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Review

Diversity of Seahorse Species (*Hippocampus* spp.) in the International Aquarium Trade

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Abstract: Seahorses (*Hippocampus* spp.) are threatened as a result of habitat degradation and overfishing. They have commercial value as traditional medicine, curio objects, and pets in the aquarium industry. There are 48 valid species, 27 of which are represented in the international aquarium trade. Most species in the aquarium industry are relatively large and were described early in the history of seahorse taxonomy. In 2002, seahorses became the first marine fishes for which the international trade became regulated by CITES (Convention for the International Trade in Endangered Species of Wild Fauna and Flora), with implementation in 2004. Since then, aquaculture has been developed to improve the sustainability of the seahorse trade. This review provides analyses of the roles of wild-caught and cultured individuals in the international aquarium trade of various *Hippocampus* species for the period 1997–2018. For all species, trade numbers declined after 2011. The proportion of cultured seahorses in the aquarium trade increased rapidly after their listing in CITES, although the industry is still struggling to produce large numbers of young in a cost-effective way, and its economic viability is technically challenging in terms of diet and disease. Whether seahorse aquaculture can benefit wild populations will largely depend on its capacity to provide an alternative livelihood for subsistence fishers in the source countries. For most species, CITES trade records of live animals in the aquarium industry started a few years earlier than those of dead bodies in the traditional medicine trade, despite the latter being 15 times higher in number. The use of DNA analysis in the species identification of seahorses has predominantly been applied to animals in the traditional medicine market, but not to the aquarium trade. Genetic tools have already been used in the description of new species and will also help to discover new species and in various other kinds of applications.

Keywords: aquaculture; CITES Trade Database; cryptobenthic fishes; FishBase; identification; pygmy seahorses; species discovery; World Register of Marine Species (WoRMS)

Citation: Koning, S.; Hoeksema, B.W. Diversity of Seahorse Species (*Hippocampus* spp.) in the International Aquarium Trade. *Diversity* **2021**, *13*, 187. https://doi.org/10.3390/d13050187

Academic Editor: Michael Wink

Received: 16 February 2021
Accepted: 23 April 2021
Published: 29 April 2021

1. Introduction

1.1. International Trade in Marine Ornamental Fishes

Apart from their role in the global food industry, marine fisheries are also engaged in the collection and export of tropical ornamental marine fishes for the international aquarium trade, which is a growing industry involving thousands of species and millions of individuals per year [1–7]. Most marine aquarium fish are still taken from the wild, in particular from coral reefs and surrounding environments, providing low-income coastal communities with a livelihood but also causing the aquarium industry to attract controversy in terms of sustainability [8–10]. This trade is connected with severe ecological risks, such as overharvesting of some species and destructive collecting methods [8,11–15] and the introduction of non-native species in the importing countries [9,16–20]. Collecting ornamental fish with the help of nets [21–23] can cause a pollution problem when the nets are lost and animals are strangled in them [24]. Other concerns are raised around the high mortality rate due to bad conditions during transport and the lack of proper husbandry facilities along the supply chain [10,25,26]. Shallow-water marine habitats are already under pressure due to the results of climate change, unsustainable fishing, land reclamation, and pollution. It is therefore vital that the collection of marine fish for aquaria does not cause further damage [27]. One group of marine animals popular in the global ornamental fish trade and vulnerable to population decline are the seahorses (*Hippocampus* spp.). The charisma of seahorses makes them iconic flagship species to address challenges and solutions in marine conservation [28].

1.2. International Trade in Seahorses (Hippocampus spp.)

Seahorse species (Syngnathidae: Hippocampus) are also among the fishes that are subject to overfishing and other anthropogenic disturbances, such as habitat loss [29]. Millions of seahorses are collected each year globally to meet the demand of the traditional Chinese medicine market and the marine ornamental industry [28,30–34], which are mostly caught by nonselective fishing methods and partly as bycatch [35–40] but also by hand [41]. *Hippocampus* species range in maximum body length from about 1.5 cm in length to 35 cm (Table 1) and are characterized by their fused jaws, prehensile tail, bony plated skeleton, and typical upright posture [42,43]. Owing to their characteristic appearance and suitable size, seahorses are popular among sea aquarium hobbyists. Seahorses have a unique reproduction style in which the female deposits eggs in an abdominal chamber of the male, where the young are incubated [43]. Seahorses are live bearers, which means that after the eggs are fertilized and brooded, the male gives birth by releasing tens to hundreds of juveniles into the water [44].

At present, there are 48 accepted *Hippocampus* species (Table 1). They occur in tropical and subtemperate shallow waters all over the world but mostly in the Indo-Pacific [30,45,46]. The combined pressure from habitat degradation as a result of anthropogenic and natural disturbances, and illegal and unregulated fishing of seahorses, has raised concerns over the overexploitation of some species [28,47]. This led to the inclusion of all *Hippocampus* species (as the first marine fishes) into Appendix II of CITES (Convention for the International Trade in Endangered Species of Wild Fauna and Flora) since 2002 with implementation in 2004 [33,48–50]. This means that all CITES Parties need to ensure that international trade does not harm wild populations; CITES does not directly address threats that are not related to international trade [51–53]. A party to CITES is a state or regional economic integration organization for which the Convention has entered into force. At present, there are 183 Parties [54]. Four Parties (Guinea, Senegal, Thailand, and Vietnam) had difficulties following the CITES regulations and became the focus of a CITES Review of Significant Trade, which eventually resulted in trade suspensions for these four countries [49]. These regulations and the concern about overexploitation have stimulated the replacement of the fishing of wild seahorses by commercial aquaculture, thereby possibly reducing the effects on natural populations as suggested earlier [55,56].

1.3. Captive Breeding

Cultivation of ornamental organisms entails the spawning, hatching, settling, and growth of juveniles and adults in an enclosed system [57]. Around 90% of freshwater ornamental fishes are cultured, whereas only 10% of marine ornamental species are estimated to come from commercial aquaculture [2,58]. The aquaculture of marine aquarium fish is significantly less advanced, and this industry has been slow to develop and is not widely accessible [59–62]. The aquaculture of seahorse species is a relatively new venture, with rising demand and market prices [43,51,63]. The commercial culture of seahorses could provide an alternative income for subsistence fishers and accommodate a future rise in global demand [55,64,65].

Table 1. *Hippocampus* species ranked by year of description, with accepted names according to WoRMS [66] and FishBase [67], threat status [68], first year of recorded live or dead specimens (with purpose T = commercial trade) in CITES Trade Database (included if >25 individuals) [69], and maximum recorded length (with references). IUCN Red List categories that apply: NE = Not Evaluated, DD = Data Deficient, LC = Least Concern, VU = Vulnerable, EN = Endangered.

Name	IUCN Status	First CITES Record		Maximum Length (cm)
		Live	Dead	
H. hippocampus (Linnaeus, 1758)	DD	1997	2003	15.0 [30]
H. erectus Perry, 1810	VU	1997	2011	19.0 [30]
H. trimaculatus Leach, 1814	LC	1997	2004	22.0 [70]
H. abdominalis Lesson, 1827	LC	1999	2007	35.0 [30]
H. guttulatus Cuvier, 1829	DD	1997		21.5 [71]
H. comes Cantor, 1849	VU	2003	2004	18.7 [30]
H. coronatus Temminck & Schlegel, 1850	DD	1997		13.3 [72]
H. kuda Bleeker, 1852	VU	1997	2003	17.0 [30]
H. mohnikei Bleeker, 1853	VU	1997	2003	8.0 [30]
H. camelopardalis Bianconi, 1854	DD			10.0 [30]
H. whitei Bleeker, 1855	EN	2002		13.0 [30]
H. algiricus Kaup, 1856	VU	2004	2004	19.0 [30]
H. histrix Kaup, 1856	VU	1997	2003	17.0 [30]
H. lichtensteinii Kaup, 1856	NE			4.0 [30]
H. ingens Girard, 1858	VU	1998	2004	31.0 [30]
H. breviceps Peters, 1869	LC	2002		10.0 [30]
H. angustus Günther, 1870	LC	1999		16.0 [30]
H. tristis Castelnau, 1872	NE			18.0 [73]
H. subelongatus Castelnau, 1873	DD	2004		20.0 [30]
H. planifrons Peters, 1877	LC	2011		11.6 [74]
H. zosterae Jordan & Gilbert, 1882	LC	1998		2.5 [30]
H. capensis Boulenger, 1900	EN	2000		12.0 [30]
H. jayakari Boulenger, 1900	LC	1998		14.0 [30]
H. kelloggi Jordan & Snyder, 1901	VU	2005	2003	28.0 [30]
H. sindonis Jordan & Snyder, 1901	LC			10.8 [72]
H. fisheri Jordan & Evermann, 1903	LC			8.0 [30]
H. barbouri Jordan & Richardson, 1908	VU	2002	2005	15.0 [30]
H. dahli Ogilby, 1908	LC			14.0 [46]
H. spinosissimus Weber, 1913	VU	1998	2004	17.2 [30]
H. reidi Ginsburg, 1933	NT	1997	2007	17.5 [30]
H. zebra Whitley, 1964	DD	2004		9.4 [30]
H. bargibanti Whitley, 1970	DD			2.4 [30]
H. minotaur Gomon, 1997	DD	2007		5.0 [30]
H. jugumus Kuiter, 2001	DD			4.4 [74]
H. colemani Kuiter, 2003	DD			2.7 [75]
H. denise Lourie & Randall, 2003	DD	2004		2.1 [30]
H. patagonicus Piacentino & Luzzatto, 2004	VU			15.0 [76]
H. pusillus Fricke, 2004	DD			2.8 [77]
H. pontohi Lourie & Kuiter, 2008	LC			1.7 [75]
H. satomiae Lourie & Kuiter, 2008	DD			1.4 [75]
H. debelius Gomon & Kuiter, 2009	DD			2.4 [78]
H. tyro Randall & Lourie, 2009	DD			6.1 [79]
H. waleananus Gomon & Kuiter, 2009	NE			1.8 [80]
H. paradoxus Foster & Gomon, 2010	DD			6.5 [81]
H. casscsio Zhang et al., 2016	DD			13.3 [82]
H. haema Han et al., 2017	NE			11.4 [72]
H. japapigu Short et al., 2018	NE			1.6 [80]
H. nalu Short et al., 2020	NE			2.2 [83]

Although available cultivation techniques already promote acceptable survival rates for some species, there still is a need to improve culture protocols, especially in terms of nutrition and microbiological aspects [57,84,85]. Moreover, over the past few decades, there have been many studies on the harmful effects of aquaculture on the environment [86–90].

The benefits and risks of aquaculture as well as the potential social and ecological implications need to be assessed before aquaculture can be considered a solution [91].

1.4. Research Aim

The aim of this study is to provide insights into the status of international trade in *Hippocampus* species for the aquarium industry and the extent to which aquaculture can meet the demands in the international trade of marine ornamental fishes. By analyzing available trade data from the CITES Trade Database [69], this review gives an overview of the worldwide seahorse diversity, their use in genetic studies, the current status of seahorse trade with regards to their extinction status according to the IUCN (International Union for Conservation of Nature) Red List of Threatened Species [68,92], maximum lengths of all species, the most traded species (popularity), the difference between numbers of wild-caught and cultured species, the most important import and export countries, and of trends in trade over time. This study also aims to give an overview of current methods of seahorse aquaculture, to highlight potential pitfalls and challenges, and to identify priorities to facilitate a sustainable seahorse trade for future years.

2. The Natural History of *Hippocampus* Species

2.1. Species Discovery: Nominal and Valid Species

In order to better understand the presence and absence of *Hippocampus* species in the international aquarium trade, an overview of the species discovery is presented. Based on data from FishBase and the World Register of Marine Species [66,67], a total of 124 nominal *Hippocampus* species have been described, 48 (39%) of which are considered valid (Figure 1; Table 1). Thus, nearly 60% of the nominal species names are unaccepted synonyms. Most species (both nominal and accepted) were described in the middle of the 19th century (1841–1860) and in the last two decades (2001–2020).

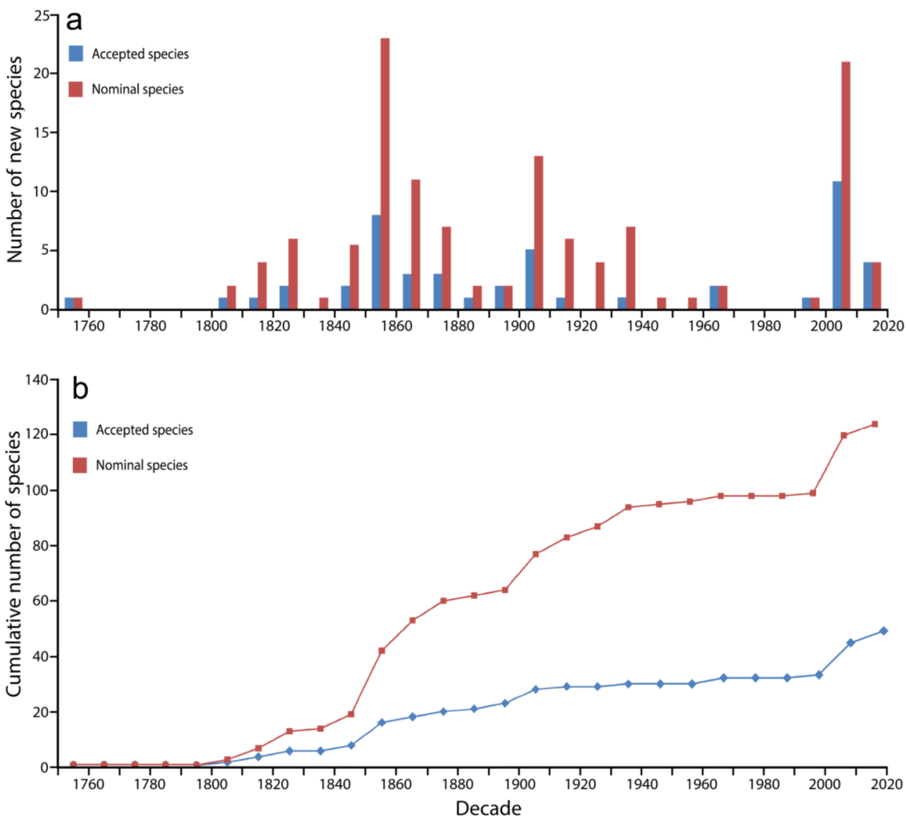

Figure 1. Description of new *Hippocampus* species, accepted and nominal (1758–2020): numbers per decade (**a**) and cumulative (**b**). Original data from FishBase and WoRMS [66,67]. Accepted species are listed in Table 1.

2.2. Body Size and Habitat Requirements

Several recently described species are relatively small and known as pygmy seahorses (Table 1). When body size is plotted against the year of description (Table 1), there appears to be a significant negative relation, indicating that many of the smaller species were discovered later than the larger ones (Figure 2). It is obvious that small species, also known as cryptobenthic fishes, are less conspicuous and therefore more difficult to find and also that they are less well-known than their larger relatives, as also seen in other fish families [93–95]. Some pygmy seahorses are considered host-specific, such as *H. denise* (Figure 3a) and *H. bargibanti*, which are usually observed when they are attached to gorgonian octocorals of the genus *Annella* or other genera [96–107]. Pygmy seahorses use camouflage, mimicking the background of their host, which in addition to their small body size, makes them difficult to detect (Figure 3a).

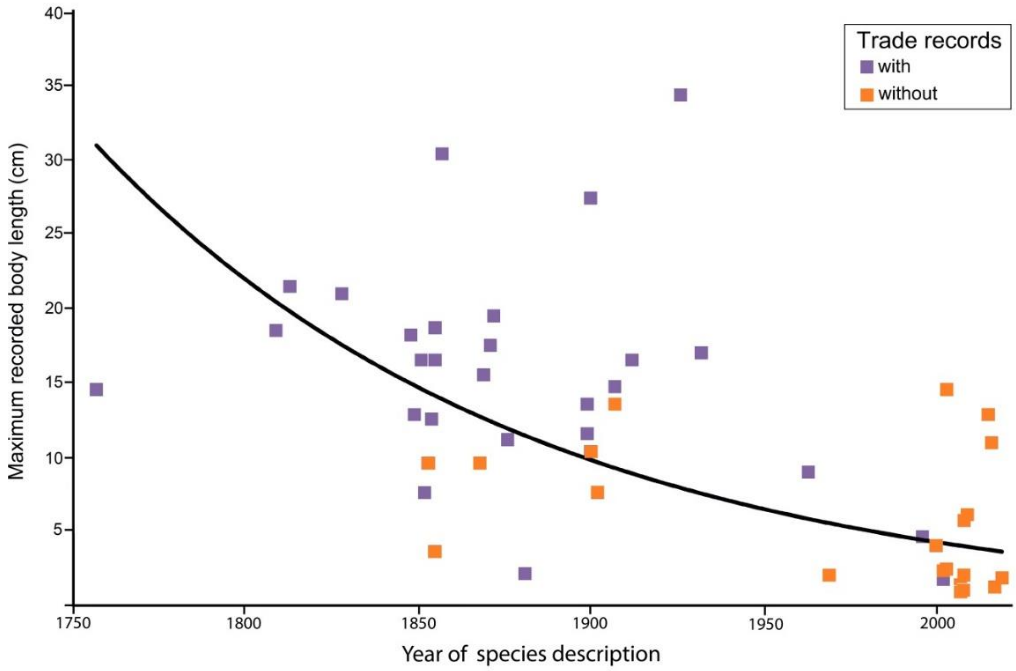

Figure 2. Maximum length of newly described *Hippocampus* species (1758–2020, n = 48), with and without trade records [69], based on data in Table 1, showing a tendency for additional new species to become exponentially smaller in size, approaching the function $y = 60.17 \times 10^6 \times e^{-0.01x}$ (Pearson correlation coefficient, ln-transformed (R = −0.675, $p < 0.00001$).

Large seahorse species that are commonly fished, such as *H. reidi* (Figure 3b), are overall less specific in their habitat requirements but share several traits with small congenerics, such as the use of camouflage and an immobile body posture while using the tail as holdfast [29,108] (Figure 3b), but some species are able to change coloration as part of their courtship behavior [109,110] or need for camouflage [103]. A few species are exceptional and show much interspecific variation in coloration, including bright tints [29,111] and biofluorescence [96,112]. Various large seahorse species are commonly found in seagrass beds [113–118], and as they can be monitored easily by recreational divers as citizen scientists [119], they can also be handpicked by professional fishermen. A broad habitat spectrum, as seen in *H. reidi* [120–122], probably enhances a species' suitability as an aquarium pet. As seahorses are poor swimmers, the availability of a holdfast is an important habitat factor [123,124], which may explain why some species have no problem in using artificial substrates to cling on [125–132].

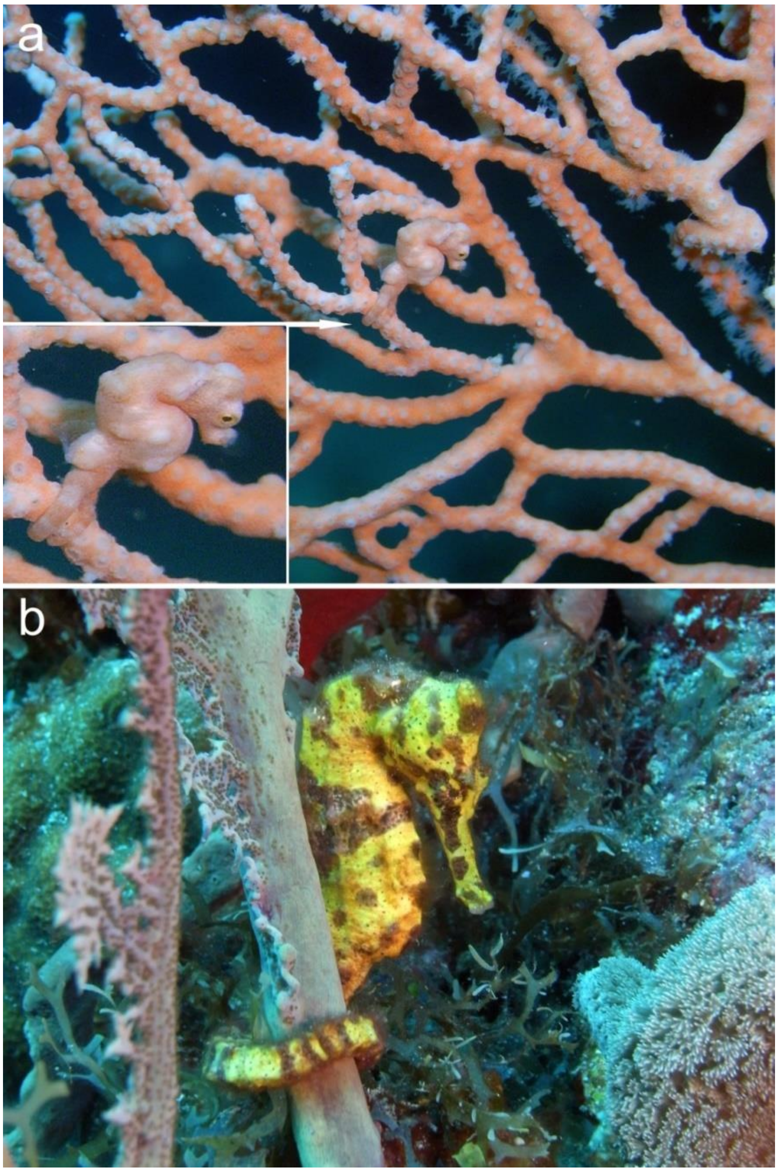

Figure 3. Two *Hippocampus* individuals clinging to gorgonian octocorals in their natural environment: (**a**) *H. denise* at Raja Ampat Islands, West Papua, Indonesia (2006); (**b**) *H. reidi* at St. Eustatius, Eastern Caribbean (2015). Photo credit: B.W. Hoeksema.

3. *Hippocampus* Species in the International Aquarium Trade

Regarding the trade of seahorses in the aquarium industry and those used as traditional medicine, there are differences in scale, species composition, source countries, and consumer countries, which can be found in primary sources, such as the CITES Trade Database [69] and also in published reports [133].

3.1. Hippocampus and CITES

For the present research, the presence of these species in the international aquarium industry was determined using the CITES Trade Database [69], as in some previous studies [33,134,135]. The data were analyzed to provide trade information based on export- and import-reported quantities of *Hippocampus* species and most important import and export countries, differences between countries, and trends over time. The search parameters in the database consist of year range, exporting and importing countries, source (e.g., wild-sourced or cultured specimens), purpose of the transaction (e.g., commercial, scientific, zoo), trade terms (e.g., live specimens, dead bodies), and taxon (species, genus). The quantities of the transaction could be either expressed in weight or number of individuals, but only number of individuals was used in the present analysis concerning live animals. Data extracted from the database were available for the years 1997–2018, but we need to keep in mind that not all data represent global trade before CITES, as those of 1997–2004 only denote trade reported by EU member states (seahorses have been listed on EU Annex D since 1997) and some voluntarily reports from other countries. Only data reported since 2004 are global in scope.

In our analyses, all importing and exporting countries and all trade purposes were included. Only "live" specimens were considered in the trade terms. Sources only included codes "W" (taken from the wild), "U" (unknown), "C" (captive-bred), and "F" (born in captivity as F1 generation from wild-caught parents F0). When a source is "U" or not mentioned, the trade database assumes that it concerns "W". This is most evident in pre-CITES data, when there was no recorded trade in cultured specimens (Table 2). Seahorses that were reared in captivity are considered cultured (coded as "C" and "F"). Numbers of seahorses that were ranched were negligible and therefore not taken into account. Re-exports, although uncommon, were excluded from the analyses to prevent duplicates. For example, 200 specimens of *H. zosterae* (W) were exported from the United States to the Netherlands in 2017 and re-exported to Mexico in 2018 [69]. Individuals of the same species were exported to Canada in 2010, Germany in 2012, South Africa in 2015, and returned to the United States in the same years [69]. The CITES trade database does not include data on domestic trade, mortality of seahorses in captivity, or cultivation in import countries.

Table 2. Import numbers (individuals) of live-traded *Hippocampus* species in the EU over 1997–2003 [69] (ranking 1 to 12). *Hippocampus* spp. = other species and unidentified. Source: C = captive-bred, F = born in captivity, W = wild-caught, U = unknown and unmentioned. Re-exports are excluded.

Species	C	F	W	U	Total
H. abdominalis (6)	0	0	769	0	769
H. barbouri (11)	40	0	0	0	0
H. comes (10)	0	0	35	6	41
H. erectus (2)	0	0	21,107	6632	27,739
H. hippocampus (3)	0	0	1727	3838	5565
H. histrix (9)	0	0	104	0	104
H. ingens (5)	0	0	1	1000	1001
H. kelloggi (12)	0	0	0	0	0
H. kuda (1)	0	0	29,285	22,156	51,441
H. reidi (4)	0	0	3557	1070	4627
H. spinosissimus (8)	40	0	70	58	168
H. zosterae (7)	0	0	233	0	233
Hippocampus spp.	40	0	40,409	10,254	50,703
Total	**120**	**0**	**97,297**	**45,014**	**142,431**

Of the 48 recognized *Hippocampus* species, 27 are represented in the international aquarium trade (Table 1). According to EU import data, in 1997–2003 more than 142,000 live *Hippocampus* individuals were exported to the EU alone (Table 2). In 2004–2018, after CITES became effective, a total of almost 680,000 live *Hippocampus* individuals were recorded as import (Table 3) and more than 1,090,000 as export (Table 4). Export data are generally higher because countries are not obliged to report imports, although some source countries also do not report exports. In some cases, annual species numbers reported by an import country appear to be higher than those of the export country [69].

Before 2004, there was almost no trade in cultured specimens (Table 2), but this changed when CITES became effective (Tables 3 and 4). Among the cultured animals, several species were predominantly reported as C (e.g., *H. reidi*, *H. abdominalis*, and *H. ingens*) and others mostly as F (e.g., *H. kuda*, *H. comes*, and *H. histrix*), which may depend on the biology of the species or perhaps on the preferred cultivation method in the source countries.

There were also shifts in species composition. In 2005–2013, *H. kuda* was by far the most important traded *Hippocampus* species, followed by *H. reidi* and *H. comes* (Figure 4). For some species, such as *H. barbouri*, *H. histrix*, *H. kelloggi*, and *H. spinossimus*, reported quantities were relatively large around 2004–2005. For a few species, it appears that the number of traded individuals was highest before 2004 (e.g., *H. erectus* and *H. abdominalis*) and gradually decreased after CITES became implemented (Figure 4).

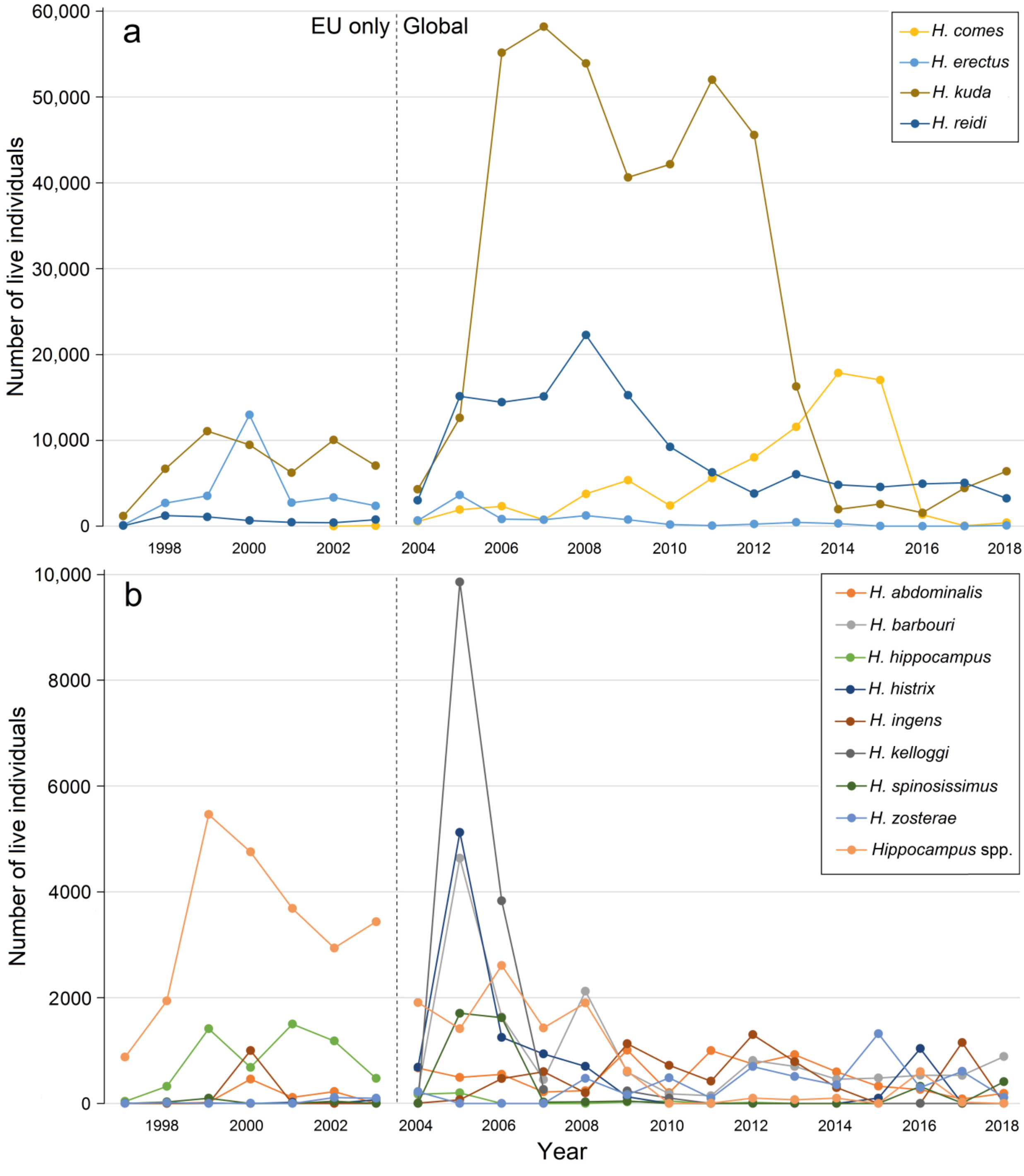

Figure 4. Annual trade records of live seahorses based on import data of the 12 internationally most traded species in the periods 1997–2003 (pre-CITES records from the EU) and 2004–2018 (global) [69]: (**a**) high annual numbers; (**b**) lower numbers.

The most important difference in species composition between the aquarium trade and the traditional medicine market is that the first is richer in species [133]. Rare species are absent in both markets, but some additional species have a low market value as dried specimens because they are generally too small, such as *H. mohnikei*, which is widespread in Asia [136–138]. Some species are rarely traded alive but commonly traded as dried specimens, such as *H. trimaculatus*, which occurs in the central Indo-Pacific [139] and is fished in several Asian countries [38,139–143]. A number of species are much marketed both as live specimens (Tables 2–4) and dried material, such as *H. comes*, *H. erectus*, *H. kelloggi*, and *H. kuda* [133,134,144].

Table 3. Import numbers (individuals) of the most live-traded *Hippocampus* species worldwide over 2004–2018 [69] (ranking 1 to 12). *Hippocampus* spp. = other species and unidentified. Source: C = captive-bred, F = born in captivity, W = wild-caught, U = unknown and unmentioned. Re-exports are excluded.

Species	C	F	W	U	Total
H. abdominalis (8)	6748	0	243	156	7147
H. barbouri (5)	5167	906	8235	0	14,308
H. comes (3)	6972	61,867	9480	5	78,324
H. erectus (7)	179	1060	7684	160	9083
H. hippocampus (12)	200	20	86	82	388
H. histrix (6)	1037	100	8578	20	9735
H. ingens (9)	3968	0	3146	8	7122
H. kelloggi (4)	0	300	14,037	0	14,337
H. kuda (1)	54,951	231,079	103,337	1065	390,432
H. reidi (2)	105,357	1038	18,723	116	125,234
H. spinosissimus (11)	627	80	3424	0	4131
H. zosterae (10)	4	1448	2805	190	4447
Hippocampus spp.	5919	1607	6997	123	14,646
Total	**191,129**	**299,505**	**186,775**	**1925**	**679,334**

Table 4. Export numbers (individuals) of the most live-traded *Hippocampus* species worldwide over 2004–2018 [69] (ranking 1 to 12). *Hippocampus* spp. = other species and unidentified. Source: C = captive-bred, F = born in captivity, W = wild-caught, U = unknown and unmentioned. Re-exports are excluded.

Species	C	F	W	U	Total
H. abdominalis (4)	26,732	60	165	828	27,785
H. barbouri (5)	6170	2354	14,630	0	23,154
H. comes (3)	30,690	110,986	13,185	0	154,861
H. erectus (9)	1509	505	9786	0	11,800
H. hippocampus (12)	24	0	20	0	44
H. histrix (6)	0	5650	14,637	0	20,287
H. ingens (8)	11,532	0	3216	0	14,748
H. kelloggi (7)	0	0	15,024	0	15,024
H. kuda (1)	71,009	367,645	60,372	0	499,026
H. reidi (2)	291,464	0	12,340	0	303,804
H. spinosissimus (10)	431	0	7029	0	7460
H. zosterae (11)	1644	194	1880	0	3718
Hippocampus spp.	3114	81	6547	324	10,066
Total	**444,319**	**487,475**	**158,831**	**1152**	**1,091,777**

3.2. Threat Status and Body Size of Hippocampus Species in the Aquarium Trade

Various *Hippocampus* species (33%) present in the trade are classified as "Data Deficient" (DD), which are mostly species that have been discovered in the last two decades (Table 1). This may indicate that abundances of these species are very low, sightings are rare, and that they may actually be endangered [145]. Most of the recently discovered species have an IUCN Red List status of Data Deficient (DD) or have not yet been evaluated (NE) (Table 1). The 12 most traded *Hippocampus* species in the aquarium industry

(Table 2, Figure 4) are among the species that were discovered early, in the period 1758–1933 (Table 1). Eight of these species have the conservation status "Vulnerable" (VU).

Most species of no commercial value are relatively small and have been discovered recently, two factors that appear to be related (Figure 2). This is also reflected in a minimum size limit of 10 cm height proposed in fisheries [146–148], which is not relevant for most species that are not of commercial importance. It is plausible that species that have been discovered recently (Table 1) are not yet known in the international trade of ornamental fishes and have not been listed in the CITES Trade Database. Among the small species, the dwarf seahorse, *H. zosterae*, described in 1882 (Table 1), is an exception because it is among the 12 internationally most traded *Hippocampus* species (Tables 2–4; Figure 4). There is no export to the United States as this species is native to that country [40,149,150].

3.3. Life History Traits and Habitats of Hippocampus Species

Whether *Hippocampus* species are suitable as aquarium pets depends on their life histories and whether they can survive outside their natural habitats. There are various special handbooks that give advice to hobby aquarists regarding the husbandry of seahorses [151–156], and some deal exclusively with the dwarf seahorse, *H. zosterae* [157–159]. Specific information on seahorse husbandry in public aquariums is also available [103,160]. Because the life span of seahorses is very short, varying from 1 to 5 years [29], aquarium owners have to replace individuals very quickly, either by new purchases or by breeding. The number of newborn young released from the male's brooding pouch varies between 5 and 2000, mostly depending on the body size of the species [29].

The absence of some *Hippocampus* species in the trade is related to their late discovery and their cryptic lifestyle (Section 2.2), but it is also possible that they are just too rare for wild capture [102] or that their habitat requirements are very specific and cannot be copied in an aquarium environment [103]. Because host occupancy rates were observed to be low in some symbiotic pygmy seahorses [97] and underwater photographers tend to disturb their natural environment [161,162], it is fortunate that these species appear to be uncommon in the aquarium industry. In 2004–2006, 1800 individuals of *H. denise* were recorded as exported from Indonesia, whereas only 504 specimens were listed as imported in Europe and the United States [69]. In contrast, the dwarf seahorse, *H. zosterae*, can be found abundantly in shallow seagrass beds in the Gulf of Mexico and the east coast of Florida [30,163], where they can be collected with the help of nets [40,149,150,164], which explains why they are available in the aquarium industry [157–159]. This species produces much offspring [149,164], whereas *H. denise* in association with gorgonians shows low population densities [97,102] and a low reproduction rate [107].

Some larger species (at least 8 cm long) cannot be found in the international aquarium trade because they may be rare or occur in a relatively small distribution range. An example is *H. camelopardalis*, which has a restricted range in the southwestern part of the Indian Ocean [30,165], although there is also an incidental record from northwestern India [166]. Another example is *H. tristis,* a relatively large and very rare species, which is endemic to southern Australia and only known from a few museum specimens and a recent photograph [73]. Other species with restricted ranges are *H. sindonis*, which is only known from Japan and Korea [167], and *H. fisheri* from the Hawaiian Islands [168] with some doubtful records from eastern Australia and New Caledonia [30]. The absence of these rare species in CITES trade records does not imply that they are never caught for the aquarium trade, although this is unlikely for the extremely rare *H. tristis.* Another explanation for the absence of trade records is that some species cannot be kept alive in aquariums, such as *H. fisheri* [169]. Some trade records are based on misidentifications, such as those of *H. capensis*, an endemic to South Africa [111,115,129] (Section 4.5). Sixty live specimens of this species were reported as export from South Africa: 30 captive-bred (C) to China in 2010 for education and 30 that were born in captivity to a zoo in Hong Kong in 2014. These records do not count as commercial trade [69].

3.4. Sources of Live Hippocampus Spp.

As trade numbers of seahorses at the species level for 1997–2018 are only available as import records, trends in source data (wild-caught vs. cultured) can only be analyzed for that period, but with a distinction between pre-CITES EU-only records and CITES global records (Figure 4). Importing countries appeared to be most consistent in reporting over that period. Before 2004, trade records of *H. barbouri*, *H. histrix*, *H. ingens*, *H. kelloggi*, *H. kuda*, *H. spinosissimus* were close to zero. Later import records of these species increased and reached a peak. *Hippocampus histrix*, *H. kelloggi* and *H. spinossimus* reached this trade peak around 2005. Overall, trade in most species decreased over the years. Exceptions are *H. abdominalis*, *H. ingens*, and *H. zostera*. *Hippocampus erectus* and *H. hippocampus* show relatively high trade numbers before 2004 (before CITES), with a strong decline in trade after that year. Before CITES became implemented (before 2004), all live-traded *Hippocampus* individuals were sourced from the wild (Figure 5). A shift from wild-caught to captive-bred export became evident after 2004, when the regulation became implemented [50], although the quantity of wild-caught seahorses still dominated trade numbers. The turning point came around 2007, when the number of traded wild-caught seahorses started to decline and the quantity of traded cultured seahorses began to increase (Figure 5).

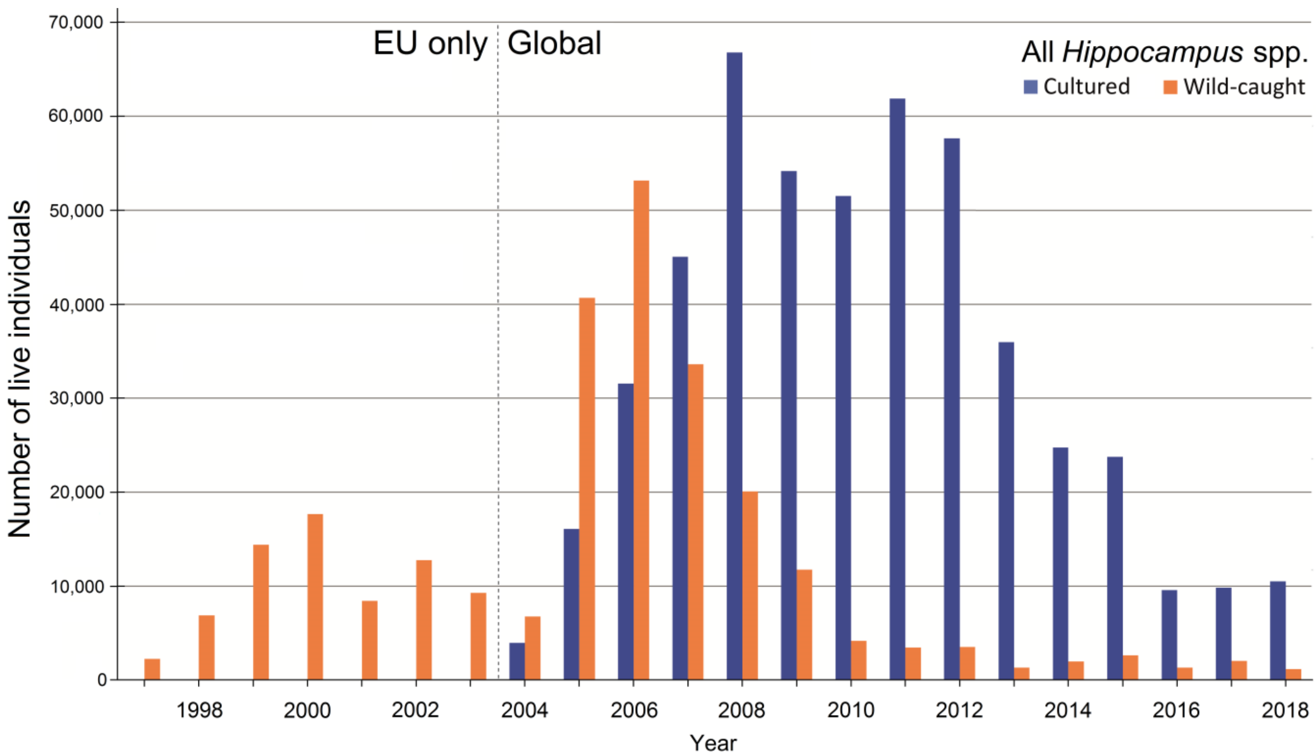

Figure 5. International trade in cultured (C + F) and wild-caught (W + U) *Hippocampus* specimens based on CITES import data for the period 1997–2018 [69]. Data from before 2004 concern the EU only.

For the whole period 1997–2018, most internationally traded live seahorses came from a cultured source (Tables 2–4). The majority of the specimens of *H. kuda*, *H. reidi*, *H. comes*, *H. abdominalis*, and *H. ingens* came from cultivation (Figure 6a–c,i,j), whereas the majority of individuals of *H. barbouri*, *H. erectus*, *H. hippocampus*, *H. histrix*, *H. kelloggi*, *H. spinosissimus*, and *H. zosterae* came from the wild (Figure 6d–h,k,l).

In 2004–2018, Vietnam was the main exporting country of live *Hippocampus*, covering almost 50% of the traded individuals (Figure 7a). Since 2004, there was a substantial increase in cultured seahorses reported from this country, which could have been facilitated by advances in seahorse husbandry and captive breeding [170]. Foster et al. [33] suggest that this could partly be due to misreporting of wild-caught animals as captive-bred, intentionally or as a mistake. The possibility of continued illegal and unregulated trade resulting in poor-quality trade data makes it difficult to assess the results of seahorse culture on the exploitation of wild populations [51]. The majority of traded seahorses from Indonesia and Brazil were wild-caught. For most source countries, it is unclear how many seahorse individuals are caught for the domestic market or for private use, depending on whether it is allowed to take live animals (with or without permits).

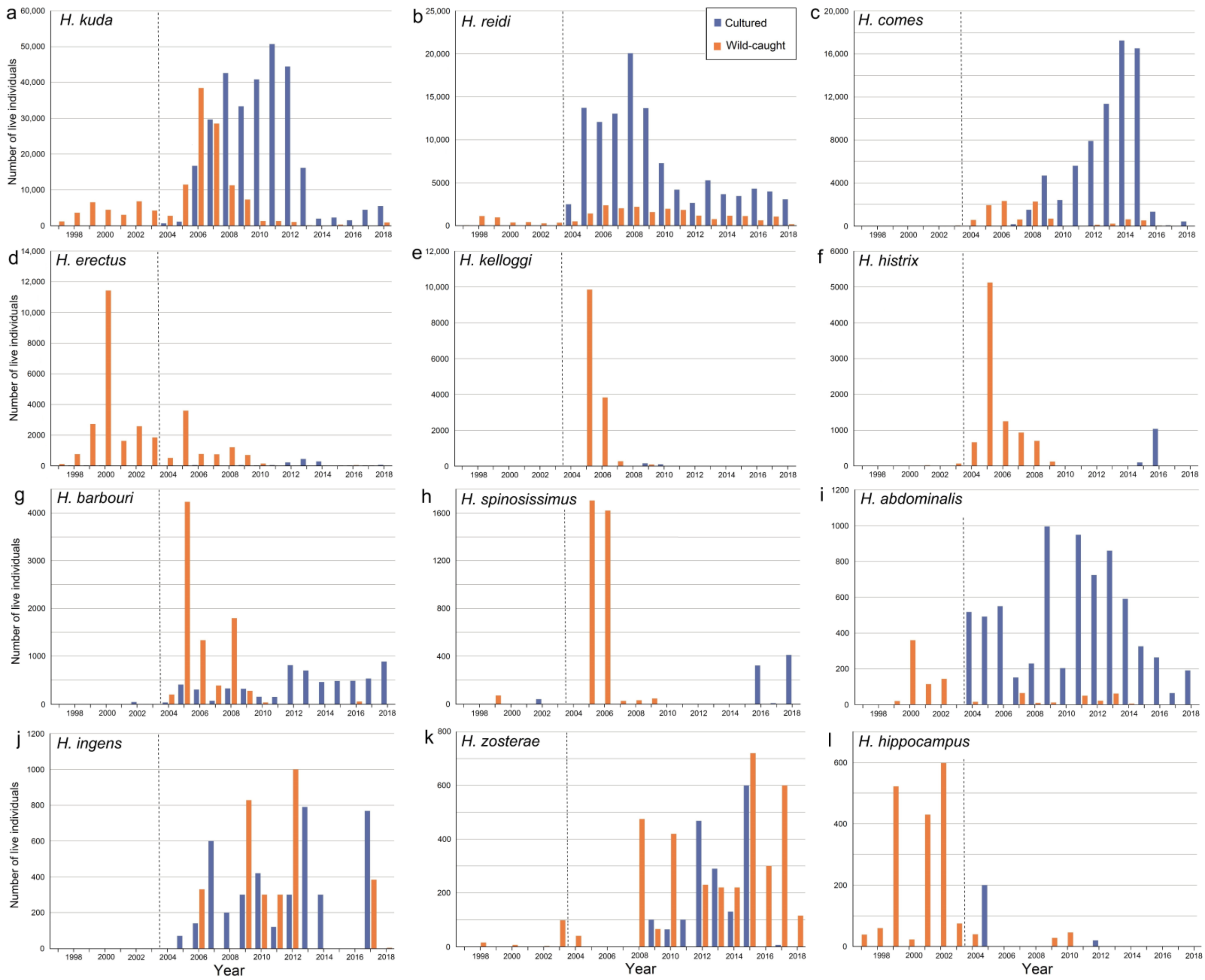

Figure 6. Import data for the 12 most traded *Hippocampus* species in the period 1997–2018 [69]. Data from before 2004 concern the EU only. Cultured = C + F; wild-caught = W + U.

The United States was by far the largest importer of live *Hippocampus* (Figure 7b), while it also has domestic trade of the native *H. zosterae* [171,172]. Almost a third of the imported seahorses came from a cultured source. Apart from the US, Canada, Japan, and Singapore, other important importing countries are located in Europe. For the EU single-market, trade among member states is not recorded in the CITES trade database.

3.5. International Trade in Live Animals vs. Dead Bodies

Trade in live seahorses is as young as the international aquarium industry, catering to hobbyists all over the world, whereas the use of seahorses as traditional medicine has its roots in China [173,174]. With growing imports from other countries and Chinese consumers migrating to other countries, this market became larger and more international. Although most seahorses in the international trade are dried, in some source countries the trade in live specimens for the international aquarium industry has been a threat for natural populations before CITES became effective [30], and many specimens are still wild-caught (Tables 3 and 4). CITES trade records for live *Hippocampus* individuals and (dried) dead bodies show striking differences in composition and timing (Table 1). While 27 traded species have been recorded as live animals, only 18 have also been listed as dried bodies [33]. With the exception of *H. kelloggi*, the first trade record of each species concerned living animals, whereas dead bodies were recorded one to several years later, suggesting that trade in live animals is more transparent than that of dried specimens.

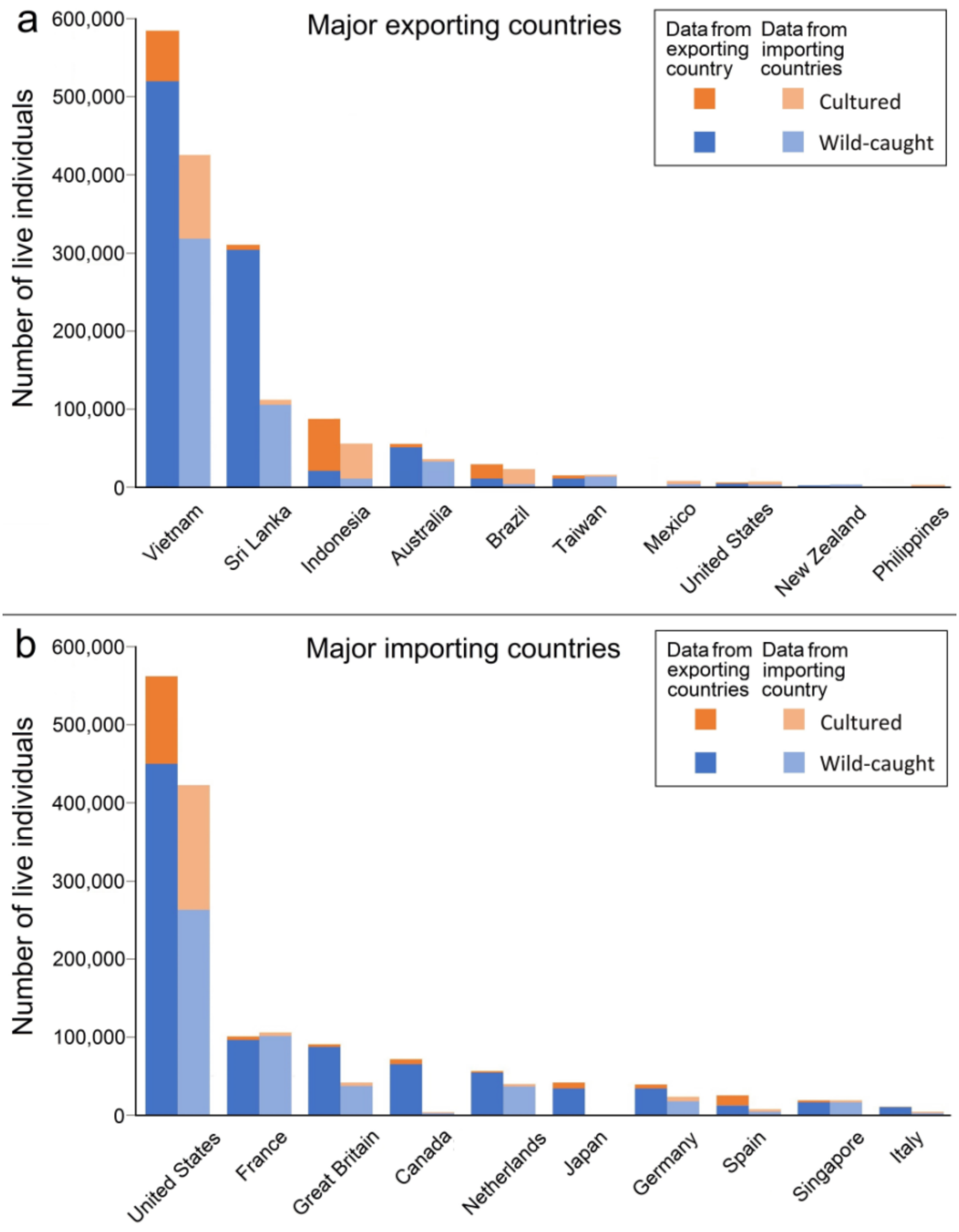

Figure 7. Trade in live *Hippocampus* individuals by source category, wild-caught (W + U) or cultured (C + F), for the 10 most important exporting (**a**) and importing (**b**) countries in 2004–2018 [69]. A distinction is made between data from exporting countries and importing countries.

The international trade of *Hippocampus* is divided into two separate markets. For instance, *H. algiricus* from West Africa is rare in the aquarium trade and commonly sold as medicine [33,175]. Most early import data (1997–2003) are pre-CITES records from the EU, which are mostly unrelated to the medicine market (Section 3.1). However, it is likely that since 2004, large proportions of dead seahorses in the international trade have also not been reported [176,177]. Because of their dry conservation, they are of low weight and they can be densely packed (in concealing packaging), which makes them easy to store and inexpensive to ship. Nevertheless, in the Philippines, dried seahorses appear to provide 2–4 times better prices to fishermen than live individuals [41]. An increase in the market price of dried seahorses was noticed after the CITES listing in 2002 [178].

Trade in live specimens is more difficult because the animals need to be packed in water and shipped as quickly as possible (as air freight) in order to prevent mortality [179,180]. The overall trade in *Hippocampus* spp. showed a decrease in the issue of export permits after CITES became effective in 2004, but this did not concern live individuals (Figure 5) as much as dried specimens [50]. Possible explanations are (1) some countries were unable to shift towards sustainable trade, (2) there was a lack of support because not enough people were involved in the fisheries, or (3) the export volume might have been too low [50]. This trend is particularly shown by *H. histrix*, *H. kelloggi*, and *H. spinosissimus*, almost all of which were wild-caught. The declining trend in trade volume may also have been the result of declining seahorse populations instead of trade regulations [50]. Therefore, depending on the species, (illegal) trade of dried specimens may also affect seahorse populations exploited for the international aquarium trade.

4. Aquaculture of *Hippocampus*

Less than 5% of the ca. 1500 marine ornamental fish species in the international aquarium trade are kept in aquaculture [181,182], and various *Hippocampus* species (Figure 6) are part of this minority. The cultivation of *Hippocampus* spp. is currently only serving the trade in ornamental fishes, as attempts of large-scale farming for the traditional medicine markets have not been successful [44]. As mentioned in Section 3.1, the trade data indicate large differences among species in source preference for either breeding in captivity (C) or born in captivity (F), which may depend on whether species can be cultivated easily or not (Tables 3 and 4).

4.1. Methods of Seahorse Aquaculture

Aquaculture of seahorses can be divided into three parts: production of live prey (usually *Artemia* sp. and copepods), keeping of breeders, and maintenance of a nursery facility for juveniles as they grow into an appropriate size [43,44,51,181,183]. There is no larval breeding stage because fertilized eggs are incubated inside the male's pouch [43,184–187]. Seahorse species in captivity usually become sexually active at ages of around 3 to 6 months. During the breeding season, they maintain a long-pair bond and are generally monogamous in a single breeding cycle; therefore, selection of the male is important for the fitness and survival of the young [109,114,183]. Hatching periods usually vary between 14 and 40 days but can be shorter at high temperatures [188]. The pygmy seahorse *H. denise* has shown a gestation period of only 11 days in captivity [107]. Many seahorse species have multiple batches of eggs during a breeding season, when temperatures and photoperiods are kept constant in culture operations [189].

In terms of husbandry, seahorses are sensitive to changes in water chemistry. It is therefore important that the aquarium habitat mimics their natural habitat [43]. Moreover, the keeping of good broodstock and the selection of healthy mating pairs are very important. Seahorses that are kept in optimal conditions will spawn naturally [43]. The diet of seahorses in the wild predominantly consists of small pelagic crustaceans, such as amphipods, copepods, and mysids [190–196], but nematodes are also important prey, depending on the habitat [197,198]. Prey shape and size are very much determined by the form of the seahorse head, in particular the long and tubular snout, and by their special feeding behavior, including suction and pivot feeding [199–205]. Most seahorse culture operations rely on cultured live food such as *Artemia* (brine shrimp), copepods, mysid shrimps, rotifers, and amphipods, but some also rely on wild-collected food [206–208]. Studies have demonstrated a variety of diets for different species, but enriched food seems to benefit both juvenile and adult seahorses and their reproduction success [51,209,210]. Skin color in seahorses, which can be variable in some species [109,110,211], is an important attribute in the aquarium industry and can depend on diet [2,212]. Individuals with the brightest color are sold for prices up to USD 500, or even higher in exceptional cases [43].

4.2. Challenges in Seahorse Aquaculture

Although aquaculture of seahorses is often thought of as a commercial venture and as a means to reduce pressure on wild populations, it could also result in negative effects on the marine environment and its populations. Firstly, the economic viability of seahorse aquaculture poses a concern. As rearing brood to market size can take months, it is still unclear whether the aquaculture industry can provide sufficient volumes of *Hippocampus* specimens in a cost-effective way to supply the demand [213]. Low survivorship of juveniles is a major problem in seahorse aquaculture [63,189,214,215]. Moreover, the acceptability and price of cultured seahorses are matters that need to be determined beforehand [216]. Economic constraints include costs of local electricity and water and heating unit efficiency [63]. Until production costs can be optimized or market prices rise, expansion of seahorse cultivation can be limited in developed countries. In developing countries, on the other hand, the main challenge of seahorse aquaculture is related to technical problems, such as rearing and diseases [51]. Under farmed conditions, seahorses experience stress, which increases their susceptibility to infection and diseases [217].

A variety of seahorse diseases have been reported to cause mass mortalities and damage to aquaculture operations, including bacterial, fungal, viral, parasitic, and noninfectious diseases [182,218]. For example, vibriosis is a bacterial infection found in aquarium and aquaculture operations worldwide, causing severe ulcers in the skin of species such as *H. kuda* [218–220], while other microbes can cause enteritis, which is also found in other cultured fish species [221–225]. Thus, apart from the problems these pathogens create for current aquaculture operations and the extra control and prevention measures that are required, the pathogens pose a danger to other fish species [218]. This highlights the requirement of further research into potential drugs and the development of disease resistance in seahorses.

The need for proper maintenance and water changes, water quality, cleaning, and feeding regimes are extremely important in aquaculture [182,226]. Most aquaculture operations rely on the use of intensive monoculture systems, which means that the animals are kept in aquaria under controlled water parameters and depend on exogenous feeding to survive. Feeding can create various challenges regarding the type of diet for different species at different life stages [227]. Moreover, cultivation of high volumes of live food can be inefficient, expensive, and difficult, while it also can facilitate the introduction of diseases [63,66,67,228–230]. Furthermore, as most culture operations have open or semiclosed systems, problems related to effluent, water use, and escapes are very common in seahorse cultivation [51]. Aquaculture can therefore also result in potential damage to the marine environment. Lastly, the success of aquaculture practices also partly depends on how well it can accommodate alternative livelihoods for subsistence fishers in source countries [51,55,231]. Aquaculture is likely to be most effective in reducing pressure on wild populations if seahorse fishers in source countries are facilitated to shift towards a more sustainable seahorse trade.

4.3. Aquaculture in Different Source Countries

CITES Parties strive to record all transactions, but some countries (e.g., Sri Lanka) recorded large volumes of seahorses for some years while having no records for other years [33]. According to the CITES trade data [69], the number of captive-bred seahorses increased after the listing of *Hippocampus* species in CITES, especially for Vietnam and Sri Lanka. Even though the export of live *Hippocampus* individuals in Vietnam is well documented in the CITES database, it appears that there are some doubts concerning the renaming of cultured species [232]. After the ban on the export of *H. kuda* in 2013, reported exports of *H. kuda* born in captivity (source code F) decreased by 99%, whereas exports of *H. comes* (with F) increased 5 times. However, Vietnamese companies reported to have only produced low numbers of *H. comes* in the past. Moreover, just one aquaculture farm remained in operation and reported that they only cultured *H. kuda*. It seems that Vietnam clearly has been dependent on wild-caught seahorses for its export, whereas its import of live seahorses from other countries, such as Cambodia and Indonesia [133,232], has only rarely taken place [69]. Aquaculture facilities struggle to close the life cycle. They primarily produce F1 generation—the offspring is born in captivity, but pregnant males are caught in the wild. Therefore, it appears that the commercial culture of seahorses is still reliant on wild broodstock [232].

In Sri Lanka, researchers were able to establish a successful culturing protocol to breed *H. reidi* artificially. Hettiarachchi and Edirisinghe [233] describe broodstock management and rearing of *Hippocampus* juveniles and how to develop various color varieties. The broodstock feeding consisted of a mixed diet of enriched *Artemia*, mysid shrimps, and estuarine copepods. After 5–6 months, *H. reidi* individuals reached marketable size with mean survival rates at 65 $\pm$ 5%. By culturing non-native *Hippocampus reidi*, culture operations in Sri Lanka were able to prove that their export was captive-bred and thus allowed to continue export under CITES regulations [28].

Indonesia is the main exporter of *H. barbouri* (W), and exporters have indicated a willingness to shift towards seahorse culture [231]. A study on the success of implementing a culture project for *H. barbouri* in Indonesia found that aquaculture could not fully replace fishing in livelihoods but instead could partly supplement and diversify fishing and collecting from the wild [231]. Exporters had great interest in cultivated seahorses, as they also experienced the results of depleted marine environments, but the economic feasibility and aquaculture technology need to be improved. Moreover, aquaculture needs to be part of a larger and multifaceted approach that also targets and improves habitat protection and restoration, makes livelihoods and stakeholders more diverse, and improves the enforcement of fishing regulations [234].

For some countries, such as the Philippines, the live trade of seahorses ceased after the listing of *Hippocampus* species under CITES. No records are known of illegal or unreported trade. However, according to Foster et al. [22], the Philippines used to run some seahorse aquaculture companies in the past and continues to show interest in this industry, leaving room for potential aquaculture operations in the future.

4.4. Opportunities for Hippocampus Aquaculture

When aquaculture operations struggle with diet and disease, systems provisioning natural food might be more efficient and could enhance results [181]. One example is an integrated multitrophic aquaculture system (IMTA) that uses the cage-culture approach. Fonseca et al. [213] developed a system in which *H. reidi* individuals were cultured in free-moving cages inside a shrimp and oyster farm, proving to be technically feasible, profitable, and resilient.

Another example concerns a cage culture of *H. reidi* that was set in mangrove estuaries in Brazil [235]. When cages with seahorses are installed in mangrove ecosystems, the fish have direct access to their natural prey [29,236,237]. In the Philippines, artificial light was used in an experiment to lure copepods into cages containing *H. barbouri* in order to provide the seahorses with prey [238]. Another study demonstrated a successful integrated eco-aquaculture system in which *H. kuda* individuals were cultured in artificial ponds with fertilized water to nourish natural seahorse food and co-cultured seaweed in order to regulate water quality and light and to provide holdfasts and prey for seahorses [239]. Another study showed that integrating macroalgae in the production system was beneficial for the survival and growth rate of juvenile *H. erectus* [240]. These low-cost culturing methods offer numerous opportunities for subsistence fishers and could potentially increase environmental and social sustainability in low-income communities. Commitment of local stakeholders can contribute to reduced reduction of the illegal, unregulated, and undeclared collection of wild seahorses [181]. However, there are also some constraints related to these production systems, such as creating an ecological imbalance in estuaries, net blockage, predators, and escapees [235].

Over the years, seahorse aquaculture methods and techniques have improved, but this sector is still facing many challenges, such as cost-effective production, diet, and diseases. Seahorse aquaculture still mainly relies on wild broodstock to continue its culture operations [51,57]. This will become effective if subsistence fishers are encouraged to shift towards a more sustainable way of seahorse trade. The marine ornamental fish industry is a great opportunity for source countries to become involved in community-based conservation-focused aquaculture initiatives [231,241]. Therefore, seahorse aquaculture should be encouraged to focus on the cultivation of local species and operate in the source countries.

Unless seahorse fishers can derive enough income from aquaculture to sustain their livelihood, there will be no incentive to protect their biological resources and shift towards more sustainable measures [51,216]. By involving local communities in aquaculture practices, it will be easier to reduce the illegal trade of wild seahorses and increase ecological and social sustainability [181]. In recent years, more research has been done on developing low-cost aquaculture techniques such as IMTA aquaculture systems that use the cage-culture approach. These newer aquaculture methods are promising as they are low-cost, feasible, profitable, resilient, and most of all can be more easily implemented in important export countries.

Even if there is a shift towards aquaculture operations, this will not motivate fishers to prevent the capture of seahorses as bycatch because they still use nonselective fishing methods such as trawling [140,242]. Therefore, increased efforts are needed to improve seahorse-fishing methods [23]. Since CITES records cannot keep track of domestic trade; illegal, unregulated, or unreported exports; or misidentifications [144,243,244], it is important that representative trade field surveys are maintained in areas that are known to export wild seahorses [245].

To better understand why some seahorses are more popular in the aquarium trade, it is also important that more research be done on the relationship between, for example, the length of seahorse species and their presence in trade. Moreover, to improve differentiating between cultured and wild-caught seahorses, tagging methods should be developed for captive-bred seahorses along with a certification and registration system for aquaculture facilities in which they are bred [51]. Furthermore, efforts should be made to motivate aquarium hobbyists to choose cultured seahorses instead of wild-caught ones, as long as these come from original source countries [51]. Lastly, there are still some constraints with IMTA systems that should be dealt with in order to develop a trustworthy cultivation protocol. Economic, environmental, and social sustainability should be assessed to ensure that cage culture is realistic and sustainable [235].

Public awareness of the diversity of seahorses and their reproductive biology, ecology, and iconic shape may also play a role in their conservation. The number of scientific publications on seahorses published each year is growing steadily (around 40 yr^{-1} in 2011–2016), most of them dealing with *Hippocampus kuda*, *H. guttulatus*, *H. reidi*, *H. abdominalis*, *H. erectus*, *H. hippocampus*, and *H. trimaculatus* [181]. Interestingly, among these most-studied species, *H. guttulatus* and *H. trimaculatus* are not among the 12 species that are most common in the aquarium trade (Tables 2–4). Among these 12, seven are not well investigated: *H. comes*, *H. barbouri*, *H. kelloggi*, *H. histrix*. *H. ingens*, *H. zosterae*, and *H. spinosissimus*. In other words, there is a discrepancy between seahorse species popular in trade and science, with some traded species appearing to be understudied.

Fishers can be a valuable source of useful information regarding the trade and aquaculture of seahorses, not only for scientists but also for tourists [143,246–250]. Public aquariums can help in the development of seahorse breeding, which is particularly important for endangered species [57,231,251–255]. Thanks to aquarium experiments, we know more about the reproduction of pygmy seahorses [103,107], but little is known about the lifespan of these rare species because they are hard to keep [104]. Public aquariums can also be used to study stress displayed by seahorses in captivity [251]. Although it may seem controversial, hobby aquarists and the aquarium industry can assist in the research on seahorse husbandry and conservation [255–257].

4.5. Use of Molecular Tools in Hippocampus Diversity Research

Animals and plants in the international trade, their organs or body parts, and particular products derived from them may be difficult to identify based on morphological characteristics alone. This problem is also recognized in the international trade of seahorses, with less than 10% of the specimens consisting of live animals and the rest of dried carcasses that are traded in large quantities, possibly composed of mixed species [258]. One of the latest developments in scientific research on the diversity of seahorses concerns the identification of specimens with the help of modern molecular techniques.

DNA analyses of various CITES-listed species groups have been performed on specimens found in markets or in international shipments, which helped to identify them at the species level. Since 2003, this technique became known as barcoding and started by using the universal mitochondrial gene cytochrome *c* oxidase I (COI) as a marker [259]. Recently, new technologies have allowed the development of more specific markers and studies of entire genomes [260]. It is a prerequisite that material used as original reference should be identified by taxonomic experts before they become deposited in barcoding libraries (such as GenBank) and that these libraries are as complete as possible [256,261].

There are many examples of barcoding applied to CITES-listed taxa, most of which concern terrestrial plants [262–267] and vertebrates [268–272]. Barcoding of marine animals in the international trade has been widely applied to sharks [273–279], for which advanced genetic technologies are available [280]. Regarding the international marine aquarium trade, identification with the help of barcoding has been applied only to an illegally traded scleractinian coral, which was published in 2020 [281], whereas the need for the barcoding of marine ornamental fish species was already promoted in 2009 [282].

Molecular studies on *Hippocampus* species are not scarce, involving 35 of 48 species (Table 5). The first paper in which genetics was applied to distinguish seahorse species was a study by Lourie et al. in 1999 [32], which was based on specimens sampled from Vietnamese markets.

Table 5. *Hippocampus* species (Table 1), with geographical range, and numbers of molecular studies for five categories of application (with references; e.g., [283–382]). $ = in international aquarium trade, ¥ = in traditional medicine [69,133].

Species Name	Geographical Range	Application of Molecular Analyses				
		Barcoding/ Genomics	Forensics/ Conservation	Phylogeny Reconstructions	Phylogeography	Functional Genetics
H. abdominalis $¥	SW Australia, New Zealand [165,347,348]	1 [283]	1 [32]	13 [186,287,305,308, 309,323,331–337]	2 [347,348]	3 [128,361, 362]
H. algiricus $¥	West Africa [39,165]	1 [283]	1 [320]	11 [288,289,295,299,302, 323,333,335,338–340]	1 [339]	—
H. angustus $¥	N Australia, South P.N.G. [165]	—	—	3 [322,335,341]	—	1 [363]
H. barbouri $¥	Central Indonesia, Philippines [165,341,342]	3 [284,285,344]	4 [321–324]	24 [186,284,287,288,299, 302,305,308,309,314, 315,317,322,323,333– 338,341,343,344,380]	2 [341,342]	—
H. bargibanti	Central Indo–West Pacific [165]	1 [83]	—	4 [42,331,334,335]	—	—
H. breviceps $	Southern Australia [165]	1 [286]	—	5 [42,76,323,335,338]	—	—
H. camelopardalis $¥	SW Africa [165]	1 [287]	1 [325]	7 [287,295,305,323, 325,335,338]	—	—
H. capensis	Southern tip of Africa [165,339,349,350]	4 [283,288, 289,350]	3 [320,324, 325]	11 [288,289,295,305, 309,323,325,335, 338,339,345]	3 [339,349, 350]	—
H. casscsio	South China Sea (SE China) [82]	3 [82,289,344]	—	3 [82,289,344]	—	—
H. colemani	Lord Howe Is., E Australia [165]	—	—	—	—	—
H. comes $¥	Central Indo–West Pacific [165]	5 [284,290–292, 344]	[32,321, 322,324]	26 [76,186,284,287,288, 299,302,305,308,309, 314,315,317,322,323, 333–338,341,343,344, 380,381]	—	—
H. coronatus $	Japan, South Korea [72,165]	—	—	6 [72,76,323,333,335,338]	—	1 [364]
H. dahlia	N, E Australia [165]	—	—	—	—	—
H. debelius	N Red Sea (Gulf of Suez) [78,165]	—	—	—	—	—
H. denise $	Central Indo–West Pacific [165]	2 [83,283]		2 [331,334]	—	—
H. erectus $¥	W Atlantic, Caribbean Sea [165,339,340,351,352]	6 [284,293–297]	1 [324]	23 [76,186,284,287,288, 295,299,302,305,311, 314,315,317,322,323, 332,333,335,337– 339,343,380]	4 [339,340, 351,352]	6 [365– 369,382]
H. fisheri	Hawaii [165,168,339]	1 [168]	—	6 [308,309,335,336, 339,340]	1 [339]	—
H. guttulatus $¥	W Europe, Mediterranean, Black Sea [165,339,353]	1 [298]	4 [326–329]	8 [295,323,333–335, 338–340]	2 [339,353]	4 [370–373]
H. haema	Japan, South Korea [72]	—		2 [72,333]	—	—

Table 5. *Cont.*

Species Name	Geographical Range	Application of Molecular Analyses				
		Barcoding/ Genomics	Forensics/ Conservation	Phylogeny Reconstructions	Phylogeography	Functional Genetics
H. hippocampus $¥s	E Atlantic, Mediterranean [165,339]	1 [299]	2 [326,329]	12 [76,295,299,305,311, 323,333–335,338–340]	1 [339]	2 [373,374]
H. histrix $¥	Indo–West Pacific [165]	5 [168,284,300, 344,378]	4 [32,320, 323,324]	20 [284,287,288,299,302, 305,309,314,315,317, 323,332–335,338,343, 344,380,381]	—	—
H. ingens $¥	East Pacific [165]	4 [284,301, 325,344]	5 [321–325]	27 [42,284,287–289, 299,305,308,309,314,315, 317,322,323,325,331–335, 337–339,343–345,380]	2 [339,354]	—
H. japapigu	Japan [80]	2 [80,83]	—	—	—	—
H. jayakari $	Red Sea, NW Indian Ocean [165]	1 [302]	1 [324]	4 [287,302,305,333]	—	—
H. jugumus	Lord Howe Is., Eastern Australia [165]	—	—	—	—	—
H. kelloggi $¥	Indian Ocean, West Pacific [165,339]	3 [284,303, 344]	6 [32,34,320–322,324]	21 [284,287,288,299, 302,303,305,308,316, 317,322,323,332–335, 338,339,343,344,381]	1 [339]	—
H. kuda $¥	Indo–West Pacific [165]	9 [168,283, 284,291,304–307,344]	7 [32,320–322,324, 325,330]	35 [76,82,186,284,287–289,299,302,307–309, 314–317,322,323,325, 331–339,343–346, 379–381]	8 [300,339, 342,345, 355–358]	1 [375]
H. lichtensteinii	Red Sea [30]	—	—	—	—	—
H. minotaur $	SE Australia [165]	—	—	—	—	—
H. mohnikei $¥	East, South, SE Asia [136,138,165,359,360]	7 [284,293,303, 308,309, 344,380]	4 [32,321, 322,324]	20 [81,284,287,288,299, 302,303,305,308,309, 322,323,325,333–335,338,344,380,381]	4 [136,138, 359,360]	—
H. nalu	E South Africa [83]	1 [83]	—	—	—	—
H. paradoxus	SW Australia [81,165]	—	—	—	—	—
H. patagonicus	SW Atlantic [165]	5 [76,295,310–312]	—	4 [76,295,311,334]	—	—
H. planifrons $	Western tip of Australia [165]	—	—	—	—	—

Table 5. *Cont.*

Species Name	Geographical Range	Application of Molecular Analyses				
		Barcoding/ Genomics	Forensics/ Conservation	Phylogeny Reconstructions	Phylogeography	Functional Genetics
H. pontohi	Central Indo–West Pacific [165]	2 [80,83]	—	1 [331]	—	—
H. pusillus	New Caledonia [165]	—	—	—	—	—
H. reidi $¥	W Atlantic, Caribbean Sea [165,339]	4 [283,295,313, 314]	2 [324,377]	25 [42,76,287–289,295,299,302,305,308, 309,314,317,323,325,331, 333–335,337–339, 343,345,380]	1 [339]	2 [365,375]
H. satomiae	Eastern Indonesia [165]	—	—	—	—	—
H. sindonis	Japan, South Korea [72,163]	—	—	5 [72,287,305,333,335]	—	—
H. spinosissimus $¥	Central Indo–West Pacific [165]	4 [284,315–317, 344]	6 [32,34,320–322,324]	17 [284,287,288,299,302, 305,315–317,323,333–335,338,339,344,381]	3 [339,342, 358]	—
H. subelongatus $	SW Australia [165]	1 [286]	—	6 [308,314,323,335,338,341]	—	1 [361]
H. trimaculatus $¥	Central Indo–West Pacific [139,165,300,342,356,358,360]	4 [284,307,318] [344]	6 [32,34,320,321] [322,324]	24 [284,287,288,299,302, 305,307–309,314,315, 317,322,323,325,331, 333–335,338,343, 344,380,381]	6 [139,300,342, 356,358,360]	—
H. tristis	Southern Australia [73]	—	—	—	—	—
H. tyro	Seychelles [165]	—	—	—	—	—
H. waleananus	Eastern Indonesia [78]	—	—	—	—	—
H. whitei $¥	S, E Australia, P.N.G., Solomon Is. [165]	2 [283,319]	—	6 [323,331,334,335, 338,341]	—	—
H. zebra $¥	Northern Australia [165]	—	—	—	—	—
H. zosterae $	Gulf of Mexico, E Florida, Bahamas, Bermuda [164,165,172,339]	1 [283]	—	10 [42,76,186,311, 323,331,335–339]	2 [172,339]	1 [376]

The use of dry seahorses from markets was continued in later genetic studies [34,282,286,287,320,323–325], one of which was based on a single specimen originally identified as *H. capensis* [287]. Because this rare species is a South African endemic protected under CITES, its record from a foreign market triggered suspicions, and a subsequent molecular study has led to the conclusion that the specimen was misidentified [288]. This could not prevent a notice in a recent publication stating that this species is exported from Africa [178].

Molecular techniques may help to detect which species are represented in large shipments of dried seahorse, which are expected to be composed of multiple species mixes [258]. Another future application for molecular analyses could be the examination of gut contents of possible predators for the presence of seahorse DNA (as "environmental DNA" or eDNA). There appear to be very few reports on seahorse predators, such as crabs, cephalopods, fish, and sea turtles [248,383–385], while for the keeping of seahorses in mariculture and aquariums it may be useful to know more about their natural enemies.

Since 2003, various studies were aimed at the conservation genetics of rare species, starting with *H. capensis* [282,284]. Since 2013 [318], an increasing number of publications have presented the entire mitochondrial genome of *Hippocampus* species for identification purposes (Table 5), and many of these results were used in phylogeny reconstructions. So far, no studies were found in which barcoding was applied to the identification of seahorses in the aquarium trade. Thirteen apparently rare species with restricted distribution ranges in the Indo-Pacific have not been studied from a phylogenetic perspective: *H. debelius* and *H. lichtensteinii* in the Red Sea, *H. tyro* in the Seychelles, *H. satomiae* and *H. waleananus* in eastern Indonesia, *H. planifroms* in western Australia, *H. paradoxus* in southwestern Australia, *H. tristis* in southern Australia, *H. zebra* in northern Australia, *H. dahlia* in northern and eastern Australia, *H. colemani* and *H. minotaur* at Lord Howe Island (off southeastern Australia), and *H. pusillus* in New Caledonia (Table 5).

Most molecular seahorse studies involved phylogeny reconstructions, particularly those on species in the traditional medicine trade (Table 5). Molecular studies were also used to determine the taxonomic status of some *Hippocampus* species [32,168,316,319], including new ones [72,81–83]. They also found species that had been misidentified in local faunas [32]. For the conservation of seahorses, it is important to know which taxonomic names are valid and where species occur.

Phylogeographic studies tell us about how lineages within species populations are distributed (Table 5). In future studies, genetics can be applied to find out which seahorses and related species form unique phylogenetic lineages within the family Syngnathidae. This information, in combination with IUCN red list data, can be used to select evolutionary distinct taxa that need priority regarding research effort to support their conservation management, as previously done for corals and various other groups of organisms [386–388]. Meanwhile, it is very likely that new, cryptic species are going to be discovered in the coming years.

5. Conclusions

Most recent reports on the international trade in seahorses concern dead specimens, whereas live seahorses have received relatively little attention. This makes sense as live animals form a clear minority in the seahorse trade [389], but this does not mean that the market in live animals does not form a threat to the natural populations [30].

Nevertheless, in the international trade of marine ornamental fishes, seahorses form an important example by being the first species group for which trade is regulated under CITES. Because the popularity of these ornamental fishes is much related to their iconic appearance and reproduction mode [28,390], lessons learned from the seahorse trade may be useful for the protection of aquarium fishes that will enter future CITES listings. This will likely stimulate the cultivation of these other ornamental fish species and reduce the risk of overfishing, but it should not distract us from the need for the protection of their natural habitats.

The diversity of seahorse species present and absent in the aquarium industry is the central theme of this study, and therefore, much emphasis is placed on the history of species discovery, ecology, and body size. Specimen identification remains a common and recurrent problem in this industry. An overview of genetic studies shows that many seahorse species have been subjected to molecular analyses and that rare species in particular are not well represented. Hopefully, in the future, similar studies will be applied to other species in the international aquarium trade.

Author Contributions: Both authors contributed to the conceptualization, methodology, analyses, writing—original draft preparation, writing—review and editing, and project administration. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: The authors are very grateful to Sarah Foster (Project Seahorse, University of British Columbia) and two anonymous reviewers for constructive comments on the manuscript and to Martine Maan (GELIFES, University of Groningen) for remarks on the MSc essay by the first author that formed the basis for the present paper. The editors and managers of WoRMS [66], FishBase [67], the IUCN Red List [68], and the CITES Trade Database [69] are acknowledged for keeping seahorse data up to date.

Conflicts of Interest: The authors declare no conflict of interest.

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