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The diet of predatory fish in drinking water reservoirs – how can they contribute to biomanipulation efforts?

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Abstract. Efforts to positively influence ecological processes and water quality by manipulating the fish community (biomanipulation) are of particular importance in drinking water reservoirs. One of the principle measures employed is to increase the abundance of predatory fish species as a means of reducing planktonophagous and benthophagous cyprinids. However, there is little information available on the effectiveness of different predatory fish in biomanipulation exercises. We examined the diet of the five dominant predatory species (pike *Esox lucius*, zander *Sander lucioperca*, asp *Leuciscus aspius*, European catfish *Silurus glanis*, and perch *Perca fluviatilis*) in five representative reservoirs in the Morava River drainage basin (Czech Republic). Fish prey made up 75 % of total food intake, with undesirable small cyprinids dominant by biomass (40 %). European catfish and asp were not taken as prey and showed no sign of cannibalism. On the other hand, predation on conspecific predatory species (including cannibalism) was relatively high in perch, pike and zander, thereby reducing their net benefit overall. This little-considered aspect of predatory feeding needs to be taken into consideration in future biomanipulation stocking strategies.

Key words: food habits, *Esox lucius*, *Sander lucioperca*, *Leuciscus aspius*, *Perca fluviatilis*, *Silurus glanis*

Introduction

Biomanipulation is a process that aims to positively influence ecological processes and water quality in lakes and reservoirs by manipulating the food-web (Mehner et al. 2002, Vašek et al. 2013). In effect, phytoplankton development is reduced through changes to the fish community (fish stock), principally by reducing populations of planktonophagous and benthophagous species, particularly roach *Rutilus rutilus* L., common bream *Abramis brama* L., silver bream *Blicca bjoerkna* L., rudd *Scardinius erythrophthalmus* L., and gibel carp *Carassius gibelio* (Bloch), be it by direct removal of such undesirable fish or through suppression by stocking predators. By reducing the abundance of planktonophagous fish, grazing pressure on zooplankton is limited, allowing development of larger filtering zooplankton (i.e. cladocerans of the genus *Daphnia* in particular) that effectively eliminates small planktonic algae from the water column, ultimately leading to increased water transparency. Biomanipulation, therefore, represents targeted influencing of the lower components of the food chain through a hierarchically higher link of the aquatic food chain, i.e. fish. In a broader sense, biomanipulation efforts also tend to focus on reducing benthivorous fish in addition to planktonophagous species (Jurajda et al. 2016), whose feeding habits may support eutrophication processes in reservoirs through bioturbation (Adámek & Maršálek 2013). In the Czech Republic, there are a number of ongoing biomanipulation projects aimed at improving water quality in drinking water reservoirs through ecological measures rather than through chemical intervention. As early as 1978, a framework range of stocking densities was defined for Czech reservoirs (Lusk & Vostradovský 1978) and, more recently, Seďa et al. (2000) proposed additional stocking of > 5 kg of piscivorous fish per hectare annually in order to ensure efficient biomanipulation impact. In order to assess the effectiveness of such measures, however, and for effective planning of future biomanipulation measures, it is essential to have a good knowledge of the current state of fish stocks in each reservoir. To address this, Jurajda et al. (2018) undertook a series of comprehensive ichthyological surveys at five representative drinking water reservoirs between 2016

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and 2017. At the same time, samples of predatory fish were taken for dietary analysis. Here, we assess the diet and feeding strategies of individual predatory species in the reservoirs and discuss their roles in the biomanipulation process.

Material and Methods

Study sites

Five reservoirs situated in the Morava River basin were selected for this study (Hubenov (HU), Bojkovice (BO), Landštejn (LA), Ludkovice (LU) and Nová Říše (NR); Table 1). All were constructed primarily as drinking water resources, though they also serve as a means of stabilising downstream river discharge. Two of the reservoirs (BO and LU) are situated in the eastern part of the Morava River basin at an altitude of around 300 m a.s.l. Both are relatively small and receive high levels of nutrient and organic input from the sewage treatment plants of adjacent villages, making them eutrophic. The remaining three reservoirs (LA, HU and NR) are located in forested countryside in the western part of the basin at altitudes between 500 and 600 m a.s.l. and receive much lower levels of nutrient input. Fisheries management at all five reservoirs is limited to supportive stocking of predatory fish species, mainly pike *Esox lucius* L., zander *Sander lucioperca* L., asp *Leuciscus aspius* (L.), and European catfish *Silurus glanis* L. (Table 1). No other biomanipulation efforts (e.g. large-scale removal of cyprinids) have been undertaken to date.

Fish sampling

The sampling process used in this study followed the routine monitoring schedule of the Morava River Authority (principally corresponding to the methodology of Kubečka et al. 2010), though the sample area and the number of gill nets exposed was extended (Table 1). Fish were sampled along the shoreline during daylight from late May to early July 2016 by boat electrofishing (one hand-held anode, EFKO FEG 13000, Honda 13kW, 300 V, 60 A, 50-80Hz), the stunned fish being collected with a 5 mm mesh hand net. Standard benthic (Pokorný s.r.o., Czech Republic; 12 panels, 1.5 m high) and pelagic (12 panels, 3.0 m high) multi-mesh gill nets were exposed overnight, the actual number of gill nets exposed depending on reservoir size and feasibility. The average proportions of examined fish, caught by electrofishing and gill nets were 58 and 42 % respectively (for more details see Table 2). All fish were determined to species, individually measured to the nearest mm (standard length – SL) and weighed to the nearest g for fish stock assessment (Jurajda et al. 2018). From these, 922 predatory fish (147 age-1 perch (*Perca fluviatilis* L.), 658 > 1+ perch, 43 zander, 39 pike, 24 asp and 11 catfish) were taken and examined for diet analysis (for numbers per reservoir, see Table 2).

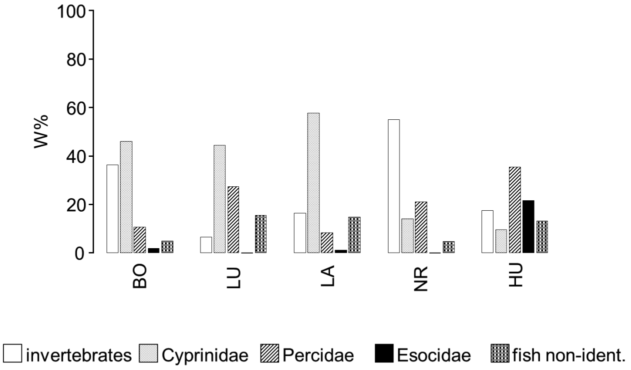

Fig. 1. Percentage by weight (%m) of food items in the diet of predatory fish from the five reservoirs under study. Reservoir abbreviations – BO Bojkovice, LU Ludkovice, LA Landštejn, NR Nová Říše, HU Hubenov.

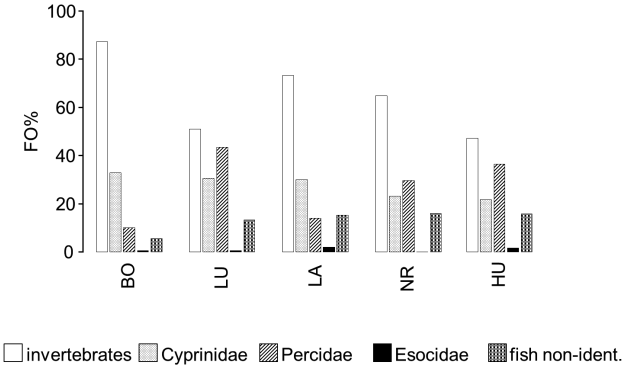

Fig. 2. Frequency of occurrence (%FO) of food items in the diet of predatory fish from the five reservoirs under study. For abbreviations see Fig. 1.

Diet analysis

All fish were sacrificed by deep clove oil anaesthesia (0.4 ml l^{-1}) and immediately stored in crushed ice in a portable cool box for transportation to the laboratory. Before removal of the digestive tract, each fish was weighed more precisely to the nearest 0.1 g. The digestive tract was then removed and weighed to the nearest 0.001 g before and after removal of ingested food, the difference being considered the mass of food. Stomach and gut contents were then preserved in 4 % formaldehyde. Fish with empty digestive tracts were noted and excluded from further analysis. Wherever possible, fish food items in the stomach and gut were determined to species level on the basis of scales (own comparative collection) and recognisable bones – pharyngeal teeth (cyprinids – Horoszewicz 1960) and only sporadically mandible/dental (pike, zander, perch, ruffe *Gymnocephalus cernua* (L.) – Čech

Table 1. Main characteristics of the five drinking water reservoirs sampled in 2016.

Reservoir	Hubenov	Bojkovice	Landštejn	Ludkovice	Nová Říše
Abbreviation	HU	BO	LA	LU	NR
GIS coordinates	49°23′40″ N 15°29′7″ E	49°3′10″ N 17°50′52″ E	49°1′28″ N 15°14′28″ E	49°7′28″ N 17°43′45″ E	49°9′19″ N 15°32′40″ E
Year put into operation	1972	1966	1973	1968	1985
Volume (10^6 m^3)	3.385	0.965	3.266	0.690	3.090
Catchment area (km^2)	19.9	13.8	12.7	13.1	21.3
Altitude (m a.s.l.)	520	320	570	285	555
Max depth	19	16	23	15	20
Area (ha)	55.0	15.5	40.5	12.5	53.5
Average depth (m)	6.2	6.2	8.9	5.5	5.8
Chlorophyll-a (μg/L)	18	17	13	22	8
Av. summer water temp. (°C)	20-24 °C	20-27 °C	19-25 °C	21-26 °C	19-24 °C
Electrofishing (m)	3190	1567	1897	1488	1687
Benthic/pelagic gill nets (n)	8/5	5/5	11/5	5/5	8/5
Species stocked 2011-2015	zander, catfish, asp	pike, zander, catfish	pike, zander, catfish, asp	pike, zander, catfish	pike, zander, catfish, asp

et al. 2008). Where identification was impossible, fish remains were summarised as "unidentified fish remains". For the purposes of this study, invertebrates were pooled and presented as "invertebrates". Tracts containing only "non-food" items (grains of sand, plant and wooden debris) were considered as empty and excluded from further analyses. Since there is a supposed distinct shift in food preference during perch ontogeny, perch were divided into two size/age categories (age-1 and > 1+), with the boundary between the two categories set at 75 mm SL, based on the findings of Dörner & Wagner (2003).

Frequency of occurrence (%FO) and percentage contribution by weight (estimated as relative weight percentage, %m) were determined for all prey categories/items according to Manko (2016), using the equations below:

$$\%FO = (n_i/n) * 100$$

where n_i is the number of fish with food item i in their digestive tract and n is the total number of fish with digestive tracts containing food, and

$$\%m = \frac{m_i}{m_t} * 100$$

where m_i is the wet weight of prey item i and m_t is the total weight of digestive tract contents in the entire sample. The degree of digestion of individual prey items was not taken into consideration in this calculation.

Results

All predators

Fish represented 74.6 %m (64 %FO) of all prey items recorded in the alimentary tracts of predatory fish at the five reservoirs investigated, with cyprinid species dominant (40.6 %m, 24 %FO) and percids as secondary prey (18.9 %m, 25 %FO) (Tables 3, 4). Unidentifiable fish remains contributed 10.8 %m (13 %FO). Invertebrates made up 23.4 %m (64 %FO) of the overall food bulk, their proportion ranging from 2 %m (22 %FO) in pike to 69.5 %m (83 %FO) in age-1 perch. Predatory species represented 23.2 %m (26 %FO) of predator diet, with perch taken most often (14.7 %m, 17 %FO) and pike and zander making up

Table 2. Number of fish examined at each drinking water reservoir caught by electrofishing (E) and/or gill nets (GN). Note: numbers of fish with empty alimentary tracts are in parentheses.

Fish/Reservoir	Hubenov	Bojkovice	Landštejn	Ludkovice	Nová Říše
Perca fluviatilis age-1	60 (0) GN	28 (0) E	4 (0) E	7 (0) E/17(0) GN	2(0) E
Perca fluviatilis ≥ 1+	28 (2) E/64 (0) GN	78 (0) E/3 (0) GN	107 (1) E/116 (3) GN	50 (0) E/79 (2) GN	31 (1) E/79 (2) GN
Sander lucioperca	3 (0) E	8 (4) E/4 (0) GN	6 (2) E	15 (1) GN	1 (0) GN
Esox lucius	8 (1) E	4 (0) E	10 (1) E	3 (0) E/13 (0) GN	1 (0) GN
Leuciscus aspius	-	8 (1) GN	-	14 (1) GN	-
Silurus glanis	2 (0) E	1 (0) E	3 (0) E	2 (0) GN	3 (1) GN

Table 3. The diet (%m, percentage by weight) of predatory fish from the five reservoirs under study – summary of all data recorded. Note: + = < 0.05.

Item/fish	*P. fluviatilis* age-1	*P. fluviatilis* ≥ 1+	*S. lucioperca*	*E. lucius*	*L. aspius*	*S. glanis*	Total
SL range (mm) min.	58	76	90	55	95	380	
max.	75	420	565	825	410	960	
R. rutilus	5.2	20.5	11.4	11.9	14.2	4.1	14.7
S. erythrophthalmus	1.7	0.5	0.0	36.5	0.0	1.6	12.1
A. brama	1.0	2.1	3.5	10.5	0.0	25.2	8.3
A. alburnus	1.4	3.9	0.0	0.1	18.3	3.2	2.8
L. aspius	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyprinidae non-ident.	2.4	4.0	3.7	0.6	12.6	1.0	2.6
Cyprinidae total	11.7	31.0	18.6	59.7	45.0	35.1	40.6
P. fluviatilis	5.8	15.0	43.0	16.9	16.4	3.3	14.7
S. lucioperca	1.3	4.4	13.2	0.2	1.3	0.0	2.3
G. cernuus	1.6	2.5	2.7	0.2	0.0	0.1	1.3
Percidae non-ident.	1.2	1.1	1.1	+	1.1	0.0	0.6
Percidae total	9.8	22.8	59.9	17.3	18.8	3.4	18.9
E. lucius	0.0	0.3	0.0	13.0	0.0	0.0	4.3
S. glanis	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pisces non-ident.	8.0	10.5	7.5	7.4	16.8	21.1	10.8
Pisces total	30.1	64.7	86.0	97.4	80.7	59.6	74.6
A. astacus	0.8	9.0	0.0	1.8	0.0	37.6	11.2
Invertebrates total	69.5	34.2	14.0	2.0	18.6	37.6	23.4
Non-food items	1.0	1.1	0.0	0.7	0.8	2.8	2.4

4.3 %m (1 %FO) and 2.3 %m (5 %FO), respectively. Asp and catfish were not recorded in the diet of any predator. Overall, cannibalistic feeding represented 11.5 %m (27 %FO), with highest rates of cannibalism recorded in ≥ 1+ perch (15 %m, 34 %FO), followed by zander (13.2 %m, 11 %FO), pike (13 %m, 16 %FO) and age-1 perch (6 %m, 10 %FO). Asp and catfish did not display signs of cannibalism.

The proportion of fish prey in predator diet at different reservoirs ranged between 40.3 %m (69 %FO) at NR and 87.6 %m (75 %FO) at LU (Figs. 1, 2). Cyprinids were the dominant prey at three of the reservoirs, representing 57.6 %m (30 %FO) at LA, 46 %m (33 %FO) at BO and 44.5 %m (31 %FO) at LU, while percids were dominant at HU (35.4 %m, 36 %FO) and NR (21.3 %m, 30 %FO) (Figs. 1, 2). Invertebrates were the most frequently occurring food item in the total food bulk (61 %FO) of predatory fish at all reservoirs, with proportions ranging from 47 %FO at HU to 87 %FO at BO (Fig. 2). Percids occurred more frequently than cyprinids in predator diet at LU, NR and HU, while cyprinids were taken more frequently at BO and LA (Fig. 2).

Perch

The dominant food items in age-1 perch diet were planktonic and benthic invertebrates, which represented more than two thirds of the total food bulk (69.5 %m, 83 %FO) (Tables 3, 4). Overall, zooplankton were the dominant component, the remaining prey consisting of water louse (*Asellus aquaticus* L.), mayfly (*Caenis*, *Baetis*) nymphs and subimagos, water bugs (*Micronecta*), caddisfly (*Ecnomus*, *Hydroptila*, Limnephilidae, Leptoceridae), chironomid larvae and damselfly (*Calopteryx*) nymphs. Overall, fish prey represented 30.1 %m (42 %FO) of age-1 perch diet, with cyprinids and percids making up 11.7 and 9.8 %m, respectively. While roach fry were the dominant component of the cyprinids taken at 5.2 %m, cannibalistic feeding on perch fry made up 5.8 %m (10 %FO). The other predatory fish species consumed was zander, though only occasionally (1.3 %m, 1 %FO).

Fish represented around two thirds of ≥ 1+ perch diet (64.7 %m, 64 %FO), the other third almost entirely comprising invertebrates (34.2 %m, 67 %FO) (Tables 3, 4). The dominant prey fish taken were roach and

Table 4. Frequency of occurrence (%FO) of food items in the diet of predatory fish at the five reservoirs under study – summary of all data recorded.

Item/fish	*P. fluviatilis* age-1	*P. fluviatilis* ≥ 1+	*S. lucioperca*	*E. lucius*	*L. aspius*	*S. glanis*	Total
R. rutilus	9	13	14	19	10	11	12
S. erythrophthalmus	3	1		3		11	2
A. brama	1	1	6	8		22	2
A. alburnus	3	3		5	15	11	3
L. aspius	0	0	0	0	0	0	0
Cyprinidae non-ident.	5	6	3	8	15	11	6
Cyprinidae total	21	27	22	43	40	67	24
P. fluviatilis	10	34	31	27	10	11	17
S. lucioperca	1	6	11	5	5		5
G. cernuus	1	2	3	3		11	2
Percidae non-ident.	1	1	6	3	10		1
Percidae total	15	43	50	11	25	22	25
E. lucius		5		16			1
S. glanis	0	0	0	0	0	0	0
Pisces non-ident.	7	14	8	14	20	44	13
Pisces total	42	64	90	89	85	71	64
A. astacus	1	5	0	3	0	44	1
Invertebrates total	83	67	22	22	55	44	61

perch at 20.5 %m and 15 %m, respectively. Predatory species made up a relatively large part of the diet, with cannibalistic feeding on perch the most common component (15 %m, 34 %FO), followed by zander (4.4 %m) and pike (0.3 %m). Invertebrate dietary items comprised zooplankton; water bugs; mayfly, damselfly and dragonfly (Gomphidae) nymphs; caddisfly and chironomid larvae; and water beetle (Dytiscidae) larvae.

Zander

The diet of zander comprised almost exclusively fish (86 %m, 90 %FO), with percids representing 59.9 %m and cyprinids 18.6 %m (Tables 3, 4). Of the percids taken, 13.2 %m (11 %FO) represented cannibalistic consumption of young zander. Invertebrates made up 14.0 %m (22 %FO) of the diet, with noble crayfish (*Astacus astacus* L.) being taken alongside smaller prey such as mayfly nymphs (*Ephemera*, *Caenis*) and chironomid larvae.

Pike

As with zander, pike diet comprised almost exclusively fish (97.4 %m, 89 %FO), with invertebrate prey (noble crayfish and mayfly nymphs *Baetis* and *Ephemera*) representing just 2 %m (22 %FO) (Tables 3, 4). Cyprinids were the dominant prey taken (59.7 %m), with percids contributing 17.3 %m and cannibalistic consumption of pike 13 %m (16 %FO). Pike predation on other predatory species was low, with zander representing just 0.2 %m (5 %FO).

Asp

Fish represented 80.7 %m (85 %FO) of asp diet, with cyprinids the dominant item (45 %m, 40 %FO) and percids at 18.8 %m (25 %FO) (Tables 3, 4). While invertebrates were the most frequently taken item (55 %FO), they represented just 18.6 %m of the total food bulk taken. Invertebrate prey principally comprised caddisfly (*Hydroptila*) and chironomid larvae and imagos.

European catfish

Catfish diet comprised around two thirds fish (59.6 %m, 71 %FO) and one third (37.6 %m, 44 %FO) large invertebrate items, with common bream the most common prey fish (25.2 %m, 22 %FO) and noble crayfish the most common invertebrate prey (Tables 3, 4).

Discussion

The principal measure employed in biomanipulation projects is increasing the density and biomass of predatory fish (e.g. Lathrop et al. 2002, Skov et al. 2002, Vašek et al. 2013). However, if such measures are to be effective as regards water quality management of drinking water reservoirs, the feeding habits of the predatory fish stocked need to be monitored and understood so that the most effective balance can be achieved. Though "apex predators" are known to play a key role in ecosystem stability across environments, their numbers are generally decreasing (Vejřík et al. 2017a), and those of freshwater reservoir ecosystems are no exception. In recreational reservoirs, for example, larger/older predatory fish tend to be relatively rare as they are usually removed by anglers (Jurajda et al. 2018). Predatory fish populations in waterbodies subject to management, whether for food production, biomanipulation or angling, are particularly vulnerable as they are largely dependent on stocking. In the Czech Republic (and elsewhere), drinking water reservoirs are subject to specific management regimes that a) limit public entrance and use, including a ban on angling, and b) aim improve water quality by reducing planktivorous and benthivorous cyprinid populations through annual stocking of predatory fish (e.g. pike, zander, catfish and asp). In this study, we set out to assess the diets of stocked predators in five Czech drinking water reservoirs and discuss our findings in relation to their intended role in controlling cyprinid populations and improving water quality.

The fish assemblages at all five reservoirs corresponded with the "stable cyprinid stage" typical of most European lowland lakes and reservoirs, with roach and common bream together contributing > 50 % of fish stock abundance (Kubečka 1993, Jurajda et al. 2018). Annual stocking of predatory fish (Table 1), however, has led to a relatively high abundance of predatory species, with a non-predatory/predatory biomass ratio ranging between 0.5 and 3 (Jurajda et al. 2018) while in other reservoirs it is markedly higher – e.g. 6.1-6.3. at Brno Reservoir (Jurajda et al. 2015).

Overall, fish made up three quarters (74.6 %m) of predatory fish food bulk and were recorded in two thirds of all fish examined (64 %FO). Both the abundance and species/sizes taken by each of the predatory species differed, however, and this may have had an impact on their role as regards biomanipulation of planktivorous and benthivorous fish species.

Target species (roach, rudd, bream, bleak and ruffe) in perch diet, for example, represented 41.9 % of identifiable prey. Assuming that these species were taken at a similar level amongst unidentifiable fish remains (10.8 %m) then a further 4.5 %m may be added, making a total of 46.5 % of target species in the overall diet. As perch are also known to feed on cyprinid eggs, with consumption reaching 29 %m of the diet during the spawning season (Zapletal et al. 2016), they may also contribute to lowering cyprinid recruitment success. On the other hand, cannibalism and consumption of other predatory species by both age-1 and ≥ 1+ perch were relatively high at 21.9 %m, or 24.1 %m when including a 2.3 % proportion from unidentified prey. Overall, therefore, perch may be considered as having a negative impact as predatory species, they are considered desirable as regards biomanipulation (or at least have the potential to play a future role). If the figures for perch were to be removed from the dataset (i.e. if perch were absent from the reservoirs), then the potential predator impact on cyprinid target species would alter dramatically. In this case, planktivorous and benthivorous fish prey would represent 57.2 %m (or 63.4 %m including the appropriate proportion of unidentifiable fish remains), with predatory species as prey representing just 4.3 %m (5 %m). The vast majority of studies on juvenile perch diet, however, report their benthivorous and planktivorous feeding (Vašek et al. 2006, Kratochvíl et al. 2008, Vejřík et al. 2016, Estlander et al. 2017) or planktivory associated with macroinvertebrate consumption (Prejs 1976, Persson et al. 2000, Tolonen et al. 2000, Reszu & Specziár 2006, Schleuter & Eckmann 2008); indeed, in years with strong perch recruitment, planktivory may reach levels that induce a strong depression in pelagic zooplankton (Persson et al. 2000). Conversely, larger perch are considered to be predominantly predators (Jeppesen et al. 1990). Consequently, removal of perch juveniles, larvae and eggs may be undertaken as a biomanipulation measure, while larger perch are left behind (e.g. Jurajda et al. 2016). However, what constitutes a "large piscivorous perch" differs considerably between studies, e.g. > 9 cm SL (Prejs 1976), > 12 cm (Tolonen et al. 2000, Rezsu & Specziár 2006), > 13 cm TL (Schleuter & Eckmann 2008), > 20 cm TL (Kahl & Radke 2006), > 20 cm SL (Didenko & Gurbyk 2016) and 25.5-37.5 cm TL (Jacobsen et al. 2002). Moreover, both our own results and those of previous authors (e.g. Mehner et al. 1998) show that fish prey are regularly taken by juvenile perch, with almost one third (30.6 %m) of food ingested by 42 % (n = 108) of the age-1 perch examined in this study being fish. It should also be remembered that most of the fish taken by juvenile perch will be larvae, which rapidly become unidentifiable after ingestion. Schooley et al. (2008), for example, showed that the larvae of razorback sucker (*Xyrauchen texanus* Abott, 1861) were only identifiable in the gut content of green sunfish (*Lepomis cyanellus* Rafinesque, 1819) and bluegill (*L. macrochirus* Rafinesque, 1819), relatives of the European perch, within 15 min of consumption, and undetectable at 60 min. Logistic models predicted a 50 % or lower probability of identifying razorback sucker larvae within 35 min of consumption (Schooley et al. 2008). Likewise, Lohr & Fausch (1996) obtained similar results for green sunfish allowed to feed freely for 24 h on larval plains killifish (*Fundulus zebrinus* Jordan & Gilbert, 1883). As stated above, cannibalism in perch reached 21.9 %m (24.1 %m) overall, of which 0+ perch made up almost 6 %m.

McCormack (1970) reported onset of carnivorous feeding in perch at > 9 cm TL with cannibalism first occurring at 11.5-13.9 cm TL, while Brabrand (1995) reported intra-cohort cannibalism as early as the perch larval stages. Considering the regular occurrence and relatively high rate of conspecific predation recorded in our own (15 %m) and other studies (e.g. 12.3 % in Yazicioglu et al. 2016), the role of perch in biomanipulation efforts becomes questionable. As a general conclusion, we would suggest that the role of perch is to be assessed on a case-by-case basis, taking full account of the time of year and, especially, the current status of perch recruitment.

Zander, like perch, show an ontogenic shift in feeding, the diet consisting almost entirely of fish from 150 mm SL (Specziár 2011). At both our own sites (Tables 3, 4) and elsewhere (e.g. Didenko & Gurbyk 2016), fish are the dominant item in zander diet, with roach and perch the most important in terms of %FO and numerical and weight dominance. Cannibalism in zander is almost certainly more extensive than assumed under present fish farm management and stocking practices. Unlike the recommendations for pike stocking strategy, for example, the relevant handbooks and manuals (e.g. Ličko et al. 2013, Randák et al. 2014) tend not to consider cannibalistic behaviour in zander. In our own study, however, predation on conspecific juveniles was relatively high at 13.2 %m and 11 %FO (Tables 3, 4). In Hungary (Lake Balaton, Specziár 2011), the rate of cannibalism in zander ranged between 0.1 and 88 % (mean 19 %, summary data for all size categories between 5-800 mm SL), while at other sites in the Czech Republic (e.g. Lipno Reservoir), values of up to 34 %m have been recorded (Vašek et al. 2018). In Ukraine (Kaniv Reservoir), values ranged from 5.7 %FO (zander < 40 cm SL) to 14.8 %FO (40-54 cm SL), with small zander the third most common prey (both by %m and %FO) after roach and perch in the largest zander size groups (Didenko & Gurbyk 2016), as also found in our study (Tables 3, 4). Significant inter- and intra-cohort cannibalism of zander both under natural lake and indoor farm conditions was also highlighted by Frankiewicz et al. (1999) and Policar et al. (2016), respectively.

With respect to feeding habits, pike are considered an ideal fish species for biomanipulation purposes as they are extremely “plastic” in their choice of prey type and size and their response to prey behaviour (Craig 2008). Indeed, its position in a biomanipulated reservoir is irreplaceable due to the numerous predator effects displayed (Vejřík et al. 2017a). Adult pike are model piscivorous predators, with a diet composed almost exclusively of fish (99 %m) and a relatively balanced prey spectrum with no clear preference for systematic groups and/or ecological guilds (Mikl et al. 2017). In the Kaniv Reservoir (Ukraine), roach, perch and gobiids (Gobiidae) were dominant in the diet, though gibel carp exceeded other species by weight (40.3 %m), followed by roach (13.4 %m), bream (13.3 %m) and perch (12.6 %m) (Didenko & Gurbyk 2016). By comparison, cyprinids (59.7 %m), represented mainly by rudd (36.5 %m), roach (11.9 %m), bream (10.5 %m), and perch (16.9 %m) were the most important pike food items in our own study (Table 3). However, cannibalism was also relatively high in pike, contributing 13 %m to the total food ingested (Table 3). Cannibalism in pike is primarily a result of intraspecific interactions as both parties usually share the same resources and habitats and, therefore, are commonly involved in competitive interactions (Polis 1988). Non-fish prey tends to be reported only exceptionally and in negligible amounts in pike diet, with such prey usually comprising larger macroinvertebrates such as crayfish (Elvira et al. 1996, this study), macrozoobenthos (Mikl et al. 2017, Yazicioglu et al. 2018) and frogs (Didenko & Gurbyk 2016). The occurrence of crayfish in pike of around 550 mm SL in our own reservoirs (Jurajda et al. 2018) suggests targeted predation as none of the reservoirs suffered from inadequate prey fish resources. On the other hand, it is questionable whether the occurrence of smaller benthic animals (mayfly nymphs, chiromomid larvae) in the diet, especially of larger zander (and pike) individuals, comes from the food of digested prey or results from direct predation.

European catfish showed a high level of feeding plasticity in this study, with fish and macroinvertebrate prey accounting for 59.6 and 37.6 %m, respectively

(Tables 3). Aside from age-1 perch, this was the lowest predation rate on fish displayed by any predatory species and the highest predation rate on invertebrates. The most important invertebrate food item in catfish diet were noble crayfish, which occurred regularly in individuals up to 960 mm TL (8 kg), thus confirming the assumption that European catfish are more opportunistic in feeding habits than other predators in European freshwater ecosystems (Syväranta et al. 2010). Such high levels of dietary adaptability have also been recorded by Vejřík et al. (2017a), who reported the regular occurrence of semiaquatic vertebrates such as waterfowl, frogs and water-bound mammals in catfish diet, though the catfish examined in their study was somewhat larger (up to 11.8 kg) than those in our own study (max. 8 kg). Moreover, the newly revealed ability of European catfish to utilise perch egg strands as a food source documents its opportunistic feeding behaviour (Vejřík et al. 2017b).

According to Vejřík et al. (2017a), both catfish and pike can coexist in aquatic ecosystems without major problems as the catfish tends to be a nocturnal feeder while pike hunts during the day. Further, Vejřík et al. (2017a) recorded rudd, tench (*Tinca tinca*) and perch as the preferred prey fish of catfish (based on electivity indices), while roach tended to dominate in pike diet, suggesting a relatively low niche overlap. In comparison, roach were the most important prey of both pike and catfish in Ukraine (Kaniv Reservoir), suggesting a higher level of niche overlap in some habitats (Didenko & Gurbyk 2016). On the other hand, catfish diet in the Kaniv Reservoir was relatively restricted, with roach, perch and gobiids along with zebra mussel, *Dreissena polymorpha* (Pallas), the only important food organisms taken. The other items (rudd) did not exceed 2.3 %. According to the literature, European catfish show a very low level of cannibalism; indeed, only Vejřík et al. (2017a) has recorded low levels in natural habitats, the only other records being of regular cannibalism under intensive larviculture (Król et al. 2014).

Asp undergo considerable ontogenic shifts in diet through their lifetime, with four trophic guilds represented by i) zooplanktivory in earliest life stages, ii) an ephemeral period (May-June) of extended feeding on surface arthropods at 16-40 mm SL, and iii) facultative and iv) obligate piscivory at 121-500 mm SL (Specziár & Reszu 2009). This partitioning corresponds with that of Vašek et al. (2018), who observed mostly terrestrial invertebrates and emerged aquatic insects being consumed by juvenile asp of < 100 mm SL, while larger individuals of > 100 m were predominantly piscivorous. The discovery of zander as prey in asp diet, albeit a single occurrence, may also point to possible predation on other piscivorous fish species (Vašek et al. 2018). In this study, terrestrial insects occurred regularly in the diet of both juveniles (110-130 mm SL) and adult asp (max. 358 mm SL) together contributing 18.6 %m of the total food consumed (Table 3). Overall, however, piscivory represented 80.7 %m of the diet, confirming its suitability for food web manipulation in drinking water reservoirs. Asp predation, therefore, has no, or no significant, effect on the populations of other predatory species, with coexisting asp and zander populations, for example, utilising different prey resources, thereby reducing potential negative competitive interactions (Vašek et al. 2018).

It is very difficult (rather impossible) to state any conclusion regarding optimal selection of appropriate species for biomanipulation purposes based just on food analyses. It depends upon many factors and issues which cannot be generalized and might be related optimally to particular reservoirs or conditions. Nevertheless, the analyses of predatory fish diet may serve as a guide for optimization of their stocking strategy. If considering the trophic and climatic factors as driving aspects for the recommendations for appropriate fisheries management of the reservoirs under study, they are to be separated into two groups – moderately eutrophic ones at altitudes ~ 550 m a.s.l. (HU, NR and LA) and eutrophic reservoirs at ~ 300 m a.s.l. (BO and LU).

As demonstrated by Jurajda et al. (2018), predatory species represented up to 60 % of biomass, with the F/C index (biomass of non-predatory fish/biomass of predatory fish) ranging from 0.5-3 in these reservoirs. This implies a high abundance of predators and their appropriate stocking strategy. Hence, the moderately trophic reservoirs (HU, NR and LA) located at higher altitudes should maintain their composition and intensity of predatory fish stocking. However, based on the predatory fish food analyses, it is recommended that the stocked zander yearlings be released along the whole shoreline in small batches and in late morning in order to minimize perch predation on them. While this recommendation also applies to the lower positioned eutrophic reservoirs BO and LU, these should also benefit from the high feeding plasticity of European catfish and increased stocking rates.

If increasing the density and biomass of predatory fish as a means of improving water quality in drinking water reservoirs is to be truly effective, then the feeding habits of the predatory fish stocked need to be fully understood so that the most effective balance can be achieved. Our own results show that, while most of the species stocked did indeed prey on the target cyprinids, relatively high levels of cannibalism and/or preying on other small predatory species (especially in perch, pike and zander) may counterbalance their potential effectiveness, and this factor needs to be fully taken into account in future plans for biomanipulation through top-down predator impact.

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