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Dietary variability in fishes: the roles of taxonomic, spatial, temporal and ontogenetic factors

András Specziár*, Tibor Erős

Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. u. 3., H-8237 Tihany, Hungary

*Corresponding author. Tel.: +36 87448244; email: specziar.andras@okologia.mta.hu

Abstract In spite of the general use of diet data in ecological research, still very little is known about the relative roles of spatial, temporal and biotic (e.g. taxonomic identity, size, sex) factors in dietary variability of fishes. Here, we applied canonical correspondence analysis and variation partitioning to examine the roles of taxonomic, annual, seasonal, lake basin, habitat and ontogenetic (standard length, L_S) factors in the dietary variation of fishes in large and shallow Lake Balaton, Hungary. The analyses were performed at the assemblage (15 fish species) and the individual species levels, and based on high (24 fine resource categories) and low resolution (nine broad resource categories) diet data. As hypothesized, most of the explained variation related to interspecific differences, while the roles of sampling year, season, lake area, habitat and L_S proved to be unexpectedly low at the assemblage level. In addition, no regularity was found in how the relative roles of these factors change between fish species. The high ratio of the unexplained variation suggests that individual variations in foraging strategies and resource use of fishes and unascertained stochastic processes had a strong influence on dietary variability both at the assemblage and the individual species levels.

Keywords Fish assemblage, Food resource, Individual feeding strategy, Size-dependent pattern, Spatio-temporal variability, Variation partitioning.

35 **Introduction**

36

37 Analysis of feeding relationships forms a fundamental part of ecological research. For fishes
38 the direct analysis of the stomach (gut) content is frequently used to provide information
39 about their food resource use, suitability of the habitat, potential biotic interactions and
40 individual feeding strategies (e.g. Bergman, 1990; Kakareko et al., 2005; Gliwicz et al., 2006;
41 Adámek et al., 2007; Ginter et al., 2012a). In a wider, ecosystem level context, diet data helps
42 to more directly quantify functional composition and food web organization and in general
43 the role of fishes in aquatic ecosystems (Power, 1990).
44 Separating the components of the dietary variation provide information about how different
45 environmental (e.g. seasonality and habitat) and/or biological factors (i.e. any morphological,
46 biological and behavioural traits) determine diet composition (Hovde et al., 2002; Chassot et
47 al., 2008; Quevedo et al., 2009; Pusey et al., 2010). Diet of fishes varies due to a diversity of
48 factors. At the assemblage level, interspecific differences in the feeding behaviour and food
49 preference generally have predominant role in dietary variability (Piet et al., 1999; Mérona &
50 Rankin-de-Mérona, 2004; Pusey et al., 2010). At the species level, ontogenetic changes are
51 one of the most characteristic components of the dietary variability. For fishes, shifting
52 between resources is one way to follow the increasing energy requirement during growth
53 (Werner & Gilliam, 1984). Moreover, ontogenetic diet shifts decrease intraspecific
54 competition for food between the adults and their offspring (Werner & Gilliam, 1984;
55 Persson, 1988; Mittelbach & Persson, 1998). The diet of fishes varies considerably with time
56 primarily due to the heterogeneity of food resources along seasonal and annual scales
57 (Warburton et al., 1998; Mérona & Rankin-de-Mérona, 2004; Ginter et al., 2012b; Nunn et
58 al., 2012). Diet of fish can also vary between habitat types (Vinni et al., 2000; Svanbäck &
59 Eklöv, 2002; Platell et al., 2007) and along spatial resource gradients (Mittelbach et al., 1992;

60 Francis & Schindler, 2009). In addition, it has been shown that variations among individuals
61 may comprise a large proportion of the population's niche breath, especially for some species
62 which exhibit generalized feeding at the population level (Bolnick et al., 2003; 2007). Inter-
63 individual dietary variation has two major components. The stochastic component is related to
64 the small-scale heterogeneity in the density and taxonomic composition of food resources.
65 This component is responsible for the short-term individual specialization and for the
66 observed dietary differences between individuals of a fish species that forage in the same
67 habitat but among different resource patches (Malone & McQueen, 1983; Downes et al.,
68 1993; Ritchie, 1998). The persistent component is related to phenotypic or behavioural
69 differences of individuals (Bolnick et al., 2003). Finally, results of diet analyses are inherently
70 variable because stomach or gut content provide only a snap shot picture of what a fish has
71 been eating in a very short time period (i.e. from 1 hour to one day). In spite of the general
72 use of diet data in ecological research, still very little is known about the relative roles spatial,
73 temporal and biotic (e.g. taxonomic identity, size, sex) factors play in dietary variability of
74 fishes. The few studies performed on marine (Hovde et al., 2002; Chassot et al., 2008) and
75 tropical lotic fish species and assemblages (Pusey et al., 2010) identified low to moderate
76 explainable proportion of dietary variation. However, to the best of our knowledge no
77 comprehensive work has been published for temperate freshwater fish assemblages.
78 This study aims to investigate the main components of intra- and interspecific dietary
79 variability of fishes in Lake Balaton, Hungary. Feeding ecology of fishes has been extendedly
80 studied in Lake Balaton (Specziár & Rezsu, 2009), and by now, there is a significant data
81 base providing a perfect opportunity for analysing dietary variability and its components.
82 Previous investigations showed that the diet of cyprinids vary considerably between the main
83 littoral habitats (i.e. macrophyte free zone, macrophyte covered area and ripraps – lake bank
84 sections stabilised with rocks) due to the differences in the food resources they provide

85 (Specziár et al., 1998; Specziár, 1999). The characteristic trophic gradient along the
86 longitudinal axis of the lake influences the diet composition of several fish species (Bíró et
87 al., 1991; Simonian et al., 1995; Rezsu & Specziár, 2006). Seasonal differences are evident in
88 the diet of most fish species (Bíró, 1973, 1974; Bíró et al., 1991; Simonian et al., 1995), and
89 year-to-year changes in the abundance of some food organisms were also proved to affect the
90 feeding of fishes (Bíró, 1973 and references therein; Bíró, 1974). Recent studies focused on
91 ontogenetic diet patterns (Bíró et al., 1991; Bíró & Muskó, 1995; Specziár & Bíró, 2003;
92 Specziár, 2005; Rezsu & Specziár, 2006; Specziár & Rezsu, 2009; Specziár 2011), and it was
93 found that 13 out of the 15 fish species investigated showed marked size-related dietary
94 changes in the lake (Specziár & Rezsu, 2009). However, it was also proved that individuals of
95 different species do not unequivocally separate based on their diet composition (e.g. for five
96 cyprinid species, see Fig. 4 in Specziár et al., 1997), and feeding guilds are organized from
97 specific size groups of more than one fish species (Specziár & Rezsu, 2009). Although, the
98 above studies provide important information about the dietary variation among fish species
99 and along specific spatial, temporal and ontogenetic scales, the relative importance of these
100 scales still remained unknown.
101 Particular goals of the present study were to quantify the importance of taxonomic (i.e.
102 between species), temporal (i.e. year and season), spatial (i.e. lake basin and habitat), and
103 ontogenetic factors in the dietary variation of fishes in Lake Balaton, and to explore how the
104 relative importance of these factors (except the taxonomic factor) vary among fish species. It
105 was hypothesized that (i) at the assemblage level (i.e. all fish species analysed together), the
106 largest fraction of the total variance would be related to interspecific differences, and (ii) at
107 the species level, the relative importance of different explanatory factors would vary markedly
108 among species according to their taxonomic relationship and guild membership. Additionally,
109 since ecological studies consider diet composition at variable resolution levels (i.e. taxonomic

level to which food items are identified), it was investigated how the observed patterns change between high (i.e. 24 fine resource categories) and low resolution (i.e. nine broad resource categories) diet composition data.

Materials and methods

Study area

Balaton is the largest shallow lake (surface area: 593 km^2; mean depth: 3.2 m) in Central Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea level. The lake is meso-eutrophic with mean annual chlorophyll-a concentrations of 3.6-18.7 mg m^{-3} (Istvánovics et al., 2007). The lake is slightly alkaline (400 mg l^{-1} of Ca^{2+} and $Mg^{2+}(HCO_3^-)_2$), pH ranges 8.2-9.1, and has a conductivity of 550-671 µs cm^{-1}. In general the lake is turbid with a Secchi disc depth varying between 0.2 m and 0.8 m. Oxygen deficiency has never been registered in the lake, and concentrations of pollutants are low or insignificant. Forty-seven percents of the lake shore is covered by reed grass *Phragmites australis*. Submerged macrophytes occur sparsely in the littoral zone. Significant part of the lake shore was stabilized with stones, and these riprap habitats are covered by filamentous algae (mainly *Cladophora* spp.) and inhabited by dense invertebrate community (Muskó et al., 2007; Balogh et al., 2008). There are also several boat harbours along the lake, which provide specific habitat because they are sheltered from swash. Detailed information on the limnology and fish fauna of the lake can be found in studies of Herodek et al. (1988), Bíró (1997), Specziár et al. (2009, 2013) and Istvánovics et al. (2007).

Sampling

135

136 Explanatory factors for this study were the sampling parameters. Fish samples representing
137 wide (i.e. lifespan in most species) size ranges of 15 species (Table 1) were collected between
138 1995 and 2007, from three seasons (spring, summer and autumn) and in three lake basins
139 (Keszthely, Zánka and Siófok basins; Fig. 1.) along the longitudinal axis of the lake. Five
140 habitats were distinguished as follows: 1) offshore area, sampled at >2 km distance off the
141 nearest shore, 2) macrophyte-free inshore area, sampled at 50 to 200 m distance off the shore,
142 3) reed grass stand, 4) riprap, sampled at 1 to 5 m distance off the shore, and 5) boat harbour
143 (Fig. 1). Applied sampling techniques included multi-mesh gillnetting (5 to 80 mm mesh
144 sizes), battery powered electrofishing (1 and 6 mm anode ring mesh sizes), benthic sledging
145 (2 mm mesh size), surface trawling (2 mm mesh size) and dip netting (1 mm mesh size).
146 Gillnets were set for half to two hours in the morning. With gillnet most fish species could be
147 collected effectively at sizes >50 mm standard length (L_S). Sampling of the littoral species,
148 especially of those hiding among macrophytes or living along the ripraps (i.e. pumpkinseed
149 sunfish *Lepomis gibbosus*, monkey goby *Neogobius fluviatilis*, perch *Perca fluviatilis* and
150 rudd *Scardinius erythrophthalmus*) was supplemented with electrofishing using a battery
151 powered Smith-Root 12-B POW type equipment (www.smith-root.com) from a small rubber
152 boat. Electrofishing proved to be an appropriate tool for catching all size-groups of littoral
153 species, except the earliest life stages. To capture the earliest life stages ($L_S \leq 20$ mm) of
154 littoral species a dip net with 1 mm mesh-size was used, while the earliest life stages ($L_S \leq 50$
155 mm) of offshore species were captured with a benthic sledge being 1 m wide and 0.34 m high,
156 and a framed surface trawl 1 m wide and 0.5 high. Both the benthic sledge and the framed
157 surface trawl had a 2 mm mesh and were towed with a boat at 5.4-5.8 km h^{-1} for 5 to 10 min.
158 per haul.
159

160 Diet analysis

161

162 Just after the capture, small fishes ($L_S \leq 100$ mm) were euthanized in an overdose of tricaine
163 methanesulfonate (MS 222; 1.0 g l^{-1}) or clove oil (0.4 g l^{-1}; more recently) and then preserved
164 in 4-10% formalin (depending on the mass of the sample). Larger specimens were instantly
165 killed by severing the central nerve system. Then they were measured for L_S to the nearest 1
166 mm, dissected and their stomachs or guts (in cyprinids) were also preserved in 4-10%
167 formalin.

168 Protocol of the diet analysis was the same as described in Specziár & Rezsu (2009).
169 Samples were generally stored for few weeks before being leached in water and analysed.
170 Diet remains were removed from the stomachs or guts and analysed in the laboratory under a
171 microscope, a stereo microscope or by eye (in large piscivores) depending on the size of the
172 diet components. The present study is based on altogether 8756 examined guts and stomachs
173 containing food remains (Table 1). Since the goal of the present study was to investigate
174 components of the dietary variability of fishes, empty stomachs and guts were not considered
175 in the analysis. Although, empty stomachs and guts could provide very useful information on
176 resource availability of specialized predators, still their inclusion in the analysis can yield
177 uncontrollable bias derived from the unknown feeding period of fishes. For example, it is
178 impossible to differentiate between non-feeding periods and resource limitation from empty
179 stomachs or guts. Food items were classified into taxonomic groups and prey >0.5 mg were
180 weighted to the nearest 0.1 mg, while in other cases their biomasses were calculated from
181 length-weight relationships (Vuille, 1991; Kawabata & Urabe, 1998; Benke et al., 1999;
182 Johnston & Cunjak, 1999; Specziár, 2011; Specziár, unpublished data).

183 Food items were grouped into 24 fine and nine broader resource categories to represent
184 cases of high and low resolution diet analyses, respectively. High resolution resource

185 categories were: (1) *Dreissena polymorpha* larvae, (2) Rotatoria, (3) Copepoda, (4) Cladocera
186 except *Leptodora kindtii*, (5) *L. kindtii*, (6) Ostracoda, (7) Oligochaeta, (8) benthic
187 Chironomidae larvae (species which typically inhabit in or on the sediment, see also Specziár
188 & Bíró, 1998), (9) non-benthic Chironomidae larvae (all other species), (10) Chironomidae
189 pupae, (11) *Chelicorophium curvispinum*, (12) *Dikerogammarus* spp., (13) *Limnomysis*
190 *benedeni*, (14) Isopoda, (15) *D. polymorpha* adults, (16) Gastropoda, (17) other soft-bodied
191 aquatic Arthropoda (e.g. Collembola, Ephemeroptera, Odonata, Heteroptera, Coleoptera,
192 Trichoptera, Acaridea), (18) 'surface Arthropoda' (including flying imagos of aquatic insects
193 and all non-aquatic arthropods occurring in the diet of fishes), (19) diatoms, (20) filamentous
194 (green) algae, (21) macrophytes, (22) detritus, (23) fishes, and (24) others (e.g. fish eggs and
195 bait material used by anglers). While, low resolution resource categories were as follows:
196 zooplankton (including high resolution categories: 1-5), soft-bodied benthic (i.e. organisms
197 living in and on the sediment) macroinvertebrates (6-8), soft-bodied non-benthic (i.e.
198 invertebrates using algae, macrophytes and artificial structures, concrete buildings and ripraps
199 as substrate, and including Chironomidae pupae) macroinvertebrates (9-14, 17), molluscs (15-
200 16), surface arthropods (18), live plant material (19-21), detritus (22), fishes (23) and others
201 (24). Individual diet composition of fish was expressed in mass percentages based on both
202 high and low resolution diet data. For brevity, diet composition data of the 15 fish species is
203 not presented here, but some basic information is available in Table 1 and Appendix A.
204
205 Statistical analysis
206
207 Diet composition data and their dependence on fish species, place (i.e. lake basin and habitat)
208 and time (i.e. year and season) of sampling, and ontogeny (i.e. fish size, L_S) were investigated
209 by performing canonical correspondence analysis (CCA) using CANOCO version 4.5

210 software (ter Braak & Šmilauer, 2002). Ordination techniques are widely used to investigate
211 patterns in multivariate species-environmental data sets, especially when the distribution of
212 data do not support the application of general linear models (e.g. multivariate analysis of
213 variance, MANOVA) requiring samples for all possible factor state × species combinations
214 (Lepš & Šmilauer, 2003). The method of CCA was chosen because preliminary detrended
215 correspondence analysis (DCA) indicated relatively long gradient length at both the
216 assemblage and most species level data sets (≥4 in standard deviation units; Lepš & Šmilauer,
217 2003). The CCA analysis was performed at both the entire assemblage level (the entire
218 database where all 15 fish species were analysed together and where the 15 fish species were
219 included to explanatory variables) and at the level of individual fish species. The analyses
220 were based on both the high and the low resolution diet data. Correspondingly, 32 sets of
221 CCA analyses were performed, two (high and low diet resolution) at the assemblage level and
222 30 (15 species × high and low diet resolution) at the species level. Individual diet data (i.e.
223 each fish represented a separate diet sample) were used throughout the analysis. In each
224 analysis, rare food categories (i.e. <0.5% total representation or <2% frequency of occurrence
225 in the concerning data set) were merged with the resource category called others. Response
226 variables (i.e. relative diet composition data) were arcsin($x^{0.5}$) transformed prior to analysis
227 according to the most preferred method of handling proportional data ranging between 0 and
228 1 (Podani, 2000; but see Warton & Hui, 2011). This transformation gives more weight to food
229 items with low (i.e. with values close to 0) and high (i.e. with values close to 1) relative
230 abundances. Of the explanatory variables, fish species (in the assemblage level analysis only),
231 lake basin, habitat, sampling year and season were treated as categorical factors and re-coded
232 into binary dummy variables (Lepš & Šmilauer, 2003); whereas L_S was treated as quantitative
233 variable. Since we assumed that a unit change in the L_S has much less effect on the diet of
234 fishes at the higher end (i.e. in adults) than at the lower end (i.e. at the early of the ontogeny)

235 of its range (e.g. see L_S intervals for identified ontogenetic species size groups in Specziár &
236 Rezsu, 2009), the data were $\log_{10}(x)$ transformed prior to analysis.
237 In each analysis (i.e. assemblage × diet resolution or fish species × diet resolution), first,
238 a preliminary overall CCA model was built, which included all potential explanatory
239 variables (Lepš & Šmilauer, 2003). The relative contribution of each variable to the model
240 was assessed by using the forward stepwise selection procedure, and their significance was
241 studied by Monte-Carlo permutation test with 9 999 permutations under the full model. On
242 the basis of this selection procedure, only significant explanatory variables ($P < 0.05$) were
243 retained in the final CCA model. Similarly, statistical significance of ordination axes and the
244 whole model (i.e. including all axes) were studied using the Monte-Carlo permutation test
245 with 9 999 permutations. Next, a series of CCA and partial CCAs were conducted to partition
246 the effects of taxonomic (i.e. fish species; only in the assemblage level analyses), temporal
247 (year and season), spatial (lake basin and habitat) and fish size (L_S) on diet composition
248 (Cushman & McGarigal, 2002).
249 Relative position of fish species in a multidimensional space based on the importance of
250 temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and ontogenetic (i.e. L_S)
251 factors in the variation of their diet composition was done using hierarchical cluster analysis
252 (CA) and principal component analysis (PCA). Prior to analyses, variation partition data (%)
253 extracted from diet composition matrixes were $\arcsin(x^{0.5})$ transformed (Podani, 2000). CA
254 was based on the unweighted-pair-group method with arithmetic mean (UPGMA) and the
255 Euclidean distance. Significant groups of species in the cluster diagrams were identified
256 according to the randomization method described by Jaksić & Medel (1990). This method
257 employs a bootstrap randomization of the raw data (fish species × variation partitions
258 extracted from diet data) to generate a distribution of Euclidean distances reflecting the null
259 hypothesis of no ordinate source of variation in the diet among the investigated fish species

(Gotelli & Graves, 1996). Data were iterated 10 000 times and their distributions were used to find the critical value of distance below which the probability of occurrence by chance is <5% (Jaksić & Medel, 1990). CA was performed in Statistica 8.0 (www.statsoft.com) while the bootstrapping procedure was done with a macro written for Excel 2010 (www.office.microsoft.com). Finally, main trends in the distribution of the identified partitions of dietary variability among the 15 fish species investigated were explored with PCA in Statistica 8.0 (www.statsoft.com).

Results

Assemblage level variation in the diet

At the assemblage level, total identified variation (i.e. eigen value, a measure of the explanatory power of each ordination axis; Table 2) was 16.3 in the high and 6.8 in the low resolution diet data, and 20.8% and 36.9% of them could be explained, respectively. Most of the explained variation in the individual diet composition data belonged to between species differences (Fig. 2). This factor explained alone 10.3% and 18.2%, and as shared effect mainly with the sampling year and the habitat additional 3.4% and 8.0% of the total variation in the high and low resolution diet data, respectively. A moderate part of the variation was explained by spatial and temporal factors, mainly by the sampling year and the habitat, while, effect of the L_S was small.

Species level variation in the diet

Similarly to assemblage level patterns, total identified variation (i.e. eigen value; Table 2) was significantly lower at low (mean: 3.0; range: 1.6-5.2) than at high (mean: 6.8; range: 4.4-13.5) diet resolution for all species, and the explained proportion of the variation was higher in the low (mean: 29.3%; range: 14.3%-54.8%) than in the high (mean: 20.2%; range 13.3%-30.6%) resolution data in all species except the *S. erythrophthalmus*. However, both the portion and the source of the explained variation in the diet data varied markedly between fish species (Fig 3 and Table 2). On average, temporal factors accounted for most of the explained variation in both the high and the low resolution diet data (7.9% and 8.4% as pure and 3.9% and 6.1% as shared effect, respectively), followed by fish size (L_S; 3.7% and 6.9% as pure and 3.7% and 6.9% as shared effect, respectively) and spatial factors (3.8% and 5.6% as pure and 3.3% and 6.0% as shared effect, respectively) (Fig. 3).

Based on the high resolution diet data, CA identified three multi–species groups and four separate species according to the importance of the investigated factors in the variation of the diet. Pikeperch *Sander lucioperca* separated from other species mainly due to the high influence of habitat and asp *Aspius aspius* due to the high proportion of shared effect of L_S. Diet of razor fish *Pelecus cultratus* and bleak *Alburnus alburnus* were relatively strongly influenced by sampling season and lake basin, while diet of *P. fluviatilis*, *S. erythrophthalmus* and ruffe *Gymnocephalus cernuus* by pure effect of L_S. The other eight species formed two less interpretable clusters (Fig. 4). Results of the PCA were highly congruent with that of the CA and supported the separation of two obligate piscivores *S. lucioperca* and *A. aspius*, and two zooplanktivores *P. cultratus* and *A. alburnus* from the other species and also from each other. The first three principal components (PC) explained 61.1% of between species variation, and PC 1 represented a gradient based on the importance of different spatial and temporal scales, PC 2 a gradient mainly based on the importance of L_S and PC 3 a gradient primarily based on season and lake basin (Fig. 5).

For the low resolution data the explained variation proportions were highest in fishes with marked ontogenetic resource shift (either diet or habitat), such in *A. aspius*, *G. cernuus*, *S. lucioperca*, Volga pikeperch *Sander volgensis*, *P. fluviatilis* and *L. gibbosus* (Fig. 3b and Table 2). CA identified only one cluster with six non-piscivorous, benthic species, while, the other nine species separated significantly from this cluster and from each other (Fig. 6). PC 1 in the PCA represented a gradient from the planktivorous *P. cultratus* and *A. alburnus*, which are species with no marked ontogenetic habitat and diet shifts, to the piscivorous *S. lucioperca*, which could be characterized with a marked ontogenetic diet shift and diverse resource use. While, PC 2 correlated positively with L_S and negatively with the importance of the shared effect of lake basin and habitat, and PC 3 correlated positively with the influence of sampling year and the shared effect of temporal and habitat factors and negatively with the importance of season in dietary variability (Fig. 7).

Discussion

The present study showed that the larger part of the dietary variability observed among individuals of 15 fish species could not be explained by between species and the considered temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and ontogenetic (i.e. L_S) factors. As hypothesized, most of the explained variation related to interspecific differences at the assemblage level. This result is similar to the finding of Pusey et al. (2010) who examined a tropical fish assemblage in Australia and found that species identity accounted for 31% of the total dietary variance. Although the explanatory power of their data set was twofold higher than what we found in the present study. According to the niche concept, differences between species facilitate their long term coexistence (Whittaker et al., 1973; Leibold, 1995; Piet et al., 1999), although on a short time or habitat scale, especially when one or more food

334 resources are abundant, interspecific dietary differences may decrease (Baker-Dittus, 1978;
335 Feyrera et al., 2003). Moreover, interspecific deviations are generally weaker at the onset of
336 larval feeding and increase with development (Nunn et al., 2007; Specziár & Rezsu, 2009),
337 which may result in a stronger taxonomic component in the dietary variability in studies
338 concentrating on adult fishes. Our results thus revealed that taxonomic identity provides only
339 a very rough picture on the diet for an individual fish, because diet composition depends on
340 individual or instantaneous feeding strategies (Ritchie, 1998; Bolnick et al., 2003; Reid et al.,
341 2010) and also can be highly variable in both time and space (Svanbäck & Eklöv, 2002;
342 Platell et al., 2007; Ginter et al., 2012b; Nunn et al., 2012). Note that further part of the
343 discussion is based primarily on the results obtained from the high resolution data, using the
344 same food item categories that were successfully used in most previous studies in Lake
345 Balaton.
346 Many fishes reveal pronounced size-dependent trend in their diet composition (Bergman,
347 1990; Mittelbach & Persson, 1998; Specziár & Rezsu, 2009). Recently, Specziár & Rezsu
348 (2009) found that 13 out of the 15 fish species investigated here showed significant
349 ontogenetic dietary changes. In the light of this, it is a bit surprising that the proportion of
350 mean variation explained by the L_S was low in the present study. However, the relative
351 importance of L_S was high in some species (e.g. *P. fluviatilis*, *G. cernuus*, *S.*
352 *erythrophthalmus*, *A. aspius*), at least compared with the importance of temporal and spatial
353 factors. Conversely, in some typical ontogenetic diet switchers (e.g. *S. lucioperca*, *S.*
354 *volgensis*, *L. gibbosus*), influence of temporal (i.e. year and season) and spatial (i.e. lake basin
355 and habitat) factors on dietary variability exceeded that of the L_S, suggesting a versatile
356 feeding behaviour in these species. In addition, L_S is closely correlated with season in younger
357 age classes (most evidently in 0+ and 1+ age classes) and the habitat use of some fish species
358 is also size-specific (Table 1), and therefore, part of the variance related to ontogenetic

359 changes were shared with the effect of these (i.e. season and habitat) factors. For example,
360 these shared effects were important in three typical ontogenetic diet switchers, *A. aspius*, *S.*
361 *lucioperca* and *S. volgensis,* and accounted for 7.5% to 9.7% of the dietary variation.
362 Discrepancy between the results of Specziár & Rezsu (2009) and the present study may also
363 be due to the difference in the study question and the statistical approach used. Specziár &
364 Rezsu (2009) concentrated only on ontogenetic patterns in the diet of 15 fish species and used
365 cluster analysis based on average data of each species size group. That approach characterized
366 trends of ontogenetic dietary changes at the population level in the 15 fish species, but
367 without estimating their significances compared to other factors. In turn, the direct ordination
368 method (CCA) used in the present study retained among individual variance as well, and
369 quantified the relative importance of temporal (i.e. year and season), spatial (i.e. lake basin
370 and habitat) and ontogenetic (i.e. L_S) factors in dietary variability for the 15 fish species.
371 The role of sampling year was evident in most fish species suggesting that the quality and
372 quantity of the food resource can significantly vary between years in Lake Balaton. This
373 finding is in accordance with the results of previous studies on the temporal dynamics of
374 several invertebrate groups, including zooplankton (G.-Tóth et al., 2011), benthic
375 chironomids (Specziár & Vörös, 2001), littoral molluscs (Balogh et al., 2008) and amphipods
376 (Muskó et al., 2007).
377 Season and lake basin accounted for >3% of the dietary variability only for *A. alburnus*
378 and *P. cultratus*, both of which are offshore living, non-benthic planktivores. These species
379 consume mainly zooplankton and periodically the swarming imagos of chironomids.
380 Availability of chironomid imagos, in turn, varies primarily between seasons and basins
381 (Specziár & Vörös, 2001; Specziár, 2008). In shared effect with predator L_S, lake basin also
382 influenced the diet of *A. aspius* and *L. gibbosus*, indicating that the response of these species
383 to the trophic gradient (i.e. between basins) was size-dependent. While, considerable joint

384 effect of L_S and temporal factors suggested some size-dependent temporal variability in the
385 diet ontogeny of *S. lucioperca*, *A. aspius* and common bream *Abramis brama*.
386 It is interesting that the habitat itself affected only weakly the diet composition of most
387 fish species, given that there are numerous examples that show how between habitat
388 differences in food resource can significantly influence the diet of fishes (e.g. Mittelbach et
389 al., 1992; Vinni et al., 2000; Svanbäck & Eklöv, 2002). For example, Platell et al. (2007)
390 found that in yellowfin seabream *Acanthopagrus latus* dietary differences were related more
391 to the habitat than to the season and fish size. In Lake Balaton, both the diversity and the
392 abundance of potential food resources vary significantly among habitats. This difference is
393 most pronounced between the offshore and the littoral areas, the former characterised by
394 highly homogeneous planktonic (G.-Tóth et al., 2011) and benthic chironomid (Specziár &
395 Vörös, 2001) food resources, whereas the four littoral habitats (i.e. macrophyte-free inshore
396 zone, reed grass stand, riprap and boat harbour) with more abundant and diverse food
397 resources including also molluscs, amphipods, isopods and macrophytes (Muskó, 1990;
398 Specziár & Bíró, 1998; Muskó et al., 2007; Balogh et al., 2008). In Lake Balaton, the highest
399 habitat effect was found in *S. lucioperca*. Juveniles of *S. lucioperca* fed on different food
400 resource in the offshore (dominantly *Leptodora kindtii*) than in the littoral zone (dominantly
401 *Limnomysis benedeni*). Previous studies showed that the diet of five abundant cyprinids (i.e.
402 roach *Rutilus rutilus*, *A. brama*, white bream *Blicca bjoerkna*, gibel *Carassius gibelio* and
403 common carp *Cyprinus carpio*) differed between the main habitats of the littoral zone in Lake
404 Balaton (Specziár *et al.*, 1998; Specziár, 1999). Why the habitat seemed to be relatively
405 unimportant in the present study could be explained by at least three reasons. Most fish
406 species did not occur in all habitats sampled (Table 1), and their habitat choice likely included
407 a filtering for available food resources as well. Therefore, species-specific habitat use resulted
408 in some overlap (i.e. shared effect) between the dietary variance related to taxonomic and

habitat factors. Second, in some fish species ontogenetic diet shift is coupled with a habitat shift that could result in a shared effect between the L_S and the habitat factors. Third, the relatively weak effect of the habitat may also suggest that the investigated fishes have highly similar ranges of food preferences and feeding strategies over their habitats at both the species and the individual levels.

As showed above, a significant amount of the explained variance could be related to two or more explanatory factors. Overall, the relatively high importance of shared factor effects in the dietary variability indicated the presence of complex processes, such as species- and size-specific habitat choice, seasonality of the presence of the earliest life stages, coupled ontogenetic diet and habitat shifts, between habitats differences in the diet ontogeny and likely several other phenomenon which are hard to disentangle based purely on field observations.

Unexplained variation in the diet composition data was high at both the assemblage and the species levels suggesting that unmeasured factors also contributed to the observed patterns. Explainable variance was similarly low in individual diet data of Northeast Arctic Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) (Hovde et al., 2002) and in Celtic Sea fish predators (Chassot et al., 2008), but bit higher in the fish assemblage of a tropical Australian river (Pusey et al., 2010). In field datasets, it is usual that a large proportion of the variation remains unexplained due to the presence of unidentified effects and/or factors (including stochastic) which are hard to quantify. In this case, for example, within season changes were not discriminated. Further, the present study concentrated on factors affecting dietary variability primarily at the group level (i.e. species, species size groups or guilds), while individual level effects were not (practically, could not be) discriminated. The importance of individual feeding strategies has been recognized in many animal taxa including fish (Bolnick et al., 2003; Quevedo et al., 2009; Smith et al, 2011).

434 Considering the high proportion of the unexplained variation in the diet data, it is likely that
435 individual level processes could be important in the present study as well.
436 Heterogeneous (patchy) food resource (Luo et al., 1996; Lehtiniemi et al., 2007) and/or
437 temporal search image (Werner et al., 1981) may result in temporal individual specialization
438 in fishes. For example, observations of Specziár (1999) showed that there is a marked duality
439 in the feeding strategy of individual *R. rutilus*, especially in the littoral zone, where they
440 exhibited short-term specialization either for molluscs or filamentous algae. Temporality of
441 this specialization could be proved by that in some individuals the first part of the gut
442 contained only one, while the second part of the gut only the other of the above food items.
443 Temporal individual specialization is sometimes highly stochastic; the diet of individual fish
444 foraging for unevenly distributing food resource is strongly influenced by the stochastic order
445 different food items are encountered (Luo et al., 1996; Lehtiniemi et al., 2007). Similarly,
446 water turbidity in shallow Lake Balaton changes stochastically in space and time (Herodek et
447 al., 1988) that contributes to variability of prey encounter rate, and therefore, the prey
448 selectivity of fishes (Shoup & Wahl, 2009; Carter et al., 2010).
449 Another type of individual specialization is when individuals of a species persistently
450 differ in their feeding strategy due to consistence in phenotypic and behavioural variability
451 (Bolnick et al, 2003; Quevedo et al., 2009; Reid et al., 2010; Kim et al., 2012). For example,
452 persistence individual differences can be observed in 0+ *S. lucioperca*. This fish species may
453 reveal an ontogenetic shift during the first growing season from zooplankton either to
454 macroinvertebrates (i.e. *L. kindtii* in the offshore and *L. benedeni* in the inshore habitats) or
455 straight to fish prey (Specziár, 2005). Such individual deviations in the timing of ontogenetic
456 diet switching were described for other species as well (Post, 2003).
457 The present study showed that due to the high intraspecific dietary variation the total
458 dietary niche ranges of the 15 fish species considerably overlapped in Lake Balaton. This

finding supports recent arguments that modelling of population level processes should consider individual level variation of organism functioning (Bolnick et al., 2003). However, the effects of short-term (including stochastic processes) and persistence individual differences in the feeding strategy, unfortunately, cannot really be separated in large-scale field studies, and can only be limitedly addressed by stable isotopic analysis, specific experiments and modelling. High individual variability in resource use should have a significant effect on intra- and interspecific resource partitioning and also on individual level growth rate and survival of fish that, in turn, influence population and community level processes. Moreover, high individual variability and wide niche breath at the population level support the adaptive generalization in the investigated fishes (Bolnick et al, 2003). Future studies should thus concentrate on quantifying the importance of individual level variations on the population's niche breath and total dietary variability, and their influence on population and community level interactions.

One would suppose some regularity in how the relative role of different factors influencing dietary variability change between fish species, but the present study could not identify any general pattern. CA and PCA did not show any consequent grouping of fish species neither based on their taxonomic relationships nor on their feeding mode, maximum size or any evident ecological traits. Since most species belong to more than one feeding guilds during their life-span (Specziár & Rezsu, 2009), it is likely that such patterns, if exist, might be organized rather based on species size groups than on species. Moreover, since most fish species show high plasticity in their resource use, these patterns probably also vary between habitats and in time.

Similarly to the findings of Chassot et al. (2008), we showed that data resolution influenced the amount of the dietary variability detected. Both the total variation identified and the proportion of variation explained differed between the high and low resolution diet

484 composition data. Lower detected variability indicates that food resource use of fishes is
485 relatively stable at the level of broad compared to fine resource categories. Results also
486 suggest that individual feeding strategies (both the short-term and the persistent variations)
487 differentiate mainly at the fine resource scale. How the proportion of the explained variation
488 changes with diet resolution likely also depends on the nature of the explanatory factors
489 considered, and supposedly follows a bump shape pattern (i.e. it will be highest at a specific
490 level of diet resolution). When the resolution of the diet categories is too low, important
491 relationships may remain hidden. Conversely, when the precision of the diet analysis
492 significantly exceeds the analytical limit of the sampling design, the high amount of the
493 unexplainable variance might be confusing. It is suggested thus that the optimal level of diet
494 resolution (i.e. taxonomic composition or size distribution) applied in particular studies
495 should be set to the descriptive power of the explanatory variables investigated.
496 In conclusion, this study showed that taxonomic (i.e. between species), temporal (i.e. year
497 and season), spatial (i.e. lake basin and habitat) and ontogenetic factors (i.e. L_S) explained
498 only a moderate part of the total dietary variability of fishes in a large and shallow lake
499 ecosystem. Moreover, no regularity was found in how the relative roles of these factors
500 change between fish species. Considering the high ratio of the unexplained variation, it is
501 likely that short-term and persistence variations in individual foraging strategies and resource
502 use of fishes and unascertained stochastic processes had a strong influence on dietary
503 variability.
504
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510

511 **References**

512

513 Adámek, Z., J. Andreji & J. J. Gallardo, 2007. Food habits of four bottom-dwelling Gobiid
514 species at the confluence of the Danube and Hron Rivers (South Slovakia). International
515 Review of Hydrobiology 92: 554–563.
516 Baker-Dittus, A. M., 1978. Foraging patterns of three sympatric killifish. Copeia 1978: 383-
517 389.
518 Balogh, Cs., I. B. Muskó, L. G.-Tóth & L. Nagy, 2008. Quantitative trends of zebra mussels
519 in Lake Balaton (Hungary) in 2003–2005 at different water levels. Hydrobiologia 613:
520 57-69.
521 Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length-mass relationships
522 for freshwater macroinvertebrates in North America with particular reference to the
523 southeastern United States. Journal of the North American Benthological Society 18:
524 308-343.
525 Bergman, E., 1990. Effects of roach *Rutilus rutilus* on two percids, *Perca fluviatilis* and
526 *Gymnocephalus cernua*: importance of species interactions for diet shifts. Oikos 57:
527 241-249.
528 Bíró, P., 1973. The food of pike-perch (*Lucioperca lucioperca* L.) in Lake Balaton. Annales
529 Instituti Biologici (Tihany) 40: 159-183.
530 Bíró, P., 1974. Observations on the food of eel (*Anguilla anguilla* L.) in Lake Balaton.
531 Annales Instituti Biologici (Tihany) 41: 133-152.

532 Bíró, P., 1997. Temporal variation in Lake Balaton and its fish populations. Ecology of
533 Freshwater Fish 6: 196-216.
534 Bíró, P. & I. B. Muskó, 1995. Population dynamics and food of bleak (*Alburnus alburnus* L.)
535 in the littoral zone of Lake Balaton, Hungary. Hydrobiologia 310: 139-149.
536 Bíró, P., S. E. Sadek & G. Paulovits, 1991. The food of bream (*Abramis brama* L.) in two
537 basins of Lake Balaton of different trophic status. Hydrobiologia 209: 51-58.
538 Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey & M. L.
539 Forister, 2003. The ecology of individuals: incidence and implications of individual
540 specialization. The American Naturalist 161: 1-28.
541 Bolnick, D. I., R. Svanbäck, M. S. Araújo & L. Persson, 2007. Comparative support for niche
542 variation hypothesis that more generalized populations also are more heterogeneous.
543 Proceedings of the National Academy of Sciences of the United States of America 104:
544 10075-10079.
545 Carter, M. W., D. E. Shoup, J. M. Dettmers & D. H. Wahl, 2010. Effects of turbidity and
546 cover on prey selectivity of adult smallmouth bass. Transactions of the American
547 Fisheries Society 139: 353-361.
548 Chassot, E., T. Rouyer, V. M. Trenkel & D. Gascuel, 2008. Investigating trophic-level
549 variability in Celtic Sea fish predators. Journal of Fish Biology 73: 763-781.
550 Cushman, S. A. & K. McGarigal, 2002. Hierarchical, multi-scale decomposition of species-
551 environment relationships. Landscape Ecology 17: 637-646.
552 Downes, B. J., P. S. Lake & E. S. G. Schreiber, 1993. Spatial variation in the distribution of
553 stream invertebrates: implications of patchiness for models of community organization.
554 Freshwater Biology 30: 119–132.

555 Feyrera, F., B. Herboldb, S. A. Maternc & P. B. Moylec, 2003. Dietary shifts in a stressed fish
556 assemblage: Consequences of a bivalve invasion in the San Francisco Estuary.
557 Environmental Biology of Fishes 67: 277–288.
558 Francis, T. B. & D. E. Schindler, 2009. Shoreline urbanization reduces terrestrial insect
559 subsidies to fishes in North American lakes. Oikos 118: 1872–1882.
560 Ginter, K., K. Kangur, A. Kangur, P. Kangur & M. Haldna, 2012a. Diet niche relationships
561 among predator and prey fish species in their early life stages in Lake Võrtsjärv
562 (Estonia). Journal of Applied Ichthyology 28: 713-720.
563 Ginter, K., K. Kangur, A. Kangur, P. Kangur & M. Haldna, 2012b. Shifts in prey selection
564 and growth of juvenile pikeperch (*Sander lucioperca*) over half a century in a changing
565 Lake Võrtsjärv. Open Journal of Applied Sciences 2: 168-176.
566 Gliwicz, Z. M., J. Slon, & I. Szynkarczyk, 2006. Trading safety for food: evidence from gut
567 contents in roach and bleak captured at different distances offshore from their daytime
568 littoral refuge. Freshwater Biology 51: 823-839.
569 Gotelli, N. J. & Graves, G. R. (1996). Null Models in Ecology. Smithsonian Institution Press,
570 Washington and London.
571 G.-Tóth, L., L. Parpala, Cs. Balogh, I. Tátrai & E. Baranyai, 2011. Zooplankton community
572 response to enhanced turbulence generated by water-level decrease in Lake Balaton, the
573 largest shallow lake in Central Europe. Limnology and Oceanography 56: 2211-2222.
574 Herodek, S., L. Laczkó & Á. Virág, 1988. Lake Balaton: Research and Management. Nexus,
575 Budapest.
576 Hovde, S. C., O. T. Albert & E. M. Nilssen, 2002. Spatial, seasonal and ontogenetic variation
577 in the diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). ICES
578 Journal of Marine Science 59: 421-437.

579 Istvánovics, V., A. Clement, L. Somlyódy, A. Specziár, L. G.-Tóth & J. Padisák, 2007.
580 Updating water quality targets for shallow Lake Balaton (Hungary), recovering from
581 eutrophication. Hydrobiologia 581: 305-318.
582 Jaksić, F. M. & R. G. Medel, 1990. Objective recognition of guilds: testing for statistically
583 significant species clusters. Oecologia 82: 87-92.
584 Johnston, T. A. & R. A. Cunjak, 1999. Dry mass-length relationships for benthic insects: a
585 review with new data from Catamaran Brook, New Brunswick, Canada. Freshwater
586 Biology 41: 653-674.
587 Kakareko T., J. Żbikowski & J. Żytkowicz, 2005. Diet partitioning in summer of two syntopic
588 neogobiids from two different habitats of the lower Vistula River, Poland. Journal
589 Applied Ichthyology 21: 292-295.
590 Kawabata, K. & J. Urabe, 1998. Length-weight relationships of eight freshwater planktonic
591 crustacean species in Japan. Freshwater Biology 39: 199-205.
592 Kim, S. L., M. T. Tinker, J. A. Estes & P. L. Koch, 2012. Ontogenetic and among-individual
593 variation in foraging strategies of northeast Pacific white sharks based on stable isotope
594 analysis. PLoS ONE 7: e45068.
595 Legendre, P., J. Oksanen & C. J. F. ter Braak, 2011. Testing the significance of canonical
596 axes in redundancy analysis. Methods in Ecology and Evolution 2: 269-277.
597 Lehtiniemi, M., T. Hakala, S. Saesmaa & M. Viitasalo, 2007. Prey selection by the larvae of
598 three species of littoral fishes on natural zooplankton assemblages. Aquatic Ecology 41:
599 85-94.
600 Leibold, M. A., 1995. The niche concept revisited: mechanistic models and community
601 context. Ecology 76: 1371-1382.
602 Lepš, J. & P. Šmilauer, 2003. Multivariate analysis of ecological data using CANOCO.
603 Cambridge University Press, New York.

604 Luo, J., S. B. Brandt & M. J. Klebasko, 1996. Virtual reality of planktivores: a fish's
605 perspective of prey size selection. Marine Ecology Progress Series 140: 271-283.
606 Malone, B. J. & D. J. McQueen, 1983. Horizontal patchiness in zooplankton populations in
607 two Ontario kettle lakes. Hydrobiologia 99: 101-124.
608 Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological
609 consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454-1465.
610 Mittelbach, G. G., G. W. Osenberg, & P. C. Wainwright, 1992. Variation in resource
611 abundance affects diet and feeding morphology in the pumpkinseed sunfish (*Lepomis*
612 *gibbosus*). Oecologia 90: 8-13.
613 Mérona, B. de & J. Rankin-de-Mérona, 2004. Food resource partitioning in a fish community
614 of the central Amazon floodplain. Neotropical Ichthyology 2: 75-84.
615 Muskó, I. B., 1990. Qualitative and quantitative relationships of Amphipoda (Crustacea)
616 living on macrophytes in Lake Balaton (Hungary). Hydrobiologia 191: 269-274.
617 Muskó, I. B., Cs. Balogh, Á. P. Tóth, É. Varga & Gy. Lakatos, 2007. Differential response of
618 invasive malacostracan species to lake level fluctuations. Hydrobiologia 590: 65-74.
619 Nunn, A. D., J. P. Harvey & I. G. Cowx, 2007. The food and feeding relationships of larval
620 and 0+ year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic
621 shifts and interspecific diet similarity. Journal of Fish Biology 70: 726-742.
622 Nunn, A. D., L. H. Tewson & I. G. Cowx, 2012. The foraging ecology of larval and juvenile
623 fishes. Reviews in Fish Biology and Fisheries 22: 377-408.
624 Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations.
625 In Ebenman, B. & L. Persson (eds), Size-structured Populations: Ecology and Evolution
626 Springer-Verlag, Berlin: 203-218.

627 Piet, G. J., J. S. Pet, W. A. H. P. Guruge, J. Vijverberg & W. L. T. Van Densen, 1999.
628 Resource partitioning along three niche dimensions in a size-structured tropical fish
629 assemblage. Canadian Journal of Fisheries and Aquatic Sciences 56: 1241-1254.
630 Platell, M. E., H. P. Ang, S. A. Hesp & I. C. Potter, 2007. Comparisons between the
631 influences of habitat, body size and season on the dietary composition of the sparid
632 *Acanthopagrus latus* in a large marine embayment. Estuarine, Costal and Shelf Science
633 72: 626-634.
634 Podani, J., 2000. Introduction to the exploration of multivariate biological data. Backhuys,
635 Leiden, The Netherlands.
636 Post, D. M., 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth
637 bass. Ecology 84: 1298-1310.
638 Power, M. E., 1990. Effects of fish in river food webs. Science 250: 811-814.
639 Pusey, B. J., A. H. Arthington, B. Stewart-Koster, M. J. Kennard & M. G. Read, 2010.
640 Widespread omnivory and low temporal and spatial variation in the diet of fishes in a
641 hydrologically variable northern Australian river. Journal of Fish Biology 77: 731-753.
642 Quevedo, M., R. Svanbäck & P. Eklöv, 2009. Intrapopulation niche partitioning in a
643 generalist predator limits food web connectivity. Ecology 90: 2263-2274.
644 Reid, A. L., F. Seebacher & A. J. W. Ward, 2010. Learning to hunt: the role of experience in
645 predator success. Behaviour 147: 223-233.
646 Rezsu, E. & A. Specziár, 2006. Ontogenetic diet profiles and size-dependent diet partitioning
647 of ruffe *Gymnocephalus cernuus*, perch *Perca fluviatilis* and pumpkinseed *Lepomis*
648 *gibbosus* in Lake Balaton. Ecology of Freshwater Fish 15: 339-349.
649 Ritchie, M. E., 1998. Scale-dependent foraging and patch choice in fractal environments.
650 Evolutionary Ecology 12: 309-330.

651 Shoup, D. E. & D. H. Wahl, 2009. The effects of turbidity on prey selection by piscivorous
652 largemouth bass. Transactions of the American Fisheries Society 138: 1018-1027.
653 Simonian, A., I. Tátrai, P. Bíró, G. Paulovits, L. G.-Tóth & Gy. Lakatos, 1995. Biomass of
654 planctonic crustaceans and the food of young cyprinids in the littoral zone of Lake
655 Balaton. Hydrobiologia 303: 39-48.
656 Smith, J. A., L. J. Baumgartner, I. M. Suthers & M. D. Taylor, 2011. Generalist niche,
657 specialist strategy: the diet of an Australian percichthyid. Journal of Fish Biology 78:
658 1183-1199.
659 Specziár, A., 1999. Food habits and feeding strategy of five cyprinids in the main habitats of
660 Lake Balaton. Halászat 92: 124-132 (in Hungarian with an English summary).
661 Specziár, A., 2005. First year ontogenetic diet patterns in two coexisting *Sander* species, *S.*
662 *lucioperca* and *S. volgensis*, in Lake Balaton. Hydrobiologia 549: 115-130.
663 Specziár, A., 2008. Life history patterns of *Procladius choreus*, *Tanypus punctipennis* and
664 *Chironomus balatonicus* in Lake Balaton. Annales de Limnologie - International Journal
665 of Limnology 44: 181-188.
666 Specziár, A., 2011. Size-dependent prey selection in piscivorous pikeperch *Sander lucioperca*
667 and Volga pikeperch *S. volgensis* shaped by bimodal prey size distribution. Journal of
668 Fish Biology 79: 1895-1917.
669 Specziár, A. & P. Bíró, 1998. Spatial distribution and short-term changes of benthic
670 macrofauna in Lake Balaton (Hungary). Hydrobiologia 389: 203-216.
671 Specziár, A. & P. Bíró, 2003. Population structure and feeding characteristics of Volga
672 pikeperch, *Sander volgensis* (Pisces, Percidae), in Lake Balaton. Hydrobiologia 506-
673 509: 503-510.
674 Specziár, A. & E. Rezsu, 2009. Feeding guilds and food resource partitioning in a lake fish
675 assemblage: an ontogenetic approach. Journal of Fish Biology 75: 247-267.

676 Specziár, A. & L. Vörös, 2001. Long term dynamics of Lake Balaton's chironomid fauna and
677 its dependence on the phytoplankton production. Archiv für Hydrobiologie 152: 119-
678 142.
679 Specziár, A., L. Tölg & P. Bíró, 1997. Feeding strategy and growth of cyprinids in the littoral
680 zone of Lake Balaton. Journal of Fish Biology 51: 1109-1124.
681 Specziár, A., P. Bíró & L. Tölg, (1998). Feeding and competition of five cyprinid fishes in
682 different habitats of the Lake Balaton littoral zone, Hungary. Italian Journal of Zoology
683 65 (Suppl.): 331-336.
684 Specziár, A., T. Erős, Á. I. György, I. Tátrai & P. Bíró, 2009. A comparison between the
685 Nordic gillnet and whole water column gillnet for characterizing fish assemblages in the
686 shallow Lake Balaton. Annales de Limnologie – International Journal of Limnology 45:
687 171-180.
688 Specziár, A., Á. I. György & T. Erős, 2013. Within-lake distribution patterns of fish
689 assemblages: the relative roles of spatial, temporal and random environmental factors in
690 assessing fish assemblages using gillnets in a large and shallow temperate lake. Journal
691 of Fish Biology 82: 840-855.
692 Svanbäck, R. & P. Eklöv, 2002. Effects of habitat and food resource on morphology and
693 ontogenetic growth trajectories in perch. Oecologia 131: 61-70.
694 ter Braak, C. J. F. & P. Šmilauer, 2002. CANOCO reference manual and CanoDraw for
695 Windows user's guide: software for canonical community ordination (version 4.5).
696 Microcomputer Power, Ithaca, New York.
697 Vinni, M., J. Horppila, M. Olin, J. Ruuhijärvi & K. Nyberg, 2000. The food, growth and
698 abundance of five co-existing cyprinids in lake basins of different morphometry and
699 water quality. Aquatic Ecology 34: 421-431.

700 Vuille, T., 1991. Abundance, standing crop and production of microcrustacean populations
701 (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. Archiv für
702 Hydrobiologie 123: 165-185.
703 Warburton, K., S. Retif & D. Hume, 1998. Generalists as sequential specialists: diets and prey
704 switching in juvenile silver perch. Environmental Biology of Fishes 51: 445-454.
705 Warton, D. I. & F. K. C. Hui, 2011. The arcsine is asinine: the analysis of proportions in
706 ecology. Ecology 92: 3-10.
707 Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in size-
708 structured populations. Annual Reviews of Ecology and Systematics 15: 393-425.
709 Werner, E. E., G. G. Mittelbach & D. J. Hall, 1981. The role of foraging profitability and
710 experience in habitat use of the bluegill sunfish. Ecology 62: 116-125.
711 Whittaker, R. H., S. A. Levin & R. B. Root, 1973. Niche, habitat, and ecotope. The American
712 Naturalist 107: 321-338.

713 **Table 1** List of species, their ontogenetic food resource and habitat use, number of stomachs or guts with food analysed (*n*) and explanatory

714 variables and their ranges investigated

				Investigated ranges of the explanatory variables				
	Ontogenetic guild memberships*	Ontogenetic habitat use (juvenile/adult)	*n*	Year	Season	Lake basin	Habitat	L_S range (mm)
Assemblage level	I-XI	all/all	8756	1995-2007	spring, summer, autumn	K, Z, S	reed, riprap, harbour, inshore, offshore	4-750
Species level								
Cyprinidae								
Alburnus alburnus	I	all/all	364	2005-2007	spring, summer, autumn	K, Z, S	inshore, offshore	7-129
Aspius aspius	I, XI, VII, VIII	littoral/all	311	1997, 2002-2007	spring, summer, autumn	K, Z, S	reed, harbour, inshore, offshore	8-530
Abramis brama	I, VI	offshore/all	831	1995-2000, 2002, 2004, 2005	spring, summer, autumn	K, Z, S	reed, riprap, inshore, offshore	8-345
Blicca bjoerkna	I, II, V	littoral/littoral, rarely offshore	602	1995-1998, 2004-2007	spring, summer, autumn	K, Z, S	reed, inshore, offshore	7-269
Cyprinus carpio	V	littoral/littoral, rarely	361	1995-1998, 2004-	spring, summer,	K, Z, S	reed, harbour,	155-680

		offshore		2006	autumn		inshore, offshore	
Carassius gibelio	III	littoral/littoral, rarely offshore	514	1995-1998, 2000, 2003-2006	spring, summer, autumn	K, Z, S	reed, harbour, inshore, offshore	22-349
Pelecus cultratus	X, VII	offshore/offshore, rarely inshore	261	1997-1998, 2003, 2006-2007	spring, summer, autumn	K, Z, S	inshore, offshore	105-336
Rutilus rutilus	I, II, III, V	littoral/all	772	1995-2000, 2004-2006	spring, summer, autumn	K, Z, S	reed, riprap, harbour, inshore, offshore	6-282
Scardinius erythrophthalmus	I, IV	reed, harbour/reed, harbour	413	2004-2006	spring, summer, autumn	K, Z, S	reed, harbour	16-260
Centrarchidae								
Lepomis gibbosus	I, IX, X	$L_S \leq 15$ mm offshore/$L_S > 15$ mm reed, harbour	463	2002-2004, 2006	spring, summer, autumn	K, S	harbour, offshore	7-172
Percidae								
Gymnocephalus cernuus	I, VI	all/all	718	1998, 2001-2002, 2004, 2006	spring, summer, autumn	K, Z, S	inshore, offshore	4-115
Perca fluviatilis	I, IX, X	reed, harbour/reed, harbour	274	2001-2002, 2004, 2006-2007	spring, summer, autumn	K, S	reed, harbour	15-225

Sander lucioperca	I, VII, VIII	all/all	1453	1999-2007	spring, summer, autumn	K, Z, S	reed, harbour, inshore, offshore	6-750
Sander volgensis	I, VIII	mainly offshore/ mainly inshore	1018	1997-2002, 2004-2007	spring, summer, autumn	K, Z, S	inshore, offshore	6-340
Gobiidae								
Neogobius fluviatilis	VI	littoral/littoral	401	2003-2007	spring, summer, autumn	K, S	riprap, inshore	6-127

*Main resources utilized by ontogenetic guilds identified by Specziár & Rezsu (2009) are as follows: I, zooplankton; II, cladocerans, benthic chironomids and other invertebrates; III, detritus and diatoms; IV, macrophytes and filamentous algae; V, molluscs; VI, benthic chironomids; VII, fishes, *Leptodora kindtii* and *Limnomysis benedeni*; VII, fishes; IX, non-benthic chironomids and crustaceans; X, *Dikerogammarus* spp.; XI, imagos of chironomids.

L_S, standard length of fish; littoral, all littoral habitats including inshore macrophyte-free area, reed-grass stands, ripraps and boat-harbours; inshore, inshore macrophyte-free area; K, Keszthely-basin; Z, Zánka-basin; S, Siófok-basin.

Table 2 Results of the canonical correspondence analyses describing the relationship between the diet compositions of fishes and forward selected, significant (at $P < 0.05$) explanatory variables in Lake Balaton, for high and low resolution diet data

	High diet resolution								Low diet resolution							
	Eigen value	Number of resource categories	Number of significant explanatory variables	Explained variation (%)	*F*	$d.f._{num.}$	$d.f._{den.}$	*P*	Eigen value	Number of resource categories	Number of significant explanatory variables	Explained variation (%)	*F*	$d.f._{num.}$	$d.f._{den.}$	*P*
Assemblage level	16.3	24	35	20.8	47.9	840	209280	<0.001	6.8	9	34	36.9	110.0	306	78489	<0.001
Species level																
Alburnus alburnus	4.4	7	7	17.7	8.6	49	2492	<0.001	1.8	3	6	17.7	9.9	18	1071	<0.001
Aspius aspius	4.7	7	6	30.6	16.7	42	2128	<0.001	3.3	5	6	42.3	27.8	30	1520	<0.001
Abramis brama	5.8	15	13	18.3	10.5	195	12255	<0.001	2.8	6	10	20.6	15.9	60	4920	<0.001
Blicca bjoerkna	9.0	15	11	18.3	6.1	165	8850	<0.001	5.2	8	11	21.1	7.3	88	4720	<0.001
Cyprinus carpio	5.1	14	10	13.7	7.5	140	4900	<0.001	3.7	8	8	14.3	4.6	64	2816	<0.001
Carassius gibelio	6.3	13	14	21.2	6.2	182	6487	<0.001	2.9	6	12	25.0	9.0	72	3006	<0.001
Pelecus cultratus	6.1	8	9	25.4	5.7	72	2008	<0.001	2.8	4	7	29.9	9.3	28	1012	<0.001
Rutilus rutilus	13.5	17	13	18.2	9.7	221	12886	<0.001	4.4	6	14	28.4	16.0	84	4542	<0.001

Scardinius erythrophthalmus	6.5	12	7	16.2	6.5	84	4860	<0.001	3.2	5	3	14.8	19.2	15	2045	<0.001
Lepomis gibbosus	9.1	15	8	21.3	11.9	120	6810	<0.001	2.8	5	4	36.6	51.4	20	2290	<0.001
Gymnocephalus cernuus	4.8	8	6	18.6	11.0	48	5688	<0.001	1.6	3	5	42.8	83.1	15	2136	<0.001
Perca fluviatilis	6.4	10	6	17.8	7.5	60	2670	<0.001	1.7	3	5	28.9	16.8	15	804	<0.001
Sander lucioperca	6.2	9	13	30.3	32.7	117	12951	<0.001	2.7	4	14	54.8	84.5	56	5752	<0.001
Sander volgensis	6.1	10	13	21.6	17.5	130	10040	<0.001	2.9	5	12	39.3	44.5	60	5025	<0.001
Neogobius fluviatilis	8.4	12	6	13.3	8.8	72	4728	<0.001	3.5	5	6	22.5	16.7	30	1970	<0.001
Mean of species level data	6.8			20.2					3.0*			29.3*				

d.f.$_{num.}$, degrees of freedom of the numerator; d.f.$_{den}$, degrees of freedom of the denominator. Note, that CANACO version 4.5 software do not list degrees of freedom data, these were calculated independently according to Legendre et al. (2011).

* denotes significant differences between species level eigen values and explained variation proportions between the high and the low diet resolution data according to the Student *t*-test at $P < 0.05$.

728 **Figure captions**

729

730 **Fig. 1** Distribution of sampling sites in Lake Balaton, Hungary. ●, offshore sites; ○, inshore
731 macrophyte-free sites; △, reed-grass stands; □ boat harbours and ripraps

732

733 **Fig. 2** Result of the variation partitioning of the influence of taxonomic, temporal (i.e. year
734 and season), spatial (i.e. lake basin and habitat) and ontogenetic (i.e. standard length,
735 L_S) factors on the diet of fishes at the assemblage level (i.e. all 15 fish species
736 examined together) in Lake Balaton, Hungary, at high (a) and low (b) diet resolution.
737 The area of each rectangular cell is proportional to the variance accounted for by that
738 component. The total explained variance proportion was 20.8% for the high and
739 36.9% for the low diet resolution data. Note that variance partitions <0.5% are not
740 specified on the figure.

741

742 **Fig. 3** Result of the variation partitioning of the influence of temporal (i.e. year and season),
743 spatial (i.e. lake basin and habitat) and ontogenetic (i.e. standard length, L_S) factors on
744 the diet of 15 fish species in Lake Balaton, Hungary, at high (a) and low (b) diet
745 resolution. ■, year; ■, season; ■, year × season (shared effect); ■, basin; ■, habitat; ■,
746 basin × habitat; ■, size (i.e. L_S); ■, temporal × spatial; ■, temporal × size; ■, spatial ×
747 size; ■, temporal × spatial × size

748

749 **Fig. 4** Unweighted-pair-group clustering of 15 fish species based on the importance of
750 temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and size (i.e. L_S)
751 related factors in their dietary variability at high diet resolution in Lake Balaton,
752 Hungary. Broken line at 53.3% distance indicates the existence of seven clusters at $P <$

753 0·05 probability level based on the bootstrap method of Jaksić & Medel (1990).
754 Explanatory variable groups separating the particular dendogram branch are indicated
755
756 **Fig. 5** Principal component (PC) analysis plots of 15 fish species based on the importance of
757 temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and size (i.e. L_S)
758 related factors in their dietary variability in Lake Balaton, Hungary, at high diet
759 resolution along PC 1 and PC 2 (a) and PC 1 and PC 3 (b). Score of each fish species is
760 indicated by a pictogram (explained in the down right corner of the figure) showing the
761 pure (dark grey) and shared (light grey) influences of year, season, lake basin, habitat
762 and L_S on dietary variability. Percentage variances represented by PCs are shown in
763 parentheses after the axis name. Arrows indicate the characteristic gradients represented
764 by the axes based on the significant ($P < 0.05$) factor correlations (r; given in
765 parentheses)
766
767 **Fig. 6** Unweighted-pair-group clustering of 15 fish species based on the importance of
768 temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and size (i.e. L_S)
769 related factors in their dietary variability at low diet resolution in Lake Balaton,
770 Hungary. Broken line at 28.4% distance indicates the existence of 10 clusters at $P <$
771 0·05 probability level based on the bootstrap method of Jaksić & Medel (1990).
772 Explanatory variable groups separating the particular dendogram branch are indicated
773
774 **Fig. 7** Principal component (PC) analysis plots of 15 fish species based on the importance of
775 temporal (i.e. year and season), spatial (i.e. lake basin and habitat) and size (i.e. L_S)
776 related factors in their dietary variability in Lake Balaton, Hungary, at low diet
777 resolution along PC 1 and PC 2 (a) and PC 1 and PC 3 (b). Score of each fish species is

778 indicated by a pictogram (explained in the down right corner of the figure) showing the
779 pure (dark grey) and shared (light grey) influences of year, season, lake basin, habitat
780 and L_S on dietary variability. Percentage variances represented by PCs are shown in
781 parentheses after the axis name. Arrows indicate the characteristic gradients represented
782 by the axes based on the significant ($P < 0.05$) factor correlations (r; given in
783 parentheses)
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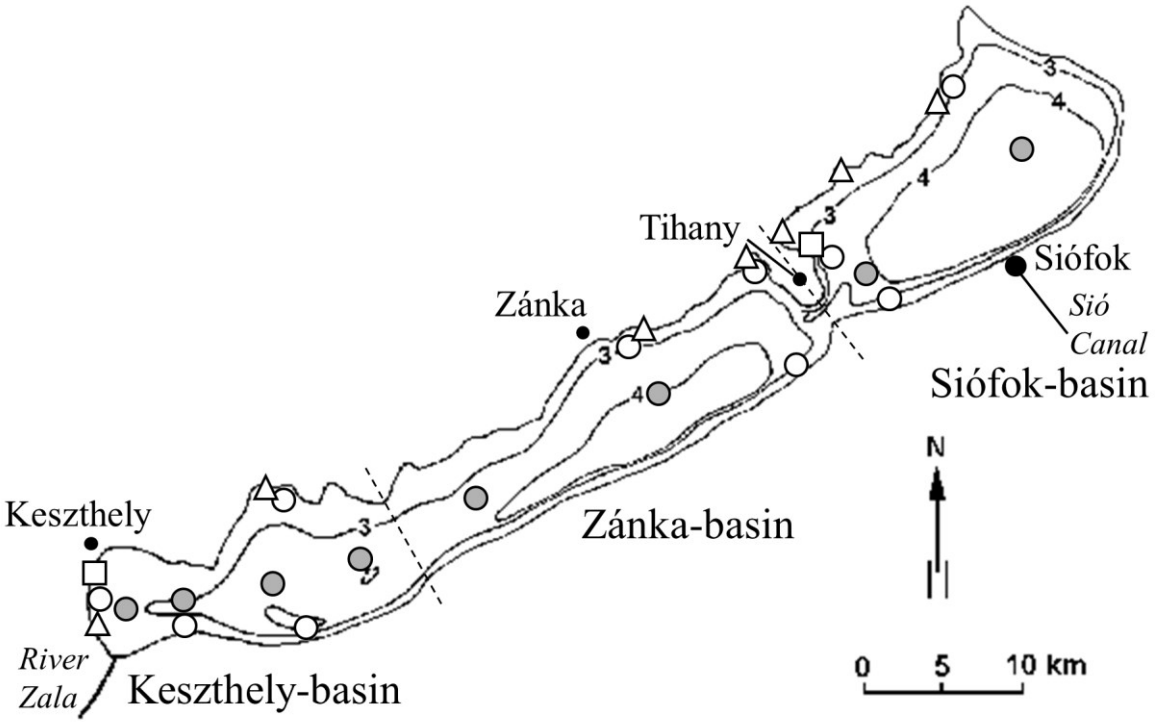

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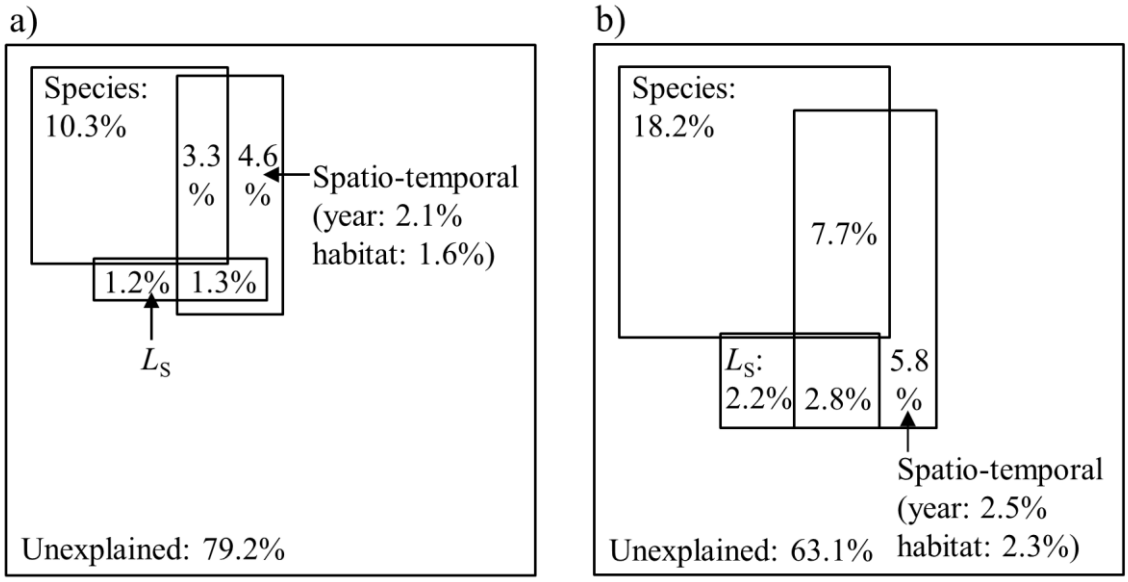
a)
Species:
10.3%
3.3
%
4.6
%
Spatio-temporal
(year: 2.1%
habitat: 1.6%)
1.2%
1.3%
L_S
Unexplained: 79.2%
b)
Species:
18.2%
7.7%
L_S:
2.2%
2.8%
5.8
%
Spatio-temporal
(year: 2.5%
habitat: 2.3%)
Unexplained: 63.1%

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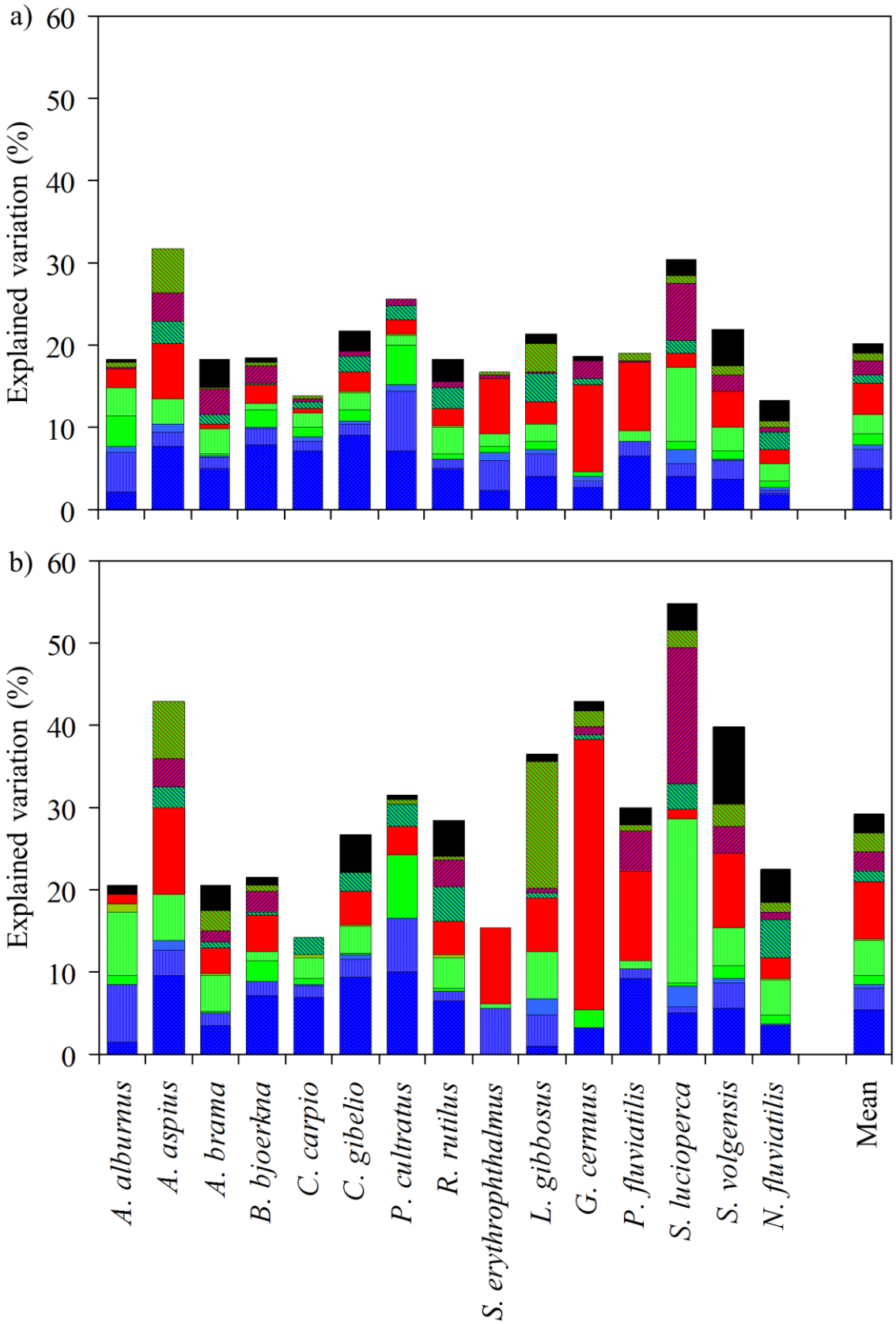
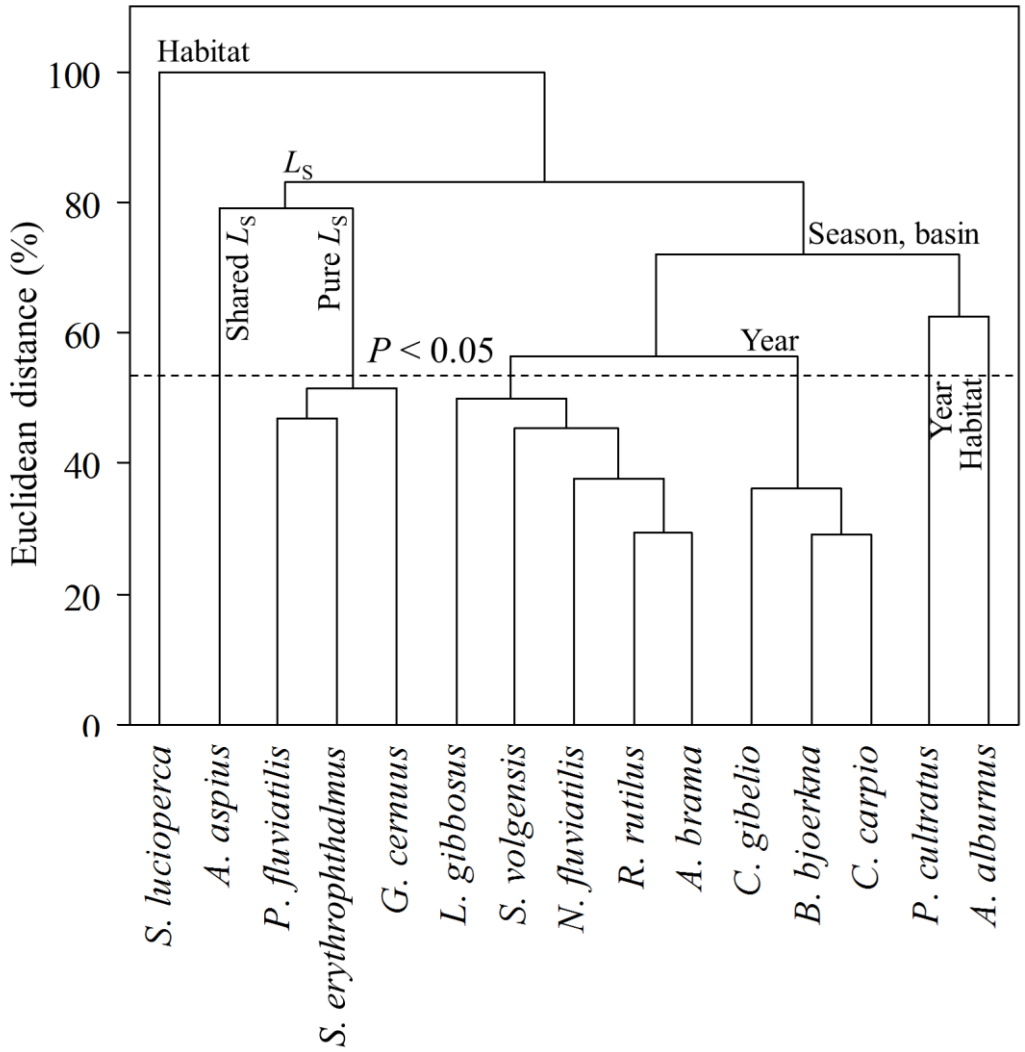

a)
b)
Explained variation (%)
0
10
20
30
40
50
60
A. alburnus
A. aspius
A. brama
B. bjoerkna
C. carpio
C. gibelio
P. cultratus
R. rutilus
S. erythrophthalmus
L. gibbosus
G. cernuus
P. fluviatilis
S. lucioperca
S. volgensis
N. fluviatilis
Mean

803

804


Habitat
L_S
Shared L_S
Pure L_S
Season, basin
Year
$P < 0.05$
Year
Habitat
Euclidean distance (%)
100
80
60
40
20
0
S. lucioperca
A. aspius
P. fluviatilis
S. erythrophthalmus
G. cernuus
L. gibbosus
S. volgensis
N. fluviatilis
R. rutilus
A. brama
C. gibelio
B. bjoerkna
C. carpio
P. cultratus
A. alburnus

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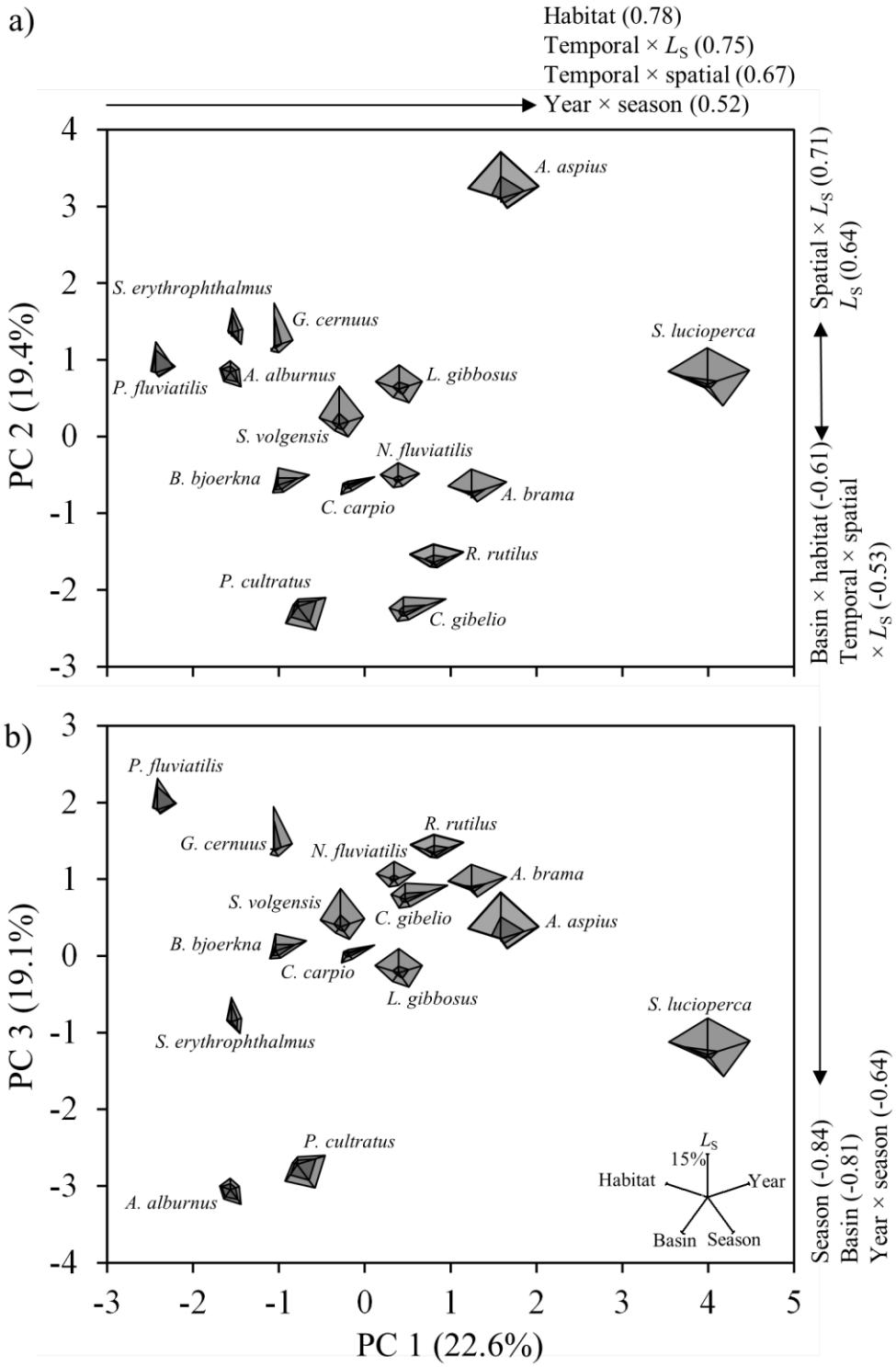
a)
Habitat (0.78)
Temporal × L_S (0.75)
Temporal × spatial (0.67)
Year × season (0.52)
PC 2 (19.4%)
A. aspius
S. erythrophthalmus
G. cernuus
S. lucioperca
P. fluviatilis
A. alburnus
L. gibbosus
S. volgensis
N. fluviatilis
B. bjoerkna
A. brama
C. carpio
R. rutilus
P. cultratus
C. gibelio
Spatial × L_S (0.71)
L_S (0.64)
Basin × habitat (-0.61)
Temporal × spatial × L_S (-0.53)
b)
PC 3 (19.1%)
P. fluviatilis
R. rutilus
G. cernuus
N. fluviatilis
A. brama
S. volgensis
C. gibelio
A. aspius
B. bjoerkna
C. carpio
L. gibbosus
S. lucioperca
S. erythrophthalmus
P. cultratus
A. alburnus
L_S
15%
Habitat
Year
Basin
Season
Season (-0.84)
Basin (-0.81)
Year × season (-0.64)
PC 1 (22.6%)

807

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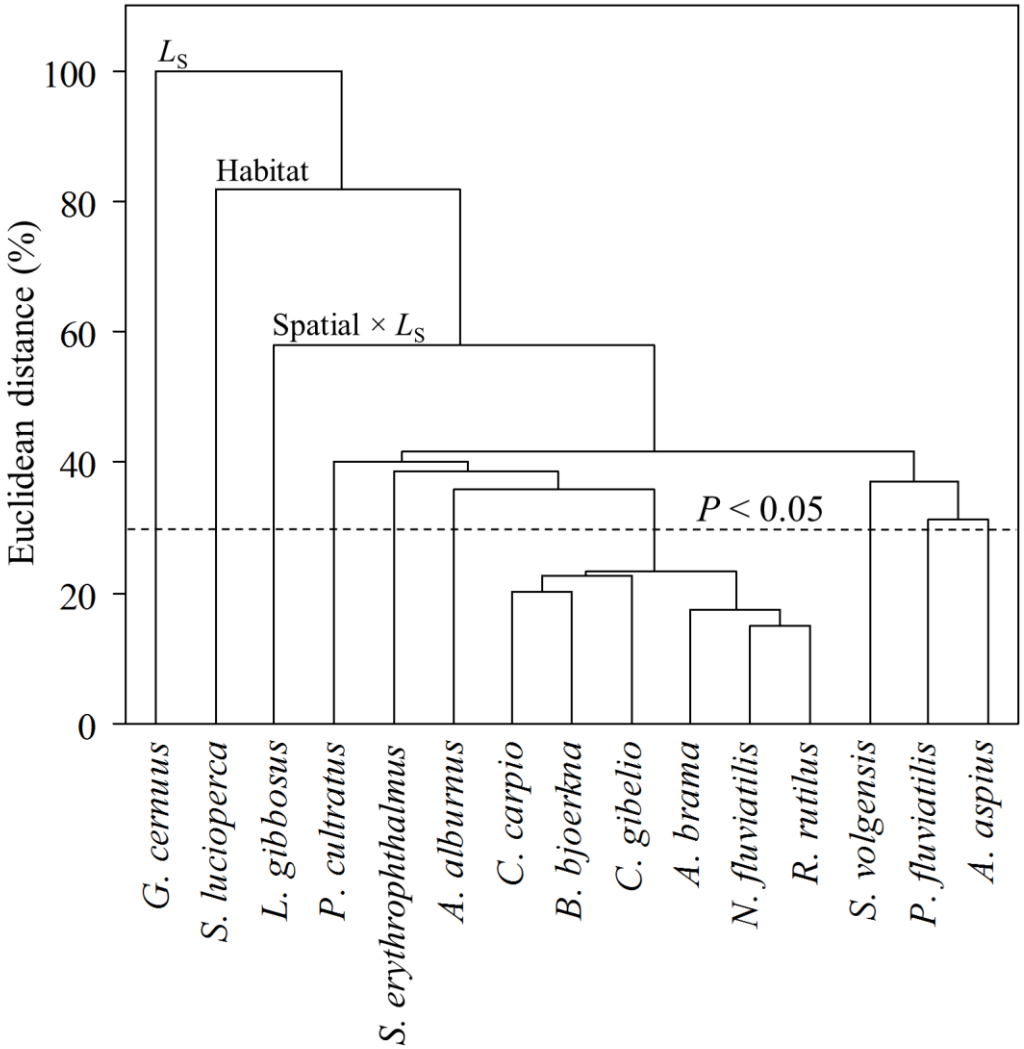
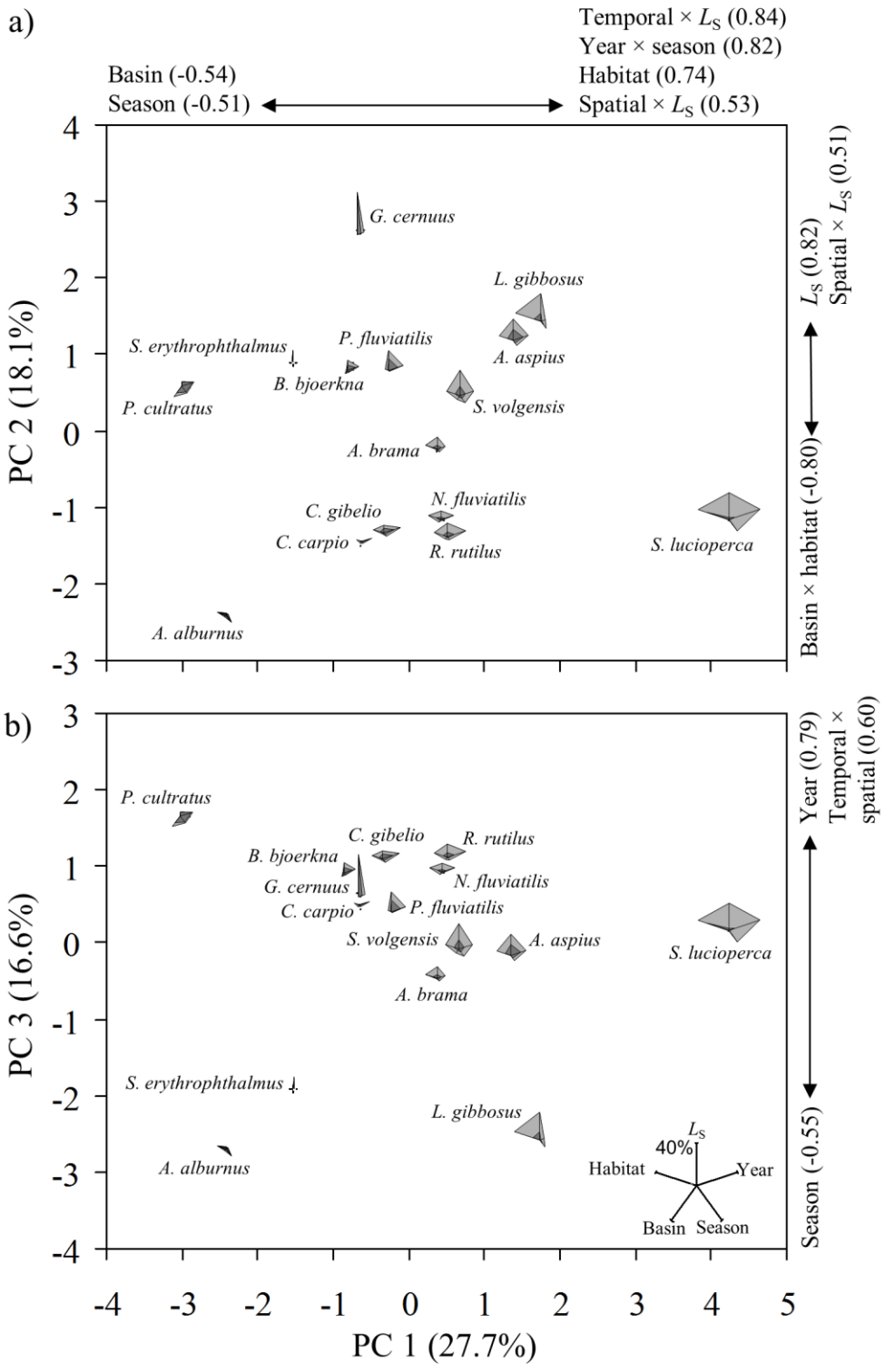

L_S
Habitat
Spatial × L_S
$P < 0.05$
Euclidean distance (%)
100
80
60
40
20
0
G. cernuus
S. lucioperca
L. gibbosus
P. cultratus
S. erythrophthalmus
A. alburnus
C. carpio
B. bjoerkna
C. gibelio
A. brama
N. fluviatilis
R. rutilus
S. volgensis
P. fluviatilis
A. aspius

809

810


a)
Temporal × L_S (0.84)
Year × season (0.82)
Habitat (0.74)
Spatial × L_S (0.53)
Basin (-0.54)
Season (-0.51)
PC 2 (18.1%)
L_S (0.82)
Spatial × L_S (0.51)
Basin × habitat (-0.80)
G. cernuus
L. gibbosus
S. erythrophthalmus
P. fluviatilis
A. aspius
B. bjoerkna
P. cultratus
S. volgensis
A. brama
N. fluviatilis
C. gibelio
C. carpio
R. rutilus
S. lucioperca
A. alburnus
b)
PC 3 (16.6%)
Year (0.79)
Temporal × spatial (0.60)
Season (-0.55)
P. cultratus
C. gibelio
R. rutilus
B. bjoerkna
G. cernuus
N. fluviatilis
C. carpio
P. fluviatilis
S. volgensis
A. aspius
S. lucioperca
A. brama
S. erythrophthalmus
L. gibbosus
A. alburnus
L_S
40%
Habitat
Year
Basin
Season
PC 1 (27.7%)

811