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9 **Feeding ecology of the invasive Amur sleeper (*Perccottus glenii* Dybowski, 1877) in**
10 **Central Europe**

11 S. Kati^{1*}, A. Mozsár^{1,2}, D. Árva^{1,2}, N. J. Cozma³, I. Czeglédi¹, L. Antal¹, S. A. Nagy¹, T. Erős²

12 ¹Department of Hydrobiology, University of Debrecen, H-4032 Debrecen, Egyetem sqr. 1.,
13 Hungary

14 ²MTA Centre for Ecological Research, Balaton Limnological Institute, H-8237 Tihany,
15 Klebelsberg K str. 3., Hungary

16 ³Department of Ecology, University of Debrecen, H-4032 Debrecen, Egyetem sqr. 1.,
17 Hungary

18 *Corresponding author: S. Kati: ksara936@gmail.com

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27 **Abstract**

28 In the last two decades, the invasion of the Amur sleeper (*Percottus glenii* Dybowski, 1877)
29 originating from the Far East can be observed in Eastern and Central Europe. Since the Amur
30 sleeper is a non-game fish species, few detailed studies exist on its feeding ecology both in its
31 native and invaded habitats. We examined the seasonal feeding ecology of Amur sleeper in a
32 lentic and in a lotic habitat. Chironomid larvae, zygopteran larvae, crustaceans and
33 ephemeropteran larvae dominated the diet. No clear differences between the two habitats were
34 found. The diet composition was mainly regulated by the body size that had stronger effect
35 than the habitat and the season. Although fish consumption was uncommon, we anticipate this
36 finding to the structure of the examined populations, in which large bodied individuals were
37 rare. Our study shows that the Amur sleeper may influence several levels (compartments) of
38 the aquatic food web, although the species proved to be an especially important predator of
39 the invertebrate assemblage.

40

41 **1. Introduction**

42 Besides habitat degradation, the spread of non-native invasive species is the main concern for
43 the decline of biodiversity (Clavero & Garcia-Berthou 2005, Casal 2006, Khan & Panikkar
44 2009). For example, invading plant and animal species have caused drastic changes in the
45 receiving biota both in terrestrial ecosystems like in New Zealand, Hawaii, Australia (Lövei
46 1997) and in aquatic ecosystems like in Lake Victoria (Gurevitch & Padilla 2004). In the past
47 centuries the rates of invasion by non-native species have been increasing worldwide,
48 especially in aquatic environments, with wide ranging consequences for the invaded
49 ecosystems (Puntilla et al. 2013). Therefore, the investigation of the ecology of invasive
50 species has become an important topic of the scientific community to aid management plans
51 for biodiversity conservation (Gozlan 2008).

52 One of the most important ecological questions about new invaders is how they can affect the
53 trophic relationships in the recipient communities. Previous studies emphasized that their
54 ecological impacts on the native community are cannot be assessed (Vitule et al. 2009,
55 Lenhardt et al. 2010). Invasion of alien fish species may have important economic and
56 ecological consequences, as they can substantially affect the structure and functioning of
57 native communities. Predation and competition exerted by non-native species may lead to
58 changes in the relative abundance of indigenous prey species or competitors and may
59 ultimately results in their local extinction (Zaret & Paine 1973, Lodge 1993, Khan & Panikkar
60 2009).

61 Amur sleeper is one of the most invasive fish species in Eurasia in the last few decades (Copp
62 et al. 2005, Reshetnikov & Ficetola 2011, Reshetnikov 2013). The original distribution of the
63 Amur sleeper is the Russian Far East, North-East China, and the northern part of the Korean
64 Peninsula (Berg 1949, Nikolsky 1956, Jurajda et al. 2006). The expansion from its native
65 range started in 1916 when the species was introduced to a garden pond in St Petersburg,
66 eastern Russia (Reshetnikov 2004). The species accommodated to the environment in its non-
67 native habitat soon, and it has been spreading extremely fast in Eastern and Central European
68 river systems (Reshetnikov 2004, Reshetnikov & Ficetola 2011). The first occurrence of
69 Amur sleeper in Hungary was recorded in 1997 in a reservoir of the River Tisza (Harka
70 1998). The species spread along the Tisza catchment within a decade. Today one of the
71 westernmost documented distribution of the species in Europe is the Balaton catchment,
72 Hungary (Reshetnikov 2010), where the species was presumably arrived via game fish
73 transport from the Tisza Catchment (Erős et al. 2008). Interestingly, the species was also
74 recently discovered in fish ponds in Germany, more than 500 km away from the hitherto
75 known westernmost records in the canals of Lake Balaton, Hungary (Reshetnikov &
76 Schliewen 2013).

77 Due to their extreme fast invasion and numerical dominance in many locations in the invaded
78 range it can be assumed that the Amur sleeper soon become an integrated element of the
79 aquatic food web in both lotic (lowland streams and rivers) and lentic (ponds and lakes)
80 habitats in Europe. Detailed knowledge about the role in the food web would be essential for a
81 variety of aquatic habitats and ecoregions to base any management actions. The few studies
82 on its non-native range confirms previous knowledge and suggest that the Amur sleeper is a
83 versatile predator of a variety of macroinvertebrate taxa, but also consumes fish, and can be
84 dangerous even to the larvae of amphibians (Szító & Harka 2000, Bogutskaya & Naseka 2002,
85 Reshetnikov 2003, Orlova et al. 2006, Koščo et al. 2008, Grabowska et al. 2009). Although
86 these studies give some insight into the feeding ecology of the species, several aspects of the
87 feeding ecology of Amur sleeper still need more information to estimate the impact of this
88 species in the newly invaded areas including the detailed elaboration of habitat, time or
89 ontogenetic changes in diet, or the examination of prey preference. Consequently, the goals of
90 this study were to investigate the feeding ecology of the Amur sleeper in a lotic and in a lentic
91 habitat in one of the westernmost part of the species' distribution, Hungary. Specifically, we
92 (i) examine the seasonal composition of the potential food resource macroinvertebrate
93 assemblage, (ii) provide detailed data on the diet composition of the species including
94 seasonal, ontogenetic and habitat dependent comparisons, and (iii) contrast diet data with the
95 composition of the macroinvertebrate assemblage.

96

97 **2. Materials and methods**

98 Study area

99 Fish and macroinvertebrate samples were taken in a lentic (Rakamaz-Tiszanagyfalui-Nagy-
100 morotva hereafter: RNM; N48°05'45.2", E21°27'45.8") and a lotic (Lónyay-főcsatorna
101 hereafter: LOF; N48°08'38.6", E21°37'47.1") habitat. The RNM is an oxbow lake of the Tisza

102 River, which is the second largest tributary of the Danube River. The RNM oxbow has a
103 length of 4.4 km, a mean width of 200 m, and a mean depth of 1.8 m. The LOF is a lowland
104 canal, which is connected to the Tisza River. The length of LOF is 91 km. Its mean width is
105 6-7 m, mean depth is 1-2 m, and its velocity is 40-60 cm s⁻¹ at average discharge. Both
106 habitats are densely vegetated with macrophytes (mainly *Stratoides aloides*, *Hydrocharis*
107 *morsus-ranae*, *Ceratophyllum demersum*, *Phragmites australis*, *Potamogeton* sp.,
108 *Ceratophyllum demersum*, *Lemna* sp.).

109

110 Sampling protocol and laboratory analyses

111 Samples were taken in spring (07.04.), summer (02.07.), and autumn (10.10.) in 2011.
112 Macroinvertebrates were collected according to the AQEM protocol with a standard net
113 (aperture: 25 cm, mesh size: 250µm) (Hering et al. 2004) and preserved in 5% formaldehyde
114 solution at the study area. Nine samples were taken from a variety of meso/microhabitats at
115 both sites and in all seasons in areas where fish sampling was performed. Fish samples were
116 taken in the littoral zone by electrofishing (Hans-Grassl IG200/2B, PDC, 75-100 Hz, 350-650
117 V, max. 10 kW; Hans Grassl GmbH, Germany). Collected specimens were euthanized with
118 overdose of clove oil and preserved in 5% formaldehyde. We collected at least 50 individuals
119 at both sampling sites and every season, so altogether 330 individuals were captured and used
120 for the laboratory analysis.

121 In the laboratory macroinvertebrate samples were identified to the lowest reasonable
122 taxonomic level, depending on the difficulty of the identification (e.g. Chironomidae). To
123 assess the relative biomass of the groups their wet weight was measured. Fish were measured
124 for standard and total length (mm) and wet weight of fish were recorded. Based on the
125 standard lengths four size groups were distinguished (0: 0-20mm, I: 20-40mm, II: 40-60, III:
126 60<) (Table 1.). Individuals were dissected to remove the first 1/3rd of the gut which is the

127 stomach. Diet components were identified corresponding to the macroinvertebrate samples.
128 The percentage occurrence of every single food category from the total stomach content was
129 estimated (Hyslop 1980).

130

131 Data analysis

132 Only fish with non-empty stomachs were included in the analyses. Wet weight of the food
133 items from the Amur sleepers' stomach were measured directly to the nearest 0.0001g. We
134 calculated the gut fullness coefficient as follows

135
$$\text{GFC} = [W_{gc} / (W - W_{gc})] \times 1000$$

136 where W_{gc} is the weight of the stomach content and W is eviscerated fish weight (Grabowska
137 & Grabowski 2005).

138 The diet of Amur sleeper was characterised by calculating percentage occurrence and the
139 percentage prey specific abundance (average weight percentage of the prey taxon considering
140 fish only in which it occurred) of each prey type (Amundsen et al. 1996). We also compared
141 weight percentage of each prey taxa in the macroinvertebrate community with their weight
142 percentage in diet by plotting the data on the x and y axes, respectively (Borza et al. 2009).
143 Points above the 1:1 regression line may indicate positive selection for the taxon, whereas
144 points below it show rejection, which may give a rough picture on prey preferences.

145 We examined the effects of habitats (lotic vs lentic), seasons (spring, summer, autumn) and
146 size groups (0, I, II, III) on diet contents (volume %) using cluster analysis. We used the
147 Euclidean distance and the Unweighted Pair Group Means algorithm (UPGMA) for
148 classification (Podani 1997, Czeglédi & Erős 2013).

149 We tested the homogeneity of variances with Bartlett test and since the result was only
150 marginally insignificant ($p=0.065$) we used three way analysis of variance (ANOVA) to test
151 whether stomach fullness differed between sampling sites, size and season. Outliers, and

152 extreme values were omitted from the statistical analysis (see Fig 5.). We did not use the 0
153 group for the ANOVA (and consequently for the analyses about gut fullness) because it did
154 not appear in all treatments or treatment combinations. We used the program STATISTICA
155 for all analyses.

156

157 **3. Results**

158 Composition of the macroinvertebrate assemblage (% biomass) showed high variations
159 between seasons and habitats (Fig. 1.). The most abundant groups were molluscs (81%),
160 platyhelminthes and annelids (4%), crustaceans (4%), heteropteras (2%). Other important
161 groups were zygopteran larvae (>1%). In the oxbow lake trichoptera larvae (2%) reached
162 notably high proportion. In every season molluscs represented the highest bulk of the
163 biomass, mainly *Bithynia tentaculata*, *Radix balthica*, *Segmentina nitida* (Table 2.). The
164 biomass of platyhelminthes and annelids decreased from spring to autumn, whereas odonata
165 larvae number and biomass increased. Chironomid larvae had low share on the total biomass,
166 although they were very abundant in both habitats in every season.

167 Chironomid larvae, zygopteran larvae, crustaceans and ephemeropteran larvae were the most
168 abundant groups in the diet of Amur sleeper (Table 3.). Chironomid larvae dominated in the
169 diet in both habitat types in all seasons (Fig. 2.). In the spring asellids (*Asellus aquaticus*) was
170 the dominant food content in the RNM. Zygopteran larvae were frequent prey in the LOF and
171 chironomid larvae were the other important food category in both site. In the summer the
172 abundance of ephemeropteran larvae, chironomid larvae and planktonic crustaceans increased
173 in the diet in the RNM. In the LOF the importance of zygopteran larvae decreased.
174 Chironomid larvae were the most important prey category besides fish larvae which were also
175 frequently eaten. In the autumn the most important food categories were Chaoboridae and
176 chironomid larvae in the RNM. In the LOF the number of chironomid larvae decreased in the

177 stomach content; gastropods and zygopteran larvae were the firstly and secondly most often
178 preyed food categories, respectively.

179 The Amur sleeper showed a rather opposite food choice between the two habitats in the spring
180 (Fig. 3.). In the RNM the species preferred asellids and rejected zygopterans and chironomids.
181 In the LOF it relied on zygopterans and avoided asellids. In the RNM the species preferred
182 ephemeropterans in summer and Chaoboridae larvae in autumn. In LOF it still relied on
183 zygopteran larvae in summer, and hirudineas in autumn, but it preferred zygopteran larvae in
184 all seasons.

185 The diet composition was mainly determined by body size that had stronger effect than
186 habitat and season (Fig. 4.). The diet of 0 size group contained mainly planktonic crustaceans,
187 while I-II size groups contained mainly chironomid larvae, and other small
188 macroinvertebrates. The diet of II-II. size groups were diverse. The importance of chironomid
189 larvae was lower, although fish and gastropods importance were higher than for smaller
190 (younger) individuals. In both habitats, II-III size groups (LOF_T_3, RNM_T_3, RNM_T_2)
191 preyed mainly on asellids in spring.

192 Gut fullness varied between 0.00 and 48.95 with a mean value of 3.61 (Fig. 5.). The three-
193 way ANOVA did not reveal significant differences between gut fullness coefficient data
194 between sampling sites or size classes or seasons (Table 4.). Significant differences were
195 found only in the interaction between sampling site and season ($p < 0.001$), and between
196 season and size ($p < 0.001$). .

197

198 **4. Discussion**

199 The diet of Amur sleeper included a variety of animal taxa, but mainly macroinvertebrates in
200 both habitats. In all investigated seasons chironomid larvae, ephemeropteran larvae,
201 zygopteran larvae and amphipods dominated in the diet. There was not a single most

202 important food category. Most of the prey taxa were on the left side of the Amundsen
203 diagrams, which means that these prey categories occurred rarely but in high density in the
204 stomach content samples. Such a pattern may indicate, but cannot prove unambiguously, that
205 individuals in the population divide the potential food sources to reduce intraspecific
206 competition (Amundsen et al. 1996).

207 The two habitats (RNM and LOF) maintained diverse and relatively similar macroinvertebrate
208 assemblages, where Molluscs were the most dominant assemblage constituting group in terms
209 of biomass besides Crustaceans (Asellus), Oligochaeta, Platyhelminthes, Odonata,
210 Heteroptera and Trichoptera taxa. No consistent seasonal changes in assemblage composition
211 could be observed. It is thus not surprising that the food of the Amur sleeper showed a
212 diversity of food categories, and we did not find clear differences between seasons and
213 habitats in diet composition. In fact, diet composition was mainly determined by body size
214 (i.e. fish length) that had stronger effect than habitat and season. Therefore, ontogenetic
215 changes in diet preferences seem to be more important than habitat and seasonality for the diet
216 of the Amur sleeper. Size dependent differences in diet support the results of previous studies
217 (Koščo et al. 2008, Grabowska et al. 2009).

218 The diet of small sized juvenile (0+) individuals contained mainly one type of prey category
219 with high volume. Planktonic crustaceans were dominant in the diet of 0 individuals, but this
220 category was also found in relatively high abundance in the diet of II and III individuals, too.
221 Large individuals of Ostracoda, Cladocera and Copepoda have been reported to often occur in
222 the diet of matured Amur sleeper (Koščo et al. 2008). With growing body size the diet
223 composition widened out, and consisted mainly of macroinvertebrate taxa (Koščo et al. 2008,
224 Grabowska et al. 2009). Fish and gastropod consumption was observed at bigger individuals,
225 but chironomid larvae consumption was more frequent at smaller ones.

226 Fish have been frequently found in the diet of large Amur sleeper, mainly from a size of 60
227 mm (Sinelnikov 1976, Koščo et al. 2008, Grabowska et al. 2009). In fact, this invasive species
228 has been considered as a harmful predator of small bodied fishes of lowland ponds and
229 streams including the endangered and endemic European mudminnow (*Umbra krameri*) (Erős
230 et al. 2008, Ambrus & Sallai 2014), which also occupies lowland waterbodies with dense
231 aquatic vegetation (Pekárik et al. 2014). Although fish was not common in the stomach in our
232 study, we anticipate this finding to the structure of the populations. Amur sleeper showed
233 dense populations in both habitats, and as a consequence the populations consisted mainly of
234 small bodied individuals. The relatively low ratio of large bodied individuals in these
235 populations can be caused by colonization effects of recently invaded habitats (Gutowsky &
236 Fox 2001). It is also true that preying on macroinvertebrates can be more profitable for small
237 predatory fish than catching fish which is more energy-consuming (Polačik et al. 2009).
238 Nevertheless fish was observed in the diet all year round in LOF, but in spring and autumn
239 occurred with low frequency, while in summer we found fish in every fifth individuals. In
240 summer the increasing abundance of fish in the diet was due to preying on fish larvae (i.e.
241 young of the year individuals). In the literature the most prevalent preys were cyprinids,
242 mostly bitterling (*Rhodeus amarus*) (Grabowska et al. 2009). Interestingly, bitterling was an
243 abundant species in LOF, but it was lacking from the diet. The most important fish prey was
244 tubenose goby (*Proterorhinus semilunaris*). Both species prefer almost the same habitat, and
245 it is likely that the young, slow moving tubenose gobies were a relatively easily available prey
246 for the Amur sleeper. Cannibalism was found to be frequent at some populations (Koščo et al.
247 2008), but we found Amur sleeper larvae only in few individuals.

248 Gastropods and zygopteran larvae were important part in the diet in autumn. Considering the
249 data from both sites 70% biomass of the consumed individuals were molluscs in autumn. In
250 the literature Amur sleeper was found to eat gastropods, but mostly the bigger individuals,

251 and generally in autumn (Koščo et al. 2008, Grabowska et al. 2009). In LOF small gastropod
252 species were abundant in all year, which can be optimal prey item for Amur sleeper. Their
253 importance in the diet in autumn cannot be explained by the occurrence of the new gastropod
254 generation. In case of other mollusc-consuming fish species this food content occurs just as a
255 secondary group (Borza et al. 2009, Polačik et al. 2009). In our opinion these food resources
256 were secondary for Amur sleeper too; although in the oxbow-lake they were in high
257 abundance, but they were relatively rare in the stomach content. Our results suggest that
258 Amur sleeper eat gastropods if other food resources are getting depleted, like in the LOF,
259 where the gastropods and zygopteran larvae were the most abundant prey items (60% of all).
260 Interestingly, stomach fullness did not depend on fish size, season and habitat. However, gut
261 fullness was rather low in each group which suggest intraspecific competition for diet in both
262 habitats in these invasive populations.

263 In conclusion, most of the food categories identified in the diet of Amur sleeper in both
264 habitats are also common preys of this species in its natural range of distribution as well as in
265 the areas already colonised (Spanovskaya et al. 1964, Sinelnikov 1976, Litvinov & O’Gorman
266 1996, Reshetnikov 2003, Miller & Vasil’eva 2003, Grabowska et al. 2009). Generally, the
267 populations in the oxbow lake and the lowland canal fed rather on macroinvertebrates,
268 tending to shift to piscivorous behaviour with the growing body size. The large number of
269 food categories found in the stomach of Amur sleeper confirms previous findings that this fish
270 species is a non-selective predator with a broad diet spectrum.

271

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277

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394

395 **Figure legends**

396 *Fig. 1. Percentage of biomass (without molluscs) of macroinvertebrate taxa in the lentic*
397 *(RNM) and lotic (LOF) sites. The percentage values of molluscs are shown above the columns*

398 *Abbreviations: PAN - Platyhelminthes+Annelida, CRU - Crustacea, CLA - Coleoptera*
399 *larvae, CIM - Coleoptera imago, HET - Heteroptera, ODO - Odonata, TRI - Trichoptera,*
400 *MEG - Megaloptera, LEP - Lepidoptera, EPH- Ephemeroptera, ODI - Other Diptera, CHI -*
401 *Chironomidae*

402

403 *Fig. 2. Seasonal diet composition of Amur sleeper according to the method of Amundsen et al.*
404 *(1996) (SL - Mean standard length (mm), SD - Standard deviation)*

405 *Abbreviations: Ase - Asellus aquaticus, Ani - Anizoptera, Zyg - Zygoptera, Gas - Gastropoda,*
406 *Chi - Chironomidae, Ann - Annelida, Pis - Pisces, Oth - Other, Lep - Lepidoptera, Het -*
407 *Heteroptera, Mph - Macrophyta, Cim - Coleoptea imago, Eph - Ephemeroptera, Cha -*
408 *Chaoboridae, Pcr - Zooplankton, Cla - Coleoptera larvae, Tri - Trichoptera, Cer -*
409 *Ceratopogonidae, Oli - Oligochaeta, Pla - Platyhelminthes, Odi - Other Diptera, Hir -*
410 *Hirudinea, Ost - Ostracoda*

411

412 *Fig. 3. Graphical representation of food preference of Amur sleeper in the lentic (RNM) and*
413 *lotic (LOF) sites (SL - Mean standard length (mm), SD - Standard deviation)*

414 *Abbreviations: Ase - Asellus aquaticus, Zyg - Zygoptera, Gas - Gastropoda, Chi -*
415 *Chironomidae, Ann - Annelida, Lep - Lepidoptera, Eph - Ephemeroptera, Cha - Chaoboridae,*
416 *Cla - Coleoptera larvae, Tri - Trichoptera, Hir - Hirudinea*

417

418 *Fig. 4. Dendrogram of diet composition data*

419 *Abbreviations indicate habitat (RNM, LOF), season (spring, SP; summer, SU; autumn AU)*
420 *and categories of standard length*

421

422 *Fig. 5. Box plots of the gut fullness coefficient values. The box represents the 25 and 75 %*
423 *quartiles, and the band in the box is the median. The whiskers represent the highest and*
424 *lowest values that are not outliers or extreme values. Open circles and asterisks denote*
425 *outliers and extreme values, respectively.*

426 *Abbreviations indicate habitat (RNM, LOF), season (spring, SP; summer, SU; autumn AU)*
427 *and categories of standard length*

428

429 *Table 1. Number of individuals in each size group (above) and number of individuals with*
 430 *non-empty stomach which were used in further analyses (below)*

431 *Abbreviations: SP - Spring, SU - Summer, AU - Autumn, RNM - Rakamaz-Tiszanagyfalui-*

432 *Nagy-morotva, LOF - Lónyay-főcsatorna, 0, I, II, III - Size groups (standard length)*

Number of individuals in each size groups

	Mean size						Total	Mean size					
	Spring	Summer	Autumn	(mm)	SD	Spring		Summer	Autumn	(mm)	SD	Total	
RNM 0.	0	4	0	18.3	1.1	4	LOF 0.	0	5	0	18.5	0.7	5
RNM I.	23	5	9	31.6	5.2	37	LOF I.	34	10	0	30.2	5.6	44
RNM II.	18	46	36	48.0	5.2	100	LOF II.	11	38	43	49.7	5.3	92
RNM III.	14	4	12	79.9	18.3	30	LOF III.	5	6	7	73.4	12.6	18
Total	55	59	57			Total	50	59	50				330

Number of individuals which used in further analyses (Individuals with non-empty stomach)

	Mean size						Total	Mean size					
	Spring	Summer	Autumn	(mm)	SD	Spring		Summer	Autumn	(mm)	SD	Total	
RNM 0.	0	4	0	18.3	1.1	4	LOF 0.	0	5	0	18.5	0.7	5
RNM I.	21	5	5	31.1	5.3	31	LOF I.	26	10	0	30.2	6.0	36
RNM II.	17	41	23	47.9	5.2	81	LOF II.	10	26	20	49.7	5.2	56
RNM III.	14	3	7	76.0	15.3	24	LOF III.	3	4	6	71.9	11.6	13
Total	52	53	35			Total	39	45	26				250

433

434 Table 2. Food categories in the benthos of Rakamaz-Tiszanagyfalui Nagy-morotva (RNM) and Lónyay-főcsatorna (LOF)(%N, relative numeric
 435 abundance of macrozoobenthos, W% weight of macrozoobenthos)

Subphylum/Classis	Ordo	Subordo/Familia	Species	RNM								LOF							
				Spring		Summer		Autumn		Together		Spring		Summer		Autumn		Together	
				N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%
Hexapoda/Insecta	Coleoptera	Haliplidae	0.24		0.15		0.56	0.11	0.31	0.01	2.26	0.08	11.68	0.25	0.50	0.07	4.89	0.17	
		Noteridae									0.79	0.10	0.07				0.34	0.04	
		Dytiscidae	0.24	0.02			1.37	0.28	0.52	0.02	0.73	0.17	1.37	0.13				0.75	0.14
		Hydrophilidae	0.16		0.07				0.08		0.06		0.48	0.02				0.18	0.01
		Helophoridae										0.27	0.02				0.09	0.01	
	Heteroptera	Gyrinidae					0.08	0.16	0.03	0.01									
		Pleidae																	
		Nepidae	<i>Plea minutissima</i>	8.81	0.10	1.19	0.03	0.56	0.09	3.50	0.07	1.86	0.05	2.41	0.05	0.08	0.01	1.56	0.05
			<i>Ranatra linearis</i>	0.16	0.22	0.07	0.10	0.08	1.12	0.10	0.22			0.14	0.05	0.08	1.40	0.07	0.10
		Nepidae	<i>Nepa cinerea</i>			0.07	0.09			0.03	0.03			0.34	0.23			0.11	0.12
			<i>Ilyocoris cimicoides</i>	2.12	2.06	0.22	0.05	0.24	2.52	0.86	1.43	0.51	1.07	1.58	0.36			0.72	0.64
		Corixidae	<i>Sigara sp.</i>									1.52	0.29	0.21	0.03			0.68	0.14
			<i>Cymatia coleoprata sp.</i>	0.94	0.01					0.31	0.01	0.17	0.01					0.07	
		Corixidae	<i>Micronecta sp.</i>	0.08	0.01					0.03	0.01					0.17	0.19	0.05	0.01
			<i>Micronecta</i>					0.08		0.03									
		Gerridae	<i>Gerris argentatus sp.</i>									0.06							0.02
			<i>Aquarius paludum</i>			0.07	0.01			0.03				0.14				0.05	
			<i>Aquarius paludum</i>											0.21	0.09			0.07	0.05
	<i>Notonecta sp.</i>						0.08	0.84	0.03	0.04	0.11	0.29					0.05	0.12	
	<i>Notonecta sp.</i>																		
	Diptera	Chironomidae	16.82	0.16	48.92	0.35	13.63	1.56	26.97	0.29	33.99	0.68	27.90	0.09	9.55	0.48	25.38	0.36	
		Ceratopogonidae	2.44	0.02	2.09	0.06	0.81	0.08	1.79	0.04	6.66	0.25	5.09	0.15	0.67	0.09	4.52	0.19	
		Simuliidae										0.06		0.27			0.11		
		Stratiomyidae	0.94	0.28	0.07				0.34	0.18			0.07	0.04			0.02	0.02	
		Chaoboridae	0.24						0.08										
		Tabanidae						0.09					0.07	0.05			0.02	0.03	
		Sciomyzidae		0.01			0.08		0.03										
		Sciomyzidae														0.25	0.21	0.07	0.01
Lepidoptera	Nymphulinae	0.47	0.03			0.56	0.71	0.34	0.05										
	<i>Cataclista lemnata</i>			0.15	0.05			0.05	0.02			0.07				0.02			
		<i>Parapoonyx stratiotata</i>			0.07	0.03			0.03	0.01			0.07	0.03		0.02	0.01		
Odonata	Anisoptera	0.71	2.76			1.13	4.68	0.60	1.95	0.06	0.24	0.62	0.37			0.23	0.29		
	Zygoptera	2.44	0.45	4.33	0.77	16.61	12.62	7.66	1.09	4.35	1.70	3.44	0.61	19.68	14.81	8.19	1.77		
Ephemeroptera	Baetidae	5.66	0.13	0.30	0.01	3.23	0.27	3.01	0.10	1.47	0.16	0.76	0.02			0.84	0.08		
	Caenidae	1.18	0.00	4.55	0.16	3.39	0.19	3.06	0.06	0.51	0.01	0.21		0.50	0.04	0.41	0.01		

436

Subphylum/Classis	Ordo	Subordo/Familia	Species	RNM								LOF							
				Spring		Summer		Autumn		Together		Spring		Summer		Autumn		Together	
				N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%	N%	W%
	Trichoptera	Polycentropodidae										0.06	0.01			0.08	0.02	0.05	
		Limnephilidae										0.17	0.16					0.07	0.07
		Phryganeidae		0.08	0.22					0.03	0.14								
		Beraeidae		0.55						0.18									
		Sericostomatidae												0.14				0.05	
		Leptoceridae				0.75	0.03	2.26	0.29	0.99	0.02								
		Polycentropodidae				2.91	0.23	12.34	5.80	4.98	0.33								
		Other														0.08	0.21	0.02	0.01
Clitellata	Hirudinea			5.90	2.42	5.67	0.44	4.19	0.64	5.27	1.70	0.23	0.26	3.92	0.33	0.08	0.41	1.40	0.30
	Oligochaeta			7.15	0.56	12.01	1.08	19.68	5.94	12.87	0.96	29.25	6.86	21.79	1.10	14.15	1.15	22.71	3.54
Turbellaria	Tricladida	Platyhelminthes						1.94	0.28	0.62	0.01	0.06	0.01			15.41	2.46	4.19	0.12
	Megaloptera	Sialidae				0.52	0.14	0.32	1.15	0.29	0.10								
Crustacea/Malacostraca	Isopoda	Asellidae		12.89	2.26	7.31	0.13	0.81	0.27	7.06	1.48	0.56	0.17	0.21	0.01			0.29	0.07
	Amphipoda	Gammaridae		0.79	0.07					0.26	0.04	0.06						0.02	
	Mysida	Mysidae						1.05	0.22	0.34	0.01								
Gastropoda				29.01	88.21	7.01	93.99	14.11	49.00	16.56	88.35	14.40	84.73	16.15	92.16	38.69	78.45	21.54	88.34
Bivalvia						1.42	2.18	0.81	11.13	0.75	1.20	0.06	2.69	0.34	3.81			0.14	3.15

437

438

439 Table 3. Relative numeric abundance (%N) and relative percentage of volume (V%) of food items in gut of Amur sleeper (*P. glenii*) from 2 sites
 440 in Rakamaz-Tiszanagyfalui Nagy-morotva (RNM) and Lónyay-főcsatorna (LOF)

Subphylum/Classis	Ordo	Subordo/Familia	Species	RNM								LOF							
				Spring		Summer		Autumn		Together		Spring		Summer		Autumn		Together	
				N%	V%	N%	V%	N%	V%	N%	V%	N%	V%	N%	V%	N%	V%	N%	V%
	Coleoptera					0.47	2.03	0.12	0.68			0.81	0.09	13.01	8.59	4.96	2.89		
Hexapoda/Insecta		Dytiscidae		0.40	0.29					0.12	0.10							0.29	0.70
		Hydrophilidae										0.81	2.10					0.29	0.74
		Hydrochidae										0.81	2.21					0.29	0.74
	Heteroptera													0.81	1.96	0.29	0.65		
		Pleidae	<i>Plea minutissima</i>			0.28	0.19			0.12	0.06								
	Diptera	Chironomidae		45.24	23.22	32.12	19.94	10.80	21.32	30.62	21.50	52.58	35.56	48.78	24.48	1.63	2.28	32.94	20.78
		Ceratopogonidae		0.40	0.39	0.56	1.02			0.36	0.47			0.81	0.02			0.29	0.01
		Chaoboridae		6.35	6.96	0.56	0.19	69.95	39.49	20.29	15.55								
		Tabanidae												0.81	2.19			0.29	0.73
	Lepidoptera			0.40	0.98	0.56	2.45			0.36	1.14					1.63	0.54	0.58	0.18
	Odonata	Anisoptera										1.03	0.13	0.81	0.77			0.58	0.30
		Zygoptera		3.17	9.12	2.51	4.28	1.88	9.41	2.55	7.60	24.74	35.87	4.07	6.62	21.95	18.15	16.33	20.22
	Ephemeroptera			0.79	0.43	23.46	42.51	2.82	5.38	11.18	16.11	4.12	6.79	3.25	4.19	0.81	0.65	2.62	3.88
		Baetidae		3.97	10.87					1.22	3.62	3.09	4.23					0.87	1.41
	Trichoptera			0.40	1.67	7.26	9.19	4.69	10.27	4.50	7.04			3.25	2.54			1.17	0.85
Annelida															4.88	8.91	1.75	2.97	
Clitellata	Hirudinea			0.79	1.94					0.24	0.65								
	Oligochaeta					0.84	1.25			0.36	0.42	3.09	5.10					0.87	1.70
Turbellaria	Tricladida	Platyhelminthes				0.28	0.85			0.12	0.28								
Crustacea/Malacostraca	Isopoda	Asellidae		32.94	36.13	6.42	9.60			12.88	15.25	3.09	3.85					0.87	1.28
	Cladocera			3.17	4.16	21.51	1.02	5.16	0.89	11.66	2.02	2.06	2.59					0.58	0.86
	Copepoda					0.56	2.26			0.24	0.75	5.15	3.36	11.38	2.76			5.54	2.04
	Ostracoda			0.79	1.96	1.40	0.13			0.85	0.70								
Mollusca						1.12	2.55			0.49	0.85								
	Gastropoda							4.23	11.22	1.09	3.74			6.50	15.28	52.03	52.07	20.99	22.45
Terrestrial Arthropods				0.40	0.59					0.12	0.20			0.81	2.21			0.29	0.74
Pisces		Odontobutidae	<i>Perccottus glenii</i>									1.03	2.51					0.29	0.84
		Gobiidae	<i>Proterorhinus semilunaris</i>			0.28	1.70			0.12	0.57			9.76	20.31	1.63	4.35	4.08	8.22
Plant														3.25	5.63	0.81	0.43	1.46	2.02
Other				0.79	1.28	0.28	0.85			0.36	0.71			4.07	8.61	0.81	2.07	1.75	3.56

442 *Table 4. Three-way ANOVA results of gut fullness coefficient data*

	SS	d.f.	MS	F	P
Sampling Site	0.02	1	0.02	0.16	0.69
Season	0.21	2	0.10	0.86	0.43
Size	0.16	2	0.08	0.66	0.52
Sampling site : Season	1.65	2	0.82	6.62	<0.001
Sampling site : Size	0.13	2	0.07	0.53	0.59
Season : Size	2.81	4	0.70	5.65	<0.001
Sampling site : Season : Size	0.46	4	0.12	0.93	0.44
Error	38.50	315	0.12		

443