seventeen "new" species were present (in bold in Appendix). Among the 100 species listed in the FAO database, 35 were no longer produced in 2013, 24 had a production less than 100 tons, 13 had a production between 100 and 1000 tons, 13 species between 1001 and 10,000, nine species between 10,001 and 100,000, and only six have a production higher than 100,000 tons. The domestication level of marine species ranged from one to five (Figure 5). The domestication level for each species is provided in the Appendix. There are only slight differences between 2009 and 2013: only the numbers of species at levels 1, 2 and 3 have increased.

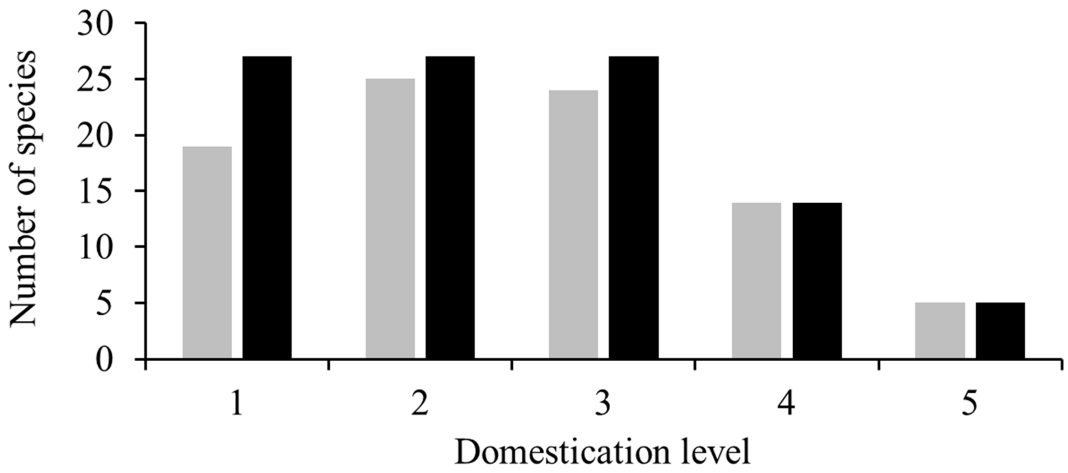

Figure 5. Domestication level of marine fish species in 2009 (**grey**) and 2013 (**black**).

The top ten marine farmed species in 2013 totaled 86.5% of the global production, which was 1,241,149 tons (when excluding groups not identified at the species level). These species are almost exclusively produced in Asia, except for the two leading species, gilthead seabream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax*), for which about half of the production is in Europe (Figure 6).

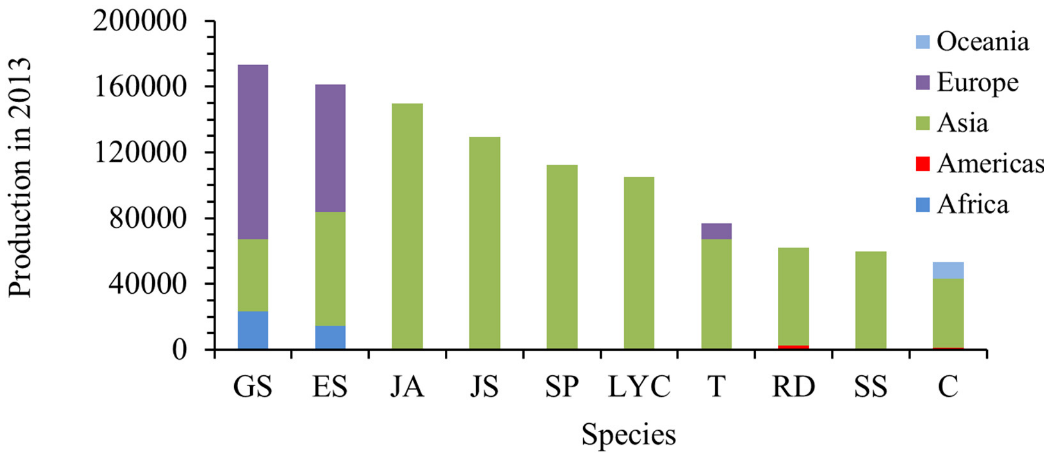

Figure 6. Aquaculture production of the top ten farmed marine species. Gilthead seabream (GS); European seabass (ES); Japanese amberjack (JA); Japanese seabass (JS), subnose pompano (SP); large yellow croaker (LYC); turbot (T); red drum (RD); silver seabream (SS) and cobia (C) (see Appendix for scientific names).

4. Discussion

4.1. Evolution of Marine Fish Aquaculture Production

Aquaculture, the farming of aquatic organisms, including fish, shellfish and mollusks (excluding plants), is the fastest growing food production system globally, with an increase in production of about 9.3% per year since 1985 [14]. In 2012, aquaculture production has reached 66.7 million tons [2]. Despite a strong increase in the past two decades, the production of marine fish species is still small compared to global aquaculture, and particularly mariculture, which is dominated by mollusks and crustaceans [7]. In comparison, fish is totally dominant in freshwater aquaculture (>99%) [7].

When compared with the two other groups of fish listed in the FAO database, it appears that marine fish species represent a very small amount of global fish production (Figure 2). This is partly due to the fact that farming of most marine fish species is very recent, and thus the life cycle is controlled in captivity for only a handful of species (see below). In addition, several constraints have restricted the expansion of aquaculture of marine fish species, particularly in North America and Europe (Figure 3), among which limited areas sheltered from ocean swells, regulatory restrictions on sites, other competitive factors, such as tourism and port development, the relatively high costs (e.g., investments in infrastructure, maintenance, cost and transport of feed), and the high developmental costs and risks associated with off-shore aquaculture technologies [7,9,24–28].

Today, the marine environment contributes less than two percent of the human food supply [27,29]. It is largely because the development of controlled food production in the ocean lags several millennia behind that on land [12,27,29]. The space used for mariculture production is estimated at about 0.01 million km^2, or about 0.04% of the global shelf area [29]. Mariculture production is concentrated in a selected number of countries (e.g., China, Spain, Greece, Norway, Chile, and Scotland), particularly in sheltered bays and lagoons [29]. In future decades, it is anticipated that mariculture would increase significantly [9,27,29]. The FAO forecasts that mariculture will reach 54 million metric tons to 70 million metric tons by year 2020 [29]. However, further development of mariculture will run into major bottlenecks concerning the availability, suitability, and cost of feed; space availability; and adverse environmental impacts, which must be overcome if mariculture is to become a major component of global food production [28,29].

4.2. Evolution of the Number of Farmed and Domesticated Marine Species

The number of farmed marine species has strongly increased in the past decades, as observed for other fish groups [5,13,28]. However, only 10 percent of the marine species listed in the FAO in 2013 accounted for nearly 90% of global production (Figure 6). Eight of the top ten farmed species have reached the domestication level 4 (n = 5) or 5 (n = 3). This implies that the entire life cycle of these species has been closed in captivity without the need to use wild inputs, and for three of them, breeding programs have been developed: five for the gilthead seabream (*Sparus aurata*), three for the European sea bass (*Dicentrarchus labrax*) and two for the turbot (*Psetta maxima*) [25]. However, reaching level 4 and 5 does not necessarily imply that the entire aquaculture production of the 19 marine fish species classified at these two domestication levels (Figure 5) is based on domesticated or genetically improved stocks only [11,20]. For instance, even though sea bass has reached the level 5, most farms still rely today on wild broodstock for reproduction or, to lesser extent, from first-generation (F1) individuals and rarely from selected F2 or F3 fish [11].

Achieving full life cycle in captivity over several generations, which could then be called domesticated fish, thus appears an important progress in mastering the sustainability and the increase of production [17]. However, domestication (and notably selection) of a new species is a long and difficult process [30] that requires, among others, broodstock management (production of high quality broodstock, gonad and gamete development, ovulation/oviposition in females and ejaculation of milt in males), incubation of eggs, and rearing of larvae and juveniles [20,25,31]. Therefore, domestication needs access to specific skills, knowledge, and technology, and both long-term public and private funding [2,8,9,13]. This explains why it is has been primarily carried out in developed countries, notably in Europe [25,32].

For all the top ten farmed species, except the large yellow croaker (*Larimichthys croceus*), the aquaculture production now strongly exceeds capture fisheries (Figure 7). This may be caused by competition between these two sources, because a wild caught fish can commonly be sold at a relatively low price, but cannot be cultured at this low price for a profit. As capture fisheries decline because of overharvesting, the prices of target species often increase dramatically. Under these conditions, aquaculture can thrive, thereby further reducing the value of that capture fishery [14].

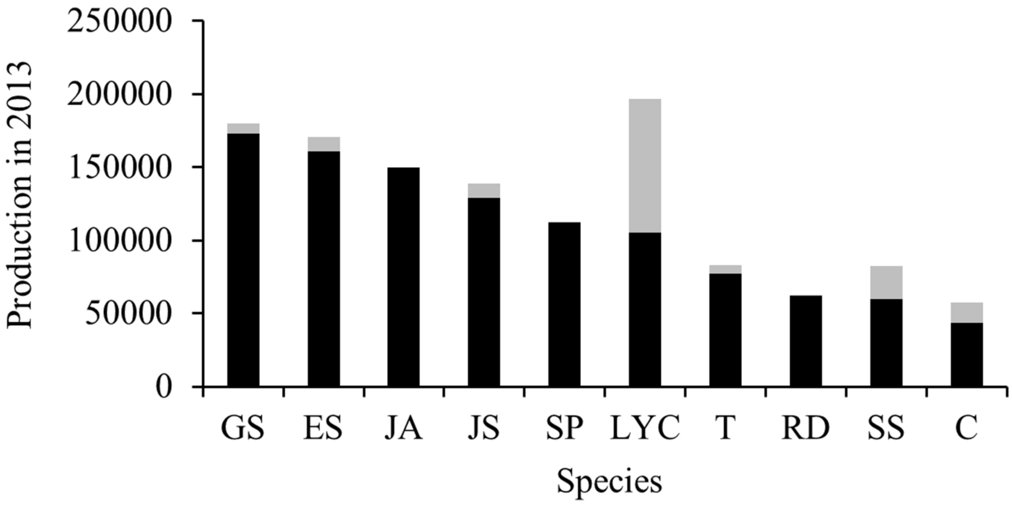

Figure 7. Global production of the top ten farmed marine species, aquaculture (**black**) and fisheries (**grey**). Gilthead seabream (GS); European seabass (ES); Japanese amberjack (JA); Japanese seabass (JS); subnose pompano (SP); large yellow croaker (LYC); turbot (T); red drum (RD); silver seabream (SS) and cobia (C). The fisheries production of JA, SP and RD are 0, 79, and 204 tons respectively (see Appendix for scientific names).

Two among the top ten farmed species, the Japanese amberjack (*Seriola quinqueradiata*) and the snubnose pompano (*Trachinotus blochii*), have only reached level 2, which implies that the entire aquaculture production is based on wild input. This method of production, known as capture-based aquaculture, consists of growing and fattening individuals removed from wild populations [17]. Tuna fattening and much of the marine cage culture in Asia, relies directly on wild-caught small pelagic fish with relatively low market price [19,28,31]. The aquaculture process transforms fish protein from low to high value for human consumption [28]. However, such systems can only function as long as survival and sustainable utilization of the affected wild stocks are warranted [17,19,31]. Therefore, capture-based aquaculture can only be seen as a transitory form of fish production, viable only as long as the wild resource is still available for seed withdrawal [17,31]. Efforts have to be made to domesticate species (*i.e.*, the closing of the life cycle in captivity) to allow a reliable production, independent of wild inputs, and then improve desirable traits through selective breeding [2,25,31].

One-third of the marine species listed in FAO in 2013 are no longer produced, and 50 percent more have a production less than 1000 tons. Nearly all species with a production inferior to 1000 tons have a domestication level between 1 and 3 (Appendix). This highlights that for most species, farming corresponds to one or a few years of aquaculture trial before being abandoned [15,20]. The main reason why numerous attempts with new species fail is that premature attempts to develop industrial enterprises were based on overly optimistic speculation about market demand, rather than on biological and technical knowledge and adequate information about economic feasibility [20,27].

5. Conclusions

Compared to the domestication of land animals, the domestication of aquatic animals, and particularly marine fish species, is a recent phenomenon. Mariculture of fish has only started a few decades ago, and today only a handful of species can be considered domesticated. In contrast, for numerous species, farming was only performed for a few years before being stopped. The future growth and sustainability of mariculture will depend partly on our ability to domesticate (*i.e.*, control the life cycle in captivity) of both currently farmed and new species.

Acknowledgments

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Conflicts of Interest

The author declares no conflict of interest.

Appendix

Table A1. Domestication level for marine fish species listed in the 2013 FAO report (n = 100 species). Group of species were excluded. Species on the list for the first time are in bold (n = 17). Aquaculture production is in tons. When no reliable scientific information was found, species were arbitrarily considered to belong to level 1 when their production was less than five continuous years (n = 15) to the level 2 when their production was between five and up to 10 continuous years (n = 3), and to the level 3 when their production was greater than 10 years (n = 3).

Scientific Name	Common Name	Production in 2013	Domestication Level	Main Reference
Anarhichas lupus	Atlantic wolffish	0	1	Gunnarsson *et al.*, 2009, [33]

Table A1. *Cont.*

Atherina boyeri	**Big-scale sand smelt**	**0**	**1**	**Dulcic *et al.*, 2008, [34]**
Bolbometopon muricatum	**Green humphead parrotfish**	**1**	**1**	
Carangoides malabaricus	**Malabar trevally**	**387**	**1**	
Caranx hippos	Crevalle jack	0	1	
Caranx sexfasciatus	**Bigeye trevally**	**1**	**1**	
Centropristis striata	Black seabass	0	1	Rezek *et al.*, 2010, [35]
Chaetodipterus faber	**Atlantic spadefish**	**0**	**1**	**Gaspar 2005, [36]**
Dentex tumifrons	Yellowback seabream	0	1	
Dicentrarchus punctatus	**Spotted seabass**	**2**	**1**	**Ly *et al.*, 2012, [37]**
Labrus bergylta	Ballan wrasse	25	1	Muncaster *et al.*, 2010, [38]
Lethrinus miniatus	Trumpet emperor	45	1	
Lutjanus bohar	Two-spotted red snapper	0	1	
Megalops atlanticus	**Tarpon**	**0**	**1**	
Micropogonias furnieri	Whitemouth croaker	5	1	Velloso and Pereira Jr. 2010, [39]
Mugil liza	Lebranche mullet	7	1	
Muraenesox cinereus	Daggertooth pike conger	0	1	
Mycteroperca bonaci	**Black grouper**	**2**	**1**	
Pagrus major	**Japanese seabream**	0	**1**	
Platichthys flesus	European flounder	0	1	Engel-Sørensen *et al.*, 2004, [40]
Pleurogrammus azonus	Okhotsk atka mackerel	0	1	
Pomatomus saltatrix	Bluefish	0	1	
Scophthalmus rhombus	Brill	0	1	Cruzado *et al.*, 2004, [41]
Siganus canaliculatus	White-spotted spinefoot	1	1	Xu *et al.*, 2011, [42]
Siganus javus	Streaked spinefoot	0	1	

Table A1. *Cont.*

Siganus rivulatus	Marbled spinefoot	0	1	El Dakar *et al.*, 2011, [43]
Valamugil seheli	Bluespot mullet	0	1	Belal 2004, [44]
Acanthopagrus berda	Goldsilk seabream	0	2	Liao *et al.*, 2001, [45]
Argyrosomus japonicus	**Japanese meagre**	**130**	**2**	**Mirimin and Roodt-Wilding, 2015, [46]**
Boleophthalmus pectinirostris	**Great blue spotted mudskipper**	**0**	**2**	**Zhang *et al.*, 1989, [47]**
Centropomus undecimalis	Common snook	0	2	Carter *et al.*, 2010a, [48]
Eleutheronema tetradactylum	Fourfinger threadfin	4173	2	Liao *et al.*, 2001, [45]
Epinephelus areolatus	Areolate grouper	47	2	Ottolenghi *et al.*, 2004, [49]
Epinephelus coioides	Orange-spotted grouper	492	2	Ottolenghi *et al.* 2004, [49]
Epinephelus fuscoguttatus	Brown-marbled grouper	86	2	Ottolenghi *et al.*, 2004, [49]
Epinephelus lanceolatus	**Giant grouper**	**36**	**2**	**Peng *et al.*, 2015, [50]**
Epinephelus malabaricus	Malabar grouper	68	2	Ottolenghi *et al.*, 2004, [49]
Gnathanodon speciosus	Golden trevally	58	2	Liao *et al.*, 2001, [45]
Liza ramada	Thinlip grey mullet	0	2	Marino *et al.*, 1999, [51]
Lutjanus goldiei	Papuan black snapper	0	2	
Lutjanus guttatus	Spotted rose snapper	2	2	García-Ortega 2009, [52]
Lutjanus johnii	John's snapper	278	2	Liao *et al.*, 2001, [45]
Miichthys miiuy	**Mi-iuy (brown) croaker**	**0**	**2**	**An *et al.*, 2012, [53]**
Mugil soiuy	So-iuy mullet	905	2	
Plectropomus maculatus	Spotted coralgrouper	7	2	
Polydactylus sexfilis	Sixfinger threadfin	0	2	Deng *et al.*, 2011, [54]
Psammoperca waigiensis	Waigieu seaperch	5,704	2	Pham *et al.*, 2010, [55]
Seriola quinqueradiata	Japanese amberjack	149,766	2	Bilio 2007b, [56]
Seriola rivoliana	**Longfin yellowtail**	**400**	**2**	**Roo *et al.*, 2014, [57]**

Table A1. *Cont.*

Thunnus albacares	Yellowfin tuna	171	2	Wexler *et al.*, 2011, [58]
Thunnus maccoyii	Southern bluefin tuna	3,482	2	Carter *et al.*, 2010b, [59]
Thunnus thynnus	Atlantic bluefin tuna	3,445	2	Carter *et al.*, 2010b, [59]
Trachinotus blochii	Snubnose pompano	112,499	2	Liao *et al.*, 2001, [45]
Trachinotus carolinus	Florida pompano	350	2	Pfeiffer and Riche 2001, [60]
Cromileptes altivelis	Humpback grouper	2	3	Hong and Zhang 2003, [61]
Dentex dentex	Common dentex	54	3	Suquet *et al.*, 2009, [62]
Diplodus sargus	White seabream	24	3	Suquet *et al.*, 2009, [62]
Diplodus vulgaris	Common two-banded seabream	0	3	Suquet *et al.*, 2009, [62]
Epinephelus akaara	Hong Kong grouper	0	3	Hong and Zhang 2003, [61]
Epinephelus tauvina	Greasy grouper	5,354	3	Hong and Zhang 2003, [61]
Evynnis japonica	Crimson seabream	0	3	
Liza vaigiensis	Squaretail mullet	0	3	
Lutjanus argentimaculatus	Mangrove red snapper	5,357	3	Hong and Zhang 2003, [61]
Lutjanus russelli	Russell's snapper	13	3	Hong and Zhang 2003, [61]
Melanogrammus aeglefinus	Haddock	0	3	Roselund and Skretting 2006, [63]
Pagellus bogaraveo	Blackspot seabream	2	3	Suquet *et al.*, 2009, [62]
Pagellus erythrinus	Common pandora	0	3	Suquet *et al.*, 2009, [62]
Platax orbicularis	**Orbicular batfish**	**8**	**3**	**Coeurdacier and Gasset 2013, [64]**
Pollachius pollachius	Pollack	0	3	Roselund and Skretting 2006, [63]
Pseudocaranx dentex	White trevally	3,155	3	
Rhabdosargus sarba	Goldlined seabream	3	3	Hong and Zhang 2003, [61]
Sciaena umbra	Brown meagre	0	3	Bilio 2007a, [65]
Seriola dumerili	Greater amberjack	0	3	Hong and Zhang 2003, [61]

Table A1. *Cont.*

Solea senegalensis	Senegalense sole	640	3	Imsland 2010, [66]
Solea solea	Common sole	45	3	Imsland 2010, [66]
Sparidentex hasta	Sobaity seabream	551	3	Teng *et al*., 1999, [67]
Takifugu obscurus	**Obscure pufferfish**	**4,860**	**3**	**Kim *et al.*, 2010, [68]**
Takifugu rubripes	**Tiger pufferfish**	**19,359**	**3**	**Wu *et al.*, 2015, [69]**
Thunnus orientalis	Pacific bluefin tuna	16,624	3	Carter *et al*., 2010b, [59]
Trachurus japonicas	Japanese jack mackerel	958	3	Masuda 2006, [70]
Umbrina cirrosa	Shi drum	1,070	3	Suquet *et al.* 2009, [62]
Acanthopagrus latus	Yellowfin seabream	0	4	Hong and Zhang 2003, [61]
Acanthopagrus schlegeli	Blackhead seabream	1,161	4	Hong and Zhang 2003, [61]
Anarhichas minor	Spotted wolfish	0	4	Le François *et al.* 2010, [71]
Argyrosomus regius	Meagre	6,659	4	Lazo *et al*., 2010, [72]
Diplodus puntazzo	Sharpsnout seabream	250	4	Suquet *et al*., 2009, [62]
Hippoglossus hippoglossus	Atlantic halibut	1,485	4	Imsland 2010, [66]
Larimichthys croceus	Large yellow croaker	105,230	4	Bilio 2007b, [56]
Lateolabrax japonicus	Japanese seabass	129,334	4	Hong and Zhang 2003, [61]
Mugil cephalus	Flathead grey mullet	12,245	4	Hong and Zhang 2003, [61]
Pagrus auratus	Silver seabream	59,616	4	Suquet *et al*., 2009, [62]
Pagrus pagrus	Red porgy	350	4	Suquet *et al*., 2009, [62]
Rachycentron canadum	Cobia	43,395	4	Bilio 2007a,b, [56,65]
Sciaenops ocellatus	Red drum	62,197	4	Lazo *et al*., 2010, [72]
Sebastes schlegeli	Korean rockfish	23,757	4	Bilio 2007b, [56]
Dicentrarchus labrax	European seabass	161,059	5	Jobling *et al*., 2010, [73]
Gadus morhua	Atlantic cod	4,252	5	Björnsson *et al*., 2010, [74]

Table A1. *Cont.*

Paralichthys olivaceus	Bastard halibut	39,445	5	Bilio 2007b, [56]
Psetta maxima	Turbot	76,998	5	Hulata 2001, [75]
Sparus aurata	Gilthead seabream	173,062	5	Jobling and Perruzi 2010, [76]

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