The food niche overlap of five fish species in the Úpoř brook (Central Bohemia)

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ABSTRACT

Key-words:
food
competition,
brown trout,
bullhead,
chub,
dace,
stone loach,
$Mtot_p$

The diet and food niche overlap of five fish species in the Úpoř brook was evaluated. The supply of food represented by benthos was studied, and the proportion of total food particles in the intestine of brown trout *Salmo trutta* L., chub *Squalius cephalus* (L.), dace *Leuciscus leuciscus* (L.), bullhead *Cottus gobio* (L.) and stone loach *Barbatula barbatula* (L.) was measured. Evaluations were performed using a new index ($Mtot_p$). All fish species except stone loach exhibited a balanced consumption of the food supply. The food components were systematically grouped, but no differences in the ingestion of these groups were found. However, a new approach in the evaluation of food competition based on observation of species-specific preferences/avoidance in ingestion of food particles was applied. The particles were divided into four ecological categories according to their availability for fish. Brown trout concentrated on easily accessible sources of benthos or that hiding below stones, and also distinctly preyed on terrestrial insects. Chub displayed a similar feeding habit, though concentrating more on drift and allochthonous sources. The food spectrum of dace was mostly composed of easily accessible benthic organisms, consuming fewer hidden benthos and terrestrial insects. The food of bullhead and stone loach was similar, both preferring benthos. Bullhead consumed hidden species while stone loach consumed more accessible species rather than hidden ones.

RÉSUMÉ

Le chevauchement de niche alimentaire de cinq espèces de poissons dans le ruisseau Úpoř (Bohême centrale)

Mots-clés :
concurrence
alimentaire,
truite,
chabot,
chevesne,

Le régime alimentaire et le chevauchement de niche alimentaire de cinq espèces de poissons dans le ruisseau Úpoř été évalués. La disponibilité en nourriture représentée par le benthos a été étudiée, et la proportion de toutes les particules alimentaires dans l'intestin de la truite *Salmo trutta* L., du chevesne *Squalius cephalus* (L.), de la vandoise *Leuciscus leuciscus* (L.), du chabot *Cottus gobio* (L.) et loche franche *Barbatula barbatula* (L.) a été mesurée. Les évaluations ont été effectuées en utilisant un nouvel indice ($Mtot_p$). Toutes les espèces de poissons à

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vandoise,
loche franche,
$Mtot_p$

l'exception de la loche franche présentaient une consommation équilibrée de la nourriture disponible. Les composants alimentaires ont été regroupés suivant les ordres ou classes, mais aucune différence dans l'ingestion de ces groupes n'a été trouvée. Cependant, une nouvelle approche dans l'évaluation de la compétition alimentaire basée sur l'observation des préférences / évitement à l'ingestion de particules alimentaires spécifiques à chaque espèce a été appliquée. Les particules ont été réparties en quatre catégories écologiques en fonction de leur disponibilité pour les poissons. La truite se tourne vers des sources facilement accessibles du benthos ou cachées en dessous des pierres, et significativement vers les insectes terrestres. Le chevesne affiche des habitudes alimentaires similaires, bien que se concentrant plus sur la dérive et les sources allochtones. Le spectre alimentaire des vandoises était principalement composé d'organismes benthiques facilement accessibles, consommant moins de benthos caché et d'insectes terrestres. La nourriture du chabot et de la loche franche étaient similaires, les deux préfèrent le benthos. Le chabot consomme des espèces cachées alors que la loche franche consomme des espèces accessibles, plutôt que celles qui sont cachées.

INTRODUCTION

During complex studies of fish assemblages, one cannot disregard the trophic demands of particular species and possible competition between them. Often, basic parameters of fish assemblages such as abundance and biomass can be the result of food competition (Holmen *et al.*, 2003) as well as the distribution of species and their preference of microhabitats (Cavalli *et al.*, 1998; Fischer, 2000; Hestagen and Heggenes, 2002; Jansen *et al.*, 2002). Interspecies trophic competition among morphologically similar species or species using the same microhabitats (Adámek *et al.*, 2003; Hardwood *et al.*, 2001; Pouilly *et al.*, 2003; Volpe *et al.*, 2001), or even other species (Baltz *et al.*, 1982; Holmen *et al.*, 2003) is generally expected and has often been demonstrated.

Food competition has often been discussed in the literature (Copp *et al.*, 1994; Dyk, 1932; Fischer, 2000; Gatz *et al.*, 1987; Maitland, 1965; Welton *et al.*, 1991). Holmen *et al.* (2003) highlighted the fact that the most effective method for discovering competition is to compare sympatric and allopatric populations of evaluated species. Some authors have found it most appropriate to carry out experiments to evaluate the selectivity of a given species to a certain food component (Holmen *et al.*, 2003; Jansen *et al.*, 2002). In this light, it is advisable to observe the specifics of the food supply when evaluating fish diets. Not even large overlaps in food components necessarily mean a high level of competition. The species observed could have merely been consuming the same abundantly available food components (Holmen *et al.*, 2003).

In this work, the food of five fish species (brown trout *Salmo trutta*, chub *Squalius cephalus*, dace *Leuciscus leuciscus*, stone loach *Barbatula barbatula* and common bullhead *Cottus gobio*) was studied. All these fish species are common in the stream studied, and many authors have studied diet and/or competition in these species (Albertová, 1982; Cavalli *et al.*, 1998; Dyk, 1932, 1956; Fochetti *et al.*, 2008; Hesthagen *et al.*, 2004; Horton, 1961; Hughes *et al.*, 2003; L'abée-Lund *et al.*, 2002; Legalle *et al.*, 2005; Maitland, 1965; Markovič *et al.*, 2007; Saksgard and Hesthagen, 2004; Yevsin and Ivanov, 1979).

The aim of this work was to examine the diet of these five fish species and to evaluate the level of competition as the overlap in their food niches. Moreover, a new approach was used to identify food competition: in addition to systematically categorized food particles, a comparison in the utilization of four food categories (based on their availability for fish) was applied.

MATERIAL AND METHODS

The study was conducted in the Úpoř brook. This brook is a right-hand tributary of the Berounka River (Central Bohemia), into which it flows near the village of Týřov. The drainage

Figure 1
Map of the Úpoř brook.

Table I
Length and weight structure of the examined fish (mean, SD...standard deviation, min...minimum, max...maximum).

species	N	length (mm)				weight (g)			
		mean	SD	min	max	mean	SD	min	max
S. trutta	164	120.8	41.8	46	270	38.3	41.3	0.8	250
S. cephalus	56	155.5	40.1	79	263	83.7	66.2	9.5	352
L. leuciscus	49	135.1	44.8	60	194	55.7	41.4	2.1	125
B. barbatula	34	99.6	16.2	64	125	11.1	4.3	3.2	18.3
C. gobio	38	83	19.1	36	108	13.9	7.7	0.75	27

area is 39.5 km^2, the length of the flow is 11.2 km and the average flow in the estuary is 0.08 m$^3 \cdot$s^{-1}. The brook is typically heterogeneous, divided into pools and rapids and riffle areas. The brook is a part of the Křivoklátsko Landscape Protected Area, Týřov National Nature Reserve, UNESCO Biosphere Reserve (see Figure 1) and is not managed by fishery organizations.

The food of the dominant species of fish assemblages in the Úpoř brook mentioned above, *e.g.* brown trout, chub, dace, bullhead and stone loach, was investigated. Food was evaluated for 164 brown trout individuals, 56 chub, 49 dace, 38 bullhead, and 34 stone loach. The length and weight structure of the samples is shown in Table I.

Fishing was performed during a long-term sampling campaign from 1999–2004. In total, 181 samples in 35 different localities placed along the investigated stream were taken. Fish were caught by electrofishing (devices TRA 2 – pulsed 450V; MK-1 pulsed 225/300V; LENA pulsed 225/300V), measured (standard length – L$_c$ (*longitudo corporis*)), weighed and fixed in 4% formaldehyde. Afterwards, autopsies of the caught fish were performed, and alimentary

tracts were transferred to 85% ethanol, stored and later evaluated. When evaluating the intestines, the number of particular food particles and their original volume were estimated with the help of a binocular microscope. The original volume was estimated based on the volumes of particular food components as determined below.

For all species, the average proportional representation (N_p) and the average proportional volume (V_p) of every food component was estimated as the percentage of the overall amount or volume, respectively, of the food in the intestines. As a further indicator, the proportion of the food component as a percentage of the body weight ($Mtot_p$) was calculated according to the relationship:

$$Mtot_p = \frac{V_p \cdot (m - m_1)}{m};$$

where V_p is the proportional volume of the given food components, m is the weight of the fish and m_1 is the weight without the intestines. For consistency, a V_p value of $\rho = 1$ kg·dm^3 was used in the calculations.

During 7 sampling campaigns, nine quantitative samples of benthos were taken. Samples were taken throughout the year (18.4.1998, 19.7.1998, 9.9.1998, 23.5.1999, 27.8.2001, 18.4.2002, 16.6.2003), collected in the same places where fish were caught. The collection was carried out by a combination of floating the benthos into a net, or by gathering benthos with tweezers from a delineated area of 1 m^2 (1 × 1 m) or 0.25 m^2 (0.5 × 0.5 m). Samples were fixed in 75% ethanol or 4% formaldehyde. Identification of particular components was carried out with a binocular microscope. Allochthonous food sources such as terrestrial insects and other terrestrial organisms and plants were not identified. The average amount and proportional volume of benthos components was calculated as the weighted mean of particular components from all samples. The density of particular components was calculated according to the volume of particular components (acquired using direct measurements of volume and linear regressions between the volume and number of the given components on the overall contents of the intestines of each fish) and their number at the site.

The use of the macrozoobenthos supply was evaluated by comparing the average proportion of each individual constituent in the supply and the average (weighted mean) proportion of the food constituents in the intestines of all specimens of each species (V_p) using χ^2 tests. Significance was tested at the level of 5%.

Interspecific food competition was evaluated by comparing the particular food components as a percentage of body weight ($Mtot_p$) for each species.

All food components were first grouped into families and 4 food categories according to where fish could most easily find the given food component, as follows:

- Category I included food sources living hidden under stones or in the substrata (mud, sand) and staying hidden except for the time of hatching, pupating or during possible disturbances. This category included gammarids, *Sialis fuliginosa*, caddisflies from the families Rhyacophilidae and Hydropsychidae, mayflies from the family Heptageniidae, and finally, dipteran juveniles.
- Category II included species which are more easily accessible, that is, living on the bottom, on stones (occasionally partly under stones and therefore hidden), and sometimes migrating in the water current. This group was made up primarily of caddisflies, stoneflies and mayflies from the families Limnephilidae, Odontoceridae, Leuctridae, Nemouridae, Baetidae, Caenidae and Leptophlebiidae, as well as annelids and detritus.
- Category III consisted of drifting food particles, *i.e.* terrestrial plants, water coleopterans and heteropterans, fish, reptilians, amphibians, dipteran larvae and pupae from the family Culicidae, and other hyponeustic species.
- Category IV consisted of terrestrial insects and epineustic species.

One-way ANOVA and the Tukey-Kramer test were used for comparisons. The level of competition was also evaluated using Detrended Corresponding Analysis (DCA) using matrices consisting of food particle proportions ($Mtot_r$) for particular fish species.

Statistical analyses were carried out using OpenOffice software, the statistical program NCSS, and Canoco 4.5.

Table II
Number, proportional volume and density of particular macrozoobenthos components in the Úpoř brook.

taxa	number (%)	volume (%)	density (g·m^{-2})
Baetidae	1.30	0.49	0.058
Caenidae	0.02	0.02	0.002
Ephemeridae	0.27	0.17	0.018
Ephemerillidae	0.05	0.002	0.001
Heptageniidae	8.03	11.53	1.395
Leptophlebiidae	15.46	6.82	0.815
Leuctridae	4.60	2.76	0.334
Nemouridae	0.86	0.62	0.076
Perlidae	0.02	0.01	0.018
Athericidae	0.02	0.16	0.02
Ceratopogonidae/Chironomidae	17.30	7.95	0.711
Limoniidae	0.08	0.002	0.001
Simuliidae	7.15	7.97	0.746
Limnephilidae tr. *Stenophylacini*	13.47	27.30	2.661
Odontoceridae	9.08	14.76	1.657
Hydropsychidae/Rhyacophilidae/Philopotamidae	4.77	2.95	0.223
***Sialis* sp.**	1.66	3.47	0.379
***Gammarus* sp.**	15.56	12.90	1.539
***Asellus* sp.**	0.01	0.00	0.001
Oligochaeta	0.29	0.12	0.526

Table III
Use of food components by particular fish species (as proportional volume – V_p). Only food particles found in digestive systems of fish are presented (i.e. 96.4% of the benthos).

taxa/food particle	food supply (%)	*S. trutta* (%)	*S. cephalus* (%)	*L. leuciscus* (%)	*C. gobio* (%)	*B. barbatula* (%)
plants		0.00	11.50	4.71	0.00	0.00
detritus		0.00	2.65	6.11	0.00	0.00
Baetidae	0.49	4.65	0.12	5.81	5.14	28.71
Ephemeridae	0.17	0.36	0.57	0.00	6.00	0.00
Heptageniidae	11.53	19.23	9.80	11.13	9.87	4.01
Leptophlebiidae	6.82	0.46	0.06	2.04	0.00	0.87
Diptera	15.98	11.62	0.72	25.00	29.43	15.45
Limnephilidae	27.30	31.68	70.94	25.97	40.23	46.10
Odontoceridae	14.76	19.67	8.22	25.33	0.00	0.10
Hydropsychidae*	2.95	0.29	0.00	0.00	2.97	0.00
***Sialis* sp.**	3.47	0.93	0.00	0.27	0.00	0.00
***Gammarus* sp.**	12.90	7.49	5.96	0.81	2.74	1.14

* Hydropsychidae/Rhyacophilidae/Philopotamidae.

RESULTS

> FOOD SUPPLY

During the whole period, the largest component of macrozoobenthos was undoubtedly insect juveniles, comprising five orders and twenty families.

The average number, proportional volume and density of benthos are given in Table II.

> FOOD SUPPLY CONSUMPTION

In spite of some differences in the use of certain constituents, as seen in Table III (generally; fish preferred dipteran juveniles, juveniles of both caddisflies and mayflies from the families Limnephilidae and Baetidae, whereas the supply of mayflies from the family Leptophlebi-idae, megalopteridians and gammarids was stable), the overall use of the food supply by all
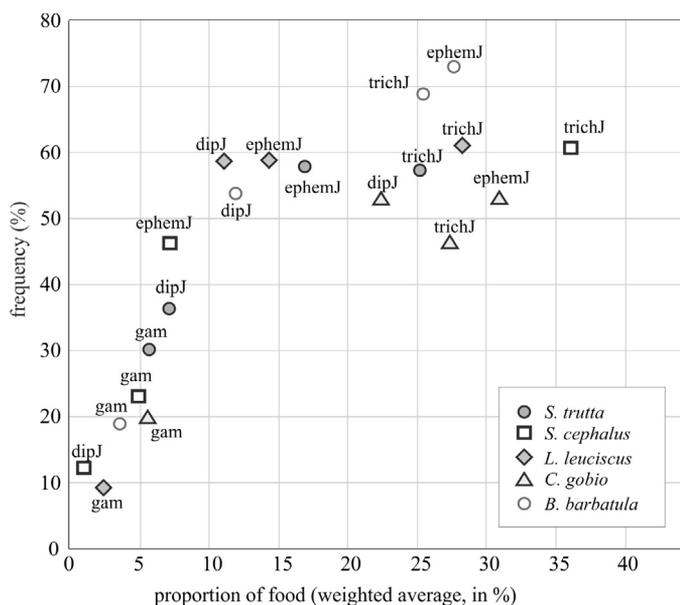
Figure 2

Frequency and proportion of some food particles in the diet of the fish species studied. trichJ – Trichoptera juveniles, dipJ – Diptera juveniles, ephemJ – Ephemeroptera juveniles, gam – Gammarus sp.

species except stone loach (χ^2 test, $P < 0.05$) was similar. This difference in consumption by stone loach was primarily caused by a strong preference for juveniles from the family Baetidae and, in contrast, by the lower use of juveniles of the species *Odontocerum albicorne*. The frequency and proportion of some of the food categories are shown in Figure 2. Both the low proportion and frequency of gammarids in all observed fish species is noticeable. On the other hand, fish frequently consumed larvae of caddisflies, which also comprised the largest proportion of their food. Differences were found in the intake of dipteran larvae, which played a dominant role in the food of dace, bullhead and stone loach, whereas they were negligible in the food of brown trout and chub. Mayfly larvae were consumed often; however, there are differences in their contribution to the overall diet of particular species.

> EVALUATION OF FOOD COMPETITION

The categories of food sources can be seen in Figure 3, showing the following significant differences resulting from ANOVA ($P < 0.05$) and the Tukey-Kramer Post-Hoc Test ($P = 0.05$, Critical Value = 3.88): both dace and chub utilized plants more than other species (*d.f.* = 271, F = 17.3), larvae of stoneflies were used significantly less by chub than by stone loach and bullhead (*d.f.* = 271, F = 3.58), plecopterian larvae were utilized more by stone loach than by other fish species (*d.f.* = 271, F = 9.91), and dipteran larvae were utilized more by bullhead (*d.f.* = 271, F = 5.56). Piscivory was detected only in brown trout and chub, and was only significantly different from other species in brown trout (*d.f.* = 271, F = 3.00). When evaluating the use of terrestrial insects, there seems to be a higher utilization by chub and brown trout in comparison with bullhead and stone loach (*d.f.* = 271, F = 12.22).

Other differences (molluscs, gammarids) were not statistically significant, and could have been caused by single, sporadic, or even intensive intakes.

Due to the considerable importance of some particular food components, *i.e.* caddisflies from the families Limnephilidae tribus *Stenophylacini*, Rhyacophilidae and Hydropsychidae and mayflies from the families Heptageniidae, Baetidae, Leptophlebiidae and Ephemeridae, individual comparisons were also performed.The differences in intakes of these food components, represented by the weighted average values of $Mtot_p$ for particular species, correspond with the results of ANOVA and the Tukey-Kramer Post-Hoc Test ($P = 0.05$, Critical
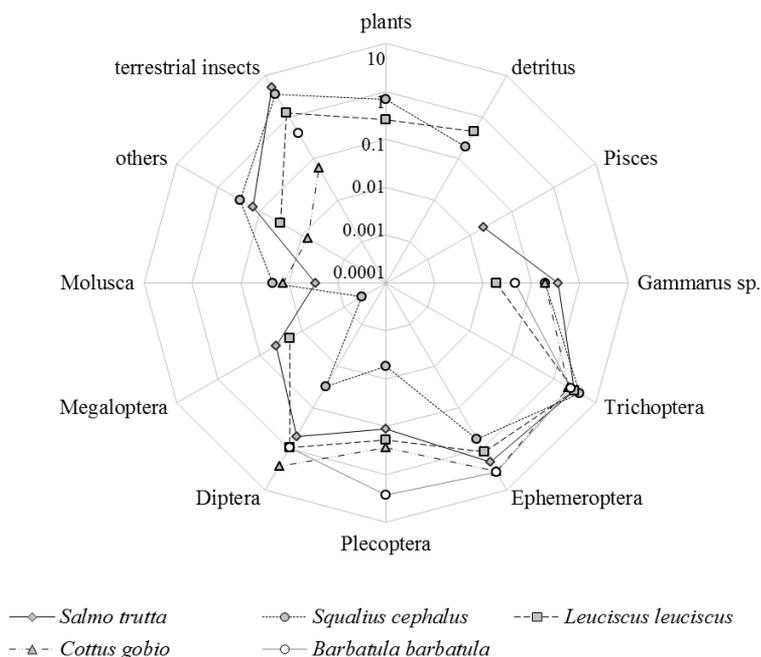
Figure 3
The use of particular food components in the diet of the studied fish species (log-transformed Mtot_p).
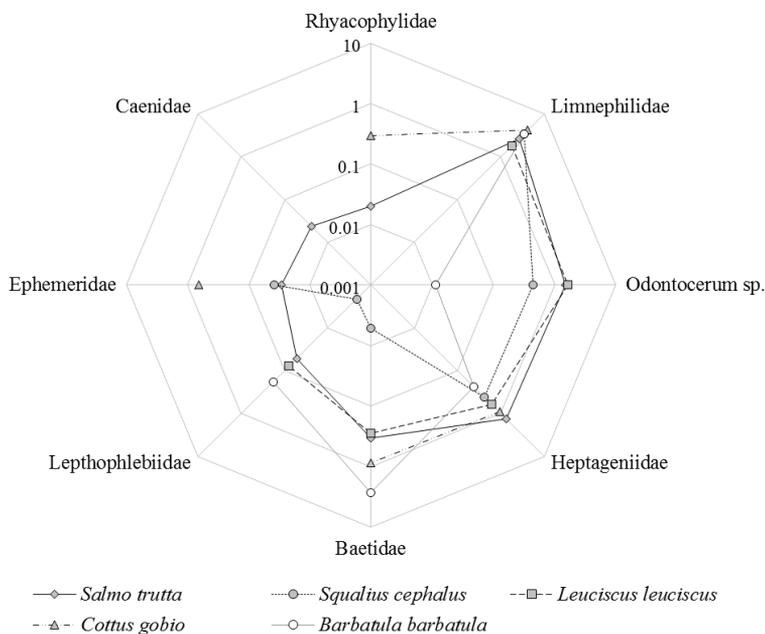

Figure 4
Use of particular families and species of macrozoobenthos in the diet of the studied fish species (log-transformed Mtot_p).

Value = 3.88) (see Figure 4). Bullhead used caddisflies from the families Rhyacophilidae and Hydropsychidae significantly more than chub and dace (*d.f.* = 271, *F* = 2.93), caddisflies of the genus *Odontocerum* were consumed less by bullhead and stone loach than by dace and brown trout (*d.f.* = 271, *F* = 3.84), mayflies from the family Ephemeridae were used mostly by bullhead, significantly more than by other species (*d.f.* = 271, *F* = 4.96) and mayflies from the family Baetidae comprised a greater part of the food of stone loach than for other species (*d.f.* = 271, *F* = 4.62).
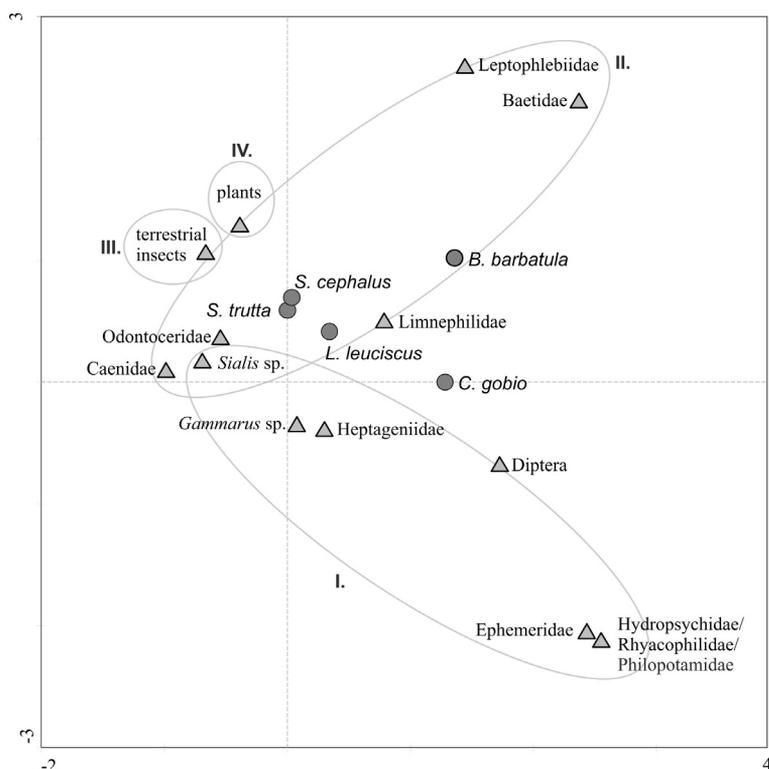
Figure 5

First and second axes of the DCA biplot (matrix fish × food components). Numerals and ovals refer to food particles summarized as food categories (I – IV): I – food sources living hidden under stones or in the substrata and usually staying hidden, II – more easily accessible, living on the bottom, on stones; III – drifting food particles (e.g. plants, water coleopterans and heteropterans, fish, etc.); IV – terrestrial insects.

The ingestion of the food components from four categories (as *Mtotp*) were also compared (see Material and methods), and differences were analyzed by ANOVA and the Tukey-Kramer test ($P < 0.05$):

1. Organisms in the first category comprised a large (approximately 18%) proportion primarily in the food of brown trout and bullhead. In the food of dace, they made up the smallest proportion (5.9%), with the difference between brown trout and dace being significant.
2. The second category was the dominant constituent of all species. It comprised the largest percentage in the food of bullhead (80%) and stone loach (92%). Stone loach used this constituent significantly more than brown trout, chub and dace.
3. The third category was only represented in dace and chub, primarily caused by the large amount of water plants present in their diet, as well as the occurrence of water coleopterans, heteropterans and vertebrates in chub. Significant differences, however, were only found between chub and other species.
4. The fourth category played the largest role in the food of brown trout and chub, where it comprised over 30% of the food supply. On the other hand, for bullhead and stone loach it made up less than 1%; these large differences were significant.

The categories of food and data about the use of important food components were used to evaluate competition using DCA (see Figure 5). From these analyses, it is possible to conclude that the closest relationship was between chub and brown trout. When examining the DCA results, it is clear that the food components formed gradients, which is homologous with the above-mentioned ecological food categories (see ovals in Figure 5). A relationship between bullhead and stone loach can also be seen, which are separated from the other group of brown trout-dace-chub.

The relationship of particular species to food categories can be interpreted as follows: brown trout consumed all food sources relatively equally, with the closest relationship to easily accessible benthos or that hiding below stones, and also distinctly using terrestrial insects. Chub had almost the same food usage as brown trout, though using food from category III, *i.e.* drift and allochthonous sources, more than brown trout. The food spectrum of dace was most similar to chub, though consuming fewer hidden species of benthos and terrestrial insects. The main components of its food consisted of easily accessible benthic organisms. The food of bullhead was most similar to that of stone loach. Bullhead primarily used benthos, and terrestrial insects and drift the least. They also consumed hidden species more than easily accessible species. The food of stone loach was very similar to that of bullhead (minimally using drift and terrestrial insects); they consumed fewer hidden species, but more easily accessible species.

DISCUSSION

Many recent as well as older studies have focused on food competition (Copp *et al.*, 1994; Dyk, 1932; Fischer, 2000; Fochetti *et al.*, 2008; Gatz *et al.*, 1987; Markovič *et al.*, 2007), sometimes under experimental conditions (Holmen *et al.*, 2003; Jansen *et al.*, 2002). One common method of processing data about food components in such studies is the grouping of individual components into systematic categories, as was also done in our study. It is difficult to find conclusive differences for these systematic groups in our data; generally, all fish consumed large quantities of caddisflies, mayflies and dipteran juveniles, as has been found by, *e.g.*, Fochetti *et al.* (2008), Maitland (1965), Markovič *et al.* (2007), Straškraba *et al.* (1966) and Welton *et al.* (1991). In the Úpoř brook mayflies comprised 34% and caddisflies 45% of the food supply, respectively, and differences in this supply and the consumption of particular species were not significant (χ^2 test, $P > 0.8$). From Figure 2, it is clear that these numerous components comprised a large proportion of the fish diets and were often ingested. This would indicate very strong competition among individual fish species with regard to benthos. For the above-mentioned reasons, competition according to particular families and individual species of benthos was also evaluated, and significant differences were found. Many of the preferences/avoidance result from the typical habitats preferred by particular fish species (Straškraba *et al.*, 1966). This can explain, for instance, the increased use of hidden mayflies and caddisflies from the Heptageniidae, Ephemeridae and Rhycophilidae families observed in bullhead. Differences found in the consumption of the species *Odontocerum albicorne* (preferably selected by dace and negatively selected by bullhead and stone loach) could be influenced by the character and size of its cases whereas bullhead and stone loach preferred mayflies from the Baetidae family. Such preferences in bullhead were experimentally demonstrated by Dahl (1999). The preference of brown trout for the Baetidae family has been reported by Straškraba *et al.* (1966) and Teixeira and Cortes (2006). On the other hand, Zimmerman and Vondracek (2007) as well as Dahl (1999) reported strong preferences for the Gammaridae family in brown trout diets, but this was not reflected in our results.

The food of the fish species studied here did not only consist of macrozoobenthos. Fish, plants, terrestrial insects and detritus were also found in their diet. Piscivory played a very small role in the food of the fish observed, only appearing considerably in the food of brown trout (and in one case in the food of both chub and bullhead). In brown trout it comprised 2.9% (and less than 1% when using the weighted average). Dyk (1956) drew attention to selective piscivory in large brown trout, with reference to both stone loach and bullhead (Dyk, 1932) as food sources. In the Úpoř brook, fish (5 bullheads and 1 lamprey juvenile) were found in individuals of brown trout measuring longer than 148 mm (129 mm in the case of lamprey). Horton (1961) found a 12% incidence of piscivory in the Walla stream, and Yevsin and Ivanov (1979) 7% piscivory in the river Pulonga; however, the average lengths of these samples were 600 and 400 mm, respectively. Hesthagen *et al.* (2004) reported only one occurrence of piscivory in a sample of 207 brown trout from 70–120 mm in length. In the former Czechoslovakia, Dyk (1956) found a piscivory incidence of 12% in 641 brown trout, representing the 7th most

important food source. This also calls attention to the higher nutritional value of fish and the related lower frequency of food ingestion. A similar phenomenon was observed by L'abée-Lund et al. (2002), who observed changes in piscivory by brown trout over a long period, and noted differences in growth in this changing population.

Piscivory in chub was identified in only one case (with 1 brown trout as prey). As for brown trout, piscivory occurs primarily in larger chub individuals (Maitland and Campbell, 1992), whereas small chub of about 160 mm in length were dominant in the Úpoř brook. Markovič et al. (2007) mentioned piscivory in chub aged 6 years and older. Piscivory was even identified in bullhead, with a juvenile brown trout appearing as food in one case. Sporadic piscivory in bullhead has also been mentioned by Andreasson (1971) and Hesthagen et al. (2004). Maitland and Campbell (1992) even found piscivory (juvenile individuals) in 3% of the bullhead they examined.

Competition can also be reduced by fish preferring different microhabitats. Cavalli et al. (1998), Jansen et al. (2002), and Saksgard and Hesthagen (2004) have described the character displacement of brown trout and the brook char Salvelinus fontinalis in lakes, where brown trout concentrated on littoral and epibenthic habitats and brook char on epipelagic habitats. Hestagen and Heggenes (2002) and Hesthagen et al. (2004) also described the preference of bullhead for deeper substrata compared with brown trout. The opposite preference is generally thought to be more common, as in our location, where bullhead preferred coarse stone substrata and shallower depths. Microhabitat preferences were studied in this locality by Vlach et al. (2005).

Moreover, not only fish prefer different habitats, but the way benthos use the water column is species-specific. Hieber et al. (2003) pointed out that certain species of mayflies are often a part of drift (Rhitrogena sp., Baetis sp.), while others, even though also often occurring in benthos, are almost non-existent in drift (Ecdyonurus sp.). This is in accordance with the very different ecological demands and habitat preference of mayfly juveniles. If the main source of benthic organisms in drift is primarily disturbance due to changes in water flow (Lake, 2000) that moves substratum particles and therefore causes food items to become dislodged (Death, 2003), it is clear that crawling or swimming mayfly larvae will be dislodged more often than hidden or burrowed larvae. Although the larvae of hidden species may appear during faster flows or during hatching (Mann, 1974), from the perspective of the whole season this may be disregarded.

From the evaluation of competition with respect to benthos, it is clear that a systematic summary of food components may not always be appropriate. Therefore, in this work a new approach was also used, attempting to compare food categories while taking into account the distribution of all food components. These food categories indicate the availability of the food components for particular fish species with respect to their habitat preferences. It can be seen from Figure 5 that data about the composition of particular species evaluated by DCA showed such gradients in food ingestion that correspond to the food categories. Moreover, evaluating these categories and the consumption of particular species (or families) of benthos using DCA demonstrated further divergence in food demands. The competitor groups formed by bullhead-stone loach and chub-dace reflect two competing morphologically similar species with a preference for the same microhabitat and the same niche (Adámek et al., 2003; Gatz et al., 1987; Pouilly et al., 2003; Volpe et al., 2001).

The results from DCA, shown in Figure 5, clearly demonstrate the main findings of this study. The relatively close relationship of all species on the basis of food consumption is evident in the center of Figure 5. This resulted from the fact that benthos comprised the largest proportion in the food of all observed species, as also reported by Maitland (1965) and Straškraba et al. (1966). It can also be seen that the highest competition is between brown trout and chub, reflected in the fact that in addition to benthos they also often consumed (as rheophilic species) allochtonous material consisting of terrestrial insects from the water surface or drifting through the water column. From this point of view, the relatively low competition between the brown trout – chub – dace group and the stone loach – bullhead group is not surprising, because the second group did not consume allochtonous material. Differences between

bullhead and stone loach are in accordance with their habitat preference and ecology, with bullhead consuming more hidden macrozoobenthos species (food category I.) than stone loach. Unlike many studies that have considered bullhead to be a strong temporary or permanent food competitor of brown trout, (Andreasson, 1971; Hestagen and Heggenes, 2002; Hesthagen *et al.*, 2004; Holmen *et al.*, 2003), no such relationship was found in our data. The position of dace among these species is governed by its close relationship to benthos and drifted plants and detritus. Differences between stone loach and dace (both species preferred particles in food category II.) are clear from their consumption of individual species of benthos; dace prefers larger morsels with a special preference for *Odontocerum albicorne*, whereas stone loach prefers smaller morsels such as stonefly and mayfly juveniles from the Baetidae and Leptophlebiidae families.

ACKNOWLEDGEMENTS

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