

## Research Article

## Alien prey in the diet of the indigenous Eurasian otter in Vistula River, Poland

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## Abstract

Several non-native fish species were recorded in the studies of Eurasian otter *Lutra lutra* diet in south European and English rivers. To document the role of alien species as a prey of this aquatic top predator in central Europe, the diet of the otter was studied by spraint analysis in the Vistula, a large European river. Fresh spraints were collected at the study site in central Poland from 2012 to 2016, and in south Poland in 2015. At both sites, fish were the staple food of otters, constituting over 90% of prey consumed. The food niche breadth of otters was relatively high. Among 20 fish species registered in the diet, there were four alien species: prussian carp *Carassius gibelio*, common carp *Cyprinus carpio*, topmouth gudgeon *Pseudorasbora parva*, and round goby *Neogobius melanostomus*. Besides alien fish species, the invasive spiny cheek crayfish *Orconectes limosus* was present in the diet of otters at both localities. Altogether, the five invasive species constituted a large proportion of the diet of otters at both sites (over 30%). According to the literature data and results of this study, at least 18 non-native fish species were preyed on by otters in Europe. It is suggested that alien prey will constitute an increasing fraction of the diet of the indigenous Eurasian otter.

**Key words:** predation, seminatural rivers, biological invasions, *Lutra lutra*, *Neogobius melanostomus*, *Orconectes limosus*, *Pseudorasbora parva*

## Introduction

Biological invasions are considered a major threat to biological diversity (Simberloff 2011). Most studies focus on the negative effects of alien species on native species and communities. However, the interactions of non-native species in new ecosystems are more complex and involve long-term direct and indirect impacts (Pyšek et al. 2020). Invasive alien species can transmit parasites, affect the behavior of native animals and modify trophic networks, e.g., by becoming the prey of indigenous predators (Canning-Clode 2016).

There are currently around 14,000 alien species (including more than half originating from outside territories) in Europe and their number is constantly growing (Roy et al. 2019). Among these species, there are those whose presence in the aquatic habitats is particularly unfavorable for native fauna and flora (Vilà et al. 2010). Inland aquatic habitats are considered

one of the most vulnerable to biological invasions (Gherardi 2007). Out of over 160 alien fish species (Teletchea and Beisel 2018), 32 species have been identified as established in Europe (Sultana and Hashim 2016). Among 37 alien fish species in freshwater habitats of Poland most came from North and South America (14 species), and East Asia including Siberia (11 species). Among them, 26 species have acclimatized and formed established populations (Witkowski and Grabowska 2012).

In the last decades, several alien fish invaded the drainage area of the Vistula River, the largest river in Poland. Round goby *Neogobius melanostomus* (Pallas, 1814), was first documented in Zatoka Gdańska in 1990 (Skóra and Stolarski 1993; Skora and Rzeznik 2001; Corkum et al. 2004), and after ten years the species was reported 130 km upstream in the Vistula River (Głowaciński et al. 2011). Topmouth gudgeon (stone morocco) *Pseudorasbora parva* (Temminck & Schlegel, 1846) was first recorded in fishponds and rivers in western and southern Poland in the 1990s (Wisniowska 1996; Witkowski 2011). Amur sleeper *Perccottus glenii* Dybowski, 1877 was introduced to Poland around 1993 and inhabits lower and middle Vistula River including oxbows and various aquatic habitats in the river valley (Terlecki and Pałka 1999; Nowak et al. 2008). Prussian carp *Carassius gibelio* (Bloch, 1782) invaded many aquatic habitats in the whole of Poland since the 19th century (Holcik 1980). Freshwater systems in Poland were additionally invaded by the spiny cheek crayfish *Orconectes limosus* (Rafinesque, 1817) of American origin, that entirely displaced native crayfish in the Vistula River (Szaniawska et al. 2017).

Otters are top predators of aquatic ecosystems. The Eurasian otter is widespread in Poland and recent surveys documented the expansion of its population in the central part of the country. There, the species inhabits numerous aquatic habitats, e.g., Vistula River, large and small rivers, lakes, fishponds, and regulated channels (Brzeziński et al. 1996; Romanowski 2006; Romanowski et al. 2013). Eurasian otters prey on various fish species and other, mostly aquatic animals including amphibians, crustaceans, birds, and mammals (Erlinge 1967; Chanin 1981; Jędrzejewska et al. 2001; Krawczyk et al. 2016). They are opportunistic fish predators, and usually consume various species of fish proportionally to their occurrence. The variation in diet composition depends mainly on habitat. When availability of fish is low, otters shift their diet primarily to amphibians, and, secondarily, to birds and mammals (Jędrzejewska et al. 2001). Several non-native fish species play a role as prey of otters, with the common carp *Cyprinus carpio* Linnaeus, 1758 being the widely known example. This species forms about 20% of the otter diet at fish ponds in central Europe (Kloskowski 1999). Several other non-native fish species, including *Lepomis gibbosus* (Linnaeus, 1758), and *Carassius auratus* (Linnaeus, 1758) were recorded in the studies of otter diet in south European and English rivers (Blanco-Garrido et al. 2008; Miranda et al. 2008).



**Figure 1.** Location of study sites in the Vistula River in Poland.

Our study aimed to document the role of alien prey in the diet of otters inhabiting the Vistula River. Most of the earlier studies of otters analyzed the diet on medium and small watercourses (Brzeziński et al. 1993, 2006; Krawczyk et al. 2011) leaving large European rivers out of focus. To put these findings in a wider context, we also compare the available information on the presence of non-indigenous fish species in the diet of otters and freshwater habitats in Europe.

### *Study area*

The Vistula is one of the largest semi-natural rivers in Central and Western Europe. Diverse riparian vegetation between the dykes and forests located inside the river valley provides an important refuge for fauna and flora and make up an ecological corridor, recognized in the European ecological network EECNET (Liro et al. 1995). Large sections of the Vistula are characterized by a dynamic process of formation and erosion of islands and sandy bars (Kajak 1993). Two study sites characteristic of the Vistula River and located app. 430 km apart were selected for this study: one in the middle course of the river (Warsaw study site, 52.3042; 20.9512), and the other in the upper course of the Vistula (Cracow study site, 50.0515; 19.9581) (Figure 1).

At the Warsaw study site, almost entire banks of the urban and suburban sections of the Vistula from its entry to Warsaw are protected with willow bundles and rocky windrows, except for 3.5 km long west bank in the city center, reinforced with stone and concrete walls. The width of the riverbed ranges from 400 m to 1400 m. The vegetation of river banks and accumulation terrace consists of herbaceous plants, shrubs, and trees, including fragments of riparian *Salici-Populetum* forests, except for the left bank in the city center, which is developed into boulevards.

At the Cracow study site, within the city limits of Cracow, the Vistula flows in a valley cut in Jurassic formations and chalk marls located mainly on its left bank. The bottom of the river is gravel and sand. The width of the riverbed ranges from 80 m to 110 m. On both sides, there are high banks overgrown with herbaceous plants and riparian vegetation dominated by willows *Salix* sp. (*Salicetum triandro - viminalis*, *Salicetum pentadro - cinereae* and *Salicetum albo - fragilis*) (Baścik and Degórska 2015). The exception is the city center where the river flows within the banks reinforced with stones and concrete (about 3.5 km on the west bank and 1.5 km on the east bank).

## Materials and methods

A field study of the diet of the Eurasian otter was undertaken in the Warsaw study site from 2012 to 2016 and in the Cracow study site in 2015. At each study site, fresh otter spraints were collected along river banks, placed in separate labeled containers and stored frozen. Each spraint was soaked for 12 h before analysis, washed through a sieve with 0.5 mm mesh, and was oven-dried at 60 °C. All undigested remains were separated and identified under a stereoscopic microscope (Webb 1976). All prey remains were segregated into fractions and weighed with 0.1 g accuracy.

Mammals and birds were identified based on fur, teeth, vertebrae, and feathers, amphibians – based on *frontoparietale* and *illeum* (Webb 1976; Pucek 1981; Engelmann et al. 1985; Teerink 2003). Fish were identified based on scales, jaw apparatus, skull bones, and some other parts of the skeleton. Fish vertebrae were identified according to Webb (1976), *ossa pharyngea inferiora* – according to Horoszewicz (1960), *praoperculum* and *interoperculum* – according to Libois et al. (1987). Round goby (*Neogobius melanostomus*) remains were identified based on comparative material. Invertebrates were identified based on fragments of chitin carapaces. Remains of *Carassius* sp. were classified as prussian carp *Carassius gibelio* based on the results of studies showing the absence of native crucian carp *C. carassius* in the study sections of Vistula (Backiel et al. 2000; Epler et al. 2003; Wiśniewolski and Ligięza 2011).

The composition of the otter diet was presented using two methods recommended in the analysis of food of this predator (Erlinge 1968; Carss and Parkinson 1996): 1) as a relative frequency of occurrence “RFO” of

**Table 1.** Main prey of otters in study sites on Vistula river, expressed by relative frequency of occurrence of prey items (RFO%) and percentage of biomass consumed (BC%).

|                    | Warsaw |       | Cracow |       |
|--------------------|--------|-------|--------|-------|
|                    | RFO%   | BC%   | RFO%   | BC%   |
| Number of spraints | 102    |       | 152    |       |
| Number of items    | 128    |       | 159    |       |
| Prey type          | RFO%   | BC%   | RFO%   | BC%   |
| Fish               | 77.34  | 91.75 | 94.34  | 99.75 |
| Birds              | 1.56   | 1.55  | 0.63   | 0.03  |
| Amphibians         | 10.16  | 5.30  | 3.14   | 0.13  |
| Insects            | 2.34   | 0.05  | 0      | 0     |
| Crayfish           | 8.59   | 1.35  | 1.89   | 0.08  |

each prey item, expressed as the percentage of occurrence of the particular item compared with the total number of occurrences of all items in the sample; 2) as a percentage of biomass consumed “BC”. To calculate the contribution of the main types of prey in the diet, the following coefficients of digestibility were used: fish – 25, birds – 12, amphibians – 18, crayfish – 7, insects – 5 (Jędrzejewska and Jędrzejewski 1998).

The food niche breadth was calculated according to Levins (1968):  $B = \sum(p_i^2)^{-1}$ , where  $p_i$  is a fraction of a given prey group in the diet. For this calculation, the following groups of prey were used: mammals, birds, amphibians, crayfish, insects, and, due to the importance of fish in the otter diet, all recognized fish species.

## Results

Fish made up the greatest part of the otter diet, both in terms of biomass consumed and relative occurrence, accounting for 99.8% of the food biomass (RFO = 94.3%) at the Cracow site and over 91.8% of the biomass (RFO = 77.3%) at the Warsaw site (Table 1). Amphibians accounted for 5.3% of biomass consumed at the Warsaw site, the remaining categories such as birds, crustaceans, and insects made up small parts of the biomass in both localities (Table 1). The food niche breadth of otters was higher in the Cracow site ( $B = 9.74$ ) as compared to the Warsaw site ( $B = 7.36$ ).

The analysis of 152 otter spraints collected in the Cracow site documented the presence of 18 species of fish representing the following families: Cobitidae, Cyprinidae, Percidae, Esocidae, and Salmonidae (Table 2). Prussian carp constituted the most numerous fish species preyed on by otters (RFO = 11.4%). Among Cyprinidae single occurrence of alien topmouth gudgeon was detected. The analysis of 102 spraints collected in the Warsaw site revealed the presence of 11 fish species representing the following families Cyprinidae, Percidae, and Esocidae. Round goby constituted the most numerous fish species preyed on by otters (RFO = 25.7%). The share of round goby in the diet of otters in the Warsaw site increased from 14% in 2012 to 28.7% in 2016 ( $\chi^2 = 6.67$ ,  $p = 0.0098$ ,  $df = 1$ ) (Table 3). Besides four (including common carp *Cyprinus carpio*) alien fish species, the invasive spiny cheek crayfish *Orconectes limosus* was present in the diet of

**Table 2.** Variation in otter diet in study sites on Vistula river, expressed by relative frequency of occurrence of prey (RFO%). Non-native species marked in bold.

| Prey                                 |                         | Warsaw       | Cracow       |
|--------------------------------------|-------------------------|--------------|--------------|
| <i>Cobitis taenia</i>                | Spined loach            | 0            | 1.90         |
| Cobitidae unidentified               |                         | 0            | 1.42         |
| <i>Abramis brama</i>                 | Bream                   | 0            | 4.74         |
| <i>Alburnus alburnus</i>             | Bleak                   | 2.34         | 2.37         |
| <i>Abramis bjoerkna</i>              | White bream             | 0            | 1.42         |
| <b><i>Carassius gibelio</i></b>      | <b>Prussian carp</b>    | <b>1.40</b>  | <b>11.37</b> |
| <i>Chondrostoma nasus</i>            | Common nase             | 0.47         | 0            |
| <b><i>Cyprinus carpio</i></b>        | <b>Carp</b>             | <b>0</b>     | <b>1.90</b>  |
| <i>Gobio gobio</i>                   | Gudgeon                 | 5.61         | 1.42         |
| <i>Leuciscus (Squalius) cephalus</i> | Chub                    | 0            | 1.42         |
| <i>Leuciscus idus</i>                | Ide                     | 0            | 1.90         |
| <i>Leuciscus leuciscus</i>           | Common dase             | 1.40         | 2.37         |
| <i>Leucaspis delineatus</i>          | Sunbleak                | 0.47         | 0.95         |
| <b><i>Pseudorasbora parva</i></b>    | <b>Topmouth gudgeon</b> | <b>0</b>     | <b>0.47</b>  |
| <i>Rutilus rutilus</i>               | Roach                   | 0.93         | 1.90         |
| <i>Scardinius erythrophthalmus</i>   | Rudd                    | 1.87         | 4.27         |
| Cyprinidae unidentified              |                         | 29.44        | 37.44        |
| <i>Perca fluviatilis</i>             | Perch                   | 0.93         | 2.84         |
| <i>Gymnocephalus cernuus</i>         | Ruff                    | 0            | 0.95         |
| Percidae unidentified                |                         | 17.29        | 11.85        |
| <i>Esox lucius</i>                   | Pike                    | 3.74         | 0.95         |
| <b><i>Neogobius melanostomus</i></b> | <b>Round goby</b>       | <b>25.70</b> | <b>0</b>     |
| <i>Salmo t. trutta</i>               | Sea trout               | 0            | 0.47         |
| Fish unidentified                    |                         | 8.41         | 5.69         |

**Table 3.** Variation in otter diet in Warsaw study site in two periods, expressed by relative frequency of occurrence of prey (RFO%). Non-native species marked in bold.

| Prey                                 | 2012         | 2015–2016    |
|--------------------------------------|--------------|--------------|
| Cyprinidae                           | 58.14        | 40.35        |
| Esocidae                             | 6.98         | 2.92         |
| Percidae                             | 16.28        | 18.71        |
| <b><i>Neogobius melanostomus</i></b> | <b>13.95</b> | <b>28.65</b> |
| Fish unidentified                    | 4.65         | 9.36         |

otters at both localities with RFO = 8.6% in Warsaw and RFO = 1.9% in Cracow sites (Tables 1, 2). Altogether the five invasive species constituted a large proportion of the diet of otters at both sites (Warsaw RFO = 33.2%, Cracow RFO = 30.8%).

## Discussion

Otters are opportunistic predators that prey on fish and various aquatic prey proportionally to their availability (Erlinge 1967; Jędrzejewska et al. 2001; Kruuk 2006; Krawczyk et al. 2016). The results of our study are in agreement with the above general rule of broad food niche of this predator. Fish were the staple food of otters in the Vistula. Their contributions to the diet, both in terms of biomass consumed (Table 1) and relative frequency of occurrence (Table 2) were high as compared to results of the analysis of the diet of otters inhabiting rivers of different sizes in eastern Poland (Brzeziński et al. 2006). Similarly the food niche of otters at both study sites

was relatively broad, which can be attributed primarily to a high number of fish species registered in the diet. The total number of 20 fish species preyed on by otters in the Vistula River is the highest number reported from the lowland rivers in central Europe studied so far. We relate it to the unique nature value of the Vistula River (van der Sluis et al. 2007). As a large and seminatural river, the Vistula River has high species richness of ichthyofauna, consisting of at least 33 species of fish (Wiśniewolski and Ligęza 2011). Most of the fish preyed on by otters in the Vistula River are common species in lowland rivers, except Common nase *Chondrostoma nasus* and dace *Leuciscus leuciscus*, recognized as least concern (LC) species IUCN Red List.

Worth noting is the high contribution of alien aquatic organisms in the diet of otters, exceeding 30%, at both study sites. This group consists of five species, including invasive round goby, topmouth gudgeon, common carp, prussian carp, and spiny cheek crayfish. Common carp was introduced widely at least as early as the Roman Empire (Balon 2006). It is regularly reported as prey of otters in many studies, with the highest contributions in aquaculture habitats that offer concentrated food resources for the predators (Kłoskowski 1999; Adámek et al. 2003; Lanszki et al. 2007). Similarly, records of topmouth gudgeon in otter diets come from studies of fish ponds (Kortan et al. 2007; Lanszki et al. 2007; Orłowska 2019). The high frequency of round goby in the diet (25.7%) is somewhat unexpected as the species is recorded for the first time as a prey of otters. This benthic fish occupies shallow rocky littoral waters, which makes it an easy prey for otters (Kruuk 2006). Most probably high frequency of round goby in the diet of otters indicates the high contribution of this species in fish communities of the Vistula River. The other indication of a high abundance of round goby is its high share in sport fisherman's catches in Warsaw (Romanowski *unpublished*).

The analysis of results of diet studies from seminatural freshwater habitats revealed at least 18 non-native fish species that were preyed upon by otters in Europe (Table 4). Common carp was the most often reported species (10 studies from 8 countries, for reports see Table 4), followed by *Lepomis gibbosus* (Linnaeus, 1758) (6 countries), *Carassius auratus* (Linnaeus, 1758), and *Pseudorasbora parva* (4 countries each). Generally otters in southern Europe tend to prey on more non-native fish species (15 species) as compared to west and central Europe (11 species) (Table 4). This tendency can be explained by higher number of non-native fish species that invaded freshwater habitats in southern European countries (Supplementary material Appendix 1). However, non-native fishes have been reported to be preyed upon by otters less frequently as compared to native fishes in freshwaters in Iberia (Blanco-Garrido et al. 2008), Italy (Prigioni et al. 2006), and England (Miranda et al. 2008; Almeida et al. 2012). Our study failed to record *Perccottus glenii* Dybowski, 1877, which inhabits oxbows in Vistula River valley (Terlecki and Pałka 1999). Interestingly,

**Table 4.** Non-native fish registered in otter diet and in freshwater (excluding aquaculture) habitats in 26 European countries. For detailed list of the non-native fish country reports and references see Appendix 1.

| Species                            | Countries where species was recorded in otter diet  | Number of countries where species was recorded in freshwater habitats |
|------------------------------------|---|---|
| <i>Alburnus alburnus</i>           | Spain [1]   | 3   |
| <i>Ameiurus nebulosus</i>          | Hungary [2], Poland [3]   | 18  |
| <i>Carassius auratus</i>           | Bulgaria [4], Czech Republic [5], Portugal [6], Spain [7, 14]   | 15  |
| <i>Carassius carassius</i>         | France [8], Italy [9]   | 5   |
| <i>Carassius gibelio</i>           | Bulgaria [4], Poland [ <b>this paper</b> ]  | 13  |
| <i>Ctenopharyngodon idella</i>     | Bulgaria [4], Hungary [2]   | 13  |
| <i>Cyprinus carpio</i>             | Czech Republic [10], France [8], Hungary [2], Italy [9], Poland [3; <b>this paper</b> ], Portugal [11], Spain [1; 7], U.K. [12] | 16  |
| <i>Gambusia holbrooki</i>          | Portugal [11], Spain [13; 14]   | 8   |
| <i>Hypophthalmichthys molitrix</i> | Bulgaria [4]  | 10  |
| <i>Hypophthalmichthys nobilis</i>  | Bulgaria [4]  | 11  |
| <i>Lepomis gibbosus</i>            | Bulgaria [4], France [8], Hungary [2], Italy [15], Portugal [11], Spain [7],  | 19  |
| <i>Leucaspis delineatus</i>        | France [8], U.K. [12]   | 5   |
| <i>Micropterus salmonides</i>      | Italy [9], Portugal [11], Spain [14]  | 14  |
| <i>Neogobius melanostomus</i>      | Poland [ <b>this paper</b> ]  | 13  |
| <i>Oncorhynchus mykiss</i>         | Czech Republic [10], Spain [14]   | 23  |
| <i>Perca fluviatilis</i>           | Italy [15]  | 4   |
| <i>Pseudorasbora parva</i>         | Bulgaria [4], Czech Republic [10], Hungary [2], Poland [ <b>this paper</b> ]  | 17  |
| <i>Silurus glanis</i>              | Italy [16]  | 7   |

1 Ruiz-Olmo and Jiménez (2009); 2 Lanszki et al. (2009); 3 Kloskowski et al. (2013); 4 Georgiev (2006); 5 Jurajda et al. (1996); 6 Simoes (2017); 7 Blanco-Garrido et al. (2008); 8 Libois (1997); 9 Smiroldo et al. (2009); 10 Lych and Cech (2017); 11 Pedrosa and Santos-Reis (2006); 12 Miranda et al. (2008); 13 Barrientos et al. (2014); 14 Martínez-Abraín et al. (2020); 15 Remonti et al. (2008); 16 Smiroldo et al. (2019).

this invasive species has not been reported in the dietary study of otters within its secondary range in Europe. In addition to alien fish, various non-native crayfish species may also constitute prey of otters: in Doñana (Spain) non-native crayfish became the main prey of this predator even in aquatic habitats inhabited by fish (Delibes and Adrian 1987).

The significant contribution of alien fish and crayfish in the diet of otters in the Vistula probably reflects their high availability and may be promoted by human alteration of habitat in urban and suburban sections of the river, as indicated by Crooks et al. (2011). This study confirms the predictions of Balestrieri et al. (2013) that the progressive spread of non-native fish in European freshwaters is expected to drive changes in the foraging behavior of top predators. This suggests that alien prey will constitute an increasing fraction of the diet of the indigenous Eurasian otter. The high share of alien fish and crayfish in the diet of otters, revealed in this study, represents a rare documented case of predation on invasive species. There are a few examples of native predators preying on alien species. In the well-studied guild of 27 species of vertebrate predators in Białowieża Primeval Forest, only six mammalian and avian predators consumed alien prey with low frequency (from 0.3%–2.7% of prey) (Jędrzejewska and Jędrzejewski 1998). The successful invasions of alien species are often attributed to decreased control of their populations by natural predators and parasitism, predicted



by the enemy release hypothesis (Elton 1958). The enemy release was considered as a possible mechanism contributing to the rapid spread and increase of the harlequin ladybird *Harmonia axyridis*, one of the most successful insect invaders in recent decades (Ceryngier et al. 2018). In this short review of otter feeding habits we demonstrated the opposite case of one native predator preying upon at least 18 non-native fish species in Europe. The interesting question of whether otters could have a potential limiting effect on the distribution and numbers of invasive fish remains open for future studies. It is worth noting that our results support the need to call for more conservation of native predators in Europe. The potential to control invasive aquatic species adds a new perspective to efforts to reconcile conflicts between otter conservation and perceived economic damage caused by the otters to aquaculture and fisheries.

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### Authors' contribution

LO research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft and review; JR research conceptualization, investigation and data collection, data interpretation, writing – original draft, review and editing

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## Web sites and online databases

- IUCN (2022) The IUCN Red List of Threatened Species. Version 2021-3. <https://www.iucnredlist.org> (accessed 12 December 2021)

## Supplementary material

The following supplementary material is available for this article:

**Appendix 1.** List of countries in Europe where the presence of non-native fishes has been found.

This material is available as part of online article from:

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