Does the non-native European catfish Silurus glanis threaten French river fish populations ?

Nicolas Guillerault, Sebastien Delmotte, Stéphanie Boulêtreau, Christine Lauzeral, Nicolas Poulet, Frédéric Santoul

doi:10.1111/fwb.12545

Does the non-native European catfish *Silurus glanis* threaten French river fish populations?

NICOLAS GUILLERAULT*,†, SÉBASTIEN DELMOTTE‡, STÉPHANIE BOULÊTREAU*,†, CHRISTINE LAUZERAL§, NICOLAS POULET¶ AND FRÉDÉRIC SANTOUL*,†

*Université de Toulouse, UPS, INP, EcoLab (Laboratoire Ecologie Fonctionnelle et Environnement), Toulouse, France
†EcoLab, CNRS, Toulouse, France
‡MAD Environnement S.A.R.L, Nailloux, France
§Laboratoire Evolution et Diversité Biologique, UMR 5174, CNRS Université Paul Sabatier, Toulouse, France
¶Direction Générale 'Le Nadar', French National Agency for Water and Aquatic Environment (Onema), Vincennes, France

SUMMARY

1. The European catfish, *Silurus glanis*, was widely introduced in western Europe, and it has now established self-sustaining populations in numerous large rivers of western France. Using data collected from surveys conducted by the French National Agency for Water and Aquatic Environment (Onema) from 1989 to 2010 in more than 500 sites throughout the country (10636 electrofishing surveys), we investigated the potential impact of the European catfish on fish communities in French rivers.
2. In the first part of the analysis, we compared trends observed before and after the European catfish was established at given sites (before after analysis). Species richness, evenness and diversity decreased significantly after the European catfish was established at 1.4%, 1.4% and 5.8% of the sites, respectively. Total fish biomass and density decreased significantly at 6.6% and 2.9% of the sites, respectively. In the second part of the analysis, we compared sites with European catfish against sites lacking European catfish during the same period (with without analysis). Fish species richness was significantly higher in sites with European catfish. No significant differences in fish diversity, evenness, total fish biomass or density were found between sites with or without European catfish.
3. While our results indicate that the European catfish may in a few cases impact fish communities or populations, it does not appear to be responsible for a countrywide collapse in fish assemblages.

Keywords: alien predator, before after analysis, biological invasion, control impact analysis, impact assess ment

Introduction

Several threats to inland water ecosystems have been identified, among which invasions are recognised as serious menaces (Dudgeon *et al*., 2006). Often resulting from accidental or intentional translocations of species by humans, invasions affect a wide range of plant and animal taxa in many lakes and rivers worldwide (García-Berthou, 2007; Ricciardi & MacIssac, 2011). Freshwater fish are among the most introduced animals worldwide (Copp *et al*., 2005; Elvira & Almodóvar, 2001), mainly because of escapes from aquaculture or intentional releases for recreational fisheries (Copp, Templeton & Gozlan, 2007; Welcomme *et al*., 2010; Cucherousset & Olden, 2011). Non-native game fish are often significantly larger than native species and occupy significantly higher trophic levels (Donaldson *et al*., 2011). In freshwater ecosystems subject to strong top-down control (Shurin *et al*., 2002), fish introductions may have important effects (Vander Zanden, Casselman & Rasmussen, 1999) such as changes to prey-size refugia and thus to predator prey equilibria (Chase, 1999; Clavero & García-Berthou, 2005) or energy fluxes (MacAvoy *et al*., 2000).

One of the most popular and successful fish introductions in Europe has involved the European catfish, *Silurus glanis*. Originating in eastern Europe and western Asia, the species was introduced to France at the end of

Correspondence: Nicolas Guillerault, Ecolab, Université Toulouse III Paul Sabatier, Bât 4R1, 31062 Toulouse CEDEX 9 (France).
E mail: nicolas.guillerault@univ tlse3.fr

the 19th century and has now established self-sustaining populations in many French rivers (Copp *et al.*, 2009; Poulet, Beaulaton & Dembski, 2011). This long-lived predator may reach a total length of over 2.5 m, becoming twice as large as the native piscivore, northern pike (*Esox Lucius*).

The large number of videos broadcast and articles published in newspapers and angling magazines, feeding myths about the size or behaviour of specimens caught, and even some scientific publications (e.g. Cucherousset *et al.*, 2012), have resulted in strong views for or against *S. glanis* and deep concerns about its foraging behaviour and impact on freshwater biota. Although *S. glanis* has been hypothesised to affect waterbird populations in Spanish reservoirs (Carol *et al.*, 2009), little is known about the ecology of the introduced *S. glanis* and there is no evidence that it as a voracious predator (Copp *et al.*, 2009; Syväranta *et al.*, 2010).

Using data collected from 10636 electrofishing surveys conducted within the last two decades in more than 500 sites throughout France, we aimed to evaluate the potential impact of *S. glanis* on riverine fish populations in the metropolitan area of France. Fish species richness, evenness, diversity, density and biomass were compared in different rivers (i) prior to and after *S. glanis* establishment (before after analysis) and (ii) between sites with and without *S. glanis* (with without analysis).

Methods

Fish survey

The French National Agency for Water and Aquatic Environments (Onema) has been monitoring freshwater fish populations in the whole river network of France for several decades. Sites were sampled during the low-flow period (from May to October) using standardised electrofishing procedures appropriate to prevailing river widths and depths. Streams were sampled by wading (mostly two-pass removal), while fractional sampling strategies were used in larger rivers (see Poulet *et al.*, 2011). Fish were identified to species, counted, weighed and then released.

Data analysis

Only surveys performed with the same sampling protocol at a given site were selected. Density and biomass were expressed as fish number and biomass per 100 m^2. Species diversity was described using Shannon's diversity index and evenness using Pielou's evenness index. Analyses were conducted using R software (R Development Core Team, 2014). The impact of *S. glanis* was defined from the standpoint of a quantifiable negative effect on the recipient environment (*sensu* Gozlan, 2008).

Before after analysis

We considered impact as a significant decrease in total fish richness, native fish richness, diversity, evenness, biomass or density after *S. glanis* establishment at a site. Fish assemblages were so different among sites that it was impossible to perform a global analysis.

Silurus glanis was considered established at a given site as soon as one individual was caught (t_0). Sites that were sampled at least once before t_0 and after t_0 were selected. Among these, sites with at least four years of *S. glanis* presence were used for the analysis (n 112).

Differences between the descriptive variables in each site (total species richness, native species richness, diversity, evenness, biomass and density) recorded before t_0 and after t_0 were tested using the Mann Whitney test. When a significant negative difference was identified, the Spearman correlation and autocorrelation tests (rank 1) with time before t_0 were used to detect a general negative temporal trend experienced prior to t_0 and not attributable to the presence of *S. glanis*.

The before after analysis does not allow the assignment of negative trends observed in the field to *S. glanis* (i.e. correlation does not imply causation). We performed the before after analysis with a comparison of sites with and without *S. glanis* (with without analysis) to parallel the intervention analysis (IA) and impact versus references sites (IVRS) analyses of Stewart-Oaten & Bence (2001).

With without analysis

The impact of *S. glanis* was judged according to whether sites with *S. glanis* (W-sites) exhibited significantly lower total species richness, native species richness, diversity, evenness, biomass or density than sites where environmental conditions would allow the presence of *S. glanis* but where it has never been recorded (while electrofishing or angling; Wt-sites).

The W-sites were selected using species distribution models (set from 236 occurrence and 874 absence sites throughout France), taking into account elevation, distance from source, slope, catchment surface, mean temperature in January and mean temperature in July. Because of the non-native status of *S. glanis*, many of these absences were not environmentally caused. We

thus chose an iterative ensemble modelling approach (Lauzeral, Grenouillet & Brosse, 2012) that combined six different statistical methods. Two-thirds of the sites were chosen at random and used to calibrate the models, and the other third was kept for independent evaluation. The calibrated model was then projected over France, giving rise to a potential species distribution. The selection of the calibration data set was repeated ten times. The ten resulting distributions were then summed, giving rise to a map of the level of habitat suitability. Each model-selected site (n 521) was submitted to the expertise of field technicians from Onema. First, the experts were asked to judge the probability of *S. glanis* presence in or near the site. In fact, especially in large rivers, European catfish is not always detected using electrofishing and the field technicians were sometimes aware of the presence of the species (from anecdotal evidence of anglers). Then, the experts were asked to judge the suitability of habitat at each site, to refine results from the model ($10' \times 10'$ resolution). Some model-selected sites had local habitat features (not previously used in the model) that were not suitable for *S. glanis* (e.g. water velocity). Finally, 47 stations were confidently selected.

The previously selected Wt-sites were compared with W-sites showing homogenous environmental conditions. To identify these W-sites, a hierarchical classification (HC, Ward's method) was performed on the environmental data set containing both W-sites and Wt-sites. This hierarchical classification generated four groups. A redundancy analysis (RDA) showed significant differences between the groups (99% randomisation test, ADE4 package for R), although two groups of stations overlapped, revealing very close environmental conditions. These two groups, containing 46 of the 47 sites without *S. glanis*, were retained for further analysis.

To detect a potential time lag in *S. glanis* impact, Wt-sites were compared with W-sites colonised for 0 2 years, 3 5 years, 6 10 years or more than 10 years during the same period of time (here, the last data recorded in the database, that is from 2006 to 2010). Significant difference in fish richness, native fish richness, diversity, evenness, biomass or density between Wt-sites and W-sites was identified using the Mann Whitney test.

Results

Before after analysis

Total fish species richness, native fish richness, evenness and diversity were potentially affected by *S. glanis* in 1.4% (1/69), 1.4% (1/69), 1.4% (1/69) and 5.8% (4/69) of sites, respectively. Total fish biomass was potentially affected at 6.6% (4/61) of sites, while total biomass of fish other than *S. glanis* was potentially affected at 13.1% (9/61) of sites. The total density of sampled fish was potentially affected after *S. glanis* establishment at 2.9% (3/69) of sites, while total density of fish other than *S. glanis* was affected at 5.8% (5/69) of sites.

The biomass of the three fish species most strongly represented (in terms of biomass) in the data set was potentially impacted by *S. glanis* in 3.3% (chub, *Squalius cephalus*) and 4.1% (barbel, *Barbus barbus*) of sites but with no impact identified for the European eel, *Anguilla anguilla* (Table 1).

The densities of the three fish species most strongly represented (in terms of density) during electrofishing (roach, *Rutilus rutilus*; chub and bleak, *Alburnus alburnus*) were significantly lower at 13%, 1.4% and 2.9% of sites, respectively, in relation to *S. glanis* introduction.

For the top predators, a significant decrease in biomass was detected in 8.3% (northern pike, *Esox lucius*) and 1.8% (Eurasian perch, *Perca fluviatilis*) of sites and a significant change in densities was found in 5.5% and 6.2% of sites, respectively. No significant change, however, was observed in either biomass or density of pikeperch, *Sander lucioperca*.

With without analysis

Irrespective of time since *S. glanis* introduction, no difference was found between W-sites and Wt-sites with respect to total evenness, diversity, biomass or density. A significant difference in total species richness was found between W-sites and Wt-sites (K W test; P 0.0036); most Wt-sites held fewer fish species than W-sites (mean values: Wt 14; $W_{[0\text{-}2]}$ 17; $W_{[2\text{-}5]}$ 17; $W_{[5\text{-}10]}$ 18; $W_{>10}$ 19). This difference originates from significant differences in both native and non-native fish species richness (K-W test; P 0.04 and $P < 0.001$, respectively).

The with without analysis showed no differences in biomass of the three most represented species (carp, European eel and chub), or densities of the three most numerically represented species (roach, chub and bleak) or biomass and density of the top-predators (northern pike, pikeperch and Eurasian perch) (Table 2).

Discussion

Comparisons between sites with and without *S. glanis* did not highlight any drastic changes in species richness during the study period, and no fish species extinction

Table 1 Results of the before after selection procedure of the sites exhibiting the *Silurus glanis* impact on biomass or density of the main freshwater fish species

	Biomass				Density			
Species	Sampled sites	B>A	rs	B<A	Sampled sites	B<A	rs	B<A
Abramis brama (N)	38	1	1 (2.6%)	0	44	1	1 (2.3%)	2
Alburnus alburnus (N)	59	2	2 (3.4%)	1	69	2	2 (2.9%)	5
Ameiurus melas (NN)	21	0		2	22	0		1
Anguilla anguilla (N)	54	0		3	58	1		3
Barbus barbus (N)	49	2	2 (4.1%)	0	51	1	1 (2.0%)	2
Cyprinus carpio (NN)	23	0		0	24	0		0
Esox lucius (N)	48	4	4 (8.3%)	0	55	3	3 (5.5%)	0
Perca fluviatilis (N)	57	1	1 (1.8%)	0	65	4	4 (6.2%)	0
Rutilus rutilus (N)	60	7	5 (8.3%)	0	69	10	9 (13.0%)	0
Sander lucioperca (NN)	25	0		2	29	0		4
Squalius cephalus (N)	60	2	2 (3.3%)	1	69	1	1 (1.4%)	0
Tinca tinca (N)	42	0		0	53	0		0

(*N*), native species; (*NN*), non native species (Poulet *et al.*, 2011). B>A: number of sites with a significant decrease in before after analysis, using the Mann Whitney test. rs: number of sites where the significant decrease in fish population was not associated with a temporal trend already established before *S. glanis* settlement, using the Spearman correlation test. The value of rs in % corresponds to the proportion of sites where *S. glanis* potentially affected fish species biomass or density. Significant increases in biomass or density (Mann Whitney test) are displayed in the column B<A.

was attributed to *S. glanis*. On the contrary, sites with *S. glanis* had higher mean total, native and non-native species richness. Sites without catfish are probably less prone to colonisation because of low local habitat suitability, physical barriers such as dams or waterfalls, or lower anthropogenic propagule pressure (Lockwood, Cassey & Blackburn, 2005), which limit the spread of *S. glanis* as well as other species of fish and thus do not permit a rise in species richness (Daufresne & Boët, 2007).

The with without analysis also revealed no significant differences in fish evenness, biomasses or fish densities, regardless of time since the invasion began. Nor was there a time lag between *S. glanis* establishment and any change over a period ranging from 0 to more than 10 years since *S. glanis* was first caught (i.e. when old and large individuals were probably not well represented). Some river basins are considered as non-equilibrium islands in which species extinctions (related to historical events) are not fully balanced by colonisations from neighbouring river basins (Oberdorff, Hugueny & Guégan, 1997; Reyjol *et al.*, 2007). Species-unsaturated rivers are more susceptible to invasion by non-native species because ecological space is less densely packed and interspecific competition is less intense (Hutchinson, 1959; Kennedy *et al.*, 2002). In addition, *S. glanis* appears to be a scavenging predator, able to exploit a wide variety of prey sources (Copp *et al.*, 2009) so that, despite its size, the species does not occupy the highest trophic position in fish communities of large rivers in France (Syväranta *et al.*, 2009). Feeding on a wide spectrum of available prey alleviates predation pressure on any particular category or species of prey (except for some specialised *S. glanis* individuals; see Syväranta *et al.*, 2009; Cucherousset *et al.*, 2012).

Few sites have experienced a significant impact of *S. glanis* introduction, and this lessens the effect of *S. glanis* as one among the numerous variables driving river ecosystems. Some systems, such as ponds or streams, are known to be more sensitive to invasion than large systems (Elton, 2000; Gozlan, 2008), and anthropogenic alterations may have an additive or synergistic impact with *S. glanis* on the host system (Light & Marchetti, 2006).

Possible impacts on a given species were detected in a small percentage (usually <5%) of sites in our analysis. Roach decreased to the greatest extent after *S. glanis* establishment. Wysujack & Mehner (2005) reported that *S. glanis* (TL ranging from 40 to 100 cm) feeds mostly on crayfish and roach. Predation by *S. glanis* on mostly smaller roach individuals, in comparison with predation by either northern pike or pikeperch, could explain why 15% of the sites experienced a significant decrease in roach density. Nevertheless, sites without *S. glanis* did not hold significantly more roach than sites with the invader, and neither roach biomass nor density decreased with time since *S. glanis* establishment. Climate change may affect roach reproduction (Geraudie *et al.*, 2009), and efforts to enhance water quality made

Table 2 Mean values ± SD (*n* sites) of (a) fish biomass (kg 100 m^{-2}) and (b) density (number of individuals 100 m^{-2}) sampled while electrofishing from 2006 to 2010 *P*-value from Kruskal–Wallis test between groups

	Time since *S glanis* arrival (years)	Total	*Abramis brama*	*Alburnus alburnus*	*Ameiurus melas*	*Anguilla anguilla*	*Barbus barbus*	*Cyprinus carpio*
(a)	No *S glanis*	1200 ± 802 (24)	284 ± 345 (6)	26 ± 46 (16)	119 ± 149 (3)	237 ± 255 (17)	216 ± 389 (13)	-(0)
	0–1	1507 ± 1523 (122)	82 ± 102 (61)	16 ± 28 (101)	44 ± 62 (21)	298 ± 336 (91)	218 ± 388 (76)	471 ± 472 (30)
	2–4	1458 ± 1218 (39)	180 ± 554 (18)	13 ± 17 (36)	139 ± 257 (10)	235 ± 205 (28)	123 ± 193 (28)	670 ± 1092 (11)
	5–9	1977 ± 1451 (35)	96 ± 96 (17)	20 ± 41 (29)	119 ± 206 (9)	288 ± 414 (25)	156 ± 211 (20)	439 ± 678 (14)
	>10	1365 ± 768 (9)	136 ± 126 (4)	19 ± 15 (9)	81 - (1)	313 ± 302 (5)	188 ± 247 (6)	305 ± 380 (6)
	P-value	*0 874*	*0 555*	*0 565*	*0 526*	*0 902*	*0 576*	*0 579*
(b)	No *S glanis*	57 ± 45 8 (24)	0 8 ± 0 5 (6)	5 1 ± 8 7 (17)	1 2 ± 1 3 (4)	1 9 ± 1 9 (17)	3 8 ± 5 6 (13)	0 7 ± 0 6 (2)
	0–1	57 ± 59 8 (122)	1 0 ± 1 6 (66)	7 2 ± 11 6 (107)	0 9 ± 1 3 (23)	1 3 ± 2 1 (91)	3 0 ± 5 4 (80)	0 5 ± 0 7 (34)
	2–4	61 ± 60 2 (39)	1 4 ± 2 6 (20)	10 1 ± 18 9 (37)	6 0 ± 10 6 (10)	0 8 ± 1 0 (29)	2 7 ± 2 7 (28)	1 2 ± 1 2 (12)
	5–9	83 ± 90 9 (35)	1 7 ± 2 4 (19)	16 4 ± 26 3 (30)	3 9 ± 6 1 (9)	1 2 ± 2 1 (25)	4 0 ± 5 7 (20)	0 2 ± 0 2 (16)
	>10	102 ± 74 4 (9)	0 8 ± 0 8 (4)	9 8 ± 8 6 (9)	3 9 - (1)	1 2 ± 1 4 (5)	4 6 ± 8 2 (6)	0 2 ± 0 2 (6)
	P-value	*0 266*	*0 724*	*0 118*	*0 506*	*0 390*	*0 892*	*0 620*

	Time since *S glanis* arrival (years)	*Esox lucius*	*Perca fluviatilis*	*Rutilus rutilus*	*Sander lucioperca*	*Squalius cephalus*	*Tinca tinca*
(a)	No *S glanis*	191 ± 271 (8)	53 ± 66 (12)	113 ± 162 (20)	91 ± 128 (2)	417 ± 450 (18)	58 ± 51 (6)
	0–1	95 ± 125 (78)	51 ± 46 (108)	118 ± 157 (113)	21 ± 65 (38)	450 ± 497 (115)	47 ± 67 (69)
	2–4	81 ± 84 (25)	116 ± 431 (35)	77 ± 74 (36)	40 ± 92 (11)	439 ± 413 (38)	60 ± 81 (21)
	5–9	94 ± 108 (21)	44 ± 40 (33)	123 ± 133 (35)	21 ± 33 (13)	397 ± 366 (35)	47 ± 58 (20)
	>10	68 ± 91 (5)	44 ± 64 (9)	113 ± 106 (8)	10 ± 14 (5)	308 ± 249 (9)	34 ± 58 (5)
	P-value	*0 885*	*0 753*	*0 737*	*0 822*	*0 964*	*0 574*
(b)	No *S glanis*	1 1 ± 1 3 (10)	1 8 ± 1 8 (15)	7 2 ± 14 4 (22)	0 2 ± 0 1 (2)	5 7 ± 5 3 (20)	0 3 ± 0 3 (6)
	0–1	0 3 ± 0 4 (81)	1 7 ± 1 9 (112)	9 2 ± 13 8 (117)	0 2 ± 0 2 (44)	9 0 ± 11 6 (120)	0 4 ± 0 4 (72)
	2–4	0 4 ± 0 3 (26)	1 7 ± 1 7 (36)	8 1 ± 10 3 (37)	0 4 ± 0 8 (13)	9 7 ± 9 4 (39)	0 3 ± 0 2 (24)
	5–9	0 5 ± 0 3 (23)	1 5 ± 1 4 (33)	11 2 ± 9 9 (35)	0 6 ± 1 1 (13)	10 6 ± 12 9 (35)	0 6 ± 0 9 (23)
	>10	0 4 ± 0 3 (5)	1 2 ± 1 6 (9)	22 7 ± 42 4 (8)	0 3 ± 0 3 (5)	7 2 ± 5 3 (9)	0 2 ± 0 1 (5)
	P-value	*0 093*	*0 859*	*0 737*	*0 786*	*0 420*	*0 666*

Values in italics are the *P*-value from Kruskal–Wallis test

during the study period led to a decrease in pollution by phosphorus and organic substances (Crouzet, 1999), while river incision led to an increase in water velocity (Wyźga, 2001; Kondolf, Piégay & Landon, 2002). These changes could be responsible for declines in limnophilic or eurytopic populations such as those of roach or perch (Jeppesen *et al.*, 2000; Olin *et al.*, 2002; Poulet *et al.*, 2011).

Silurus glanis might potentially affect predatory species such as northern pike or pikeperch via predation or competition for food or habitat. However, densities of predators are often low (<1 individual 100 m^{-2}), and the number of sites holding these species is often small; this may limit the robustness of our analysis for such species. Predatory fish are also very popular with anglers, potentially creating a significant pressure on their populations through harvesting. The population dynamics of such species are also blurred by numerous stocking episodes, for which statistics are often absent and where stocking efficiency may vary widely from year to year (Arlinghaus *et al.*, 2007; Arlinghaus, Matsumura & Dieckmann, 2010.

Our study showed no generalised impact of *S. glanis* on fish biomass, density or community structure in French rivers. Nevertheless, *S. glanis* may have local effects on fish populations since significant changes in fish biomass and density after *S. glanis* establishment were identified at several sites. Future studies should determine in greater detail whether *S. glanis* might change the structure of the food web in the decades after its establishment. Additionally, research should focus on potential effects on migratory species (MacAvoy *et al.*, 2000) whose populations are not monitored by Onema's electrofishing survey.

Acknowledgments

The authors wish to thank the numerous engineers and technicians who perform electrofishing and maintain the database. The authors also thank anonymous reviewers and the editor for useful comments on the manuscript.

References

Arlinghaus R., Cooke S.J., Lyman J., Policansky D., Schwab A., Suski C., *et al.* (2007) Understanding the complexity of catch and release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, **15**, 75 167.

Arlinghaus R., Matsumura S. & Dieckmann U. (2010) The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. *Biological Conservation*, **143**, 1444 1459.

Carol J., Benejam L., Benito J. & García Berthou E. (2009) Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, **174**, 317 328.

Chase J.M. (1999) Food web effects of prey size refugia: var iable interactions and alternative stable equilibria. *The American Naturalist*, **154**, 559 570.

Clavero M. & García Berthou E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, **20**, 110.

Copp G.H., Bianco P.G., Bogutskaya N.G., Erős T., Falka I., Ferreira M.T., *et al.* (2005) To be, or not to be, a non native freshwater fish? *Journal of Applied Ichthyology*, **21**, 242 262.

Copp G.H., Britton R.J., Cucherousset J., García Berthou E., Kirk R., Peeler E., *et al.* (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and intro duced ranges. *Fish and Fisheries*, **10**, 252 282.

Copp G.H., Templeton M. & Gozlan R.E. (2007) Propagule pressure and the invasion risks of non native freshwater fishes: a case study in England. *Journal of Fish Biology*, **71**, 148 159.

Crouzet P. (1999) L'eutrophisation des rivières en France : où en est la pollution verte ? *Les Données de l'Environne ment*, **48**, 1 4.

Cucherousset J., Boulêtreau S., Azémar F., Compin A., Guil laume M. & Santoul F. (2012) 'Freshwater killer whales': beaching behavior of an alien fish to hunt land birds. *PLoS ONE*, **7**, e50840.

Cucherousset J. & Olden J.D. (2011) Ecological impacts of non native freshwater fishes. *Fisheries*, **36**, 215 230.

Daufresne M. & Boët P. (2007) Climate change impacts on structure and diversity of fish communities in rivers. *Global Change Biology*, **13**, 2467 2478.

Donaldson M.R., O'Connor C.M., Thompson L.A., Ginge rich A.J., Danylchuk S.E., Duplain R.R., *et al.* (2011) Con trasting global game fish and non game fish species. *Fisheries*, **36**, 385 397.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z. I., Knowler D.J., Lévêque C., *et al.* (2006) Freshwater bio diversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, **81**, 163 182.

Elton C.S. (2000) *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago 60637.

Elvira B. & Almodóvar A. (2001) Freshwater fish introduc tions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology*, **59**, 323 331.

García Berthou E. (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology*, **71**, 33–55.

Geraudie P., Gerbron M., Hill E. & Minier C. (2009) Roach (*Rutilus rutilus*) reproductive cycle: a study of biochemical and histological parameters in a low contaminated site. *Fish Physiology and Biochemistry*, **36**, 767–777.

Gozlan R.E. (2008) Introduction of non native freshwater fish: is it all bad? *Fish and Fisheries*, **9**, 106–115.

Hutchinson G.E. (1959) Homage to Santa *Rosalia* or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.

Jeppesen E., Peder Jensen J., Søndergaard M., Lauridsen T. & Landkildehus F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology*, **45**, 201–218.

Kennedy T.A., Naeem S., Howe K.M., Knops J.M.H., Tilman D. & Reich P. (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.

Kondolf G.M., Piégay H. & Landon N. (2002) Channel response to increased and decreased bedload supply from land use change: contrasts between two catchments. *Geomorphology*, **45**, 35–51.

Lauzeral C., Grenouillet G. & Brosse S. (2012) Dealing with noisy absences to optimize species distribution models: an iterative ensemble modelling approach. *PLoS ONE*, **7**, e49508.

Light T. & Marchetti M.P. (2006) Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, **21**, 434–446.

Lockwood J.L., Cassey P. & Blackburn T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

MacAvoy S.E., Macko S.A., McInnich S.P. & Garman G.C. (2000) Marine nutrient contributions to freshwater apex predators. *Oecologia*, **122**, 568–573.

Oberdorff T., Hugueny B. & Guégan J. F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, **24**, 461–467.

Olin M., Rask M., Ruuhljärvi J., Kurkilahti M., Ala Opas P. & Ylönen O. (2002) Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *Journal of Fish Biology*, **60**, 593–612.

Poulet N., Beaulaton L. & Dembski S. (2011) Time trends in fish populations in metropolitan France: insights from national monitoring data. *Journal of Fish Biology*, **79**, 1436–1452.

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R project.org.

Reyjol Y., Hugueny B., Pont D., Bianco P.G., Beier U., Caiola N., *et al.* (2007) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography*, **16**, 65–75.

Ricciardi A. & MacIssac H.J. (2011) Impacts of biological invasions on freshwater ecosystems. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (Ed. D.M. Richardson), pp. 211–224. Blackwell Publishing Ltd, Chichester, UK.

Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B., *et al.* (2002) A cross ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785–791.

Stewart Oaten A. & Bence J.R. (2001) Temporal and Spatial variation in environmental impact assessment. *Ecological Monographs*, **71**, 305–339.

Syväranta J., Cucherousset J., Kopp D., Crivelli A., Céréghino R. & Santoul F. (2010) Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquatic Biology*, **8**, 137–144.

Syväranta J., Cucherousset J., Kopp D., Martino A., Céréghino R. & Santoul F. (2009) Contribution of anadromous fish to the diet of European catfish in a large river system. *Die Naturwissenschaften*, **96**, 631–635.

Vander Zanden J.M., Casselman J.M. & Rasmussen J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, **401**, 464–467.

Welcomme R.L., Cowx I.G., Coates D., Béné C., Funge Smith S., Halls A., *et al.* (2010) Inland capture fisheries. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **365**, 2881–2896.

Wysujack K. & Mehner T. (2005) Can feeding of European catfish prevent cyprinids from reaching a size refuge? *Ecology of Freshwater Fish*, **14**, 87–95.

Wyźga B. (2001) Impact of the channelization induced incision of the Skawa and Wisłoka Rivers, southern Poland, on the conditions of overbank deposition. *River Research and Applications*, **17**, 85–100.