Alien Fish Species in France with Emphasis on the Recent Invasion of Gobies

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Abstract

Introduction of alien species constitutes worldwide one of the major threats to biodiversity, particularly in freshwater ecosystems. In France, the number of alien aquatic plant and animal species has increased exponentially over time in freshwater ecosystems and shows no sign of decreasing. For fish only, more than 40 alien species have been either voluntary or involuntary introduced in the past decades. About two-thirds are still present today and at least 26 are naturalized. As in many European countries, the fish introduction history in France switched from voluntary introduction in the nineteenth century (aquaculture, sport fishing, and management of ecosystems) to unintentional but human-aided introductions (aquarium trade and global ship transport). The negative impacts of alien species on native species and ecosystems are most often unknown in France and needs further studies to develop a functional policy on alien species introductions and the protection of aquatic ecosystems integrity. The information gathered allow discussing the possible reasons explaining whether an alien species is able or not to establish sustainable populations in France and thereafter became invasive, such as gobies recently arrived.

Keywords: inland waters, invasive species, gobies, climate change

1. Introduction

Introduction of alien species (also sometimes called non-native, transplanted, or exotic with a slightly different meaning, see **Table 1**) constitutes worldwide one of the major threats to biodiversity, with alteration or destruction of habitats, pollution, overexploitation, and climate change [1, 2]. In freshwater ecosystems, the introduction of fish is considered as a significant component of human-caused environmental changes [3]. The rate of introductions has strongly

Term	Definition
Non-native or foreign	Species not occurring naturally in a geographic area
Exotic	Species introduced from other biogeographic realms
Indigenous or native	A species occurring naturally in a specific geographical area without human intervention
Introduced population	Population that arrives at locations not normally achievable by that species, with intentional or accidental human assistance
Naturalized	Self-sustaining populations in the wild of a non-native species
Invasive	Non-native species that spread and cause significant ecological changes or cause severe economic losses
Translocated	Species that is transported from a region where it is native to another part within the same country

Table 1. Definitions of the main terms used in the literature on fish introduction (modified after [16, 18, 34].

increased in the past century [4–7]. In France, for instance, the number of alien aquatic plant and animal species has increased exponentially in freshwater ecosystems from less than 10 prior to the beginning of the nineteenth century up to 148 today and shows no sign of decreasing [7].

For fish, the main causes of introduction of alien species are aquaculture [3, 6, 8], commercial and recreational fisheries [9, 10], aquarium fish market [11], and management of aquatic ecosystems [3, 12]. Introductions could also result from a spread following the human modifications of hydrosystems, such as the construction of canals [3, 13] or dams [14] that allow species to disperse by their own means or transported by ship ballasts [3, 15]. Today, more than 600 freshwater fish species have been introduced into areas outside their native range globally [16], which resulted in that more than half of the river basins across the world host at least one alien fish species [17]. Among these 600 species, Toussaint et al. [18] found that 14 are present into at least one of the 1054 river basins studied in the 6 biogeographic realms defined by [19]: Afrotropical, Australian, Nearctic, Neotropical, Oriental, and Paleartic. Three species are present in all six realms: rainbow trout (*Oncorhynchus mykiss*), common carp (*Cyprinus carpio*), mosquitofish (*Gambusia affinis*), and three more, goldfish (*Carassius auratus*), sea trout (*Salmo trutta*), and Eastern mosquitofish (*Gambusia holbrooki*) in five realms [18]. These few alien species contribute the most to the global homogenization pattern, whereas most introduced species have low impact on the global change in dissimilarity, i.e., beta-diversity [18]. The authors thus concluded that focusing conservation efforts in controlling the spread of these few species may be more relevant to counteract the global homogenization trend [18].

Most often, exotic species freshly introduced are not able to survive in their new environment and it is generally considered that only a low percentage succeeds to establish sustainable populations and become invasive [1, 20]. However, García-Berthou et al. [21] found that the average percentage established of the 123 alien aquatic species into six European countries (United Kingdom, France, Spain, Sweden, Germany, and Italy) is 63% (167 of 264 introductions), much higher than the 5–20% suggested by Willamson's "tens" [21]. Once established, the eradication of a freshwater non-native species is almost impossible [17], which is a real problem because it is still today very difficult to prevent new introductions and to predict the success and effects of invading species [20]. There is indeed no consensus about what makes a successful invader, even though some biological attributes have been proposed, among which a high environmental tolerance (e.g., eurythermal and euryhaline), a high genetic variability, a short generation span, a rapid growth, an early sexual maturity, a high reproductive capacity, and a broad diet [22]. Based on the analysis of 10 life-history traits between 13 non-native and 46 native freshwater fish species inhabiting the Central European biogeographical region, Grabowska and Przybylski [23] found that the former were significantly different from the latter. Non-native species tend to be small or medium in size, have a short longevity and mature early, a rather low fecundity but with large eggs, spawn at least twice each year over an extended reproductive season, and exhibit some form of parental care. MacDougall et al. [24] assume that the divergence in at least one biological attribute (on the basis that it results in a “fitness difference”) can better explain invasion success than a particular suite of specific life-history attributes [23]. For instance, the gibel carp (*Carassius gibelio*) possess a unique reproductive attribute (the eggs can be activated by the sperm of other cyprinid species, allowing the production of progeny in the absence of conspecific males), which probably partly explain why it is one of the most successful invader in Poland and more generally in Central Europe [23]. More broadly, the theory of MacDougall et al. [24] belongs to a vein of interest related to the ecosystem naiveté, with at least two hypotheses that can be extended to freshwater fish even if the latter has been mostly tested for terrestrial plants. Ricciardi and Atkinson [25] proposed the phylogenetic distinctiveness hypothesis: larger impacts are caused by exotic species that add novel taxa to the community. The evolutionary naïveté hypothesis [26, 27] assumes that impact of exotic species depends on the recipient community’s evolutionary experience with functionally similar species. Both hypotheses have originally been produced to explain the ecological impact of exotic species but can also be used to investigate their success in terms of establishment.

The success or failure of an alien species relies probably partly on its biological attributes (or on one or a few specific attributes) but also depends on the recipient ecosystem characteristics, including both biotic and abiotic factors [20, 28, 29]. All aquatic ecosystems seem potentially colonizable even though some might be more susceptible to invasion: simple systems (i.e., with rather low native species richness) or complex systems (i.e., species-rich communities) [17], geographically and historically isolated environments (e.g., islands), disturbed or anthropogenic habitats, or regions where no co-adapted foes, including competitors, predators, parasites, or diseases are present [30]. At last, the human-mediated propagule pressure (the number of individuals introduced as well as the frequency of introductions in a given area) is positively correlated with the establishment of alien species [1, 17]. Commensalism with human activity has also been found as one of the most consistent attribute of the success of invasive species [22, 30].

Most alien fish species have generally low impacts on native species and ecosystems [1], but high-impact invaders comprise at least 10% of the total number of invaders [31]. The main consequences of alien species on native species and ecosystems are varying and non-exclusive: hybridization, predation, competition, extirpation, dissemination of diseases and parasites, habitat change, and food web alteration [3, 12, 15, 32, 33]. In metropolitan France, more than one-third of the freshwater fish species are alien [7, 34]. Even though none has yet been documented in France as the cause of native species extinction, several of them are well known as causing major ecosystem disturbances.

The aim of the present chapter is first to reassess the knowledge acquired on alien fish species in France in the past years, and second to focus on the recent invasions of gobies in the north-east of the country [35] to dissect possible factors enhancing successful invasion.

2. Alien species in Europe and France

Several atlas and field guides have been written on the European fish fauna, among which the last and most completed was published 10 years ago [36]. It appears that this fauna is one of the poorest across the world as these authors only recognized 579 species in European freshwaters west of the Urals, particularly in comparison with the 13,000 freshwater fish species described in the world [19]. Among these 579 species, 33 have been introduced from regions outside Europe (North America and Asia in a large majority [37]), of which 28 are established [36]. Besides, much more species have been moved between European countries [34]. Consequently, Leprieur et al. [17] have highlighted that western and southern Europe regions are among the six areas where introduced species represent more than a quarter of all species. A database developed from the project DAISIE (Delivering Alien Invasive Species Inventories for Europe) was launched about a decade ago [38], and includes now more than 12,000 alien animals and plants in Europe (http://www.europe-aliens.org/). A total of 162 alien fish species (including diadromous) are listed in European freshwaters (an update of the 136 analyzed in [39]), among which 3: the round goby (*Neogobius melanostomus*), the pseudorasbora (*Pseudorasbora parva*), and the brook trout (*Salvelinus fontinalis*), are classified within the 100 of the worst alien species.

The French fish fauna has also been extensively studied in the past decades (e.g., [40–43]. Traditionally about 80 species were recognized [34], yet with the advent of the DNA barcoding and integrative taxonomy [44] several taxonomic revisions have been done: some new species have been described [45–47], others have been invalidated [48]. For instance, it was thought that the Northern pike (*Esox Lucius*) was the only species present in Europe, but recent integrative analyses based on both morphological and molecular characters concluded that three species are actually present in France, the Northern pike (which is the most common), *E. aquitanicus* (from the Charente to the Adour drainages), and *E. cisalpinus* (mostly in the Lake Geneva). Besides, more than 40 alien species have been either voluntary or involuntary introduced in the past decades in France [42]. Nearly one-third are no longer present in France (or their presence is very doubtful), among which several salmonids (*Oncorhynchus tschawytscha*, *O. kisutch*, and *Coregonus* spp.) and centrarchids (*Pomoxis* spp., *Lepomis* spp.) [42]. Among those that are still present today, most have established self-sustaining populations (**Table 2**); even though some occupied a very restricted area, such as the rock bass (*Ambloplites rupestris*) [49]. Few other alien species are probably not established, such as the rainbow trout *Oncorhynchus mykiss* or the grass carp *Ctenopharyngodon idella*. In total, the fish species richness has increased in the past decades [49] and there are today more than 100 species inhabiting France, which belong to 26 families. The two most speciose families are Cyprinidae (n = 40) and Salmonidae (n = 9), whereas 12 are monotypic, among which Gadidae [50].

The timing and reasons of introductions of alien species in France are, in general terms, similar to other European countries [3, 16, 34], such as in Belgium [51], Germany/Austria [52, 53],

Latin name	Date of first observation in France	Vectors of introduction	Native range	French name	References
Ambloplites rupestris	1904	Release: recreational fishing		Crapet des roches	[5, 41]
Ameirus melas	1871	Escape: from the "Museum National d'Histoire Naturelle"	North America	Poisson chat	[5, 40, 42]
Aspius aspius	1976	?		Aspe	[5, 40, 42]
Carassius auratus	Around 1750	Release: ornamental purposes		Carassin doré	[5, 40]
Carassius carassius	Around 1750	Release: aquaculture		Carassin commun	[5, 40]
Carassius gibelio	Around 1850	Release: aquaculture		Carassin argenté	[5]
Cobitis bilineata	Around 1995	Unintentionally introduced		Loche transalpine	[42]
Coregonus albula	1860	Release: recreational fishing		Petite marène	[5, 40]
Cyprinus carpio	Around 1250	Release: aquaculture		Carpe commune	[5, 42, 40]
Gambusia affinis	1924	Release: anti-mosquito biological control		Gambusie	[5, 42, 40]
Gambusia holbrooki	1924	Release: anti-mosquito biological control		Gambusie	[5, 42, 40]
Lepomis gibbosus	1977	Release: recreational fishing	North America	Perche soleil	[5, 42, 40]
Leuciscus idus	Around 1950	Dispersal: unintentionally introduced during stock enhancement		Ide mélanote	[5, 42, 40]
Micropterus salmoides	1890	Release: recreational fishing		Black-bass à grande bouche	[5, 42, 40]
Neogobius fluviatilis	2014	Dispersal: shipping	Ponto-caspian	Gobie fluviatile	Unpublished data
Ponticola kessleri	2011	Dispersal: shipping	Ponto-caspian	Gobie de Kessler	[35, 42]
Neogobius melanostomus	2011	Dispersal: shipping	Ponto-caspian	Gobie à taches noires	[35, 42]
Pachychilon pictum	Around 1980	?		Epirine lippue	[5, 42]
Proterorhinus semilunaris	2007	Dispersal: shipping	Ponto-caspian	Gobie demi-lune	[35, 42, 90]
Pseudorasbora parva	Around 1978	Escape: from aquaculture production unit		Pseudorasbora	[5, 42, 91]
Salvelinus fontinalis	1876	Release: recreational fishing		Omble de fontaine	[5, 42, 40]

Latin name	Date of first observation in France	Vectors of introduction	Native range	French name	References
Salvelinus namaycush	1886	Release: recreational fishing		Cristivomer	[5, 42, 40]
Sander lucioperca	Around 1880	Release: recreational fishing		Sandre	[40–42]
Silurus glanis	1857	?		Silure glane	[5, 40, 42, 92]
Umbra pygmea	1910	Release: aquaculture		Umbre pygmée	[5, 42, 93]
Vimba vimba	1989	Dispersal		Vimbe	[5, 42]

Silurus glanis is included in this table but its alien status remains questionable. Vectors of introductions have been classified into: Dispersal (range expansion by active or passive means from populations of neighboring countries. It includes accidental transport by human means), Escape (escaped from captivity) or Release (deliberately released into the wild)

Table 2. List of alien fish considered as naturalized in French inland waters.

Bulgaria [55], Poland [56], or Norway [57]. The first species that was introduced in France is the common carp *Cyprinus carpio* in roman times, followed by the goldfish *Carassius auratus* [41, 42]. Nevertheless, this is only during the second half of the nineteenth century that more frequent introductions occurred under the auspices of the Imperial Society of zoological acclimatization ("Société impériale zoologique d'acclimatation") [41, 42], which was established in 1855 [34]. Introductions were first motivated by research curiosity and to improve fish stocks for fishery. Introductions concerned exclusively European and North American fish, among which various salmonids and centrarchids [41, 42]. Then, new species were deliberately introduced to improve the fish market economy by diversifying the market of native species, for sport fishing, to act as biological control agents of algal blooms in eutrophic ecosystems, or to control mosquitoes [3]. More recently, because of stricter legislation and change in fisheries management practices away from stocking with non-natives [34], the main pathways for alien fish introduction are via either the ornamental trade and subsequent unintentional introduction [6, 11] or angling practices, such as for the asp (*Aspius aspius*), which is one of the three alien species that showed the most spectacular colonization in France during the past decades [49]. Besides, several introductions were accidental (e.g., during stocking events), which is probably the case for species not favored for fishing, such as *Pseudorasbora parva*, *Pachychilon pictum*, and pumpkinseed *Lepomis gibbosus* [49]. Other introductions result from natural species range expansion accelerated by several human activities and infrastructures, such as fluvial transport and artificial canals [56]. In conclusion, the attitude to the introduction of non-native fish have changed over time from efforts made to seek out and introduce new species actively to the protection of hydrosystems face from all new species [33, 34].

The negative impacts of alien species on native species and ecosystems, as for other countries [16], such as Belgium [51], Norway [57], Bulgaria [55], or Poland [56], are most often unknown in France and needs further studies [5, 41, 42] to develop a functional policy on alien species introductions and the protection of aquatic ecosystems integrity [51]. The recent European Union legislation addressing the problem of invasive alien species or IAS (EU Regulation No. 1143/2014) identifies different types of intervention including prevention, early warning, and rapid response. It required member states to develop a list of invasive alien species of concern in addition to a list of Union concern (see EU 2016/1141 and 2017/1263). These lists are dynamic at the Member State and EU levels and need scientific evidences to identify and prioritize IAS of regional and indeed global concern. We still need a quantitative methodology to assess potential impacts of invasive fish even if some recent proposals have been done [58, 59].

2.1. Two alien fish species intentionally introduced but not acclimatized: the rainbow trout and grass carp

The rainbow trout (*Oncorhynchus mykiss*), which is a salmonid originating from the west coast of North America, was one of the first fish species to be domesticated and introduced globally: today it is present in more than 90 countries [60, 61]. In France, it was first introduced in the beginning of 1880 for angling [41]. Thereafter, with the control of artificial production, it has become one of the leading species in inland European aquaculture [62] and accounts for more than three-quarters of the French fish production [61]. Yet, rainbow trout is still considered non-established in France [49], and in most European countries, except in few Norwegian drainage basins where only six self-reproducing populations are confirmed by the mid-1990s [57], as well as in few Alpine rivers in Austria, Slovenia, Switzerland, and Italy [36]. The failure of rainbow trout to establish in most parts of Europe may to a large extent be caused by its susceptibility to whirling disease, a myxozoan parasite *Myxobolus cerebralis* [57]. Nevertheless, even though it is not established, it is still very common in France, because of escapees from aquaculture and intentional releases in lakes, rivers, and particularly private ponds for sport fishing [16, 51]. The impacts of rainbow trout on native species and ecosystems is poorly documented in France [5], but it is generally considered that this species do not show severe environmental impacts across Europe [3].

The grass carp (*Ctenopharyngodon idella*) is native from East Asia and was first introduced in France in the end of 1950s [41], similar to other European countries [34]. As rainbow trout and two Asian carps (silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*), the grass carp does not breed in natural conditions in France because it requires very specific conditions that are not met in this country: large rivers with a strong current (1 m/s), important and rapid water level variations (1–2 m), water temperatures comprised between 20 and 25°C during several weeks in summer, and long unregulated water courses in which the pelagic eggs can incubate [63]. Yet, easy artificial reproduction has allowed this species to be spread in numerous countries [55], even though it is only very occasionally found in open waters in France [63] or Belgium [51]. However, it is present in numerous ponds across France [63]. The impact of grass carp is poorly document in France [41, 63]. Yet in other countries, it is considered that several parasites were transferred, which infested the common carp in Bulgaria [55] and Poland [56]. More generally, it is considered that grass carp can significantly influence native ecosystems because of their prevalence in some water bodies [56]. For instance, they are reported to destroy the spawning grounds of native phythophilous fish species through foraging on macrophytes, which could led to the decreased of fishing of some species in several lakes or depletion of wild fowl fauna, particularly those feeding on soft aquatic vegetation, e.g., coot, *Fulica atra*, and swan, *Cygnus* sp. [56]. Nevertheless, it is important to mention that the use of grass carp has allowed in certain cases to effectively control macrophyte development while avoiding the use of more costly and environmentally unacceptable alternatives such as insecticides or herbicides [16].

These two examples illustrated what has occurred in the past in France (and more generally in Europe) to improve angling, aquaculture production, and management of ecosystems. Today, it would be a futile and potentially a controversial exercise to try to eradicate these two species and more generally already established alien fish species because of high expense, difficulty of success, and the likelihood of imposing substantial collateral damage [56, 64]. However, as the possible outcomes of introductions are still very poorly documented, the precautionary approach ("guilty until proven innocent") is most appropriate for dealing with new alien species introductions [3, 51]. Because, nowadays, aquaculture is the main pathway of initial introduction of new fish species in Europe [6], one possible way to decrease risks while increasing production [16] would be therefore to rely more on the production of local species with valuable qualities such as pikeperch (*Sander lucioperca*) or European perch (*Perca fluviatilis*) ([54], Teletchea et al. 2009).

2.2. One unwanted invasive species: *Pseudorasbora parva*

The topmouth gudgeon is a small cyprinid originating from East Asia, including Japan, the Korean section of the Amur River Basin, China (basins of the rivers Yangtze and Hoanghe), and Taiwan [65]. It was accidentally released in Europe in early 1960s with stocking material of Asian herbivorous cyprinids [51, 56, 65–67]. Then, because of both stocking and natural range expansion, it has rapidly spread across Europe [51, 56, 67] and more generally in numerous countries in the world, being now classified as a worldwide pest [66]. It still continues today to expand its range, and represent one of the most common alien species in France [49]. Similarly, following its introduction into lakes in the UK in 1996, populations appear to establish rapidly and become dominant in the fish community (often >97% by number) [64]. The reason for its success is its very high reproductive rate, which gives rise to dense populations of fish that compete with fry of other species [65]. Besides, this species is opportunist and has a wider ecological and physiological tolerance than many European fish species and can survive to a moderate degree of pollution, elevated temperatures, and low water levels. The ability to spawn on any smooth-surfaced object, such as branches, leaves, and artificial substrata, is another important factor likely to have contributed to the rapid dispersal of this species [65]. The impact of the topmouth gudgeon is poorly documented in France [42]. Yet, in other countries, it has been shown that it can compete for food with other species such as *Aphanius anatolie* and *Orthrias* sp. [65]. It was also described that populations of *Leucapius delineatus* decreased when topmouth gudgeon increased, the latter being a vector of a lethal pathogen for the former [49, 64, 65]. More generally, their high abundance provokes concerns of detrimental ecological impacts through, for example, high competition for resources such as food and spawning habitat, and they become a pest species to anglers [64]. The topmouth gudgeon is included in the list of exotic species of concern in the framework of European Union legislation addressing the problem of invasive alien species (EU Regulation No. 1143/2014).

3. Recent invasion of gobies: why?

The recent, spectacular invasion of French hydrosystems by gobies is a good medium to discuss about what makes the success of an invasion. Since 2007, four freshwater Gobiidae species have been introduced in French hydrosystems: the tubenose goby (*Proterorhinus semilunaris*) in 2007, the bighead goby (*Ponticola kessleri*) in 2010, the round goby (*Neogobius melanostomus*) in 2011, and the monkey goby (*Neogobius fluviatilis*) in 2015. All that Ponto-Caspian species have moved in Europe with a contiguous East to West range expansion, with a spread from the Black Sea to the Rhine Delta observed as early as in the 1960s for the tubenose goby. Here, we focused on the round goby that reach locally high densities in many locations of the Upper Rhine and the Moselle River [35, 68]. This species has begun to spread in the 1990s [69]. It was observed for the first time in a downstream section of the Upper Rhine in Germany (between Düsseldorf and Cologne) in 2008, upstream of the confluence with the Neckar in 2010, in the French Upper Rhine (the Gambsheim fishway) in 2011 and in Basel harbor, 143 km upstream the Gambsheim fishway, in 2012 [35, 70]. Five years after its first observation, the round goby represented in several locations along the Upper Rhine more than 80% of the total catch by electrofishing (100 fishing points). The relative density of the round goby never fall below 25% of the total catch 1 year after its first observation, with a maximum value reaching 90% in a location dominated by rip-rap embankment [68]. This population dynamic is an amazing success that we dissected considering first the species bio/ecological traits and secondly the characteristics of its recipient ecosystems.

3.1. A profile of invader

Potential reasons for the proliferation of the round goby include (1) its reproductive success, (2) its singular behavior by comparison with native species, and (3) its tolerance to a wide range of physicochemical conditions. The fecundity per round goby female during a reproductive season ranges between some hundreds and a maximum of 5200 eggs that are divided in up to six spawns per year (unpublished results and values reported in [71, 72]). This number of eggs is not important by comparison with native species but the round goby exhibits two characteristics that make them prolific: multiple spawning combined to a protracted reproductive season and some forms of parental cares [73, 74]. The male occupies and defends a nest—an enclosed cavity—to which females are attracted to spawn adhesive eggs on the undersize of rocks [75–77]. In laboratory experiments conducted in Canada, up to three females were selected by a male and spawned sequentially in a nest [78], but field observations reported that up to 15 different females could enter a nest to spawn [76]. Inside the nest, eggs are regularly inspected by males and constantly ventilated using pectoral and caudal fins. In Europe, gobies are the most typical species of guarders—nest spawners according to the typology of parental investment recently used by [23] in a comparative study between exotic and native fish.

Gobies lack a swimbladder, which makes their positioning in the water column predominantly benthic. They stand at the bottom and are considered bad swimmers in that they cannot fight against an important current or make jumps. A consequence is that at any stage of their biological cycle the gobies need numerous shelter and hiding places in their environment.

Mineral structures (pebble, stones, and blocks) or macrophytes are useful habitats but in a given environment they would be more frequent in hard substrates as typically rip-rap embankments [79–81]. Few other native species, such as the European bullhead (*Cottus gobio*), the freshwater blenny (*Salaria fluviatilis*) or the ruffe (*Gymnocephalus cernua*), have these characteristics [43, 82]. *Neogobius melanostomus* inhabits a wide range of temperate freshwater and brackish-water ecosystems [72]. It has also demonstrated its capacity to adapt to local conditions in terms of prey availability [72]. This species exhibits a wide thermal tolerance, ranging from −1 to 30°C, but its energetic optimum temperature is estimated to be 26°C [72]. They would also be fairly little sensitive to pollutions. The distinguishing ecological features of the round goby by comparison with native ones make them singular in the range of bio/ecological profiles of species in place, a distinctiveness that could promote its success [25].

3.2. Hydrosystems prone to invasions

There are multiple potential and non-exclusive hypotheses to explain the gobie's success from the hydrosystem point of view. Among these, we emphasize the ideas (1) that the environments are not saturated in species and (2) that the rivers were man-modified in a way favoring the installation of exotic species.

The environments invaded by exotic species are not saturated in species for two main reasons. First, they correspond to hydrosystems that were largely defaunated during the Würm glaciation (80,000–10,000 BP). At the end of this period, the Rhine basin was recolonized by fish species from refuge areas that were outside ice range extension [83]. This recolonization by natural process takes a long time in the Rhine River considering the isolation of this basin and its geographical orientation with the downstream part to the North. The process was artificially accelerated these last centuries by human-aided introduction and the opening of the hydrographic basin with canals. Nowadays, the Upper Rhine is the main navigating way in Europe with two-third of goods transported on that fluvial road (330 millions of tons per year). Man activities allowed species from refuge area during the last glaciation, in particular the Ponto-Caspian area, to reach this unsaturated ecosystem. The Rhine has hence become the main entrance point for the dispersal of many invasive aquatic animal species in France over recent decades [7]. Another reason why ecosystems are not saturated in species is that pollution and human activities have profoundly modified natural communities, leaving vacant ecological niches within the hydrosystem. The decline of the Atlantic salmon (*Salmo salar*) or the European eel (*Anguilla anguilla*) in French inland waters are for example well documented. In conclusion, the ecosystems are not saturated because the post-glaciation process of recolonization is not achieved and several native species in place have already declined.

Second, the river stretches that served as entrance point in French hydrosystems are highly modified in terms of structure, quality, and functioning. The alteration of their habitats has placed the native species in a situation of anachronism: they are un-adapted to their own natural environment. The changes of habitats were too fast since the nineteenth century to allow a real adaptive response from species in place. Most of them disappeared, and the others can have a declining level of competition. The resulting consequence is that the remained native species in place is not efficient to compete with some euryecious and prolific species. Furthermore, the rule of biotic factors in the success of gobies can be explained from a theoretical point of view by the invasional meltdown [84] and the enemy release hypotheses [85, 86, 87]. To be explained, the invasional meltdown can be drawn schematically. The propagule pressure received by a navigated and highly modified hydrosystem, such as the Rhine, is so important that a first exotic species always finished successfully. This one became a factor favoring a second exotic species, for example, because it will decrease the pressure of a potential predator. The two exotic species can then pave the way for a third exotic species and so on. This concept could probably be applied to the round goby in that it was preceded by the invasion of crustaceans and molluscs fed massively by this fish [88]. The enemy release hypothesis assumes the advantage of the loss of the original parasite burden of an invader. A recent study [89] revealed that 3 years after its first observation, the round goby hosted only one macroparasite in the French Upper Rhine, whereas in all other locations along its invasive pathway or its native range a minimum of three macroparasites were reported. This is typically an example of the enemy release an introduced species can benefit at least at the beginning of the invasion process.

4. Conclusions

The main goal of the present chapter is to give an update picture of alien fish species in France and their fate in the past decades. We dissected how the fish introduction history in France switched from voluntary introduction in the nineteenth century to unintentional but human-aided introductions (aquarium trade and global ship transport). The 28 alien fish established represent one-third of the fish species in France and >25% of the European exotic fish. Four species of our list are included among the 100 worst invasive species of Europe (DAISIE) and three others among the 100 worst invasive species of the world (IUCN). The information gathered will allow discussing the possible reasons explaining whether an alien species is able or not to establish sustainable populations in France and thereafter became invasive, such as gobies. Now and in the near future, natural resource managers have no other choice than to deal with them because no invasive fish have spontaneously collapsed up to a local extinction in France.

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