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Original article

Resource availability and use by Eurasian otters *Lutra lutra* in a heavily modified river-canal system

Janusz Kloskowski, Jacek Rechulicz & Barbara Jarzynowa

The freshwater habitats of semi-aquatic carnivores in Europe have undergone substantial alterations due to regulation and construction of artificial watercourses. We compared seasonal estimates of otter *Lutra lutra* food composition with concomitantly collected data on fish availability and otter holt location in a strongly human-modified ecosystem comprising the upper stretches of the Wieprz-Krzna Canal, the longest artificial waterway in Poland, and an associated regulated river. Concrete lining of the canal, extreme water level variation and regular vegetation clearance to enhance water flow substantially limited otter food and shelter resources, yet the canal offered attractive habitats for some fish and hibernating amphibians, while otter resting sites were available at the closely adjacent river. The taxonomic composition of fish in the otter diet, reconstructed based on faecal analysis, was largely reflected in electrofishing catches. Fish communities in our study area were numerically dominated by small-sized species and otters fed on very small fish (median seasonal total lengths: 46-54 mm). Either the smaller fish in the population were taken or prey sizes did not differ from those available. The significant contribution of amphibians and waterbirds to otter diet (seasonally 41-75% in terms of biomass) indicated poor fish supplies for otters in the canal-river system. High trophic diversity, compared to other otter studies in temperate climatic conditions, indicates that otters facing unstable food conditions exhibit great flexibility in their diet, which may facilitate colonisation of anthropogenic, depauperate environments. Otter occurrence provides little opportunity for conflict with human economic interests in ecosystems that are highly managed for purposes other than fish production. Since anthropogenic habitats are typically poor in some resources, such as shelter structures, their suitability for otters can be enhanced by ensuring good connectivity with nearby less-disturbed habitats, where the necessary resources can be supplemented.

Key words: artificial waterways, Eurasian otter, human-modified habitats, Lutra lutra, prey selectivity, trophic diversity

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Riverine ecosystems in Europe have changed substantially over the last few centuries due to large-scale anthropogenic influences such as river management, water pollution and construction of artificial watercourses. These changes have precipitated biodiversity loss, including declines in semi-aquatic carnivores (e.g. Mason 1995, Lodé et al. 2001). Human alteration of freshwater ecosystems is now so pervasive that most carnivore populations live in habitats modified and (in varying degrees) managed by humans. While research and conservation efforts have traditionally focussed on natural ecosystems as strongholds for wildlife and points of reference for restorative management, carnivore adaptations to, and performance in, novel habitats merit more attention than they have received (*cf.* Gallagher &

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Carpenter 1997, Western 2001). The Eurasian otter *Lutra lutra*, a top aquatic predator, has long been characterised as a flagship species of undisturbed, healthy environments (Stevens et al. 2011), and habitat loss is considered the major cause of the decline of this species over much of its range in Europe. River regulation and construction of dams, canals and draining dykes have been blamed for destruction of riparian cover and impoverishment of fish populations, which constitute the principal food resource for otters (reviewed by Mason 1995). However, following the recent population recovery in Europe (e.g. Chanin 2003, Romanowski 2006), otters have been reported to (re)settle in habitats previously deemed unfit because of scarce food supplies or human disturbance (Romanowski 2006). Their ability to colonise anthropogenic, low-biodiversity environments casts doubt on the use of otters as a flagship species and an indicator of ecosystem health.

Since otter populations are food-limited (Kruuk et al. 1993, Ruiz-Olmo et al. 2001), assessment of potential prey resources and understanding of dietary preferences is essential for conservation and management of the species. It may also help to mitigate conflicts with human interests wherever otters exploit economically valuable fish resources (Kloskowski 2005, Almeida et al. 2012). However, with the exception of pond fisheries (Kloskowski 1999, Lanszki et al. 2001), the use of prey by otters in anthropogenically-impacted ecosystems remains poorly explored (see Sales-Luís et al. 2007). Fish abundance may affect otter distribution, timing of reproduction and natural mortality (Kruuk et al. 1987, Ruiz-Olmo et al. 2001; see also Lodé 2002). Captivity experiments have demonstrated otter preference for fish and, among fish, for larger (intermediate) sizes, although prey size may interact with energetic content (Erlinge 1968, Topping & Kruuk 1996). On the other hand, most studies on free-living otters have indicated an opportunist foraging strategy, although some fish species and size ranges may be preferred, presumably due to species- or size-specific vulnerability or nutritional value (e.g. Adrián & Delibes 1987, Kruuk et al. 1993, Almeida et al. 2012). In their review, Clavero et al. (2003) showed a latitudinal gradient in otter food composition, from a generalist strategy and diverse diet in the unstable food and hydrological conditions of Mediterranean areas to specialisation as piscivorous predators in relatively predictable temperate freshwater ecosystems. Also, otters are reported to breed more regularly in complex and stable habitats, i.e. those providing predictable water, food and shelter resources (Ruiz-Olmo & Jiménez 2009).

Here, we investigated the use of food resources by otters in relation to fish availability in a highly-modified riverine habitat in eastern Poland. We compared seasonal estimates of otter diet from faecal analysis with results of concurrently conducted electrofishing catches in a system comprising a large, concrete-lined irrigation canal and an associated small regulated river, typical for the canal catchment area. We compared fish (in terms of abundance and diversity) and shelter resources provided by the canal and the adjacent river. We also searched for otter holts along these watercourses, as an indicator of availability of cover structures. Based on the characteristics of modified riverine ecosystems, we predicted that the habitat created by the heavily anthropogenically-influenced canal area would provide poor food resources for otters, especially in terms of fish abundance because of flow alteration, poor habitat structure and temporary dewatering; moreover, due to human alteration of hydrological cycles, fish supplies would be unstable in a manner inconsistent with their natural seasonality (Poff et al. 1997, Wolter 2001, Roberts & Rahel 2008). Also, owing to increased landscape homogeneity and concrete lining, shelter resources such as holts would be deficient (Chanin 2003), while availability of breeding and resting sites has been claimed as one of the factors limiting otter occurrence, especially in areas of high human activity (Mason & Macdonald 1986, Romanowski 2006). Our second prediction was that under conditions of low food abundance and predictability, otters should exhibit high dietary flexibility and little or no selectivity of prey species and size categories. Theoretical approaches based on optimality criteria (foraging theory), as well as empirical research, suggest that foragers broaden their diet to include lower-value prey taxa as the availability of higher-value prey declines (e.g. Schoe-ner 1971, Dill 1983; but see Juanes 1994). Analogously, with regard to prey size preferences, under conditions of poor fish availability, we would not expect any size selection by otters, even though large-sized fish are more profitable food than small fish due to greater energy return (Hislop et al. 1991). Since capture success is generally negatively correlated to prey size, smaller individuals may in fact be disproportionately taken from fish populations (*cf.* Temple 1987, Christensen 1996).

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Material and methods

Study area

Our study area was the upper reaches of the Wieprz-Krzna Canal and the lower reaches of the Świnka River in the southern part of the Polesie region of eastern Poland (51°3'N, 23°0'E; Fig. 1). The 142-km-long canal connecting the rivers Wieprz and Krzna is the longest artificial waterway in the country. Constructed in 1954-1961 as the main stem of a drainage/irrigation system to boost agricultural production, the canal affects hydrological relations in an area of > 500,000 ha. The extensive canal network has brought about degradation of vast peatland areas and serious decline of aquatic biodiversity in the zone of its hydrological influence (Radwan 1994), exacerbated by regulation of small rivers linked with the canal system. The uniform, trapezoidal canal bed is 4-7 m wide at its base. The slopes are lined with concrete slabs and the flow, regulated by numerous weirs, can be reversed in some stretches. Due to the trapezoidal profile, there can be a great variance in the width of the canal by season, with peak flows in spring and occasionally in autumn, when waters from the Wieprz River are conveyed for irrigation purposes and to feed storage reservoirs and ponds situated at the canal's lower reaches. In the summer, some canal sections can be nearly emptied due to maintenance which is carried out regularly, including clearance of vegetation (mainly Canadian waterweed *Elodea canadensis* and pondweed *Potamogeton* sp.) from the canal bed and margins to improve flow conditions. During electrofishing sessions, water depth at the deepest part varied between ca 0.6 m in the summer and 1.2 m in the autumn and spring. The Świnka River is a 37-km-long tributary of the Wieprz River. In its lowest reaches, it is ca 4 m wide and up to 1.1 m deep. As part of the canal system management scheme, large sections of the river were straightened and the banks rivetted with branches, but the natural, meandering bed, with scattered patches of common reed *Phragmites australis* and mannagrass *Glyceria* sp., has been partly preserved. The sampled river stretch runs roughly parallel to the canal at a distance of a few hundred metres and crosses it (see Fig. 1). Water from the canal can be conveyed to the Świnka River through a siphon structure in case of relative water surplus/deficit in the canal, but normally the concrete bed of the canal flows like an aqueduct over the river. As both watercourses receive sewage from many sources, concentrations of industrial and organic effluents locally exceed the acceptable limits set by the Polish State Inspection of Environmental Protection (WIOŚ 2000). Although the area surrounding our study sites is agricultural, the adjacent landscape (ca 2 km north of the canal) is dominated by the Bogdanka coal mine. Bank-side vegetation is sparse and, at some stretches, human settlements are clustered close to the banks. While fishing is prohibited in the canal, poaching might locally affect fish communities.

During an otter field survey in the region in 1995 (Kloskowski 2005), numerous sightings of tracks and faeces in the canal zone indicated that it was intensively frequented by otters.

Prey population sampling

Between October 1997 and October 1998, whole-day electrofishing sessions were conducted by a 7-8 person team on a seasonal basis along the same sections of the Wieprz-Krzna Canal and the Świnka River in: 1) 1997, in October (representing autumn) and December (winter) and 2) 1998, in March (spring), May and June (summer) and October (autumn). Estimates of fish abundance were obtained using a three-pass depletion technique (Zippin 1956): two to three 50-m reaches of both the river and the canal were enclosed using 7-mm mesh blocking nets, each pass taking 0.5 hour, with a break of approximately 1 hour between fish removals. Fish were caught using portable, battery-powered equipment IUP-12 (220-250V, 7A, DC) across the whole width of the river/canal bed, wading upstream. All fish captured were identified to species and counted, and their total lengths (TL) were measured (nearest mm) with the exception of individuals < 25 mm TL, since such small fish were only exceptionally retained in otter faeces, as they were either neglected as prey or completely digested. Subsamples of captured fish were weighed. In case the number of fish of a given species increased between successive passes, the total catches were used as a minimum estimate of species abundance in the blocked-off sections. In the analyses we used proportionate numerical representation of fish taxa, but we also estimated biomass proportions as the product of average individual weight and estimated population size. We did not attempt to estimate absolute fish densities per unit volume of water due to the limited number of sampling sites (Bohlin et al. 1989) and rapidly changing water levels in the canal. Nonetheless, we calculated fish biomass abundance per 50-m reach to assess seasonal changes in food supplies for otters in the canal and in the river; however, the two watercourses differed seasonally in

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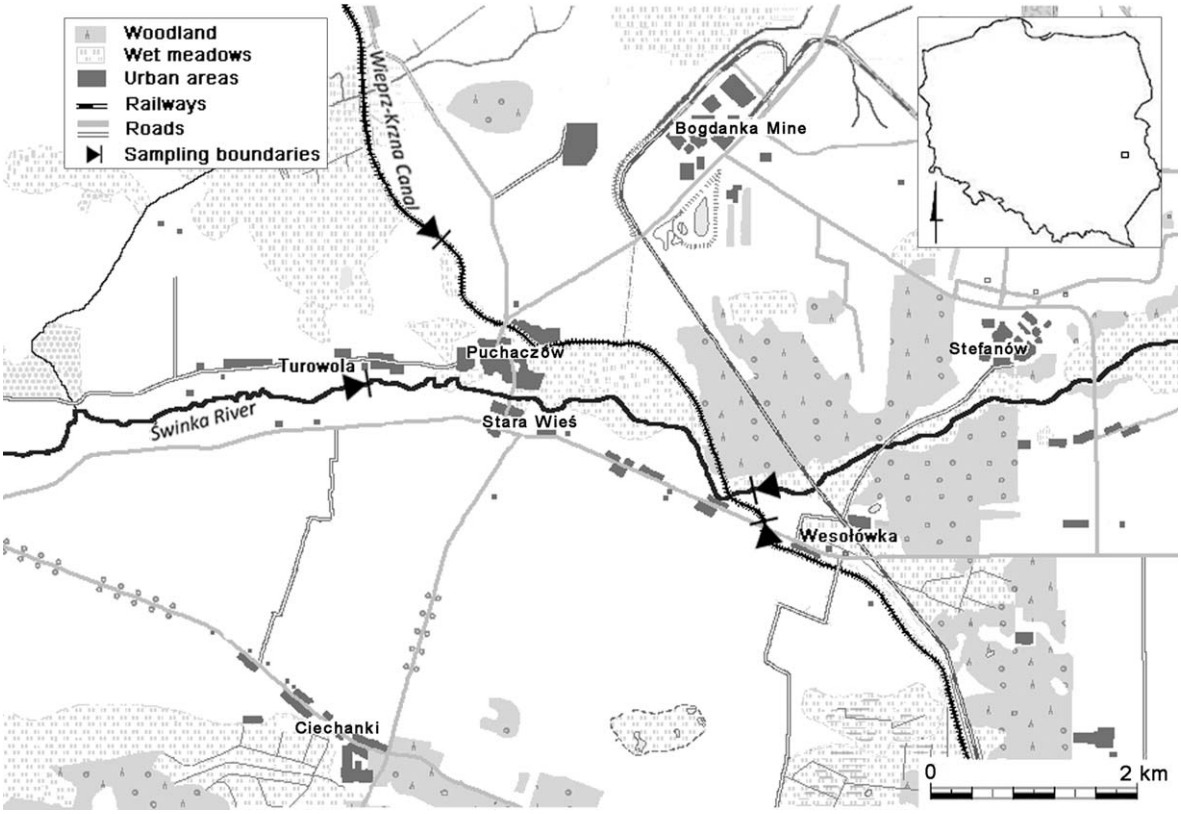

Figure 1. Map of the Wieprz-Krzna Canal and the Świnka River in eastern Poland where fish communities and otter spraints were sampled during 1997-1998. The upstream and downstream boundaries of the sampled reaches are indicated.

depth, and fish abundance was likely to be comparatively underestimated by electrofishing in the canal during high-water periods (*cf.* Bohlin et al. 1989).

Otter home ranges in freshwater habitats are larger than the reaches we sampled for fish populations (Kruuk et al. 1993). However, as the upper Wieprz-Krzna Canal was environmentally and morphologically homogeneous throughout, as were the middle and lower courses of the Świnka River, the fish-collection sites were taken to be representative of them (see also Przybylski & García-Berthou 2004).

To check for crayfish presence in our study area, mesh traps baited with beef liver (as used by local fishermen for commercial catches) were set at irregular intervals in the electrofished reaches between June and September 1998. The trapping proved unsuccessful, but crayfish remains, apparently left by otters, were occasionally found on the Świnka River banks (but never along the canal margins), indicating that crayfish identified in otter faeces (see Results), albeit apparently rare in the area studied, originated from the river. Amphibians and waterbirds sighted within the sampled sections were recorded, but no quantitative abundance estimates were attempted. In the canal area, waterbirds had severely limited breeding opportunities due to poor development of riparian cover.

Spraint sampling and analysis

Otter faeces (hereafter: spraints) were collected seasonally from the banks, on standard routes ca 4-km long (see Fig. 1) overlapping with the electrofished sections of the Wieprz-Krzna Canal and the Świnka River, within two weeks of the electrofishing sessions. Owing to the exposed character of the banks and frequent water level fluctuations, the persistence of spraints, which were apparently washed away quickly, was low in the canal area (*cf.* Mason & Macdonald 1986). Therefore, we assumed that the spraints collected were representative of the months when electrofishing samples were taken. Faecal material was stored in individual bags, dried and washed. During field visits, we also searched for the presence of otter holts. A holt was defined as any underground cavity with signs of use by otters.

We used two methods to present the results of

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spraint analysis: the percentage of the estimated number of individuals of a prey category relative to the total number of prey individuals (this technique was used for assessment of similarity between diet and available prey) and the percentage of the estimated total biomass of individuals of a prey category relative to the total biomass of all categories (Pierce & Boyle 1991). The validity of the most popular method in studies of otter diet, based on relative frequencies of occurrence of taxa in spraints, has been questioned (Pierce & Boyle 1991, Carss & Parkinson 1996), so we used it only for calculation of dietary diversity indexes with regard to the same prey categories (fish, amphibians, reptiles, birds, mammals, crayfish and other invertebrates), as in the review by Clavero et al. (2003), to make them directly comparable with other studies on otter trophic ecology.

For fish and amphibians, the minimal number of individuals of species represented in spraints was defined as the highest total of any of the species-specific bones present in each spraint. Where possible we used 'key bones', species-diagnostic hard parts that occurred with relatively high frequency in spraints, and for which predictive equations were available, allowing reconstruction of the original prey size. Length-weight regressions were then used to convert fish length to weight (e.g. Libois et al. 1987). Key bones used were pharyngeal teeth structures, maxillae and dentaries in cyprinids and cobitids, and dentaries, operculae and premaxillae or articularies in other fish taxa. In amphibians (only anurans were identified from the remains), ilea, frontoparietales and maxillae were used; body masses were estimated dependent on bone size, with three weight classes adopted for each species. When species level identification was not possible, weight classes for the most likely species were applied. To avoid possible overestimation of some prey items due to retrieval of remains of the same individuals from multiple spraints (Carss & Parkinson 1996), vertebrae and fish scales from the entire monthly sample of spraints, when identified to the same taxon and size/age, were considered to represent one prey individual. Also, they were used only when other species-specific bones were either absent (missing) in the sample or indicated different fish size. Invertebrate, mammal and bird numbers were defined likewise as the highest total of any of the identifiable parts present in the entire sample because the remains retrieved (exoskeleton parts, hair or feathers) obviously represented single prey individuals in many spraints. Mammals and birds were identified to family level (Day 1966, Brom 1991). For birds, mean adult body weights of the most common species in our study area were taken from Brom (1991). For crayfish, we used the mean weight (27 g) estimated in an earlier study in this region for European crayfish *Astacus astacus* specimens preyed on by otters (Kloskowski 1999). Weights of molluscs (unionids) and mammals (rodents) were approximated to 10 g, and insect weights to 1 g.

Data analysis

The spraint samples collected at the canal and the river were lumped for the analyses because otter tracks indicated that at least some resident individuals frequented both watercourses. We estimated fish composition in the canal and in the river separately to compare their fish resources. However, electrofishing samples from the two watercourses were combined for analyses of otter food selection. Fish species diversity in the two watercourses and trophic niche width of otters were examined using the Shannon-Wiener index (H'). To account for temporal autocorrelation of seasonal data, differences in fish density and diversity between the canal and the river were estimated by fitting a linear mixed model with season as a random effect. To obtain an overview of seasonal changes in fish communities in the canal and in the river, the Bray-Curtis coefficient of similarity (BCS) was calculated for each season and the similarity between seasons was then displayed by non-metric multidimensional scaling (NMDS). The goodness of fit of the NMDS model was estimated with a stress function (values close to zero indicating a good fit). The taxonomic similarity of fish assemblages in the two habitats, and of the proportional abundance of fish taxa in the electrofishing catches and in the diet of otters, was evaluated by means of analysis of similarity (ANOSIM), a non-parametric permutation procedure which generates probabilities of observing the test statistic R reflecting the degree of similarity between groups. ANOSIM is based on the Bray-Curtis similarity measure, which has a robust monotonic relationship with ecological distance and can also handle data with excess zeros (Faith et al. 1987, Legendre & Legendre 1998). Fish species that contributed most to differences in the taxonomic composition of spraints and electrofishing samples were subsequently identified by SIMPER (similarity percentages) analysis using PAST

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software v. 2.17b (Hammer et al. 2001). To test our prediction on prey selection, we assessed preference/avoidance value for individual fish taxa using Jacobs' selectivity index (Jacobs 1974). The standardised index varies from -1.0 (total avoidance) to +1.0 (absolute preference) and statistical significance was obtained by testing the seasonal index values against the expected value of 0 (prey used as available) with the Wilcoxon test. No Bonferroni correction for multiple tests was applied. For the analyses, we grouped taxonomically similar species to genus or family when at least one of them occurred at an average frequency < 1%, both in the electrofishing catches and in otter diet: two *Carassius* species, two *Leuciscus* species, cobitids and percids. For graphical presentation, cobitids and gasterosteids were grouped to family level (see Table 1 for species list).

We compared length frequency distributions of gudgeon *Gobio gobio* and roach *Rutilus rutilus* (overall TL ranges in the catches: gudgeon, 30-155 mm; roach, 47-190 mm; for roach, only the October 1997 samples were large enough for analysis) collected by electrofishing to those derived from spraints. Since the lengths were not distributed normally, median tests (Zar 1999) were applied. Additionally, selectivity for different size classes was calculated using the Jacobs' index. Other fish in our study area were either small-sized species (< 80 mm TL), with little variation in size, or occurred too infrequently in the electrofishing/spraint samples to permit statistical analyses.

We amalgamated May and June (hereafter: summer) electrofishing and spraint samples (catches were conducted on 21 May and 3 June) because numbers of detected spraints were distinctively smaller than in other study months (May: N = 28, June: N = 14); species composition of the two monthly electrofishing samples was similar (BCS = 84%). Differences in faecal sample sizes may bias dietary comparisons (Carss & Parkinson 1996); however, we assumed that our seasonal samples were sufficiently large for reliable analyses.

Results

Otter resource availability in the Wieprz-Krzna Canal and the Świnka River

Altogether, 13 fish species were recorded in the catches from the Wieprz-Krzna Canal and 15 species in the Świnka River. With the exception of summer, the estimated total fish biomass per 50 m of bank length was 1.8-3.2 larger in the canal (which was approximately 2-2.5 times wider) than in the river (linear mixed model on log-transformed data: $F_{1,4} = 10.11$, $P = 0.034$). In both the canal and the river, fish biomass peaked during spring (2,327 g/50 and 7,063 g/50 m, respectively). In other seasons, it was relatively stable in the canal (1,166-1,579 g/50 m) and in the river (495-672 g/50 m), but in the canal, it fell to 571 g/50 m (vs 598 g/50 m in the river) in the summer.

Fish species diversity did not consistently differ between the canal and the river when the seasonal values of Shannon-Wiener H' ($F_{1,4} = 2.47$, $P = 0.191$; ranges: 0.232-1.350 vs 0.419-1.715) were compared. However, there were distinct differences between fish assemblages of the two watercourses (Fig. 2A and B) as indicated by ANOSIM ($R = 0.384$, $P = 0.032$, 9,999 permutations) and NMDS (Fig. 3). Bitterling *Rhodeus sericeus* (on average 48% by numbers and 38% by biomass in the seasonal catches) and gudgeon (25 and 26%, respectively) were the most abundant species in the canal (see Fig. 2A). The fish community of the river was dominated numerically by three-spined stickleback *Gasterosteus aculeatus*

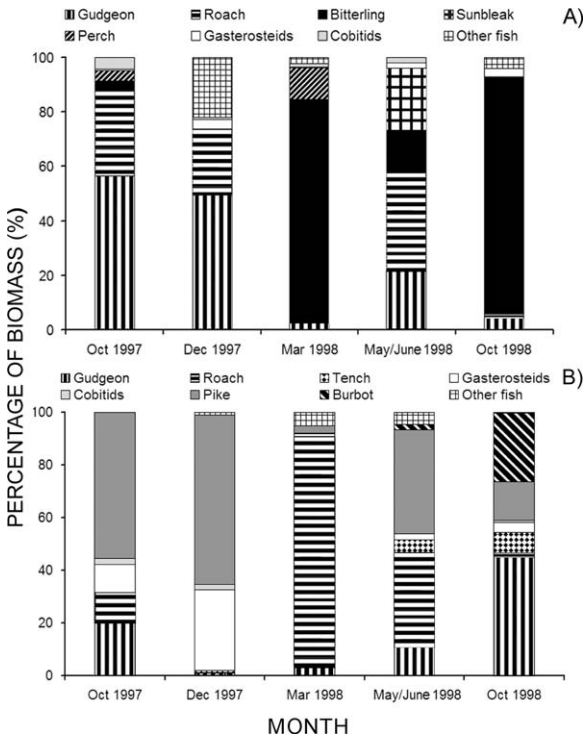

Figure 2. Biomass composition of fish communities in the Wieprz-Krzna Canal (A) and in the Świnka River (B) estimated by the Zippin multi-pass depletion method (Zippin 1956). The estimated fish numbers were converted to biomass using average masses of fish caught.

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Table 1. Seasonal diet composition of the otters in the canal-river system. Relative frequencies of number (% N) and weight (% W) for each food category are indicated. *Carassius* sp. were crucian carp *C. carassius* and Prussian carp *C. gibelio*. *Leuciscus* sp. were ide *L. idus* and common dace *L. leuciscus*. The remains of these species were difficult to distinguish from each other.

	Month									
	October 1997		December 1997		March 1998		May/June 1998		October 1998	
Food category	N (%)	W (%)	N (%)	W (%)	N (%)	W (%)	N (%)	W (%)	N (%)	W (%)
Crayfish *Astacidae*	0.2	1.4	-	-	-	-	1.7	4.0	0.3	1.3
Other aquatic invertebrates	0.2	0.1	0.6	0.7	0.7	0.1	6.7	0.9	1.6	0.5
Bitterling *Rhodeus sericeus*	37.5	6.0	36.0	4.6	47.9	7.7	10.9	0.7	64	17.4
Bleak *Alburnus alburnus*	3.6	4.2	0.5	0.2	3.0	1.5	-	-	0.5	0.8
Common carp *Cyprinus carpio*	0.2	1.7	-	-	-	-	-	-	-	-
Gudgeon *Gobio gobio*	12.0	18.7	27.4	28.1	13.9	16.9	10.1	4.6	15.7	26.8
Roach *Rutilus rutilus*	4.5	2.5	4.3	2.0	0.6	0.4	2.5	1.0	3.2	2.6
Sunbleak *Leucaspius delineatus*	0.5	0.1	1.1	0.3	0.6	0.3	0.8	0.3	0.3	0.1
Tench *Tinca tinca*	1.6	1.7	0.5	2.5	-	-	0.8	1.6	0.8	0.7
White bream *Blicca bjoerkna*	0.3	0.2	-	-	-	-	-	-	-	-
Carassius sp.	2.2	1.5	1.6	0.4	1.8	0.6	-	-	-	-
Leuciscus sp.	2.0	3.8	1.1	0.6	-	-	-	-	0.3	0.3
Loach *Misgurnus fossilis*	2.5	2.0	3.8	2.2	1.2	0.6	10.1	4.5	0.3	0.4
Stone loach *Barbatula barbatula*	3.3	1.7	1.1	0.3	3.0	3.4	2.5	0.3	-	-
Spined loach *Cobitis taenia*	1.1	0.3	0.5	0.3	0.6	0.7	-	-	-	-
Three-spined stickleback *Gasterosteus aculeatus*	11.6	2.4	3.8	0.4	0.6	0.1	33.6	3.6	5.6	1.2
Nine-spined stickleback *Pungitius pungitius*	2.3	0.5	0.5	-	2.4	0.3	3.4	0.3	0.5	0.1
Burbot *Lota lota*	0.2	0.1	3.2	1.8	-	-	-	-	0.5	0.4
Brown bullhead *Ameiurus nebulosus*	0.2	0.2	0.5	2.0	0.6	1.3	-	-	-	-
Ruffe *Gymnocephalus cernua*	-	-	1.1	2.6	-	-	-	-	0.3	0.5
European perch *Perca fluviatilis*	1.2	1.1	0.5	0.1	3.6	8.3	0.8	0.3	1.1	3.5
Pike *Esox lucius*	1.2	10.4	1.6	2.8	2.4	15.0	2.5	7.3	0.5	3.8
Amphibians	11.3	38.7	9.2	14.2	17.0	42.7	11.8	22.9	4.3	15.6
Birds	-	-	1.1	33.9	-	-	1.0	46.5	0.3	24.0
Mammals	0.3	0.8	-	-	-	-	0.8	1.2	-	-
H'	1.3		1.1		1.1		2.0		1.5	

(on average 45% in the seasonal catches), followed by gudgeon (25%). However, in terms of biomass (see Fig. 2B), pike *Esox lucius* (35%) and roach (27%) were more important than gudgeon (16%) and stickleback (8%), their relative biomass importance being influenced by a few large individuals. Bitterling, seasonally dominant in the canal, was recorded in the river only in October 1998 (2% by numbers). By contrast, three-spined stickleback made up < 10% of catches in the canal, except for winter (29%). Of the predatory species, pike was absent in the canal, while perch *Perca fluviatilis* was rarely caught in both watercourses (on average < 1% by numbers) and its biomass contribution was significant only in spring (12% in the canal and 5% in the river). The NMDS plot indicated pronounced seasonal changes in the fish assemblages, especially in the canal (see Fig. 3); consequently, the overall taxonomic composition of fish supplies in our study area fluctuated strongly (Fig. 4A). The instability of fish communities was particularly indicated by differences in October catches between 1997 and 1998 (see Figs. 3 and 4A). Small-sized species were numerically dominant in both watercourses. Bitterling (upper end of TL range = 76 mm), three-spined stickleback (67 mm) and sunbleak *Leucaspius delineatus* (73 mm) together accounted for > 60%, on average, of the combined catches.

We did not detect any amphibian breeding sites along the sampled reaches. However, during electrofishing operations in the winter, we observed aggregations of frogs (*Rana* spp.), containing thousands of individuals, hibernating beneath the concrete slabs fastening the slopes of the canal. Also, in October and March, numerous frogs were observed on the banks, apparently congregating before hibernation and emerging from it.

During field visits, we detected otter holts in the Świnka River banks, especially at sites where beaver *Castor fiber* had damaged the revetement. The over-

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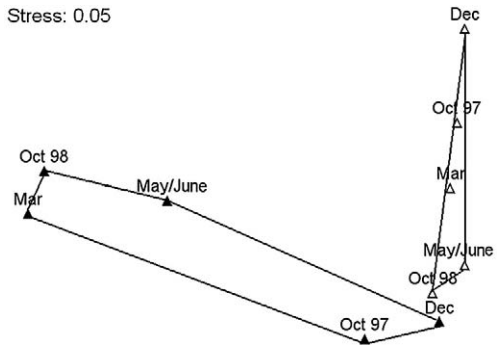

Figure 3. NMDS ordination of the fish communities sampled seasonally from October 1997 to October 1998 in the canal (▲) and in the river (△). Distances between symbols represent similarities. Convex hulls are shown for each habitat. The stress coefficient represents goodness-of-fit criteria.

all holt density was 0.5/km of watercourse. No holts were found in the canal embankments.

Fish in otter diet

In total, 1,465 prey items were identified from remains in 478 spraints (330 in the Wieprz Krzna Canal and 148 in the Świnka River). The most numerous species in the otters' fish diet were bitterling (average 40%), gudgeon (16%) and three-spined stickleback (13%; see Fig. 4B). The rankings of fish prey taxa, in terms of numbers and biomass, were similar (Spearman r: in all seasons $P \leq 0.02$). Gudgeon comprised the largest percentage by weight with a mean of 36% of the fish biomass consumed by otters, which corresponded to 19% of the overall diet (i.e. including non-fish food items; see Table 1). The main differences between the numerical and biomass importance of prey items in the otters' fish diet concerned the largest- and smallest-size species: the contribution of pike, the second prey item by biomass, was greater by biomass than by numerical frequency (17 vs 2%), while the reverse pattern was observed for three-spined stickleback (4 vs 13%). Bitterling ranked third in percentage biomass (13%).

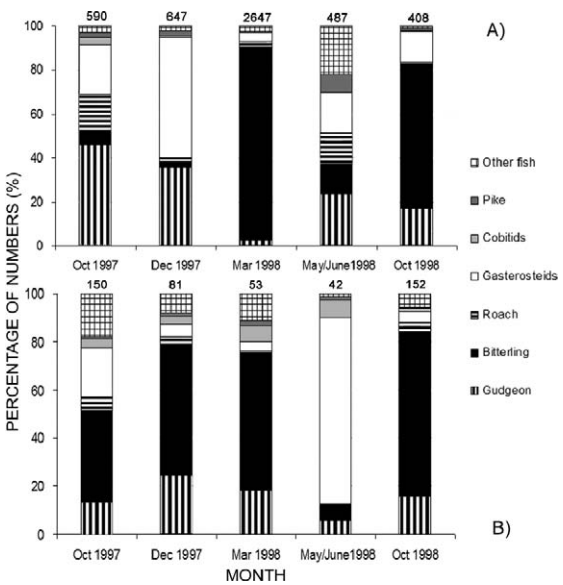

Figure 4. Relative percent frequency by number of major fish taxa in the combined electrofishing catches from the canal-river system (A), and in the fish diet of otters (B). The figures above the columns denote sample sizes (numbers of individuals caught and numbers of spraints, respectively).

All species present in the electrofishing catches were also identified in spraints. Ruffe *Gymnocephalus cernua*, common carp *Cyprinus carpio* and white bream *Blicca bjoerkna* were represented by single individuals in the otter diet (see Table 1), but were absent from the catches. Composition of fish taxa in the electrofishing samples and in spraints did not differ significantly (ANOSIM: $R = 0.088$, $P = 0.220$). Bitterling, gudgeon and three-spined stickleback, consumed most frequently by otters, were also the most abundant species in the combined catches (on average 35, 25 and 21%, respectively; see Fig. 4A and B). Also, these three species together contributed to most (75%) of the observed dissimilarity in proportional abundance in spraints and electrofishing catches (SIMPER: 38, 20 and 17%, respectively). In no fish taxon, with > 5% contribution to Bray-Curtis dissimilarity, were the deviations in Jacobs' selectivity index scores from the value for non-selective feeding consistently in the same direction (Wilcoxon test: all $P > 0.3$); only cobitids, which contributed 6% to dissimilarity, were marginally significantly (positively) selected ($P = 0.079$). However, cobitids formed a minor component of otter food (see Table 1).

The fish diet of otters consisted predominantly of small individuals, the seasonal median lengths of fish prey varying between 46 and 54 mm, while those in the combined catches ranged from 53 to 95 mm. However, the interquartile ranges overlapped in all months except October 1997. For those species for which sample size was sufficient for size selectivity analysis, the median sizes from the diet were either significantly smaller (roach; gudgeon in October 1997 and 1998, all $P < 0.001$) or did not significantly differ from those derived from the electrofishing samples (all $P > 0.13$; Fig. 5).

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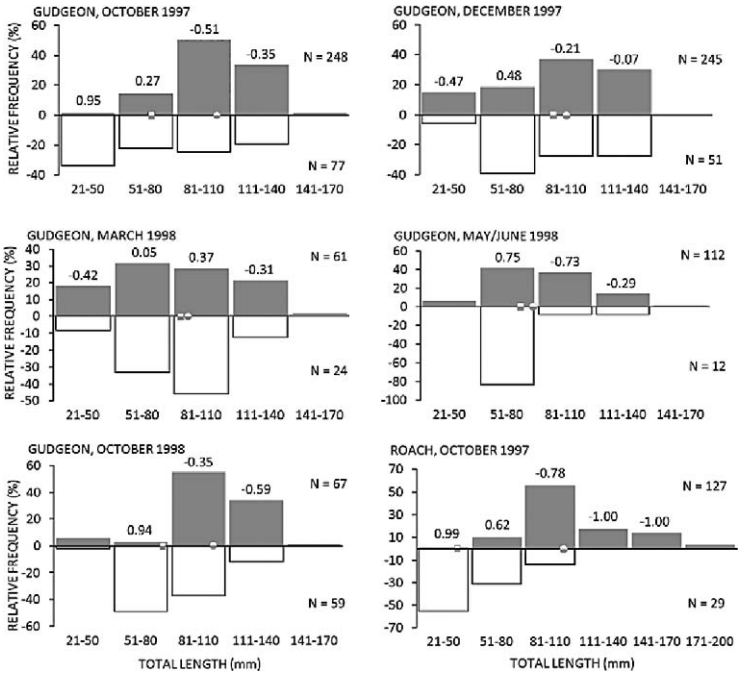

Figure 5. Size frequency distributions of gudgeon and roach captured by electrofishing (positive y-axis) and taken by otters (negative y-axis) in the canal-river system. Prey fish were divided into 30-mm length classes for both availability and diet. Circles and squares indicate median sizes of fish in the electrofishing samples and in the otters' diet, respectively. Values over bars are Jacobs' selectivity indices for each size class (the indices were calculated only for size classes that had > 10 individuals either in the diet or in the electrofishing samples).

Non-fish prey

Overall, the estimated contribution by non-fish prey biomass to otter diet exceeded 41% in all seasons and reached 75% in summer (see Table 1). Anurans substantially contributed to the diet in October 1997 and March 1998 (an estimated 39 and 43% by biomass, respectively). In these months, a few small piles of uneaten frog carcasses, marked by spraints, were detected at the banks along the sampled reaches. Avian prey were exclusively waterbirds (Anatidae, Podicepidae, Phalacrocoracidae) with a significant summer peak (46% by biomass). Crayfish, aquatic insects and rodents were of lesser importance. Unionid shell remains were retrieved from one spraint in winter. Dietary diversity was lowest in winter and spring and highest in the summer (see Table 1).

Discussion

The canal-river system as otter habitat

Our results support the prediction that the heavily altered ecosystem provides poor fish resources for otters (*cf.* Chanin 2003 for discussion of minimum fish densities needed by otters to survive). Small-sized species comprised the majority of fish collected during electrofishing sessions. It might be argued that at high densities, small fish may form a rich food supply (Topping & Kruuk 1996), but with the very small prey size, the energetic costs of hunting and daily calorific requirements of otters may be difficult to balance (Mason & Macdonald 1986). The contention that fish made a poor food base for otters in the canal-river system was substantiated by the significant contribution of non-fish prey, especially amphibians, to the otter diet. Otters appear to shift to amphibians, which are energetically less valuable food than fish (Nelson & Kruuk 1997), when fish resources are scarce (Brzeziński et al. 1993, Remonti et al. 2009, Almeida et al. 2012). However, as indicated by the incidence of surplus killing, anurans congregating at hibernation sites were seasonally an abundant and easy prey, and thus, analogous to the exploitation of small fish, potentially profitable despite their relatively low calorific content.

Fish assemblages in the Wieprz-Krzna Canal were roughly typical for artificial lowland waterways of Central Europe (Wolter 2001). Both the estimated fish density and taxonomic composition were subject to strong fluctuations, dependent on the water flow regime and influxes of fish entrained from the Wieprz River. Fish biomass was highest in the canal-river system in spring, when the largest volumes of water were conveyed. In summer, the seasonally lowest fish biomass in the canal corresponded with the greatest contribution of alternative prey to otter diet. Many otter habitats are characterised by seasonal fish scarcity or extreme water-level fluctuations, and an increase in alternative prey in otter diet in summer is

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reported from various habitats, since birds, amphibians and crayfish are particularly vulnerable to predation during this period (Miranda et al. 2008, Remonti et al. 2009). However, in our study area, non-fish prey played an important part in the food of otters in all seasons.

Water level instability and the poor structure of the habitat, resulting from the concrete lining and regular vegetation removal, apparently adversely affected the abundance of carnivorous fish such as pike (*cf*. Wolter 2001). This view is supported by fairly successful pike stocking since 2006 in the neglected sections (with poorly-cleared aquatic vegetation) of the canal (Polish Angling Association in Chełm, unpubl. data). The same factors are likely to account for the paucity of some food resources (crayfish and waterbirds) and the absence of otter dens in the canal margins. On the other hand, the concrete embedding of the canal has created an attractive habitat for some small fish species and hibernating anurans; the substantial occurrence of bitterling in spring was presumably fostered by abundance of unionids (Przybylski & García-Berthou 2004), which are used for spawning by this species. Kushlan (1976) showed that predominance of small-sized fish could be favoured by the scarcity of piscivorous fishes in unstable environments. Even with small-sized species prevailing, fish resources of the canal were intensely exploited by otters, as indicated by the dietary importance of bitterling, which was numerous in the canal while virtually absent in the Świnka River. In fact, the canal, mimicking a medium-sized river, was likely to offer better feeding opportunities than most of the small rivers within the boundaries of its hydrological network, simply because of its size. Fish biomass per unit bank length was higher in the canal than in the neighbouring Świnka River, while species diversity did not differ between the two watercourses. Owing to poor fish productivity of the small, mostly regulated rivers in the region, during seasonal periods of food stress local otter populations rely to some extent on carp stocks of fish farms (although no farms operate in the upper canal area), where they are severely persecuted (Kloskowski 1999, 2005).

Prey availability vs use

Quantification of diet based on faecal analysis should be interpreted with caution when samples are not assigned to individuals, e.g. insights into the predator's functional response to changes in relative prey availability are restricted. Also, although we used taxon-specific hard parts resistant to digestion (key bones) to determine the relative frequency of prey in the diet, as recommended by Carss & Parkinson (1996), the extent to which estimates of food composition were biased, due to differential recovery of undigested parts of fish vs non-fish prey and large vs small prey, remains unknown.

Sampling limitations associated with assessment of fish availability, which need to be acknowledged, include differences in catchability related to fish size and behaviour. Also, the electrofishing results might be biased by the patchy distribution of shoaling fish (Bohlin et al. 1989). In our study, this may particularly concern bitterling and three-spined stickleback, which were occasionally observed in large schooling aggregations during the electrofishing operations. Overall, fish communities in engineered canals are subject to rapid temporal variation, dependent on whether fish are allowed to enter and pass through the headgate and weirs. However, we believe that this has not seriously affected the patterns observed because spraint sampling and electrofishing were conducted concurrently at the same sites.

Despite the potential for bias in the estimates of otter diet and fish relative abundance, some general conclusions on otter feeding patterns in relation to prey availability can be drawn. As predicted, we did not find consistent preference/avoidance of any fish species common in our study area. Some dietary patterns could be linked to fluctuations in fish abundance; in the summer, the increased exploitation of gasterosteids, which were less likely to be a profitable food item because of their small body size and the presence of spines, coincided with the seasonally low water levels in the canal (but see Taastrøm & Jacobsen 1999, Miranda et al. 2008 for positive selection of gasterosteids). Otters consumed very small fish and took fish sizes that were either smaller or proportionate to their relative availability. In other studies on otters, prey fish taken were larger (but see Adrián & Delibes 1987), and small fish like those mainly preyed upon in the canal-river system often appeared to be ignored (e.g. Kruuk et al. 1993, Taastrøm & Jacobsen 1999, Sales-Luís et al. 2007, see also Kruuk & Moorhouse 1990 for selection of larger sizes). In fish pond areas, i.e. habitats with ample food supplies, otters have been observed to select lower to intermediate sizes; however, again, mean sizes of consumed fish were considerably in excess of median sizes in our present study (Kloskowski 2000, Lanszki et al. 2001). Underestimation of larger sizes due to incomplete ingestion (Pierce & Boyle 1991) is

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unlikely because seasonal TL ranges of species analysed for size preference only exceptionally exceeded 15 cm, and such small fish are typically completely eaten by otters (Erlinge 1968). Overall, the results suggest that under conditions of poor fish abundance, otters show no preference for any fish species; neutral or negative size selectivity was displayed (*cf.* Temple 1987). Since smaller fish individuals are more vulnerable to predation, the negative size selection can be a passive process (Juanes 1994).

Management implications

Otter trophic diversity in the canal-river system was very high (particularly in the summer, when fish abundance in the canal was lowest) compared with other studies from temperate Europe (reviewed in Clavero et al. 2003). The broad trophic niche suggests that otters may display high trophic flexibility, irrespective of the latitudinal pattern of food diversity when faced with unpredictable food and hydrological conditions. Such an increase in niche breadth, from a specialised diet to a wide array of trophic resources, has been observed in other medium-sized mammalian carnivores, depending on the local availability of prey, especially when their main prey resources are in short supply (Roper 1994, Lozano et al. 2006; see also Remonti et al. 2009). Adaptability to changing food conditions may be the key to successful colonisation of anthropogenic, apparently unfavourable habitats. Since otters can be exposed to seasonal food shortages or extreme variation in water flow even in pristine environments (e.g. Brzeziński et al. 1993, Ruiz-Olmo et al. 2001), dietary plasticity may have evolved as a highly adaptive trait in natural settings, and it can help otters to utilise both marginal and novel habitats. On the other hand, otter persistence in impoverished habitats, and conflicts with fisheries, undermine their usefulness as a flagship species (or an umbrella species representing habitat requirements of a suite of other species) sensitive to degradation of aquatic communities and riverside landscapes (*cf.* Bifolchi & Lodé 2005).

Artificial waterways, built for water conveyance and irrigation purposes, raise important conservation issues because of their adverse impact on aquatic communities (e.g. Mason & Macdonald 1986, Roberts & Rahel 2008). Paradoxically, such ecologically impoverished, highly managed watercourses, which are a widespread feature of riverine landscapes in Europe, may offer habitats in which otter protection efforts will be less contentious, due to reduced competition for fish supplies with humans. Particularly in areas with poor otter habitats, they may help to sustain local populations and facilitate metapopulation dynamics. However, they can be severely limited with regard to some types of resources, such as shelter structures (Sales-Luís et al. 2007) and, seasonally, also some food supplies. An obvious liability of the Wieprz-Krzna Canal zone as otter habitat was the sheer absence of potential breeding or resting places. While conservation activities to revitalise otter habitats may be beneficial in terms of 'ecosystem services' (*cf.* Medina-Vogel & Gonzalez-Lagos 2008), considering wildlife in management of man-made waterways is often unrealistic because of their specific hydrological functions, e.g. concrete lining and removal of vegetation are regarded as necessary measures to prevent water seepage and maintain proper water flow. Instead, we recommend managing the nearby aquatic habitats to augment resources critical for otters. As a mobile species with extensive individual home ranges (Kruuk et al. 1993), otters can easily utilise a mosaic of diverse habitats in a supplementary or complementary fashion (Dunning et al. 1992). Therefore, conservation strategies on a landscape scale should recognise anthropogenic systems of potential suitability for otters and integrate them in terms of good structural habitat connectivity (*cf.* Lodé 2002) with adjacent, less disturbed habitats which, even when of overall low quality themselves, may supplement the deficient resources.

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