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7 **Stable isotopes and gut contents indicate differential resource use by**
8 **coexisting asp (*Leuciscus aspius*) and pikeperch (*Sander lucioperca*)**

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22 Running title: Resource use by coexisting asp and pikeperch

23

24 Abstract

25 Differential use of habitat and prey resources is an important mechanism that may allow
26 coexistence of sympatric species. Unlike interactions between smaller cyprinid and percid
27 fishes, the resource use by coexisting predatory asp (*Leuciscus aspius*) and pikeperch (*Sander*
28 *luciperca*) is relatively unknown. Here, gut content and stable isotope analyses were used to
29 study ontogenetic dietary shifts and interspecific trophic niche overlap between asp and
30 pikeperch coexisting in two reservoirs. The hypothesis that both species show an ontogenetic
31 dietary shift from small invertebrates to large fish prey, but at the same time use different prey
32 resources to reduce potential competitive interactions, was validated. The isotopic niches of
33 the two predators showed no, or only a moderate, degree of overlap (0–65%). The ontogenetic
34 changes in the degree of interspecific isotopic niche overlap were different in the two
35 reservoirs, suggesting that trophic segregation can be dynamic and variable among systems.
36 Gut contents revealed that small (<100 mm standard length) asp consumed mostly terrestrial
37 invertebrates and emerged aquatic insects, whereas small pikeperch foraged on zooplankton,
38 larval and pupal stages of aquatic insects and fish. Larger individuals (>100 mm) of both
39 species were predominantly piscivorous, with asp consuming more cyprinid prey and
40 pikeperch more percid prey. Coexisting asp and pikeperch populations are able to utilise
41 different prey resources, thereby reducing potential negative competitive interactions.

42

43 Keywords: dietary ontogeny, foraging strategy, interspecific competition, piscivory, stable
44 isotopes

45

46 1 Introduction

47 Differential resource use is perceived as an important mechanism allowing the coexistence of
48 species within ecological communities (Schoener, 1986; Chesson, 2000; Chase & Leibold,
49 2003). This view is based on the competitive exclusion principle (Hardin, 1960), which states
50 that species cannot stably coexist unless the utilisation of limiting resources is well
51 differentiated. The segregation of coexisting species can occur along various dimensions such
52 as the time of activity, the habitat used, or the type of prey eaten (Schoener, 1986). A
53 comprehensive review of resource use in fish communities by Ross (1986) suggested that
54 niche segregation among coexisting species is mainly driven by partitioning of available food
55 resources rather than habitat or time segregation. Species coexistence can, however, be
56 influenced also by other mechanisms. For example, stochastic events (e.g., unpredictable
57 environmental fluctuations) that affect demographic attributes of species may result in their
58 coexistence (Sale, 1978; Warner & Chesson, 1985; Grossman et al., 1998). Therefore, one
59 approach to improve our understanding of the ecological mechanisms that determine the
60 coexistence of species is to examine resource overlap among potential competitors. Most
61 studies of dietary segregation between coexisting fish species have focused on adult life
62 stages (e.g., Hodgson et al., 1997; Schulze et al., 2012; Walker et al., 2013; Zaia Alves et al.,
63 2017). Ontogenetic variations in the resource use among potential competitors have been
64 examined less frequently (Werner & Gilliam, 1984; Amundsen et al., 2003; Davis et al.,
65 2012) although this knowledge is important to fully understand the structure and functioning
66 of fish communities.

67 Asp (Cyprinidae, *Leuciscus aspius*) and pikeperch (Percidae, *Sander lucioperca*) are
68 important piscivorous fishes in freshwater communities of western Eurasia where they
69 naturally coexist in large rivers, lakes and reservoirs (Kottelat & Freyhof, 2007; Vašek et al.,
70 2013). Adults reach similar sizes (usually up to 1000 mm in total length) and prey on small

71 fish (Baruš & Oliva, 1995; Mittelbach & Persson, 1998). Juveniles of pikeperch forage on
72 aquatic invertebrates whereas juveniles of asp may also feed on terrestrial insects fallen on the
73 water surface (Baruš & Oliva, 1995). The feeding ecology of pikeperch has been explored
74 extensively and thus it is well-known that this species usually shifts to piscivory in the first
75 summer of its life (Buijse & Houthuijzen, 1992; van Densen et al., 1996; Mittelbach &
76 Persson, 1998). Less is known, however, about the size and age at which asp become
77 piscivorous. Moreover, only limited attempts have been made to quantitatively characterise
78 the diets of coexisting asp and pikeperch populations (Specziár & Rezsú, 2009). In general,
79 similar feeding habits (i.e., invertivory followed by piscivory) suggest that the two species
80 may interact strongly. Sympatric populations of asp and pikeperch thus provide a good
81 opportunity to investigate whether and how the two predators differ in resource use
82 throughout their lives.

83 In this study, gut content (GCA) and stable isotope (SIA) analyses were used to
84 explore ontogenetic dietary shifts and niche segregation between asp and pikeperch co-
85 occurring in two artificial lakes (i.e., reservoirs). It was expected that both species undergo an
86 ontogenetic dietary shift from invertebrates to fish prey, but this shift occurs later (i.e., at a
87 larger body size) for asp due to its higher tendency to feed on invertebrates. It was also
88 hypothesised that coexisting asp and pikeperch use different prey resources, but the degree of
89 trophic segregation diminishes with increasing body size, i.e. when both species become
90 piscivorous.

91

92

93 2 Methods

94 2.1 Study sites

95 The study was carried out in two reservoirs located in South Bohemia, Czech Republic. Lipno
96 Reservoir (hereafter Lipno; 48°37'58"N, 14°14'13"E), situated on the upper Vltava River, is
97 a relatively shallow water body (Table 1). Due to its shallowness and frequent wind action,
98 most of the reservoir area does not thermally stratify during the summer season. In contrast,
99 Římov Reservoir (hereafter Římov; 48°51'00"N, 14°29'28"E), situated on the Malše River, is
100 a deep canyon-type lake (Table 1) that is strongly thermally stratified during the summer
101 season. Both reservoirs have similar water clarity and a moderately eutrophic trophic status
102 (Table 1).

103 Due to seasonal water level fluctuations, the littoral zone vegetation is poorly
104 developed and submerged macrophytes are practically missing in both reservoirs. The adult
105 fish community compositions are similar in Lipno and Římov, with a dominance of cyprinid
106 species (mostly roach *Rutilus rutilus*, bleak *Alburnus alburnus*, bream *Abramis brama* and
107 white bream *Blicca bjoerkna*) accompanied by perch *Perca fluviatilis* and ruffe
108 *Gymnocephalus cernua* (Čech et al., 2009; Vašek et al., 2016). Asp and pikeperch naturally
109 reproduce in both reservoirs (Jůza et al., 2013; Blabolil et al., 2016). In Římov, however,
110 populations of the two predators are also regularly supported by stocking with pond-reared
111 fingerlings in autumn (Vašek et al., 2013).

112

113 2.2 Sample collection

114 Fish sampling and treatment was conducted in compliance with guidelines from the
115 Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech
116 Republic. Asp, pikeperch and their fish prey were sampled from Lipno in August/September
117 2012 and 2013, and from Římov in August 2013 and 2014. Sampling was carried out with
118 multi-mesh survey gillnets set overnight in littoral, profundal and pelagic zones at four to five
119 different stations within each reservoir (for details of the gillnet sampling, see Vašek et al.,

120 2016). Additional samples of young-of-the-year (YOY) asp and pikeperch, as well as prey
121 fish, were collected from the littoral and pelagic zones of both reservoirs using a beach seine
122 net and a trawl, respectively (for details of these sampling methods, see Jůza et al., 2014).

123 Each fish was measured for standard length (mm) and a sample of dorsal muscle was
124 dissected and stored at -20°C until processed for stable isotope analysis. The analysed prey
125 fish included YOY perch, ruffe and roach, and one-year old bleak. The digestive tracts of asp
126 and pikeperch were dissected and preserved in a 10% formaldehyde solution for later diet
127 analysis. Scales and otoliths were taken and used for age determination following validated
128 methods described by Ruuhijärvi et al. (1996) and Krpo-Četković et al. (2010). To evaluate
129 ontogenetic changes in the short-term diets (based on GCA that represents the recently
130 ingested prey items) and long-term diets (based on SIA that represents the assimilated food
131 sources over several weeks to months) of asp and pikeperch, individuals of both species were
132 grouped into <100 , $100-199$, $200-299$, and ≥ 300 mm size classes that corresponded
133 approximately to age categories 0+, 1+, 2+, and $\geq 3+$, respectively.

134 At both reservoirs, invertebrate samples for SIA were collected from three to four
135 sampling stations and three to four times (June to August) during the same summers when the
136 fish were captured. Bulk zooplankton was collected from the pelagic zone by taking several
137 vertical hauls through the upper 5 m (Lipno) or 10 m (Římov) of the water column with a
138 $200\text{-}\mu\text{m}$ mesh plankton net. The live zooplankton was immediately sieved through a $350\text{-}\mu\text{m}$
139 mesh and stored frozen at -20°C . Before preparation for SIA, defrosted samples were visually
140 inspected using a stereomicroscope. Most of the samples were dominated by herbivorous
141 crustaceans, mainly cladocerans (*Daphnia*) and calanoid copepods. Bulk samples of
142 macroinvertebrates from the littoral zone (<2 m depth) were collected with a kick net (mesh
143 size 0.7 mm) and hand-picked from stones. Only non-predatory organisms (primary
144 consumers) were considered and they included mainly trichopteran, ephemeropteran and

145 chironomid larvae, and also waterlouse (*Asellus aquaticus*) and small snails (Lymnaeidae).
146 All the trichopteran larvae and snails were removed from their cases or shells. Bulk samples
147 of terrestrial insects were collected with a sweep net from the shoreline grasses and shrubs.
148 Adults of the aquatic insects (Trichoptera, Ephemeroptera, Odonata and Diptera) were
149 excluded when present, and thus the samples contained adult insects of purely terrestrial
150 origin, i.e. Hymenoptera, Hemiptera, Coleoptera, Lepidoptera, Brachycera and Orthoptera.
151 All littoral and terrestrial invertebrate samples were stored frozen at -20°C until further
152 processed for SIA.

153

154 2.3 Gut content analysis

155 In the laboratory, digestive tracts were opened and the contents were examined under a
156 stereomicroscope. Since asp lack a true stomach, the contents of the entire gut from the
157 oesophagus to the anus were analysed, whereas only stomach contents were analysed from
158 pikeperch. The total gut or stomach fullness was first visually estimated on a percentage scale
159 ranging from empty (0%) to full (100%). The prey items were identified to the lowest feasible
160 taxonomic level, and their contribution to the total gut or stomach fullness was then
161 determined by the indirect volumetric method (Hyslop 1980). In addition, the number of prey
162 fish individuals discernible to species level was recorded for each digestive tract. When
163 possible, characteristic remains (e.g., scales, pharyngeal arches, opercula and other bones of
164 fish prey, and head capsules, thoraxes, tail spines and other exoskeleton parts of invertebrate
165 prey) were used for identification of masticated and partially digested prey items. The prey
166 items were subsequently grouped into six categories: (1) crustacean zooplankton, (2) larval
167 and pupal stages of aquatic insects, (3) emerged aquatic insects, (4) terrestrial insects, (5)
168 cyprinid fish, and (6) percid fish.

169

170 2.4 Stable isotope analysis

171 Fish muscle and invertebrate samples were dried at 60°C for 48 h and ground to a fine powder
172 using either a porcelain mortar or a mixer mill MM 200 (Retsch GmbH, Haan, Germany).
173 Stable carbon and nitrogen isotopes and the element (C, N) composition of all samples were
174 measured using a Europa Scientific elemental analyser interfaced with a Europa Scientific 20-
175 20 isotope ratio mass spectrometer (Sercon Ltd, Crewe, UK) at the Iso-Analytical Ltd, Crewe,
176 UK. Vienna Pee Dee Belemnite and atmospheric N₂ were used as the international standards
177 for carbon and nitrogen, respectively, while NBS-1577B (powdered bovine liver, $\delta^{13}\text{C}_{\text{V-PDB}} =$
178 -21.60‰ , $\delta^{15}\text{N}_{\text{Air}} = 7.65\text{‰}$) was used as a working standard. NBS-1557B was calibrated in-
179 house as a secondary reference material and is directly traceable to IAEA-CH-6 (sucrose,
180 $\delta^{13}\text{C}_{\text{V-PDB}} = -10.43\text{‰}$) and IAEA-N-1 (ammonium sulphate, $\delta^{15}\text{N}_{\text{Air}} = 0.40\text{‰}$). Isotope ratios
181 in each sample were expressed in conventional delta notation ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) as parts per
182 thousand (‰) differences from the international standard. The analytical error (standard
183 deviation), estimated from replicated runs of the reference material, was less than 0.1‰ for
184 both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Every fifth sample was run in duplicate and the mean difference \pm
185 standard deviation (SD) between replicates was $0.03 \pm 0.04\text{‰}$ for $\delta^{13}\text{C}$ and $0.06 \pm 0.06\text{‰}$ for
186 $\delta^{15}\text{N}$. The fish muscle $\delta^{13}\text{C}$ values were not corrected for lipids due to the generally low C:N
187 ratios (<3.5) indicating negligible lipid content in the samples (Hoffman et al., 2015).

188 The relative contributions of different diet sources assimilated by each size class of
189 asp and pikeperch were modelled using the SIAR package in R (Stable Isotope Analysis in R;
190 Parnell et al., 2010). Inputs to the model were the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the individual
191 consumers (asp and pikeperch) and the reservoir-specific mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of
192 the potential prey resources (Figure A1). In both reservoirs, pelagic zooplankton and littoral
193 macroinvertebrates did not differ in isotope values (t -tests, $P > 0.05$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)
194 and hence they were grouped as “aquatic invertebrates” for SIAR. Furthermore, the isotope

195 data collected in the subsequent years were pooled because isotope values for major trophic
196 level groups (i.e. predatory fish, prey fish, aquatic invertebrates and terrestrial insects) did not
197 substantially differ between years. Therefore, diet composition for both asp and pikeperch
198 was estimated from three possible diet sources: aquatic invertebrates, terrestrial insects, and
199 fish. Fractionation factors (mean \pm SD) between resources and the consumers were assumed
200 to be $0.91 \pm 1.04\text{‰}$ for $\delta^{13}\text{C}$ and $3.23 \pm 0.41\text{‰}$ for $\delta^{15}\text{N}$ (Vander Zanden & Rasmussen,
201 2001). Element concentrations (proportions of C and N) directly measured in the prey
202 resources were included into the model (Phillips & Koch, 2002).

203 Trophic position (TP) of individual asp and pikeperch was estimated from stable
204 isotope data, using the equation described by Cabana and Rasmussen (1996):

$$205 \text{TP}_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.23 + 2$$

206 where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value of asp or pikeperch, $\delta^{15}\text{N}_{\text{baseline}}$ is the $\delta^{15}\text{N}$ value of the
207 baseline organisms (calculated as the average value from aquatic invertebrates), 3.23 is the
208 assumed diet-tissue enrichment in $\delta^{15}\text{N}$ per trophic level (Vander Zanden & Rasmussen,
209 2001), and the constant 2 refers to the trophic position of the baseline organisms.

210 Finally, the isotopic niche widths of each size class of asp and pikeperch were
211 calculated as sample size-corrected standard ellipse areas (SEAC) using the SIBER package in
212 R (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011). SEAC was also used to
213 determine the degree of isotopic niche overlap between the two species, using the equation of
214 Stasko et al. (2015):

$$215 \% \text{ Overlap} = [\{ (\text{area of overlap between } \text{SEAC}_1 \text{ and } \text{SEAC}_2) \times 2 \} / (\text{SEAC}_1 + \text{SEAC}_2)] \times 100$$

216 where SEAC_1 and SEAC_2 are the ellipse areas calculated from asp and pikeperch samples,
217 respectively.

218

219 2.5 Statistical analysis

220 Non-parametric one-way analysis of similarities (ANOSIM) was run in PAST ver. 3.19
221 (Hammer et al., 2001) to compare volumetric proportions of different prey categories in the
222 digestive tracts of different size classes of asp and pikeperch in the Lipno and Římov
223 reservoirs. ANOSIM was based on Bray-Curtis similarity index and the one-tailed
224 significance was computed by permutation of group membership with 9,999 replicates. The
225 size at piscivorous shift was compared between the species by using binomial data of prey
226 fish presence in gut contents (0 = no fish remains in gut, 1 = fish remains in gut) as the
227 response variable and fish length and species as the predictor variables in logit-regression
228 models. Furthermore, the ontogenetic (i.e., size-related) changes in asp and pikeperch TP
229 were analysed by fitting asymptotic regression models using the SSasymp function in R (Ritz
230 et al., 2015). The differences in TP between asp and pikeperch of each size class in each
231 reservoir were also compared using *t*-test. Finally, the likelihood test in the SIBER (Jackson et
232 al., 2011) was used to test for between-species differences in isotopic niche widths of asp and
233 pikeperch size-classes. All statistical analyses except ANOSIM were performed in the R
234 computing programme ver. 3.4.1 (R Core Team, 2017).

235

236

237 3 Results

238 Both GCA and SIA data demonstrated clear ontogenetic dietary shifts and differential use of
239 the prey resources by coexisting asp and pikeperch. The GCA results indicated significant
240 between-species differences in the prey compositions (ANOSIM: $R = 0.457$, $P < 0.001$), but
241 the diets of asp and pikeperch became more similar with increasing size (Table 2). Small
242 (<100 mm) asp fed on terrestrial and emerged aquatic insects, whereas larger asp consumed
243 mostly fish (Fig. 1). Correspondingly, small (<100 mm) pikeperch foraged on zooplankton,

244 larval and pupal stages of aquatic insects and fish, whereas larger pikeperch were mainly
245 piscivores (Fig. 1). Contrary to asp, no terrestrial insects or emerged aquatic insects were
246 found in pikeperch stomachs. The two species showed contrasting prey fish compositions,
247 with asp feeding more often on cyprinid prey fish and pikeperch feeding mostly on percid fish
248 (Fig. 1). When only prey fish discernible to species level were considered, the most abundant
249 species found in asp guts were ruffe in Lipno and bleak in Římov, whereas the most abundant
250 species observed in pikeperch stomachs were perch and conspecifics in Lipno and ruffe in
251 Římov (Table 3). The logit-regression models (Fig. 2) demonstrated that pikeperch shifted to
252 piscivory at a smaller size than asp, both in Lipno (parameter estimate \pm SE for species effect:
253 2.4 ± 0.9 ; $Z = 2.6$, $P = 0.009$) and Římov (2.3 ± 0.6 ; $Z = 3.7$, $P < 0.001$).

254 The SIA results confirmed the ontogenetic dietary shifts of asp and pikeperch to
255 piscivory, as illustrated by the positive non-linear relationship between size and TP (Fig. 3,
256 Table 4) and by the SIAR estimates showing a shift from invertebrate to fish prey with
257 increasing predator size (Fig. 4). In Lipno, small (<100 mm) asp had a significantly lower TP
258 than similar-sized pikeperch, whereas no between-species differences were observed among
259 larger size classes (Table 5). An opposite pattern was observed in Římov, where no between-
260 species differences in TP were observed for small asp and pikeperch, whereas larger asp had
261 consistently lower TP as compared to similar-sized pikeperch (Table 5). The results from
262 SIAR isotopic mixing model suggested that terrestrial insects contributed only little to the
263 long-term diet of all size classes of asp and pikeperch in Římov but had a relatively high
264 contribution to the long-term diet of both small (<100 mm) asp (54%) and pikeperch (32%) in
265 Lipno (Fig. 4).

266 The isotopic niche widths generally did not differ between the coexisting asp and
267 pikeperch populations (Table 5). In Lipno, there was no overlap between isotopic niches
268 (SEAc) of small (<100 mm) asp and pikeperch, whereas the isotopic niches of larger asp and

269 pikeperch overlapped partially (i.e., 49–65%; Table 5). An opposite pattern was observed in
270 Římov, where the interspecific SEAC overlap was highest (65%) in the <100 mm size class,
271 intermediate (42%) in the 100–199 mm size class, and none in the 200–299 and \geq 300 mm size
272 classes (Table 5).

273

274

275 4 Discussion

276 Both GCA and SIA suggested that there were clear ontogenetic dietary shifts and interspecific
277 niche segregation between asp and pikeperch in the two reservoirs examined. So far, only
278 limited information on resource use has been available for co-occurring asp and pikeperch
279 populations (Specziár & Rezsú, 2009), and the current study is also the first that applied SIA
280 approach (together with conventional GCA method) to characterise dietary niches of the two
281 sympatric predators. Consequently, findings of this study provide important insights into the
282 trophic ecology of coexisting asp and pikeperch populations and their roles in freshwater food
283 webs.

284

285 4.1 Ontogenetic dietary shifts in asp and pikeperch

286 Gut content and stable isotope data both showed that asp and pikeperch consumed more fish
287 prey with increasing body size. According to the GCA and SIAR results, fish prey
288 overwhelmingly dominated in the short- and long-term diets of large- and medium-sized
289 predators, whereas they contributed only around 50% or less to the diets of small-sized (<100
290 mm) asp and pikeperch. Our results demonstrate that asp and pikeperch can begin feeding on
291 fish as early as their first summer (i.e., as YOY), although shifting to piscivory was completed
292 in their second summer of life (i.e., at length >100 mm). Both the logit-regression models
293 (based on absence/presence of prey fish in predators' digestive tracts) and SIA-based TP

294 estimates consistently indicated that pikeperch shifted to piscivory at a smaller size than asp.
295 These results confirmed the expectation that juvenile asp have a higher tendency to feed on
296 invertebrates and shift to piscivory somewhat later (i.e., at a larger size) than pikeperch.
297 However, although piscivory occurred later for asp, the TP estimates suggest that both species
298 accomplished shifting to predominantly piscivorous feeding in their second summer of life
299 since individuals of the 100–199 mm size class attained mean TP values of ≥ 3.5 , indicating
300 piscivory. Consequently, both species can be characterised as “specialist piscivores” (sensu
301 Keast, 1985) because they shift to piscivory relatively early in life.

302 GCA indicated that small-sized (<100 mm) asp consumed mainly terrestrial and
303 emerged aquatic insects in both reservoirs. SIAR results suggested that terrestrial insects
304 dominated (54%) the long-term diet of small-sized (<100 mm) asp in Lipno, whereas small
305 asp in Římov showed a greater reliance upon prey fish. Hence, the SIAR results indicate that
306 small-sized Římov asp probably consumed more fish than suggested by GCA which reflects
307 only recently ingested prey items (e.g., Paradis et al., 2008). According to GCA, small-sized
308 (<100 mm) pikeperch fed on zooplankton, aquatic insects and fish, but not on terrestrial and
309 emerged aquatic insects. Although terrestrial insects were absent in pikeperch digestive tracts,
310 we always included terrestrial invertebrates as a third prey source (besides aquatic
311 invertebrates and fish) to make the SIAR analysis consistent between asp and pikeperch.
312 Consequently, the SIAR results confirmed that terrestrial insects generally represented an
313 unimportant prey source for pikeperch of all size classes. Small-sized (<100 mm) Lipno
314 pikeperch were, however, an exception because the SIAR suggested that terrestrial insects
315 might be a substantial diet source (32%) for these fish. This apparent bias (i.e., overestimation
316 of the terrestrial prey contribution to pikeperch diet) can be explained by the fact that stable
317 isotope values of terrestrial and aquatic invertebrates partially overlapped (particularly in
318 terms of $\delta^{13}\text{C}$) in Lipno, hindering assessment of the relative contributions of these prey

319 sources to higher trophic levels. Nevertheless, the SIAR results appropriately revealed the
320 ontogenetic niche shift from feeding on invertebrates to piscivory in both species.

321 Previous studies have shown that, under favourable growth conditions (i.e., higher
322 optimum temperature and food availability), pikeperch become piscivorous during their first
323 summer and reach sizes well above 100 mm (Buijse & Houthuijzen, 1992; van Densen et al.,
324 1996). In contrast, under less suitable conditions, YOY pikeperch either remain invertivorous
325 and reach generally small sizes (Specziár, 2005; Vinni et al., 2009, Ginter et al., 2011) or
326 develop a bimodal size distribution with a minor group becoming piscivorous and a majority
327 staying invertivorous (van Densen, 1985; Frankiewicz et al., 1996). Information on
328 ontogenetic dietary shifts in asp is limited. Yet, the data available from Lake Balaton
329 (Specziár & Rezsú, 2009) correspond well with the current study: the <40 mm asp were
330 invertivorous, the 41–120 mm asp had a diet containing both invertebrates and fish, and the
331 121–500 mm fish were entirely piscivorous. The fact that transition to piscivory in our study
332 systems was not completed during the first summer implies growth-limiting conditions for
333 juvenile stages of both species. Persson & Brönmark (2002) highlighted the importance for
334 YOY predators to be synchronised with fluctuations in resource availability. Hence, we can
335 speculate that discontinuous availability of suitable food resources might reduce growth and
336 delay shifting to piscivory in our study systems. However, growth rates of YOY predators
337 might have also been restricted by water temperatures. Římov is a deep reservoir situated in a
338 canyon and hence it warms slowly in spring which may delay the spawning period and
339 shorten the first-year growth season (cf., Wysujack et al., 2002; Jůza et al., 2013). In contrast,
340 Lipno is a shallow reservoir, but because of its location at a higher altitude, thermal
341 conditions may delay spawning and reduce the growth of juvenile stages similarly to that in
342 Římov.

343

344 4.2 Interspecific niche segregation between asp and pikeperch

345 The isotopic niche widths generally did not differ between the coexisting asp and pikeperch
346 populations, indicating a similar extent of trophic specialisation in both species. Moreover,
347 the isotopic niches of the two predators showed no or only a moderate degree of overlap (i.e.,
348 0–65%). Interestingly, overlap between the isotopic niches of asp and pikeperch increased
349 with increasing predator size in Lipno but decreased in Římov. These findings do not support
350 the hypothesis that the degree of trophic segregation between asp and pikeperch should
351 diminish with increasing body size (i.e., with a shift to piscivory). Instead, the results suggest
352 that size-related trophic segregation between asp and pikeperch may be dynamic and variable
353 among systems, probably reflecting varying availability of prey sources.

354 The results also demonstrate that coexisting asp and pikeperch used rather different
355 prey resources both at small and large sizes. The GCA and SIA data both indicated that the
356 interspecific trophic segregation in the smallest (<100 mm) predator size class was likely due
357 to the exclusive utilisation of terrestrial invertebrates and emerged aquatic insects by asp,
358 whereas pikeperch used zooplankton, larval and pupal stages of aquatic insects, and small
359 fish. Similarly, Specziár & Rezsú (2009) observed that small (16–40 mm) asp foraged mostly
360 on adult Chironomidae, whereas co-occurring similar-sized pikeperch relied on zooplankton.
361 Moreover, the GCA results showed that piscivorous stages of the two predators consumed the
362 same fish species, but in different proportions. The fact that asp used relatively more cyprinid
363 prey fish while pikeperch consumed more percoid fish might be another reason for the
364 observed segregation of the isotopic niches of the two predators, particularly those of
365 medium- and large-sized classes. Because pikeperch ingest prey intact, with no mastication, it
366 was usually possible to identify (at least to family level) most of prey fish. In contrast,
367 ingested prey fish in asp were often strongly masticated by pharyngeal teeth and digested
368 beyond recognition. Hence, we suppose that the relative contribution of cyprinid prey fish in

369 the diet of asp might even be higher than suggested by the GCA, because small and soft
370 cyprinid species such as bleak were probably under-represented due to their rapid digestion.

371 This study provides novel empirical data on piscivorous diets of coexisting asp and
372 pikeperch populations. Previous single-species studies indicated that the piscivorous diets of
373 both asp and pikeperch are dominated by cyprinid (Wysujack et al., 2002; Krpo-Ćetković et
374 al., 2010; Specziár, 2011) and by percid prey fish (Vostradovský & Váša, 1981; Frankiewicz
375 et al., 1999, Keskinen & Marjomäki, 2004). Hence, both predators can behave rather
376 opportunistically and consume the most abundant fish species. However, in sympatry, asp and
377 pikeperch can differentiate prey fish resources as illustrated by this study. In summary, by
378 using a combination of GCA and SIA, our study indicates that coexisting asp and pikeperch
379 populations can use different prey resources at both juvenile and adult life stages, thereby
380 reducing the potential negative competitive interactions (Vanni et al., 2009).

381

382 4.3 Conclusion and recommendation for future studies

383 The present study demonstrates that coexisting asp and pikeperch forage at the top of the food
384 webs and thereby play similar functional roles in lake ecosystems. Notably, the trophic niches
385 of the two predators were relatively well separated, both at juvenile and older life stages. The
386 observed niche segregation may help to reduce potential interspecific resource competition
387 between coexisting asp and pikeperch populations.

388 Asp and pikeperch can induce top-down cascading impacts on lower trophic levels
389 (Benndorf, 1990; Brabrand & Faafeng, 1993; Donabaum et al., 1999). They are also popular
390 game fishes for anglers and therefore often stocked into various systems (e.g., Ruuhijärvi et
391 al., 1996; Wysujack et al., 2002; Vašek et al., 2013). Our results are relevant to fisheries
392 management, because they indicate that different use of the prey resources may potentially
393 mitigate interspecific competition between co-occurring asp and pikeperch populations. In

394 future studies, comparison of trophic niches of the two species under conditions of allopatry
395 and sympatry could help to determine whether relatively low overlap in resource use is the
396 consequence of interspecific competition or different foraging strategies that evolved in the
397 past.

398

399

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409

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- 564

565 Tables

566 Table 1. Basic environmental characteristics of the two reservoirs studied. Mean values for
567 the growing season (May–September) are shown for Secchi depth, total phosphorus and
568 chlorophyll-*a*.

Characteristic	Lipno	Římov
Year of filling	1960	1978
Surface altitude (m a.s.l.)	725	471
Surface area (km ²)	48.7	2.1
Mean depth (m)	6	16
Maximum depth (m)	22	43
Hydraulic retention time (days)	244	85
Secchi depth (m)	1.9	2.6
Total phosphorus (µg L ⁻¹)	25	27
Chlorophyll- <i>a</i> (µg L ⁻¹)	14	19

569

570 Table 2. Sample sizes in gut content analysis (GCA) (*n*) and results from pairwise one-way
 571 analysis of similarities (ANOSIM) comparisons of volumetric prey proportions in digestive
 572 tracts of asp and pikeperch in the Lipno and Římov reservoirs. Statistically significant
 573 differences ($P < 0.05$) are shown in bold.

Reservoir	Size class (mm)	<i>n</i>		ANOSIM
		Asp	Pikeperch	<i>P</i>
Lipno	<100	16	17	<0.001
	100-199	4	7	0.024
	200-299	6	11	0.262
	≥300	7	6	0.217
Římov	<100	12	20	<0.001
	100-199	14	10	0.043
	200-299	15	11	<0.001
	≥300	7	5	0.176

574

575

576 Table 3. List of fish species preyed upon and their total numbers found in all digestive tracts
 577 of asp and pikeperch collected from the Lipno and Římov reservoirs.

Prey fish species (family)	Asp		Pikeperch	
	Lipno	Římov	Lipno	Římov
Perch (Percidae)	3	2	14	8
Pikeperch (Percidae)	1	-	11	2
Ruffe (Percidae)	7	-	6	13
Bleak (Cyprinidae)	3	9	1	-
Bream (Cyprinidae)	-	-	-	1
Roach (Cyprinidae)	1	1	-	6
Total number of prey fish discernible to species level	15	12	32	30

578

579 Table 4. Parameter estimates and corresponding *t*- and *P*-values for the non-linear
580 (asymptotic) regression models with trophic position (TP) as a response variable and standard
581 length (mm) as a predictor variable, given for asp and pikeperch in Lipno and Římov
582 reservoirs. The models are fitted using SSasympt function in R (R Core Team 2017),
583 producing estimates for the horizontal asymptote on the right side (Asym), the response value
584 (i.e., TP) when length is zero (R0), and the natural logarithm of the rate constant (lrc). See
585 Fig. 3 for sample sizes and predicted regression curves.

Reservoir	Species	Parameter	Estimate	SE	<i>t</i>	<i>P</i>
Lipno	Asp	Asym	3.85	0.08	45.79	<0.001
		R0	0.22	0.88	0.25	0.806
		lrc	-4.29	0.27	-16.00	<0.001
Lipno	Pikeperch	Asym	3.77	0.05	81.09	<0.001
		R0	2.03	0.26	7.93	<0.001
		lrc	-4.16	0.20	-21.28	<0.001
Římov	Asp	Asym	3.91	0.07	54.77	<0.001
		R0	2.50	0.39	6.35	<0.001
		lrc	-4.45	0.35	-12.90	<0.001
Římov	Pikeperch	Asym	4.31	0.08	51.30	<0.001
		R0	2.86	0.18	16.07	<0.001
		lrc	-4.66	0.24	-19.16	<0.001

586

587 Table 5. Mean trophic position (TP; standard deviation in parentheses), isotopic niche width
 588 measured as standard ellipse area (SEAC) and niche overlap for asp and pikeperch of four size
 589 classes collected from the Lipno and Římov reservoirs. P^\dagger and P^\ddagger refer to statistical
 590 significances for TP comparisons and for niche width comparisons, respectively, between asp
 591 and pikeperch in each size class. Statistically significant differences ($P < 0.05$) are highlighted
 592 in bold. For number of predators analysed for stable isotopes in each size class see Fig. 4.

Reservoir	Size class (mm)	TP (SD)		P^\dagger	SEAC		P^\ddagger	Overlap (%)
		Asp	Pikeperch		Asp	Pikeperch		
Lipno	<100	2.5 (0.3)	3.1 (0.2)	<0.001	2.6	3.9	0.88	0.0
	100-199	3.5 (0.2)	3.6 (0.3)	0.64	3.0	2.9	0.38	48.8
	200-299	3.7 (0.3)	3.7 (0.2)	0.94	3.2	1.3	0.03	54.9
	≥ 300	3.8 (0.2)	3.8 (0.2)	0.64	2.1	1.1	0.08	64.7
Římov	<100	3.3 (0.3)	3.5 (0.3)	0.07	2.7	2.7	0.51	65.2
	100-199	3.7 (0.2)	3.9 (0.1)	<0.001	1.0	1.2	0.74	42.3
	200-299	3.8 (0.1)	4.2 (0.2)	<0.001	1.2	1.1	0.28	0.0
	≥ 300	3.9 (0.2)	4.2 (0.2)	<0.001	1.4	0.9	0.18	0.0

593

594 Figure Legends

595 Figure 1. Mean volumetric proportion of different prey categories in the digestive tracts of
596 different size classes of asp and pikeperch in the Lipno and Římov reservoirs. Predators that
597 contained unidentified prey fish in their digestive tracts are not shown to better illustrate
598 interspecific differences in piscivorous foraging on percid and cyprinid fish. The number of
599 examined digestive tracts with discernible prey items is indicated above the bars.

600

601 Figure 2. Logistic regressions showing the probability of finding fish remains in gut contents
602 as a function of asp ($n = 43$ & 65) and pikeperch ($n = 56$ & 69) standard length in the Lipno
603 and Římov reservoirs.

604

605 Figure 3. Trophic positions of asp ($n = 43$ & 77) and pikeperch ($n = 62$ & 88) in the Lipno and
606 Římov reservoirs as a function of standard length. Lines indicate predicted values for the non-
607 linear (asymptotic) regression models (see parameter estimates in Table 4).

608

609 Figure 4. Proportional contribution (mean \pm 95% credibility intervals) of different prey types
610 (aquatic invertebrates, terrestrial insects and fish) to the diet of different size classes of asp
611 and pikeperch in the Lipno and Římov reservoirs, estimated using SIAR mixing model. The
612 number of predators analysed for stable isotopes in each size class is indicated across the top
613 of the graphs.

614

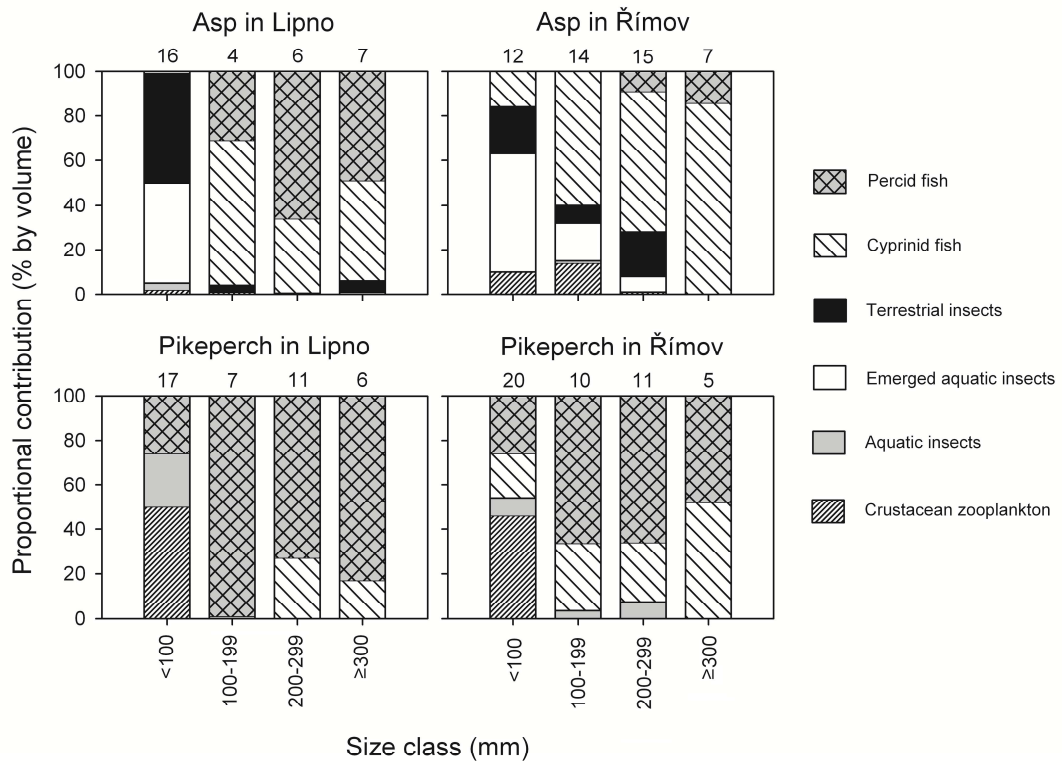
615 Appendix

616 Figure A1

617 Bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual asp (circles; $n = 43$ & 77) and pikeperch
618 (triangles; $n = 62$ & 88), and their principal diet sources in the Lipno and Římov reservoirs.
619 Filled squares represent mean \pm standard deviation for pelagic zooplankton, littoral
620 macroinvertebrates, terrestrial insects and prey fish. All diet sources were corrected for
621 trophic fractionation using values ($\delta^{13}\text{C} = 0.91$, $\delta^{15}\text{N} = 3.23$) from Vander Zanden &
622 Rasmussen (2001). Because pelagic zooplankton and littoral macroinvertebrates did not differ
623 in their isotope values, they were merged as “aquatic invertebrates” for the purpose of SIAR
624 estimates (see Fig. 4).

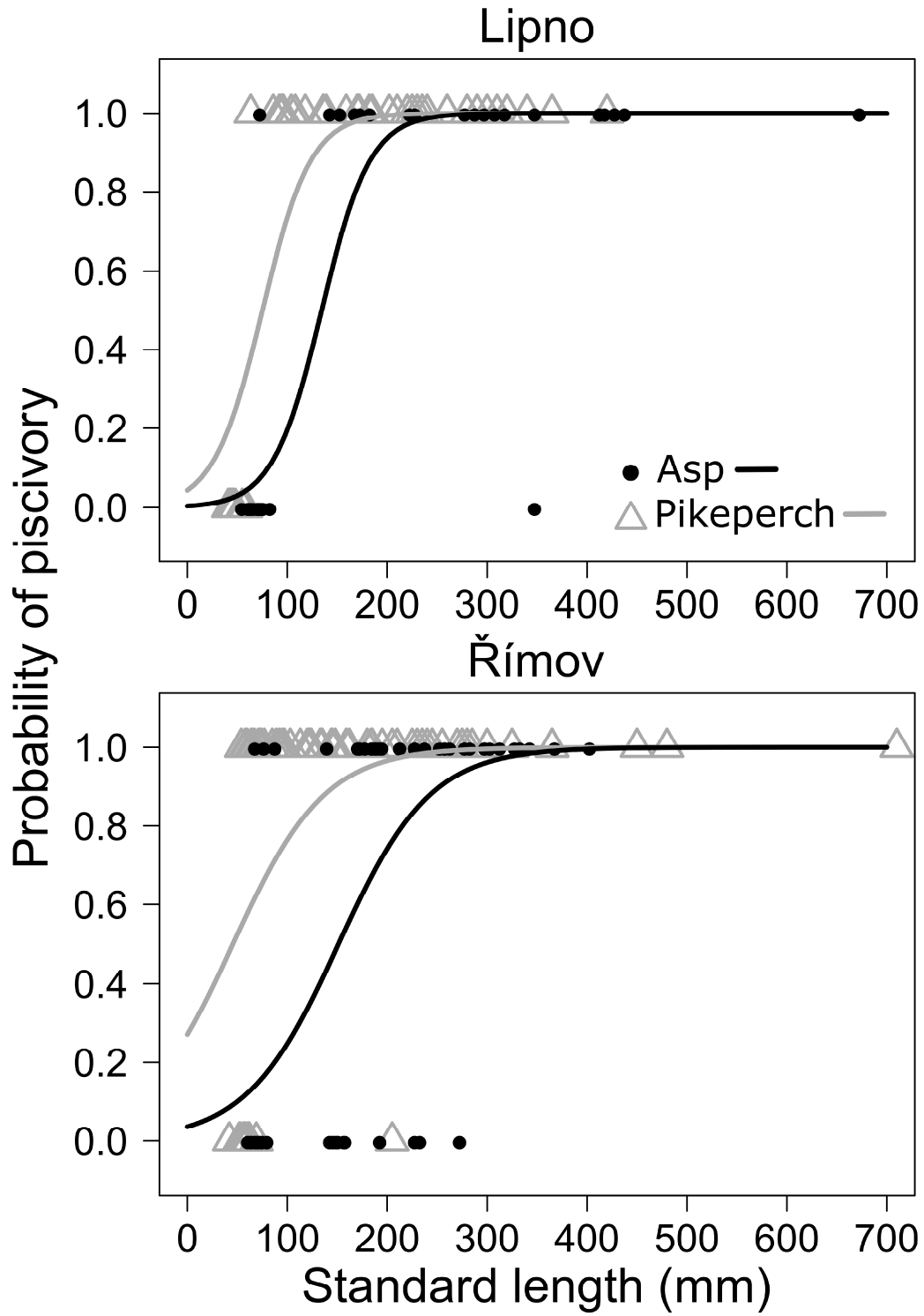
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626 **FIGURE 1**



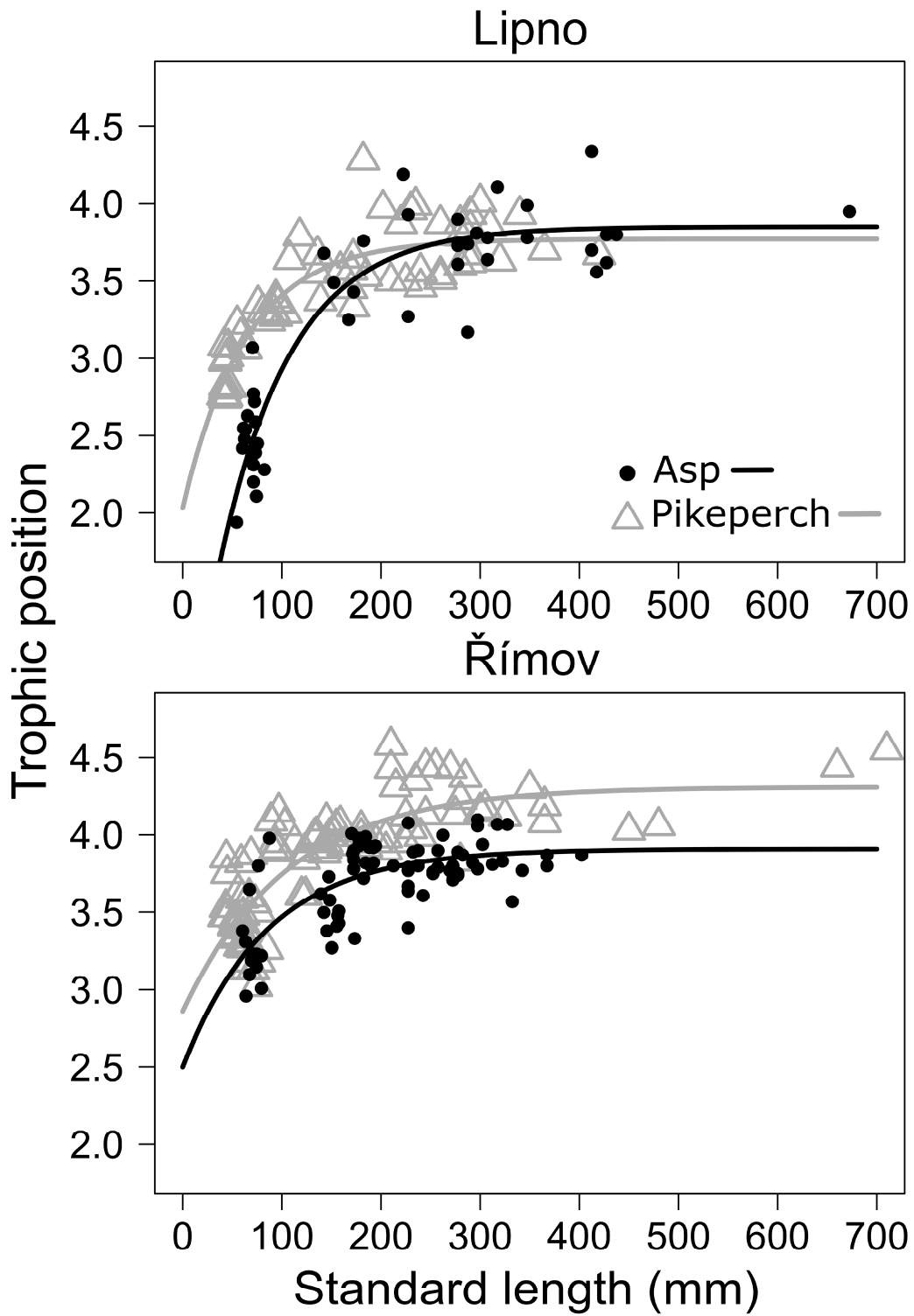
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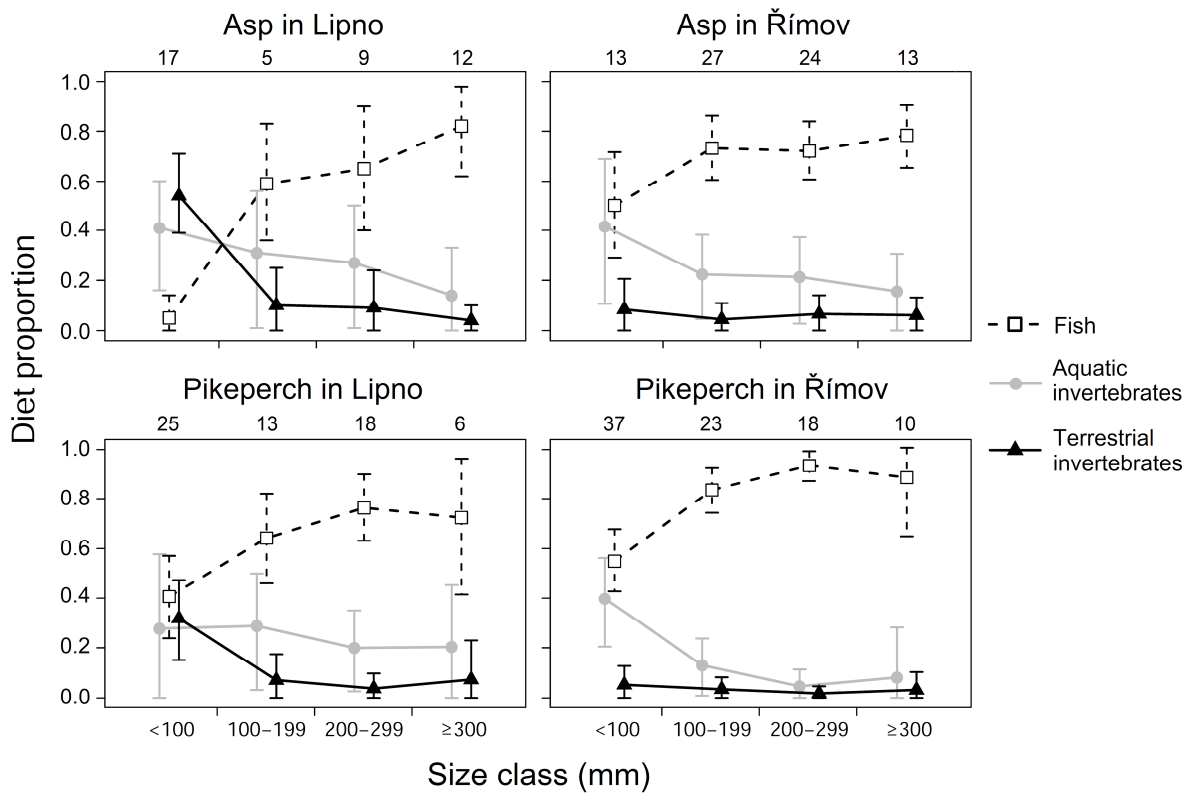
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633

634

635 **FIGURE 4**



636

637

