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Authors: Didenko, Alexander V., and Gurbyk, Alexander B.

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Spring diet and trophic relationships between piscivorous fishes in Kaniv Reservoir (Ukraine)

Alexander V. DIDENKO and Alexander B. GURBYK

Institute of Fisheries of the National Academy of Agrarian Sciences of Ukraine, Obukhivska St. 135, 03164 Kyiv, Ukraine; e-mail: al_didenko@yahoo.com

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Abstract. Four piscivorous fishes such as pike, *Esox lucius*, European catfish, *Silurus glanis*, pikeperch, *Sander lucioperca*, and Eurasian perch, *Perca fluviatilis*, co-occur in Kaniv Reservoir (Ukraine). In total, 47 food items were identified in their diets including remains of fish and invertebrates. Sixteen prey items were identified in pike diet including 15 fish species; 33 prey items in European catfish diet, among which 20 fish species; 21 prey items in pikeperch diet, among which 18 fish species; and 28 prey items in perch diet, among which 12 fish species. The most important prey for pike were roach, *Rutilus rutilus* (%IRI = 25.9 %), Prussian carp, *Carassius gibelio* (34.7 %), and perch (18.4 %); for catfish – roach (55.5 %) and perch (20.6 %); for pikeperch – roach (52.8 %) and perch (34.1 %); and for perch – monkey goby, *Neogobius fluviatilis* (85.7 %). Highest diet overlap indices were observed between catfish and pikeperch (84.8 %) while the lowest between catfish and perch (33.7 %). No significant difference was observed between the average sizes of fish prey in the stomachs of pikeperch and European catfish (*t*-test, $P > 0.05$), but there were significant differences between all other pairs of piscivorous species (*t*-test, $P < 0.001$).

Key words: *Esox lucius*, *Silurus glanis*, *Sander lucioperca*, *Perca fluviatilis*, fish diet

Introduction

Piscivorous fish comprise an essential component of aquatic ecosystems, playing an important top-predator regulatory role for fish community composition and food-web structure (Post et al. 1997, Juanes et al. 2002). Piscivores occupy the third or fourth trophic level and tend to stabilize fish communities by consuming the most abundant species and thus balancing all the links of the food chain (Popova & Sytina 1977). They may also depress planktivorous fish populations, thereby allowing large-bodied zooplankton to flourish, which results in relatively low phytoplankton biomass and subsequently, in higher water quality (Post et al. 1997).

The most abundant freshwater piscivorous fish in Europe are northern pike, *Esox lucius*, European catfish, *Silurus glanis*, pikeperch, *Sander lucioperca*, and Eurasian perch, *Perca fluviatilis* (Kottelat & Freyhof 2007). These fish species regularly coexist, and as piscivores, may compete for prey fish resources. However, they are native to European freshwaters and co-evolved which may have resulted in the development of feeding habits that reduce the trophic relationships between them. Multispecies interactions in fish communities have attracted increasing interest among fish scientists, including the potential for food and habitat niche separation among co-occurring species (Fortunatova & Popova 1973, Ross 1986, Kahilainen & Lehtonen 2003). Studies of piscivore diets and trophic relationships are hereby important for understanding piscivore ecology, and thereby also central for rational fisheries management and conservation biology in freshwater environments (Fortunatova & Popova 1973, Alp et al. 2008).

Piscivorous fishes such as pike, European catfish, pikeperch, and perch, are the most preferred game fish for recreational fishermen in Ukrainian freshwaters, especially in the Dnieper Rivers reservoirs, and are also highly valued targets for local commercial fisheries. According to official fishery statistics (State Agency of Fisheries of Ukraine), the commercial landings averaged 520 tons (5.2 % of the total fish catch) per year during 2009-2013. However, these numbers are underestimated due to the lack of complete landing reports (Mezhzherin 2008). The highest proportion of piscivorous fishes in commercial landings is observed in Kaniv Reservoir, where the piscivore percentage has increased from 8.2 % in 2004 to 14.0 % in 2013 (35.0 to 69.7 tons). Their average annual commercial catch in Kaniv Reservoir during 2009-2013 according to the State Agency of Fisheries of Ukraine was 36.4 ± 2.1 tons of pikeperch, 13.1 ± 1.0 tons of perch, 11.5 ± 0.4 tons of catfish, and 6.6 ± 0.6 tons of pike.

In light of the importance of piscivores as a structuring force in aquatic ecosystems, the aim of the present study is to describe and evaluate diet compositions and overlaps, prey selectivities, and trophic relationships of pike, European catfish, pikeperch and perch. The study was conducted in spring period, when spawning of both predators and their prey occur and that fact can affect their diets. The obtained results will complement and expand the information regarding these piscivorous fishes that can be used to enable sustainable fisheries and conservation development in the region.

Material and Methods

Study area

Fish samples were collected in the middle part of Kaniv Reservoir (Fig. 1). The shallow Kaniv Reservoir was created in 1972 on the River Dnieper between Kiev and Kremenchuk reservoirs within Kiev and Cherkassy regions of Ukraine (Grynzhevsky 1998). It has an area of 675 km^2, length of 123 km, maximum width of 8 km, an average depth of 3.9 m and the maximum depth of 21 m (Denisova et al. 1989). The middle part of the reservoir is relatively shallow and has many islands and areas covered by dense aquatic vegetation. According to fishery statistics, the most abundant, non-piscivorous, commercial fishes in Kaniv Reservoir in the studied years were roach, *Rutilus rutilus*, (40.0 % of the total commercial catch by weight); bream, *Abramis brama*, (13.8 %); Prussian carp, *Carassius gibelio*, (12.9 %); silver bream, *Blicca bjoerkna*, (9.0 %), and artificially stocked Chinese carps, *Hypophthalmichthys* spp., (4.7 %).

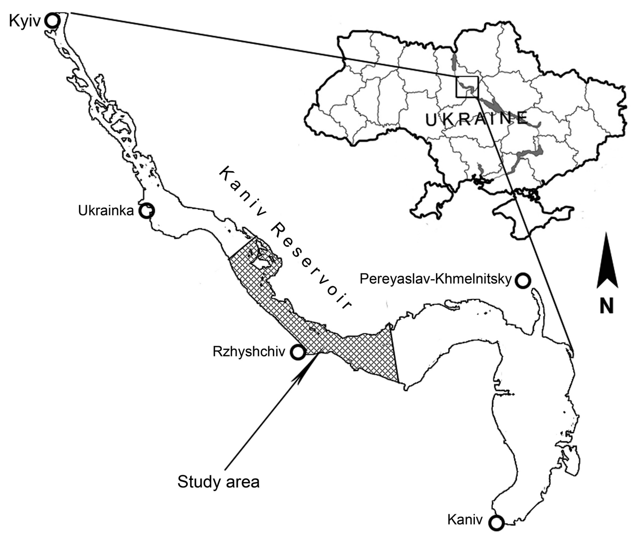

Fig. 1. Study area in Kaniv Reservoir, the River Dnieper.

Data collection

Fish were sampled with commercial gillnets (bar mesh sizes of 30, 36, 40, 45, 50, 55, 60, 65, 70, 75, 80, 90, 100, 110, 120 mm, individual lengths 70 m, heights from 1 to 4 m) during April-May of 2010-2012 and 2014. The nets were set in different habitats and depths (from approximately 1 to 7 m) on the bottom and open waters within the studied area. Nets were set in the morning (from 6:00 to 10:00) and lifted in the morning of the next day (with a fishing period of approximately 24 hours). All caught fish were immediately processed on the fish landing site. Individuals were measured to the nearest 1 cm (standard length, SL) and weighed to the nearest 10 g, gut contents of piscivorous were removed by dissection or by flushing their stomachs (Bowen 1996) and weighed to the nearest 0.01 g using electronic scales. Individual prey items were identified to the lowest possible taxonomical level, counted, measured to the nearest 1 mm SL (if possible), and weighed to the nearest 0.01 g. Overly digested and unidentifiable fish stomach contents were classified as “unidentified fish remains”. Empty stomachs were recorded but later removed from analysis.

Data processing

The wet weights of partly digested prey items were estimated using empirically established and species-specific length to weight relationships from Kaniv Reservoir collected in 2010-2012 with commercial gillnets (large species) and a 10 m beach seine with 1.0 mm mesh size (small species). Literature data (Grabowska et al. 2011, Verreycken et al. 2011) were used for some prey species, which have never been caught in the reservoir or caught in very small numbers, such as weatherfish, *Misgurnus fossilis*; Chinese sleeper, *Perccottus glenii*; ruffe, *Gymnocephalus cernuus*.

The focal piscivorous species were divided into three length groups each: pike (< 40 cm, 45-59 cm, > 59 cm), catfish (< 65 cm, 65-79 cm, > 79 cm), perch (< 20 cm, 20-24 cm, 25-29 cm, > 29 cm), pikeperch (< 40 cm, 40-54 cm, > 54 cm). Prey items from stomach samples of each piscivore-species specific length group were described as frequency of occurrence (the percentage of non-empty stomachs containing a particular prey, %FO), percentage by number (%N), percentage by weight (%W), index of relative importance (IRI = (%N + %W) × %FO), and percent index of relative importance (%IRI = 100 × IRI_i/Σ IRI_i) (Liao et al. 2001).

Paired *t*-tests were used to compare the lengths of prey fish in the stomachs of different piscivorous fishes (α = 0.05). The *t*-tests were performed by testing all possible pairs of four piscivores and comparing the lengths of all prey fish species combined. The lengths of the most abundant prey species such as roach and perch in the stomachs of pike, European catfish, and pikeperch were compared separately.

Linear regressions were used to find the relationships between predator and prey fish sizes (all prey fish combined and some most abundant prey fishes separately).

Diet overlap indices (DOI) were calculated according to the Shorygin (1952) formula:

$$DOI = \sum_{i=1}^{n} \min(a, b), \text{ where}$$

a – percent weight of a given prey item in the diet of species A; *b* – percent weight of a given prey item in the diet of species B. This index ranges from 0 % (no overlap) to 100 % (complete overlap). Diet overlap was considered significant if DOI ≥ 60 (Wallace 1981).

Partial correlations were used to examine the co-occurrence of piscivorous species, which was assumed as the number of fish of different species caught in the same gillnets per day. Only daily net catches with more than one species were used in this analysis.

All calculations and statistical evaluation were performed in MS Excel 2010 and JMP IN 4 (SAS Institute), respectively.

Results

Four piscivorous fishes comprised on average, 8.9 % by number and 19.0 % by weight, of the total catch in survey gillnets in the studied years: pike – 0.8 % by number and 4.1 % by weight, catfish – 0.8 % and 7.5 %, pikeperch – 1.9 % and 4.7 %, perch – 5.4 % and 2.8 %. The average length of the studied piscivores was 51 ± 2 cm for pike (min 33 cm, max 98 cm, n = 156), 78 ± 2 cm for European catfish (min 32, max 134 cm, n = 201), 40 ± 1 cm for pikeperch (min 15 cm, max 78 cm, n = 246), and 22 ± 1 cm for perch (min 12 cm, max 35 cm, n = 212 cm).

In total, 47 food items were identified in the diet of the focal piscivorous fishes, including remains of fish, frogs, invertebrates, and aquatic vegetation (Tables 1-4).

Pike

Stomachs of 47.4 % of pike were empty. Only vertebrate preys, including 15 different fish species

Table 1. Diet composition of pike of Kaniv Reservoir (%FO = frequency of occurrence, %IRI = percent index of relative importance).

Prey items	Length groups (cm)							
	< 44 (n = 29)		45-59 (n = 36)		> 59 (n = 17)		All lengths (n = 82)	
	%FO	%IRI	%FO	%IRI	%FO	%IRI	%FO	%IRI
Fish	96.6	99.1	100.0	100.0	100.0	100.0	98.8	99.9
Rutilus rutilus	17.2	20.4	30.6	47.3	11.8	4.1	22.0	25.9
Scardinius erythrophthalmus	13.8	8.8	13.9	8.3			11.0	5.3
Abramis brama			8.3	6.3	5.9	3.3	4.9	3.5
Blicca bjoerkna	27.6	37.6	5.6	1.7	5.9	0.9	13.4	7.8
Alburnus alburnus	3.4	0.3	5.6	1.0			3.7	0.4
Tinca tinca	3.4	1.0			5.9	0.9	2.4	0.3
Carassius gibelio	6.9	2.1	16.7	21.2	35.3	69.4	17.1	34.7
Hypophthalmichthys sp.			2.8	1.3			1.2	0.3
Neogobius fluviatilis	3.4	0.7	5.6	1.4	5.9	2.5	4.9	1.7
Neogobius melanostomus	6.9	1.6			5.9	1.3	3.7	0.6
Mesogobius batrachocephalus	3.4	1.2					1.2	0.1
Proterorhinus semilunaris	3.4	0.3	2.8	0.2			2.4	0.2
Perca fluviatilis	24.1	25.0	11.1	7.6	23.5	17.0	18.3	18.4
Sander lucioperca			8.3	3.5			3.7	0.7
Syngnathus abaster			2.8	0.2			1.2	< 0.01
Unidentified fish remains					5.9	0.6	1.2	< 0.01
Frogs	3.4	0.9					1.2	0.1

and frogs, were recorded in the diet of pike (Table 1). Roach and perch were the dominant species by the frequency of occurrence, followed by Prussian carp, silver bream, and rudd, *Scardinius erythrophthalmus*. These species also dominated numerically, but Prussian carp significantly exceeded other species by

Table 2. Diet composition of European catfish of Kaniv Reservoir (%FO = frequency of occurrence, %IRI = percent index of relative importance).

	Length groups (cm)							
Prey items	< 65 (n = 43)		65-79 (n = 61)		> 79 (n = 50)		All lengths (154)	
	%FO	%IRI	%FO	%IRI	%FO	%IRI	%FO	%IRI
Fish	88.1	83.3	93.4	90.5	92.0	96.6	90.9	92.5
Rutilus rutilus	9.3	10.8	18.0	39.8	36.0	78.0	21.4	55.5
Scardinius erythrophthalmus	2.3	0.3	8.2	5.6	6.0	0.8	5.8	2.3
Abramis brama					2.0	0.1	0.6	< 0.01
Blicca bjoerkna	2.3	0.1	1.6	< 0.01	2.0	0.1	1.9	0.1
Alburnus alburnus					2.0	< 0.01	0.6	< 0.01
Rhodeus amarus			1.6	< 0.01			0.6	< 0.01
Tinca tinca	2.3	0.3	1.6	0.1			1.3	< 0.01
Carassius gibelio	4.7	3.6			8.0	1.7	3.9	0.9
Cobitis taenia	4.7	0.7	6.6	0.5	2.0	< 0.01	4.5	0.2
Misgurnus fossilis	2.3	0.5			2.0	0.1	1.3	< 0.01
Neogobius fluviatilis	23.3	15.6	9.8	1.6	6.0	0.5	12.3	2.9
Neogobius melanostomus	18.6	14.4	14.8	6.8	8.0	1.6	13.6	5.3
Neogobius kessleri			1.6	< 0.01	2.0	0.1	1.3	< 0.01
Neogobius gymnotrachelus			6.6	0.6			2.6	0.1
Proterorhinus semilunaris	20.9	10.0	8.2	1.0	2.0	< 0.01	9.7	1.3
Perccottus glenii			1.6	0.1			0.6	< 0.01
Perca fluviatilis	16.3	25.5	26.2	28.8	22.0	11.4	22.1	20.6
Sander lucioperca	2.3	0.6	6.6	1.4	8.0	1.4	5.8	1.4
Gymnocephalus cernuus	4.7	0.6	13.1	3.1	6.0	0.6	8.4	1.3
Syngnathus abaster	2.3	0.2	4.9	0.2			2.6	0.1
Unidentified fish remains	2.3	0.1	9.8	1.0	2.0	< 0.01	5.2	0.3
Frogs	7.0	4.6	1.6	0.1	6.0	0.5	4.5	0.6
Invertebrates	23.8	11.2	29.5	9.3	22.0	2.9	25.3	6.9
Astacus leptodactylus	2.3	0.5	3.3	0.4	8.0	0.8	4.5	0.5
Spiders			1.6	< 0.01			0.6	< 0.01
Odonata larvae (Anisoptera)	7.0	0.7	4.9	0.4	2.0	< 0.01	4.5	0.3
Aphelocheirus aestivalis			3.3	0.1			1.3	< 0.01
Coleoptera larvae	2.3	0.1					0.6	< 0.01
Coleoptera imago	2.3	0.1			2.0	< 0.01	1.3	< 0.01
Dreissena polymorpha	11.6	9.8	14.8	7.6	8.0	1.9	11.7	5.9
Anodonta cygnea			4.9	0.4			1.9	< 0.01
Viviparus sp.			4.9	0.3			1.9	< 0.01
Planorbarius corneus			1.6	< 0.01	4.0	0.1	1.9	< 0.01
Plants	7.0	0.9	1.6				2.6	< 0.01
Trapa natans fruits			1.6	< 0.01			0.6	< 0.01
Other aquatic vegetation	7.0	0.9					1.9	< 0.01

weight (40.3 %), followed by roach (13.4 %), bream (13.3 %), and perch (12.6 %). Prussian carp, roach, and perch can be considered as the most important prey for pike according to the Index of Relative Importance.

Diet differed between pike length groups (Table 1). While silver bream, perch, and roach were more important in the diet of smaller pike, Prussian carp became more important in larger pike, and significantly exceeded all other species in the largest length group of pike. The share of roach in the stomach content increased with pike length up to length group 45-59 cm, but dropped drastically in the largest fish.

The length of fish prey in pike diet varied from 4.0 to 27.0 cm with an average length of 12.8 ± 0.7 cm; the average length of roach was 12.1 ± 1.2 cm and that of perch was 12.7 ± 1.5 cm. The average number of fish prey in pike stomachs was 1.3 ± 0.1. The predator-prey fish length relationship was y = 0.308x – 2.745, ($R^2 = 0.53$, $P < 0.001$) (Fig. 2); for roach prey: y = 0.193x + 2.667 ($R^2 = 0.15$, $P > 0.05$); for perch prey: y = 0.253x – 0.479 ($R^2 = 0.73$, $P < 0.001$).

European catfish

Altogether, 23.4 % of catfish stomachs were empty. Thirty-three food items, including frogs, 20 fish species, 10 taxa of invertebrates, and aquatic plants, were recorded in the diet of catfish, while fish was the dominant prey (Table 2). The most frequently encountered prey items were roach and perch, followed by round goby, *Neogobius melanostomus*, and monkey goby, *Neogobius fluviatilis*, and zebra mussel, *Dreissena polymorpha*. Roach and perch were the most important prey items by number (23.0 % and 12.4 %, respectively) and by weight (54.7 % and 15.6 %, respectively).

The share of fish prey in catfish diets increased with catfish size, albeit it was somewhat lower in the largest catfish compared to the 65-79 cm length group, while the share of invertebrates decreased (Table 2). Gobiids, especially round and monkey gobies, were the most important fish prey in the smallest catfish. The proportion of roach in the diet increased with catfish size, and was the dominant prey species in the largest catfish. Perch was a very important prey for the 65-79 cm length group, and to a lesser degree for the smaller length group (< 65 cm). Although its overall importance is comparatively low, Prussian carp also becomes more frequently encountered with increasing size of catfish. All other prey items seem to be occasional in catfish diet.

The length of fish prey in catfish diet varied from 3.0 to 29.0 cm with an average length of 9.6 ± 0.3 cm; the average length of roach was 12.0 ± 0.5 cm and that of perch was 9.4 ± 0.5 cm. The average number of fish prey in the stomachs was 3.2 ± 0.4 fish. The predator-prey fish length relationship was y = 0.196x – 5.597, ($R^2 = 0.51$, $P < 0.001$) (Fig. 2); for roach prey: y = 0.189x – 4.142 ($R^2 = 0.46$, $P < 0.001$); for perch prey: y = 0.162x – 2.534 ($R^2 = 0.51$, $P < 0.001$).

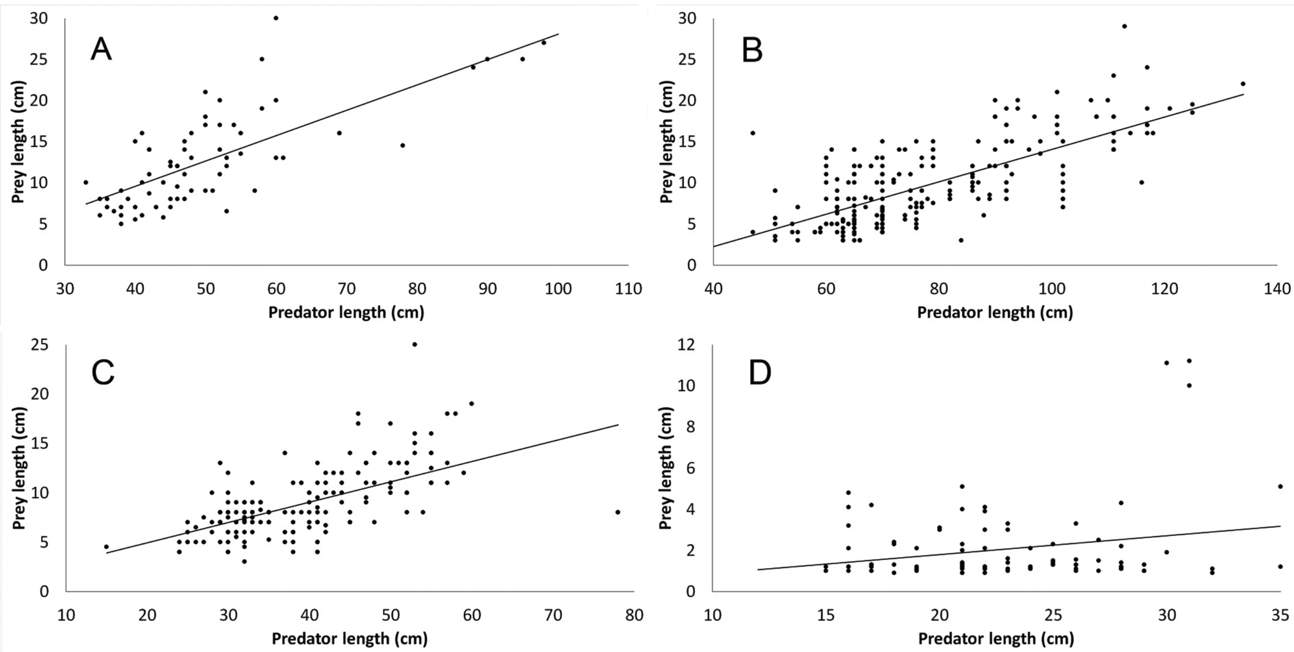

Fig. 2. Relationships between predator length and prey fish length: A – pike, B – European catfish, C – pikeperch, D – perch.

Table 3. Diet composition of pikeperch of Kaniv Reservoir (%FO = frequency of occurrence, %IRI = percent index of relative importance).

Prey items	Length groups (cm)							
	< 40 (n = 87)		40-54 (n = 54)		> 54 (n = 21)		All lengths (n = 162)	
	%FO	%IRI	%FO	%IRI	%FO	%IRI	%FO	%IRI
Fish	96.5	97.7	100.0	99.3	100.0	100.0	97.5	98.8
Clupeonella cultriventis			1.9	0.5			0.6	0.1
Rutilus rutilus	11.5	8.6	40.7	74.9	57.1	87.9	27.2	52.8
Scardinius erythrophthalmus	5.7	1.3	7.4	1.1			5.6	0.8
Blicca bjoerkna	5.7	1.3	1.9	0.1			3.7	0.4
Alburnus alburnus	4.6	0.5	7.4	2.1	4.8	0.3	5.6	1.1
Rhodeus amarus	1.1	< 0.01					0.6	< 0.01
Pelecus cultratus			1.9	0.4	4.8	0.5	1.2	0.2
Carassius gibelio			1.9	0.2			0.6	< 0.01
Cobitis taenia	2.3	0.1					1.2	< 0.01
Neogobius fluviatilis	20.7	11.1	7.4	1.2			13.6	4.4
Neogobius melanostomus	4.6	0.9	3.7	0.4			3.7	0.5
Proterorhinus semilunaris	2.3	0.1					1.2	< 0.01
Benthophilus nudus	1.1	< 0.01					0.6	< 0.01
Perca fluviatilis	42.5	70.1	16.7	10.4	28.6	9.3	32.1	34.1
Sander lucioperca	5.7	1.6	14.8	7.8	14.3	1.8	9.9	3.6
Gymnocephalus cernuus	6.9	2.0	1.9	0.1	4.8	0.2	4.9	0.7
Gymnocephalus acerina			1.9	0.1			0.6	< 0.01
Syngnathus abaster	1.1	< 0.01					0.6	< 0.01
Unidentified fish remains	1.1	< 0.01					0.6	< 0.01
Invertebrates	8.0	1.3	5.6	0.5			6.2	0.8
Dreissena polymorpha	8.0	1.3	5.6	0.5			6.2	0.8
Plants	9.3	1.0	3.7	0.2			6.2	0.5
Trapa natans fruits	1.1	< 0.01					0.6	< 0.01
Other aquatic vegetation	8.0	1.0	3.7	0.2			5.6	0.5

Pikeperch

In total, 34.1 % of pikeperch stomachs were empty. Twenty one food items, which included 18 fish species, zebra mussel, and debris of aquatic vegetation including water caltrop, *Trapa natans*, fruits were identified in pikeperch gut contents. Fish remains significantly exceeded all other food items (Table 3). Perch was the most frequently encountered prey type in pikeperch diets, followed by roach, monkey goby, and conspecific juveniles. By number, perch (23.8 %), roach (22.4 %), and monkey goby (11.2 %) significantly exceeded other species, while roach and perch were the most important by weight (54.8 % and 18.4 %, respectively).

The smallest pikeperch consumed mainly perch and monkey goby, and the share of perch and gobiids in the gut content decreased with pikeperch size, while the share of roach increased. An increase in frequency of occurrence of conspecific juveniles is observed from smaller to larger length groups of pikeperch, being almost identical in the two largest length groups. Small pikeperch become the third prey by number and frequency of occurrence, after roach and perch, in the largest pikeperch length groups.

The length of fish prey in pikeperch diet ranged from 4.0 to 25.0 cm, with an average length of 9.0 ± 0.3 cm; the average length of roach was 11.3 ± 0.5 cm and that of perch was 8.5 ± 0.3 cm. The average number of fish prey in pikeperch stomachs was 1.6 ± 0.1 fish. The predator-prey fish length relationship was $y = 0.206x + 0.837$, ($R^2 = 0.37$, $P < 0.001$) (Fig. 2); for roach prey: $y = 0.244x + 0.411$ ($R^2 = 0.46$,

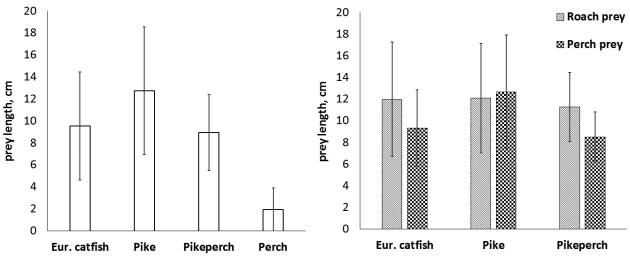

Fig. 3. Mean fish prey sizes of piscivorous fishes in Kaniv Reservoir (mean ± SD). All fish prey combined (left), roach prey and perch prey separately (right).

$P < 0.001$); for perch prey: $y = 0.189x – 1.583$ ($R^2 = 0.54$, $P < 0.001$).

Perch

Altogether, 44.8 % of perch stomachs were empty. Twenty eight food items were recorded in perch diet (Table 4), which included 12 fish species, fish eggs, 14 invertebrate taxa, and plant debris. However, fish items, among which monkey goby was the most important, significantly exceeded all other taxa. The

Table 4. Diet composition of perch of Kaniv Reservoir (%FO = frequency of occurrence, %IRI = percent index of relative importance).

Prey items	Length groups (cm)							
	< 20 (n = 36)		20-24 (n = 45)		> 24 (n = 36)		All lengths (n = 117)	
	%FO	%IRI	%FO	%IRI	%FO	%IRI	%FO	%IRI
Fish	69.4	79.6	84.4	94.5	91.7	92.7	82.1	93.2
Rutilus rutilus	2.8	0.9			16.7	10.4	6.0	2.3
Scardinius erythrophthalmus	2.8	0.3			8.3	2.0	3.4	0.5
Blicca bjoerkna			2.2	0.3	2.8	0.5	1.7	0.3
Alburnus alburnus	2.8	0.3					0.9	0.1
Cobitis taenia			4.4	0.6	2.8	0.2	2.6	0.2
Neogobius fluviatilis	38.9	69.4	57.8	90.3	44.4	73.5	47.9	85.7
Neogobius melanostomus	2.8	0.5	2.2	0.3	5.6	1.8	3.4	0.8
Proterorhinus semilunaris	11.1	6.1	2.2	0.1			4.3	0.4
Perccottus glenii			2.2	0.1			0.9	< 0.01
Perca fluviatilis	2.8	1.0	6.7	2.4	8.3	2.8	6.0	2.2
Gymnocephalus cernuus					2.8	0.1	0.9	< 0.01
Syngnathus abaster					8.3	1.0	2.6	0.1
Unidentified fish remains	5.6	1.0	4.4	0.3	2.8	0.1	4.3	0.4
Fish eggs	2.8	0.1	4.4	0.2	5.6	0.3	4.3	0.2
Invertebrates	41.7	20.1	22.2	4.5	19.4	4.7	25.6	5.5
Astacus leptodactylus			6.7	0.6	5.6	0.4	4.3	0.3
Gammarus sp.	2.8	0.1					0.9	< 0.01
Asellus aquaticus	2.8	0.3					0.9	< 0.01
Odonata larvae (Anisoptera)	8.3	1.3	4.4	1.1			4.3	0.6
Odonata larvae (Zygoptera)	2.8	0.4					0.9	< 0.01
Notonecta glauca	2.8	0.4					0.9	< 0.01
Coleoptera larvae					2.8	0.1	0.9	< 0.01
Chironomidae larvae	2.8	0.2					0.9	< 0.01
Dreissena polymorpha	8.3	1.5	2.2	0.1	11.1	2.7	6.8	1.0
Gastropoda	8.3	3.6	2.2	0.1	5.6	1.5	5.1	1.2
Oligochaeta	2.8	0.2					0.9	< 0.01
Hirudinea	16.7	11.8	8.9	2.5			8.5	2.2
Nematomorpha	2.8	0.1					0.9	< 0.01
Bryozoa			2.2	0.1			0.9	< 0.01
Aquatic plants	2.8	0.3	6.7	1.0	11.1	2.6	6.8	1.3

Table 5. Diet overlaps of four piscivorous fishes in Kaniv Reservoir.

Fish species	European catfish	Perch	Pikeperch
Pike	42.2	34.5	35.9
European catfish		33.7	84.8
Perch			33.5

second and third prey by weight after monkey goby (38.1 %) were juvenile roach and perch (13.3 % and 11.5 %, respectively), but the most important prey by number were monkey goby (37.2 %), gastropods (9.2 %), and leeches (7.6 %).

The importance of monkey goby is the highest in the length group 20-24 cm, and slightly decreases in importance for larger perch. The share of leeches is the highest in the smallest perch group, and leeches virtually disappear from the perch diet in two largest length groups. At the same time, there is an increase in the importance of roach, conspecific juveniles, and zebra mussel with increasing perch sizes.

The length of fish prey in perch diets ranged from 1.0 to 11.2 cm, with an average length of 1.9 ± 0.2 cm. The average number of fish prey in perch stomachs was 1.5 ± 0.1. The predator-prey fish length relationship was $y = 0.096x - 0.258$, ($R^2 = 0.05$, $P = 0.031$) (Fig. 2); for monkey goby prey: $y = 0.018x + 1.351$ ($R^2 = 0.005$, $P > 0.05$).

Comparison of prey sizes

No significant difference was observed between the average sizes of fish prey in the stomachs of pikeperch and European catfish (*t*-test, $P > 0.05$) (Fig. 3). There were however significant differences between all other pairs of piscivorous species (*t*-test, $P < 0.001$). As for individual species, no significant differences were observed between the average sizes of roach prey in the stomachs of all examined piscivores (*t*-test, $P > 0.05$), while the average length of perch prey somewhat differed between pikeperch and pike (*t*-test, $P = 0.015$) and between catfish and pike (*t*-test, $P = 0.045$), but not between pikeperch and catfish (*t*-test, $P > 0.05$).

Diet overlaps

The diet overlaps between European catfish and pikeperch can be considered significant (Table 5) mainly due to high prevalence of roach, while the lowest values were observed between perch and pikeperch and between perch and catfish. As for different length groups, the highest diet overlap indices were recorded between the largest size group of European catfish and 40-54 cm and > 54 cm pikeperch (79.3 % and 75.8 %, respectively). The lowest values of the diet overlap indices were recorded between the largest size group of pike and 40-54 cm and > 54 cm pikeperch (0.3 % and 0.1 %, respectively).

Co-occurrence of piscivorous fishes

Only pike and perch showed some positive relationship between their numbers caught in the same gillnets per day ($R^2 = 0.88$, $P = 0.021$) indicating that they inhabited the same biotopes. Other pairs of species did not show such significant correlations ($P > 0.05$), however, the relationship between European catfish and pikeperch was very close to be positively significant ($R^2 = 0.81$, $P = 0.054$).

Discussion

The piscivorous habits of pike, European catfish, pikeperch and perch have been demonstrated in a variety of studies (Fortunatova & Popova 1973, Popova & Sytina 1977, Diana 1979, Mann 1982, Kahilainen & Lehtonen 2003, Kangur & Kangur 2009), however their prey species composition varies in different areas. Among the studied piscivorous fishes, pike and pikeperch can be considered as exclusive predators at adult age in spring in Kaniv Reservoir, while European catfish and perch also fed on invertebrates.

Significant numbers of the studied species, especially pike and perch, had empty stomachs, which is quite common in predatory fish (Diana 1979, Kahilainen & Lehtonen 2003, Kangur & Kangur 2009). Such a peculiarity may be related to the fact that data were collected during spawning period, when these fishes, e.g. pike and perch, reduce their feeding activity (Diana 1979, Dörner et al. 2003). Pike and perch spawned earlier than catfish and pikeperch and almost the entire sampling period took place within or after spawning of the first two species. Moreover, large numbers of fish with empty stomachs may be also related to their collection method (gillnets), which is a very stressing factor causing some piscivores to regurgitate their stomach contents (Sutton et al. 2004).

Among the observed prey items, species such as roach, rudd, silver bream, bleak, monkey goby, perch, and black-striped pipefish, *Syngnathus abaster*, were found in the stomachs of all studied piscivorous fishes, however with different prevalence and importance. While roach and perch were the most important prey items for pike, catfish, and pikeperch, monkey goby comprised a significant part of the gut content of perch and smaller size groups of catfish and pikeperch.

Roach were the most important prey for the studied predators in spring (except for perch), perhaps especially during spawning when they aggregate and probably are less cautious and consequently more vulnerable to predation. In addition, roach has a body size and morphology that makes it readily accessible to piscivores (Fortunatova & Popova 1973). Roach when gathered in large spawning shoals were also the major prey item for pike in the River Vistula (Horoszewicz 1964) and for piscivorous fish in the Volga Delta and Rybinsk Reservoir, where some piscivores, e.g. perch and pikeperch, obtain up to 40-80 % of their annual ration during this period (Fortunatova & Popova 1973, Popova & Sytina 1977).

The second important prey of European catfish and pikeperch in Kaniv Reservoir was perch and this species is one of the main prey items for piscivorous fishes in many European freshwaters (Eklöv & Hamrin 1989, Peltonen et al. 1996, Keskinen & Marjomäki 2004, Kangur & Kangur 2009).

Deep-bodied species such as Prussian carp and bream were found only in pike and catfish diets (however, one occurrence of Prussian carp was observed in one pikeperch stomach), the piscivores with gape sizes large enough to consume these prey items (Fortunatova & Popova 1973, Nilsson & Brönmark 2000, Wysujack & Mehner 2005). However, small sized silver bream, another deep-bodied fish, were found in the stomachs of all examined piscivores. The frequency of occurrence of rudd was higher in pike diets compared to other piscivores, potentially due to overlap in choice of habitat such as vegetated shallow areas (Cook & Bergersen 1988). Bleak being the most abundant small sized fish in Kaniv Reservoir (Tsedyk 2000, Aleksienko et al. 2013) comprised a very insignificant part of piscivores' diets. This was probably due to its lower vulnerability as it is very fast swimmer compared to less abundant but slower percids and gobiids. Bleak is also very rarely eaten by piscivorous fish in Finnish lakes (Peltonen et al. 1996). Juvenile pikeperch were consumed by all studied species except perch, for which they were too large. They have an elongated shallow body shape and are probably relatively abundant in the reservoir, making them easy prey for piscivores. Although cannibalism is quite common in predatory fishes and it becomes more important with increasing body size of the predator (Popova & Sytina 1977, Grimm 1981, Mann 1982, Kahilainen & Lehtonen 2003, Kangur & Kangur 2009, Kopp et al. 2009), cannibalism was observed only in pikeperch and perch in Kaniv Reservoir, probably because juvenile pikeperch and perch are smaller and more abundant than other juvenile piscivores. Moreover, data were collected during spawning period of other prey fishes, which become aggregated and more vulnerable for predation.

Among the studied piscivorous fishes of Kaniv Reservoir, European catfish was characterized by having the highest diet diversity. This species is considered to be a more opportunistic fish than the other predators in European freshwater ecosystems (Syväranta 2010), and its dietary spectrum is greater, allowing it to include a wider variety of food items (Bekbergenov & Sagitov 1984). Crayfish plays an important role in catfish diet (Czarnecki et al. 2003, Wysujack & Mehner 2005, Carol et al. 2009), although crayfish contents were low in this study that may be due to their low number in the study area or to the availability of more preferred prey. Among invertebrates, zebra mussel was the most important prey to catfish.

Rare findings of plant objects in the diet of the studied fishes are probably accidental items swallowed together with the prey. Records of water caltrop fruits and zebra mussel in pikeperch stomachs may be due to the fact that this fish may instinctively catch relatively large objects moving in water. These objects, which are very common in the studied part of Kaniv Reservoir, are thrown away, sometimes in large quantities, by fishermen when they clean gillnets aboard their fishing boats. Moreover, they can be also attached to gillnets and float in water. Rare findings of zebra mussel shells in pike and pikeperch stomachs were also observed in the Lake Peipsi, Estonia (Kangur & Kangur 2009).

A comparison of the diet composition of four piscivorous fishes such as pike, European catfish, pikeperch and perch, demonstrated shifts in prey choice between piscivore's length groups (Fortunatova & Popova 1973, Mann 1982, Wysujack & Mehner 2005, Kangur & Kangur 2009). For instance, pike shifted from roach and rudd to Prussian carp and perch with increasing body size; European catfish shifted from gobiids and zebra mussel to roach and perch, and then roach becomes the most important prey in the largest catfish; pikeperch shifted from perch and gobiids to roach; and perch shifted from gobiids and invertebrates to gobiids and juvenile roach.

All species showed a positive prey-predator length relationship that has been observed also in other studies (Nilsson & Brönmark 2000, Kahilainen & Lehtonen 2003, Dörner 2007). While a positive predator-prey length relationship was found for pike, no significant relationship was found for roach prey that may be related to the fact that large pike often took both small and large roach prey. However, a more significant relationship was observed between pike and perch prey lengths, as perch were less abundant in the diet of 45-59 cm pike being one of dominating prey item in the smallest (small sized perch) and largest (large sized perch) length groups of pike. Pike, compared to pikeperch and perch, are capable of consuming larger fish. The average lengths of roach (12.1 cm) and perch (12.7 cm) prey in pike diet in Kaniv Reservoir are different from those in the Lake Peipsi (16.6 and 10.2 cm, respectively) (Kangur & Kangur 2009).

As for European catfish, despite the fact that this species had significantly larger average body size than all other piscivorous fishes in the reservoir, the average size of its fish prey was similar to that of pikeperch and significantly smaller than that of pike, indicating that it consumed mainly small prey such as coarse and juvenile fish. Such a peculiarity of eating relatively smaller fish than other piscivores despite a large gape size was also mentioned by Wysujack & Mehner (2005) for the Feldberger Haussee in Germany.

Pikeperch is a gape-limited predator (Salonen et al. 1996), and deep-bodied prey fish such as Prussian carp, bream, silver bream and rudd were very infrequent or absent in pikeperch diet. Small pikeperch in Finland eat small and elongated species such as smelt and bleak, while the larger ones feed on roach and perch (Peltonen et al. 1996). The same is partially true for pikeperch in Kaniv Reservoir, where small pikeperch consumed mainly small, elongated gobiids, while roach become more important in the diet of larger pikeperch. However, perch were more important prey in smaller length groups of pikeperch.

The coefficient of determination (R^2) of the predator-prey length relationship for pikeperch is relatively low (0.37) indicating high variation in size selectivity that is probably due to gape-limitation of this species, when shorter relatively deep-bodied fishes can have the same body depth as longer shallow-bodied fish. R^2 values are slightly higher when only one prey species is accounted for (e.g. 0.46 for roach and 0.54 for perch), and among all studied predatory species it was observed only for pikeperch. The average lengths of roach (11.3 cm) and perch (8.5 cm) preys in pikeperch diet in Kaniv Reservoir are very similar to those in the Lake Peipsi (11.4 and 7.9 cm, respectively) (Kangur & Kangur 2009).

Among the investigated species, the highest diet overlap was observed between European catfish and pikeperch, possibly indicating foraging competition between these species in the spring period. In addition to overlap in prey species, they consumed similar sizes of prey, including roach and perch. The highest diet overlap index between predatory fish in the lower River Volga was also observed between catfish and pikeperch (up to 69.5 %) as well as between catfish and pike (up to 64.9 %), while the lowest values were observed between pike and pikeperch (43.6-47.8), and the majority of their diet overlaps was due to roach (Fortunatova & Popova 1973).

Such high values of diet overlaps between catfish and pikeperch in the studied periods can be related to spawning peculiarities of predatory fishes in Kaniv Reservoir. As it was mentioned above, pike and perch spawn earlier and many of them do not eat for some period of time after spawning, and in such a way they show reduced activity during the mass spawning run of roach, which usually occurs from the end of April to the beginning of May. Such a spawning fasting and reduction of feeding activity in late April was also observed in pike in North America (Diana 1979) and in perch in German and Danish lakes (Dörner et al. 2003). At the same time, pikeperch and catfish, that spawn later, actively feed on roach during this period resulting in high diet overlap indices. This fact may also contribute to the reduction of foraging competition between pike and other piscivorous species and at the same time to the reduction of predation intensity on spawning roach.

Low diet overlap indices were usually observed between the smallest and largest length groups of piscivorous fishes of the same species due to consumption of different prey items, potentially to reduce intraspecific competition. At the same time, perch and juvenile pikeperch are prey to cannibals and other predatory fishes, resulting in predator-prey interactions between them.

Despite the high diet overlap indices between pikeperch and European catfish, the level of the competition for food can be reduced as these species have different feeding habits and occupy different habitats. For instance, catfish is characterized by nocturnal activity (Boujard 1995, Carol et al. 2007), while pikeperch and pike are more active in the morning and evening crepuscular period (Fortunatova & Popova 1973, Cook & Bergersen 1988). Pike and European catfish are considered to be ambush predators, while pikeperch and large perch are prey pursuers (Stolbunov & Pavlov 2006). Pike, as well as perch, prefer shallow, vegetated areas (Popova & Sytina 1977, Cook & Bergersen 1988, Greenberg 1995) while pikeperch avoid vegetation and stay offshore in open areas of lakes and reservoirs (Fortunatova & Popova 1973, Popova & Sytina 1977, Kangur & Kangur 2009). Pike usually has a higher predation rate in the presence of vegetation, whereas pikeperch have a higher predation rate in the absence of vegetation (Greenberg et al. 1995). The European catfish is characterized by the use of different bottom habitats from deep sites of the reservoir main channel to shallow littoral habitats, with resting places within dense vegetation or in areas over-grown with bulrushes and tree roots (Fortunatova & Popova 1973, Carol et al. 2007). In Kaniv Reservoir, pike and perch preferred shallow vegetated areas, where they co-occurred, but their diet overlap index was relatively low, indicating the absence of high forage competition between them. At the same time, perch was an important prey item for pike. Pikeperch were mainly caught offshore in deeper waters and often in the same gillnets with European catfish and considering a high diet overlap between these species they can be competitors. However, catfish occupied a higher diversity of habitats during the study period as they were caught not only in deep waters but also often in shallow vegetated areas, where they preyed on spawning fish. Such a wide distribution of catfish in the reservoir, as well as its nocturnal activity (Boujard 1995), may contribute to the reduction of forage competition with other piscivores, especially with pikeperch, with which it has the highest diet overlap indices, at least during the study period.

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