RESEARCH ARTICLE

Intraguild predation as a potential explanation for the population decline of the threatened native fish, the European mudminnow (*Umbra krameri* Walbaum, 1792) by the invasive Amur sleeper (*Perccottus glenii* Dybowski, 1877)

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Abstract

Biotic interactions exerted by invasive species have a strong effect on ecosystems. Intraguild predation may contribute to the decline in the distribution, abundance and population size of native species and may facilitate the spread of non-native taxa. In this study, we investigated the feeding ecology of the invasive fish Amur sleeper (*Perccottus glenii* Dybowski, 1877) in a lowland watercourse, where it co-exists with the threatened native fish European mudminnow (*Umbra krameri* Walbaum, 1792). We used two sampling protocols that differed in the frequency of sampling time (e.g. monthly samplings and samplings in 10-day intervals) to provide evidence of predation, an interaction that may lead to the decline of mudminnow populations with the spread of the Amur sleeper. Aquatic macroinvertebrates comprised a major part of the diet for both sampling intervals. However, finer temporal resolution revealed the importance of fish, especially mudminnow juveniles, as a periodically available food source in the Amur sleeper's diet. A high degree of dietary overlap was found between the different size groups of the Amur sleeper, but larger

specimens tended to feed on a relatively higher proportion of fish. Our results suggested that temporal resolution of stomach content analyses may largely determine inferences on the importance of predation on juvenile mudminnow. Overall, we found that intraguild predation could contribute to the decline of European mudminnow populations, which underscores the importance of effective control measures to prevent the further spread of the invasive Amur sleeper.

Keywords
Diet analysis, endemic fish species, juveniles, population decline, trophic interactions

Introduction

Over the last few decades, anthropogenic activities and climate change have accelerated the spread of non-native freshwater fishes (Copp et al. 2005; Rahel and Olden 2008; Seebens et al. 2017) with devastating consequences on native biota (da Silva et al. 2010; Strayer 2010). Adverse trophic interactions between invaders and native species are usually exerted through competition and predation (Mooney and Cleland 2001; Foley et al. 2017). However, in species sharing trophic guilds, competition and predation can be combined, a phenomenon known as intraguild predation (abbreviated as IGP). IGP, which can be facilitated by phenology (e.g. spawning, the presence of juveniles) (Wissinger et al. 1996), increases the pressure on native fauna (Polis et al. 1989; Polis and Holt 1992) and modulates resource availability and, thus, the extent of competition versus predation (Taniguchi et al. 2002; Yurkowski et al. 2017). Besides, predator-prey interaction is defined by ontogeny (Werner et al. 1983) and by seasonal and spatial variability in species distribution (Winemiller 1990; Foley et al. 2017). Overall, the phenology of the predator and prey influence their roles as predator, competitor and prey (Gotelli 1995).

The Amur sleeper (*Percottus glenii* Dybowski, 1877) is one of the most intensively spreading invasive fish species in Eurasia (Copp et al. 2005; Reshetnikov and Ficetola 2011; Reshetnikov 2013; Horvatić et al. 2022). Originally found in the Far East of Russia, it is now on the "list of invasive alien species of Union concern (Union list)" within the scope of the new Regulation (EU) No. 1143/2014 on the prevention and management of the introduction and spread of invasive alien species (European Commision 2016). Due to the adverse impact of this invasive species on the recipient ecosystems, a thorough analysis of its ecological needs and invasion biology is necessary (Simberloff 2003; Reshetnikov and Ficetola 2011).

The Amur sleeper feeds on prey from several trophic levels (Reshetnikov 2003; Grabowska et al. 2009; Kati et al. 2015). It consumes mainly invertebrates (e.g. aquatic and terrestrial arthropods, molluscs and zooplankton), but fish can also form part of its diet when Amur sleepers are above 40 mm in body length (SL) (Sinelnikov 1976; Zaloznykh 1982; Grabowska et al. 2009). Consequently, the species potentially constitutes a serious threat to the native fish fauna, especially to the strictly protected European mudminnow (*Umbra krameri* Walbaum, 1792), which is an

endemic fish to the Danube and Dniester River Basins (Manteifel and Reshetnikov 2001; Witkowski and Grabowska 2012; Tatár et al. 2017; Grabowska et al. 2019). Species with a small distribution area (e.g. endemic species), short lifespan and low fecundity, such as the European mudminnow, are amongst the species most vulnerable to invasion (Clavero and García-Berthou 2005; Strayer 2010; Arthington et al. 2016). Similar to the Amur sleeper, the European mudminnow consumes primarily invertebrates, but rarely eats fish. It even participates in cannibalism in older ages (Lovassy 1927; Bănărescu 1964; Berinkey 1966; Wanzenböck 1995). Considering overlaps in feeding habits and habitats (Grabowska et al. 2019), IGP can be assumed between the two species.

The populations of European mudminnow strongly decreased after the river regulations of the Tisza River in the 19th century. Further declines accelerated after the establishment and spread of the Amur sleeper during the last few decades (Sallai 2005; Takács et al. 2015; Fazekas et al. 2016; Tatár et al. 2017; Bănăduc et al. 2022). Although the Amur sleeper is a superior competitor and reduces the foraging efficiency of the European mudminnow (Grabowska et al. 2019), declines in European mudminnow populations in the presence of the Amur sleeper were also noticed in habitats with unlimited food resources (Takács et al. 2015; Bănăduc et al. 2022). Accordingly, predator-prey interactions can be presumed between the Amur sleeper and the European mudminnow. Reduction of juvenile recruitment has been detected in several amphibian and fish species in the presence of the Amur sleeper (Spanovskaya et al. 1964; Litvinov and O'Gorman 1996; Reshetnikov and Manteifel 1997; Manteifel and Reshetnikov 2001; Reshetnikov 2001, 2008), but these observations require further, more detailed investigations in order to unequivocally prove the significance of the Amur sleeper in the decline of native fish populations.

To better understand the processes which may lead to the reduction of European mudminnow populations, we examined the role of predation in the biotic interactions between the invasive Amur sleeper and the native European mudminnow. Specifically, we examined the stomach contents of Amur sleepers in a lowland stream, where the mudminnow still has a dense population, but where the Amur sleeper has already established a population. Our objectives were as follows: (i) What is the importance of the mudminnow or other fishes to the food supply of the Amur sleeper? (ii) How does fish consumption depend on the size of the predator and prey? (iii) How does the temporal intensity of sampling influence the results of the diet analysis? We hypothesised that the Amur sleeper is an effective predator of mudminnow and it is especially effective on small young-of-the-year individuals since the Amur sleeper is a small-bodied predatory fish. Therefore, we also hypothesised that conventional seasonal or monthly stomach content analyses may be inefficient in quantifying patterns of fish consumption correctly. Specifically, we hypothesised that even monthly samplings are not effective enough to reveal the predatory effect of the Amur sleeper on the mudminnow since this may require more intensive samplings, which are better adjusted to the presence and growth rate of the mudminnow juveniles.

Material and methods

Sample collection and laboratory process

The sampling site was the lowland Hejő stream (coordinates: 47°52.0237'N, 21°0.1433'E) which is a tributary of the Tisza River, the second largest tributary of the Danube River. Our own fish surveys showed that the fish assemblage of the Hejő consisted of the following species: Prussian carp (*Carassius gibelio*) (2%), spined loach (*Cobitis elongatoides*) (3%), pike (*Esox lucius*) (2%), weather loach (*Misgurnus fossilis*) (3%), Amur sleeper (*Perccottus glenii*) (5%), roach (*Rutilus rutilus*) (4%) and European mudminnow (*Umbra krameri*) (81%). Consequently, the mudminnow still had the most abundant population at the examined site, while the Amur sleeper had the second-most abundant population. Note, that fish assemblage surveys in the Hungarian portion of the Tisza River Basin indicated a general decline of mudminnow populations with the spread of the invasive Amur sleeper (e.g. the extent of the mudminnow population decrease was over 95% in the Upper Tisza region) (Bănăduc et al. 2022).

The mean depth of the Hejő varies between 0.8 m and 2 m and the width averages 4 m. The stream is covered with dense aquatic and hydrophilic macrophytes (mainly *Lemna minor*, *L. trisulca*, *Ceratophyllum demersum*, *C. submersum*, *Hydrocharis morsus-ranae* and *Phragmites australis*).

Fish were collected using an electric fishing device (Hans Grassl EL64 II GI, DC, 300/600V max. 7 kW, Hans Grassl GmbH, Germany; permission number: HaGF/134/2019 and HaGF/68/2021) from March 2020 to August 2021. We designed two sampling protocols, which differed in frequency over time. First, we used traditional monthly samplings to characterise the diet of the Amur sleeper, similarly to other fish diet studies (Carman et al. 2006; Grabowska et al. 2009). Second, we applied a more intensive temporal sampling design (e.g. 10-day collections, see below) to test whether monthly samplings are representative for characterising the fish-eating behaviour of the Amur sleeper. During the monthly sampling, we collected 30 Amur sleepers in each month from March 2020 to February 2021 (samples were taken every 4 weeks starting from the 23 March (n = 360; collected specimens SL: 28 mm – 93 mm). To examine diet composition at a finer temporal scale, in a period when the Amur sleeper may prey on the eggs and larvae of potential prey (e.g. in the hatching and breeding season), we collected 20 specimens at 10-day intervals from the beginning of May 2021 till the end of August 2021 (n = 240; collected specimens' SL: 45 mm – 90 mm). Note: the Kolmogorov-Smirnov test did not indicate significant difference in the size frequency distribution of Amur sleepers between the monthly and the 10-day sampling protocols (D = 0.286; p = 0.304). In addition, mean length was also highly unlikely to be biologically significant, since it was 58.8 mm and 59.6 mm in the case of the monthly and 10-day samplings, respectively.

The collected specimens were euthanised by using clove oil in the field. The standard (SL) and total length (TL) were measured to the nearest 0.01 mm with a digital calliper. Sex and stomach fullness were determined by visual examination. Exenterated guts with their contents were preserved in 96% ethanol until dietary analyses. In the laboratory, gut

contents were determined under a stereomicroscope (EduBlue – ED.1802-S) and prey items were identified to the lowest practicable taxonomic level. The stomach fullness (in volume) was determined on a scale of 0–100% (empty – full) and the fullness contribution of each prey item category was estimated such that the sum of all prey categories equalled the total stomach fullness (Hyslop 1980; Amundsen et al. 1996; Kati et al. 2015).

Statistical analyses

Fish with empty stomachs were excluded from further analyses. To estimate the importance of fish, especially the European mudminnow in the diet of the Amur sleeper, we calculated the frequency of occurrence ($F_i\%$) and the percentage of prey-specific volume ($Pi\%$) for each prey category (Amundsen et al. 1996). The frequency of occurrence and the prey-specific volume were described by the following equations:

$$F_i\% = N_i \: / \: N \times 100$$

$$P_i\% = (\textstyle\sum P_i \: / \: \sum P_{Ti})$$

where $F_i\%$ is the frequency of occurrence of the prey item i; N_i is the number of fish with prey item i in their stomach; and N is the number of fish with food content in their stomach. $P_i\%$ is the prey-specific volume of the food item i; $\sum P_i$ is the stomach content (percentage) constituted by the prey item i; $\sum P_{Ti}$ is the total stomach fullness of the fish, which contained the prey item i (Hyslop 1980; Labropoulou and Eleftheriou 1997). To investigate the food composition related to the body size of the predator, we divided the collected specimens into three size groups, based on the length-frequency distribution of the Amur sleeper population collected during the 10-day sampling protocol. The following size groups were established: small, ≤ 49 mm SL (n = 59); intermediate, 50–62 mm SL (n = 96); and large, ≥ 63 mm SL (n = 53).

We used non-metric multidimensional scaling (NMDS) with Bray–Curtis distance to evaluate the diet overlap amongst the size groups. NMDS is an indirect gradient analysis that generates an ordination, based on a specified number of dimensions and attempts to meet the conditions of a rank similarity matrix (Clarke 1993). The NMDS ordination is considered to be effective if the stress value (i.e. the measure of the match between distances in the original matrix and distances in the reduced ordination space) is below 0.2 (Clarke 1993). Diet categories that significantly (alpha = 0.05) influence the distribution pattern of the data points of the different size groups were determined using the "envfit" function (999 runs) in the freely available statistical programme "R" (version 4.2.2.) (R Core Team 2022). An analysis of similarity (ANOSIM) was also conducted to test the null hypothesis that there was no difference in the diet contents amongst the size groups. ANOSIM is a non-parametric test that compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. It produces a test statistic (R) expressed as a number between –1 and 1. An R value close to 1 suggests dissimilarity, while an R value close to 0 indicates similarity amongst groups. R values below 0 suggest that dissimi-

larities are greater within groups than between groups. The significance of the R statistic was determined by a permutation-based test (9999 runs) (Clarke 1993). Both NMDS and ANOSIM were run using the package "vegan 2.5.7" (Oksanen et al. 2020).

Dietary overlap between the Amur sleeper size groups was assessed using Schoener's (1970) dietary overlap index: $C_{xy} = 1 - 0.5\sum|p_{xi} - p_{yi}|$, where p_{xi} and p_{yi} are the proportions of prey i (based on the relative abundance of prey items) found in the diet of groups x and y, respectively. This index ranges from 0 (no diet overlap) to 1 (complete overlap). Schoener's index values > 0.6 are usually considered to be biologically meaningful in terms of consumed prey items by groups x and y (Wallace 1981; Clarke et al. 2005).

Results

Graphical analysis of the feeding strategy revealed that the Amur sleeper consumed mostly macroinvertebrates and had a broad dietary niche (Figs 1, 2). Although few food categories were consumed frequently with high prey-specific volume, the distribution of food items (points located at the upper left corner of the diagrams, see Figs 1, 2) indicated a substantial interindividual difference in diet content (resource partitioning).

In general, 15 and 12 prey categories were found, using the monthly and the 10-day protocol, respectively. Ephemeroptera and Crustacea dominated the diet, but Diptera and Coleoptera were also important in the monthly (Fig. 1) and the 10-day protocols (Fig. 2), respectively.

Diptera (March: 45%), Crustacea (May: 24%) and Ephemeroptera (*Cloeon dipterum* – April: 59%), as well as Odonata (*Coenagrion puella* – May: 23%) were the most abundant prey categories during spring in the case of the monthly protocol. The crustacean group (represented mainly by *Asellus aquaticus* and *Synurella ambulans*) was a major prey item by relative abundance in all seasons (June: 46%; November: 80%; January: 41%). Coleoptera (*Haliplus* sp.) was a main prey from summer (August: 17%) till winter (January: 17%), as indicated by its relative abundance, while Hirudinae, Heteroptera and Odonata were abundant mainly in summer (Hirudinae in August: 10%; Heteroptera in June: 6%; Odoniata in June: 14%) and autumn (Hirudinae in October: 15%; Heteroptera in September: 13%; Odonata in September: 16%).

During the 10-day protocol, the group Crustacea proved to be the most important prey (Fig. 2). Its contribution to the Amur sleeper's diet increased until the middle of summer (Fig. 2). Dragonfly larvae were a vital food resource from the end of spring till the middle of summer (Fig. 2). Amphibian tadpoles appeared continuously in the stomach from the end of June and became an essential forage base. The relative abundance of Ephemeroptera was remarkable at the end of spring (8 May: 66%; 18 May: 46%).

Piscivory was observed more frequently in the 10-day sampling protocol, with increasing importance from spring to summer. Fish eggs occasionally occurred in the diet in spring, but this diet category was amongst the less important diet categories (positioned low-right corner) (Fig. 2).

European mudminnow was the primary fish prey (Fig. 3); other fish species were identified in only two cases. Fish were usually consumed by only a few individuals

(moderate or low frequency of occurrence), but with substantial individual specialisation (high prey-specific volume). Specifically, we recorded the offspring of the spined loach and the Amur sleeper in the stomach contents in one case.
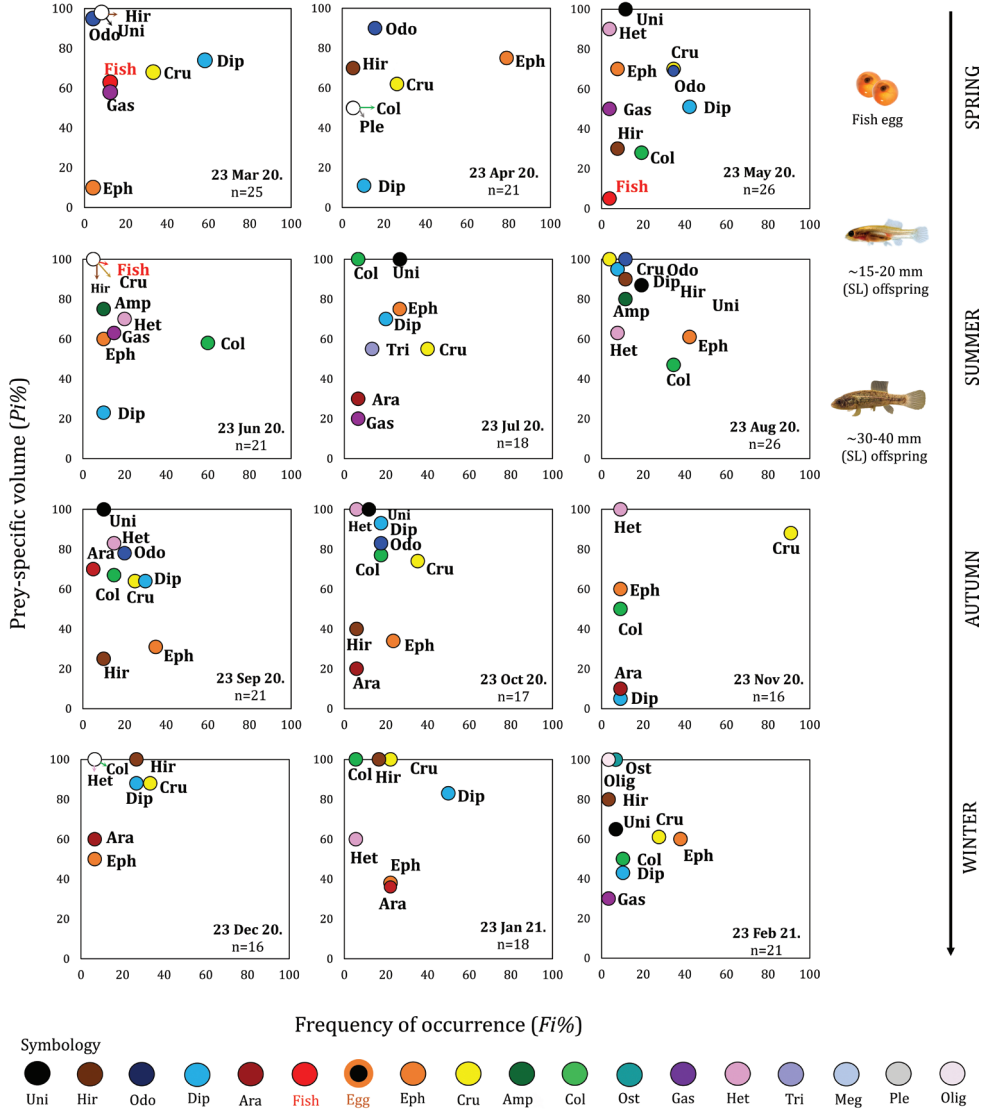

Figure 1. Graphical representation of the diet composition of Amur sleeper according to the method of Amundsen et al. (1996) during the monthly interval sampling. Prey items identified as: Fish (fish); Amp (Amphibia); Col (Coleoptera); Cru (Crustacea); Dip (Diptera); Eph (Ephemeroptera); Ost (Ostracoda); Ple (Plecoptera); Olig (Oligochaeta); Ara (Arachnida); Gas (Gastropoda); Het (Heteroptera); Hir (Hirudinea); Meg (Megaloptera); Odo (Odonata); Tri (Trichoptera); Uni (unidentified food particles). Date of the sampling occasions as well as the number (n) of the collected specimens (with non-empty stomach) are presented in the lower-right corner. The diagram on the right side represents the temporal scale of the sampling protocol and the ontogenetic development of the European mudminnow (0+).
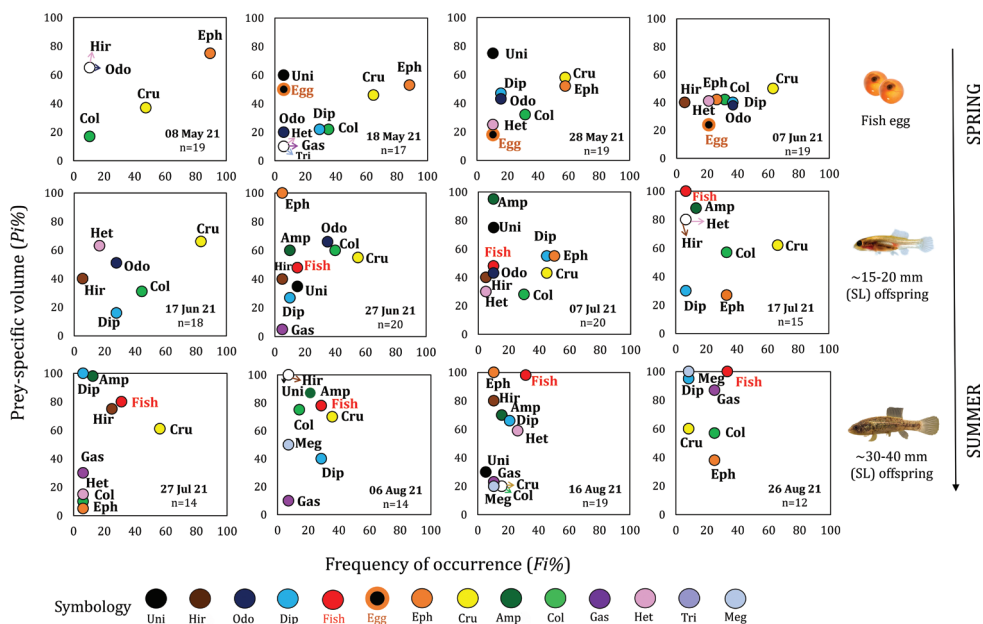
Figure 2. Graphical representation of the diet composition of Amur sleeper according to the method of Amundsen et al. (1996) during the finer temporal (10-days) sampling. Prey items identified as: Fish (fish); Amp (Amphibia); Col (Coleoptera); Cru (Crustacea); Dip (Diptera); Eph (Ephemeroptera); Gas (Gastropoda); Het (Heteroptera); Hir (Hirudinea); Meg (Megaloptera); Odo (Odonata); Tri (Trichoptera); Uni (unidentified food particles). Date of the sampling occasions as well as the number (n) of the collected specimens (with non-empty stomach) are presented in the lower-right corner. The diagram on the right side represents the temporal scale of the sampling protocol and the ontogenetic development of the European mudminnow (0+).

Figure 3. European mudminnow (*Umbra krameri*) offspring within the digestive tract of an adult Amur sleeper (*Perccottus glenii*) female.

The NMDS analysis converged in two dimensions with a stress value of 0.13. The Amur sleeper size groups showed a high degree of dietary overlap (Fig. 4), resulting in a non-significant separation of groups (ANOSIM: R = -0.0063; p = 0.6062). However, larger specimens tended to feed on a relatively higher proportion of fish and had a greater niche breadth than specimens belonging to the intermediate and small size groups (Fig. 4).

Further quantification of diet overlap using the Schoener Index confirmed the results of the NMDS and ANOSIM analyses. The index values indicated high overlaps amongst the size groups, with the lowest similarity values between the small and large size groups (0.669), intermediate between the small and intermediate size groups (0.692) and the highest similarity between the intermediate and large size groups (0.865).
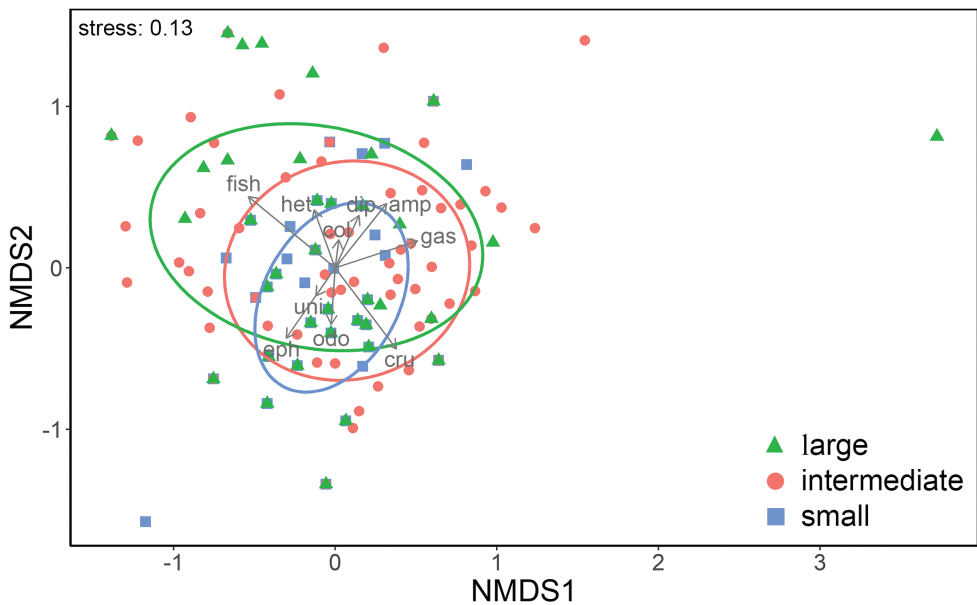

Figure 4. Non-metric multidimensional scaling (NMDS) analysis plots of Amur sleeper diet by size groups. Data points are coded and grouped by size groups. Ellipses illustrate the 95% confidence interval of the bivariate mean of a given size group calculated on standard error of the mean.

Discussion

Dietary analyses conducted at different temporal resolutions were useful to unambiguously prove the predatory effect of the invasive Amur sleeper on native taxa, especially on a small-bodied endemic fish like the European mudminnow. Conventional monthly samplings showed that the Amur sleeper is an effective predator of a variety of macroinvertebrates, but could not reveal the importance of fish in the diet. On the contrary, sampling at a finer temporal resolution highlighted that the Amur sleeper is feeding on fish eggs and is an effective predator of fish juveniles, which provides evi-

dence of predator-prey interaction. This interaction combined with competition for resources may be responsible for the decline of mudminnow populations in waterbodies that have been invaded by the Amur sleeper.

The Amur sleeper consumes predominantly macroinvertebrates (Koščo et al. 2008; Grabowska et al. 2009; Kati et al. 2015), which was also confirmed by our own samplings. However, fish consumption becomes more frequent with ontogeny (Koščo et al. 2008; Grabowska et al. 2019). As Amur sleeper is a non-selective, visual predator (Grabowska et al. 2009), motile fish larvae and tadpoles are more attractive (Reshetnikov 2008). Although we found that fish larvae and tadpoles were marginal food resources during the monthly samplings, the 10-day interval sampling highlighted the importance of fish eggs, juveniles and amphibians in the diet, especially in the hatching and breeding seasons. For example, during the monthly sampling, the frequency of occurrence ($Fi\%$) of fish in the stomach reached 12.5% (March) (Fig. 1), while during the 10-day method, this value reached 21% (egg - 7 June) and 33% (fish - 26 August) (Fig. 2). These values are remarkable compared, for example, with the results of Marsh and Douglas (1997), whose study examined the effect of predatory fishes on the endemic humpback chub (*Gila cypha*). Their results revealed that a lower frequency of prey item occurrence in the stomach (here 2% in the stomach of channel catfish (*Ictalurus punctatus*)) can indicate a considerable predation impact by non-native fishes, which can contribute to their population decline.

Amongst the consumed fish, the European mudminnow was the most dominant prey item. This is not surprising since this species was the most dominant fish in the community, which occupies the same meso- and microhabitats as the Amur sleeper (e.g. vegetated areas in the water column) (Pekárik et al. 2014; Grabowska et al. 2019). In addition, juveniles of the mudminnow grow more slowly than fingerlings of the Amur sleeper (Wanzenböck 1995; Nyeste et al. 2017). Consequently, the mudminnow juveniles are at risk of predation for a longer period than the juveniles of the Amur sleeper, especially in those populations where the Amur sleeper is gape-size limited due to the lack of large specimens in the population, such as we experienced in the Hejő. It is important to note that the narrow size range of the Amur sleeper may have influenced the results on the intensity of predation in the examined population since the predatory effect can be even stronger in those populations, where the size of the predatory fish is larger (Litvinov and O'Gorman 1996). Nevertheless, this relatively small size range is typical in most lowland streams in Hungary, where the Amur sleeper has dense populations (Nyeste et al. 2017).

IGP is determined by the predator and prey size; prey size range extends with the increasing body size of the predator (Scharf et al. 2000; Dörner and Wagner 2003). Indeed, fish consumption showed strong ontogenetic and seasonal patterns. Due to the gape-size limit, smaller Amur sleepers consumed fish sporadically (Grabowska et al. 2009; Kati et al. 2015), while the frequency of the occurrence and contribution of fish in the diet increased with increasing predator body size. High overlaps amongst the diet composition of the Amur sleeper size groups, especially between the intermediate and large size groups, were detected due to the narrow range of the body length of the

Amur sleeper population. Nevertheless, our results (i.e. Schoener Index values, NMDS and ANOSIM analyses) also suggest that the larger Amur sleepers had a greater dietary niche breadth and fed on a high portion of fish (Fig. 2), which can be even more explicit by the growing and ageing of the Amur sleeper population (Litvinov and O'Gorman 1996). Other studies found that the degree of dietary niche overlap can be smaller in populations that contain larger individuals that feed mainly on fish (Sinelnikov 1976; Zaloznykh 1982).

The seasonality patterns of IGP are driven by the availability of prey (Yurkowski et al. 2017) and IGP exerts pressure mostly on juveniles (Mehner et al. 1996; Fritts and Pearsons 2004; Hasegawa and Fukui 2021). Based on the finer temporal sampling protocol, juveniles of the European mudminnow were a periodically available resource. Feeding on fish eggs and mudminnow offspring were detected after the hatching season and consumption of juveniles increased during the survey. European mudminnow offspring over 25 mm in length has proved to be the most vulnerable ontogenetic developmental stage by the Amur sleeper predation. Fish consumption, instead of feeding on macroinvertebrates, can be more energy-consuming (Polačik et al. 2009); however, it is more valuable due to its high nutritional value (Elliott and Hurley 2000). In the following spring, one-year-old (0+) mudminnow specimens will grow over the gape size of the Amur sleeper and, thereby, the predation impact of the species decreases further. Note that, although cannibalism has been also found in the case of the Amur sleeper (Koščo et al. 2008; Interesova and Reshetnikova 2020), it was only observed once during the study.

The invasive Amur sleeper affects the food web of recipient ecosystems (Reshetnikov 2003) and threatens native species (Marsh and Douglas 1997; Reshetnikov 2008; Grabowska et al. 2009; Kati et al. 2015). Our results show that intraguild predation can play a role in the decline of the European mudminnow population by the elimination of mudminnow juveniles. The adverse effects of this multi-trophic interaction are more emphasised in species with low fecundity, short life spans and small distribution areas (Rocha et al. 2015). The absolute fecundity of the European mudminnow ranges between 100–2000 eggs/female and the maximal lifespan of the species is only 5 years (Kottelat and Freyhof 2007; Wilhelm 2008). Depending on the feeding conditions, the Amur sleeper can start feeding on fish in earlier life stages (Koščo et al. 2008) (when it reaches 45–50 mm body length in the 1st–2nd year (Nyeste et al. 2017)) and fish remains an important food resource afterwards (Sinelnikov 1976; Zaloznykh 1982; Litvinov and O'Gorman 1996; Grabowska et al. 2009; present study). This predation pressure on juveniles may lead to a collapse of European mudminnow populations within a few years after the establishment of Amur sleepers, as has previously been experienced in several cases (Bănăduc et al. 2022). Note that, although we could not investigate the direct predatory effect of mudminnow on Amur sleeper juveniles due to its conservation status (strictly protected, endemic species), large specimens of European mudminnow also consume fish (Lovassy 1927; Berinkey 1966; Wilhelm 2008). Therefore, a certain extent of predatory pressure on the Amur sleeper's offspring by the mudminnow cannot be ruled out in co-existing populations. However,

the longer life span (Nyeste et al. 2017), higher fecundity and aggressive behaviour of the Amur sleeper (Grabowska et al. 2011) increase the negative effects of IGP on the European mudminnow population. Since the distribution area of this endemic species is restricted mainly to the Carpathian Basin, further spread of the Amur sleeper may result in the extermination of the European mudminnow. Therefore, conservation measures (e.g. preventing further spread and the selective removal of the Amur sleeper) are more urgent than ever.

Acknowledgements

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