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Ecology, behaviour and management of the European catfish.

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Ecology, behaviour and management of the European catfish.

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Short title: What's new on European catfish?

Abstract: The extreme body sizes of megafishes associated with their high commercial values and recreational interests have made them highly threatened in their native range worldwide by human-induced impacts such as overexploitation. Meanwhile, some megafishes have been introduced outside of their native range. A notable example is the European catfish (*Silurus glanis*), one of the few siluriforms native to Eastern Europe. It is among the 20 largest freshwater fish worldwide, attaining a total length over 2.7 m and a documented mass of 130 kg. Its distinct phylogeny and extreme size imply many features that are rare among other European fish, including novel behaviours (massive aggregations, beaching), consumption of large bodied prey, fast growth rates, long lifespan, high fecundity, nest guarding and large egg sizes. The spread of the species is likely to continue due to illegal introductions, primarily for recreational angling, coupled with natural range extension associated with climate change. Here, the most recent knowledge on the current distribution and the ecology of the species are reviewed. A series of key research questions are identified that should stimulate new research on this intriguing, yet largely unknown, species and, more generally, on the ecology of freshwater invaders.

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Introduction

Large apex consumers are unsurprisingly rare in nature as a consequence of their long generation time coupled with the inherent properties and pyramidal structure of food webs. Shifts in their abundance can, however, have strong direct and indirect ecological effects, including modifying food web structure and ecosystem functioning (Estes et al. 2011; Ripple et al. 2014). Large predators have also been recognised as providing important ecosystem services (Wilmers et al. 2003), including economic benefits via trophy hunting, recreational fishing and photo-safari tourism (Naidoo et al. 2011; Arlinghaus et al. 2014). A challenging issue regarding the conservation and management of large apex predators is their coexistence with conflicting human activities and the associated social perceptions (Ripple et al. 2014). This is notably the case of the so-called megafishes (Stone 2007), whose extreme body size has attracted high commercial and recreational interests, rendering these fishes locally threatened by human-induced impacts such as overexploitation and habitat alteration in their native range (Allan et al. 2005; Stone 2007).

Biological invasions are a key component of the human-induced biodiversity crisis (Sala et al. 2000), and one of the main threats caused by introduced species is the alteration of the structure of recipient communities and the modification of ecosystem functioning (Chapin et al. 1996). Quantifications of the ecological impacts of invasive species are, however, often difficult (Simberloff et al. 2013), making it highly challenging for assessments of impact to be completed, despite their requirement for formulating robust risk management policies and processes (Britton et al. 2011). Due to their strong association with human activities, freshwater ecosystems have been the recipients of numerous non-native species, with fishes being among the most frequently introduced freshwater organisms (Copp et al. 2005). Because their introduction is primarily driven by aquaculture, fishery or angling purposes (Johnson et al. 2009), introduced fishes tend to be selected for traits that include larger body-sizes than native species (Blanchet et al. 2010), often resulting in them occupying high trophic positions in recipient communities (Cucherousset et al. 2012). Ecological impacts of invasive fishes are apparent across all levels of biological organisation

(Cucherousset and Olden 2011), with introductions of large-bodied predatory fishes known to impact native fish populations and modify prey community and food web structure (Vander Zanden 1999; Eby et al. 2006; Sagouis et al. 2015).

Although introduced fishes tend to be significantly larger than their native counterparts (Blanchet et al. 2010), body-size is not necessarily the biological trait that facilitates their invasion success (Miller et al. 2002). It does, however, play a crucial role in the functioning aquatic ecosystems in general, driving trophic interactions between species and the fluxes of nutrients within ecosystems (Hildrew et al. 2007). In fishes, trophic position is primarily driven by the morphological constraints during foraging that relates to gape-size limitations, given that they usually swallow their food whole (Cohen et al. 1993; Forsman 1996). Due to metabolic scaling, body-size also influences nutrient turnover and the amount of energy needed for maintenance by an organism (Cohen et al. 1993; Jennings et al. 2007). Therefore, introduced large-bodied fishes may consume high quantities of prey and sustain their metabolic activity by consuming new, unexploited, resources (Cucherousset et al. 2012).

An emblematic example of an introduced megafish that is increasingly receiving scientific interest is the European catfish *Silurus glanis* that is now invasive in western and southern European freshwaters (Figure 1). It is among the 20 largest freshwater fishes in the world and is the largest in Europe (Stone 2007; Boulêtreau and Santoul 2016). The species can measure over 2.7 m total length and a documented total weight of 130 kg (Boulêtreau and Santoul 2016), making it by far the largest species by length and mass in their introduced range where they are considered a 'giant' top predator due to adults being at least twice larger than native predators. Their extreme body sizes has resulted in them being an increasingly popular target species for recreational anglers in Europe, resulting in their intentional introductions into some western and southern European countries (Carol 2007; Gago et al. 2016, Figure 1), but also outside Eurasia (e.g. China (Chen and Wey 1995; Ren 2012; Adakebaike et al. 2015), Tunisia (Mili et al. 2016; Valadou 2007; Schlumberger et al. 2001) and more recently in Brazil (Cunico and Vitule 2014). This is despite some of these countries having legislation in place to prevent such introductions (Hickley and

Chare 2004). Moreover, in countries including France, Belgium and Spain, the species has established self-sustained populations in major river basins. Given their considerable gape size compared to native predatory fish, and their large body sizes providing them natural refuge from native predators (Wysujack and Mehner 2005), they have traits that suggest they could impact food webs, especially when these have already been disturbed by anthropogenic activities.

In a review on the environmental biology of European catfish, Copp et al. (2009) underlined the important lack of knowledge in the introduced range of the species and the need for additional scientific inquiries on this species. Since this review, many studies have investigated their invasion ecology. The aim of this new review was to build on Copp et al. (2009) by highlighting the avenues of research opportunity that arise from the most recent findings. In particular, important details are provided relating to their contemporary distribution (Figure 1), habitat use, activity, social and dispersion behaviour, trophic interactions, and socio-economic consequences, and the implications of these issues for their management. Research questions and perspectives are also developed to stimulate new research specifically on European catfish and more generally on the ecology of invasive species.

I- Habitat use and activity

The preferred habitats of European catfish are slow-moving lotic or lentic waters of considerable depth (Greenhalgh 1999; Copp et al. 2009), immediately making them inherently difficult to capture using conventional sampling techniques (e.g. Harvey and Cowx 1996). Recently, the use of different acoustic biotelemetry techniques that allow their tracking in large and deep environments has made important contributions to existing knowledge of their movements and habitat use in their invasive range. Exclusively completed in reservoirs and large rivers, these studies have revealed that European catfish individuals tend to show relatively few movements and, overall, strong site fidelity (Carol et al. 2007; Slavík and Horký 2009; Brevé et al. 2014; Capra et al. 2014). For example, in the upper Rhône River (France), the median home range of the 13 tagged catfish was 1.3 km (Capra et al. 2014). In the Meuse, over a period of several months, 89% of the 20 tracked catfish never left the 1.5 km river stretch where they were tagged (Brevé et al. 2014). These observations are consistent with Slavík et al. (2014) who demonstrated European catfish energetically defends optimal small areas rather than a large home range area, as this reduces their energy costs.

As a consequence of their physiological optimum between 25 and 27 °C (Copp et al. 2009), European catfish have mobility patterns that indicate greater activity during summer periods as water temperatures reach their maximum (Slavík et al. 2007; Capra et al. 2014). This preference for warm waters has been revealed by their movements in large rivers impacted by warm-water effluents from nuclear power plants, where individuals adapt their space utilisation and settle in the artificially heated sections of the river (Bergé 2012; Capra et al. 2014). Thus, in rivers with anthropogenic disturbances that result in the presence of heated effluents, the ability of introduced European catfish to survive and develop an invasive population is likely to be enhanced.

The species does not have high oxygen requirements because its blood contains 30 to 35% haemoglobin, meaning it can utilise relatively small amounts of oxygen efficiently, resulting in its tolerance limits for dissolved oxygen being approximately 3.0 to 3.5 mg l^{-1} (Copp et al. 2009). Daněk et al. (2014) showed that juvenile European catfish could endure values down to 2.4 mg/L in winter in an oxbow lake of the River Elbe in Czech Republic. Correspondingly, provided that deep areas are available as a winter refuge with sufficient oxygen for survival then even very cold winter periods are unlikely to be an obstacle to the invasion success of the usually warm-water adapted catfish.

A key driver of European catfish activity relates to the diel cycle, where in controlled environments, they usually show preferences for feeding at night, although they can synchronise their activity according to the feeding period without respect to the diurnal phase (Boujard 1995). In the wild, their activity tends to also peak at night, although this can vary with season (Slavík et al. 2007). Whilst important, the interaction of diel cycle and temperature only partially explains some of the behavioural patterns of European catfish, with use of electromyogram (EMG) tags showing that there is considerable individual variability in behaviours. For example, some tagged individuals had energy utilisation patterns that showed little pattern with the phase of the diurnal cycle, with peak activity use during specific periods of the day or the night (Slavík and Horký 2012). It was suggested that rather than being related to day/night phases, their behaviours were more related to their individual characteristics, and corresponded to the theory of behavioural syndromes and the classification of individuals into groups of proactive and active individuals with different abilities to use energy reserves (Øverli et al. 2005). The influence of these different behavioural syndromes could have substantial consequences for the outcome of introductions, as these potentially have strong influences on the ability of released individuals to establish new populations and colonise new regions (Chapple et al. 2012). Correspondingly, individual differences in behaviour and personality are an aspect of their invasion ecology that requires further work, and have implications for both their capacity to disperse and their ecological impacts (Juette et al. 2014) and, potentially, their likelihood of being vulnerable to recreational angling (Uusi-Heikkilä et al. 2008; Wilson et al. 2015).

II- Social and dispersion behaviour

The issue of whether European catfish shows solitary or grouping behaviours was highlighted in a recent study on France's River Rhône (France), where observations were frequently made of the formation of aggregative groups comprising of up to 44 individual fish and of estimated total biomass of up to 1132 kg (Boulêtreau et al. 2011). The reasons for these groupings remained unclear, particularly given the individual sizes of the fish released them from native predators and could result in increased individual costs from sharing resources (Slavík et al. 2014). It was also discussed that these groupings could have considerable consequences for local biogeochemical recycling. Non-random aggregations have also been described for other fishes, such as for sharks when the social context of their behaviour favours the members of the group pursuing other activities (Mourier et al. 2012).

In the context of these aggregations and their potential causal factors and ecological benefits, their behavioural patterns across both their native and invasive range then provide contrasting information. In the native range, European catfish has been reported to be a species that actively defends its access to resources, resulting in their foraging usually being completed individually (Carol et al. 2007), and increased energy utilisation tends to occur when they are in contact with conspecifics in preferred areas of habitat (Slavík and Horký 2009). Thus, it could be that solitary preferences represent an active defence of limited resources, whilst living in a group may be preferred provided that available resources are sufficient and/or that specimens can use them more effectively. Familiar conspecifics consumed less energy during repeated mutual contact under the experimental conditions (Slavík et al. 2011), hence groupings of catfish in modified environments (Boulêtreau et al. 2011) could be an adaptation towards conserving energy. Consequently, the formation of these aggregations of very large-bodied individuals is an aspect of their invasive behaviour that warrants further work, particularly in relation to the drivers of this grouping behaviour. Moreover, their consequences at the individual and group level for resource acquisition and energy expenditure, and also how these groupings potentially affect the behaviours of their prey, also requires additional work.

The behaviour of European catfish in captive situations also delivers information useful for providing insights into understanding aspects of their invasion ecology. Laboratory studies have suggested that their behaviour is dependent on the number of interacting individuals. When held in isolation, they show randomly distributed diel activity across both light and dark phases. When held together in higher numbers, they switch to feeding mainly in dark phases (Bolliet et al. 2001). Captive studies have also suggested that catfish can distinguish between familiar and unfamiliar conspecifics based on prior experiences (Slavík et al. 2011), a trait observed in other fishes more generally (Höjesjö et al. 1998; Griffiths et al. 2004). For example, unfamiliar albino catfish were co-opted into the socially established group of familiar conspecifics worse than pigmented fish (Slavík et al. 2015), probably due to colour difference, limitations in social behaviour (e.g. low aggressiveness) and/ or in physiology functions (e.g. poor vision) (Slavík et al. 2016b). Familiarity based on prior experience plays an important role in the occupancy of shelters, which shows that the species is able to make group decisions based on prior experience (Slavík et al. 2012). Furthermore, under laboratory conditions, familiar catfish utilized available resources more effectively, displaying lower movement activity needed for shelter occupancy (Slavík et al. 2016a). These aspects could have important implications for the initial behaviours of individuals following their introduction into waters and thus could influence their ability to initially survive before establishing a sustainable population.

European catfish also show a wide repertoire of other behavioural strategies that could also provide some advantages for their adaptation to new environments. Although individuals tend to show high fidelity to specific areas that would presumably naturally inhibit their dispersal (Carol et al. 2007; Slavík et al. 2007; Capra et al. 2014), when mature individuals are released into a river then individuals often undergo random downstream transfers of up to 30 km (O. Slavík and P. Horký, personal communication), providing a mechanism for short-distance dispersal. Moreover, downstream dispersal is more likely to be driven by the downstream migration of juveniles, as this would partition their habitat use from those of adult conspecifics, with this having been recorded in some lowland streams in their native range (Slavík et al. 2007). Some recent studies have indicated that, in the dispersal of animals living in groups, a potentially important role is played by differences in individual personalities. As described by the social cohesion hypothesis, sociability affects dispersal behaviour because more social individuals display a lower tendency for dispersion (Bekoff 1977; Cote et al. 2010) and show reduced movements (Cote and Clobert 2012). Correspondingly, where high aggregations of European catfish have been recorded, and where group foraging behaviours have been noted, such as beaching behaviours, then testing this hypothesis could provide some key insights into these behaviours that have only been noted in the invasive range to date.

III- Trophic ecology

Outside its native area, and especially in large rivers where it is inherently difficult to conduct ecological studies, there is limited knowledge on the feeding ecology of European catfish. Of those studies completed, indications are that, by increasing predator-invulnerable size refuges (Wysujack and Mehner 2005, Carol et al. 2009), their presence could potentially induce a new predation pressure on the largest native fish species and/or establish novel trophic interactions by foraging on prey that were not previously consumed by native predatory fish (Cucherousset et al. 2012). For instance, European catfish is abundant throughout the main stem of the Ebro river (Spain), where endemic cyprinids, in particular *Luciobarbus graellsii*, have been extirpated, probably due to multiple stressors that include predation by European catfish (Carol et al. 2009). Similarly, anadromous fish have been shown to significantly contribute to their diet in French rivers (more than 50% for some specialised individuals) (Syväranta et al. 2009). This worrying predation pressure may thus interrupt the longitudinal fluxes of energy from marine to riverine ecosystems, representing a further threat to many anadromous fishes that have already been impacted by human activity (e.g. dam construction, water pollution, fisheries). Indeed, the increased anadromous prey residence time and predator density caused by river impoundments tend to favour increased predator encounter rates (Agostinho et al. 2012) and, importantly, most of these anadromous fishes had reached a size refuge from fish predation before European catfish were introduced. While trophic impacts of European catfish have been reported locally in its introduced range, a recent study highlighted that overall, the invasive populations in France have only impacted low numbers of freshwater fish communities (Guillerault et al. 2015). Specifically, the authors observed that fish species richness, evenness and diversity decreased significantly after the establishment of European catfish in 1.4%, 1.4% and 5.8% of the 112 French studied sites, respectively.

Some terrestrial vertebrates, mainly birds and small mammals, have been reported to contribute to the diet of European catfish (Copp et al. 2009). For instance, using stable isotope analyses, Syväranta el al. (2010) reported that fin and muscle tissues from larger individuals were often considerably enriched in $\delta^{13}C$, suggesting frequent consumption of non-aquatic birds and/or mammals and that these individuals might be sustaining their high metabolic activity by feeding upon previously unexploited resources (see also Carol et al. 2009). In addition, Cucherousset et al. (2012) revealed European catfish can display trophic specialisation (*cf*. Bolnick et al. 2003) through foraging on terrestrial birds (namely pigeons *Columba livia*) through intentional beaching behaviours. Camera recordings showed that small numbers of individuals grouped together and patriated in beaching behaviours to capture these preys, with a capture efficiency of 28 %. When some individuals actively foraged in such a manner, other individuals would wait nearby, suggesting that the active foragers are the potential dominant individuals in the group. Importantly, stable isotope analyses revealed that the dietary contribution can reach up to 30-40% for the most specialised individuals.

Of importance here is developing understanding of whether trophic specialisation and the ability to display new foraging behaviours (i.e. not reported previously in the species' native range) is an adaptation to their new environment that contributes to their invasive success, or is just a context-dependent behaviour that has developed in response to a specific foraging opportunity. Moreover, quantifying the consequences of their apparent potential to modify the linkage between marine-freshwater and terrestrial-freshwater ecosystems through their trophic interactions and how it potentially amplifies the ecological consequences of some existing anthropogenic-mediated perturbations is important.

IV- Socio-economic dimensions

European catfish has constituted a valuable fisheries resource through much of its native range and has been targeted by both commercial and recreational fisheries since prehistoric times (Quinn 2011). Maybe ironically, the unique attributes of European catfish, in particular its growth and potential for reaching very large body sizes, have also facilitated the illegal introduction of the species outside its native range. Relatedly, recent work in Germany and the USA has shown that body size is a key determinant of angler motivation across a range of species (Arlinghaus et al. 2014), including catfishes (Hutt et al. 2013). Although there are no data available on numbers and sizes of released individuals, some of the introduced fisheries now support a vibrant trophy fish and catch-and-release-only tourism fishery, with numerous guides operating on both the Ebro and the Po basins, and likely in many other areas in France, Spain and Italy. In these areas, the presence of the European catfish promotes socio-economic development based on recreational angling by nonlocals (Rodríguez-Labajos 2014). There is evidence that some of these stocks were purposely created by illegal transfer of a few hundred individuals by anglers, such as in the Mequinenza reservoir in the Ebro basin (Carol 2007; Rodríguez-Labajos et al. 2009). Anecdotal observation of social media and recent introduction to new Iberian river basins suggests that some anglers are interested in further spreading the species, and there is also evidence that some discussion in social media has taken place in the U.S.A. to purposely introduce the species to North America to supplement the native species that do not nearly reach the same final body sizes. The species was also recently recorded as introduced in the wild, with uncertain establishment, in Brazil (Cunico and Vitule 2014). Johnson et al. (2009) warned that illegal release of highly demanded species constitutes a constant pathway facilitating spread of non-native species, which particularly applies to European catfish due to its attractiveness to a small, yet highly avid segment of trophy anglers (Hickley and Chare 2004; Britton et al. 2007). Trophy anglers are known to practice catch-and-release (e.g., Arlinghaus 2007), hence there is little hope that angler exploitation would contribute significantly to their removal once populations have established.

In its native range, whilst European catfish has so far not featured very prominently among the target species of the majority of anglers (Arlinghaus et al. 2008), there has been a development of a highly specialized sub-section among anglers that specifically targets trophy catfish. It is these anglers that likely feed the foreign catfish guiding businesses in the introduced ranges and that also heavily target native stocks in countries such as Germany, Hungary, or Russia. In contrast to angling, the large body sizes of European catfish are likely of low importance to commercial capture fisheries that tend to be more biomass-oriented. There is also a small aquaculture sector in central Europe focusing on European catfish, some of which are used for stocking purposes.

Perhaps due to climate change, European catfish appear to now be able to disperse and recruit highly successfully throughout its native range, in turn creating management conflicts and fostering active eradication efforts in some areas (e.g., in Germany), based on the belief that their populations exert high trophic effects as it expands its range. As a consequence, in some German states, state-level minimum size limits have been reduced or eliminated to facilitate exploitation. In Spain, European catfish is included in the National catalogue of invasive alien species and thus holding, transporting, and trading with this species is forbidden. In Belgium and France, the fishing of the European catfish is authorized during all the year, with no limit of size and number of individuals. In Belgium, restocking and introduction are not allowed. In England, introducing and keeping European catfish in inland waters requires a permit granted by the responsible government authority, with a permit generally only granted where the inland water is an enclosed stillwater where the fish has no chance of escaping into the wider environment.

Anglers targeting trophy catfish in areas like the Ebro or Po Rivers could also lead to indirect ecosystem impacts associated with catfish angling. For example, many anglers use live baitfish and hence due to the bait industry there is the possibility of unintended introduction of other fishes, parasites or diseases (Johnson et al. 2009). Moreover, in some areas, bottom fishing with large fishmeal pellets has become popular among catfish anglers. Pellets are often used in high amounts associated with groundbaiting to attract fish. This may lead to significant nutrient inputs and foster eutrophication, similar to the case in carp fishing (Arlinghaus and Mehner 2003; Niesar et al. 2004).

European catfish is also exploited for commercial purposes, notably on the Eastern European market, where its flesh is appreciated. As mostly benthic feeder, the European catfish has been shown to accumulate higher concentrations of organochlorine compounds (Babut et al. 2012; Huertas et al. 2016) and heavy metals such as mercury (Carrasco et al. 2011) than other fish species. In the Po River (North Italy), the 33% of the 54 European catfish analysed from 2006 to 2009 exceeded the maximum levels of 125 ng PCBs g^{-1} fresh weight set by the European regulations in fish (Squadrone et al. 2013a). Thus, in rivers where there are extant pollution problems (e.g. heavy metals, and organochlorine and radioactive compounds), European catfish flesh levels of PCB and heavy metals and could constitute a health human concern (Squadrone et al. 2013b; Comby et al. 2014).

V- Management and control of invasive populations

The greatest problem for managing the important extent of catfish range within Europe arises from the interaction of their attractiveness as an unique trophy fish with their apparent suitability for establishing self-sustaining populations and then achieving rapid growth rates across much of their extended range, but especially in the warmer regions of southern Europe. This has created a strong desire for introducing individuals into previously non-invaded areas, despite regulations being in place to prevent this (Hickley and Chare 2004; Genovesi et al. 2014). This continued pressure of introductions of European catfish includes Great Britain. Despite generally unsuitable current climate conditions for their fast growth and recruitment, angling demand has resulted in catfish release into over 250 lake fisheries and their escape into a number of major river basins (Britton et al. 2010a). This general introduction pressure from anglers means that any management and regulatory framework designed to prevent their further releases will be extremely difficult to implement effectively (Britton et al. 2011). Moreover, given that many of the introductions outlined have been into large open river systems with high connectivity, then in many cases the ability to extirpate local populations to prevent their dispersal is negligible, despite this being a useful management measure to prevent dispersal from connected lentic environments (Britton et al. 2010b; Britton et al. 2011). Consequently, the combination of their large body sizes making them highly attractive to specialist anglers (Hickley and Chare 2004), their relative ease of capture (Britton et al. 2007) and their invasive presence in major European river systems (Copp et al. 2009) suggests that management methods to reduce their ecological impacts in existing ranges will be futile (Britton et al. 2010a). Arguably, these conservation resources would be better targeted at preventing their introductions into river basins where they are not yet present, utilizing new policy and regulations specifically designed for this or with the use of high fines and other disincentives (Johnson et al. 2009; Genovesi et al. 2014, Piria et al. 2016). Nevertheless, the indications are that catfish introductions by anglers in Southern Europe are still ongoing (e.g. their first record in Portugal reported in 2015 (Gkenas et al. 2015)), and thus their invasive range is predicted to increase further. Climate change could also result in areas in more northern latitudes becoming increasingly vulnerable to their invasion, especially where individuals are already present but populations have yet to establish due to thermal constraints (Britton et al. 2010a).

Conclusions

To date, studies of the biology and ecology invasive European catfish populations in western Europe have provided some intriguing insights into their behaviours in novel environments. Aspects such as their large aggregations of mature fishes, trophic interactions across ecosystem boundaries and their high exploitation of anadromous fishes are all aspects of their ecology not reported in their native range. Their attainment of extremely large body sizes, utilization of areas of modified rivers unsuitable for indigenous fishes, and their incurring of additive or synergistic detrimental impacts for prey populations that are already under stress from disturbances such as impoundments, are also key aspects of their invasion ecology. Because of its unique features, we argue that quantifying the ecology of European catfish following the identified research directions in Table 1 should provide new insights into contemporary understandings of the ecology of biological invasions.

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Figure caption

Figure 1: Native (light blue) and introduced (dark blue) distributional ranges of European catfish (*Silurus glanis*) in Eurasian watersheds with an area > 1000 km^2. Watersheds where the species is present are displayed in blue; watersheds with no official evidence of introduction were in grey; < 1000 km^2 watersheds are displayed in white. European catfish in river basins of Europe were extracted from a world-wide database on freshwater fish faunas that compiles the available literature (including scientific reports, books, online data and grey literature) on species lists at the river-basin scale. Details on the database and references used per river basin are available in Brosse et al. (2013) and on the Biofresh data platform (http://www.freshwaterbiodiversity.eu/). This information was updated with information from Alp et al. (2011), Banister (1980), Benejam et al. (2007), Carol et al. (2003), Doadrio (2001), Economou et al. (2007), Gago et al. (2016), Gkenas et al. (2015), Has-Schön et al. (2015), Kamangar and Rostamzadeh (2015), Pérez-Bote and Roso (2009), Triantafyllidis et al. (2002), the surveys performed by the French National Agency for Water and Aquatic Environments (Onema 2012) and authors' personal information.

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Figure 1

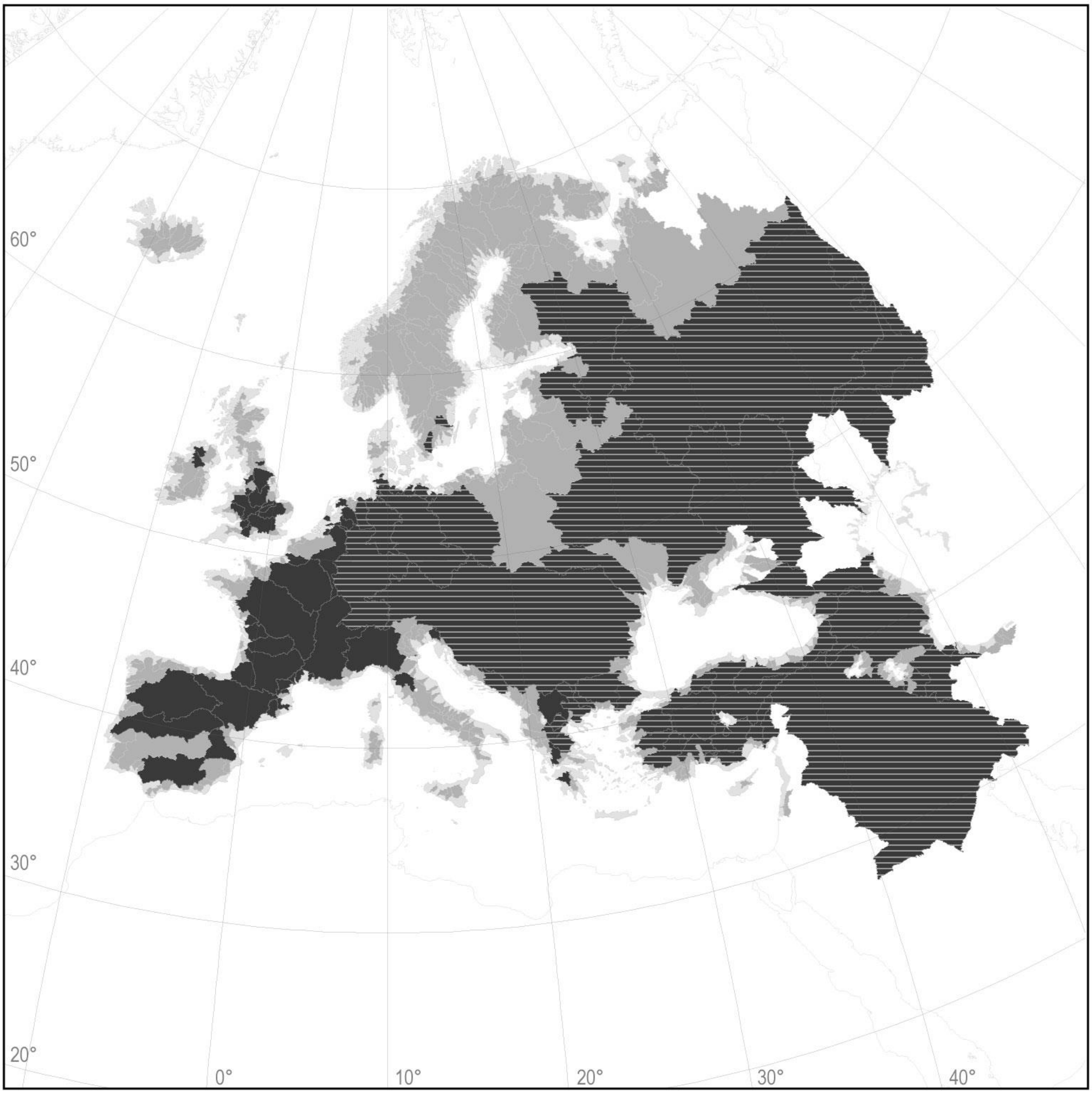

Figure caption

Figure 1: Native (striped dark grey) and introduced (dark grey) distributional ranges of European catfish (*Silurus glanis*) in Eurasian watersheds with an area > 1000 km^2. Watersheds where the species is present are displayed in dark grey; watersheds with no official evidence of introduction were in grey; < 1000 km^2 watersheds are displayed in light grey. European catfish in river basins of Europe were extracted from a world-wide database on freshwater fish faunas that compiles the available literature (including scientific reports, books, online data and grey literature) on species lists at the river-basin scale. Details on the database and references used per river basin are available in Brosse et al. (2013) and on the Biofresh data platform (http://www.freshwaterbiodiversity.eu/). This information was updated with information from Alp et al. (2011), Banister (1980), Benejam et al. (2007), Carol et al. (2003), Doadrio (2001), Economou et al. (2007), Gago et al. (2016), Gkenas et al. (2015), Has-Schön et al. (2015), Kamangar and Rostamzadeh (2015), Pérez-Bote and Roso (2009), Triantafyllidis et al. (2002), the surveys performed by the French National Agency for Water and Aquatic Environments (Onema 2012) and authors' personal information.

Figure 2: A large, close to 2 m long, European catfish (*Silurus glanis*) in a natural Southern European river. Photo credit: Rémi Masson.

Table 1. An overview of the subject covered by the review in relation to general ecological themes and hypotheses, and the associated research questions that could be addressed on European catfish.

Subject area	**Invasion ecological theme / hypothesis**	**Research questions**
Part I: Habitat use and activity	Invasion probabilities	How does high individual site fidelity in European catfish populations influence their patterns of dispersal?
	Invasion probabilities	What is the relationship between ecosystem anthropization and the survival, establishment and invasion probability of European catfish?
Part II: Social behaviour	Invasion probabilities	How do individual differences in behaviour and personality influence the ability of released European catfish individuals to disperse, to establish new populations and to colonise new regions?
	Intra-population variability in behaviour	How do aggregative behaviours influence intra-population variability in time budgets and foraging behaviours, and can these influence prey communities?
	Behavioural syndromes and invasions outcomes	How do native prey populations adapt to an invasive species with a new behaviour (e.g. nocturnal habits)?
	Behavioural syndromes and invasions outcomes	How do animal personalities influence dispersal mechanisms, introduction/invasion outcomes and angler exploitation rates?

	Social cohesion hypothesis	How does intra-population variability in sociability affect the formation of aggregations?
Part III: Foraging and trophic ecology	Novel trophic interactions	What are the drivers of the creation of novel trophic links by invasive species, particularly at ecosystem boundaries? How important are social interactions in this?
	Food web energy flux	What is the ecological significance of invasive species interrupting the longitudinal energy flux from marine to freshwater systems via their predation of anadromous fishes?
	Prey-size refuges	What are the ecological and evolutionary consequences of introductions of large-bodied species that means prey species are no longer within size refuges from predation?
Part IV: Socio-economic dimensions	Pathways of introduction	Can recreation of the pathways of introduction via genetic analyses help characterise the influence of donor regions on invasive outcomes, including adaptation processes?
	Propagule pressure	Where information is available in the invasive range on the numbers of fish released, and their frequency of release, can these inform how propagule pressure influences invasion probabilities?
	Anthropogenic impacts	Can invasive species act as biological pollution sinks?
Part V: Management and control of invasive E	Management	What are the most cost-effective management tools to prevent introductions into new river basins?
	Management	How to effectively reduce the number of illegal introductions by anglers?

catfish populations	Management	Following successful introduction and establishment, can such species be controlled efficiently and cost-effectively?

4