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Endangered aquatic macrophytes in the diet of rudd (*Scardinius erythrophthalmus*)

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Abstract. Oxbow lakes are specialised standing water bodies that often support unique macrophyte and animal communities. Between 2015 and 2016, we assessed the diet composition of adult rudd (*Scardinius erythrophthalmus*) in one such macrophyte-rich lake. Over 2016, we also undertook a series of feeding behaviour tests under artificial conditions, the aim being to assess whether adult rudd represent a threat to the endangered sharp-leaved pondweed (*Potamogeton acutifolius*). In total, we examined 100 digestive tracts of rudd feeding under natural conditions and 100 from rudd feeding under artificial conditions. Our results show that i) *P. acutifolius* is deliberately consumed by rudd, and ii) pondweeds, periphyton and invertebrates were the dominant dietary components in the diet. A reluctance to consume cleaned *P. acutifolius* suggests a link with periphyton and invertebrate consumption. While rudd clearly consume *P. acutifolius*, we found no evidence of any negative impact on either pondweed development or on the macrophyte community as a whole.

Key words: herbivorous fish, diet composition, oxbow lakes, *Potamogeton acutifolius*, feeding habits

Introduction

Oxbow lakes are a distinctive form of shallow standing waterbody, formed when a wide meander from the main stem of a river is cut off. Such lakes provide optimal conditions for submerged macrophytes, with high nutrient availability, plenty of light and warm water temperatures. As such, many of these lakes support unique macrophyte and animal communities, often including endangered macrophyte species. The sharp-leaved pondweed (*Potamogeton acutifolius*) is typically found in mesotrophic to mid-eutrophic lentic habitats along lowland rivers (e.g. oxbow lakes), but has shown a recent decline, possibly due to the increasing occurrence of longer dry period leading to a drop in water levels and increased eutrophication. The species is currently included in the European Red List data book for vascular plants as an endangered species and is classified as endangered in the Czech Republic according to Red List of Protected Species (Danihelka et al. 2012).

The rudd, *Scardinius erythrophthalmus*, is a widespread European cyprinid species found in most still or slow-flowing freshwaters (Wolnicki et al. 2009). As rudd are phytophilic and spawn on soft aquatic macrophytes, they are usually associated with abundant submerged vegetation (Hicks 2003). Rudd fry consume unicellular algae and phytoplankton and switch to zooplankton and small chironomids when they reach ca. 10 mm standard length (SL) (Kennedy & Fitzmaurice 1974). Older rudd (> 149 mm SL) may also consume chironomids; however, the greater part of their diet consists of soft submerged macrophytes (Baruš & Oliva 1995, Tomec et al. 2003). The predominance of different food categories in the diet depends strongly on season (Nurminen et al. 2003), with rudd usually preferring zooplankton and small invertebrates in spring and autumn, with macrophytes and algae increasing in importance in summer (García-Berthou & Moreno-Amich 2000, Vejříková et al. 2016).

As rudd commonly occupy the same habitat as *P. acutifolius*, they could theoretically pose a threat to this endangered species (Guinan et al. 2015), either through grazing to the plant or through other, as yet unidentified, impacts. To the best of our knowledge, such interactions have yet to be examined in the native

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habitat of both species. The aim of this study, therefore, was to assess whether rudd is a significant consumer of *P. acutifolius* in small, shallow macrophyte-rich oxbow lakes, and whether they have any impact on macrophyte-rich aquatic systems as a whole.

Material and Methods

Study area

This study was undertaken in a shallow (max. depth 2 m) 0.4 ha oxbow lake associated with the River Orlice (the Elbe River basin), situated near the town of Hradec Králové in north-eastern Bohemia, Czech Republic (50°13′04″ N, 15°53′82″ E, altitude 230.5 m a.s.l.; Fig. 1).

The locality is situated within the Pekelská jezera Nature Park and the alluvial wetlands are artificially flooded at least once each five years. While the oxbows come under the control of the Czech Anglers Union, no fish had been stocked in the oxbows for at least five years before this study. The most common species in the oxbows are cyprinids, with crucian carp (*Carassius carassius*) and rudd (*Scardinius erythrophthalmus*) usually dominant. Common carp (*Cyprinus carpio*) also occur rarely due to earlier stocking efforts.

The aquatic macrophyte community in the oxbow is dominated by hornworth (*Ceratophyllum demersum*), Eurasian watermilfoil (*Myriophyllum spicatum*), *P. acutifolius* and water crowfoot (*Batrachium trichophyllum*).

Macrophyte sampling

For the purposes of this study, submerged aquatic macrophytes were sampled manually along a 15 m stretch at four littoral sites (Fig. 1) in April, June, August, October and December of 2015 and 2016, based on the methods of Grulich & Vydrová (2006). For organisational reasons, monitoring was undertaken each two months at the same time as fish monitoring. Macrophytes were determined to species level and expressed as relative frequency over the study stretch. These values were then expressed gravimetrically and used to determine Ivlev's index of electivity (see below).

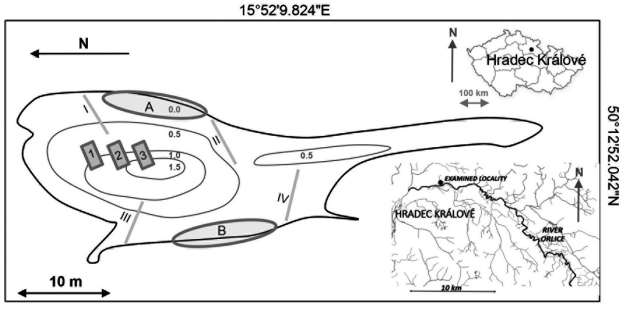


Fig. 1. The oxbow study area in the Pekelská jezera Nature Park, with monitoring and experimental sites indicated. A + B = beach seining sites, I-IV aquatic macrophyte monitoring sites, 1-3 experimental cages.

Fish sampling

Rudd sampling was performed in April, June, August, October and December of 2015 and 2016 using a 20 m 2 cm mesh beach seine along both long banks (Fig. 1). All fish caught were identified to species, measured to the nearest 1 mm (SL) and species other than rudd released back to the oxbow alive.

Fish caught in 2015 were used for dietary analysis (100 individuals), while those in 2016 were used for a field test of feeding preference under artificial conditions (100 individuals). All rudd in the feeding experiment were >180 mm SL and aged five years or older, this being the dominant category in the oxbow, i.e. the main potential threat to submerged macrophytes (Baruš & Oliva 1995, Tomec et al. 2003). In addition, we captured and examined 20 sub-adult rudd < 180 mm SL in June 2015, though this cohort was not expected to consume macrophytes. Immediately after capture, all fish were euthanised with an overdose of clove oil, placed separately into laboratory zip-lock bags and kept on ice in a cooler box until examined in the laboratory (Taraborelli et al. 2010, Mikl et al. 2017).

Diet analysis: 2015

Rudd were weighed to the nearest 0.1 g and the first third of the digestive tract removed and weighed to the nearest 0.001 g. The final two thirds of the gut were not examined due to excessive food digestion (Vøllestad 1985). The gut was again weighed after removal of ingested food, the difference being considered the mass of food. Gut contents were frozen for further analysis. Fish with empty digestive tracts were noted and excluded from further analysis.

Nutritional analysis

Protein, lipid and ash content were analysed in order to determine the basic biochemical composition of *P. acutifolius* and filamentous algae, protein being quantified using the Kjeldahl method, lipids using extraction with trichloroethylene and ash assessed following incineration in a muffle furnace at 525 °C for six hours (see Tomec et al. 2003). While other macrophyte species may also contribute significantly to the diet, we concentrate on *P. acutifolius* only as a) we are specifically interested in the value of this

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particular species as a food item, and b) previous studies have already determined the nutritional value of *P. crispus* (Shaltout et al. 2016) and *C. demersum* (Esteves & Suzuki 2010, Laining et al. 2016).

Field experiment: 2016

Three 2 m^3 (2 × 1 × 1 m) 20 mm mesh cages were placed on the lake bottom and stabilised with iron rods. All three cages covered an area of submerged macrophytes of similar density and composition (including *P. acutifolius*) to that under natural pond conditions. The macrophytes in cage 3 were cleaned of invertebrates and algae using a soft toothbrush and pressurised water. Rudd were only stocked (or restocked) in the cage after full sedimentation of solid particles to the bottom. While recolonisation is, to some extent, inevitable during the exposure period, we expect no bias toward colonisation from previously cleaned invertebrates.

Twenty rudd of > 180 mm SL were stocked in two of the cages and the third cage (Group 1 – no fish; control) contained submerged macrophytes only (Fig. 1). In one of the two stocked cages, the macrophytes were left in their natural state (Group 2) while those in the second cage were regularly cleaned of epiphytic organisms (Group 3). Between April and December 2016, the rudd were removed from both stocked cages each month and replaced with 20 new individuals of the same size cohort. The removed rudd were euthanised with an overdose of clove oil, placed separately into laboratory zip-lock bags and kept on ice in a cool box until laboratory processing. Each fish was measured to the nearest 1 mm SL and weighed to the nearest 0.1 g. The gut contents in the first third of the digestive tract were removed and weighed to the nearest 0.001 g. Dietary composition was determined as set out below.

Data analysis: 2015-2016

A modification of the gravimetric method (Hyslop 1980) was used to analyse food content in the laboratory. The bulk of the sample consisted of aquatic macrophytes and these were separated from determinable taxa under a binocular microscope. Invertebrate taxa were determined to the lowest taxonomic level by examining identifiable remains (e.g. chironomid head capsules and chitinous remains (carapace, exopodites, post-abdomens) of cladocerans under a 40-450× magnification binocular microscope. *Simocephalus* sp., for example, were determined using the reconstruction method of Orlova-Bienkowskaya (2001). The proportion of

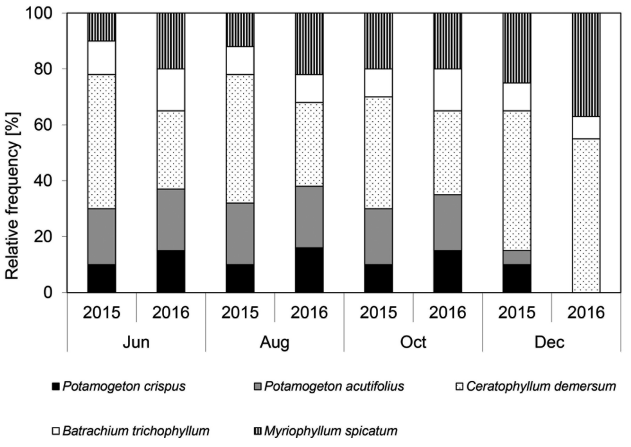


Fig. 2. Temporal variation in macrophyte composition over 2015 and 2016 at the oxbow study site in the Pekelská jezera Nature Park.

total food intake represented by each category was evaluated by the indirect method of Manko (2016), using the following formula:

$$\%m = (m_i/m_t) \times 100$$

where m_i is the weight of a particular food component and m_t is the weight of all food components combined. This value was then combined with frequency of occurrence and expressed as the index of preponderance (IP) according to Natarajan & Jhingran (1961):

$$\%IP = 100 \times ((m_i \times FO_i)/\Sigma(m_i \times FO_i))$$

where m_i is the weight percentage of a particular food component and FO_i is the frequency of occurrence of that food component (Pivnička 1981). The degree of selectivity for all dietary items found in rudd digestive tracts was evaluated using Ivlev's index of electivity (E; Ivlev 1961):

$$\%E = (r_i - n_i)/(r_i + n_i)$$

where r_i is the relative abundance of prey item i in the gut and n_i is the relative abundance of the same prey item in the environment. Prey items in the

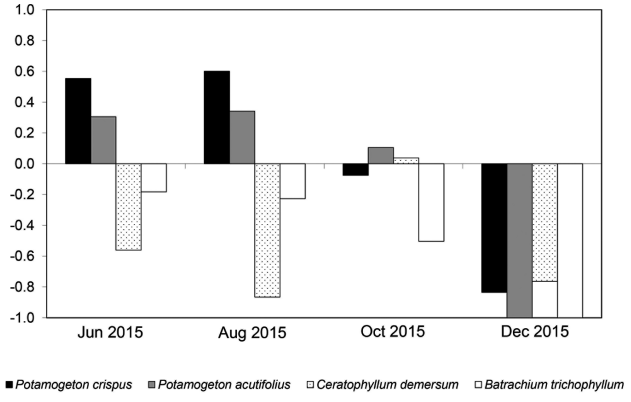


Fig. 3. Ivlev's index of electivity for macrophytes at the oxbow study site in the Pekelská jezera Nature Park (2015 only).

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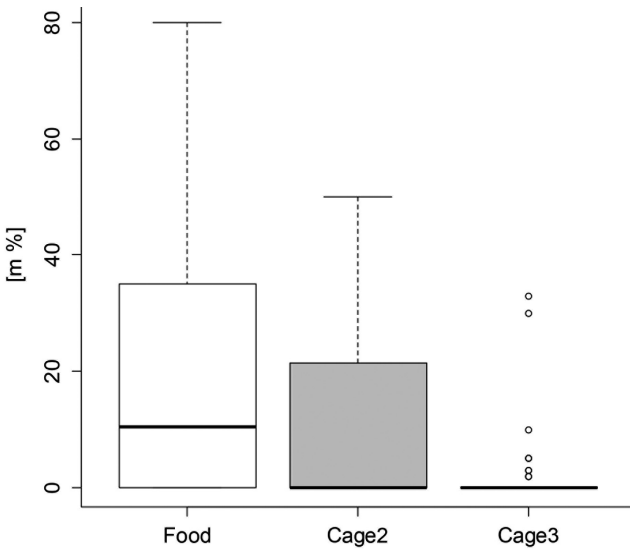


Fig. 4. Consumption of *P. acutifolius* by free-living rudd in 2015 (Food) and in the experimental cages 2016 (Cage 2 – uncleaned, Cage 3 – cleaned). Boxplots = quartiles (Q1, median and Q3), whiskers = maximum, dots = outliers.

environment were expressed gravimetrically as n_i. A value of E = 0 means a particular food item was taken in direct relation to its availability, –1 < E < –0.01 indicates avoidance (consumed less than expected from estimates in the environment) and 0.01 < E < 1 represents preference (consumed more than expected from estimates in the environment). The index of electivity was evaluated in 2015 only in order to assess the diet preferences of free-living fish. In 2016, the same site was used for the caged experiments.

Statistical evaluation

Differences between macrophyte and dietary groups compared during field observation and during the cage experiment were evaluated using one-way ANOVA ($P < 0.05$) with post-hoc Tukey-tests. All analyses were performed using the R software package v. 3.5.1 – R Core Team 2018 (Crawley 2007).

Results

Macrophyte composition

From April to December in both 2015 and 2016, *C. demersum* dominated in the macrophyte community (32.7 %), followed by *P. acutifolius* (13.1 %) and *M. spicatum* (16.6 %) (Fig. 2.) Both *P. crispus* (8.6 %) and *B. trichophyllum* (9 %) were recedent. Surface water macrophyte coverage was 72.5 % in 2015 and 80 % in 2016, with no significant difference in the overall proportion of *P. acutifolius* observed in 2015 and 2016 ($P > 0.05$). By December 2015, however, *P. acutifolius* abundance had decreased to 5 %, and it was not found at all in December 2016 (Fig. 2). Likewise, *P. crispus* was down to 10 % in December 2015 and was not found in December 2016. In both cases, these represent standard seasonal successional declines over the winter period.

Diet composition

Three items dominated the diet of adult rudd under natural conditions, *P. acutifolius* (%IP = 35.7 ± 8.3), filamentous algae (%IP = 31.9 ± 32.4) and *P. crispus* (%IP = 21.1 ± 16.7). These were followed by *C. demersum* (%IP = 16.7 ± 15.8) and detritus (%IP = 11.4 ± 9.5), with *B. trichophyllum* (%IP = 6.0 ± 2.1) and aquatic invertebrates (mainly chironomids and *Simocephalus* sp.; %IP = 1.8 ± 1.4) recedent (Table 1). *Potamogeton acutifolius* was observed in June, August and October 2015 only, being replaced by *C. demersum* in October 2015.

Table 1. Index of preponderance (IP) of main food items under natural conditions. SL = standard length (mm), Wt = total weight (g), SD = standard deviation.

	Apr 2015	Jun 2015	Aug 2015	Oct 2015	Dec 2015	Mean
Potamogeton crispus	-	34.8	40.1	8.6	0.9	21.1
Potamogeton acutifolius	-	37.6	44.8	24.7	-	35.7
Ceratophyllum demersum	-	13.5	3.3	43.2	6.7	16.7
Batrachium trichophyllum	-	8.3	6.3	3.3	-	6.0
Filamentous algae	74.0	3.3	1.4	12.3	68.5	31.9
Aquatic invertebrates	3.9	0.6	0.5	2.3	-	1.8
Detritus	22.1	1.9	3.6	5.6	23.9	11.4
n fish	20	20	20	20	20	
n fish with no food	4	0	0	0	2	
SL (SD)	214.4 (18.7)	271.5 (13.8)	292.3 (19.5)	297.0 (12.1)	292.5 (14.5)	
Wt (SD)	280.9 (92.5)	469.6 (55.4)	369.3 (23.0)	338.2 (55.9)	312.6 (50.7)	

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Table 2. Index of preponderance (IP) of main food items in experimental Cage 2 – uncleaned macrophytes. SL = standard length (mm), Wt = total weight (g), SD = standard deviation.

	Apr 2016	Jun 2016	Aug 2016	Oct 2016	Dec 2016	Mean
Potamogeton crispus	-	22.7	18.9	5.6	-	15.7
Potamogeton acutifolius	-	21.5	22.3	13.1	-	19.0
Ceratophyllum demersum	-	2.8	5.4	4.9	-	4.4
Batrachium trichophyllum	-	0.2	0.5	0.4	-	0.4
Filamentous algae	21.5	6.8	17.3	11.6	3.1	12.1
Aquatic invertebrates	46.2	12.5	6.6	19.0	78.3	32.5
Detritus	32.3	33.5	29.0	45.4	18.6	31.8
n fish	20	20	20	20	20	
n fish with no food	12	3	0	0	12	
SL (SD)	220.4 (24.5)	292.5 (9.7)	289.9 (11.7)	298.9 (11.7)	226.0 (31.9)	
Wt (SD)	288.5 (106.1)	437.6 (54.6)	389.63 (64.3)	323.1 (43.9)	260.5 (98.9)	

Table 3. Index of preponderance (IP) of main food items in experimental Cage 3 – cleaned macrophytes. SL = standard length (mm), Wt = total weight (g), SD = standard deviation.

	Apr 2016	Jun 2016	Aug 2016	Oct 2016	Dec 2016	Mean
Potamogeton crispus	-	0.4	0.7	1.7	-	0.9
Potamogeton acutifolius	-	0.5	0.6	6.6	-	2.6
Ceratophyllum demersum	-	0.3	0.1	0.3	-	0.2
Batrachium trichophyllum	-	0.1	0.1	0.0	-	0.1
Filamentous algae	2.1	0.9	1.7	2.3	-	1.8
Aquatic invertebrates	80.1	59.6	37.0	24.1	70	54.2
Detritus	17.8	38.2	59.8	65.0	30	42.2
n fish	20	20	20	20	20	
n fish with no food	15	4	7	13	19	
SL (SD)	211.9 (20.7)	285.4 (11.6)	278.5 (10.0)	278.5 (10.0)	219.0 (35.9)	
Wt (SD)	240.2 (68.3)	390.9 (49.6)	298.8 (46.1)	285.0 (47.9)	249.9 (108.0)	

Table 4. Nutritional analysis of *P. acutifolius* and filamentous algae in the experimental cages (Cage 2 – uncleaned, Cage 3 – cleaned).

Parameter	Unit	Uncleaned *P. acutifolius*	Cleaned *P. acutifolius*	*Filamentous algae*
Protein	%	12	13.5	8.7
Fat	%	7.1	7.3	2.9
Ash	%	34.1	24.8	31.6

Over the whole sampling season, rudd consumed significantly more *P. acutifolius* and *P. crispus* than all other dietary items together ($P < 0.05$), with no significant difference between the quantities of *P. acutifolius* and *P. crispus* taken ($P > 0.05$). The mean index of electivity value was 0.25 for *P. acutifolius* and 0.36 for *P. crispus* (Fig. 3), suggesting intentional consumption of these food items (December [winter] values excluded). Mean values for *C. demersum* (–0.46) and *B. trichophyllum* (–0.30) indicated avoidance of these food items.

Field experiment

Macrophyte community development was similar in all three cages (Group 1 – control, Group 2 – uncleaned, Group 3 – cleaned) over the whole experiment, with no significant difference in the quantity of *P. acutifolius* available throughout ($P > 0.05$). Rudd dietary composition, however, showed significant differences between the stocked cages (Tables 2 and 3), with invertebrates (%IP = uncleaned 32.5 ± 26.6, cleaned 54.2 ± 20.7) and detritus (%IP = uncleaned

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31.8 ± 8.6, cleaned 42.2 ± 17.8) dominant items in the cage with cleaned macrophytes (Group 3), and all macrophyte species and filamentous algae recedent (Tables 1-3). In the uncleaned cage (Group 2), *P. acutifolius* (%IP = 19.0 ± 4.2), *P. crispus* (%IP = 15.7 ± 7.3) and filamentous algae (%IP = 12.1 ± 6.7) were all important dietary items, with all other items recedent. Fish consumed significantly more macrophytes (including *P. acutifolius*) in the uncleaned cage ($P < 0.05$); with significantly less ($P < 0.05$) *P. acutifolius* remaining Fig. 4; (Tables 1-3).

Nutritional content

Nutritional analysis indicated only slight differences between cleaned and uncleaned *P. acutifolius*, with fat at 7.3 % and 7.1 %, respectively and protein at 12 % and 13.5 %, respectively (Table 4). In comparison, filamentous algae contained a much lower proportion of fat (2.9 %) and protein (8.7 %) (Table 4).

Discussion

In this study, we investigated the potential influence of rudd on *P. acutifolius*, an endangered aquatic macrophyte, in a shallow oxbow lake. Conditions within the oxbow lake (small area and a relatively low rudd density [max. 500 ind./locality, or 0.125 ind./m^2]) limited our experiment somewhat by preventing us undertaking the field experiment and dietary analysis in the same year. Further, significant changes occurred in the 2017 plant and fish community (attributable to a particularly hard winter over 2016/2017) and this prevented us undertaking replicates of the experiment under similar conditions. Despite this, we strongly believe that our study truly reflected natural conditions in this oxbow lake and, as such, the conclusions can be applied to similar habitats along many waterbodies throughout Europe. It should also be noted that many of the organisms taken as food were unidentifiable due to different stages of digestion and the absence of more durable body parts (e.g. Rotifera, Cnidaria, Oligochaeta). Such organisms could still represent important dietary items and their absence in the total identified prey may have had an impact on the relative quantities of macrophytes and invertebrates in the dietary analysis. Nevertheless, we feel the relative proportions are generally accurate and certainly allow comparisons between samples. Finally, while the density of fish in the cage experiments was higher than that in the oxbow itself (10 ind./m^2 *vs.* 0.125 ind./m^2), and hence there may have been density dependant impacts of observed diet, the fact that a significant proportion of *P. acutifolius* remained in the cage at the end of each experimental run would tend supported our findings, i.e. that rudd, even at relatively high densities, were not having a significant impact on *P. acutifolius*.

Dietary analysis indicated that rudd deliberately consumed submerged macrophytes throughout the year, as also noted by Losos et al. (1980), Prejs (1984) and García-Berthou & Moreno-Amich (2000). On the other hand, Tomec et al. (2003) noted that rudd from Lake Vrana (Croatia) mainly consumed algae, with macroinvertebrates (e.g. chironomids and Trichoptera larvae) always forming an accompanying but important part of the diet and submergent macrophytes only representing a minor proportion. Several other authors have also recorded rudd diet as including macroinvertebrates, especially gammarids, *Asellus* and trichopteran larvae (e.g. Martyniak et al. 1996, García-Berthou & Moreno-Amich 2000). Our own data confirm that macrophytes are indeed taken alongside algae and macroinvertebrates at significant levels; however, we suggest that further studies are needed to clarify the relative importance of the three food types in rudd diet and the specific roles played by different macroinvertebrate taxa in different environments and seasons.

There are several reasons why *P. acutifolius* may have been consumed at the level observed in this study. Our results showed that some macrophyte species at the study site were consumed more or less often by rudd than their availability would suggest. While *C. demersum* was the dominant species at the study site, for example, its proportion in the diet was very low, while *M. spicatum*, which was also abundant, was not consumed at all. In these cases, we suggest that the species were avoided due to the shape of the plant, deposition of inorganic substances in the cell walls (Stanković & Pajević 2001) and presence of aromatic oils (Wang et al. 2015). In comparison, both pondweed species were frequently consumed by rudd, probably due to the relative absence of inorganic substances and the presence of partially decomposed and soft peripheral parts. The proportion of *P. crispus* in the diet decreased strongly over autumn, probably reflecting the end of the *P. crispus* growing season. Our comparative experiments indicated that rudd consumed *P. acutifolius* significantly more often when confronted with macrophytes covered with algae and macroinvertebrates. As algae also represent a significant source of nutrition (Table 4), it is likely that the fish increase their intake of *P. acutifolius* (either accidentally or intentionally) while feeding on the algae attached to the plant's surface. Interestingly,

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we noted a significant difference between fish feeding naturally (i.e. outside the cages) and those feeding in Cage 2 (uncleaned), possibly as a result of differing feeding behaviour due to an increased relative fish density in the enclosed space and a more restricted potential diet. Further studies would be needed to clarify this observation. In comparison, macroinvertebrates dominated the diet in Cage 3 (cleaned), despite the macrophytes being regularly cleaned of periphyton/algae. Owing to its upturned mouth (which allows it to feed at the water's surface or on the underside of leaves), the rudd is morphologically ill-adapted to feeding on the bottom substrate (Eklöv & Hamrin 1989). As such, we assume that the fish were forced to support consumption of incoming phytophilous invertebrates with those from bottom habitats due to the temporary absence of a periphyton/algal community on the macrophyte surface.

We suggest that the leaves of some aquatic plants, including *P. acutifolius*, may become an attractive food source, or are taken more often accidentally, as they gradually decompose and soften, particularly when covered in periphyton/algae and invertebrates. In our case, increased consumption of filamentous algae may have a similar cause, being taken from the oxbow bottom at the same time as invertebrates. Periphyton and benthic filamentous algae in standing waters are commonly inhabited by ciliates, rotifers, cnidarians, small oligochaetes, larval stages of Chironomidae, Trichoptera, Mollusca and small cladocerans (Lodge 1990, Ravera & Jamet 1991). Such items represent a more profitable food source for rudd than macrophytes alone (Lodge 1990, Ravera & Jamet 1991), and are found in the diet more often at times when there are not enough macrophytes (e.g. in April and December). Our study showed that rudd consumed a significant quantity of *P. acutifolius*, and that macrophyte consumption increased when the leaves were covered in periphyton, algae and invertebrates. When regularly cleaned, macrophytes were only consumed at low levels, suggesting that *P. acutifolius* may not always have been the primary target of the rudd. Despite the relatively high levels of consumption, there appeared to be no negative impact on the *P. acutifolius* population, as also indicated by the long-term co-existence of the two species in the oxbow.

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