

This manuscript is contextually identical with the following published paper: Kati S, Mozsár A, Árvai D, Cozma NJ, Czeglédi I, Antal L, Nagy SA, Erős T (2015) **Feeding ecology of the invasive Amur sleeper (*Perccottus glenii* Dybowski, 1877) in Central Europe**. International Review of Hydrobiology Volume 100, Issue 3-4, Pages 116-128. DOI: 10.1002/iroh.201401784

The original published pdf available in this website:

<http://onlinelibrary.wiley.com/doi/10.1002/iroh.201401784/abstract>

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

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

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

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

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

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

Keywords: invasive species, diet resources, seasonality

Running title: Feeding ecology of the Amur sleeper

Abstract

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

1. Introduction

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

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

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

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

2. Materials and methods

Study area

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

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

Sampling protocol and laboratory analyses

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

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

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

Data analysis

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

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

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

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

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

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

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

3. Results

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

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

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

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

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

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

4. Discussion

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

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

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

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

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

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

5. Acknowledgements

We would like to express our thanks to our colleagues from the University of Debrecen, Department of Hydrobiology. This research was supported by the European Union and the

275 State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP-
276 4.2.4.A/ 2-11/1-2012-0001 ‘National Excellence Program’.

277

278 **6. Literature Cited**

279 Ambrus, A. & Sallai, Z. 2014: Distribution and conservation of the European mudminnow
280 (*Umbra krameri* Walbaum, 1972) at the range of the Fertő-Hanság National Park (North-West
281 Hungary). *Pisces Hungarici* **8**, 97–100. [in Hungarian]

282 Amundsen, P. A., Gabler, H. M., Staldvik, F. J. 1996: A new approach to graphical analysis
283 of feeding strategy from stomach content data – modification of the Costello (1990) method.
284 *Journal of Fish Biology* **48**, 607–614.

285 Berg, L.S. 1949: *Ryby presnyh vod SSSR i sopredel'nyh stran*. [Fishes of the USSR and
286 adjacent countries.] 3. Moskva–Leningrad. [In Russian]

287 Bogutskaya, E. P. & Naseka, A. M. 2002: *Perccottus glenii* Dybowski, 1877. Freshwater
288 Fishes of Russia, Zoological Institute, RAS.

289 Borza, P., Erős, T., Oertel, N. 2009: Food resource partitioning between two invasive gobiid
290 species (Pisces, Gobiidae) in the litoral zone of the River Danube, Hungary. *International*
291 *Review of Hydrobiology* **94**, 609–621.

292 Casal, C. M. V. 2006: Global documentation of fish introductions: the growing crisis and
293 recommendations for action. *Biological Invasion* **8**, 3–11.

294 Czeglédi, I. & Erős, T. 2013: Characterizing the long-term taxonomic and functional
295 variability of a stream fish assemblage. *Fundamental and Applied Limnology* **183**, 153–162.

296 Clavero, M. & Garcia-Berthou, E. 2005: Invasive species are a leading cause of animal
297 extinctions. *Trends in Ecology and Evolution* **20(3)**, 110.

298 Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Erős, T., Falka, I., Ferreira, M. T., Fox, M. G.,
299 Freyhof, J., Gozlan, R. E., Grabowska, J., Kováč, V., Moreno–Amich, R., Naseka, A. M.,

300 Penáz, M., Povž, M., Przybylski, M., Robillard, M., Russell, I. C., Stakėnas, S., Šumer, S.,
 301 Vila–Gispert, A., Wiesner, C. 2005: To be, or not to be, a non–native freshwater fish? Journal
 302 of Applied Ichthyology **21**, 242–262.

303 Erős, T., Takács, P., Sály, P., Specziár, A., György, Á. I., Bíró, P. 2008: Occurence of Amur
 304 sleeper, *Perccottus glenii* Dybowski, 1877 in the water basin of Lake Balaton. Halászat
 305 **101(2)**, 75–77. [in Hungarian]

306 Gozlan, R. E. 2008: Introduction of non-native freshwater fish: is it all bad? Fish and
 307 Fisheries **9**, 106–115.

308 Grabowska, J. & Grabowski, M. 2005: Diel-feeding activity in early summer of racer goby
 309 *Neogobius gymnotrachelus* (Gobiidae): a new invader in the Baltic basin. Journal of Applied
 310 Ichthyology **21**, 282–286.

311 Grabowska, J., Grabowski, M., Pietraszewski, D., Gmur, J. 2009: Non-selective predator – the
 312 versatile diet of Amur sleeper (*Perccottus glenii* Dybowski, 1877) in Vistula River (Poland), a
 313 newly invaded ecosystem. Journal of Applied Ichthyology **25**, 451–459.

314 Gurevitch, J. & Padilla, D. 2004: Are invasive species a major cause of extinctions? Trends in
 315 Ecology and Evolution **19**, 9.

316 Gutowsky, L. F. G. & Fox, M. G. 2011: Occupation, body size and sex ratio of round goby
 317 (*Neogobius melanostomus*) in established and newly invaded areas of an Ontario river.
 318 Hydrobiologia **671**, 27–37.

319 Harka, Á. 1998: New fish species in the fauna of Hungary: *Perccottus glehni* Dybowski,
 320 1877. Halászat **91(1)**, 32–33. [in Hungarian]

321 Hering, D., Moog, O., Sandin, L., Verdonschot, P. F. M. 2004: Overview and application of
 322 the AQEM assessment system. Hydrobiologia **516**, 1–20.

323 Hyslop, E. J. 1980: Stomach contents analysis-a review of methods and their application.
 324 Journal of Fish Biology **17**, 411–429.

325 Jurajda, P., Vassilev, M., Polačik, M., Trichkova, T. 2006: A First Record of *Perccottus glenii*
 326 (*Perciformes: Odontobutidae*) in the Danube River in Bulgaria. *Acta Zoologica Bulgarica* **58**,
 327 279–282.

328 Khan, M. F. & Panikkar, P. 2009: Assessment of impacts of invasive fishes on the food web
 329 structure and ecosystem properties of a tropical reservoir in India. *Ecological Modelling* **220**,
 330 2281–2290.

331 Koščo, J., Manko, P., Miklisová, D., Košuthová, L. 2008: Feeding ecology of invasive
 332 *Perccottus glenii* (*Perciformes, Odontobutidae*) in Slovakia. *Czech Journal of Animal Science*
 333 **53(11)**, 479–486.

334 Lenhardt, M., Markovic, G., Hegedis, A., Maletin, S., Cirkovic, M., Markovic, Z. 2010: Non-
 335 native and translocated fish species in Serbia and their impact on the native ichthyofauna.
 336 *Reviews in Fish Biology and Fisheries* **21(3)**, 407–421.

337 Libosvářský, J. & Kux, Z. 1958: Contribution to the knowledge of biology and food of mud
 338 minnow *Umbra krameri* (Walbaum). *Zoologické Listy* **7**, 235–248. [in Czech with German
 339 summary]

340 Litvinov, A. G. & O’Gorman, R. 1996: Biology of Amur sleeper (*Perccottus glehni*) in the
 341 delta of Selenga River, Buryatia, Russia. *Journal of Great Lakes Research* **2**, 370–378.

342 Lodge, D. M. 1993: Biological invasions: lessons for ecology. *Trends in Ecology and*
 343 *Evolution* **8**, 133–137.

344 Lövei, G. 1997: Global change through invasion. *Nature* **388**, 627–628.

345 Miller, P. & Vasil’eva, E. D. 2003: *Perccottus glenii* Dybowsky 1877. In: The freshwater
 346 fishes of Europe. Vol. 8/I. Mugilidae, Atherinidae, Atherionopsidae, Blennidae,
 347 Odontobutidae, Gobiidae 1. (Miller, P. J. ed). AULA-Verlag, Wiebelsheim, pp. 135–156.

348 Nikolski, G. V. 1956: Fishes of Amur river basin. Results of Amur ichthyological expedition
 349 of 1944–1949, Moscow, Russia. pp. 551. [in Russian]

350 Orlova, M. I., Telesh, I. V., Berezina, N. A., Antsulevich, A. E., Maximov, A. A., Litvinchuk,
 351 L. F. 2006: Effects of nonindigenous species on diversity and community functioning in the
 352 Gulf of Finland (Baltic Sea). *Helgoland Marine Research* **60**, 98–105.

353 Pekárik, L., Hajdú, J., Koščo, J. 2014: Identifying the key habitat characteristics of threatened
 354 European mudminnow (*Umbra krameri* Walbaum, 1792). *Fundamental and Applied*
 355 *Limnology* **184**, 151–159.

356 Podani, J. 1997: Bevezetés a többváltozós biológiai adatfeltárás rejtelmeibe. Scientia Kiadó,
 357 Budapest. pp. 412. [in Hungarian]

358 Polačik, M., Janáč, M., Jurajda, P., Adámek, Z., Ondračková, M., Trichkova, T., Vassilev, M.
 359 2009: Invasive gobies in the Danube: invasion success facilitated by availability and selection
 360 of superior food resources. *Ecology of Freshwater Fish* **18**, 640–649.

361 Puntila, R., Vilizzi, L., Lehtiniemi, M., Copp, G. H. 2013: First application of FISK, the
 362 Freshwater Fish Invasiveness Screening Kit, in Northern Europe: example of Southern
 363 Finland. *Risk Analysis* **33**, 8.

364 Reshetnikov, A. N. 2003: The introduced fish, Amur sleeper (*Perccottus glenii*), depresses
 365 populations of aquatic animals (macrovertebrates, amphibians, and a fish). *Hydrobiologia*
 366 **510**, 83–90.

367 Reshetnikov, A. N. 2004: The fish *Perccottus glenii*: history of introduction to western
 368 regions of Eurasia. *Hydrobiologia* **522**, 349–350.

369 Reshetnikov, A. N. 2010: The current range of Amur sleeper *Perccottus glenii* Dybowski,
 370 1877 (Odontobutidae, Pisces) in Eurasia. *Russian Journal of Biological Invasions* **1(2)**, 119–
 371 126.

372 Reshetnikov, A. N. & Ficetola, G. F. 2011: Potential range of the invasive fish Amur sleeper
 373 (*Percocottus glenii*) in the Holarctic. *Biological Invasions* **13**, 2967–2980.

374 Reshetnikov, A. N. 2013: Spatio-temporal dynamics of the expansion of rotan *Perccottus*
 375 *glenii* from West-Ukrainian centre of distribution and consequences for European freshwater
 376 ecosystems. *Aquatic Invasions* **8(2)**, 193–206.

377 Reshetnikov, A. N. & Schliewen, U. K. 2013: First distribution of the invasive alien fish rotan
 378 *Perccottus glenii* Dybowski, 1877 (Odontobutidae) in the Upper Danube drainage (Bavaria,
 379 Germany). *Journal of Applied Ichthyology* **29**, 1367– 1369.

380 Sinelnikov, A. M. 1976: Pitanie Amur sleepera v pojmenykh vodoetmahbassejna r.
 381 Razdolnaja (Primorski Krai) [Feeding of Amur sleeper in flood plain water body of the basin
 382 of Razdolnaya River (Primorski Krai)]. *Biology of fishes of the Far East*, DGU, Vladivostok,
 383 pp. 96–99. [in Russian]

384 Spanovskaya, V. D., Savvaitova, K. A., Potapova T. L. (1964): Variation of Amur sleeper
 385 (*Perccottus glehni* Dyb., fam. Eleotridae) in acclimatization. *Voprosy Ikhtiologii* **4**, 632–643.
 386 [in Russian]

387 Szító, A. & Harka, Á. 2000: The food sources of Amur sleeper (*Perccottus glehni* Dybowski,
 388 1877) in Hungary. *Halászat* **93(2)**, 97–100. [in Hungarian]

389 Vitule, J. R. S., Umbria, S. C., Aranha, J. M. R. 2006: Introduction of the African catfish
 390 *Clarias gariepinus* (BURCHELL, 1822) into Southern Brazil. *Biological Invasion* **8**, 677–
 391 681.

392 Zaret, T. M. & Paine, T. R. 1973: Species introduction in a tropical lake. *Science* **182**, 449–
 393 455.

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						Mean size							
	Spring	Summer	Autumn	(mm)	SD	Total	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						Mean size							
	Spring	Summer	Autumn	(mm)	SD	Total	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
		Gyrinidae						0.08	0.16	0.03	0.01								
	Heteroptera	Pleidae	<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
		Nepidae	<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
			<i>Nepa cinerea</i>			0.07	0.09			0.03	0.03			0.34	0.23			0.11	0.12
		Naucoridae	<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</i>	0.94	0.01					0.31	0.01	0.17	0.01					0.07	
			<i>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</i>									0.06						0.02	
			<i>sp.</i>			0.07	0.01			0.03				0.14				0.05	
			<i>Aquarius paludum</i>											0.21	0.09			0.07	0.05
	Diptera	Notonectidae	<i>Notonecta sp.</i>					0.08	0.84	0.03	0.04	0.11	0.29					0.05	0.12
		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									
	Lepidoptera			0.47	0.03			0.56	0.71	0.34	0.05					0.25	0.21	0.07	0.01
		Nymphulinae				0.15	0.05			0.05	0.02			0.07				0.02	
			<i>Cataclista lemnata</i>			0.07	0.03			0.03	0.01			0.07	0.03			0.02	0.01
			<i>Paraponyx stratiotata</i>			0.07	0.05			0.03	0.02								
	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

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%
Hexapoda/Insecta	Coleoptera							0.47	2.03	0.12	0.68			0.81	0.09	13.01	8.59	4.96	2.89
		Dytiscidae		0.40	0.29					0.12	0.10								
		Hydrophilidae												0.81	2.10			0.29	0.70
	Heteroptera	Hydrochidae												0.81	2.21			0.29	0.74
																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								
	Lepidoptera	Tabanidae												0.81	2.19			0.29	0.73
				0.40	0.98	0.56	2.45			0.36	1.14					1.63	0.54	0.58	0.18
		Anisoptera										1.03	0.13	0.81	0.77			0.58	0.30
	Odonata	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
				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
		Ephemeroptera																	
	Trichoptera	Baetidae		3.97	10.87					1.22	3.62	3.09	4.23					0.87	1.41
				0.40	1.67	7.26	9.19	4.69	10.27	4.50	7.04			3.25	2.54			1.17	0.85
																4.88	8.91	1.75	2.97
Annelida	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	Gastropoda					1.12	2.55			0.49	0.85								
								4.23	11.22	1.09	3.74			6.50	15.28	52.03	52.07	20.99	22.45
				0.40	0.59					0.12	0.20			0.81	2.21			0.29	0.74
Terrestrial Arthropods																			
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		