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Do invasive bighead goby *Neogobius kessleri* and round goby *N. melanostomus* (Teleostei, Gobiidae) compete for food?

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ABSTRACT

Key-words: *biological invasions, diet composition, feeding strategy, diet competition, Danube*

Bighead goby (*Neogobius kessleri*) and round goby (*Neogobius melanostomus*) have been invading new non-native areas about two decades successfully. In this study, diet spectrum, seasonal variation, feeding strategy and diet overlap between these two invasive species were assessed. Materials were collected from the Danube at Bratislava by fishing rods and/or electrofishing. The diet spectrum of both species was diverse: a total of 46 food types in bighead goby and 51food types in round goby were observed. *Dikerogammarus* sp., chironomid larvae and *Corophium* sp. were the most predominant food types in bighead goby, whereas in round goby, chironomid larvae, *Corophium* sp., bryozoans and Cladocera predominated. The diet varied over seasons. In the Slovak part of the Danube, bighead goby and round goby have adapted to local food resources, consuming diverse food from small to large items, both with soft and/or hard body. This enhances the capability of these invasive species to spread successfully. It appears that even if both exploit similar food resources, their proportional content differs. Further differences between these gobies were also found in their food behaviour and feeding strategy. Both species tend to be specialists where possible, but round goby demonstrates higher flexibility towards general feeding strategy.

RÉSUMÉ

Les gobies invasifs de Kessler *Neogobius kessleri* et le gobie à tâches noires *N. melanostomus* (Teleostei, Gobiidae) sont-ils en compétition pour la nourriture ?

Mots-clés : *invasions biologiques, régime alimentaire, stratégie d'alimentation, compétition alimentaire, Danube*

Le gobie de Kessler (*Neogobius kessleri*) et le gobie à tâches noires (*Neogobius melanostomus*) ont envahi de nouveaux milieux en deux décennies avec succès. Dans cette étude, le spectre de l'alimentation, sa variation saisonnière, la stratégie d'alimentation et le chevauchement du régime alimentaire entre ces deux espèces envahissantes ont été évalués. Les échantillons ont été recueillis par pêche à la ligne et/ou pêche électrique dans le Danube à Bratislava. Le spectre alimentaire des deux espèces était différent : un total de 46 types d'aliments pour le gobie de Kessler et 51 pour le gobie à tâches noires ont été observés. *Dikerogammarus sp*., des larves de chironomes et *Corophium sp*. étaient les types d'aliments prédominants chez le gobie de Kessler, alors que chez le gobie à tâches noires, les larves de chironomes, *Corophium sp*., des bryozoaires et *Cladocera* prédominaient. Le régime alimentaire varie au fil des saisons. Dans la partie slovaque du Danube,

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le gobie de Kessler et le gobie à tâches noires se sont adaptés à des ressources alimentaires locales, consommant une nourriture variée allant de petites à de grandes proies, à corps mou et/ou dur. Cela augmente la capacité de ces espèces envahissantes à se propager avec succès. Il semble que même si les deux espèces exploitent des ressources alimentaires similaires, leurs proportions diffèrent. D'autres différences entre ces gobies ont également été trouvées dans leur comportement alimentaire et leur stratégie d'alimentation. Les deux espèces ont tendance à être des spécialistes lorsque cela est possible, mais le gobie à tâches noires démontre une plus grande flexibilité allant vers une stratégie alimentaire plus généraliste.

INTRODUCTION

The bighead goby, *Neogobius kessleri* (Günther 1861) and round goby, *Neogobius melanostomus* (Pallas, 1814) have been expanding from Black and Caspian Seas over the last decades (Copp *et al*., 2005). Together with other two non-native gobiid species – *Neogobius gymnotrachelus* (Kessler 1857), and *Neogobius fluviatilis* (Pallas 1814), bighead goby and round goby have successfully inhabited the upper and middle Danube (Jepsen *et al*., 2008). Round goby and bighead goby have not only become the most abundant gobies in the upper and middle Danube (Ahnelt *et al*., 1998; Jurajda *et al*., 2005; Wiesner, 2005) but both species have reached high relative abundance in the fish communities of upper (10.8% and 2.3%, respectively) and especially middle Danube (10.9% and 5.4%; Kováč, 2013). Moreover, both species continue on spreading and establishing new populations, and have also penetrated the River Rhine to reach finally the North Sea (Skóra and Stolarski, 1993; Copp *et al*., 2005; Borcherding *et al*., 2011). Such a fast and effective expansion of the original area of distribution of a species poses several questions that should be of interest not only for fish biologists but also for ecologists and biologists in general. For example, such important questions are: 1) what makes these invaders so successful? 2) how can such successful invaders coexist and spread simultaneously? and/or 3) do the two species occupy the same dietary niche – do they compete for food? Along with our previous studies devoted mainly to the first of these questions (L'avrinčíková *et al*., 2005; L'avrinčíková and Kováč, 2007; Kováč *et al*., 2009; Grul'a *et al*., 2012), this study contributes in searching for answers of all the three.

Within this context, it is essential to understand the use of food resources by the invading fish, including their primary prey and feeding ecology. Bighead goby and round goby are now very abundant, which implies that they could play an important role in foodweb interactions in the River Danube. A few studies devoted to diet of invasive populations of bighead goby and/or round goby have brought some basic information on the species diet composition (Simonović *et al*., 2001; Adámek *et al*., 2007; Copp *et al*., 2008; Polačik, 2009), some of them being more comprehensive, analysing seasonal and habitat variation (Borza *et al*., 2009). However, none of these papers provide a complex insight into the diet niche of these successful invaders. Nevertheless, recently, two comprehensive studies on the diet of invasive gobies have been published. The first is from the Lower Rhine (Borcherding *et al*., 2013), and the second from the Upper Danube (Brandner *et al.*, 2013). Thus, to complement the picture, a detailed taxonomic analysis of the diet spectrum of bighead goby and round goby from the Middle Danube, including seasonal changes in its composition, was undertaken in this study. The main aim was to assess the diet overlap between bighead goby and round goby in the Middle Danube and to shed light on how these species can coexist in the same habitat. Specific objectives were to 1) undertake a comprehensive taxonomic analysis of the diet spectrum of invasive populations of both bighead goby and round goby and to characterize seasonal changes in its composition; 2) determine the feeding strategy of invasive populations of both species; 3) analyse the diet overlap between the invasive populations of these two species and to assess their competition for food.

Table I

Data on the bighead goby and round goby examined at the Slovak part of the River Danube, n = numbers of individuals, SL = standard length, SD = standard deviation.

Bighead goby		Spring	Summer	Autumn	Total
n		58	52	201	311
SL(mm)	**Range**	37–131	19–110	37–140	19–140
	Mean	69	52.5	68.6	65.9
	SD	18.2	27.4	24.9	24.9
Male (*n*)		19	32	98	149
Female (*n*)		39	20	103	162
Empty digestive tracts		0	0	1	1

Round goby		Spring	Summer	Autumn	Total
n		97	155	197	449
SL(mm)	**Range**	33–106	25–120	31–143	25–143
	Mean	66.1	67.7	61.3	65.6
	SD	13.4	15.5	15.9	16.2
Male (*n*)		42	79	104	225
Female (*n*)		55	76	93	224
Empty digestive tracts		1	0	6	7

MATERIALS AND METHODS

> *STUDY AREA, COLLECTION AND PROCESSING OF SAMPLES*

Specimens of bighead goby and round goby were sampled at two sites located in the middle section of the River Danube (Slovakia). Fish were collected by fishing rod and/or electrofishing during the seasonal cycle from the Karloveské side arm (r. km 1873, N48°08′, E17°04′) and from the Čunovo Reservoir (r. km 1851, N48°02′, E17°13′). The Čunovo Reservoir is not a typical reservoir, it is a widened part of main channel of the Danube, without any barrier separating it from the Karlova Ves side arm. Thus, specimens from both sites were considered one population. A total of 311 specimens of bighead goby and 449 specimens of round goby were collected from these sites (Table I). The samples were immediately anesthetized and preserved in 4% formaldehyde for the laboratory analysis.

The fish were measured using vernier calliper to the nearest 0.01 mm – Standard length (SL) – and weighed to the nearest 0.01 g before dissection. The gut contents of each specimen were removed, weighed (to 0.1 mg) and analysed under stereomicroscope to identify prey categories (individual fish were analysed separately). Prey items were identified to the lowest recognisable taxa and counted, and the relative weight of each food category to the biomass of total contents was estimated as described by Hyslop (1980), and then recalculated into weights based on the weight of total gut content. The food items, which were represented by less than 1%, were included into the relative abundance and frequency of occurrence but excluded from the relative biomass calculations.

Diet composition was expressed in terms of relative abundances (%N_i), percentage of biomass (%B_i) and frequency of occurrence (%F). These were calculated for each food item from the entire food bulk as

$$\%N_i = \frac{100\sum N_i}{\sum N_t} \quad \text{and} \quad \%B_i = \frac{100\sum B_i}{\sum B_t}$$

where $N_i(B_i)$ = total digestive tract content (by numbers or weight) composed by food item i and N_t (B_t) = total digestive tract content (by numbers or weight) of all digestive tracts in the entire sample. The frequency of occurrence (%F) was defined as proportion of fish containing given prey category.

The Costello graphical method (1990) modified by Amundsen *et al*. (1996) was used to visualise the diet patterns and seasonal changes of bighead goby and round goby. The diet was characterized by frequencies of occurrence and relative prey-specific abundance that is defined as the percentage of a prey taxon from all prey items in only those specimens in which the actual prey really occurs. This method describes feeding strategy, and identifies dominant prey items in individuals from the Slovak part of the river Danube. All macroinvertebrates which were sorted to the lowest recognisable taxa were combined to the family level, except of chironomid larvae, chironomid pupae, *Dikrogammarus* sp., *Corophium* sp., *Gammarus* sp. and undetermined amphipods.

Diet overlap between round and bighead goby was calculated using the Morisita's (1959) index as modified by Horn (1966), which was calculated using the formula:

$$C\lambda = 2\sum_{i=l}^{s} XiYi/\left(\sum_{i=l}^{s} Xi^2 + \sum_{i=l}^{s} Yi^2\right)$$

where s is the total number of all food categories distinguished, Xi, and Yi are the proportions of food item i (expressed as $\%N_i$ for countable food items and $\%B_i$ for uncountable food items) in the guts of species X and Y respectively. Zaret and Rand (1971) assumed that $C\lambda$ values $\geqslant 0.6$ to indicate significant overlap (Cailliet and Barry, 1979). Diet overlap between bighead goby and round goby was assessed for total samples, as well as for males, females, smaller specimens, larger specimens, and for seasonal samples, separately. Division between smaller (25–57 mm·SL, bighead goby $n = 134$, round goby $n = 142$) and larger (58–143 mm·SL, bighead goby $n = 177$, round goby $n = 307$) specimens was based on the breakpoint that had been found in proportional size of maxilla during ontogeny of round goby from the same sites (L'avrinčíková *et al*., 2005). For individual items overlap, a modified version of the above formula in the form $C\lambda = 2XiYi/(Xi^2 + Yi^2)$ was used.

> *STATISTICAL ANALYSES*

Season-to-season differences in the important food categories (numeric abundance and biomass) were evaluated using Kruskal-Wallis test (Zar, 1984).

Before testing the overlaps, normal distribution of the data was tested first, using the Kolmogorov-Smirnov test. Because the Morisita's (1959) index modified by Horn (1966) indicated a significant diet overlap between the two species (except summer), for season, sex and size group, a null hypothesis that the indication of diet competition between bighead and round gobies is not real was subsequently tested using the one tailed t-test. To test the null hypothesis, values from the above Morisita's index were used. If the p-value for any of the tests was greater than or equal to 0.05, the null hypothesis was rejected at the 95.0% confidence level.

RESULTS

DIET SPECTRUM

The diet spectrum of bighead goby contained a total of 46 food types, whereas that of round goby comprised of 51 food types (Table II), though the presence of sand in the gut is considered to be rather accidental.

In bighead goby, chironomid larvae were the most prevalent food type in terms of relative abundance, followed by *Dikerogammarus* sp. and *Corophium* sp. (Table II). Concerning biomass, *Dikerogammarus* sp. represented the most important contribution to the total consumed food. The second most prevalent food type was represented by small fishes (consumed by specimens of 63–135 mm·SL). Concerning frequency of occurrence, *Dikerogammarus* sp. was present in almost every analysed stomach, followed by chironomid larvae and *Corophium* sp. (Table II).

Table II
Diet of bighead goby and round goby expressed as relative abundance (%N_i), percentage of biomass (%B_i) and frequency of occurrence (%F) of prey at the Slovak part of the River Danube. Abbreviations: nd - not determined, l. - larvae, p. - pupae.

		Bighead goby			Round goby		
Food items		%N_i	%B_i	%F	%N_i	%B_i	%F
Turbellaria		0.03	0.06	0.32	0.01	0.08	0.23
Bryozoa			0.01	0.96		27.66	63.12
Gastropoda							
	Potamopyrgus sp.	0.17	0.07	1.29	0.16	0.09	3.62
	Viviparus sp.	0.09	0.51	0.64			
	Eggs of gastropods	0.78	0	0.32			
	Gastropoda (nd)				0.02	0.05	0.90
Bivalvia							
	Bithyniidae				0.05	0.15	0.23
	Pisidium sp.	0.03	0.08	0.32	0.12	0.85	2.49
	Sphaerium sp.				0.11	1.95	2.26
	Valvata sp.				0.10	0.04	1.36
	Bivalvia (nd)				0.08	0.39	2.49
Polychaeta							
	Hypania invalida (Grube, 1860)	0.06	0.05	0.64	0.07	0.60	1.81
Oligochaeta		1.39	2.15	8.4	0.93	1.56	15.84
Hirudinea		0.06	0.25	0.64			
Nematomorpha		0.03	0.04	0.32	0.09	0	0.68
Hydracarina		0.38	0.02	3.22	0.51	0.02	13.57
Cladocera		0.66	0	4.5	9.32	0.40	33.03
Ostracoda		0.84	0.01	1.93	3.14	0.24	17.87
Copepoda		0.12	0	0.64	4.81	0.16	19.23
Mysidacea							
	Limnomysis benedeni (Czerniavsky, 1882)	0.17	0.05	0.96	0.01	0	0.23
Isopoda							
	Jaera istri (Veuille, 1979)	0.32	0.35	3.22	0.35	0.19	8.60
Amphipoda							
	Corophium sp.	11.93	4.85	30.23	14.39	16.12	76.24
	Dikerogammarus sp.	18.69	44.87	61.74	1.79	12.96	28.51
	Gammarus sp.	1.56	1.15	8.36	0.56	0.97	10.41
	Amphipoda (nd)	3.3	3.42	18.1	0.36	0.92	5.88
Ephemeropteran l.							
	Baetidae	0.06	0.05	0.32	0.01	0	0.23
	Caenidae	0.12	0.12	0.96	0.11	0.21	3.39
	Potamanthus luteus (Linnaeus, 1767)	0.06	0.01	0.64	0.03	0.05	1.13
	Ephemeroptera (nd)	0.06	0.15	0.64			
Odonata larvae							
	Coenagrionidae	0.03	0.01	0.32			
	Gomphidae	0.03	0.29	0.32			
Heteroptera							
	Micronecta sp.	0.03	0	0.32	0.04	0	0.90
	Heteroptera (nd)	0.06	0.16	0.64			
Coleopteran larvae							
	Dytiscidae	0.06	0.01	0.64	0.02	0	0.68
	Elmidae	0.03	0	0.32	0.01	0	0.23
	Hydraenidae				0.01	0.01	0.23
Coleopteran imagines							
	Dytiscus sp.	0.06	0.13	0.64	0.01	0.15	0.45

Table II
Continued.

	Bighead goby			Round goby		
Food items	$\%N_i$	$\%B_i$	%F	$\%N_i$	$\%B_i$	%F
Trichopteran larvae						
Brachycentridae	0.03	0.07	0.32			
Goeridae				0.02	0.08	0.68
Hydropsychidae	1.76	0.83	4.82	0.01	0.02	0.45
Hydroptilidae	0.12	0.01	0.96	0.12	0.05	2.94
Limnephilidae				0.01	0.04	0.23
Polycentropodidae				0.02	0.01	0.90
Sericostoma sp.				0.15	0.09	3.62
Trichoptera (nd)	0.17	0.05	1.61			
Dipteran larvae						
Ceratopogonidae	0.12	0	0.96	0.10	0.01	3.17
Ephydridae				0.01	0	0.23
Chironomidae	50.25	1.86	47.59	58.38	11.23	84.62
Limoniidae	0.32	0.03	1.93	0.10	0.06	1.13
Psychoda sp.				0.01	0	0.23
Simulidae	0.2	0.03	0.96	0.01	0	0.23
Syrphidae	0.03	0.04	0.32	0.01	0.02	0.23
Diptera (nd)				0.01	0.05	0.23
Dipteran pupae						
Chironimidae	2.48	0.93	16.4	2.3	1.84	32.35
Fish						
Cyprinidae	0.06	0.96	0.32			
Gymnocephalus sp.	0.03	5.8	0.32			
Gobiidae	0.03	2.6	0.32			
Neogobius sp.	0.14	6.35	1.61			
Bighead goby	0.09	2.68	0.64			
Round goby	0.03	1.79	0.32	0.01	3.62	0.23
Tubenose goby	0.03	0.41	0.32			
Fish (nd)	1.27	12.3	13.5	0.43	0.74	13.80
Embryos of round goby				0.84	2.92	1.13
Eggs	1.76	0.07	3.22	0.52	0.00	11.31
Detritus		2.41	21.54		11.33	56.11
Macrophytes		2.7	10.29		1.60	26.70
Sand		0.07	4.82		0.42	3.17
Terrestrial arthropods						
Linyphiidae				0.01	0	0.23
Auchenorrhyncha				0.01	0.01	0.23
Diplopoda				0.01	0.03	0.23
Dipteran imagines				0.01	0.01	0.23
Chilopoda	0.09	0.05	0.64			
Thysanoptera				0.01	0	0.23
Terrestrial items (nd)	0.03	0.24	0.32			
Undetermined items	0.06	0.02	0.64			

Table III
Relative numeric abundance (%N_i) and percentage of biomass (%B_i) of food categories representing >5% of the total gut content in the diet of bighead goby and round goby from the Slovak part of the River Danube during the seasonal cycle 2008–2010. Abbreviations as in Table II.

Bighead goby	Spring	Summer	Autumn	%*Ni* max
Dikerogammarus **sp.**	14	33	17	33
Corophium **sp.**	17	5	12	17
Chironomidae l.	53	46	50	53
	Spring	**Summer**	**Autumn**	**%*Bi* max**
Dikerogammarus **sp.**	51	73	36	73
Corophium **sp.**	14	1	3	14
Amphipoda (nd)	7	1	3	7
Oligochaeta	6	3	1	6
Neogobius kessleri	0	12	1	12
Neogobius **sp.**	0	0	10	10
Gymnocephalus **sp.**	0	0	9	9
Fish (nd)	4	3	17	17

Round goby	Spring	Summer	Autumn	%*Ni* max
Dikerogammarus **sp.**	1	5	1	5
Corophium **sp.**	7	30	10	30
Chironomidae l.	51	37	71	71
Cladocera	7	13	9	13
Copepoda	20	0	1	20
Ostracoda	2	1	4	4
	Spring	**Summer**	**Autumn**	**%*Bi* max**
Dikerogammarus **sp.**	10	15	12	15
Corophium **sp.**	13	18	15	18
Chironomidae l.	17	8	14	17
Oligochaeta	5	0	1	5
Round goby	0	0	14	14
Embryos of round goby	0	6	0	6
Bryozoa	24	35	16	35
Detritus	12	9	16	16

5–25%
25–50%
>50%

Similarly, in round goby, chironomid larvae were also the most prevalent food type, but in this species the larvae were followed by *Corophium* sp. and Cladocera by (Table II). Concerning biomass, bryozoans represented the most important contribution to the total food consumed by round goby. The second most prevalent food types were *Corophium* sp. followed by *Dikerogammarus* sp. The other important food types were chironomid larvae and detritus (Table II). Chironomid larvae, *Corophium* sp. and bryozoans were present in almost every analysed stomach (Table II). In two specimens (100–143 mm·SL), small fishes were also found in their stomachs.

> SEASONAL VARIATION

In spring, bighead goby consumed mainly chironomid larvae, followed by *Corophium* sp. and *Dikerogammarus* sp. (Table III). In summer, chironomid larvae also formed their most abundant food but the second most abundant prey was *Dikerogammarus* sp., and *Corophium* sp. occupied the third place. The same order of food items was recorded in autumn. The proportion of chironomid larvae and *Dikerogammarus* sp. differed significantly between seasons but that of *Corophium* sp. did not (Kruskal-Wallis test: chironomid larvae H (2, $N = 309$) = 8.79, $p < 0.05$; *Corophium* sp. H (2, $N = 311$) = 13.95, $p < 0.01$; *Dikerogammarus* sp. H (2, $N = 311$) = 7.44, $p < 0.05$).

However, when expressed in biomass, amphipods (*Dikerogammarus* sp., *Corophium* sp., and undetermined amphipods) constituted the major proportion of total gut content in spring, occupying the first three most important items (Table III). *Dikerogammarus* sp. represented the highest proportion of total biomass also in summer and autumn, though fishes were also very important diet during these two seasons – bighead goby and various undetermined fishes in summer, and undetermined fishes, *Neogobius* sp. and *Gymnocephalus* sp. in autumn. Concerning fish preys, bighead goby, *Neogobius* sp. and *Gymnocephalus* sp. were not present in every season (see also the seasonal changes in feeding strategy below). The proportion of *Corophium* sp. and Oligochaeta, that were also an important item in spring in the bighead goby diet, differed significantly between the seasons (Kruskal-Wallis test: *Corophium* sp. H (2, $N = 311$) = 16.43, $p < 0.01$; Oligochaeta H (2, $N = 311$) = 8.95, $p < 0.05$) but *Dikerogammarus* sp., undetermined amphipods and fishes did not (Kruskal-Wallis test: *Dikerogammarus* sp. H (2, $N = 311$) = 3.93, $p = 0.14$; undetermined Amphipoda H (2, $N = 311$) = 4.85, $p = 0.09$; undetermined fish H (2, $N = 311$) = 3.83, $p = 0.15$).

In round goby, chironomid larvae predominated numerically in all seasons, followed by Copepoda, Cladocera and *Corophium* sp. in spring (Table III). *Corophium* sp. and Cladocera were the second and third most abundant food types in summer and autumn. Other food items represented by more than 5% in some season were *Dikerogammarus* sp. and Ostracoda. All items mentioned above varied significantly among seasons (Kruskal-Wallis test: *Dikerogammarus* sp. H (2, $N = 448$) = 75.38, $p < 0.01$; *Corophium* sp. H (2, $N = 448$) = 48.97, $p < 0.01$; chironomid larvae H (2, $N = 448$) = 40.95, $p < 0.01$; Cladocera H (2, $N = 448$) = 6.32, $p < 0.05$; Copepoda H (2, $N = 448$) = 66.15, $p < 0.01$; Ostracoda H (2, $N = 448$) = 25.80, $p < 0.01$).

Concerning biomass, bryozoans predominated in all seasons, though in autumn, detritus had the same percentage proportion as bryozoans. The subsequent most important food items were chironomid larvae and *Corophium* sp. in spring, *Corophium* sp. and *Dikerogammarus* sp. in summer, and *Corophium* sp. in autumn (Table III). In autumn, the own species, i.e. round goby, also appeared to form high biomass in round goby diet, however, the intensity of this cannibalism should be taken with caution, since the high biomass values resulted from one single big prey specimen found in the gut of one round goby. Other food items representing more than 5% of biomass in some seasons were Oligochaeta and embryos of round goby. All these items differed significantly among seasons (Kruskal-Wallis test: *Dikerogammarus* sp. H (2, $N = 449$) = 42.89, $p < 0.01$; *Corophium* sp. H (2, $N = 449$) = 37.25, $p < 0.01$; chironomid larvae H (2, $N = 449$) = 63.46, $p < 0.01$; Oligochaeta H (2, $N = 449$) = 21.98, $p < 0.01$; bryozoans H (2, $N = 449$) = 69.05, $p < 0.01$; detritus H (2, $N = 449$) = 13.44, $p < 0.01$).

> *FEEDING STRATEGY*

The graphical method for bighead goby indicated a mixed feeding strategy with varying degrees of specialization on different prey types (Figures 1a, 1e) in spring and autumn. A relatively specialized feeding strategy was found in summer (Figure 1c), when bighead goby specialized on two types of food (*Dikerogammarus* sp. and chironomid larvae). All individuals of bighead goby fed on these dominant prey taxa, but small proportions of other prey types were also present in the diet of a few individuals (Figure 1c).

In terms of biomass, the graphical analysis suggests a specialization to one prey type in every season, most frequently to *Dikerogammarus* sp., but alternatively to fish, Ephemeroptera and Nematomorpha in some specimens (Figures 1b, 1d, 1f). In other words, most predators specialized on *Dikerogammarus* sp., though individual predators specialized on fish, Ephemeroptera and Nematomorpha, and the contribution of this prey to stomach content was high.

For round goby, a feeding strategy between two types of specialization and generalization appeared. The first type suggests a specialization towards only one single prey type, namely chironomid larvae in spring and autumn (Figures 2a, 2e). In other words, chironomid larvae were eaten by more than half of the population, and their average contribution to the stomach

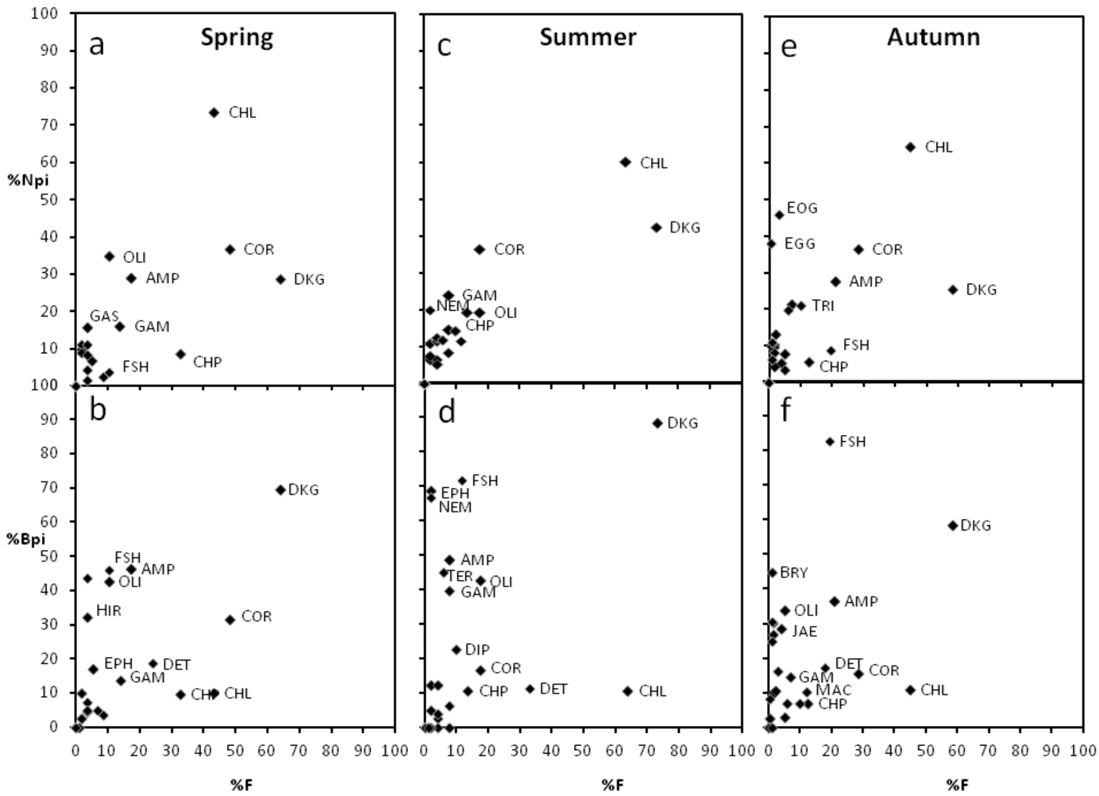

Figure 1
Feeding strategy of bighead goby from the Slovak part of the River Danube over the seasonal cycle, %Npi – prey specific abundance, %Bpi – prey specific biomass, %F – frequency of occurrence. Abbreviations (only the major categories are indicated): DKG – Dikerogammarus sp., GAM – Gammarus sp., COR – Corophium sp., AMP – Amphipoda (not determined), JAE – Jaera istri, CHL – Chironomid larvae, CHP – Chironomid pupae, DIP – Diptera others, GAS – Gastropoda, EOG – Eggs of gastropods, BIV – Bivalvia, COI – Coleopteran imagines, EPH – Ephemeroptera, TRI – Trichoptera, OLI – Oligochaeta, TUR – Turbellaria, NEM – Nematomorpha, ZOP – Zooplankton, FSH – Fish, ERG – Embryos of round goby, EGG – Eggs of fish, BRY – Bryozoa, DET – Detritus, MAC – Macrophyta, TER – Terrestrial arthropods.

contents of these fishes was high. Whereas, in summer, the analysis suggests generalized feeding strategy, with the second type of specialization. This means that individual predators specialized on round goby embryos and that this item was consumed by only a limited fraction of predators ($<$3% of individual round goby ate embryos) but its contribution to stomach content was high (Figures 2c).

On the other hand, analysis of biomass in round goby demonstrates a rather generalized feeding strategy in all seasons, which means that the most important prey items were eaten by more than half of the population, but their contribution to the stomach contents in these fishes was not high (Figures 2b, 2d, 2f). This generalized feeding strategy has some exceptions, such as round goby embryos in summer and fishes in autumn (Figures 2d, 2f). These exceptions suggest that individual predators specialized on these food items and that these items were consumed by only a limited fraction of predators but their contribution to stomach content was high.

> DIET OVERLAP BETWEEN BIGHEAD GOBY AND ROUND GOBY

In general, the diet of bighead goby and round goby appeared to overlap considerably, though the overlap in individual diet items varied from item to item (Table IV). The same pattern was

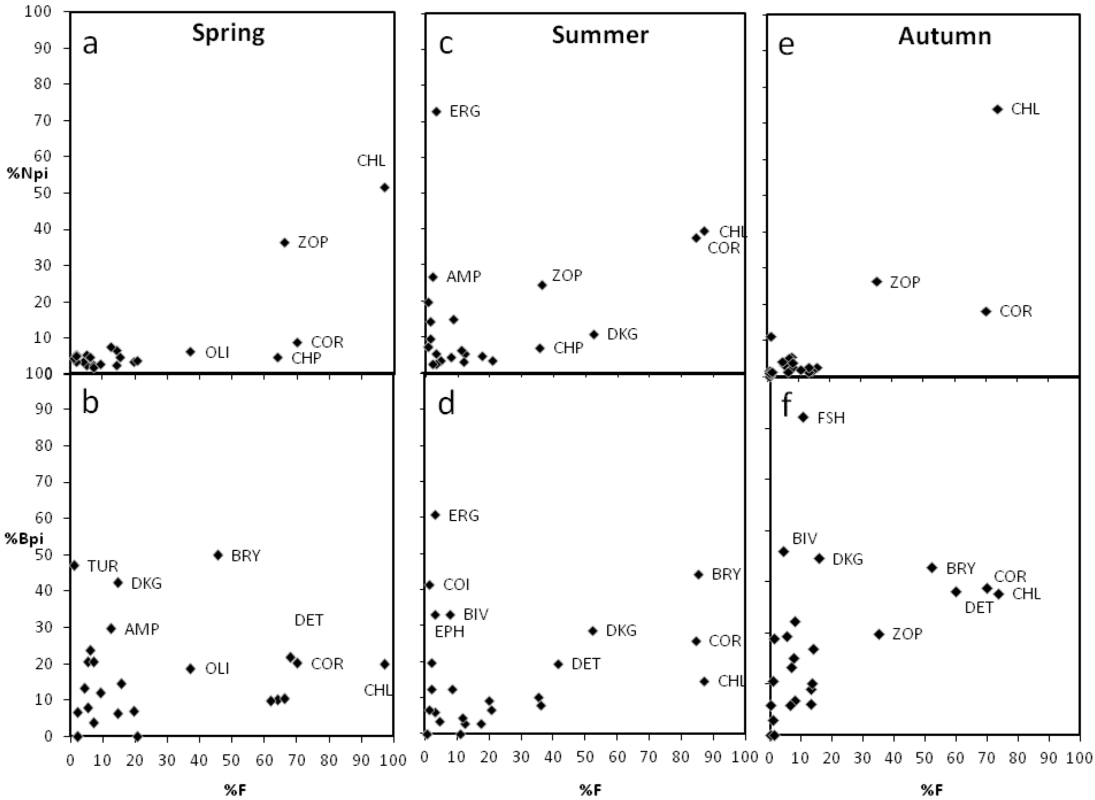

Figure 2
Feeding strategy of round goby from the Slovak part of the River Danube over the seasonal cycle, %Npi – prey specific abundance, %Bpi – prey specific biomass, %F – frequency of occurrence. Abbreviations as in Figure 1.

observed when males, females, smaller and/or larger specimens were analysed separately. The overall diet overlap between bighead goby and round goby was also found to be considerable in spring and autumn but not in summer (Table IV). However, one tailed *t*-tests did not confirm indication of real diet competition between the two species (one tailed *t*-test: General $t = -0.35$, $p = 0.63$; Males $t = -2.66$, $p = 0.99$; Females $t = -1.97$, $p = 0.97$; Smaller $t = -1.32$, $p = 0.90$; Larger $t = -2.55$, $p = 0.99$; Spring $t = -2.73$, $p = 0.99$; Summer $t = -3.37$, $p = 0.99$; Autumn $t = -4.23$, $p = 0.99$).

DISCUSSION

Correlation often exists between morphological traits and food-orientation of species because the traits determine how a fish can feed and so what it can eat (Wootton, 1998). Bighead goby has the biggest mouth from among all four invasive gobies in the River Danube (with protruding lower jaw). This allows bighead goby to catch larger prey, including fishes, which gives them the advantage in exploiting energy-rich food resources. Indeed, although fish prey were represented in their stomachs only in small numbers, biomass was high (Table II; Figures 1d, 1e). In the gut of bighead goby, diverse fish prey, such as round goby, tubenose goby, *Gymnocephalus* sp. and cyprinids were recorded, and cannibalism was also observed. Similarly, bighead goby exploit the genus of amphipods with the largest body size (*Dikerogammarus* sp.) almost everywhere in their invaded area (Table II; Borza *et al*., 2009). Round goby is not reported to be piscivorous in its native range (Pinchuk *et al*., 2003), nevertheless remnants of fish were found in stomachs of a relatively high number of individuals from the invasive Slovak population (Table II). However, in most cases these remnants were

Table IV

Diet overlap between bighead goby and round goby calculated using the Morisita's (1959) index as modified by Horn (1966) from the Slovak part of the River Danube during the seasonal cycle 2008–2010. Proportions of food items used in the index are expressed as $\%N_i$ for countable items and $\%B_i$ for uncountable items. $C\lambda$ values $\geqslant 0.6$ indicate significant overlap (marked by bold and shading). Abbreviations as in Table II, also a – adult.

Round vs. bighead goby	All individuals	Males	Females	Smaller	Larger	Spring	Summer	Autumn
***Dikerogammarus* sp.**	0.19	0.21	0.17	0.16	0.18	0.11	0.45	0.07
***Gammarus* sp.**	**0.63**	**0.99**	0.35	**0.83**	0.49	0.09	**0.99**	**0.83**
***Corophium* sp.**	**0.98**	**0.83**	**0.99**	**0.88**	**1**	**0.66**	0.22	**0.99**
Amphipoda (nd)	0.23	0.08	0.52	0.01	0.33	0.46	0.34	0.13
Jaera istri	**1**	**0.99**	**1**	**0.97**	**0.98**	**0.97**	0.43	**0.95**
Limnomysis benedeni	0.07	0.15	0	0	0.11			0.08
Chironomidae l.	**0.99**	**0.99**	**0.99**	**0.98**	**0.89**	**1**	**0.90**	**0.94**
Chironimidae p.	**0.98**	**0.89**	**1**	**0.73**	**1**	**1**	**0.99**	0.51
Ceratopogonidae	**0.99**	0	0.47	**0.99**	**0.97**	**1**	**0.70**	
Syrphidae	0.40	0	0		0.33			0.46
Simulidae	0.06	0	0.10		0.05	0.08		0
Limonidae	0.56	**0.60**	0.54	0.12	**0.72**	**0.68**	0	0
***Potamopyrgus* sp.**	**1**	**0.60**	**0.80**	**0.88**	**0.98**	0.58	0	**0.90**
***Pisidium* sp.**	0.45	**0.92**	0	0	0.57	0	**0.70**	0
***Micronecta* sp.**	**0.97**	0	**0.98**	0.54	0	0	0.39	0
Dytiscus a.	0.40	**0.74**	0		0.33		0	0
Dytiscidae l.	**0.72**	0	0.55	0.54	0		0	0
Elmidae l.	0.40	0.42		0	0		0	0
Potamanthidae	**0.83**	0	0.39	0	0.47	0		0
Caenidae	**1**	**0.74**	**0.94**	0.54	**0.69**	**0.75**	**0.89**	0.24
Baetidae	0.21	0	0		0.17			0.24
Hydroptylidae	**1**	**0.91**	0.89	**0.82**	0	0	0	**0.84**
Hydropsychidae	0.01	0.03	0.01	0	0.01	0.31		0.01
Oligochaeta	**0.92**	**0.86**	**0.96**	0.41	1	**0.99**	0.29	**0.69**
Turbellaria	0.40	0	0		0.33	0.31		
Nematomorpha	0.57	**0.92**	0		**0.69**	0	0	
Polychaeta	**0.99**	0	**0.94**	0	**0.93**	**0.95**	0	0
Cladocera	0.14	0.19	0.10	0.09	0.21	0.09	**0.83**	0.15
Copepoda	0.05	0.03	0.07	0.04	0.04	0.02	0	0.32
Ostracoda	0.50	0.38	0.57	0.58	0.26	0	0	0.57
Hydracarina	**0.96**	**0.87**	0.49	**1**	0.53	0	0	**0.92**
Round goby	0.40	0.42			0.33			0.46
Fish (nd)	**0.61**	**0.81**	0.44	**1**	0.40	**0.75**	**0.99**	0.42
Eggs	0.55	0.24	**0.83**	**0.99**	0.40	0.52	**0.79**	0.18
Bryozoa	0	0	0	0	0	0	0	0
Detritus	0.41	0.46	0.38	**0.86**	0.36	**0.72**	0.27	0.26
Macrophytes	**0.97**	**0.74**	**0.88**	**0.95**	**0.97**	0.14	0.59	**0.62**
Diet in total	**0.83**	**0.80**	**0.85**	**0.80**	**0.73**	**0.78**	0.49	**0.86**

represented by scales only, which suggests aggressiveness towards other fish rather than predation. The aggressiveness of round goby was also recorded under laboratory condition, when round goby aggressively attacked and displaced mottled sculpin *Cottus bairdi* (Dubs and Corkum, 1996).

Seasonal variation in the diet composition of bighead goby from the Slovak stretch of the Danube (Table III; Figures 1a–1f) appeared to be limited in the case of the most important prey items - *Dikerogammarus* sp. and chironomid larvae (relative abundance and percentage biomass). A similar pattern of seasonal variation was found in bighead goby from Hungary. *Dikerogammarus* sp. was a predominant prey in each season but fishes were also important in spring (on the gravel-sand beach habitats; Borza *et al*., 2009).

On the other hand, seasonal variation in the diet of round goby supports the picture of this species as a flexible feeder. It appears that invasive round goby take the advantage of energy rich sources (embryos of round goby, *Dikerogammarus* sp.) when available (Table III). The seasonal changes found in the diet of round goby from the Slovak stretch of the Danube followed a similar scenario as those in round goby from Hungary (Borza *et al*., 2009). In spring, fishes consumed mainly the same food items, i.e. chironomid larvae. During the other seasons, populations of round goby consumed predominantly bryozoans and *Corophium* sp. in Slovakia and *Dikerogammarus* sp. in Hungary, which were followed by molluscs in Hungary (Borza *et al*., 2009), and by *Dikerogammarus* sp. in Slovakia (Table III). In the Great Lakes, seasonal variation in the diet of invasive round goby was also observed (French and Jude, 2001). In the Slovak part of the Danube, seasonal changes influenced the diet composition of round goby. Seasonal variation suggests that round goby is a more flexible feeder than bighead goby, since round goby take the advantage of energy rich sources during season, when available.

One of characteristics of a typical invasive animal is often reported to be a broad diet spectrum (Ricciardi and Rasmussen, 1998). Notwithstanding, it is difficult to define how many diet items means "broad". It may seem that the diet of invasive bighead goby and round goby in Slovakia is wider than that of the other populations (bighead goby 46 items; round goby 51 items; Table II). However, the number of food items detected depends on the taxonomic level to which food items were determined. In fact, even if bighead goby from Slovakia can utilize a broad diet spectrum, they highly prefer amphipods (percentage of biomass) and chironomid larvae (relative numeric abundance), and they thus tend to be specialists. Nonetheless, in the River Hron, where *Dikerogammarus* sp. was probably absent, the diet of bighead goby consisted mainly of trichopteran larvae and *Corophium curvispinum* (Adámek *et al*., 2007). Flexibility was also observed elsewhere in the River Danube, where the diet of invasive bighead goby differed between populations from native and non-native areas (Polačik, 2009).

Round goby also tend to be specialist since they highly prefer zebra mussels (*Dreissena polymorpha*) where this prey is abundant (Ghedotti *et al*., 1995). However when abundance of mussels decreased significantly, the importance of chironomid larvae and amphipods in round goby diet increased (Barton *et al*., 2005). Also in the Gulf of Gdansk, strong dominance of molluscs was observed in fish from 130–150 mm·TL and fish of 160–180 mm fed exclusively on molluscs (Skóra and Rzeznik, 2001).

Furthermore, in the section of Flint River in Michigan, at which zebra mussels were absent, the diet of round goby changed on a diel basis, with hydropsychid caddisfly and chironomid larvae predominating during the day, chironomid pupae dominating in the evening, and heptageniid mayflies dominating at night (Carman *et al*., 2006). This suggests not only specialization of bighead goby and round goby to a few prey items, but also an opportunistic behaviour and capacity to adapt to local conditions.

Bighead goby and round goby have already reached eudominant position at various sites within the Slovak part of the Danube (Černý, 2006; Kováč, 2013). The results indicate that bighead goby and round goby (Table II) share similar diet, which implies a potential for food competition. In the Serbian stretches of the Danube, similarity between round and bighead gobies was attributed to the presence of gammarids (Simonović *et al*., 2001). In Hungary, low diet overlap was found in spring but higher in summer and autumn (Borza *et al*., 2009). A previous study from the Slovak stretch also addressed an overlap in diet of these two invading species (Copp *et al*., 2008). As many as 38 items found to occur in the guts of both species (Table IV) raise the question on potential interspecific competition between bighead goby and round goby. In other words, how can these two species coexist at the same habitats, using the same food resources? In general, the diet of bighead goby and round goby were found to overlap considerably, though the overlap varied from item to item. In fact, a closer look at the diet composition of the two species reveals that the significant overall overlap results mainly from partial overlaps in less important food items (Table IV). The same pattern was observed when males, females, smaller and/or larger specimens were analysed separately. The overall diet overlap between bighead goby and round goby was also found to be considerable in spring and autumn but not in summer (Table IV). Indeed, from among the most important items, a significant overlap was found only in chironomid larvae and *Corophium* sp. Furthermore, chironomid larvae are the most abundant aquatic insects from among all important benthic prey in the Slovak part of the river Danube (Graf *et al*., 2008). Therefore, since chironomid larvae do not appear to be a limiting food resource, they are not likely to be a subject of competition between bighead goby and round goby. Finally, testing the hypotheses associated with diet competition between these two species (one tailed *t*-tests) did not support the indication of real competition. It is evident that even if round goby and bighead goby exploit similar food resources, they differ in their proportional content. Thus, in the Middle Danube, competition between bighead and round goby for food does not seem to be a factor that might affect the success of these two highly invasive species of fish in colonizing new habitats. Similar conclusions have been derived for the Upper Danube (Brandner *et al*., 2013) and the Lower Rhine, though in the latter, juvenile round goby were found to compete on food resources with juvenile bighead goby in spring (Borcherding *et al*., 2013).

Success of invasive organisms is often considered to result from their capability to exploit available ecological niches (Brown, 1989; Williamson, 1996). In fact, bryozoans were highly represented in the diet of round goby (Table II), which suggests that this invasive species takes the advantage of empty diet niche in order to reduce energetically costly competition (Ross, 1986; Schoener, 1986).

Differences in diet niche between the two gobies are also found in their food behaviour and strategy. Bighead goby prefer rather active hunting (fish, *Dikerogammarus* sp.), whereas round goby use grazing (bryozoan, chironomid larvae). Concerning feeding strategy, both species tend to be specialists (bighead goby: *Dikerogammarus* sp. and chironomid larvae; round goby: chironomid larvae, and bryozoan), however round goby demonstrates higher flexibility towards general feeding strategy than bighead goby, which is specialized to a lower number of food items. This feeding strategy is likely to make round goby a more successful colonizer. On the other hand, in the Upper Danube, both species were identified as predacious omnivores with high dietary overlap and a generalistic feeding strategy (Brandner et al., 2013).

It has been also found that the feeding patterns of both species in the Upper and Middle Danube strongly differ from those in their native ranges, underlining their great plasticity (see also Brandner et al., 2013). Ability to adapt to the food offer is one of the essential factors to spread very successfully. It appears that bighead goby and round goby can adapt to local food resources and consume diverse food, whether small or large food items, soft or hard bodied, though they differ in proportional content of these items. Both species are flexible enough in food electivity and thus not limited by local food resources, which enhances their capability to spread very successfully.

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