

Habitat and seasonal variations in diet of otters, *Lutra lutra* in eastern Poland

Marcin BRZEZIŃSKI¹, Jerzy ROMANOWSKI², Łukasz KOPCZYŃSKI¹ and Elżbieta KUROWICKA¹

¹ Department of Ecology, Warsaw University, ul. Banacha 2, 02-097 Warszawa, Poland;
e-mail: marcinb@biol.uw.edu.pl

² Centre for Ecological Research Polish Academy of Sciences, ul. Konopnickiej 1, 05-092 Łomianki, Poland;
e-mail: romanowski@cbe.internetdsl.pl

Received 2 February 2006; Accepted 26 September 2006

A b s t r a c t. The diet of otters *Lutra lutra* was studied by spraint analysis in six river and stream habitats in eastern Poland. In all of them fish were the staple food of otters, constituting from 29 % to 96 % of prey consumed in particular seasons. In upland (river Tanew) and mountain (river San, streams Dwernik and Głębokki) habitats, bullheads (*Cottus gobio*) were the most frequently eaten fish throughout the year (with maximum contribution of 57 % in the winter diet on river Tanew). In these habitats otters preyed on total of 10 fish species, including: brown trout (*Salmo trutta*), stone loach (*Barbatula barbatula*), brook minnow (*Phoxinus phoxinus*) and stickleback (*Gasterosteus aculeatus*). On the lowland rivers, otters relied on more fish species than on the upland and mountain rivers (14 species on river Czarna Hańcza and 12 species on the upper and lower course of river Biebrza). Beside various cyprinids, otters preyed on stickleback, perch (*Perca fluviatilis*), mud loach (*Misgurnus fossilis*), burbot (*Lota lota*) and pike (*Esox lucius*). On all rivers, except the lower Biebrza, most of fish (from 70% to 88%) captured by otters were less than 10 cm long. Amphibians and crayfish were two other important groups of prey. On small streams in the Bieszczady Mountains, frogs (mainly *Rana temporaria*) comprised up to 46% of otter prey. Crayfish (*Ortonectes limosus*) remains were recorded in otter spraints only on the lowland rivers: in summer crayfish comprised 52% of prey on the Czarna Hańcza River and 47% of prey on the upper Biebrza River. In upland and mountain habitats the food niche breadth of otters was lower (from $B=2.62$ to $B=6.12$) than on the lowland rivers (from $B=3.10$ to $B=11.09$) and did not differ much between the seasons. On the lowland rivers the food niche breadth was high in winter and low in summer, and the seasonal differences in otter diet were much more pronounced as compared to the upland and mountain habitats.

Key words: food niche, prey size, rivers

Introduction

Otters were found to be widespread in eastern Poland, where in the main river catchments from 88–100% of investigated (visited) sites were found positive in a national field survey in 1991–1994 (Brzeziński et al. 1996). Recent surveys documented an ongoing process of expansion of the otter population in central and eastern Poland, where the species now inhabits almost all available aquatic habitats: large and small rivers, lakes, fishponds, streams and regulated channels (Romanowski 2006). Although the composition of otter diet was analyzed in numerous studies within the otter distribution range (Jędrzejewska et al. 2001), the data from Poland originate only from fishponds (Wiśniewska 1996, Klośkowska 1999, 2000) and small rivers in Białowieża Primeval Forest and Bieszczady Mountains (Brzeziński et al. 1993, Harna 1993, Jędrzejewska et al. 2001).

The aim of this study was to compare the diet of otters in six different lowland and upland/mountain river habitats in eastern Poland and to quantify seasonal variation in the diet.

Study Area

Otter diet was studied in six different river habitats in eastern Poland (Fig. 1). Czarna Hańcza River (total length 142 km), the left tributary of Nemau river, runs through the north-eastern Poland in the post-glacial landscape. A ten km long section, below the Wigry National Park, was chosen for the study. In this area the Czarna Hańcza is a lowland river, with a meandering course, from 15 to 20 m wide and up to 2 m deep. The water level is stable. The river bed is sandy and partly covered by water plants. The water flow is fast, up to $2.1 \text{ m}^3\cdot\text{s}^{-1}$. Banks are overgrown with riparian vegetation, reeds, sedges and black alder *Alnus glutinosa*. Pine *Pinus silvestris* forests dominate on the slopes of the river valley.

Biebrza River, a right tributary of the Narew River, is a 155 km long, lowland river in north-eastern Poland. Two separate sections were defined as study areas, a 5 km long section in the upper Biebrza and a 12 km section in the lower Biebrza, some 50 km apart. Both were in the Biebrza National Park. In its upper part, the Biebrza River is up to 15 m wide and up to 2 m deep. It runs through meadows and pastures. The banks have narrow reed beds. Aquatic plants are numerous. The water flow is moderate – $1.1 \text{ m}^3\cdot\text{s}^{-1}$. In its lower basin the river runs through a wide marshy valley and it has many meandering courses. The river is up to 30 m wide. Its mean depth is 2 m, however in some parts, up to 6 m. The river bed is sandy and lacks aquatic vegetation. Water flow is $8.7 \text{ m}^3\cdot\text{s}^{-1}$. The banks are overgrown with dense and vast reed beds. Oxbows, up to 1.5 km long and about 2 m deep, are very numerous. Their beds are muddy and are overgrown with aquatic plants. In the lower Biebrza basin, the water level increases in the early spring to flood huge areas of the valley.

The Tanew River, a right tributary of San River, runs through the Lublin Upland in south-eastern Poland. The river is 113 km long. Studies were undertaken on an 8 km long section in the upper reaches of the river. In this area the river is shallow (less than 1 m deep) and the river bed is rocky. The river is up to 10 m wide and the water flow is very fast. Boulders and



Fig. 1. Study areas: 1 – Czarna Hańcza, 2 – upper Biebrza, 3 – lower Biebrza, 4 – Tanew, 5 – San, 6 – Dwernik and Głęboki.

stones are numerous, however, in the parts with slower water flow, the bed is sandy. Banks are forested, with black alder dominating in the vicinity of the river. In the nearby marshes several small ponds are present.

The San River, 443 km long, is the largest river in south-eastern Poland. Studies were conducted in its upper reaches, in the Bieszczady Mountains. A seven km long section was selected for collecting otter spraints. In the study area the water flow is very fast. The rocky river bed is up to 60 m wide. Rocks, boulders and stones are very numerous. Water level changes rapidly according to the rainfall. In dry periods (mainly summer) the river is only 0.5 m deep on average. After heavy rainfall, the water level can rise more than 1.5 m. The valley slopes are steep, overgrown by beeches *Fagus silvatica* and hazel *Corylus avellana*. Riparian vegetation is abundant. Flat terraces in some parts of the section are overgrown by alder *Alnus incana* and grasses.

The Dwernik and Głębokki streams are left tributaries of the San River in the Bieszczady Mountains. Due to their mountainous character they were distinguished as one, separate study area. Both streams are similar, running in narrow valleys with steep, rocky and forested slopes. The width of the streams does not exceed 5 m. They are shallow, up to 0.5 m deep. The water flow is very fast so the streams usually do not freeze in the winter. The food of otters was studied on 3 km long sections which were about 5 km distant from the San River.

Material and Methods

Otter spraints were collected in all study areas throughout one year, usually twice in the season. Results are presented for each season: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). Altogether 4039 spraints were analyzed. Each spraint was oven dried at 50 °C, washed through a sieve with 1 mm mesh and dried again. All undigested remains were separated and identified according to the keys of H o r o s z e w i c z (1960), P u c e k (1981), M ä r z (1987) and collection of comparative material. Fish, which dominated in the otter diet, were identified on the basis of scales, jaw apparatus, skull bones and some other parts of the skeleton. The size of fish eaten was estimated by measuring vertebrae, according to indexes calculated by W i s e (1980) and our own collection of fish skeletons. Four size groups of fish were distinguished: < 10 cm, 11–20 cm, 21–30 cm and >31 cm.

The composition of otter diet is presented as a relative percentage occurrence (relative frequency) of 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).

The food niche breadth was calculated according to L e v i n s (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 otter diet, all recognized fish species (Table 1).

Results

Czarna Hańcza River

Fish were the dominant prey of otters inhabiting the Czarna Hańcza River, however, crayfish *Ortonectes limosus* and frogs (mainly common frog *Rana temporaria*) comprised a

Table 1. Food niche breadth (index B after L e v i n s 1968) in winter, spring, summer and autumn in six studied habitats in Poland and the seasonal variability in otter diet expressed by χ^2 test.

River	Index of food niche breadth B				χ^2	p
	Winter	Spring	Summer	Autumn		
Czarna Hańcza	9.31	11.09	3.10	8.08	1099.5	<0.001
Biebrza - upper	7.37	5.52	3.84	7.31	675.3	<0.001
Biebrza - lower	7.82	5.30	5.97	7.62	716.2	<0.001
Tanew	2.62	3.21	3.50	3.53	174.8	<0.001
San	5.57	4.84	6.12	6.05	201.6	<0.001
Dwernik and Głębokki	3.43	4.12	3.71	3.37	49.7	<0.001

significant part of the diet (Table 2). In winter, spring and autumn, the overall contribution of fish to the diet of otters was stable – about 70% of all eaten prey items. Only in summer was it smaller, due to the high proportion of crayfish remains (52.1%). There were 5 fish species which dominated the diet: stickleback *Gasterosteus aculeatus*, bullhead *Cottus gobio*, brook minnow *Phoxinus phoxinus*, perch *Perca fluviatilis* and bitterling *Rhodeus sericeus*. Despite significant seasonal variability of prey occurrence in spraints ($\chi^2=1099.5$, $p<0.001$), these five fish species were eaten by otters in all seasons and composed from 35.4% of prey items eaten in summer to 51.7% in winter (Table 2). Other fish species were less important, comprising

Table 2. Seasonal variation in otter diet on Czarna Hańcza River expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Stickleback (<i>Gasterosteus aculeatus</i>)	12.4	11.8	19.6	19.8
Bullhead (<i>Cottus gobio</i>)	11.6	10.9	5.4	9.2
Brook minnow (<i>Phoxinus phoxinus</i>)	13.1	8.0	1.6	8.9
Bitterling (<i>Rhodeus sericeus</i>)	8.7	3.4	0.3	4.9
Gudgeon (<i>Gobio gobio</i>)	5.1	0.9	0	0.8
Spirling (<i>Alburnoides bipunctatus</i>)	2.6	0.9	0.1	1.7
Crucian carp (<i>Carassius carassius</i>)	0	1.1	0.2	1.0
Roach (<i>Rutilus rutilus</i>)	1.0	2.8	0	0
Chub (<i>Leuciscus cephalus</i>)	0.8	0	0.1	0.5
Cyprinidae undet.	0	0	1.4	0
Spined loach (<i>Cobitis taenia</i>)	4.3	5.7	1.5	5.2
Cobitidae undet.	0.2	1.1	1.2	0.1
Percidae	5.9	8.5	8.5	4.4
Pike (<i>Esox lucius</i>)	0.3	1.8	0.3	1.5
Eel (<i>Anguilla anguilla</i>)	0.3	2.3	0.2	1.2
Salmonidae	1.4	1.1	0.6	2.2
Fish (total)	67.6	60.4	40.9	61.4
River lamprey (<i>Lampetra fluviatilis</i>)	0.6	5.7	0	0.1
Insects	0.5	2.5	3.1	2.3
Crayfish	14.3	14.6	52.1	19.2
Amphibians	15.7	13.7	1.9	14.9
Birds	1.1	2.3	1.7	2.1
Mammals	0.1	0.9	0.2	0
Number of spraints	264	151	569	218
Number of items	961	439	1023	731

not more than 20% of all prey items. Crayfish which dominated the diet in summer, comprised 14% to 19% of prey in all other seasons. Frogs were eaten in similar proportion (10–15% of prey), except of summer, when they were eaten sporadically. Food niche breadth varied between the seasons and, due to the dominance of crayfish in otter diet, was very low in summer (B=3.10) but very high in spring (B=11.09) (Table 1).

Upper Biebrza River

On the upper Biebrza River a group of prey species was taken by otters throughout the year, but the diverse diet differed significantly in particular seasons ($\chi^2=675.3$, $p<0.001$). Crayfish were most frequently eaten prey in spring and summer (35.8% and 47% respectively) but were of a minor importance during the cold seasons (Table 3). Frogs were eaten in largest numbers in autumn and winter (20.2% and 27.8% respectively). Prey which were also eaten more frequently in autumn and winter than in spring and summer were bitterling and gudgeon *Gobio gobio*. Other relatively important fish in otter diet were sticklebacks, roach *Rutilus rutilus*, perch and stone loach *Barbatula barbatula*. The seasonal changes of the diet were easily seen due mainly to the variable crayfish consumption. Food niche breadth was highest in winter (B=7.37), lowest in summer (B=3.84) (Table 1).

Lower Biebrza River

Fish, supplemented mainly with crayfish, frogs and birds were the main prey category in the diverse diet of otters on the lower Biebrza River. Seasonal variability in the diet was high

Table 3. Seasonal variation in otter diet on upper Biebrza River expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Stickleback (<i>Gasterosteus aculeatus</i>)	6.7	16.1	10.2	8.2
Bitterling (<i>Rhodeus sericeus</i>)	17.8	2.6	0.6	11.3
Gudgeon (<i>Gobio gobio</i>)	19.8	2.0	1.0	8.2
Crucian carp (<i>Carassius carassius</i>)	0	1.3	2.3	3.1
Roach (<i>Rutilus rutilus</i>)	6.3	10.2	1.4	2.7
Bleak (<i>Alburnus alburnus</i>)	0.4	2.3	0.7	0
Cyprinidae undet.	0	0.8	3.0	0
Mud loach (<i>Misgurnus fossilis</i>)	0.8	3.1	3.9	1.0
Common loach (<i>Barbatula barbatula</i>)	4.3	2.8	2.6	7.7
Spined loach (<i>Cobitis taenia</i>)	0.4	2.6	1.4	0
Perch (<i>Perca fluviatilis</i>)	9.1	5.1	0.3	2.1
Ruff (<i>Gymnocephalus cernuus</i>)	3.2	0.8	0.1	1.5
Pike (<i>Esox lucius</i>)	4.7	0.8	1.9	5.7
Fish (total)	73.5	50.4	29.4	51.5
Insects	1.2	5.3	9.6	6.8
Crayfish	4.7	35.8	47.0	12.9
Amphibians	20.2	7.9	12.3	27.8
Birds	0.4	0.5	0.7	1.0
Mammals	0	0	1.0	0
Number of spraints	65	159	345	67
Number of items	253	391	698	194

($\chi^2=716.2$, $p<0.001$) with no single prey species dominating throughout the whole year. However, fish, such as burbot *Lota lota*, roach, pike *Esox lucius*, mud loach *Misgurnus fossilis* and perch occurred regularly in the diet in all seasons. Their contribution varied according to the season (Table 4). Burbot and roach dominated in spring (23.5% and 33.2% of all prey items) and mud loach in autumn and summer (23.3%–24.3%). Altogether, the five fish species mentioned above comprised from 42.6% of all prey in winter to 89.1% in summer. Among other fish species only gudgeon contributed more than 10% of prey items in winter. In spring otters hunted many birds (10.7%). Frogs were abundant in otter diet mainly in autumn and winter (up to 18.9% of prey consumed). Crayfish played little role in the diet and their relatively high contribution was recorded not in the warm seasons but in winter (20.3%). The food niche was much broader in winter ($B=7.82$) and autumn ($B=7.62$) than in spring ($B=5.30$) and summer ($B=5.97$) (Table 1).

Table 4. Seasonal variation in otter diet on lower Biebrza River expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Stickleback (<i>Gasterosteus aculeatus</i>)	2.2	2.7	0	2.1
Gudgeon (<i>Gobio gobio</i>)	10.2	0.5	1.9	4.8
Crucian carp (<i>Carassius carassius</i>)	0.3	2.1	3.7	2.3
Roach (<i>Rutilus rutilus</i>)	10.8	33.2	15.0	10.3
Bleak (<i>Alburnus alburnus</i>)	0.1	0	0.7	0
Common bream (<i>Abramis brama</i>)	2.8	4.8	0.7	0.3
Mud loach (<i>Misgurnus fossilis</i>)	7.9	3.2	24.3	23.3
Percidae	7.2	2.7	14.5	8.9
Pike (<i>Esox lucius</i>)	5.2	4.3	15.4	12.0
Eel (<i>Anguilla anguilla</i>)	0.1	0	0	0
Wels (<i>Silurus glanis</i>)	0.1	0	0	0
Burbot (<i>Lota lota</i>)	11.5	23.5	19.9	12.7
Fish (total)	58.4	77.0	96.0	76.7
Insects	1.3	3.2	0.3	2.7
Crayfish	20.3	5.9	0.7	4.5
Amphibians	18.9	2.1	0	14.7
Birds	0.7	10.7	1.7	0
Mammals	0.4	1.1	1.2	1.4
Number of spraints	235	99	302	102
Number of items	724	187	573	292

T a n e w R i v e r

Bullhead was the dominant prey throughout the year, comprising from 43.7% to 56.9% of all eaten animals (Table 5). The overall seasonal changes in diet on the Tanew River were significant ($\chi^2=174.8$, $p<0.001$), but the contribution of bullhead in the diet did not vary seasonally. Two other fish species, brown trout *Salmo trutta* and stickleback, were supplementary prey. Trout were eaten most frequently in winter (20%) and sticklebacks in autumn (26.5%). The contribution of other fish species to otter diet was very low and in no season exceeded 15%. Frogs were abundant in otter food in all seasons in similar proportions, comprising from about 10% to 20% of prey consumed. In general, the diet of otters was based on only a few prey species. Food niche breadth was lowest, compared to other habitats, and did not differ much between the seasons (from $B=2.62$ in winter to $B=3.53$ in autumn) (Table 1).

Table 5. Seasonal variation in otter diet on Tanew River expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Stickleback (<i>Gasterosteus aculeatus</i>)	9.2	19.4	16.8	26.5
Bullhead (<i>Cottus gobio</i>)	56.9	50.3	45.5	43.7
Crucian carp (<i>Carassius carassius</i>)	0	1.9	0.9	0.3
Common loach (<i>Barbatula barbatula</i>)	0	1.4	0.6	0
Perch (<i>Perca fluviatilis</i>)	4.6	6.5	2.9	6.2
Brown trout (<i>Salmo trutta</i>)	20.0	4.5	3.4	8.7
Grayling (<i>Thymallus thymallus</i>)	0	0	0	3.3
Pike (<i>Esox lucius</i>)	1.6	0	0	0
Burbot (<i>Lota lota</i>)	0	1.9	0	0
Fish (total)	92.3	85.8	70.1	88.7
Insects	0	0	1.1	0.3
Amphibians	7.7	11.6	20.6	9.7
Birds	0	0.6	7.6	0
Mammals	0	1.9	0.6	1.3
Number of spraints	40	83	241	149
Number of items	65	155	475	309

San River

Otters inhabiting the mountainous San River had rather stable, although slightly diverse diet throughout the whole year ($\chi^2=201.6$, $p<0.001$). Food niche breadth varied from 4.84 in spring to 6.12 in summer (Table 1). Three fish species: bullhead, stone loach and brook minnow, together with frogs, comprised, according to season, from 65.3% to 79.6% of prey eaten (Table 6). Other fish, such as cyprinids, perch, brown trout and grayling *Thymallus thymallus* were of a minor importance. The most frequently eaten fish, bullhead, was taken in the same proportion in all seasons (27.2%–29.9%). The second most important prey, stone loach, was abundant in otter diet mainly in spring. Frogs were consumed from winter to autumn, being more frequently taken in the cold rather than in the warm seasons. Crayfish

Table 6. Seasonal variation in otter diet on San River expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Bullhead (<i>Cottus gobio</i>)	27.2	29.9	28.8	28.2
Brook minnow (<i>Phoxinus phoxinus</i>)	15.3	9.0	8.1	15.3
Cyprinidae undet.	8.0	9.4	8.3	4.3
Common loach (<i>Barbatula barbatula</i>)	15.3	29.1	21.4	13.4
Perch (<i>Perca fluviatilis</i>)	0.4	4.7	7.5	6.1
Brown trout (<i>Salmo trutta</i>)	4.3	1.2	5.0	5.3
Grayling (<i>Thymallus thymallus</i>)	4.3	4.9	5.1	2.1
Fish (total)	74.7	88.2	84.1	74.7
Insects	0	0	0.6	0
Crayfish	2.3	1.2	7.6	7.5
Amphibians	21.8	10.4	7.0	17.3
Mammals	1.1	0.2	0.6	0.5
Number of spraints	75	183	265	213
Number of items	456	924	1447	980

Astacus astacus was recorded in small numbers and its contribution to the diet was highest in summer and autumn, reaching nearly 8%.

D w e r n i k a n d G ł ę b o k i s t r e a m s

The diet of otters feeding on these two streams was homogenous and the food niche breadth showed little variation – the highest, recorded in spring (B=4.12), did not differ much from the lowest recorded in autumn (B=3.37) (Table 1). Only 6 main prey types were identified (5 fish species and a common frog) plus a few rodents and unidentified cyprinids. It was the only habitat in which frogs were eaten more frequently than any fish species in all seasons (Table 7). Amphibians were consumed in similar proportion throughout the year (from 36.1% to 45.9% of all eaten prey). The second most important prey was bullhead. Other fish eaten were stone loach, brown trout, grayling and brook minnow. The diet was seasonally stable, but differed slightly throughout the year ($\chi^2=49.7$, $p<0.001$). The most visible seasonal difference was the increased otter predation on brown trout in autumn and winter.

Table 7. Seasonal variation in otter diet on Dwernik and Głębok streams expressed by percentage occurrence of prey items.

Species	Winter	Spring	Summer	Autumn
Bullhead (<i>Cottus gobio</i>)	27.4	23.9	34.0	23.8
Brook minnow (<i>Phoxinus phoxinus</i>)	3.3	5.2	6.2	4.8
Cyprinidae undet.	0	1.8	3.1	2.5
Common loach (<i>Barbatula barbatula</i>)	1.6	12.9	11.3	4.1
Brown trout (<i>Salmo trutta</i>)	22.6	5.9	7.2	15.6
Grayling (<i>Thymallus thymallus</i>)	1.6	8.3	0	0.8
Fish (total)	56.5	58.1	61.9	51.6
Amphibians	40.3	39.4	36.1	45.9
Mammals	3.2	2.6	2.1	2.5
Number of spraints	25	74	49	66
Number of items	62	155	97	122

P r e y s i z e

In most habitats, otters preyed mainly on small fish (below 10 cm long) comprising 88% of individuals from the Czarna Hańcza River and 72% -81% from the upper Biebrza, Tanew and San (Fig. 2). The lower Biebrza River was the only studied habitat where fish below 10 cm long did not dominate the diet. There, most of the fish consumed were from 10 to 20 cm long (47.3%), while larger fish, over 20 cm long, comprised 17.6% of all predated individuals. The larger average size of fish eaten by otters in this habitat resulted from the abundance of large species such as burbot and pike.

D i s c u s s i o n

Otters are considered as opportunistic fish predators, and usually consume various species of fish proportionally to their occurrence (Erlinge 1967, Jenkins & Harper 1980, Chanin 1981, Taatstrøm & Jacobsen 1999, Poledník et al. 2004). In

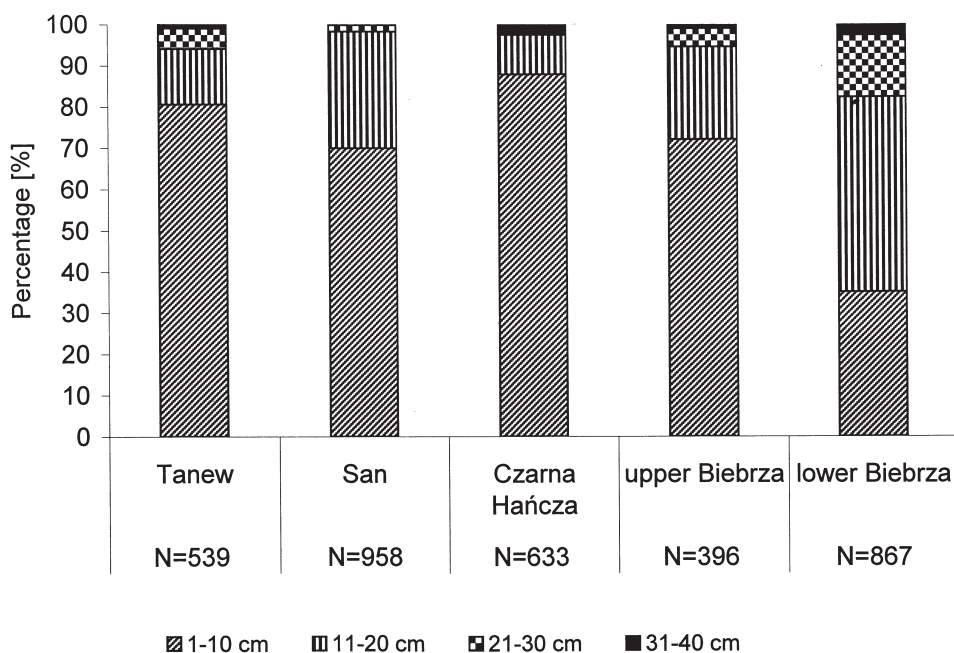


Fig. 2. Size of fish eaten by otters. N – number of specimens.

recent reviews of the literature, authors connect variation in otter diet mainly with latitude (Clavero et al. 2003) or with habitat (Jędrzejewska et al. 2001). Clavero et al. (2003) show that otter diet is more diverse in southern latitudes than in temperate zones and that otters are more piscivorous towards the north. On the contrary, Jędrzejewska et al. (2001) suggest that variation in diet composition does not change significantly with latitude depending mainly on habitat. As concluded by these authors the otter appears to be a predator strongly specialized in food resources taken from aquatic habitats: fish, crayfish and amphibians. Beside fish, crayfish seem to be a prey of special importance, especially in spring-summer (Adrian & Delibes 1987, Kyne et al. 1989, Lanszki & Molnár 2003). When both crayfish and fish are in low supply or availability, otters shift their diet primarily to amphibians, and, secondarily, to birds and mammals. The significantly increased contribution of amphibians to otter diet was recorded mainly from small rivers and streams which do not provide enough fish for otters (Brzeziński et al. 1993, Lojkásek & Grendziok 1994, Sulka 1996, Jędrzejewska et al. 2001) or/and in the places of amphibian high densities, for instance at spawning sites (Wise et al. 1981, Fairley 1984, Weber 1990).

In eastern Poland diet of otters, as found in this study, largely agrees with the above general rules. Fish were the staple food of otters but the share of alternative prey – amphibians, was relatively high in all studied habitats. The most diverse diet was recorded on the lowland rivers: on Czarna Hańcza and on Biebrza (Table 1). In the upland (Tanew River) and mountainous habitats (San River, Dwernik and Głęboki streams) the food niche breadth was lower than on the lowland rivers. On the Czarna Hańcza River and Biebrza River (both upper and lower) otters preyed on 14 and 12 fish species respectively, whereas on the two streams in Bieszczady Mountains only 5 fish species were found in the diet.

The contribution of amphibians to the otter diet was highest on mountain streams. On larger rivers, with more diverse and numerous fish communities, amphibians were preyed upon in smaller numbers. In temperate zones, amphibians become an important prey usually in cold seasons, despite their availability from autumn to spring appearing to be much lower than in summer (B r z e z i ń s k i et al. 1993). However, this low winter availability is not necessarily true, because of two reasons. Firstly, otters, similarly to polecats (*Mustela putorius*) and American mink (*Mustela vison*), are able to search for amphibians hibernating in mud, both on banks and in the bottom of water courses (S u l k a v a 1996). Secondly, in temperate zones, during winter there are usually periods of warming when frogs (mainly the common frog) move from their hibernating shelters and can be found torpid on the bottoms of rivers (S a v a g e 1961), and fall easy prey to otters.

On the rivers of eastern Poland, as in many other European habitats, alternative prey other than amphibians, were sporadically hunted by otters and played little role in the diet. Birds, mammals and insects did not contribute separately more than 10% of otter diet (the only exception was lower Biebrza where birds constituted 10.7% in spring). Only a few European studies of otter diet recorded higher percentage occurrence of birds and mammals in otter diet (J ę d r z e j e w s k a et al. 2001). Thus, these groups of prey should be treated not as an alternative prey but rather as a supplementary and occasional food of otters.

Seasonal variation in otter diet reflects more or less seasonal variation in prey availability and numbers. Availability of potential prey is determined mainly by habitat, however, it can also vary according to the season, especially in latitudes where seasonality is well pronounced. In southern Europe, where seasons are not so well pronounced, seasonal variation in prey availability and variation in otter diet is rather small (A d r i a n & D e l i b e s 1987) as compared to northern and eastern Europe (S u l k a v a 1996, S i d o r o v i c h 2000). In temperate zones, seasonal differences in prey availability concern more terrestrial than aquatic food resources, but even in inland waters, prey availability changes seasonally. However, these changes are clear only in those aquatic habitats with a diverse ichthyofauna and high fish biomass. In such habitats otters vary their diet through the year to take advantage of seasonal changes in availability (C h a n i n 1981). In aquatic habitats with only few fish species, otter diet is homogenous and its seasonal variation is small. For example, in many oligotrophic lakes and rivers, salmonids dominate the diet in all seasons (C h a n i n 1981).

Results obtained from eastern Poland show that, in habitats with a small number of fish (and other prey) species, otter diet is not only less diverse than in rich habitats, but also much more stable. On upland and mountain rivers and streams otter food niche breadth was relatively low and comparable in all seasons. On mountain streams, as well as on the San and Tanew rivers, otters preyed on bullhead, brown trout, brook minnow, stone loach and grayling – typical and most common representatives of fish communities of rapid flow mountain rivers. An earlier study of H a r n a (1993) on four rivers in Bieszczady Mountains, as well as results of P o l e d n í k et al. (2004) from Beskydy Mountains showed similar proportions of the same dominant fish species in the otter diet. On the contrary, on larger lowland rivers, a seasonal variation in diet composition was well pronounced and, in general, the indices of food niche breadth were higher. On the lowland Biebrza and Hańcza rivers, otters preyed on many fish species including roach, gudgeon, bitterling, mud loach, pike and burbot, typical for eutrophic, slow moving waters with low oxygen content. Moreover, on lowland rivers otter diet was more diverse in cold than in warm seasons. Many reports documented significant decrease in the consumption of majority fish species by

otters in summer (Erlinge 1967, Webb 1975, Chanin 1981, Kynne et al. 1989, Taastrøm & Jacobsen 1999). Such clear seasonal differences in the contribution of cyprinids to the otter diet are explained by higher energetic costs of predation on more mobile fish in warmer water and/or the easier availability of crayfish, which are usually the main alternative prey source in warm seasons (Kynne et al. 1989).

On the lowland rivers in eastern Poland, seasonal changes in diet were affected mainly by the variable consumption of crayfish. An increased contribution of crayfish in summer diet of otters was recorded on Czarna Hańcza and upper Biebrza. In both study areas of the Biebrza, the maximum values of food niche breadth were recorded in autumn and winter, and on the Czarna Hańcza in winter and spring. In temperate latitudes this inversed seasonal change of food niche breadth is not recorded for otters inhabiting inland waters with poor food resources (Brzeziński et al. 1993). It is also rarely found among carnivores and raptors of terrestrial habitats. For example, in the Białowieża Primeval Forest (eastern Poland), of the whole community of predators only two raptors (goshawk *Accipiter gentilis* and pygmy owl *Glaucidium passerinum*) had significantly more diverse diet in autumn-winter than in spring-summer (Jędrzejewska & Jędrzejewski 1998).

Otters prey mostly on small sized cyprinids and percids, with body length from 5–15 cm (Jenkins et al. 1979, Brzeziński et al. 1993, Sulikava 1996, Kučerová & Roche 1999). Fish from other families: pikes, eels and trout eaten by otters are usually larger (Adrian & Delibes 1987, Kemenes & Nechay 1990, Sulikava 1996). Small sized fish (up to 10 cm long) predominated in the diet of otters on almost all rivers studied in eastern Poland and only on the lower Biebrza were larger fish (11–20 cm long) more numerous. The size of the fish consumed by otters in the majority of aquatic habitats is positively correlated with the size of fish dominating in the environment (Wise et al. 1981, Libois et al. 1991, Taastrøm & Jacobsen 1999). This relation should be explained not only by otter selective predation on small sized individuals of species capable of further growth, but rather in terms of availability of small sized prey species. In habitats studied in eastern Poland the size of fish eaten by otters depended mainly on species predated. These were first of all bullhead (max. length 13 cm), stone loach (max. length 12 cm), brook minnow (max. length 14 cm), stickleback (max. length 10 cm), gudgeon (max. length 15 cm) and bitterling (max. length 9 cm). On the lower Biebrza otters preyed on relatively many large sized fish like pike, burbot and perch, that resulted in larger average size of fish eaten in this habitat.

LITERATURE

- Adrian M. I. & Delibes M. 1987: Food habits of the otter (*Lutra lutra*) in two habitats of the Donana National Park, SW Spain. *J. Zool. (Lond.)* 212: 399–406.
- Brzeziński M., Jędrzejewski W. & Jędrzejewska B. 1993: Diet of otters (*Lutra lutra*) inhabiting small rivers in the Białowieża National Park, Eastern Poland. *J. Zool. (Lond.)* 230: 495–501.
- Brzeziński M., Romanowski J., Cygan J. P. & Pabin B. 1996: Otter *Lutra lutra* distribution in Poland. *Acta Theriol.* 41: 113–126.
- Clavero M., Prenda J. & Delibes M. 2003: Trophic diversity of the otter (*Lutra lutra* L.) in the temperate and Mediterranean freshwater habitats. *J. Biogeogr.* 30: 761–769.
- Chanin P. 1981: The diet of the otter and its relations with the feral mink in two areas of southwest England. *Acta Theriol.* 26: 83–95.

- Erlinge S. 1967: Food habits of the fish-otter (*Lutra lutra* L.), in south Swedish habitats. *Viltrevy* 4: 372–432.
- Fairley J. S. 1984: Otters feeding on breeding frogs. *Ir. Nat. J.* 21: 372.
- Harna G. 1993: Diet composition of the otter *Lutra lutra* in the Bieszczady Mountains, south-east Poland. *Acta Theriol.* 38: 167–134.
- Horoszewicz L. 1960: Wartości kości gardłowych dolnych (*Ossa Pharyngea Inferiora*), jako kryteriów gatunkowego oznaczania ryb karpiowatych (*Cyprinidae*) [Identification of cyprinid (*Cyprinidae*) species using *Ossa Pharyngea Inferiora*]. *Rocz. Nauk. Rol.*, B 75: 237–325 (in Polish).
- Jenkins D., Walker J. G. K. & McCowan D. 1979: Analyses of otter (*Lutra lutra*) faeces from Deeside, N. E. Scotland. *J. Zool. (Lond.)* 187: 235–244.
- Jenkins D. & Harper R. J. 1980: Ecology of otters in northern Scotland II: Analysis of otter (*Lutra lutra*) and mink (*Mustela vison*) faeces from Deeside, NE Scotland in 1977–78. *J. Anim. Ecol.* 49: 737–754.
- Jędrzejewska B. & Jędrzejewski W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a Case Study. *Ecological Studies* 135, Springer Verlag, Berlin Heidelberg: 1–450.
- Jędrzejewska B., Sidorovich V. E., Pikulik M. M. & Jędrzejewski W. 2001: Feeding habits of the otter and the American mink in Białowieża Primeval Forest (Poland) compared to other Eurasian populations. *Ecography* 24: 165–180.
- Kemenes I. & Nechay G. 1990: The food of otters *Lutra lutra* in different habitats in Hungary. *Acta Theriol.* 35: 17–24.
- Kloskowski J. 1999: Otter *Lutra lutra* predation in cyprinid-dominated habitats. *Z. Säugetierkd.* 64: 201–209.
- Kloskowski J. 2000: Selective predation by otters *Lutra lutra* on common carp *Cyprinus carpio* at farmed fisheries. *Mammalia* 64: 287–294.
- Kučerová M. & Roche K. 1999: Otter conservation in the Třeboň biosphere reserve and protected landscape area. *Třeboň Otter Foundation, Strasbourg*: 1–103.
- Kyne M. J., Smal C. M. & Fairley J. S. 1989: The food of otters *Lutra lutra* in the Irish midlands and comparison with that of mink *Mustela vison* in the same region. *Proc. of the Royal Irish Acad., Sec. B* 89: 33–46.
- Lanszki J. & Molnár T. 2003: Diet of otters living in three different habitats in Hungary. *Folia Zool.* 52(4): 378–388.
- Levins R. 1968: Evolution in changing environments. *Princeton Univ. Press, Princeton*.
- Libois M., Rosoux R. & Delooz E. 1991: Ecologie de la loutre, *Lutra lutra*, dans le Marais Poitevin. III. Variations du régime et tactique alimentaire. *Cathiers d'Ethologie* 11 (1): 31–50 (in French with English summary).
- Lojkásek B. & Grendziok P. 1994: K potravě a výskytu vydry říční (*Lutra lutra* L.) na území CHKO Beskydy (On the diet and occurrence of the otter (*Lutra lutra*) in the Beskydy Protected Landscape Area). *Acta Fac. Rer. Nat. Univ. Ostraviensis (Biologica-Ekologická)* 142(2): 151–158 (in Czech with English summary).
- März R. 1987: Gewoll- und Rupfungskunde. *Akademie-Verlag, Berlin*.
- Poledník L., Mitrenga R., Poledníková K. & Lojkásek B. 2004: The impact of methods of fishery management on the diet of otters (*Lutra lutra*). *Folia Zool.* 53(1): 27–36.
- Pucek Z. (ed.) 1981: Keys to vertebrates of Poland. Mammals. *PWN-Polish Scientific Publishers, Warszawa*: 1–367.
- Romanowski J. 2006: Monitoring of the Otter recolonisation of Poland. *Hystrix It. J. Mamm. (n.s.)* 17: 37–46.
- Savage R. M. 1961: The ecology and life history of the common frog (*Rana temporaria temporaria*). *Pitman & Sons Ltd., London*.
- Sidorovich V. E. 2000: Seasonal variation in the feeding habits of riparian mustelids in river valleys of NE Belarus. *Acta Theriol.* 45: 233–242.
- Sulkava R. 1996: Diet of otters *Lutra lutra* in central Finland. *Acta Theriol.* 41: 395–408.
- Taaström H. M. & Jacobsen L. 1999: The diet of otters (*Lutra lutra* L.) in Danish freshwater habitats: comparisons of prey fish populations. *J. Zool. (Lond.)* 248: 1–13.
- Webb J. B. 1975: Food of the otter (*Lutra lutra*) on the Somerset levels. *J. Zool. (Lond.)* 177: 486–491.
- Weber J. M. 1990: Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. *J. Zool. (Lond.)* 220: 641–651.
- Wise M.H. 1980: The use of fish vertebrae in scats for estimating prey size of otters and mink. *J. Zool. (Lond.)* 192: 25–31.
- Wise M. H., Linn I. J. & Kennedy C. R. 1981: A comparison of the feeding biology of mink *Mustela vison* and otter *Lutra lutra*. *J. Zool. (Lond.)* 195: 181–213.
- Wiśniowska L. 1996: Diet of the otter (*Lutra lutra*) in fish ponds in southern Poland. *J. Wildl. Res.* 1: 272–277.