



# Ontogenetic variations in the diet of two invasive gobies, *Neogobius melanostomus* (Pallas, 1814) and *Ponticola kessleri* (Günther, 1861), from the middle Danube (Slovakia) with notice on their potential impact on benthic invertebrate communities



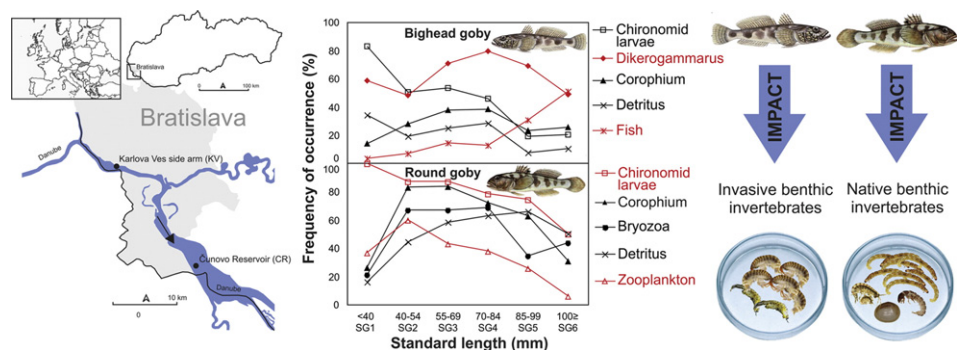
Barbora Števo<sup>\*</sup>, Vladimír Kováč

Comenius University, Faculty of Natural Sciences, Department of Ecology, Mlynská dolina, Ilkovičova 6, 842 15 Bratislava 4, Slovakia

## HIGHLIGHTS

- Bioinvasions can affect negatively native ecosystems through trophic interactions.
- Diet and impact of two invasive gobies (fish) in the Danube were examined.
- Both gobies preferred chironomids when small, bighead goby shifted to fish when large.
- In contrast to round goby, invasive species predominated in the diet of bighead goby.
- The impact of invasive gobies develops over time after the onset of the invasion.

## GRAPHICAL ABSTRACT<sup>1</sup>



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## ABSTRACT

In this study, ontogenetic variations in diet of invasive bighead goby *Ponticola kessleri* and round goby *Neogobius melanostomus* from the middle Danube were analysed. Index of stomach fullness, Fulton's condition factor, index of food importance, frequency of occurrence, biomass, electivity, and proportions of invasive organisms in their diet were examined. Changes in the diet during ontogeny of both species emphasise the differences in their trophic niches. Our results combined with literary data suggest that bighead goby may threaten small native benthic fish species as a predator (especially in the invasion front), whereas round goby can potentially impact native fish species of all ontogenetic phases by competing for food. Round goby appear to have strong impact on bivalves, especially in the invasion front. High consumption of invasive organisms by bighead goby may help the native macroinvertebrate community. Thus, in contrast to round goby, bighead goby does not seem to be a hot candidate for being a nuisance invader.

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## 1. Introduction

Thanks to a high habitat diversity and dense ecotonal structure, the Danube provides diverse combinations of environmental conditions suitable for a great variety of different fish species (Kováč, 2015),

<sup>\*</sup> Corresponding author.

E-mail addresses: [manonik@gmail.com](mailto:manonik@gmail.com) (B. Števo), [kovac@fns.uniba.sk](mailto:kovac@fns.uniba.sk) (V. Kováč).

<sup>1</sup> Pictures of bighead goby and round goby (graphical abstract): Fritz Terofal and Claus Militz (modified).

including several invasive gobies (though native in the lower Danube), such as monkey goby *Neogobius fluviatilis* (Pallas, 1814), racer goby *Neogobius gymnotrachelus* (Kessler, 1857), bighead goby *Ponticola kessleri* (Günther, 1861) and round goby *Neogobius melanostomus* (Pallas, 1814). From among these, the round goby and bighead goby appear to be the most successful, as they have been continuing on spreading and establishing new populations further through the middle and upper Danube, and have also penetrated the River Rhine (Copp et al., 2005; Kalchauer et al., 2013; Verreycken et al., 2011; Verreycken, 2013).

The rise in numbers of invasive gobies in the middle Danube, has coincided with a progressive decline in some native benthic fishes, such as bullhead *Cottus gobio* (Linnaeus, 1758), stone loach *Barbatula barbatula* (Linnaeus, 1758), and the white-finned gudgeon *Gobio alpinus* (Lukasch, 1933) (Jurajda et al., 2005). There are at least four mechanisms by which the round goby and/or bighead may have contributed to this: competition for habitat, predation, interference with spawning, and competition for food (Jude et al., 1995). Concerning the latter, round goby have been reported to have the potential for competition for food resources and habitat with native fishes (Copp et al., 2008; Vanderploeg et al., 2002), and bighead goby is also likely to have such potential. In the River Sava, bighead and round goby have been recently reported to have possible adverse impact on the native chub *Squalius cephalus* (Linnaeus, 1758) and zingel *Zingel zingel* (Linnaeus, 1766) populations, respectively (Piria et al., 2016). Also, in the River St. Clair and Great Lakes, round goby decimated populations of mottled sculpins *Cottus bairdii* (Girard, 1850) and logperch *Percina caprodes* (Rafinesque, 1818) and reduced the hatching success of native fishes by feeding on their eggs (Corkum et al., 2004; Chotkowski and Marsden, 1999; French and Jude, 2001; Jude et al., 1995). In the Gulf of Gdansk, round gobies have increased in abundance, while three-spined sticklebacks *Gasterosteus aculeatus* (Linnaeus, 1758) have declined (Corkum et al., 2004) and the similarities in the diet of round goby and flounder *Platichthys flesus* (Linnaeus, 1758) suggest potential for food competition (Karlson et al., 2007). Laboratory experiments indicated that round goby may pose risks for a wide variety of native benthic fishes (Bergstrom and Mensinger, 2009). In the goby–ruffe competition experiment with a limited food base, gobies grew faster than ruffe *Gymnocephalus cernuus* (Linnaeus, 1758), suggesting that gobies may be competitively superior at low resource levels (Bauer et al., 2007).

High abundances of round and bighead gobies in the middle Danube, as well as the period of time of their presence (approximately one decade in the former and two decades in the latter; e.g. Kováč, 2015), pose the question about their impact on native communities. However, the Danube represents a large and complex ecosystem, and it is not so simple to assess the impact of these fish invaders on native communities. In particular, it is difficult to distinguish reliably between the effect of the invaders themselves from various other effects, such as hydro-morphological modifications and other human-induced pressures, and/or other environmental variables. Nevertheless, as a part of an impact assessment, it is essential to understand the use of food resources by the invading fish, including their primary prey and feeding ecology.

Several recent studies have addressed significant differences between the populations of gobies at the edge of invasion and in the centre of invasion (Brandner et al., 2013b; Brownscombe and Fox, 2012; Brownscombe et al., 2012; Groen et al., 2012; Gutowsky and Fox, 2012; Houston et al., 2013; Raby et al., 2010). Some of these studies showed that in the invasion front females predominate over males (Brandner et al., 2013b; Brownscombe and Fox, 2012), and that largest individuals facilitating further spreading are more abundant at the invasion front than in its core (Brandner et al., 2013b; Gutowsky and Fox, 2012; Houston et al., 2013). However, the size-structure of a successfully reproducing invasive population undergoes rapid changes, and thus the proportion of juveniles and adults varies between the invasion front and the core, with a fast increase of juveniles (smaller individuals) at the invasions front. Such differences in the sex ratio and size structure suggest that the impact of invasive populations associated with

competition for food and/or predation may evolve after the onset of invasion. In order to evaluate this assumption, the first objective of the present study was to analyse ontogenetic changes in stomach fullness and diet composition, i.e. to test for the differences between smaller and larger individuals of both bighead goby and round goby. The second objective was to test differences between sexes in their index of stomach fullness, including seasonal variation. Relationships between their consumption rates and condition (Fulton's condition factor) were also examined in association with the subsequent rapid density increase of the invasive populations.

Furthermore, the invasive gobies have also been reported to consume invasive organisms (Brandner et al., 2013a; Schiphouwer, 2011), and therefore the third objective of this paper was to analyse consumption of invasive gobies on other invasive fishes and invertebrates, and to evaluate their electivity for invasive organisms, including differences between size groups. Indeed, only a few studies have focused on ontogenetic trophic niche shifts in the European rivers (Borcherding et al., 2013; Piria et al., 2016), especially in such an important European invasion pathway as the Danube, and therefore, there is limited information on feeding patterns of different size classes of bighead and round goby in the region. Quantification of feeding ecology of gobies through the detailed investigation of consumption rates and prey selectivity will permit a more informed assessment of the impacts of their predation on local fish and invertebrate communities.

## 2. Materials and methods

### 2.1. Study area

Specimens of bighead goby and round goby were sampled at two sites located in the middle section of the River Danube (Slovakia; Fig. 1). Fish were collected over the seasonal cycles 2008–2010 (September, October and November 2008, March, April, May, June, July, August and September 2009, March, April, May, July, September and October 2010) from the Karlova Ves side arm (rkm 1873, N48°08', E17°04', denoted further as KV) and from the Čunovo Reservoir (rkm 1851, N48°02', E17°13', denoted further as CR). Čunovo is not a typical reservoir; it is a widened part of main channel of the Danube, without any barrier separating it from the KV.

### 2.2. Collection and processing of samples

A total of 311 specimens of bighead goby (KV,  $n = 105$ ; CR  $n = 206$ ) and 449 specimens of round goby (KV,  $n = 249$ ; CR  $n = 200$ ) were collected from these sites by fishing rod and/or electrofishing. In most analyses, the whole samples were used, except the electivity and relative weight of biomass (%B), for which samples from CR only were used. Fish were collected between 11:00 to 15:00 from the same microhabitats as the macrozoobenthos samples. The samples were immediately anesthetized and preserved in 4% formaldehyde for the laboratory analysis. The fish were measured using vernier caliper to the nearest 0.01 mm – Standard length (SL) and weighted to the nearest 0.01 g before dissection. Fish were sexed using the genital papillae. The gut contents of each specimen were removed, weighted (to 0.1 mg) and analysed under stereomicroscope to identify prey categories.

At three sampling occasions in autumn (04/11/2008), spring (15/05/2009) and summer (25/08/2009), macrozoobenthos samples were collected at CR simultaneously with fish samples. Prior to sampling, microhabitat coverage was estimated for the site. Macrozoobenthos was sampled from four different microhabitats based on the substratum particle sizes (megallithal >40 cm, macrolithal >20 cm to 40 cm, mesolithal >6 cm to 20 cm, and akal >0.2 cm to 2 cm; AQEM consortium, 2002). For each microhabitat, an area of 25 × 25 cm was sampled by kick-sampling and a hand net (frame 25 × 25 cm, mesh size 500 μm) (Frost et al., 1971). From megallithal, samples were collected using scrubbing with brush from the same large area as kick-

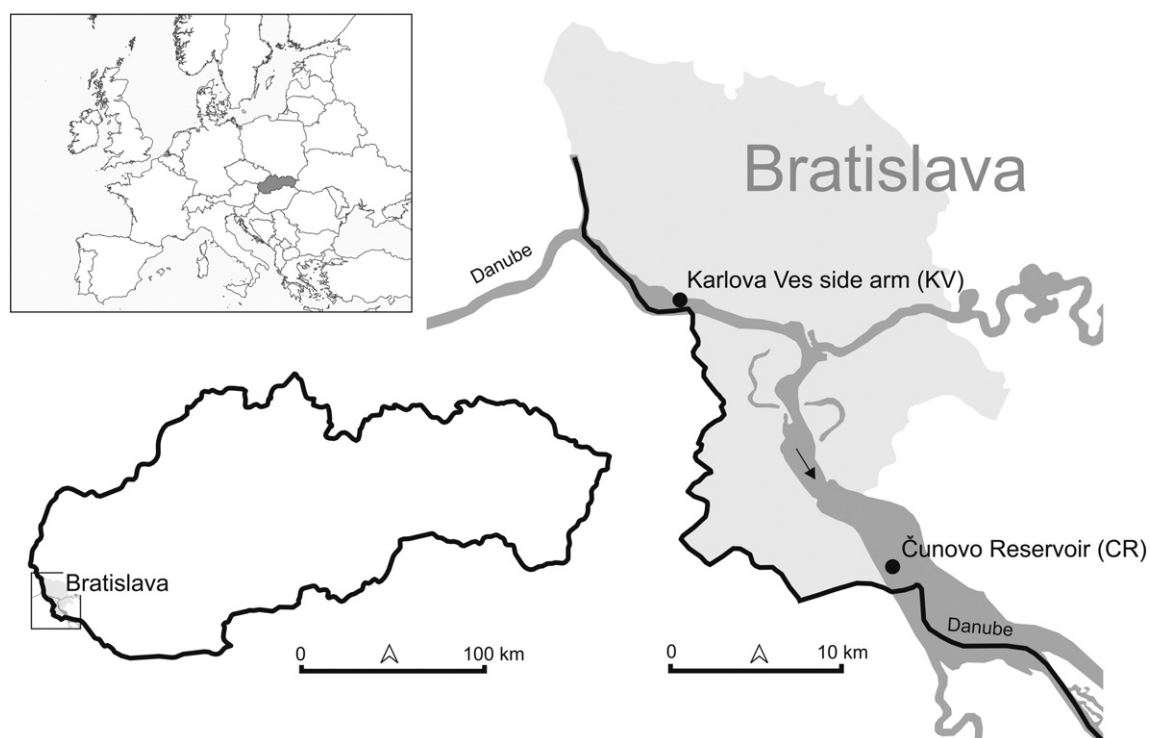


Fig. 1. Sampling sites in the Slovak part of the River Danube.

sampling methods (25 × 25 cm). At each sampling occasion, four samples were collected from each type of substrate. Material was preserved in 4% formaldehyde prior to transportation to the laboratory, where the samples were sieved using 500 µm sieves, and determined under a stereomicroscope. Macroinvertebrates were identified to the same taxonomic level as the items in the fish stomach contents. To evaluate the diet electivity, individuals of macrozoobenthos were weighted.

For the analyses associated with ontogenetic variations (growth), samples of both species were divided into 6 size groups (Table 1). For the analyses associated with seasonal feeding activity, the samples were divided into spring (March 2009 and 2010, April 2009 and 2010, May 2009 and 2010), summer (June 2009, July 2009 and 2010, August 2009) and autumn (September 2008, 2009 and 2010, October 2008 and 2010, November 2008).

**Table 1**  
Ontogenetic differences in the index of stomach fullness (*ISF*) and Fulton's condition factor (*K<sub>SL</sub>*) of bighead goby and round goby examined at the Slovak part of the River Danube; n = numbers of individuals, SL = standard length, SD = standard deviation. Statistical analysis in size-to-size groups differences in the index of stomach fullness (<sup>a</sup>) and Fulton's condition factor (<sup>b</sup>) were evaluated using Kruskal-Wallis test for bighead goby and one-way ANOVA for round goby. Subsequently, post hoc analyses were used to identify significant differences (<0.05 in bold) between the size-groups of both bighead and round gobies.

Bighead goby						Post-hoc comparison					
Size group	SL mm (n)	ISF	SD	K <sub>SL</sub>	SD	1	2	3	4	5	6
1	<40 (29)	4.38	3.44	2.52	0.6		<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>	<b>0.01<sup>b</sup></b>	
2	40–54 (83)	2.08	2.1	2.18	0.26	<b>0.00<sup>a</sup></b>		0.75 <sup>b</sup>	0.27 <sup>b</sup>	<b>0.03<sup>b</sup></b>	0.2 <sup>b</sup>
3	55–69 (95)	2.83	2.31	2.2	0.24	<b>0.00<sup>a</sup></b>	0.15 <sup>a</sup>		0.4 <sup>b</sup>	0.05 <sup>b</sup>	<b>0<sup>b</sup></b>
4	70–84 (39)	2.42	1.81	2.26	0.29	<b>0.00<sup>a</sup></b>	0.49 <sup>a</sup>	0.41 <sup>a</sup>		0.23 <sup>b</sup>	<b>0.01<sup>b</sup></b>
5	85–99 (26)	1.8	1.61	2.34	0.28	<b>0.00<sup>a</sup></b>	0.57 <sup>a</sup>	0.06 <sup>a</sup>	0.24 <sup>a</sup>		0.17 <sup>b</sup>
6	≥100 (39)	1.36	1.95	2.43	0.25	<b>0.00<sup>a</sup></b>	0.17 <sup>a</sup>	<b>0.01<sup>a</sup></b>	<b>0.05<sup>a</sup></b>	0.37 <sup>a</sup>	
Total	(311)	2.45	2.36	2.27	0.32						
Round goby						Post-hoc comparison					
Size group	SL mm (n)	ISF	SD	K <sub>SL</sub>	SD	1	2	3	4	5	6
1	<40 (19)	0.9	0.52	2.2	0.21		<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>	<b>0<sup>b</sup></b>
2	40–54 (85)	1.31	2.39	2.46	0.19	0.34 <sup>a</sup>		0.44 <sup>b</sup>	0.62 <sup>b</sup>	0.18 <sup>b</sup>	<b>0<sup>b</sup></b>
3	55–69 (186)	1.52	1.69	2.49	0.26	0.13 <sup>a</sup>	0.34 <sup>a</sup>		0.81 <sup>b</sup>	0.37 <sup>b</sup>	<b>0.01<sup>b</sup></b>
4	70–84 (108)	1.21	1.21	2.48	0.19	0.46 <sup>a</sup>	0.70 <sup>a</sup>	0.13 <sup>a</sup>		0.32 <sup>b</sup>	<b>0.01<sup>b</sup></b>
5	85–99 (35)	1.39	1.41	2.52	0.22	0.31 <sup>a</sup>	0.82 <sup>a</sup>	0.67 <sup>a</sup>	0.60 <sup>a</sup>		0.08 <sup>b</sup>
6	≥100 (16)	1.14	1.25	2.64	0.28	0.67 <sup>a</sup>	0.72 <sup>a</sup>	0.39 <sup>a</sup>	0.88 <sup>a</sup>	0.63 <sup>a</sup>	
Total	(449)	1.35	1.68	2.48	0.24						

To evaluate differences in food uptake activity between sizes classes, as well as variation in seasonal feeding activity, index of stomach fullness (*ISF*) was used. Index was calculated as  $ISF = 100W_GW_S^{-1}$ , where  $W_G$  - gut content mass (g) and  $W_S$  - eviscerated body weight (g) (Kamler, 2002).

Fulton's condition factor allows condition to be determined in living fish, but the use of somatic weight (total weight less gonad and stomach content weights) instead of total weight is believed to provide a more precise reflection of condition since feeding intensity and gonad maturation can vary significantly between individuals (Lambert and Dutil, 1997; Wong and Benzie, 2003). For each fish the Fulton's condition factor ( $K_{SL}$ ) was calculated by using the somatic weight of the fish:  $K_{SL} = 10^5 W_S L^{-3}$ , where  $W_S$  - somatic body weight (g) and  $L$  - length (mm) (Anderson and Neumann, 1996).

To assess ontogenetic changes in the diet composition of bighead goby and round goby, the index of food importance (*IFI*) expressed in Principal Component Analysis (PCA; Lepš and Šmilauer, 2003), as well as frequency of occurrence (%F) were used. For the descriptions of dietary composition, the frequency of occurrence (%F) provides the most robust and interpretable measure of diet composition (Baker et al., 2014).

The relative importance of a food items was evaluated using the index of food importance (*IFI*),  $IFI = 100FB(\sum FB)^{-1}$ , where  $F$  - % frequency of occurrence and  $B$  - % relative weight of biomass. Percentage of biomass (weight of given prey category in relation to total weight of gut content: %B) and the frequency of occurrence (defined as the proportion of fish containing a given prey category: %F) were quantified for each prey category (Grabowska and Grabowski, 2005; Hyslop, 1980). This index provides a definite and measurable basis for grading the various food elements as it gives a combined picture of frequency of occurrence as well as biomass (Brandner et al., 2013a; Herder and Freyhof, 2006; Natarajan and Jhingran, 1961). *IFI* varies from 0 to 100, with higher values corresponding to a larger contribution of one food item compared to the total gut content.

Macrozoobenthos and food items were divided in three groups: invasive, native and unassigned (species with non-allocable biogeographical origin). *IFI* was used to express the proportion of these three groups in stomachs of both gobies from both sites (CR and KV pooled together). However, to express the differences between the invasive benthic invertebrates found in the fish gut content and the invasive benthic invertebrates in the environment, relative biomass (%B, %B<sub>E</sub>) was calculated from the CR samples.

The fish samples from CR were further used to analyse the electivity of bighead goby and round goby. To express dietary electivities (electivity plot), the percentage of biomass (%B<sub>E</sub>) of each prey taxa in the macroinvertebrate community were compared with their weight percentage (%B) in diet by plotting the data on the x and y axes, respectively. Points above the 45 degrees line may indicate positive 'selection' for the taxon, whereas points below it show 'rejection', which may give a rough picture on prey preferences (i.e., electivity; Borza et al., 2009). Food items other than macrozoobenthos were excluded from the analysis.

### 2.3. Statistical analyses

To visualize the overall picture of the food items that affected the diet composition of size groups in bighead goby and round goby, PCA (Lepš and Šmilauer, 2003) was applied. Size-to-size group differences in *ISF*,  $K_{SL}$  and %F were evaluated using One-way ANOVA or Kruskal-Wallis test (Zar, 1984). Subsequently, post hoc analyses were used to identify significant differences between the size-groups of both bighead and round gobies.

To analyse  $K_{SL}$  and *ISF*, data transformation (ArcSin) was first used. Two-way ANOVA (sex and season) was applied, in order to find whether there was a significant difference between males and females, as well

as between seasons, respectively. Subsequently, based on the results of F-test (homogeneity of variance) and Kolmogorov-Smirnov test, either Mann-Whitney or t-test was used to identify the particular season during which the difference between males and females was significant.

## 3. Results

Samples from CR and KV were tested (Mann-Whitney) for potential differences in %F, *ISF* and *IFI* before pooling. No significant differences in these parameters were found between the two sites (bighead goby %F:  $U = 458.5$ ,  $p = 0.27$ ; *ISF*:  $U = 7030$ ,  $p = 0.08$ ; *IFI*:  $U = 460.5$ ,  $p = 0.49$ ; round goby %F:  $U = 668.5$ ,  $p = 0.86$ ; *ISF*:  $U = 23.023$ ,  $p = 0.22$ ; *IFI*:  $U = 352$ ,  $p = 0.29$ ). Thus, specimens from both sites were treated as one population of bighead goby and round goby, respectively.

### 3.1. Index of stomach fullness and Fulton's condition factor

The smallest individuals (size group 1) of bighead goby had highest *ISF* (4.38), and they differed significantly from the other groups (Table 1). Decreasing tendency from the smallest to the largest individuals (from size group 1 to size group 6) was reflected in the lowest *ISF* (1.36) of the largest individuals. The group with the largest individuals differed significantly from all size groups except the size groups 2 and 5 (Table 1). On the other hand, the smallest individuals of round goby had the lowest *ISF*, though *ISF* culminated at size group 3 (Table 1). However, the differences in *ISF* were not significant between the size groups of round goby (Table 1).

Bighead goby from size group 1 had the highest  $K_{SL}$  (2.52), and this group differed significantly from all the other groups except the largest individuals (Table 1). In round goby,  $K_{SL}$  was lowest (2.2) in the smallest individuals, similarly to *ISF* (Table 1). This group differed significantly from all the other groups (Table 1), and the largest round goby achieved the highest  $K_{SL}$  (2.64).

### 3.2. Diet composition

No significant differences in diet composition were found between males and females of bighead goby and round goby in terms of frequency of occurrence (Mann-Whitney test: bighead goby  $U = 683.5$ ,  $p = 0.99$ ; round goby  $U = 654.5$ ,  $p = 0.75$ ).

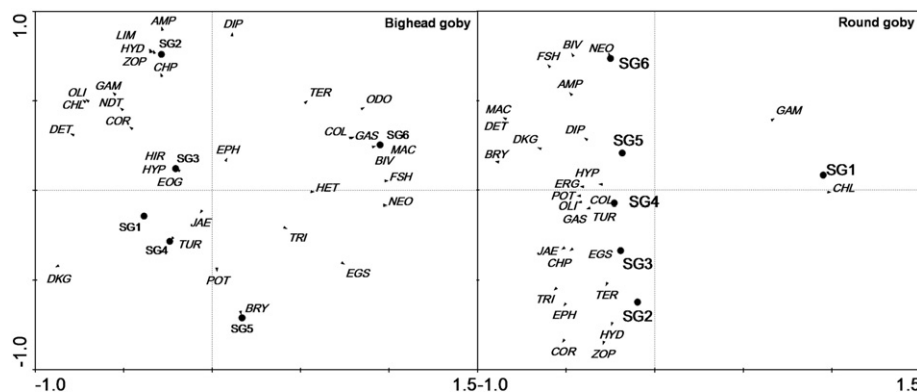
Differences between size groups in both bighead and round goby were found in their diet composition (PCA, Fig. 2). In bighead goby, the size group 6 differed from all the other size groups. In round goby, the size group 1 was the most segregated from the other size groups (Fig. 2).

Expressed in frequency of occurrence, chironomid larvae predominated in the diet of the smallest bighead goby (size group 1), though the importance of these items decreased with increasing body size (Fig. 3). Amphipods (especially *Dikerogammarus* sp. and *Corophium* sp.) predominated in almost all size groups, however, in largest individuals (size group 6), fish (tubenose goby *Proterorhinus marmoratus* (Pallas, 1814), bighead goby, round goby, *Gymnocephalus* sp., Cyprinidae and undetermined species) started to be the most important food item (Fig. 3, Table 2). In round goby, chironomid larvae predominated in all size groups, especially in the smallest individuals. With increasing body size of the gobies, zooplankton decreased, in contrast to detritus, where the trend was opposite. In the size groups 2 to 5, other food items, such as *Corophium* sp. and bryozoans prevailed (Fig. 3, Table 2).

### 3.3. Invasive organisms in the diet

In the whole sample from KV and CR, invasive species predominated in the diet of bighead goby expressed in *IFI* (79.7%, Table 3), and this also applies for each size group except the size group 6 (the largest specimens). The size group 4 reached the highest value of *IFI* for invasive organisms (95.6%, Table 3). On the other hand, invasive species formed





**Fig. 2.** A multivariate analyses (PCA) of ontogenetic variations in the diet composition of bighead goby and round goby from the Slovak part of the River Danube expressed as index of food importance (IFI). SG1 - size group 1 (<40 mm), size group 2 (40–54 mm), size group 3 (55–69 mm), size group 4 (70–84 mm), size group 5 (85–99 mm), size group 6 ( $\geq 100$  mm), AMP - Amphipoda (not determined), BIV - Bivalvia, BRY - Bryozoa, CHL - Chironomid larvae, CHP - Chironomid pupae, COL - Coleoptera, COR - *Corophium* sp., DET - Detritus, DIP - Diptera others, DKG - *Dikerogammarus* sp., EGS - Eggs of fish, EOG - Eggs of gastropods, EPH - Ephemeroptera, ERG - Embryos of round goby, FSH - Fish, GAM - *Gammarus* sp., GAS - Gastropoda, HET - Heteroptera, HIR - Hirudinea, HYD - Hydracarina, HYP - *Hypania invalida* (Grube, 1860), JAE - *Jaera istri* (Veuille, 1979), LIM - *Limnomysis benedicti* (Czerniavsky, 1882), MAC - Macrophyte, NDT - Not determined, NEO - *Neogobius* sp., ODO - Odonata, OLI - Oligochaeta, POT - *Potamopyrgus* sp., TER - Terrestrial arthropods, TRI - Trichoptera, TUR - Turbellaria, ZOP - Zooplankton. PC1 represented the size-related gradient in both species. Bighead goby, PC1 showed 78%, and PC2 12% variability of food items. Round goby, PC1 showed 60%, and PC2 26% variability of food items.

only a small proportion of the round goby diet (25.2%, Table 3), regardless size groups, with the smallest individuals (size group 1) having only 1.7% of food components represented by invasive organisms.

In CR, invasive species formed approximately a half of biomass in the benthic invertebrate community (Table 3). Invasive aquatic invertebrates predominated in the diet of each size group of bighead goby (81.9% of total biomass, Table 3). In contrast, the percentage of invasive items was much lower in round goby (36.7% of total biomass, Table 3), though it varied considerably between the size groups. The smallest individuals (size group 1) consumed only 8% of invasive organisms, however in the subsequent size groups (2–3) the proportion of invasive food

items increased to >60%. In the larger size groups, invasive organisms formed a minority compared to the overall diet (Table 3).

#### 3.4. Electivity and its ontogenetic variation

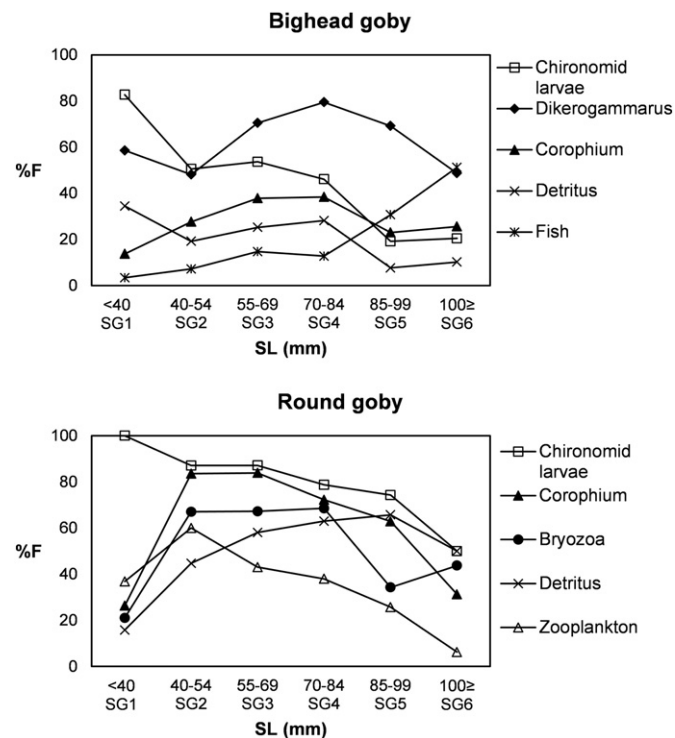
In all size groups of bighead goby, strong preference for *Dikerogammarus* sp. was recorded (Fig. 4), with a maximum in the size groups 1, 5 and 6. *Corophium* sp. was preferred by groups 2 and 4 (Fig. 4).

In round goby, the preference/avoidance was more variable. The smallest individuals (size group 1) consumed chironomid larvae, exclusively, that were present in all size groups, though not in such amounts (Fig. 4). Subsequently, the individuals shifted to *Corophium* sp. (groups 2, 3 and 4) and *Dikerogammarus* sp. (groups 3 and 4). Bivalvia began to occur in the size group 4 in small proportions, being increasingly preferred by the subsequent size groups 5 and 6 (Fig. 4).

#### 3.5. Seasonal variation and differences between sexes of ISF and $K_{SL}$

In total (all seasons taken together), ISF of bighead goby did not differ significantly between males (2.29) and females (2.62; two-way ANOVA,  $F(\text{sex}) = 1.2$ ,  $p = 0.27$ ). The ISF culminated in summer for both males and females, being slightly higher in females throughout all seasons (Table 4;  $t$ -test: spring  $t = 0.7$ ,  $p = 0.47$ , summer  $t = 0.3$ ,  $p = 0.77$ ; Mann-Whitney test: autumn  $U = 4677.5$ ,  $p = 0.4$ ). However, seasonal differences regardless of sex were significant throughout the year (two-way ANOVA,  $F(\text{season}) = 13.3$ ,  $p < 0.01$ ). On the other hand, ISF of round goby differed significantly between males (1.17) and females (1.54; two-way ANOVA,  $F(\text{sex}) = 6.4$ ,  $p < 0.05$ ). The ISF culminated in summer for both males and females, being higher in females in spring and summer (Table 4), though the differences were significant only in summer (Mann-Whitney test: spring  $U = 969$ ,  $p = 0.18$ ; summer  $U = 2386$ ,  $p < 0.05$ ; autumn  $U = 4823.5$ ,  $p = 0.98$ ). Seasonal differences in ISF of round goby regardless of sex were significant throughout the year (two-way ANOVA,  $F(\text{season}) = 17.5$ ,  $p < 0.01$ ).

For all individuals of bighead goby taken together,  $K_{SL}$  differed significantly between males (2.36) and females (2.19; two-way ANOVA,  $F(\text{sex}) = 19.6$ ,  $p < 0.01$ ), and it culminated in summer. In contrast to ISF,  $K_{SL}$  was higher in males throughout all seasons (Table 4) and differed significantly in spring and autumn ( $t$ -test: spring  $t = -6.9$ ,  $p < 0.01$ ; Mann-Whitney test: summer  $U = 291$ ,  $p = 0.59$ ;  $t$ -test: autumn  $t = -2.2$ ,  $p < 0.05$ ). Also, seasonal differences regardless of sex were significant throughout the year in  $K_{SL}$  (two-way ANOVA,



**Fig. 3.** Ontogenetic variation of main food categories of bighead goby and round goby from the Slovak part of the River Danube expressed as frequency of occurrence (%F). Abbreviations as in Fig. 2.

**Table 2**

Size-to-size group differences in the frequency of occurrence (%F) of the most important diet in bighead goby and round goby (Kruskal-Wallis test or one-way ANOVA) with post hoc analyses to identify significant differences ( $<0.05$  in bold) between the size-groups of both bighead and round gobies (see Table 1 for size group details). BRY - Bryozoa, CHL - Chironomid larvae, COR - *Corophium* sp., DET - Detritus, DKG - *Dikerogammarus* sp., FSH - Fish, ZOP - Zooplankton.

Bighead goby							Round goby						
Size group	1	2	3	4	5	6	1	2	3	4	5	6	
Post-hoc comparison DKG <sup>a</sup> , CHL <sup>b</sup>							Post-hoc comparison CHL <sup>a</sup> , COR <sup>b</sup>						
1		<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>		<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	0.72 <sup>b</sup>	
2	0.31 <sup>a</sup>		0.67 <sup>b</sup>	0.63 <sup>b</sup>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	0.16 <sup>a</sup>		0.95 <sup>b</sup>	0.06 <sup>b</sup>	<b>0.01<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	
3	0.24 <sup>a</sup>	<b>0.00<sup>a</sup></b>		0.40 <sup>b</sup>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	0.14 <sup>a</sup>	0.99 <sup>a</sup>		<b>0.02<sup>b</sup></b>	<b>0.01<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	
4	0.07 <sup>a</sup>	<b>0.00<sup>a</sup></b>	0.32 <sup>a</sup>		<b>0.03<sup>b</sup></b>	<b>0.02<sup>b</sup></b>	<b>0.02<sup>a</sup></b>	0.12 <sup>a</sup>	0.06 <sup>a</sup>		0.24 <sup>b</sup>	<b>0.00<sup>b</sup></b>	
5	0.41 <sup>a</sup>	0.05 <sup>a</sup>	0.90 <sup>a</sup>	0.40 <sup>a</sup>		0.92 <sup>b</sup>	<b>0.01<sup>a</sup></b>	0.08 <sup>a</sup>	0.06 <sup>a</sup>	0.53 <sup>a</sup>		<b>0.01<sup>b</sup></b>	
6	0.40 <sup>a</sup>	0.95 <sup>a</sup>	<b>0.02<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	0.09 <sup>a</sup>		<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.03<sup>a</sup></b>		
Post-hoc comparison FSH <sup>a</sup> , DET <sup>b</sup>							Post-hoc comparison BRY <sup>a</sup> , DET <sup>b</sup>						
1		0.13 <sup>b</sup>	0.34 <sup>b</sup>	0.49 <sup>b</sup>	<b>0.01<sup>b</sup></b>	<b>0.01<sup>b</sup></b>		<b>0.02<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.00<sup>b</sup></b>	<b>0.04<sup>b</sup></b>	
2	0.63 <sup>a</sup>		0.51 <sup>b</sup>	0.35 <sup>b</sup>	0.23 <sup>b</sup>	0.32 <sup>b</sup>	<b>0.00<sup>a</sup></b>		<b>0.04<sup>b</sup></b>	<b>0.01<sup>b</sup></b>	<b>0.03<sup>b</sup></b>	0.69 <sup>b</sup>	
3	0.23 <sup>a</sup>	0.44 <sup>a</sup>		0.74 <sup>b</sup>	0.07 <sup>b</sup>	0.12 <sup>b</sup>	<b>0.00<sup>a</sup></b>	0.98 <sup>a</sup>		0.41 <sup>b</sup>	0.40 <sup>b</sup>	0.53 <sup>b</sup>	
4	0.26 <sup>a</sup>	0.47 <sup>a</sup>	0.91 <sup>a</sup>		<b>0.04<sup>b</sup></b>	0.07 <sup>b</sup>	<b>0.00<sup>a</sup></b>	0.83 <sup>a</sup>	0.82 <sup>a</sup>		0.77 <sup>b</sup>	0.32 <sup>b</sup>	
5	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.03<sup>a</sup></b>	<b>0.03<sup>a</sup></b>		0.78 <sup>b</sup>	0.32 <sup>a</sup>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>		0.29 <sup>b</sup>	
6	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.00<sup>a</sup></b>	<b>0.05<sup>a</sup></b>		0.16 <sup>a</sup>	0.07 <sup>a</sup>	0.06 <sup>a</sup>	<b>0.05<sup>a</sup></b>	0.51 <sup>a</sup>		
Post-hoc comparison COR							Post-hoc comparison ZOP						
1													
2	0.16						0.06						
3	<b>0.01</b>	0.14					0.60	<b>0.01</b>					
4	<b>0.03</b>	0.23	0.95				0.93	<b>0.00</b>	0.39				
5	0.45	0.65	0.14	0.18			0.42	<b>0.00</b>	<b>0.05</b>	0.19			
6	0.29	0.82	0.16	0.22	0.82		0.06	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	0.18		

F (season) = 14.7,  $p < 0.01$ ). In round goby,  $K_{SL}$  differed significantly between males (2.5) and females (2.45; two-way ANOVA, F (sex) = 5.3,  $p < 0.05$ ). Again  $K_{SL}$  culminated in summer for both sexes, being higher in males throughout all seasons (Table 4), though significantly only in spring ( $t$ -test: spring  $t = -3.1$ ,  $p < 0.01$ ; summer  $t = -0.6$ ,  $p = 0.57$ ;  $t$ -test: autumn  $t = -0.4$ ,  $p = 0.69$ ). Seasonal differences regardless of sex were significant throughout the year in  $K_{SL}$  (two-way ANOVA, F (season) = 3.9,  $p < 0.05$ ).

## 4. Discussion

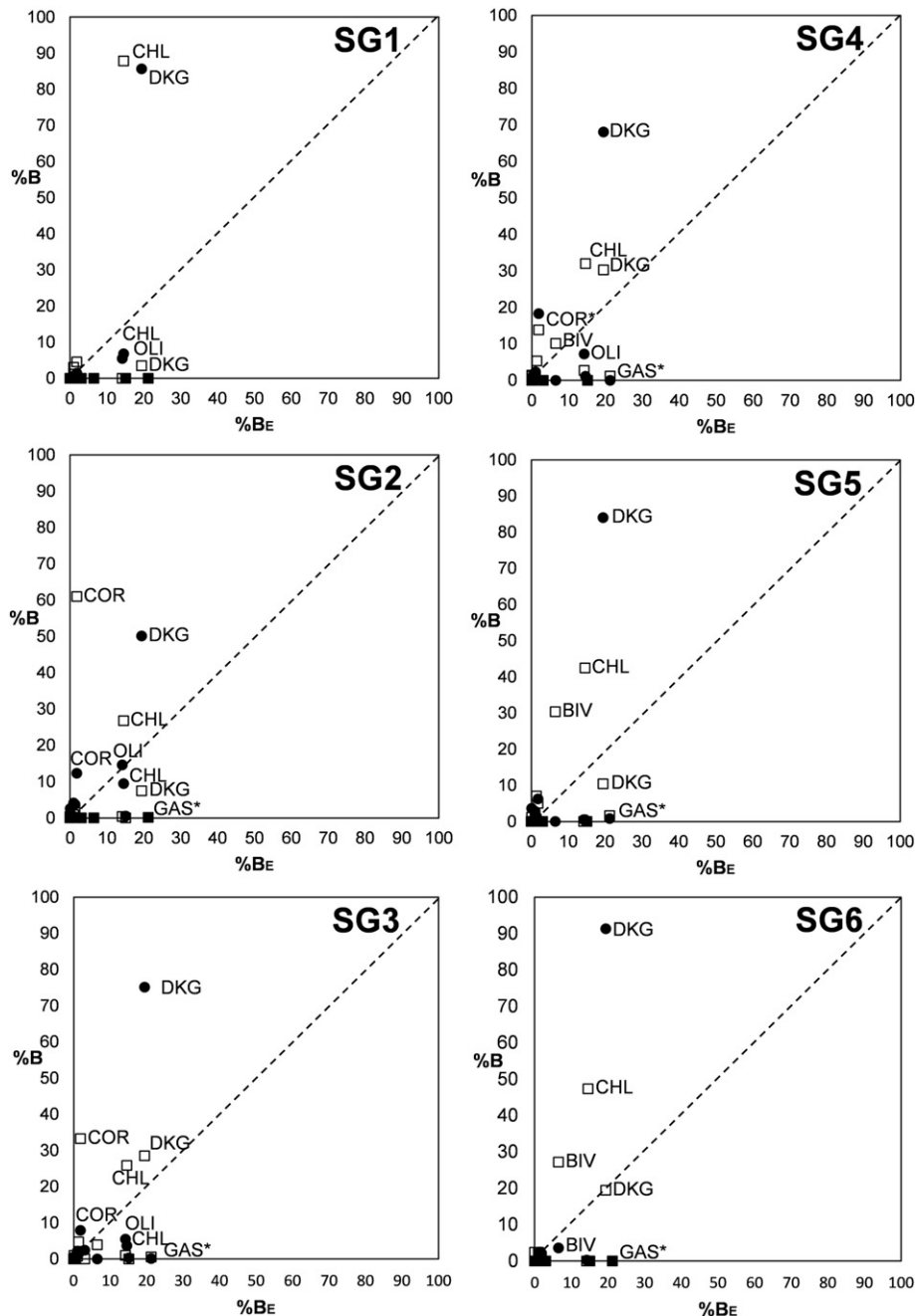
### 4.1. Ontogenetic variations in stomach fullness and condition

Smaller bighead goby from the middle Danube were found to have fuller stomachs than larger individuals, whereas in round goby it was opposite (Table 1), similar to round gobies from the River Trent and from the Latvian coastal waters in the eastern Baltic Proper (Raby

**Table 3**

Ontogenetic variations of the proportions of invasive organisms in the diet of bighead goby and round goby from the Slovak part of the River Danube;  $IFI$  = index of food importance (all food items from Čunovo Reservoir – CR and Karlova Ves – KV),  $\%B$  = relative weight of biomass (food items only invertebrate from CR),  $\%B_E$  = relative weight of biomass in environmental (from CR), SD = standard deviation, see Table 1 for size group details.

Bighead goby (proportions of food items in the stomachs of gobies)												Macrozoobenthos (proportions in environment)							
Size group	Invasive (CR + KV)		Native (CR + KV)		Unassigned (CR + KV)		Invasive (CR)		Native (CR)		Unassigned (CR)		Invasive (CR)		Native (CR)		Unassigned (CR)		
	IFI	SD	IFI	SD	IFI	SD	%B	SD	%B	SD	%B	SD	%B <sub>E</sub>	SD	%B <sub>E</sub>	SD	%B <sub>E</sub>	SD	
1	86.0	30.2	11.7	2.4	2.3	0.6	86.1	34.5	7.2	1.9	6.7	2.0							
2	77.7	24.2	13.4	2.1	8.9	2.1	59.4	17.9	17.0	2.6	23.6	5.5							
3	86.5	29.1	10.0	1.2	3.5	0.8	76.0	27.0	8.8	1.2	15.2	4.0							
4	95.6	30.7	3.3	0.4	1.0	0.2	82.4	26.1	5.6	0.7	12.0	2.8							
5	89.5	29.4	9.7	2.3	0.9	0.2	94.7	33.5	4.8	0.9	0.5	0.2							
6	43.1	10.3	52.1	12.9	4.7	1.1	93.1	36.9	6.2	1.2	0.7	0.2							
Total	79.7	25.4	16.7	2.8	3.6	0.6	81.9	29.2	8.3	1.0	9.8	2.3	52.0	8.8	29.7	3.5	18.3	4.7	
Round goby (proportions of food items in the stomachs of gobies)												Macrozoobenthos (proportions in environment)							
Size group	Invasive (CR + KV)		Native (CR + KV)		Unassigned (CR + KV)		Invasive (CR)		Native (CR)		Unassigned (CR)		Invasive (CR)		Native (CR)		Unassigned (CR)		
	IFI	SD	IFI	SD	IFI	SD	%B	SD	%B	SD	%B	SD	%B <sub>E</sub>	SD	%B <sub>E</sub>	SD	%B <sub>E</sub>	SD	
1	1.7	0.5	98.3	27.2	0.0	0.0	8.0	2.1	92.0	30.8	0.0	0.0							
2	41.3	14.4	54.8	9.9	3.9	1.2	68.6	24.4	30.6	9.3	0.8	0.2							
3	39.6	11.2	58.2	9.4	2.1	0.3	61.3	15.7	31.3	8.8	7.4	1.4							
4	31.3	7.6	66.1	10.7	2.6	0.4	46.2	12.3	40.2	11.0	13.6	4.0							
5	25.7	5.8	65.7	9.3	8.7	1.5	15.7	4.2	50.2	14.4	34.1	11.8							
6	11.7	2.3	83.2	15.4	5.1	1.2	20.7	7.8	52.2	16.5	27.2	11.1							
Total	25.2	6.4	71.1	11.2	3.7	0.5	36.7	9.3	49.4	15.1	13.8	4.7	52.0	8.8	29.7	3.5	18.3	4.7	



**Fig. 4.** Electivity plot displaying ontogenetic food preferences of bighead goby (●) and round goby (□) from the Čunovo Reservoir (River Danube, Slovakia). Points above the angle bisector indicate preference (positive selection of food items), whereas points below indicate avoidance (negative selection of food items). Abbreviations as in Fig. 2, also %B = relative weight of biomass, %BE = relative weight of biomass in environmental.

et al., 2010; Strake et al., 2013). Metabolism rates vary with the age of fish, being higher in younger individuals (Fonds et al., 1992), which could explain the emptier stomachs in younger round gobies (Strake et al., 2013). However, this is not case in bighead goby. In general, bighead goby consumed more food than round goby, and this applies for all size groups (Table 1). This higher energy intake is reflected in faster length growth but not in weight (Gruľa, 2012). Thus, it appears that bighead goby need more energy to achieve the same biomass as round goby. They are either less efficient in the use of energy from food sources or have higher energy expenditure. Different feeding strategy between these two gobies suggest the latter: bighead goby prefer active hunting (fish, *Dikerogammarus* sp.) whereas round goby use grazing (bryozoan, chironomid larvae; Števoe and Kováč, 2013).

#### 4.2. Ontogenetic variations in the diet composition

Feeding behaviour of bighead goby is more stenophagous compared to round goby (Brandner et al., 2013a; Števoe and Kováč, 2013). Higher rate of explained variability suggests that ontogenetic changes in the diet composition of bighead goby are more important than in round goby both in the Middle Danube (Slovakia) and in the Lower Rhine (Germany; Fig. 2; Borcherdig et al., 2013). If the smaller individuals consumed mainly chironomid larvae (Fig. 3) and mid-size groups (3–5) consumed mainly *Dikerogammarus* sp., then larger specimens shifted towards fishes (Fig. 3), and the largest individuals (>125 mm total length; TL) were found to become predominantly fish predators (Borcherdig et al., 2013). Some food items such

**Table 4**

Seasonal variation in the index of stomach fullness (*ISF*) and Fulton's condition factor (*K<sub>SL</sub>*) of bighead goby and round goby from the Slovak part of the River Danube; n = numbers of individuals, SD = standard deviation.

Bighead goby	Spring				Summer				Autumn				Total			
Male (n)	19				32				98				149			
Female (n)	39				20				103				162			
	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD
Male	2.74	1.59	2.38	0.23	3.57	2.39	2.55	0.58	1.79	1.77	2.29	0.27	2.29	2.02	2.36	0.37
Female	3.19	2.44	2.04	0.15	3.82	3.91	2.42	0.30	2.14	2.27	2.21	0.24	2.62	2.62	2.19	0.26
Round goby	Spring				Summer				Autumn				Total			
Male (n)	42				79				104				225			
Female (n)	55				76				93				224			
	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD	ISF	SD	K <sub>SL</sub>	SD
Male	1.27	0.92	2.50	0.23	1.51	1.17	2.53	0.26	0.86	0.65	2.47	0.26	1.17	0.96	2.50	0.25
Female	1.81	2.58	2.37	0.17	2.19	2.74	2.51	0.18	0.85	0.71	2.46	0.24	1.54	2.17	2.45	0.21

as detritus or *Corophium* sp. were supplementary for all size groups (Fig. 3).

Differences in the diet composition between size groups of round goby were found not only in the Middle Danube but also in the Lower Rhine, the River Sava, the bay of Gdansk, as well as in Lake Erie and the River Trent in North America (Borcherding et al., 2013; Campbell et al., 2009; Piria et al., 2016; Raby et al., 2010; Skora and Rzeznik, 2001). Smaller individuals of round goby are mainly benthos feeders consuming *Gammarus* sp., Ceratopogonidae, Ephemeroptera (*Caenis* sp., *Stenonem* sp., *Ephemera* sp., *Baetis* sp.), Odonata (*Macromia* sp.), Diptera (*Athrix* sp., both larvae and pupae), Oligochaeta, Ostracoda, crayfish, and Trichoptera (Barton et al., 2005; Jude et al., 1995). On the other hand, larger individuals prefer to consume larger prey, and zooplankton occurs in their diet only accidentally. Regardless the geographical area, the importance of molluscs, especially bivalves, in the diet of round goby increases progressively with body length (Barton et al., 2005; Borcherding et al., 2013; Frolova, 2009; Jude et al., 1995; Raby et al., 2010). In North America, strong dominance of bivalves was observed in specimens >90 mm TL, whereas in the Gulf of Gdansk such dominance starts at 130–150 mm TL, and individuals of 160–180 mm TL feed exclusively on bivalves (Skora and Rzeznik, 2001).

In the invasion front, e.g. currently in the River Sava, gastropods are a very important prey item for round goby, and they are also the most abundant benthic invertebrates in the environment (Piria et al., 2016). However, in the long-established population of round goby from the Middle Danube in Slovakia, molluscs represented just a small proportion of their diet, regardless the predator's size. Indeed, decreasing abundance of molluscs in the Slovak part of the Danube that began in 2004 coincides with the arrival of round goby in 2003 (Beracko and Matečný, 2016). This could explain why molluscs were not found in the stomachs of round goby in such quantities. Similarly, in the River Trent, large round gobies from a long-established population had almost no dreissenids in their guts, whereas these were the predominant prey type in gobies occupying the expansion areas (Raby et al., 2010). Zebra mussel density in the area with the long-established population was an order of magnitude lower than in the expansion areas (Raby et al., 2010).

The smallest individuals of bighead goby have a larger gape than small individuals of round goby, so they can choose more diverse food items (Fig. 3). In contrast to the smallest round gobies, they are not focused only on chironomid larvae.

To sum up, smaller individuals of both species appear to occupy a different trophic niche compared to larger individuals (see also Muñoz and Ojeda, 1998), especially if smaller round goby that feed on zooplankton (Fig. 3, Raby et al., 2010; Rakauskas et al., 2008), do not hunt only at the bottom but also in the water column.

#### 4.3. Ontogenetic variations and electivity of invasive organisms in the diet

The detailed analyses of ontogenetic shifts in consumption showed a strong focus of bighead goby on invasive organisms (*IFI*, Table 3), when all size groups highly preferred invasive benthic invertebrates (%B, %B<sub>E</sub>, Table 3), especially *Dikerogammarus* sp. (Fig. 4). Only the largest individuals of bighead goby consumed lower amounts of invasive organisms (*IFI*, Table 3), mainly due to predation on fish (Figs. 2, 3). If the pioneering populations of bighead goby from the invasion front followed the pattern observed in round goby, i.e. increased presence of large sized individuals (Brandner et al., 2013b), then native fish species would be in risk by bighead goby. In contrast, no size groups of round goby chose invasive food items (*IFI*, Table 3), and the smallest individuals (<40 mm SL), as well as individuals >85 mm SL even avoided invasive benthic invertebrates (%B, %B<sub>E</sub>, Table 3). Electivity for bivalves started in size groups from 70 to 84 mm, and increased with body size (Fig. 4). The fact that round goby consumes lower amounts of invasive organisms than bighead goby may result in a highly different impact on native benthic invertebrates and fish.

Indeed, eating invasive prey by gobies was found not only in the Middle Danube but also in the Upper Danube and in the Rhine river system (Brandner et al., 2013b; Schiphouwer, 2011). Thus, the negative impact by bighead goby on native benthic invertebrates can be potentially mitigated by their predation on various non-native benthic invertebrates. Unlike the Danube, such a "Ponto-Caspian food chain" has been established in Lake Erie, with round goby feeding heavily upon invertebrate species from its own native area (Campbell et al., 2009).

#### 4.4. Seasonal and sexual variations in the stomach fullness and condition factor

Seasonally, both species were found to be most active in feeding during summer (Table 4), i.e. during highest water temperatures (spring 9.1–15 °C, summer 17.5–23.2 °C, autumn 19.9–11.5 °C, data for the Danube in Slovakia from the Slovak Hydro-Meteorological Institute, Bratislava). The same pattern was observed in round goby from the littoral zone of the Kuibyshev and Saratov Reservoirs (Kirilenko and Shemonaev, 2012). In the Lower Rhine, both species ate significantly more food in spring and summer than in autumn (Borcherding et al., 2013). Thus, seasonal variation in *ISF* appears to be closely related to water temperature. Seasonality in feeding activities plays an important role in inter-specific competition. Feeding activity appears to vary depending on local conditions (Adámek et al., 2010; Smyly, 1955). In the Danube, Balon's ruffe *Gymnocephalus baloni* (Holčík and Hensel, 1974) and yellow pope *Gymnocephalus schraetser* (Linnaeus, 1758) were found to have highest *ISF* values in spring, whereas ruffe in autumn



(Nagy, 1985). Thus, variations in feeding activities can increase or decrease the impact of invasive gobies on native species of fish, and attention should be paid to this aspect of inter-specific interactions.

Females of both species consumed more food than males (Table 4), especially in summer, which is probably associated with higher energy needs of females due to reproduction. In contrast, males guard nests during this period, and their reception of food is limited (Pinchuk et al., 2003). Females allocate the energy from food into gonads rather than into somatic growth, whereas in males their higher  $K_{SL}$  indicates opposite (Table 4). It appears that females of both species started to allocate energy into ovaries right in early spring – they had relatively high  $ISF$ , but lowest  $K_{SL}$  (Table 4) and highest gonadosomatic index (Hôrková and Kováč, 2014, 2015). Individuals that have higher post-winter energy reserves are able to breed earlier in the spring (Schultz et al., 1991), providing early spawned offspring the advantage of a longer growing season and lower intra cohort resource competition (Houston et al., 2013).

Ecological and evolutionary processes (including shifts in species composition, accumulation of materials and interactions with abiotic variables) can increase, decrease, or qualitatively change the impacts of an invader through time (Strayer et al., 2006). Both gobies are now well established in the middle Danube (bighead goby since 1996; Stráňai, 1997, and round goby since 2003; Stráňai and Andreji, 2004), and their  $ISF$  was found to be the lowest in autumn (Table 4). In contrast, a population at the edge of an invasion had highest  $ISF$  in autumn (Raby et al., 2010). Reduced intraspecific competition for food resources (higher food availability) at the front of the invasion had a role in higher energy allocation towards autumn lipid storage, allowing round goby to overwinter in better condition and have superior allocation to reproduction in early spring at expanding range edges (Houston et al., 2013). Density-dependent resource limitation in the area of introduction influences intraspecific competition, which is low at edges of an invasion (Houston et al., 2013) in contrast to established area (Slovakia), where cannibalism was recorded in both goby species, due to high intraspecific competition (Števo and Kováč, 2013).

#### 4.5. Conclusions and comments to the possible impacts on native communities

Previous studies demonstrated significant differences in feeding strategies and/or trophic niches between bighead goby and round goby (Brandner et al., 2013a; Števo and Kováč, 2013). The present study emphasises these differences with regard to ontogenetic variations and the stage of invasion. This is especially important within the context of potential impact of both invaders on native communities. Bighead goby seems to represent a risk for small native benthic fish species as a predator, especially in the invasion front (Brandner et al., 2013b), whereas round goby has a potential to impact native fish species of all ontogenetic phases as a strong competitor for food. Indeed, a recent study from the invasion front supports the above assumption. Larger specimens of bighead goby in the River Sava, where the species was first found in 2011, consumed mainly fishes (Piria et al., 2016). Round goby also appear to have strong impact on bivalves, again especially in the invasion front, where larger females with the highest consumption rates are supposed to predominate.

The benthic invertebrates that were found to be preferred by both bighead and round gobies in the Middle Danube can be heavily affected by a significant predation impact. On the other hand, all these benthic invertebrates have always been a subject of predation of native species of fish. Therefore, in fact, the native predators are just being replaced by the invasive predators, and the resulting predation pressure on the prey, does not need to increase, necessarily. Ironically, high preferences of *Dikerogammarus* sp. by bighead goby may help to maintain or increase the abundance of other native macroinvertebrates species. *Dikerogammarus* sp. is an important predator that consumes native isopod (e.g. *Asellus aquaticus* Linnaeus, 1758), insect larvae but also small

fish and eggs of fish (Casellato et al., 2007), damaging seriously the natural foraging network of rivers and lakes (Dick et al., 2002). From this point of view, bighead goby does not seem to be – in contrast to round goby – a hot candidate for being a nuisance invader.

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