Freshwater Biology

Freshwater Biology (2013) doi:10.1111/fwb.12102

Do non-native fish as prey favour the conservation of the threatened indigenous Eurasian otter?

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SUMMARY

1. Biological invasions are considered a major threat to biodiversity. Most research has focused on the distribution, biology and impacts of non-native species on native fauna and flora. However, few studies have explored their role as prey for native predators of conservation concern.
2. To assess the incidence and intensity of predation by the Eurasian otter *Lutra lutra* on established non-native fish species, data were collated from the published literature. To be selected, studies had to cover at least 1 year, analyse more than 100 spraints and report the study period and percentage relative frequency (%RF) of all prey fish species.
3. To permit reliable, time-related comparisons with %RF of non-native fishes in otter diet, we also reviewed available information about both the distribution of non-native fishes and history of their introductions to European countries, revealing a decrease with longitude in the number of naturalised non-native fishes taken (ranging between 5 and 34) and their percentage in each fish assemblage.
4. Our selective criteria were met by 30 dietary studies from 44 study areas in 15 European countries during 1970–2010. The extent to which otters rely on non-native fishes was almost negligible (mean %RF = 4.8), with the number of non-native fishes preyed upon by otters decreasing with both latitude and longitude.
5. The %RF of non-native fish in the diet increased slightly with time, with otters preying significantly more on non-native fish in study areas where alterations of the fish assemblage had been highlighted in the reference papers. No relationship was found between otter diet breadth and the occurrence of non-native fishes in their diet.
6. The current role of non-native species in otter diet suggests that effective otter conservation management plans should focus on the maintenance and/or enhancement of native fish assemblages.

Keywords: facilitative interactions, feeding behaviour, introductions, latitudinal gradient, predator-prey

Introduction

Biological invasions are considered a major threat to biodiversity (Vitousek *et al*., 1996; IUCN/SSC/ISSG, 2000; Baillie, Hilton-Taylor & Stuart, 2004; CBD, 2005). Interactions between introduced species and invaded habitats are highly complex, being compounded by environmental factors such as habitat modification (Maguire, 2004),

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disturbance regimes (Mack & D'Antonio, 1998) and evolutionary pathways (Mooney & Cleland, 2001). As a consequence, most studies have focused on the impact of non-native species on native species or communities by both top-down (*e.g.* Grosholz & Ruiz, 1996) and bottom-up (*e.g.* Bohn & Amundsen, 2001) processes. Of the six kinds of interaction (or combinations thereof) that Ebenhard (1988) suggested as likely to occur between native and non-native species (herbivory, predation, competition, disease or toxicity transmission, hybridisation, role as prey), the role of non-native species as prey for native predators has rarely been documented (e.g. Corkum, Sapota & Skora, 2004). These 'new' food resources are expected to have major effects on the populations of food-limited predators (Beja, 1996) and may enhance the survival of rare or declining species of conservationist interest.

A Web-based search covering the period 1993–2004 revealed six references with evidence of non-native species acting as a major food resource for native predators (Rodriguez, 2006). More recently, invasive round goby *Neogobius melanostomus* was reported to have positive effects on growth rate and body size of the threatened Lake Erie water snake *Nerodia sipedon insularum* (King, Ray & Stanford, 2006), whereas the spread of North American red swamp crayfish *Procambarus clarkii* seems to be beneficial to native (Correia, 2001; Tablado *et al.*, 2010) as well as introduced (Copp *et al.*, 2009) predators in Europe.

One native mammal that is a potential predator of introduced species is the Eurasian otter *Lutra lutra* (Miranda *et al.*, 2008), a semi-aquatic carnivore that suffered a dramatic decline throughout its European range between the 1950s and 1980s (Mason & Macdonald, 1986; Macdonald & Mason, 1994). In more recent decades, as the reasons for the otter's decline (water pollution, declining food resources, habitat loss, persecution) eased, populations gradually began to recover in several European countries (Ruiz-Olmo *et al.*, 2000; Crawford, 2003; Romanowski, 2006; Prigioni, Balestrieri & Remonti, 2007). The extent of otter recovery has been suggested to depend on both the degree of connectivity amongst neighbouring river catchments (Romanowski, 2006; Remonti *et al.*, 2008) and the availability of food resources (Ruiz-Olmo, López-Martín & Palazón, 2001), the latter potentially affecting otter density, breeding success and mortality (Kruuk & Conroy, 1991; Kruuk *et al.*, 1993; Ruiz-Olmo *et al.*, 2011). Although the otter is a flexible predator, foraging on a range of prey according to their relative availability (Remonti, Balestrieri & Prigioni, 2009), fish are the predominant and optimum prey type (Kruuk, 2006), being more profitable than both amphibians and crayfish in terms of absolute mean biomass and energetic content (Ruiz-Olmo & Jiménez, 2009).

Freshwater fish assemblages have been profoundly altered by human activities (Dudgeon *et al.*, 2006), with the introduction of fish species being a major cause of these changes (Moyle, 1997; Cowx, 1998; Leprieur *et al.*, 2009; Strayer, 2010). The first introductions probably date back to Roman times, but the spread of non-native species peaked towards the end of the 19th century and in the second half of the 20th century (Welcomme, 1992). Loss of biodiversity (Courtenay & Moyle, 1992), reduction in endemism and taxonomic homogenisation of fish assemblages (Marr *et al.*, 2010) are amongst the most often cited consequences of fish introductions.

Whilst Eurasian otters have been reported to shift their diet promptly in response to the introduction of non-native crayfishes (Delibes & Adrian, 1987; Correia, 2001), data on otter use of non-native fishes as prey are less consistent. In fresh waters of both Iberia (Blanco-Garrido, Prenda & Narvaez, 2008) and England (Miranda *et al.*, 2008; Almeida *et al.*, 2012), non-native fishes have been reported to be preyed upon by otters less than expected, whereas in southern Italy, otters switched to introduced largemouth bass *Micropterus salmoides* and pumpkinseed *Lepomis gibbosus* in the river sections where these fish had replaced the native fish fauna (Prigioni *et al.*, 2006). Similarly, otter consumption of non-native fishes increased during the flooding of an artificial lake in Portugal (Pedroso, Sales-Luís & Santos-Reis, 2011), and introduced ruffe *Gymnocephalus cernuus* has become the main prey of otters in Loch Lomond (Scotland) in the 20 years after the ruffe's introduction (McCafferty, 2005). These results suggest that non-native species may represent a more important prey item in otter diet in some situations and especially in semi-natural ecosystems or those subject to human alterations.

The aim of the present article is to assess the feeding adaptive response of otters to the temporal and spatial distribution of non-native fishes throughout its European range as well as the potential role played by this 'new' resource for otter conservation through a comprehensive review and analysis of available information on (i) occurrence of non-native fishes in otter diet, (ii) history of freshwater fish introductions and (iii) current status of non-native fishes in the countries for which sound otter diet data were available. Data were analysed using Random Forest Regression (RFR), a machine learning technique that is currently considered a promising technique in ecology (Franklin, 2010; Drew, Wiersma & Huettmann, 2011; Cheng *et al.*, 2012), useful to disentangle complex ecological phenomena (Schwartz *et al.*, 2006; Sepúlveda *et al.*, 2009; Davidson *et al.*, 2012).

Methods

The definitions of 'alien' and 'non-native' are not unanimously agreed, the interpretations being influenced by socio-political and economic perspectives (Copp *et al.*, 2005a). A biogeographical approach should consider as non-native any organism occurring in an area outside its historical range as a consequence of its deliberate, accidental or even indirect release into the wild by humans (see Copp *et al.*, 2005a for a review). Particularly for fishes, this approach includes translocations (*i.e.* within country movements that involve introductions to drainage basins outside the species' native range). However, for the purposes of the present study of broad spatial and temporal patterns, non-native (alien) species were considered, within a bio-political context, as any species moved to a country outside its natural range (Welcomme, 1988) because (i) data on fish introductions and distributions were available for all studies at a national scale only (*i.e.* in most cases, no information was available on the composition of fish assemblages in the otter diet study areas), and (ii) translocations have been so common in some regions (Copp *et al.*, 2005a) that the post-glacial native ranges of many fish species remain unknown or speculative for several countries, including Italy (Bianco, 1995) and the British Isles (Wheeler, 1977). Amongst introduced fish species, only those that have established self-sustaining populations in the wild (*i.e.* naturalised or established species; stage III–V in Colautti & MacIsaac, 2004) were considered. Transient/vagrant species were ignored.

The current number of naturalised non-native fish species in European countries was taken from Elvira (2001), except where subsequent literature with more accurate information was available (*e.g.* Hill *et al.* (2005) and Zięba *et al.* (2010a), Zięba, Fox & Copp (2010b) for the U.K.). For each country, overall numbers of freshwater fishes and histories of fish introductions were compiled from Web-based searches of publications and http://www.fishbase.org. Where necessary, lamprey species were removed with reference to Blanc *et al.* (1971).

To allow sound comparisons with the percentage relative frequency (%RF) of non-native fishes in otter diet, introductions were split into four periods: prior to 1980, 1981–1990, 1991–2000 and 2001–2010. Variations in the percentage increase (%I) in the number of non-native fish for each period were tested by ANOVA and post hoc Bonferroni tests.

To assess the importance of non-native fishes in otter diet, data were collated from available published literature. To standardise the comparison of results from different time periods and geographical areas, data were selected according to the following criteria: (i) studies covered at least 1 year and were based on spraint analysis only, so as to avoid differences in food type representation due to differential digestion (Putman, 1984; Balestrieri, Remonti & Prigioni, 2011); (ii) spraint sample sizes had to be greater than 100 to distinguish moderate effect sizes (Trites & Joy, 2005); (iii) all recognisable fish species had to be reported; (iv) the study period (year) had to be reported adequately; and (v) diet composition had to be expressed as percentage relative frequency (%RF = number of occurrences of each prey item/total number of occurrences of all prey items × 100) or could be derived from values or graphs given in the paper concerned. Although %RF does not provide any information about the biomass or relative volume of each prey item, this index has the advantage of having been used frequently in dietary comparisons (Reynolds & Aebischer, 1991; Clavero, Prenda & Delibes, 2003; Lozano *et al.*, 2006; Zhou *et al.*, 2011), and in otter diet studies, %RF values have been shown to be nearly as accurate as other indices (Jacobsen & Hansen, 1996). When geographical coordinates (latitude and longitude) of the study area were not indicated, they were derived from ordinance survey maps with representative mean coordinates used when samples were collected over a large area. Results for several streams from the same area were pooled to avoid pseudo-replication (Hulbert, 1984). When only seasonal data were reported, mean annual %RF was calculated from raw data when available.

To test the hypothesis that otter predation on non-native fishes was higher where otter diet was more diverse (Hounsome & Delahay, 2005) (*i.e.* non-native fishes provided an alternative prey to compensate for a decrease in native fish abundance; Clavero *et al.*, 2003), dietary breadth was estimated by standardised Levins' index (Feinsinger, Spers & Poole, 1981): $B = 1/R \sum_{i=1}^{n} p_i^2$ where p_i is the proportion of occurrence in terms of %RF of R food categories. According to Krebs (1989), the number of categories used is that obtained by categorising otter prey to the lowest possible systematic level allowed by published data (R = 73). To permit reliable comparisons with previous studies (Clavero *et al.*, 2003), food items were also grouped into seven main categories (fishes, amphibians, crayfishes, mammals, birds, reptiles and 'others').

Random Forest Regression (RFR) was applied to test for (i) influences of dietary breadth and time on %RF for all study areas, (ii) relationship between the minimum, mean and maximum geographic coordinates of each country (downloaded from http://opengeocode.org) and both the current richness and number of naturalised non-native species per each fish assemblages, as well as the number of non-native fish preyed upon by otters and (iii) influence of food availability (total number of non-native fishes, percentage of non-native species in each fish assemblage) on otter consumption of non-native fish species (%RF) for all the study areas for which historical data about fish introductions were found.

Random Forest Regression is of particular interest for identifying non-linear relationships amongst both continuous and categorical variables without processing (no need to rescale or normalise the inputs), thus allowing the analysis of variables that are difficult to be defined using other traditional statistical methods (Cutler *et al.*, 2007; Siroky, 2009; Vincenzi *et al.*, 2011) and correcting many of the known limits of single regression trees, such as overfitting and unstable results with modification of the database (Breiman, 2001). RFR is based on the combination of a large set of regression trees (Breiman, 2001) in which each tree is trained by selecting a random bootstrap subset 'Xi' (i = bootstrap training iteration of the database X, ranging from 1 to *t*) and a random set of predictor variables (Breiman, 2001). This is the main difference compared with standard regression trees, where for each node the best split amongst all predictor variables is used (*e.g.* Vezza *et al.*, 2012). The elements not included in the training data set Xi are referred to as out-of-bag data (OOB, *e.g.*, the validation data set) for each bootstrap sample. On average, each element of X was an OOB element in one-third of the *t* iterations. For each bootstrap sample Xi, an unpruned regression tree was grown and at each node *m* variables (with *m* = square root of the number of predictor variables; Breiman, 2001) were randomly selected. The out-of-bag estimate of the error rate (E_{OOB}, which is an unbiased estimate of the generalisation error of the forest) and the percentage of explained variance are then obtained by calculating the mean of the predictions of the generated *t* trees.

Random Forest Regression quantifies the importance of the predictor variables in terms of decrease in node impurities (Breiman, 2001). Following Acharjee *et al.* (2011), we included in the algorithm a permutation test to provide a significance level for each predictor, with $\alpha = 0.05$ as significance threshold value. The RFR model was applied 1000 times, and the 95 percentile of the ordered distribution of node impurity values was taken to assess the significance level of each individual variable. Finally, the marginal effect of each predictor variable on the selected target variable was visualised by partial dependence plots (Cutler *et al.*, 2007).

Mean %RF of non-native fish in otter diet in the study areas for which fish farming (Nos. 13, 14, 16, 32, 33 in Table 3) or deep alterations of freshwater fauna (No. 34) had been emphasised in the reference papers was compared with that resulting for the rest of the sample using a *t*-test.

Results

Species richness of freshwater fish assemblages was lowest in Ireland and Scotland, and highest in Bulgaria (Table 1), and showed a positive relationship with longi-

Table 1 Freshwater fish assemblages of the 15 European countries for which the percentage relative frequency of non-native fish in otter diet was available

Country	No fresh-water fish	No non-native fish	Non-native %	References
Austria	80	17	21.3	Copp *et al.* (2005a)
Belarus	115	5	4.4	Fishbase.org*; Elvira (2001)
Bulgaria	120	6	5.0	Karapetkova *et al.* (1998); Elvira (2001)
Czech Republic	60	11	18.3	Lusk *et al.* (2010)
Denmark	60	11	18.3	Fishbase.org*; Elvira (2001)
England	58	14	24.1	Copp *et al.* (2005a)
Finland	65	11	16.9	Fishbase.org*; Elvira (2001)
France	79	32	40.5	Copp *et al.* (2005a,b)
Hungary	71	15	21.1	Copp *et al.* (2005a); Elvira (2001)
Ireland	40	11	27.5	Fishbase.org*; Elvira (2001)
Italy	78	34	43.6	Bianco & Ketmaier (2001)
Poland	76	26	34.2	Grabowska *et al.* (2010)
Portugal	43	12	27.9	Copp *et al.* (2005a,b)
Scotland	40	13	32.5	Adams & Maitland (2001)
Spain	83	25	30.1	Elvira & Almodóvar (2001)
Mean ± SE	71.2 ± 6.1	16.2 ± 2.3	24.4 ± 2.9	

*Accessed 01/08/2012.

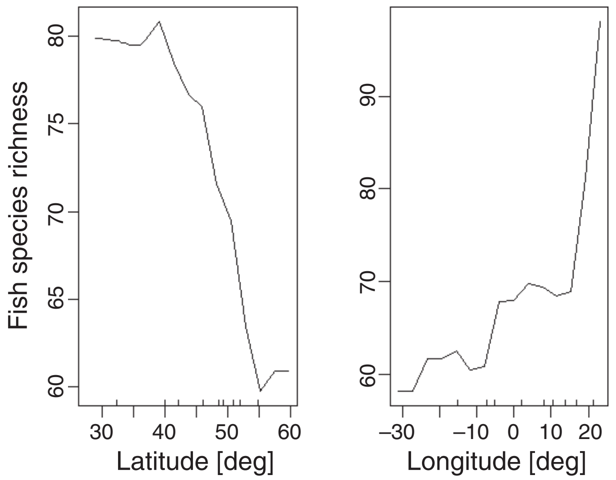

Fig. 1 RFR partial dependence plot for latitude and longitude (expressed in degrees; deg) using fish species richness as the target variable.

tude and a negative relationship with latitude ($\alpha < 0.001$ for both predictor variables). The two geographical coordinates explained 24% of the variance in species richness across Europe (Fig. 1). The number of naturalised non-native fish species was lowest in Belarus and highest in Italy (Table 1). The proportion of non-native fish in each fish assemblage was inversely related to longitude (R^2 = 12%, α = 0.02).

From the review of fish introductions into ten European countries (Table 2), an average of 67.7 ± 5.0% of naturalised species were introduced before 1980. The percentage increase in the number of non-native fish for each country did not vary between successive decades ($F_{2,27}$ = 2.78, n.s.), the mean decadal increase being 15.9 ± 4.5% (min–max = 0.0–30.6).

Data selection criteria were met by 30 diet studies (Table 3), which were carried out in 44 study areas between the early 1970s and 2010 and covered a longitudinal range from Portugal (38° 50′N, 08° 60′E) to Belarus (56° 00′N, 32° 00′E) and a latitudinal range from Finland (62° 15′N, 24° 25′E) to southern Italy (40° 25′N, 15° 15′E; Fig. 2). The %RF of non-native fish in otter diet ranged from 0 to 69.6% (mean ± SE = 4.8 ± 1.97), with only five of the 44 values exceeding 10% (Table 3). Non-native fish species were preyed upon by otters in seven of 15 European countries for which data were available. In these countries, otter used a few non-native fish species (mean = 3.6 ± 0.7; min–max = 1–6), corresponding to 23.0 ± 7.1% of the non-native fish assemblage of each country (min–max = 6.7–50.0%; Table 4). Common carp *Cyprinus carpio* and pumpkinseed were the most widespread non-native prey of otters, occurring in six and five countries, respectively, with pumpkinseed and rainbow trout *Onchorynchus mykiss* attaining the highest %RF values (Table 4).

The %RF of non-native fish in otter diet increased slightly through time (R^2 = 2%, α = 0.05), particularly from 1990 onwards (Fig 3). On average, otter preyed significantly more ($t_{df=41}$ = 3.51, P = 0.001) on non-native fishes in areas where fish farming or considerable alterations to the fish assemblages had been reported in the original references (mean %RF = 24.0 versus 1.7).

Dietary breadth (B) ranged between 0.15 and 0.56 (mean = 0.26 ± 0.01; Table 3) for seven food categories (R) and between 0.016 and 0.206 (mean = 0.078 ± 0.038) for

Table 2 History of fish introductions for ten European countries (n = cumulative number of naturalised fish for each time period; %I = percentage increase between successive periods): Albania (Shumka *et al.*, 2008), Czech Republic (Lusk *et al.*, 2010), England (Copp *et al.*, 2005a, Copp and Fox, 2007; Zięba *et al.*, 2010a,b), Greece (Zenetos *et al.*, 2009), Italy (Bianco & Ketmaier, 2001), Norway (Hesthagen & Sandlund, 2007), Poland (Grabowska *et al.*, 2010), Serbia (Lenhardt *et al.*, 2012), Slovakia (Koščo *et al.*, 2010) and Spain (Elvira & Almodóvar, 2001).

	<1980	1981–1990		1991–2000		>2001		
Country	*n*	*n*	%I	*n*	%I	*n*	%I	Mean %I
Albania	9	10	11.11	13	30.00	14	7.69	16.27
Czech Republic	11	11	0.00	11	0.00	11	0.00	0.00
England	12	14	16.67	14	0.00	14	0.00	5.56
Greece	6	7	16.67	8	14.29	10	25.00	18.65
Italy	19	26	36.84	32	23.08	34	6.25	22.06
Norway	7	9	28.57	10	11.11	11	10.00	16.56
Poland	12	18	50.00	24	33.33	26	8.33	30.56
Serbia	10	11	10.00	16	45.45	18	12.50	22.65
Slovakia	15	15	0.00	19	26.67	21	10.53	12.40
Spain	17	19	11.76	25	31.58	25	0.00	14.45
Mean	11.8	14.0	18.2	17.2	21.5	18.4	8.0	15.9
SE	1.3	1.8	5.0	2.4	4.7	2.5	2.4	4.5

 Freshwater Biology, doi:10.1111/fwb.12102

Table 3 Location, study period, number of analysed otter spraints, dietary breadth (Levin's index, B, with $R = 7$) and percentage relative frequency (%RF) of non-native fishes in otter diet for 44 European study areas

	Country	Period	Latitude	Longitude	Height a.s.l.	No spraints	B	%RF	References
1	Austria	1992–1993	49° 00′	15° 00′E	700	175	0.17	0.00	Knollseisen (1995)
2	Czech Republic	2000–2002	49° 38′	18° 43′E	400	136	0.24	0.00	Polednik *et al.* (2004)
3		2000–2003	49° 35′	18° 45′E	400	358	0.32	0.00	
4		2000–2004	49° 38′	18° 43′E	400	400	0.28	0.00	
5	Denmark	1990–1991	56° 20′	09° 10′E	0	587	0.16	0.00	Taastrøm & Jacobsen (1999)
6		1990–1991	56° 20′	09° 10′E	0	391	0.22	0.00	
7	England	1998–2000	51° 00′	04° 00′W	200	161	0.31	0.00	Bonesi *et al.* (2004)
8		2004–2005	51° 06′	02° 58′W	50	358	0.16	4.16	Miranda *et al.* (2008)
9		2009–2010	52° 53′	01° 03′E	35	215	0.20	2.62	Almeida *et al.* (2012)
10		1972–1973	50° 30′	04° 00′W	105	253	0.17	0.00	Chanin (1981)
11		1972–1973	50° 30′	04° 00′W	10	389	0.17	0.00	
12	Finland	1988–1993	62° 15′	24° 25′E	300	1506	0.30	0.00	Sulkava (1996)
13	Hungary	1996–1998	46° 14′	17° 29′E	100	801	0.16	2.62	Lanszki & Molnar (2003)
14		1999–2001	46° 18′	16° 52′E	100	116	0.56	4.68	
15		2001–2002	46° 44′	17° 45′E	100	234	0.56	0.46	
16		1992	46° 00′	18° 00′E	100	873	0.20	17.34	Lanszki & Körmendi (1996)
17		1989	47° 00′	17° 00′E	100	270	0.22	0.40	Kemenes & Nechay (1990)
18	Ireland	1996	51° 60′	09° 00′W	260	287	0.40	0.00	Ottino & Giller (2004)
19		1984–1986	53° 30′	07° 30′W	100	2349	0.42	0.00	Kyne *et al.* (1989)
20	Italy	1996–1997	40° 30′	16° 30′E	560	193	0.32	0.33	Prigioni *et al.* (2006)
21		2001–2003	40° 30′	16° 30′E	560	555	0.37	13.6	
22		2001	40° 00′	16° 30′E	480	1323	0.33	0.66	Remonti *et al.* (2008)
23		2006	40° 30′	16° 30′E	560	838	0.35	2.41	Smiroldo *et al.* (2009)
24		1987–1988	40° 10′	16° 10′E	380	490	0.19	0.00	Prigioni *et al.* (1991; unpubl. data)
25		1987–1988	42° 40′	11° 35′E	250	122	0.25	0.60	
26		1982–1983	42° 40′	11° 35′E	350	148	0.19	0.40	
27		1987–1988	40° 35′	16° 25′E	445	461	0.21	1.00	
28		1987–1988	40° 25′	15° 15′E	350	148	0.24	0.00	
29		2001	40° 25′	15° 15′E	270	564	0.26	0.49	Fusillo *et al.* (2003)
30	Poland	1988–1996	52° 60′	23° 75′E	168	396	0.24	0.00	Jedrzejewska *et al.* (2001)
31		1987–1989	49° 17′	22° 15′E	500	379	0.34	0.00	Harna (1993)
32	Portugal	2003–2005	40° 17′	06° 57′W	810	206	0.21	49.81	Marques *et al.* (2007)
33		2003–2004	38° 50′	08° 60′W	0	1680	0.19	0.19	Freitas *et al.* (2007)
34		1996–1997	40° 20′	08° 12′W	700	1328	0.23	69.63	Sales-Luís *et al.* (2007)
35	Scotland	1987–1988	57° 00′	02° 30′W	65	324	0.15	0.00	Carss *et al.* (1990)
36	Spain	1984–1996	42° 00′	00° 00′	328	755	0.21	8.60	Ruiz-Olmo & Palazón (1997)
37		1984–1996	42° 00′	00° 00′	540	596	0.22	0.00	
38		1984–1996	42° 00′	00° 00′	512	1432	0.18	0.38	
39		1984–1996	42° 00′	00° 00′	1040	610	0.16	0.00	
40		2002–2005	41° 49′	01° 53′W	500	108	0.20	1.40	Melero *et al.* (2008)
41		1979	38° 00′	04° 50′W	500	2145	0.25	16.97	López-Nieves & Hernando (1984)
42	France	1991	45° 30′	02° 20′	730	704	0.23	2.65	Libois (1997)
43	Belarus	1988–1995	56° 00′	32° 00′	100	641	0.36	0.00	Sidorovich *et al.* (1998)
44	Bulgaria	2005–2006	41° 20′	27° 00′	300	1155	0.33	8.75	Georgiev (2006)

73 categories. RFR analysis suggested there was no significant association, in terms of percentage of explained variance, between any dietary breadth index ($R = 7$ and $R = 73$) and either the %RF of non-native fishes in otter diet or latitude (α ranging between 0.371 and 0.771).

The number of non-native fish preyed upon by otters was inversely related to both latitude and longitude ($R^2 = 65\%$, $\alpha < 0.001$; Fig. 4), whereas no significant relationship was found between %RF and either the number or the percentage of naturalised non-native fish species ($\alpha = 0.723$ and 0.646, respectively).

Discussion

European freshwater fish assemblages have undergone profound changes, particularly in western Mediterranean countries. For example, the number of non-native freshwater fishes exceeds the original numbers of endemic species in both the Iberian Peninsula (Marr *et al.*, 2010)

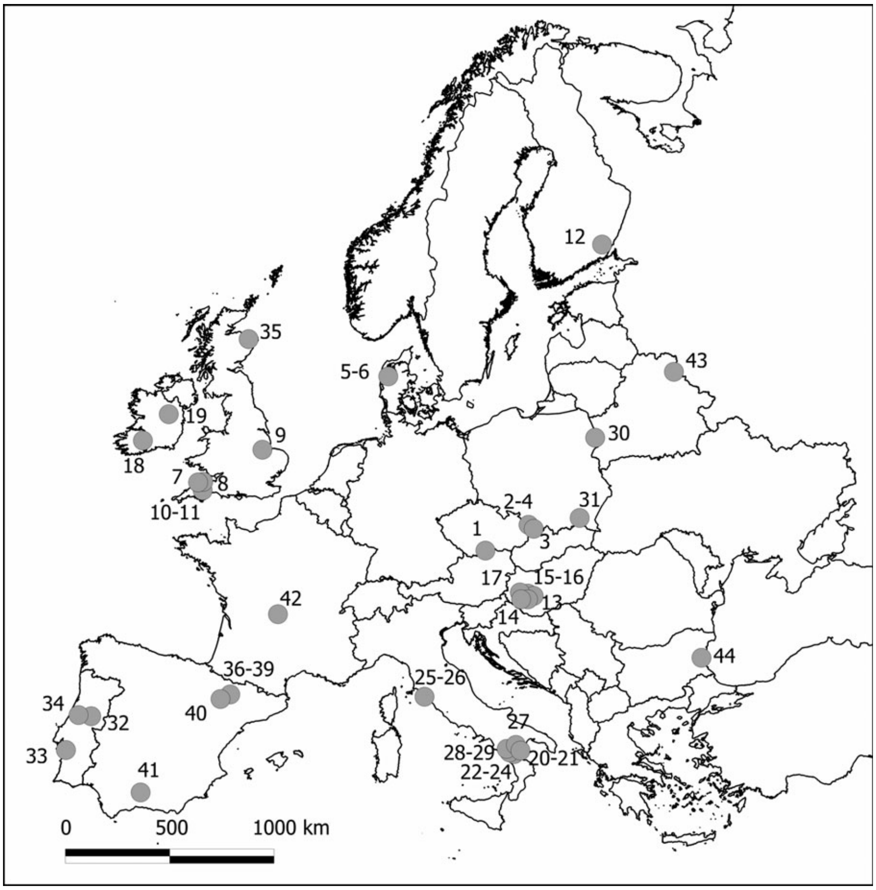

Fig. 2 Distribution of the 44 reviewed study areas in Europe for which the percentage relative frequency of non-native fish species in otter diet was reported (numbers correspond to those in Table 2).

Table 4 Mean percentage relative frequency (mean %RF ± 1.96 SE, when available) of non-native fish species in otter diet for seven European countries (see Table 1 for references)

	%RF						
Non-native fishes	Bulgaria	England	France	Hungary	Italy	Portugal	Spain
Centrarchidae					1.4 ± 2.2		
Micropterus salmoides					1.16 ± 3.7	1.15 ± 2.2	1.67 ± 3.3
Lepomis gibbosus	8.40		0.66	5.0 ± 6.2	0.02 ± 0.03	21.6 ± 42.2	
Carassius auratus	0.28				Traces	0.6 ± 0.8	
Carassius carassius			0.10				
Cyprinus carpio		0.80 ± 1.0	1.89		0.45 ± 0.4	0.04 ± 0.04	1.7 ± 2.1
Rutilus rutilus							0.12 ± 0.2
Leucaspius delineatus		0.54 ± 1.0					
Gobio sp.						0.01 ± 0.02	1.1 ± 2.1
Hypophthalmichthys sp.	0.09						
Ictalurus melas					0.03 ± 0.06		
Onchorynchus mykiss						16.6 ± 32.5	
No of non-native species eaten	3	2	3	1	6	6	4
% of total non-native fish	50.0	14.3	9.4	6.7	14.7	50.0	16.0

and Italy (Bianco, 1995). The number of introductions in Italy is the highest in Europe as a consequence of more than a century of ineffective controls on introductions (Copp *et al.*, 2005a). The longitudinal trend found in the proportion of non-native fish in each fish assemblage is in accordance with the preferential east-to-west route of

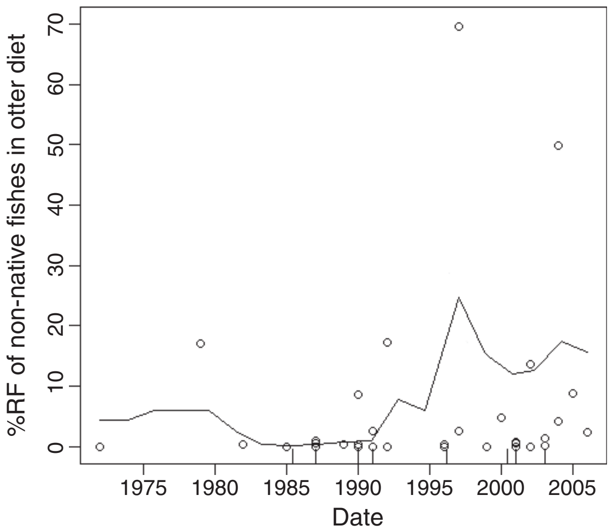

Fig. 3 Time-related variation in the percentage relative frequency of non-native fishes in Eurasian otter diet in Europe and the RFR model prediction (solid black line; $R^2 = 2\%$, $\alpha = 0.05$).

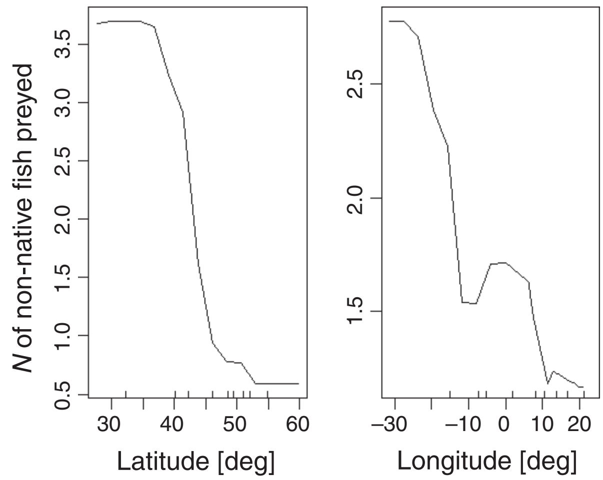

Fig. 4 RFR partial dependence plot for latitude and longitude (expressed in degrees; deg) using the number of non-native fish preyed upon by otters as the target variable.

introductions (both inter-continental and intra-continental; Copp *et al.*, 2005a), whereas the assumption that introductions were aimed mainly to increase the ichthyological biodiversity of European countries (Welcomme, 1992) is supported by the lower overall richness of western fish assemblages. Although the percentage increase in the number of non-native fish for each country has been constant in recent decades, predictive models and current evidence suggest that it will not decrease in the near future (Strayer, 2010).

Foraging strategies are adaptive responses to food abundance and availability (Sundell *et al.*, 2003; Zhou *et al.*, 2011), so the progressive spread of non-native fish in European freshwater systems is expected to drive changes in the foraging behaviour of top predators. In attempting to demonstrate such changes, the present meta-analysis encompasses an extended period and a wide geographical area, potentially constrained quantitatively by variations in data quality despite the adopted selection criteria. For example, suitable data were lacking in some cases for both introduction histories and local fish assemblage composition where otter diet was assessed.

Nonetheless, the patterns revealed in the meta-analysis suggest that otter predation on non-native fishes is a function of the latter's relative abundance, both in time and space. The overall slight increase with time of non-native fish occurrence in otter diet may depend on three, non-mutually exclusive, factors: (i) the increasing number of introduced fish species, (ii) their progressive intra-basin and inter-basin dispersal and (iii) time-lags (or 'lag phases'), possibly dependent on a minimum threshold fish density being required before predator–prey interactions are established (Correia, 2001). The first of these hypotheses is partially supported by the history of fish introductions. Regardless, otters generally preyed on a small number of widespread non-native species, with common carp and pumpkinseed being amongst the most successful. Common carp was the first species to be introduced widely, beginning at least as early as the Roman Empire (Balon, 2006), with pumpkinseed introductions beginning during the height of the 'acclimation society' epoch of the late 19th century (Copp & Fox, 2007). This suggests that some time is probably needed for the invaders to establish and expand their ranges sufficiently to become a non-negligible resource for native predators.

The greater importance of non-native species in the diet of south-western European otters probably reflects their relatively higher availability because at greater latitudes the occurrence of most non-native species is limited by less favourable environmental conditions (Copp, Templeton & Gozlan, 2007; Zięba *et al.*, 2010b).

The hypothesis that non-native fish consumption would be higher where otter diet is more diverse was not supported by our analysis. Contrary to the results of Clavero *et al.* (2003), no relationship was found between dietary breadth and latitude. Comparing their results to those of Jedrzejewska *et al.* (2001), Clavero *et al.* (2003) suggested that the lack of a latitudinal pattern in the latter study probably depended on the low proportion of Mediterranean areas included in the analysis. On the other hand, some recent studies in the Iberian Peninsula reported low Levins' index values (Nos 32, 33, 38 in

Table 3), suggesting that habitat-related variations in fish assemblage richness and stability may play a major role in shaping otter diet (Jedrzejewska *et al*., 2001; Smiroldo *et al*., 2009).

Human-altered ecosystems may favour the establishment success of non-native species (Moyle, 1986; Crooks, Chang & Ruiz, 2011). Artificial lakes and reservoirs are often wrongly considered to be suitable recipients for non-native benthic or slow-water fish species, which can be attractive to anglers and otters alike (Collares-Pereira *et al*., 2000; Prigioni *et al*., 2006; Pedroso *et al*., 2011). The same may be said of ponds in urbanised areas, which are more likely to receive non-native fishes the closer the water body is to the nearest road and footpath (Copp *et al*., 2005b). In the same way, fish farms offer concentrated food resources and are prone to predation by otters (Ludwig *et al*., 2002; Adámek *et al*., 2003). Accordingly, despite the small sample sizes available, the occurrence of non-native fishes in otter diet was higher in areas including either dams or fish farms, suggesting that, as reported in previous studies (Roche, 1998; Ludwig *et al*., 2002), otters may switch to these predictable and rich resources whenever the availability of 'natural' alternative resources is low. Although results of the present study indicate that otter predation on non-native fishes throughout their European range is still negligible, non-native prey may be important under such critical conditions, favouring the survival or expansion of otter populations in heavily human-altered areas (McCafferty, 2005; Romanowski, 2006; Pedroso *et al*., 2011). However, these limited, localised benefits of non-native fishes for otter conservation are insufficient compensation for their unpredictable, adverse effects on native fish assemblages (Moyle, Li & Barton, 1987; Leprieur *et al*., 2009), which, on the contrary, are likely to affect the diversity and abundance of native fish prey for otters. As such, the most effective management strategy for the conservation and recovery of otter populations in freshwater environments is the protection and enhancement of native fish assemblages (Beja, 1996).

Acknowledgements

The participation of GHC was funded by the UK Department of Environment, Food and Rural Affairs. D. Almeida is thanked for assisting with the preparation of data for the United Kingdom. Random Forest Regression was developed within the framework of the EU-funded HolRiverMed project (Marie Curie Actions, Intra-European Fellowships for the mobility of European researchers).

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(Manuscript accepted 28 December 2012)