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Diet seasonality and food overlap of *Perca fluviatilis* (Actinopterygii: Perciformes: Percidae) and *Rutilus rutilus* (Actinopterygii: Cypriniformes: Cyprinidae) juveniles: A case study on Bovan Reservoir, Serbia

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Abstract

European perch, *Perca fluviatilis* Linnaeus, 1758 and roach, *Rutilus rutilus* (Linnaeus, 1758) are the most common species present in mesotrophic and eutrophic lakes throughout Europe. Their biomass, especially in juvenile stages, contributes the most to the fish production of these ecosystems. In Bovan Reservoir, these two species constitute the bulk of the juvenile fish biomass. This study aimed to investigate the feeding composition of these two species in order to evaluate their niche overlap due to the availability of resources during different seasons. Traditional diet analysis indices and Kohonen artificial neural network (i.e., a self-organizing map, SOM) were used to investigate the diet of 158 individuals of both species and evaluate their food niche overlap. The indicator value (IndVal) was applied to identify indicator food categories based on which the contents of their alimentary tracts were grouped first into neurons and then into clusters on the SOM. Our results showed that juvenile fish used zooplankton and benthic prey in their diet. Roach often fed on nonanimal prey, while perch of age 0+ used fishes in the diet. Additionally, four clusters of neurons were isolated on the SOM output network. The distribution of perch and roach alimentary tracts in neurons indicated no high degree of competition between them. While diet analyses indices show which food category is generally important in specimens' diet, the SOM recognizes those specimens and arranges them together into the same or adjacent neurons based on dominant prey. Understanding fish feeding habits is critical for the development of conservation and management plans. Since Bovan is a eutrophic reservoir, our knowledge of fish feeding habits needs to be considered for stocking strategies in the future.

Keywords

feeding overlap, IndVal index, perch, roach, self-organizing map

Introduction

Dietary analysis has been used for decades in biological and ecological studies of different fish species (Manoel and Azevedo-Santos 2018). Fishes live in quite variable environments where the availability of resources varies in time and space (Nurminen et al. 2010). The feeding spectrum and share of actively feeding specimens depend to a great extent on the season (Gerasimov et al. 2018), so the seasonal differences are evident in the diet of the majority of fish species (Specziár and Erős 2014). Considering juvenile fish, seasonal shifts in the diet are usually a trade-off between prey abundance and increasing body size, which allows individuals to target larger prey (Gopalan et al. 1998). It is widely accepted that the ecology of fish feeding in the first year of life is a critical period in fish life histories (Bogacka-Kapusta and Kapusta 2010). Fishes change habitats or prey types during their ontogeny, and they are often exposed to the selection pressure on important morphological and behavioral traits at different life stages (Werner 1988). Juvenile fish are particularly susceptible to fluctuations in food availability. Thus, Dinh et al. (2017) noted that the study on the variation of food types consumed by fish at different seasons and sizes is critically important for improving our understanding of fish adaptations to their environment and habitat changes.

Studies of diet in fish assemblages at a certain location allow us to recognize distinctive trophic guilds and make inferences about their structure, the degree of importance of the different trophic levels, and the relations among their components (Novakowski et al. 2008). The ecological theory predicts that species belonging to the same ecological guild can coexist only if there are differences in their responses to the limited availability of resources. This theory also suggests that competition is an important interaction between species when the resources are scarce (Begon et al. 1996). That can affect patterns of habitat selection, niche overlap, and diet activity (David et al. 2007). Understanding the biological mechanisms, such as trophic relations, through which species interact with one another is the basis of many ecological studies, from dietary research to the elaboration of food web models (Costalago et al. 2014).

Perch, *Perca fluviatilis* Linnaeus, 1758, and roach, *Rutilus rutilus* (Linnaeus, 1758), are two fish species cohabiting the littoral zone in many European lakes (Syväranta and Jones 2008). They were selected for this study as they constitute the bulk of the young-of-the-year fish biomass in Bovan Reservoir and play a significant role in the food chain since they are intermediates between the lower stages of the food chain and predatory fish (Persson and De Roos 2012). This study aimed to investigate the feeding composition of these two species to evaluate their niche overlap due to the availability of resources during different seasons. A further aim was the assessment of the efficiency of combining the Kohonen unsupervised artificial neural network, i.e., a self-organizing map (Kohonen 1982) and IndVal index (Dufrêne and Legendre 1997) for the analysis of data regarding perch and roach diets. Self-organizing maps and IndVal index, which are widely used in biocenology, have previously been applied only twice (Dukowska et al. 2013, 2014) in ecological studies of a fish diet. This is the first study that presents fish diet assessment combining traditional diet analysis indices (Hyslop 1980; Hickley et al. 1994) and self-organizing maps.

Methods

Study area and fish sampling. Bovan is an artificial reservoir situated in the middle flow of the Sokobanjska Moravica River near the municipality of Aleksinac in southeast (43°38′46″N, 021°42′28″E) (Fig. 1). Its surface area is 4 km^2, maximum depth 50 m, and maximum width 500 m. The reservoir was formed from 1978 to 1984 in Bovanska Gorge as a multifunctional system, with the primary aim to regulate the Morava River basin and protect the Đerdap I reservoir. Its important functions are to maintain sludge and flooding waves, enrich small waters, as well as produce hydro-energy. Initially, it was not planned for a water supply. However, due to its great potential, the water treatment plant was added, and the reservoir nowadays supplies drinking water to the population of the region (Zlatković et al. 2010). Bovan is a eutrophic reservoir (Simić et al. 2006), and the fish community consists mainly of common bream, *Abramis brama* (Linnaeus, 1758); perch; pikeperch, *Sander lucioperca* (Linnaeus, 1758); roach; and Prussian carp, *Carassius gibelio* (Bloch, 1782) (see Pavlović et al. 2015). Detailed qualitative and quantitative analyses of zooplankton and bottom fauna, which represents available food for fishes in the study area, were given by Ostojić (2006) and Simić et al. (2006). The authors stated that analysis of zooplankton composition established the presence of taxa from groups Protozoa, Rotatoria, Cladocera, and Copepoda. On the other hand, the greatest number of species in the bottom fauna was recorded for groups Oligochaeta and Chironomidae.

The field-work was conducted in May and September of 2011 and 2012. Fish were sampled using gillnets of mesh size 10 mm. For each analyzed fish, the total length (TL) was measured to the nearest mm and then weighted (W) to the nearest g. Studies of fish diet, feeding ecology, and food habits are carried out commonly through dissection and examination of alimentary tracts (Hynes 1950; Hyslop 1980). Immediately after the capture and measuring, fish were preserved in 4% formalin and transported to the laboratory, where alimentary tracts were removed, transferred to a Petri dish, and analyzed under binoculars. Prey items were identified to the lowest possible taxonomic level, counted under binoculars, and preserved in 70% ethanol.

Alimentary tract content analysis. Shannon's diversity index (H) was used to assess the prey diversity of the dietary contents in each fish species during all seasons. The index was calculated as

$$H = -\Sigma(p_i)(\ln p_i)$$

where p_i is the proportion of individuals belonging to the ith species relative to the total number of individual prey items recovered for a fish species (Magurran 1988).

To determinate the most important prey in the diet, the Prominence Value (PV) of the dietary component was calculated using the following formulas (Hickley et al. 1994; Lorenzoni et al. 2002):

$$\mathrm{PV} = \%N\sqrt{(\%\mathrm{FO})}$$

$$\%\mathrm{PV} = 100\mathrm{PV} \cdot \Sigma\mathrm{PV}^{-1}$$

where %FO is the frequency of occurrence (the number of alimentary tracts containing each food item in relation to the total number of alimentary tracts with food), and %N is relative abundance (the number of individuals of each food item with respect to the total number of individuals). The vacuity index (%VI) was used to express a number of empty alimentary tracts (Hyslop 1980).

To interpret the species' feeding strategy, the Costello (1990) graphical method modified by Amundsen et al. (1996) was applied, in which prey-specific abundance of each food category is plotted against the frequency of occurrence (%FO) on a two-dimensional graph. In this approach, prey-specific abundance was calculated as

$$P_i = 100\Sigma S_i \cdot \Sigma S_{ti}^{-1}$$

where P_i is the prey-specific abundance of prey i; S_i is the alimentary tract content (by number) comprised of prey i, and S_{ti} is the total alimentary tract content in only those fish with prey i in their alimentary tracts. In the graph, prey items positioned in the upper part of the graph show a specialist feeding strategy of the fish, and those positioned in the lower part indicate a generalist feeding strategy of the fish. Besides, the diet specialization was estimated by the diet evenness index (E)

$$E = H \cdot H_{\max}^{-1}$$

where $H_{\max} = \ln S$, and S is the total number of preys in the sample. According to Oscoz et al. (2005) values close to zero mean a stenophagous diet and those closer to one represent an euryphagous diet. The evenness index was employed together with modified Costello's graphical method.

Diet similarity among different species of fish, or the same species during different seasons, was assessed using Schoener's overlap index (α). It was evaluated using the Prominence value (PV) of each food item (Lorenzoni et al. 2002) according to the following formula (Schoener 1970):

$$\alpha = 1 - 0.5(\Sigma|\mathrm{PV}_{xi} - \mathrm{PV}_{yi}|)$$

where PV_{xi} is prominence values of food item i in species x, PV_{yi} is prominence values of food item i in species y. The index has a minimum of 0 (no overlap), and a maximum of 1 (complete overlap). According to Wallace (1981), a value 0.6 or higher may be considered to be evidence of significant overlap.

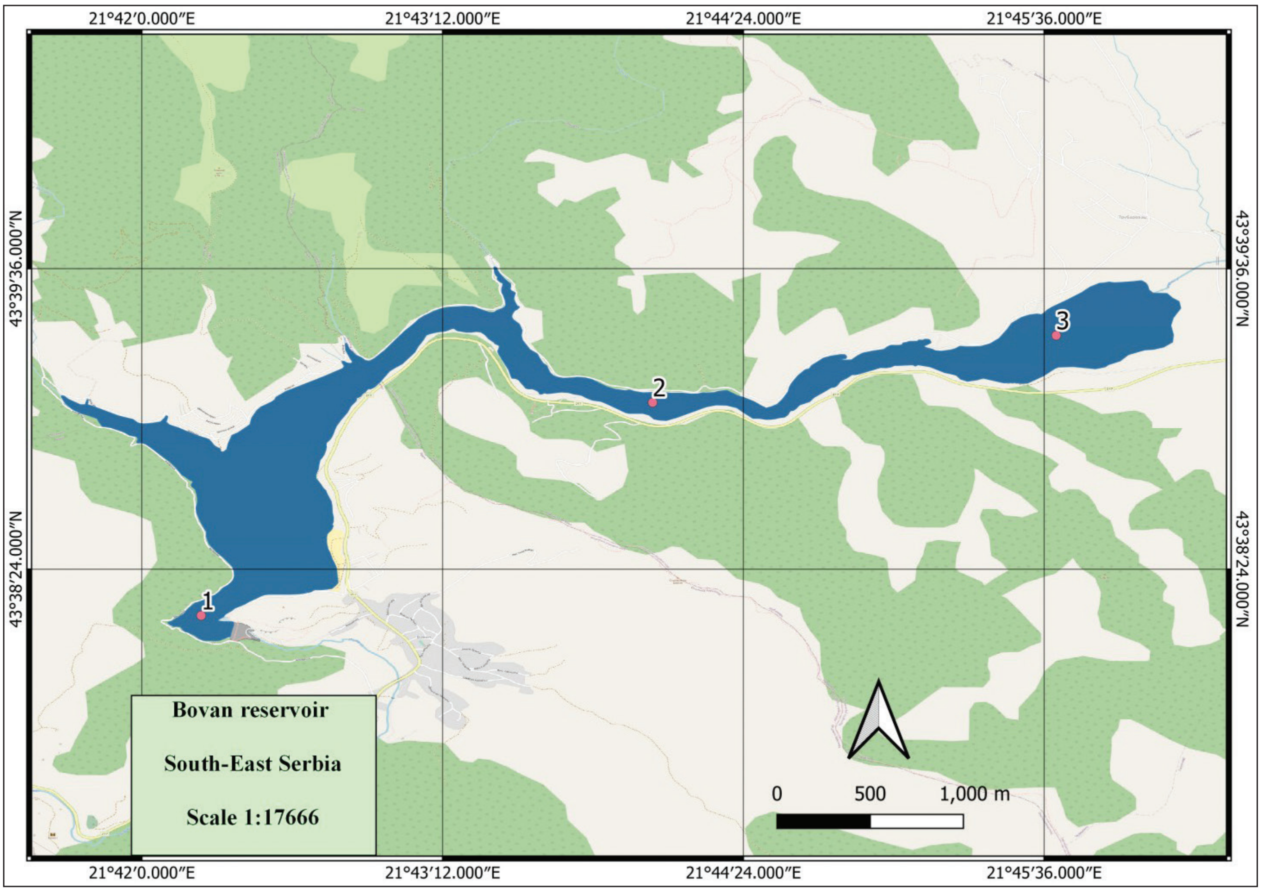

Figure 1. Map of Bovan Reservoir, southeast Serbia. Numbers on the map represent sampling sites, 1 = dam, 2 = middle part of the reservoir, and 3 = lower part of the reservoir.

Statistical data analysis. Analysis of alimentary tract content allows us to determine species' diet composition and further understand their feeding habits and trophic role in the ecosystem (Cailliet et al. 1986). On the other hand, data obtained from alimentary tracts could be noisy because many fragmented and/or digested elements cannot be identified. Moreover, it is rare that the amount of a given food category recorded in alimentary tracts equals the amount of a given food category eaten (Dukowska et al. 2013). Kohonen's unsupervised artificial neural network (i.e., a self-organizing map, SOM) (Kohonen 1982) is resistant to the noise in data (Lek and Guégan 1999; Park et al. 2006). In this work, we used them to determine patterns in the content of the alimentary tracts. The SOM technique is a useful method for the clustering and visualization of large data sets (Penczak et al. 2012; Stojković et al. 2013). It can visualize and explore linear and nonlinear relations in the high-dimensional data set.

The network structure of the SOM is composed of two layers, the input and output, each consisting of data processing units, i.e., neurons (Kohonen 1982, 2001). The input for the SOM is the input matrix. In our study, it consisted of 130 columns (one column represented one alimentary tract) and 26 rows (one row represented one prey taxa). The relative abundance data of prey taxa from the alimentary tracts of fish were log-transformed ($\log(x + 1)$), normalized, and scaled from 0 to 1. Each input neuron was sent through the network throughout the learning process. During the learning process of the SOM network, an alimentary tract content was created in each output neuron. All these neurons present the output layer represented by a codebook matrix. It consists of two-dimensional grids, where the differences between neurons, i.e., models carried by the neurons, increased in accordance with mutual distance increase. The total variability observed in the data set was covered by models from all neurons (Penczak et al. 2006). To distinguish subsets of neurons and subdivide them into clusters on the SOM map, the *k*-means method was used (Jain and Dubes 1988). The map resolution (number of output neurons) is an important parameter for the detection of deviation in the data. If the resolution is wrong, for example, too low or too high, the differences are too small for a plausible interpretation (Céréghino and Park 2009). Since there is no conventional theoretical method for determining the best optimal map resolution, we used the two most recommended methods. The first method, proposed by Vesanto et al. (2000), implies that the optimal number of neurons in the map should be close to 5 square roots of 5 where *n* is the number of training samples. The alternative method (Park et al. 2003) indicates that the optimal resolution is determined by considering the local minimum quantization error (QE) and topographic error (TE). Using these methods and trying to avoid a large number of empty output neurons (Penczak et al. 2012), we found that a 7 × 7 grid is most appropriate for our study. The SOM Toolbox also generated a visualization of the associations of food categories with SOM regions (sub-clusters of neurons) represented by shades of gray but not for the statistical verification of those associations (Lek et al. 2005). The SOM analysis was carried out using the Matlab ver. 6.1.0.450 algorithm interface (http://www.cis.hut.fi/projects/somtoolbox).

Since SOM is a visualization technique without any statistical indication, the indicator value (IndVal) by Dufrêne and Legendre (1997) was used to identify indicator food categories significantly associated with each cluster of SOM output neurons. An IndVal of the food category (*i*) in all alimentary tracts of each SOM cluster (*j*) was calculated as the product of A_{ij} (the relative abundance in % calculated as the mean mass of the food category (*i*) in the alimentary tracts of cluster (*j*) divided by the sum of the food category mean masses in all the clusters in the study) and F_{ij} (the relative frequency of occurrence of the food category (*i*) in the alimentary tracts of cluster (*j*) also expressed as a %), as follows:

$$A_{ij} = M_{ij} \cdot M_i^{-1}$$

$$F_{ij} = \mathrm{NAT}_{ij} \cdot \mathrm{NAT}_j^{-1}$$

$$\mathrm{IndVal}_{ij} = 100 A_{ij} F_{ij}$$

where M_{ij} is mean value of mass of food category (*i*) in the alimentary tracts of cluster (*j*), M_i is mean value of mass of food category (*i*), NAT_{ij} is the relative frequency of occurrence of food category (*i*) in the alimentary tracts of cluster (*j*), NAT_j is the relative frequency of occurrence of all food categories of cluster (*j*), A_i is the relative abundance in percentage (%), and F_{ij} is the relative frequency of occurrence in percentage (%) of food category (*i*) in the alimentary tracts of cluster (*j*).

The Monte Carlo significance test with 1000 permutations was applied to identify significant prey taxa with the use of PC-ORD statistical software (McCune and Mefford 2011). All indicator species with an IndVal score over 25 were interpreted as representative prey taxa of a particular group, with a relative frequency and abundance of at least 50%.

Results

A total number of 130 individuals, with 7.4–11.2 cm in TL, were used to examine diet composition. The number of analyzed specimens by season was as follows: 23 specimens for perch in spring 2011, 20 specimens in autumn 2011, then 17 specimens in spring 2012, and 12 specimens in autumn 2012. The number of analyzed specimens of roach was the same in the spring of both years (18 specimens), then in autumn of 2011 (15 specimens), and finally in the autumn of 2012 (7 specimens). Fish with empty alimentary tracts (28 individuals) were excluded (%VI = 17.72).

Values of the frequency of occurrence (%FO), relative abundance (%*N*), and prominence value (%PV) for each

Table 1. Assessment of diet composition of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 from Bovan Reservoir, Serbia, expressed as relative abundance (%*N*), frequency of occurrence (%FO), and prominence value (%PV) of food.

Taxon or group	Spring 2011						Autumn 2011					
	Perch			Roach			Perch			Roach		
	%*N*	%FO	%PV	%*N*	%FO	%PV	%*N*	%FO	%PV	%*N*	%FO	%PV
Protozoa	2.06	26.08	1.22	—	—	—	0.83	20.00	0.43	—	—	—
Rhizopoda	—	—	—	2.63	11.11	1.14	—	—	—	5.61	20.00	3.32
Rotatoria	0.51	4.34	0.12	2.63	5.55	0.81	—	—	—	3.57	6.66	1.22
Bryozoa	6.92	30.43	4.45	—	—	—	7.61	30.00	4.88	4.08	6.66	1.39
Hydracarina	0.07	4.34	0.01	—	—	—	1.39	25.00	0.81	—	—	—
Ostracoda	2.35	43.47	1.81	10.52	55.55	10.24	5.47	75.00	5.55	6.12	53.33	5.92
Anostraca	—	—	—	—	—	—	—	—	—	—	—	—
Conchostraca	0.88	13.04	0.37	—	—	—	0.18	5.00	0.04	—	—	—
Notostraca	—	—	—	—	—	—	—	—	—	—	—	—
Cladocera	0.22	4.34	0.05	—	—	—	0.37	5.00	0.09	—	—	—
Daphnia sp.	5.15	26.08	3.07	14.73	88.88	18.14	1.11	10.00	0.41	11.73	86.66	14.46
Bosmina sp.	6.84	73.91	6.86	25.78	88.88	31.75	8.72	80.00	9.14	24.48	93.33	31.32
Leptodora kindtii	0.88	17.39	0.42	—	—	—	0.09	5.00	0.02	—	—	—
Calanoida (Copepoda)	27.54	100.0	32.17	12.63	55.55	12.29	21.63	85.00	23.38	14.28	66.66	15.44
Cyclopoida (Copepoda)	35.42	95.65	40.46	20.00	55.55	19.47	43.63	90.00	48.53	18.87	66.66	20.40
Isopoda	0.07	4.34	0.01	—	—	—	—	—	—	—	—	—
Amphipoda	5.59	73.91	5.61	1.57	5.55	0.48	4.82	65.00	4.55	—	—	—
Gammaridae	0.07	4.34	0.01	—	—	—	—	—	—	—	—	—
Insecta (other)	—	—	—	—	—	—	0.09	5.00	0.02	—	—	—
Diptera (other)	—	—	—	—	—	—	0.27	5.00	0.07	—	—	—
Chironomidae	3.97	34.78	2.73	1.05	11.11	0.45	3.24	25.00	1.89	0.51	6.66	0.17
Plecoptera	0.58	8.69	0.19	—	—	—	—	—	—	—	—	—
Ephemeroptera	—	—	—	—	—	—	0.18	5.00	0.04	—	—	—
Trichoptera	0.07	4.34	0.01	—	—	—	0.09	5.00	0.02	—	—	—
Oligochaeta	0.07	4.34	0.01	8.42	22.22	5.18	0.18	5.00	0.04	10.71	20.00	6.34
Fishes	0.66	17.39	0.32	—	—	—	—	—	—	—	—	—
Detritus	—	94.44	—	—	33.33	—	—	—	—	—	100.0	—

food category found in alimentary tracts of analyzed fish are presented in Tables 1 and 2. Prey items included 27 different taxa, but they were not all represented as prey in both species during different seasons. Additionally, detritus was excluded from the calculation because the remains of animal and plant materials have degraded to a large extent, so it was not possible to put them into any category. Small crustaceans belonging to Ostracoda, Calanoida, Cyclopoida, and Cladocera were food categories consumed by both analyzed species throughout the studied seasons, but to a different extent.

The most varied diet was recorded in perch caught in the spring of 2011 ($H = 2.05$), with even 21 different prey categories detected, while the perch caught in the autumn of 2012 had the least varied diet (15 different prey categories, $H = 1.63$). Organisms categorized as Protozoa, Bryozoa, Ostracoda, *Bosmina* sp. and *Daphnia* sp. cladocerans, Calanoida, and Cyclopoida copepods, then Amphipoda, and Chironomidae, were the most common prey of all perch, but their proportion in the diet varied from season to season. Calanoid copepods were present in all analyzed perch alimentary tracts caught in spring 2011 and 2012, while cyclopoid copepods were present in all analyzed perch samples caught in autumn 2012. Only perch specimens caught in the spring of 2011 used fish fry in their diet as well as detritus and isopod crustaceans. The similarity in the diet of the analyzed perch was suggested by the high values of Schoener's overlap index (α from 0.87 to 0.95, Table 3).

Roach did not have a varied diet as perch, and, within species, they had quite a uniform diet during different seasons. Out of, in total, 12 identified prey categories in the diet of roach caught in spring 2011 and 2012, and in autumn 2011, there were as many as 11 prey categories ($H = 1.75$–1.9). Roach caught in autumn 2012 had the least diverse diet (seven prey categories, $H = 1.55$). Rhizopoda was the only prey present in the roach diet, but not in the perch diet. The most frequent food categories in the roach diet were members of the class Ostracoda, Calanoida, and Cyclopoida, as well as *Daphnia* sp. and *Bosmina* sp. (%FO $\geq$ 50 in all studied seasons) (Tables 1 and 2). In autumn 2012, *Daphnia* sp. and *Bosmina* sp. were present in all analyzed alimentary tracts of roach. Schoener's overlap index showed that the roach had a very similar diet during all seasons. However, roach (sampled in spring 2012) had significant index values with all other analyzed specimens of roach as well as perch from other seasons (Table 3).

The modified Costello graphic showed mostly a generalized feeding strategy in studied fish including some specimens that specialized on certain prey items (Fig. 2). In perch, the graphic analysis revealed that the feeding strategy of this species was a generalist feeder as all of the prey items were positioned in the lower part of the graph. Only Cyclopoida stood out according to the higher frequency of occurrence and prey-specific abundance values in relation to other prey items. Rare preys are also

Table 2. Assessment of diet composition of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2012 from Bovan Reservoir, Serbia, expressed as relative abundance (%*N*), frequency of occurrence (%FO), and prominence value (%PV) of food.

Taxon or group	Spring 2012						Autumn 2012					
	Perch			Roach			Perch			Roach		
	%*N*	%FO	%PV	%*N*	%FO	%PV	%*N*	%FO	%PV	%*N*	%FO	%PV
Protozoa	2.73	35.29	1.84	—	—	—	0.83	25.00	0.48	—	—	—
Rhizopoda	—	—	—	2.95	16.66	0.84	—	—	—	—	—	—
Rotatoria	0.91	5.88	0.25	1.68	5.55	0.47	—	—	—	—	—	—
Bryozoa	6.66	35.29	4.49	2.95	5.55	0.83	8.22	25.00	4.82	—	—	—
Hydracarina	0.10	5.88	0.02	—	—	—	0.97	16.66	0.46	—	—	—
Ostracoda	1.82	29.41	1.12	7.59	50.00	6.46	4.87	50.00	4.03	6.25	71.43	5.74
Anostraca	0.10	5.88	0.02	—	—	—	—	—	—	—	—	—
Conchostraca	—	—	—	—	—	—	0.69	8.33	0.23	—	—	—
Notostraca	—	—	—	—	—	—	0.97	8.33	0.32	—	—	—
Cladocera	—	—	—	—	—	—	1.11	8.33	0.37	—	—	—
Daphnia sp.	3.23	17.64	1.54	18.98	94.44	22.21	2.08	8.33	0.70	16.66	100.0	18.11
Bosmina sp.	4.54	70.58	4.33	18.98	94.44	22.21	5.29	83.33	5.66	36.45	100.0	39.62
Leptodora kindtii	0.20	5.88	0.05	—	—	—	—	—	—	—	—	—
Calanoida (Copepoda)	26.36	100	29.94	17.72	77.77	18.81	23.67	91.66	26.58	9.37	71.43	8.61
Cyclopoida (Copepoda)	42.93	94.12	47.30	25.32	77.77	26.88	39.97	100.0	46.89	22.92	85.71	23.06
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	5.85	94.12	6.44	—	—	—	5.57	83.33	5.96	—	—	—
Gammaridae	—	—	—	—	—	—	—	—	—	—	—	—
Insecta (other)	0.10	5.88	0.02	—	—	—	—	—	—	—	—	—
Diptera (other)	0.10	5.88	0.02	—	—	—	—	—	—	—	—	—
Chironomidae	4.04	29.41	2.48	1.68	11.11	0.67	4.45	33.33	3.01	—	—	—
Plecoptera	0.30	5.88	0.08	—	—	—	0.83	8.33	0.28	—	—	—
Ephemeroptera	—	—	—	—	—	—	—	—	—	—	—	—
Trichoptera	—	—	—	—	—	—	—	—	—	—	—	—
Oligochaeta	—	—	—	2.11	5.55	0.59	0.42	8.33	0.14	8.33	28.57	4.84
Fishes	—	—	—	—	—	—	—	—	—	—	—	—
Detritus	—	—	—	—	100.0	—	—	—	—	—	100.0	—

Table 3. Schoener's overlap index (α) for the whole sample of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 and 2012 from Bovan Reservoir, Serbia. The codes provided include P or R for fish species (perch or roach, respectively), the year (2011 and 2012) and the season (S for spring and A for autumn).

α	P2011S	R2011S	P2011A	R2011A	P2012S	R2012S	P2012A	R2012A
P2011S	—	0.54	0.87	0.58	0.93	0.65	0.94	0.65
	R2011S	—	0.31	0.93	0.49	0.84	0.54	0.86
		P2011A	—	0.61	0.89	0.68	0.95	0.54
			R2011A	—	0.56	0.84	0.57	0.83
				P2012S	—	0.61	0.93	0.46
					R2012S	—	0.54	0.83
						P2012A	—	0.50

present in the perch diet, which are located at the lower-left corner on the graph. Similarly, the graphic analysis indicated the generalist feeding strategy of roach as most prey items were at the lower part of the graph, with two exceptions of Rotatoria (autumn 2011) and Oligochaeta (autumn 2011, and spring 2012) at the upper left corner of the graph. Evenness index confirmed these results (perch 0.49 ± 0.01; roach 0.38 ± 0.01).

Four clusters of neurons (A, B, C, and D) were isolated on the SOM output network (Fig. 3). The alimentary tracts of all analyzed roach were distributed in clusters A and B. Cluster A contained two samples of perch (both sampled in autumn 2011), and cluster B had four samples of perch (without any specimen in spring 2011). Clusters C and D exclusively contained perch alimentary tracts. Cluster B had the largest number of neurons, while cluster D had the largest number of samples. In cluster A, the most numerous were alimentary tracts of the roach sampled in spring 2011 (ten samples), while the least numerous were alimentary tracts of the roach sampled in the autumn of 2012, with only one sample. According to samples within, cluster B was the most diverse. In that group, the most numerous were alimentary tracts of roach, sampled in spring 2012. Clusters C and D contained the alimentary tracts of perch sampled in spring and autumn during both study years. In both clusters, the most numerous were the alimentary tracts sampled in spring 2011, while the least numerous were those sampled in autumn 2012.

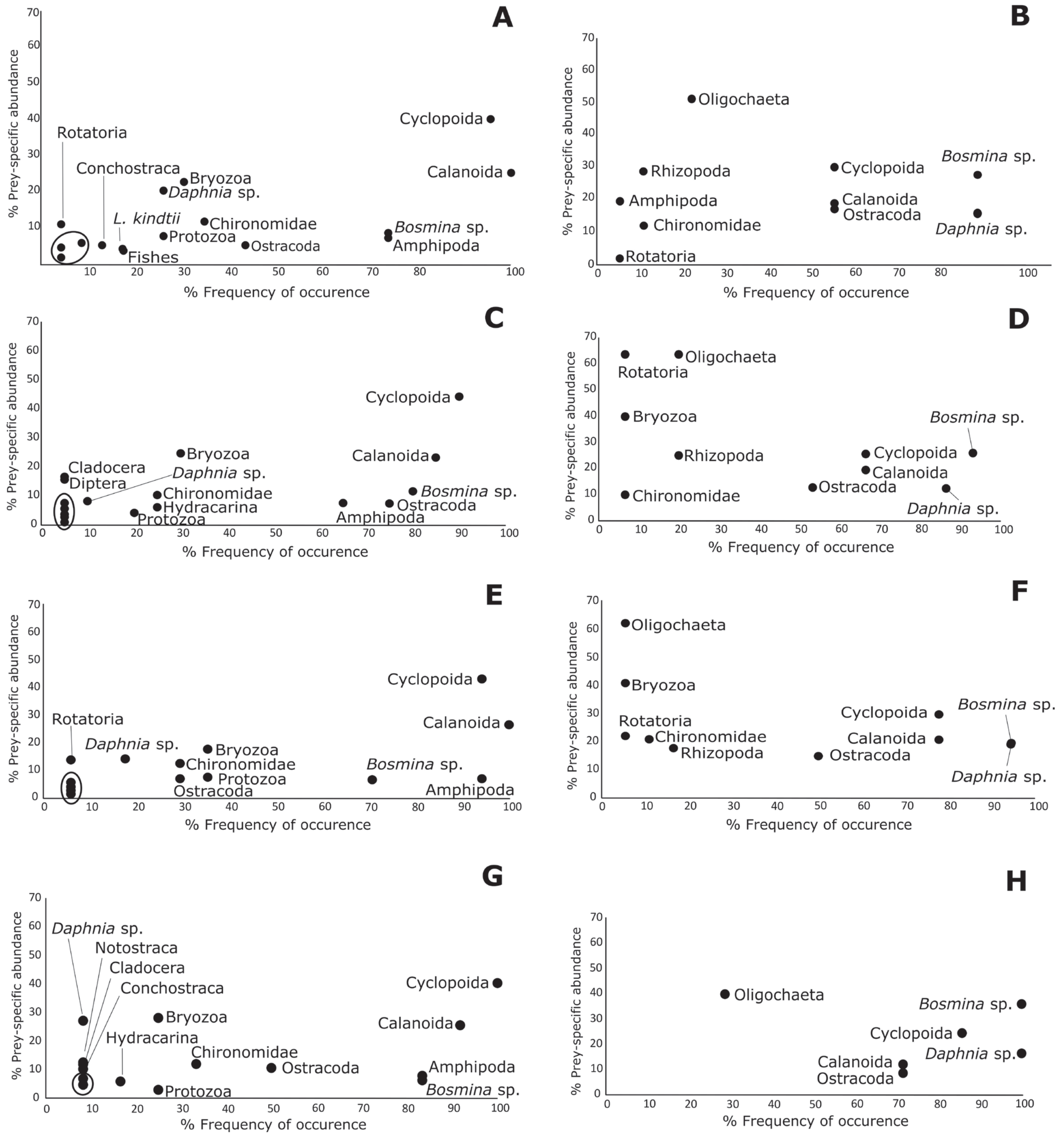

Figure 2. Costello graph. Prey-specific abundance vs. frequency of occurrence the diet of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 and 2012 from Bovan Reservoir, Serbia. (**A**) perch spring 2011, (**B**) roach spring 2011, (**C**) perch autumn 2011, (**D**) roach autumn 2011, (**E**) perch spring 2012, (**F**) roach spring 2012, (**G**) perch autumn 2012, (**H**) roach autumn 2012. Rare preys are encircled.

Significant IndVal values were recorded for 10 out of 26 food categories (Table 4, Fig. 4). One food category was significantly associated with alimentary tracts assigned to cluster A, two food categories for alimentary tracts of cluster B, six food categories for cluster C and five food categories for cluster D. Three out of 10 food categories (Cyclopoida, Calanoida, and Amphipoda) were significant for specimens whose alimentary tracts were assigned to clusters C and D, while *Bosmina* sp. were significant for specimens in clusters B and D. Oligochaeta were significant prey for specimens from cluster A and *Daphnia* sp. for specimens from cluster B. Nevertheless, they both were completely absent in the alimentary tracts of specimens assigned to cluster C. Also, Protozoa and Chironomidae were significant prey for specimens in cluster C, whereas they were absent in the alimentary tracts of specimens distributed in cluster B. On the other hand, *Bosmina* sp. were present in all the alimentary tracts of specimens assigned to cluster B, whereas Cyclopoida were also present in all the alimentary tracts of specimens assigned to clusters C and D (Table 4).

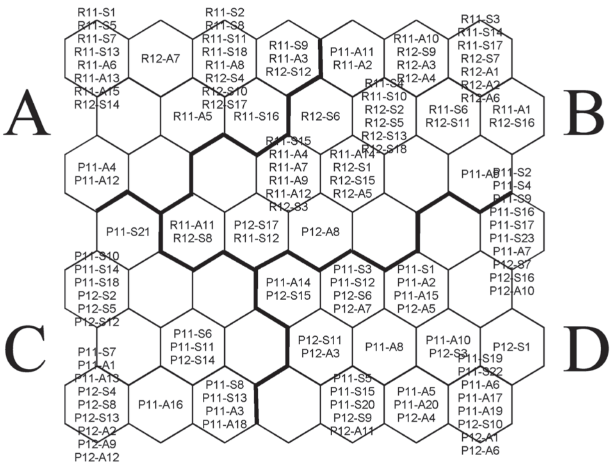

Figure 3. The 130 alimentary tracts of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 and 2012 from Bovan Reservoir, Serbia, assigned to 49 (7 × 7) SOM output neurons within clusters **A**, **B**, **C**, and **D**. The code for each alimentary tract consists of one letter for the fish species (P or R), two digits for the year of sampling 11 (2011) or 12 (2012), one letter for sampling season (S = spring or A = autumn) and the ordinal number of the individual.

Discussion

In this study, we have analyzed the food interactions between perch and roach juveniles. Although general food categories consumed by perch and roach were similar, each species had its own predominant prey items during different seasons. In general, perch changes diet during ontogeny by feeding on zooplankton, macroinvertebrates, and fish (Rezsu and Specziár 2006). In contrast, roach does not undergo notable ontogenetic dietary shifts and is considered a more efficient planktivore than perch (Werner and Gilliam 1984). There have been many papers on juvenile perch and roach diet with, in general, contradictory opinions. Persson et al. (2000), and Estlander et al. (2010) claimed that these two species have the same preferences for zooplankton, while Rezsu and Specziár (2006) and Schleuter and Eckmann (2008) stated that they have different food preferences.

Zooplankton is the essential diet of fish fry (Karus et al. 2014), and this was observed in our research. Based on the Prominence values, the food categories presented in the diet of both species throughout the entire study period were Ostracoda, *Daphnia* sp., *Bosmina* sp., Calanoida, and Cyclopoida, but in different proportions. The Prominence value showed that only roach caught in autumn 2012 had in each alimentary tract *Bosmina* sp. and *Daphnia* sp. It is noticeable in our study that perch in each of the studied seasons more often used *Bosmina* sp. than *Daphnia* sp. in the diet. This result is similar to the findings of Mehner et al. (1995, 1998), who noted that perch tend to consume small cladocerans. Frankiewicz and Frankiewicz-Wojtal (2012) and Evtimova et al. (2015) had the opposite opinion and stated that perch more often use large cladocerans such as *Daphnia* sp. in their diet. Despite these opposing views, the reason for perch consuming smaller rather than large cladocerans may be the significantly higher number of cladocerans of the genus *Bosmina* than the genus *Daphnia* in Bovan Reservoir (Ostojić 2006). According to Tarvainen et al. (2002), Vašek et al. (2006), and Peterka and Matěna (2009), zooplankton is the main food of 0+ roach. This statement agrees with our results, but among zooplankton *Bosmina* sp. stood out as the most dominant prey of roach during all studied seasons.

In Bovan Reservoir, consumption of cladocerans was higher in roach than in perch and, in contrast, perch was more likely to feed on amphipods and copepods (Cyclopoida and Calanoida) than roach. This is also indicated by Okun and Mehner (2005). Zapletal et al. (2014) reported that roach consumed far fewer copepods, while Kornijów et al. (2005) noted that copepods were not part of roach

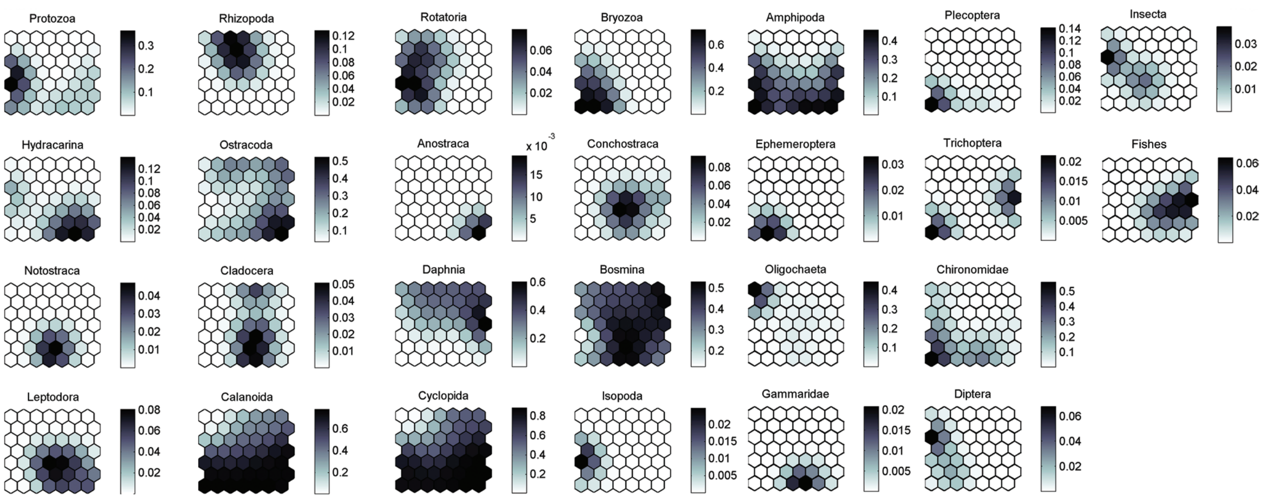

Figure 4. Distribution pattern for 26 food categories represented in the diet of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 and 2012 from Bovan Reservoir, Serbia. The shading is scaled independently for each food category. The shade of black for each food category is highly correlated with the values of the IndVal index. The degree of shading decrease is also indicated by a decline in the values of the IndVal index.

Table 4. Relative frequency (%FO), relative abundance (%*N*), and indicator values (IndVal) for food categories of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) collected in 2011 and 2012 from Bovan Reservoir, Serbia. The highest (at $P \leq 0.05$) IndVal in a given cluster (A, B, C, D) are in bold (exact significance levels are presented in Fig. 3) (modified according to Dukowska et al. 2013, 2014).

Fish diet group	A			B			C			D		
	%FO	%*N*	IndVal	%FO	%*N*	IndVal	%FO	%*N*	IndVal	%FO	%*N*	IndVal
Protozoa	4	3	0	0	0	0	43	73	**32**	18	23	4
Rhizopoda	17	51	9	10	0	5	0	0	0	0	0	0
Rotatoria	4	27	1	3	9	0	9	64	6	0	0	0
Bryozoa	4	2	0	5	3	0	87	91	**79**	2	4	0
Hydracarina	4	7	0	0	0	0	4	7	0	16	85	14
Ostracoda	54	20	11	59	18	11	26	14	4	59	48	**28**
Anostraca	0	0	0	0	0	0	0	0	0	2	100	2
Conchostraca	0	0	0	0	0	0	0	0	0	11	100	11
Notostraca	0	0	0	0	0	0	0	0	0	2	100	2
Cladocera	0	0	0	3	29	1	0	0	0	5	71	3
Daphnia sp.	75	25	19	92	32	**29**	0	0	0	25	43	11
Bosmina sp.	83	18	15	100	32	**32**	43	18	8	93	33	**31**
Leptodora kindtii	0	0	0	0	0	0	0	0	0	14	100	14
Calanoida	17	1	0	95	10	9	96	43	**42**	98	46	**45**
Cyclopoida	17	0	0	97	10	10	100	39	**39**	100	50	**50**
Isopoda	0	0	0	0	0	0	4	100	4	0	0	0
Amphipoda	8	5	0	5	1	0	83	45	**37**	77	48	**37**
Gammaridae	0	0	0	0	0	0	0	0	0	2	100	2
Insecta (other)	4	65	3	0	0	0	0	0	0	2	35	1
Diptera (other)	4	5	3	0	0	0	4	74	1	0	21	0
Chironomidae	21	5	1	0	0	0	57	74	**42**	20	21	4
Plecoptera	0	0	0	0	0	0	13	97	13	2	3	0
Ephemeroptera	0	0	0	0	0	0	4	100	4	0	0	0
Trichoptera	0	0	0	0	0	0	0	0	0	5	100	5
Oligochaeta	38	85	**32**	3	9	0	0	0	0	7	6	0
Fishes	0	0	0	0	0	0	0	0	0	9	100	9

diet. Copepods rarely occur in planktivorous fish diets, such as roach, because of their ability to escape from predators (Peterka and Matěna 2009; Karus et al. 2014). Also, Prominence values are higher for Cyclopoida than for Calanoida, although all perch specimens from the spring of both years had Calanoida in their alimentary tract content.

The large cladoceran *Leptodora kindtii* is also an important food component in the roach and perch diet (Vašek and Kubečka 2004; Vašek et al. 2006). This does not coincide with our results since *L. kindtii* has not been found in any of the alimentary tracts of the roach, and perch rarely used it in the diet. For perch as a visually oriented predator (Persson and Greenberg 1990), it is difficult to catch because of its transparency due to its extremely reduced body elements (predator defense strategy) (Liu and Uiblein 1996). However, even with the low Prominence values, it was detected in the perch diet in all studied seasons, except autumn 2012.

In general, our results showed that macroinvertebrates constituted a minor fraction of the food items found in the perch and roach alimentary tracts. The majority of juvenile perch fed on chironomids (Mehner et al. 1995, 1998), while roach fed on chironomids and Odonata larvae (Bogacka-Kapusta and Kapusta 2007). Adamczuk and Mieczan (2015) noted that juvenile specimens of both species showed the same high preference for chironomids. Our results supported this statement because chironomids were the prey of both species during all studied seasons (except roach in autumn 2012). According to Simić et al. (2006) chironomids are very abundant in Bovan Reservoir bottom fauna. Also, Oligochaeta were not recorded in the perch diet only in the spring of 2012 and throughout the research, the Prominence value was low. According to Kornijów et al. (2005), only a few roach included macroinvertebrates (mainly ephemeropteran and trichopteran larvae, seldom chironomid larvae) in their diet despite the high biomass of these prey. It could be concluded that only a few perch included macroinvertebrates such as Plecoptera, Ephemeroptera, and Trichoptera larvae, in their diet. A small and sporadic presence of these organisms in the perch diet can be assumed from the Prominence value.

During the investigated seasons, detritus was also present in the diet of juvenile perch, but to a much lower extent than in the juvenile roach diet. It was possible to detect its presence in the diet but not to quantify it, except with frequency of occurrence, the values of which were high. The importance of detritus in the roach diet has been noted by Kornijów et al. (2005) and Zapletal et al. (2014). According to Matěna (1995, 1998), the roach diet changes according to the ontogenetic stage, with the proportion of macrophytes and detritus increasing as the fish gets older. On the contrary, Lyagina (1972) and Vøllestad (1985) referred that a high proportion of detritus in the roach diet indicates the low availability of animal prey.

Also, according to Brandl (1994), roach consumed detritus before the increase of cladoceran abundance.

This study showed that the roach has better competitive abilities for cladocerans than juvenile perch. It results in a shift in feeding preferences of juvenile perch and thereafter increased competition with older perch and additionally decreased growth and recruitment to the piscivorous stage (Persson and Greenberg 1990). This is not rare, and during this research, the occurrence of 0+ perch feeding on fish was recorded. This was recorded only in the spring of 2011. Perch can feed on increasingly larger prey as gape size increases (Romare 2000) and can reach their piscivorous niche in their first growing season (Borcherding et al. 2000; Rezsu and Specziár 2006; Schleuter and Eckmann 2008). This phenomenon is useful because it is known that piscivorous juvenile perch have one of the key roles in contributing to water transparency in many lakes and reservoirs (Shapiro 1980; Gulati et al. 2008; Jacobsen et al. 2014).

The modified Costello's method suggests that some of the analyzed specimens specialized on certain types of prey, whereas the entire sample seems to have a generalized feeding strategy. This can be deduced from the fact that a few prey items have a high prey-specific abundance (%P_i) and low frequency of occurrence (%FO). Roach is considered a generalist feeder with the exception of specialization on Oligochaeta and Rotatoria. According to Costello's graph, for some roach specimens, Oligochaeta were of great importance during the whole investigation, with the exception of autumn 2012 (%$Pi < 50$). The explanation for this is the dominance of Oligochaeta in Bovan Reservoir bottom fauna (Simić et al. 2006). The generalist feeding strategy in perch is likely associated with its opportunistic feeding behavior that feeds on the most available and abundant prey in a given time and place (Gerking 1994). According to Costello's graph, Cyclopoida are positioned nearest the upper right corner during all seasons, while *Daphnia* sp. (autumn 2012) approached the upper left corner. Also, in the lower-left corner rare or unimportant preys are placed (Amundsen et al. 1996).

Due to the different degrees of digestion, information on the alimentary tracts' contents may consist of only general food categories (i.e., higher taxonomic levels) or may be identified to the lowest possible taxonomic level. If we decide to uniform the data and present the alimentary tracts' contents "roughly" or on the other hand in detail this would result in losing information on a large part of the alimentary tracts' content (Marszał et al. 1996, 1998), and could result in methodological errors, too (Dukowska et al. 2013). For these reasons, self-organizing maps could be useful in fish feeding analysis because they easily deal with nonlinear variables that are related in a complex way and that exhibit normal or skewed distributions (Lek et al. 2005; Dukowska et al. 2013).

First, there were two groups of roach specimens assigned to clusters A and B, and two groups of perch specimens assigned to clusters C and D. Those in cluster A benefited from Oligochaeta, which were used during the whole study as reflected in significant IndVal. Specimens in cluster B during all study periods most often fed on cladocerans *Bosmina* sp. and *Daphnia* sp., which is proved by significant IndVal values. All perch and roach specimens from the most diverse cluster B had *Bosmina* sp. in their alimentary tracts. Perch assigned to cluster C focused on Chironomidae and zooplankton, including Protozoa and Bryozoa (IndVal significant only for cluster C), while those in cluster D ate mostly zooplankton. Also, it is visible in cluster C that no specimens consumed *Daphnia* sp. Copepods played an important role in the diet of perch, as indicated by significant IndVals. Additionally, each specimen distributed in clusters C and D had Cyclopoida in its alimentary tract. Protozoa, Bryozoa, Ostracoda, and Amphipoda are good examples of the advantage of self-organizing maps and IndVal in relation to traditional index Prominence value. IndVal for these groups is significant only for cluster C, only for cluster D, or both, while the Prominence value for these preys is low throughout the whole research. This distribution of specimens' alimentary tracts in neurons indicates that there was no high degree of competition between perch and roach, and the segregation between them was strict. The value of Schoener's niche overlap index found in this research was indicating an almost total diet overlap within the species, as also visually shown by the results obtained using self-organizing maps, where all roach and only six specimens of perch were classified into clusters A and B. All other specimens of perch were in clusters C and D. Low trophic overlap is expected for these two species that seem to use this strategy to allow their coexistence in high abundance in Bovan Reservoir. Seasonality significantly affected both species' diet composition, indicating the different proportions of food resources between periods because similar food categories were present during all seasons, but IndVal singles out certain food categories as significant.

Self-organizing maps have proven to be most suitable for application over complex and nonlinear ecological data and are particularly suitable for application over large data sets (Kruk et al. 2007; Chon 2011; Penczak et al. 2012). Compared to various methods of linear ordination, self-organizing maps provide a better overview of community planning in ecological studies (Giraudel and Lek 2001). As Dukowska et al. (2013, 2014) stated, the diet analysis presented in this way increases the credibility of the obtained data. This is important because there were food categories used in both species' diets but represented to a lesser extent or only represented in single specimens. Presentation of fish diet in this way provided a clearer picture of the trophic relations within and between species in Bovan Reservoir.

This study shows the diet analysis based on traditional indices, which have been used for decades, and the diet analysis presented using self-organizing maps and IndVal. Comparing the results obtained in these two ways, the impression is that results are very similar or even identical. The high Prominence values and separation of certain preys on Costello's graph (upper right corner) show which preys are dominant. This is confirmed by significant IndVal. Also, there are preys like Protozoa, Bryozoa, Ostracoda, Amphipoda, and Chironomidae that are positioned in the middle of Costello's graph all the time, and the Prominence values are not particularly high or low. For these preys IndVal values are significant, and the specimens that consume them are together in a cluster on the SOM map, which means that these preys are important only for certain specimens, and not for the whole population. Oligochaeta are a good example, too. They are important prey for certain roach specimens based on Costello's graph, and IndVal is significant for them. All these specimens are arranged in cluster A. Also, there are, in the perch diet, rare or unimportant preys, for which the Prominence values are low, and on a graph, they are in the lower-left corner. Consequently, these specimens are arranged in the same cluster, and IndVal values are insignificant. Likewise, the SOM output network visually shows the results of Schoener's niche overlap index too, where the separation between species is clearly seen. It appears that the IndVal shows the same results as the Prominence value and Costello's graph, while the SOM output network shows whether there is an overlap in diet between specimens or species, as do the Schoener's niche overlap index.

Conclusions

Our results showed that juvenile fish used in diet both zooplankton and macrozoobenthos specimens; roach often fed on nonanimal prey, while perch of age 0+ also used fish in their diet. However, both species play an important role in the food web of ecosystems. Thus, the presented study provides a basis for further research on the feeding biology of these two species. Moreover, integrating these results with those previously published could be used to draw up a common strategy for managing the reservoir fish stock.

In summary, this study offers valuable insights into the dietary strategies of perch and roach. However, fish feeding analysis using self-organizing maps provides a more complete insight into the fish feeding habits, and thus the similarities and differences between them. Because as the distance in the network increases, the differences in models assigned to the neurons also increase. One neuron can contain data from several samples (i.e., specimens), and therefore there is certainly a high degree of their dietary similarity. In the end, it should be mentioned that with the identification of the alimentary tract contents, which is a complex and time-consuming process, especially in juveniles, self-organizing maps in combination with the IndVal index represents an adequate and time-saving analysis.

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