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Ecology, behaviour and management of the European catfish.

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Corresponding Author:	Frédéric Santoul Universite Toulouse III Paul Sabatier Toulouse, FRANCE
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universite Toulouse III Paul Sabatier
Corresponding Author's Secondary Institution:	
First Author:	Julien Cucherousset
First Author Secondary Information:	
Order of Authors:	Julien Cucherousset Pavel Horky Ondrej Slavík Michaël Ovidio Robert Arlinghaus Stéphanie Boulêtreau Robert Britton Emili García-Berthou Frédéric Santoul
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Abstract:	<p>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 (<i>Silurus glanis</i>), 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.</p>
Suggested Reviewers:	Zeb Hogan University of Nevada Reno zhogan@unr.edu

	Michael C Quist University of Idaho mcquist@uidaho.edu
	Janja Horvatic Associate Professor, University of Osijek jhorvatic@biologija.unios.hr
	Niels Brevé Sportvisserij Nederland breve@sportvisserij nederland.nl
	Rafael Miranda Ferreiro Universidad de Navarra rmiranda@unav.es
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1 Ecology, behaviour and management of the European catfish.

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Julien Cucherousset¹, Pavel Horky², Ondrej Slavík², Michaël Ovidio³, Robert Arlinghaus^{4,5},

Stéphanie Boulêtreau⁶, Robert Britton⁷, Emili García-Berthou⁸ and Frédéric Santoul^{6*}

6 Affiliations

¹ CNRS, Université Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.

² Czech University of Life Sciences Prague Dept. of Zoology and Fisheries 165 21 Praha 6 – Suchdol, Czech Republic.

³ UR-FOCUS, Biology of Behaviour Unit, Laboratory of Fish Demography and Hydroecology, 22 Quai E. Van Beneden, B-4020 Liège. Belgium.

⁴ Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.

⁵ Division of Integrative Fisheries Management, Faculty of Life Sciences, Invalidenstrasse 42, 10115 Berlin, Germany.

⁶ EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.

⁷ Department of Life and Environmental Sciences, Bournemouth University, Poole, BH12 5BB, United Kingdom.

⁸ GRECO, Institute of Aquatic Ecology, University of Girona, 17003 Girona, Catalonia, Spain

To whom correspondence should be addressed. E-mail: frederic.santoul@univ-tlse3.fr

Short title: What's new on European catfish?

25 **Abstract:** The extreme body sizes of megafishes associated with their high commercial values and
26 recreational interests have made them highly threatened in their native range worldwide by human-
1 induced impacts such as overexploitation. Meanwhile, some megafishes have been introduced
27 3 outside of their native range. A notable example is the European catfish (*Silurus glanis*), one of the
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7 8 few siluriforms native to Eastern Europe. It is among the 20 largest freshwater fish worldwide,
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17 18 to continue due to illegal introductions, primarily for recreational angling, coupled with natural
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21 22 distribution and the ecology of the species are reviewed. A series of key research questions are
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25 26 more generally, on the ecology of freshwater invaders.
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31 32
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41 **Introduction**

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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

68 (Cucherousset and Olden 2011), with introductions of large-bodied predatory fishes known to
69 impact native fish populations and modify prey community and food web structure (Vander Zanden
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70 1999; Eby et al. 2006; Sagouis et al. 2015).

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

82 An emblematic example of an introduced megafish that is increasingly receiving scientific
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83 interest is the European catfish *Silurus glanis* that is now invasive in western and southern
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84 European freshwaters (Figure 1). It is among the 20 largest freshwater fishes in the world and is the
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85 largest in Europe (Stone 2007; Boulêtreau and Santoul 2016). The species can measure over 2.7 m
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86 total length and a documented total weight of 130 kg (Boulêtreau and Santoul 2016), making it by
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87 far the largest species by length and mass in their introduced range where they are considered a
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88 ‘giant’ top predator due to adults being at least twice larger than native predators. Their extreme
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89 body sizes has resulted in them being an increasingly popular target species for recreational anglers
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90 in Europe, resulting in their intentional introductions into some western and southern European
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91 countries (Carol 2007; Gago et al. 2016, Figure 1), but also outside Eurasia (e.g. China (Chen and
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92 Wey 1995; Ren 2012; Adakebaike et al. 2015), Tunisia (Mili et al. 2016; Valadou 2007;
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93 Schlumberger et al. 2001) and more recently in Brazil (Cunico and Vitule 2014). This is despite
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94 some of these countries having legislation in place to prevent such introductions (Hickley and
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95 Chare 2004). Moreover, in countries including France, Belgium and Spain, the species has
96 established self-sustained populations in major river basins. Given their considerable gape size
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97 compared to native predatory fish, and their large body sizes providing them natural refuge from
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98 native predators (Wysujack and Mehner 2005), they have traits that suggest they could impact food
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99 webs, especially when these have already been disturbed by anthropogenic activities.
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100 In a review on the environmental biology of European catfish, Copp et al. (2009) underlined
101 the important lack of knowledge in the introduced range of the species and the need for additional
102 scientific inquiries on this species. Since this review, many studies have investigated their invasion
103 ecology. The aim of this new review was to build on Copp et al. (2009) by highlighting the avenues
104 of research opportunity that arise from the most recent findings. In particular, important details are
105 provided relating to their contemporary distribution (Figure 1), habitat use, activity, social and
106 dispersion behaviour, trophic interactions, and socio-economic consequences, and the implications
107 of these issues for their management. Research questions and perspectives are also developed to
108 stimulate new research specifically on European catfish and more generally on the ecology of
109 invasive species.

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1- Habitat use and activity

112 The preferred habitats of European catfish are slow-moving lotic or lentic waters of considerable
113 depth (Greenhalgh 1999; Copp et al. 2009), immediately making them inherently difficult to
114 capture using conventional sampling techniques (e.g. Harvey and Cowx 1996). Recently, the use of
115 different acoustic biotelemetry techniques that allow their tracking in large and deep environments
116 has made important contributions to existing knowledge of their movements and habitat use in their
117 invasive range. Exclusively completed in reservoirs and large rivers, these studies have revealed
118 that European catfish individuals tend to show relatively few movements and, overall, strong site
119 fidelity (Carol et al. 2007; Slavík and Horký 2009; Brevé et al. 2014; Capra et al. 2014). For
120 example, in the upper Rhône River (France), the median home range of the 13 tagged catfish was
121 1.3 km (Capra et al. 2014). In the Meuse, over a period of several months, 89% of the 20 tracked

122 catfish never left the 1.5 km river stretch where they were tagged (Brevé et al. 2014). These
123 observations are consistent with Slavík et al. (2014) who demonstrated European catfish
124 energetically defends optimal small areas rather than a large home range area, as this reduces their
125 energy costs.

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

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

142 A key driver of European catfish activity relates to the diel cycle, where in controlled
143 environments, they usually show preferences for feeding at night, although they can synchronise
144 their activity according to the feeding period without respect to the diurnal phase (Boujard 1995). In
145 the wild, their activity tends to also peak at night, although this can vary with season (Slavík et al.
146 2007). Whilst important, the interaction of diel cycle and temperature only partially explains some
147 of the behavioural patterns of European catfish, with use of electromyogram (EMG) tags showing
148 that there is considerable individual variability in behaviours. For example, some tagged individuals

149 had energy utilisation patterns that showed little pattern with the phase of the diurnal cycle, with
150 peak activity use during specific periods of the day or the night (Slavík and Horký 2012). It was
151 suggested that rather than being related to day/night phases, their behaviours were more related to
152 their individual characteristics, and corresponded to the theory of behavioural syndromes and the
153 classification of individuals into groups of proactive and active individuals with different abilities to
154 use energy reserves (Øverli et al. 2005). The influence of these different behavioural syndromes
155 could have substantial consequences for the outcome of introductions, as these potentially have
156 strong influences on the ability of released individuals to establish new populations and colonise
157 new regions (Chapple et al. 2012). Correspondingly, individual differences in behaviour and
158 personality are an aspect of their invasion ecology that requires further work, and have implications
159 for both their capacity to disperse and their ecological impacts (Juette et al. 2014) and, potentially,
160 their likelihood of being vulnerable to recreational angling (Uusi-Heikkilä et al. 2008; Wilson et al.
161 2015).

163 *II- Social and dispersion behaviour*

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

174 In the context of these aggregations and their potential causal factors and ecological
175 benefits, their behavioural patterns across both their native and invasive range then provide

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

190 The behaviour of European catfish in captive situations also delivers information useful for
191 providing insights into understanding aspects of their invasion ecology. Laboratory studies have
192 suggested that their behaviour is dependent on the number of interacting individuals. When held in
193 isolation, they show randomly distributed diel activity across both light and dark phases. When held
194 together in higher numbers, they switch to feeding mainly in dark phases (Bolliet et al. 2001).
195 Captive studies have also suggested that catfish can distinguish between familiar and unfamiliar
196 conspecifics based on prior experiences (Slavík et al. 2011), a trait observed in other fishes more
197 generally (Höjesjö et al. 1998; Griffiths et al. 2004). For example, unfamiliar albino catfish were
198 co-opted into the socially established group of familiar conspecifics worse than pigmented fish
199 (Slavík et al. 2015), probably due to colour difference, limitations in social behaviour (e.g. low
200 aggressiveness) and/ or in physiology functions (e.g. poor vision) (Slavík et al. 2016b). Familiarity
201 based on prior experience plays an important role in the occupancy of shelters, which shows that the
202 species is able to make group decisions based on prior experience (Slavík et al. 2012). Furthermore,

203 under laboratory conditions, familiar catfish utilized available resources more effectively,
204 displaying lower movement activity needed for shelter occupancy (Slavík et al. 2016a). These
205 aspects could have important implications for the initial behaviours of individuals following their
206 introduction into waters and thus could influence their ability to initially survive before establishing
207 a sustainable population.

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

225 226 ***III- Trophic ecology***

227 Outside its native area, and especially in large rivers where it is inherently difficult to conduct
228 ecological studies, there is limited knowledge on the feeding ecology of European catfish. Of those
229 studies completed, indications are that, by increasing predator-invulnerable size refuges (Wysujack

230 and Mehner 2005, Carol et al. 2009), their presence could potentially induce a new predation
231 pressure on the largest native fish species and/or establish novel trophic interactions by foraging on
1 prey that were not previously consumed by native predatory fish (Cucherousset et al. 2012). For
232 3 instance, European catfish is abundant throughout the main stem of the Ebro river (Spain), where
233 4 endemic cyprinids, in particular *Luciobarbus graellsii*, have been extirpated, probably due to
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234 8 multiple stressors that include predation by European catfish (Carol et al. 2009). Similarly,
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236 11 anadromous fish have been shown to significantly contribute to their diet in French rivers (more
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237 14 than 50% for some specialised individuals) (Syväranta et al. 2009). This worrying predation
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238 17 pressure may thus interrupt the longitudinal fluxes of energy from marine to riverine ecosystems,
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239 20 representing a further threat to many anadromous fishes that have already been impacted by human
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240 23 activity (e.g. dam construction, water pollution, fisheries). Indeed, the increased anadromous prey
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241 26 residence time and predator density caused by river impoundments tend to favour increased
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242 29 predator encounter rates (Agostinho et al. 2012) and, importantly, most of these anadromous fishes
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243 32 had reached a size refuge from fish predation before European catfish were introduced. While
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244 35 trophic impacts of European catfish have been reported locally in its introduced range, a recent
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245 38 study highlighted that overall, the invasive populations in France have only impacted low numbers
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246 41 of freshwater fish communities (Guillerault et al. 2015). Specifically, the authors observed that fish
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247 44 species richness, evenness and diversity decreased significantly after the establishment of European
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248 47 catfish in 1.4%, 1.4% and 5.8% of the 112 French studied sites, respectively.

249 Some terrestrial vertebrates, mainly birds and small mammals, have been reported to
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250 47 contribute to the diet of European catfish (Copp et al. 2009). For instance, using stable isotope
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251 50 analyses, Syväranta et al. (2010) reported that fin and muscle tissues from larger individuals were
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252 53 often considerably enriched in $\delta^{13}\text{C}$, suggesting frequent consumption of non-aquatic birds and/or
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253 56 mammals and that these individuals might be sustaining their high metabolic activity by feeding
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254 59 upon previously unexploited resources (see also Carol et al. 2009). In addition, Cucherousset et al.
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255 62 (2012) revealed European catfish can display trophic specialisation (*cf.* Bolnick et al. 2003) through
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256 65 foraging on terrestrial birds (namely pigeons *Columba livia*) through intentional beaching

257 behaviours. Camera recordings showed that small numbers of individuals grouped together and
258 patriated in beaching behaviours to capture these preys, with a capture efficiency of 28 %. When
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259 some individuals actively foraged in such a manner, other individuals would wait nearby,
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260 suggesting that the active foragers are the potential dominant individuals in the group. Importantly,
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261 stable isotope analyses revealed that the dietary contribution can reach up to 30-40% for the most
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262 specialised individuals.
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263 Of importance here is developing understanding of whether trophic specialisation and the
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264 ability to display new foraging behaviours (i.e. not reported previously in the species' native range)
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265 is an adaptation to their new environment that contributes to their invasive success, or is just a
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266 context-dependent behaviour that has developed in response to a specific foraging opportunity.
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267 Moreover, quantifying the consequences of their apparent potential to modify the linkage between
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268 marine-freshwater and terrestrial-freshwater ecosystems through their trophic interactions and how
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269 it potentially amplifies the ecological consequences of some existing anthropogenic-mediated
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290 perturbations is important.
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31 32 33 272 ***IV- Socio-economic dimensions***

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373 European catfish has constituted a valuable fisheries resource through much of its native range and
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274 has been targeted by both commercial and recreational fisheries since prehistoric times (Quinn
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275 2011). Maybe ironically, the unique attributes of European catfish, in particular its growth and
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276 potential for reaching very large body sizes, have also facilitated the illegal introduction of the
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277 species outside its native range. Relatedly, recent work in Germany and the USA has shown that
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278 body size is a key determinant of angler motivation across a range of species (Arlinghaus et al.
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279 2014), including catfishes (Hutt et al. 2013). Although there are no data available on numbers and
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280 sizes of released individuals, some of the introduced fisheries now support a vibrant trophy fish and
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281 catch-and-release-only tourism fishery, with numerous guides operating on both the Ebro and the
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282 Po basins, and likely in many other areas in France, Spain and Italy. In these areas, the presence of
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283 the European catfish promotes socio-economic development based on recreational angling by non-
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284 locals (Rodríguez-Labajos 2014). There is evidence that some of these stocks were purposely
285 created by illegal transfer of a few hundred individuals by anglers, such as in the Mequinzenza
1 reservoir in the Ebro basin (Carol 2007; Rodríguez-Labajos et al. 2009). Anecdotal observation of
286 3 social media and recent introduction to new Iberian river basins suggests that some anglers are
287 4 interested in further spreading the species, and there is also evidence that some discussion in social
288 6 media has taken place in the U.S.A. to purposely introduce the species to North America to
289 8 supplement the native species that do not nearly reach the same final body sizes. The species was
290 10 also recently recorded as introduced in the wild, with uncertain establishment, in Brazil (Cunico and
291 12 Vitule 2014). Johnson et al. (2009) warned that illegal release of highly demanded species
292 14 constitutes a constant pathway facilitating spread of non-native species, which particularly applies
293 16 to European catfish due to its attractiveness to a small, yet highly avid segment of trophy anglers
294 18 (Hickley and Chare 2004; Britton et al. 2007). Trophy anglers are known to practice catch-and-
295 20 release (e.g., Arlinghaus 2007), hence there is little hope that angler exploitation would contribute
296 22 significantly to their removal once populations have established.
297 24 In its native range, whilst European catfish has so far not featured very prominently among the
298 26 target species of the majority of anglers (Arlinghaus et al. 2008), there has been a development of a
299 28 highly specialized sub-section among anglers that specifically targets trophy catfish. It is these
300 30 anglers that likely feed the foreign catfish guiding businesses in the introduced ranges and that also
301 32 heavily target native stocks in countries such as Germany, Hungary, or Russia. In contrast to
302 34 angling, the large body sizes of European catfish are likely of low importance to commercial
303 36 capture fisheries that tend to be more biomass-oriented. There is also a small aquaculture sector in
304 38 central Europe focusing on European catfish, some of which are used for stocking purposes.
305 40 Perhaps due to climate change, European catfish appear to now be able to disperse and recruit
306 42 highly successfully throughout its native range, in turn creating management conflicts and fostering
307 44 active eradication efforts in some areas (e.g., in Germany), based on the belief that their populations
308 46 exert high trophic effects as it expands its range. As a consequence, in some German states, state-
309 48 level minimum size limits have been reduced or eliminated to facilitate exploitation. In Spain,
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311 European catfish is included in the National catalogue of invasive alien species and thus holding,
312 transporting, and trading with this species is forbidden. In Belgium and France, the fishing of the
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313 European catfish is authorized during all the year, with no limit of size and number of individuals.
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314 In Belgium, restocking and introduction are not allowed. In England, introducing and keeping
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315 European catfish in inland waters requires a permit granted by the responsible government
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316 authority, with a permit generally only granted where the inland water is an enclosed stillwater
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317 where the fish has no chance of escaping into the wider environment.
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318 Anglers targeting trophy catfish in areas like the Ebro or Po Rivers could also lead to
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319 indirect ecosystem impacts associated with catfish angling. For example, many anglers use live
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320 baitfish and hence due to the bait industry there is the possibility of unintended introduction of other
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321 fishes, parasites or diseases (Johnson et al. 2009). Moreover, in some areas, bottom fishing with
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322 large fishmeal pellets has become popular among catfish anglers. Pellets are often used in high
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323 amounts associated with groundbaiting to attract fish. This may lead to significant nutrient inputs
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324 and foster eutrophication, similar to the case in carp fishing (Arlinghaus and Mehner 2003; Niesar
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325 et al. 2004).
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326 European catfish is also exploited for commercial purposes, notably on the Eastern
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327 European market, where its flesh is appreciated. As mostly benthic feeder, the European catfish has
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328 been shown to accumulate higher concentrations of organochlorine compounds (Babut et al. 2012;
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329 Huertas et al. 2016) and heavy metals such as mercury (Carrasco et al. 2011) than other fish
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330 species. In the Po River (North Italy), the 33% of the 54 European catfish analysed from 2006 to
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331 2009 exceeded the maximum levels of 125 ng PCBs g⁻¹ fresh weight set by the European
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332 regulations in fish (Squadrone et al. 2013a). Thus, in rivers where there are extant pollution
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333 problems (e.g. heavy metals, and organochlorine and radioactive compounds), European catfish
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334 flesh levels of PCB and heavy metals and could constitute a health human concern (Squadrone et al.
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335 2013b; Comby et al. 2014).
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337 *V- Management and control of invasive populations*
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338 The greatest problem for managing the important extent of catfish range within Europe arises from
339 the interaction of their attractiveness as an unique trophy fish with their apparent suitability for
340 establishing self-sustaining populations and then achieving rapid growth rates across much of their
341 extended range, but especially in the warmer regions of southern Europe. This has created a strong
342 desire for introducing individuals into previously non-invaded areas, despite regulations being in
343 place to prevent this (Hickley and Chare 2004; Genovesi et al. 2014). This continued pressure of
344 introductions of European catfish includes Great Britain. Despite generally unsuitable current
345 climate conditions for their fast growth and recruitment, angling demand has resulted in catfish
346 release into over 250 lake fisheries and their escape into a number of major river basins (Britton et
347 al. 2010a). This general introduction pressure from anglers means that any management and
348 regulatory framework designed to prevent their further releases will be extremely difficult to
349 implement effectively (Britton et al. 2011). Moreover, given that many of the introductions outlined
350 have been into large open river systems with high connectivity, then in many cases the ability to
351 extirpate local populations to prevent their dispersal is negligible, despite this being a useful
352 management measure to prevent dispersal from connected lentic environments (Britton et al. 2010b;
353 Britton et al. 2011). Consequently, the combination of their large body sizes making them highly
354 attractive to specialist anglers (Hickley and Chare 2004), their relative ease of capture (Britton et al.
355 2007) and their invasive presence in major European river systems (Copp et al. 2009) suggests that
356 management methods to reduce their ecological impacts in existing ranges will be futile (Britton et
357 al. 2010a). Arguably, these conservation resources would be better targeted at preventing their
358 introductions into river basins where they are not yet present, utilizing new policy and regulations
359 specifically designed for this or with the use of high fines and other disincentives (Johnson et al.
360 2009; Genovesi et al. 2014, Piria et al. 2016). Nevertheless, the indications are that catfish
361 introductions by anglers in Southern Europe are still ongoing (e.g. their first record in Portugal
362 reported in 2015 (Gkenas et al. 2015)), and thus their invasive range is predicted to increase further.
363 Climate change could also result in areas in more northern latitudes becoming increasingly

364 vulnerable to their invasion, especially where individuals are already present but populations have
365 yet to establish due to thermal constraints (Britton et al. 2010a).

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367 **Conclusions**

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

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654 **Figure caption**

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Figure 1

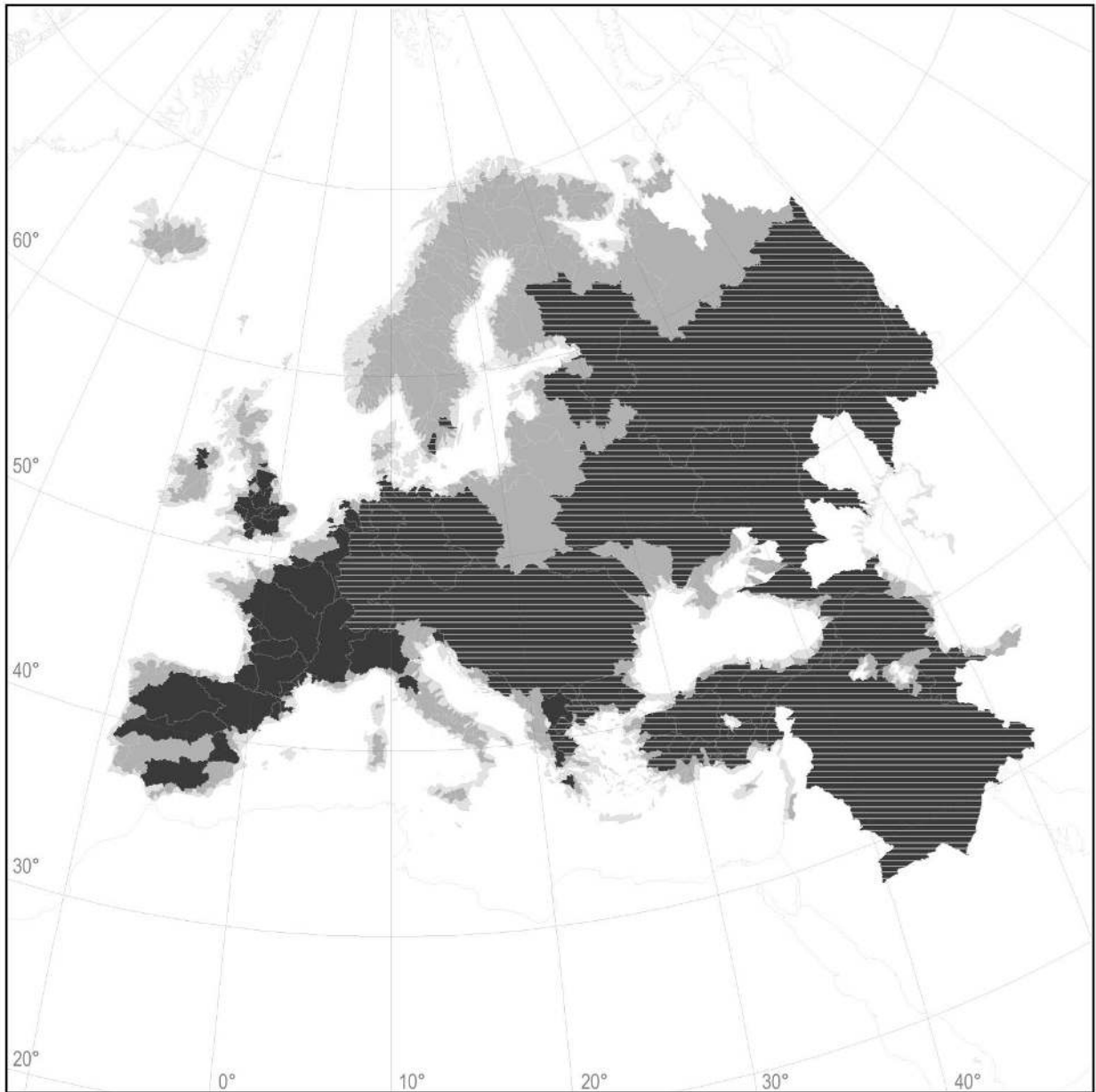




Figure caption

Figure 1: Native (striped dark grey) and introduced (dark grey) distributional ranges of European catfish (*Silurus glanis*) in Eurasian watersheds with an area > 1000 km².

Watersheds where the species is present are displayed in dark grey; watersheds with no official evidence of introduction were in grey; < 1000 km² 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.

- 1 **Table 1.** An overview of the subject covered by the review in relation to general ecological themes and hypotheses, and the associated research questions
- 2 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?
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