

# Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources

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**Abstract** – We investigated somatic condition, growth rate, diet and food resources of the native (lower Danube) and non-native (upper Danube) populations of invasive bighead goby *Neogobius kessleri* and round goby *N. melanostomus* within the Danube River to answer the question whether prey availability and type may have facilitated successful goby invasion to the upper Danube. The non-native populations of both species were in better somatic condition and grew faster. The biomass of nonmollusc macrozoobenthos, dominated by Amphipoda, was markedly higher in the non-native range while molluscs were recorded frequently in both the native and non-native ranges. Amphipods were far the most consumed prey by non-native fish, whereas native fish combined two main prey types – amphipods and fish (bighead goby) and amphipods and bivalves (round goby).

A laboratory experiment was conducted to reveal whether the low consumption of bivalves by the round goby in the non-native range reflects prey encounter rates or alternatively prey selectivity. When bivalves and amphipods were offered simultaneously in excess to the experimental fish, round goby showed strong preference towards amphipods. Molluscs are hypothesised to be an alternative rather than the most preferred prey for the round goby. Rich food resources utilised by the non-native bighead and round goby contribute to their invasive success in the upper Danube.

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**Key words:** *Apollonia*; food availability; Bivalvia; invasion success; zebra mussel

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## Introduction

Several species of the genus *Neogobius* have recently received much scientific attention for their invasive potential. The round goby *Neogobius (Apollonia) melanostomus* (Pallas, 1814) caused severe impacts on native communities and whole ecosystems in North America (e.g., Vanderploeg et al. 2002). The round goby and three other species: bighead goby *Neogobius kessleri* (Günther, 1861), monkey goby *Neogobius (Apollonia) fluviatilis* (Pallas, 1814) and racer goby *Neogobius gymnotrachelus* (Kessler, 1857) have invaded new areas within the European continent and continue to spread and establish new populations (Copp et al. 2005). All four invasive gobies are of

Ponto-Caspian origin and their historical distribution in freshwaters was historically restricted to Ponto-Caspian rivers, including the lower reach of the Danube River (Ahnelt et al. 1998). In the 1990s, the four *Neogobius* species were recorded far upstream their known historical distributions in the Danube and have established abundant non-native populations (Zweimüller et al. 1996; Wiesner et al. 2000; Zweimüller et al. 2000; revised by Ahnelt et al. 2001; Stráňai & Andreji 2001).

Research on Danubian *Neogobius* spp. ecology was scarce prior to the onset of their range expansion (e.g., Gheorghiev 1966), but invasive gobies in the Danube are at present subject to intensive scientific research (e.g., Erős et al. 2005; Jurajda et al. 2005; Wiesner

2005; Adámek et al. 2007; Ľavrínčiková & Kováč 2007; Copp et al. 2008; Borza et al. 2009; Kováč et al. 2009). However, most recent work has focused on *Neogobius* spp. populations at single sites within different stretches of the Danube, whereas a comparative approach based on a set of original and comparable data is lacking. A comparison of environmental and/or population characteristics between the native and non-native *Neogobius* spp. ranges may provide insight into relative importance of factors affecting their invasion success. For example, the predominance of the bighead and round goby in the non-native range compared to the predominance of the monkey goby in the native range can be explained by their inverse substrate preferences and corresponding substrate occurrences within the respective ranges (Erős et al. 2005; Polačik et al. 2008). However, except for the different species dominances, notable differences in the overall genus *Neogobius* density were found between the native and non-native ranges, too. The *Neogobius* spp. density was consistently about threefold higher in the non-native range compared to the native range (Polačik et al. 2008). This implies that the non-native Danube stretches may have a potential to host higher density of *Neogobius* spp. The high *Neogobius* spp. density in combination with the strikingly larger mean body size of fish from non-native populations (bighead and round goby were compared) generated the hypothesis that there was higher food availability in the non-native range (Polačik et al. 2008).

Invasive gobies are generalist benthic feeders, capable of utilising most of the macrozoobenthic prey, a feature that increases their invasive potential (Kostrzewa & Grabowski 2003; Grabowska & Grabowski 2005; Adámek et al. 2007; Copp et al. 2008). However, even within a dietary niche of a generalist predator, some prey types are preferred (i.e., more profitable) over others (e.g., Fullerton et al. 1998). In other words, generalist feeding strategy allows the

predator to utilise varying preys in new areas, but the real suitability of the new food resources for the predator will only be reflected in condition of the newly-established populations.

We hypothesised that the non-native goby populations may benefit from higher prey abundances and/or nutritionally more profitable prey available in comparison to the populations in the native range. To answer the question whether prey availability and type may have facilitated successful goby invasion to the upper Danube, we sampled the native (Bulgarian – lower Danube) and non-native (Austrian – upper Danube) populations of bighead and round goby in the respective Danube stretches. Growth rate and Fulton's condition coefficient were used to test food saturation among the populations. Furthermore, we compared the main food sources for the gobies in terms of biomass of macrozoobenthos and analysed diet patterns of both species in the upper and lower Danube. Finally, we performed a laboratory experiment to directly test whether the diet of round goby is more likely to reflect the predator's food preferences or, alternatively, the availability of certain prey types in the environment.

## Materials and methods

### Study area

The Danube consists of three sections with different geological origins. The lower Danube runs between the Danube delta and the Djerdap Gorge, the middle Danube corresponds to the area of paleolake Pannon delimited by the Danube inland delta in Slovakia, and the upper Danube consists of the portions of river upstream of the Austrian-Slovak border (Kováč et al. 2006). The native range of the bighead and round goby was represented by the Bulgarian stretch (lower Danube, r. km 770–836) and the non-native range by the Austrian stretch (upper Danube, r. km 1900–1902) of the Danube River (Fig. 1).

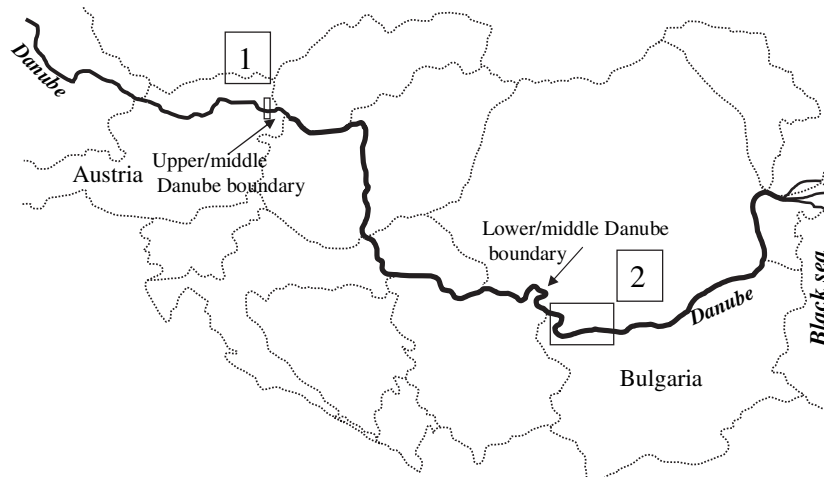


Fig. 1. The Danube River with study stretches indicated by rectangles – 1: Austrian (non-native) stretch, 2: Bulgarian (native) stretch.

Food resources in the field

Food resources in the native and non-native ranges were evaluated using quantitative (CPUE: weight per time unit) macrozoobenthos sampling in October 2006. A total of 22 (13 in Bulgaria, 9 in Austria) macrozoobenthos samples were collected using the kick sampling technique (Frost 1971) with a hand net of 0.5-mm mesh size. A sampling took from 60 s (fine substrate) to 240 s (coarse substrate) and it typically covered 1–3 m<sup>2</sup>. Spatial extent of samplings followed the occurrence of substrate types in the sampled stretches. Riprap and gravel-based substrates were equally present and sampled in the Austrian stretch whereas finer substrates – sand and mud – dominated in the samples over gravel and riprap substrates along the Bulgarian stretch. In the laboratory, nonmollusc invertebrates (preserved in 4% formaldehyde) were grouped according to taxa and weighed to the nearest 0.001 g. The weight percentages of all taxonomical groups were then calculated.

As we considered important prey mollusc species [particularly the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and *Corbicula* sp.] to be relatively resistant to the traditional kick sampling technique, only the presence or absence of molluscs was recorded (with the aim to find out whether they occurred frequently or infrequently) at 48 sites (27 in Bulgaria, 21 in Austria). The assessment of their occurrence included active visual hand-searching on the surface of stones in depths up to 50 cm and/or the presence of smaller species (e.g., *Lithoglyphus* sp., *Theodoxus* sp.) was checked in nonmollusc invertebrate samples where they occurred as a bycatch.

Condition coefficient, growth rate and diet patterns

Bighead and round goby were collected in the field using electrofishing and beach seining in October 2005 (for diet patterns, condition coefficient) and in October 2006 (for diet patterns, condition coefficient, and growth rate) (Table 1). In the field, fish were killed using a lethal dose of anaesthetic and stored in formaldehyde. In the laboratory, fish were measured to the nearest 1 mm and weighed to the nearest 0.01 g.

Differences between the native and non-native populations of both species were tested using two

food saturation indices – Fulton’s condition coefficient (Anderson & Neumann 1996) and growth rate. Fulton’s condition coefficient was calculated from eviscerated body weight for all fish used for diet patterns analysis (Table 1).

To avoid bias arising from intersexual differences in growth rate, only females were examined. Examined fish were chosen so that there were no significant within-species differences in standard length between fish from native and non-native ranges (*t*-tests, *P* > 0.05) (Table 1). Mean spacing of scale circuli was used to estimate fish growth rate, based on the finding in a pilot study that traditional age determination from scale annuli was ambiguous and prone to subjective bias (see also Miller 1975; DeCicco & Brown 2006; Ibáñez et al. 2008). Circuli spacing is known to adequately reflect growth rate in fish, with denser spacing reflecting slower growth rates (Fisher & Pearcy 2005; Ibáñez et al. 2008) and is typically expressed as mean circuli spacing for a portion of the scale (Fisher & Pearcy 1990, 2005).

Scales were removed from the anterior region of the fish’s left flank. The cleaned scale was then photographed under a light microscope equipped with U-eye 1540 camera (Imaging Development Systems, Woburn, Massachusetts, U.S.A.) and subsequently measured and analysed using LUCIA 5.0 software (Laboratory Imaging, Prague, Czech Republic). The circuli in the internal part of a small goby scale are often difficult to clearly visualise because of residual epidermal tissue, whereas the external circuli may be easily damaged during the preparation process. Therefore, the number of circuli in the middle third of a scale was counted to obtain a relative growth rate index (GRI), representing scale circuli density. The GRI was calculated as the number of circuli in the middle third of the scale per scale length (measured along the anterior-posterior axis) to compensate for potential differences in scale size. An analysis of covariance (ANCOVA) was used to compare growth rate between native and non-native populations, with standard length as a covariate.

To test for differences in diet patterns, gut contents were examined in the native and non-native populations of the bighead and round goby. The fish originated from 27 sites in Bulgaria and 21 sites in Austria (Fig. 1) and were chosen so that there was no

Table 1. Number (*N*) and mean standard length (SL, with standard deviation SD) of fish used for growth rate and diet patterns analyses.

	Non-native (Austria)						Native (Bulgaria)					
	Growth rate			Diet patterns			Growth rate			Diet patterns		
	<i>N</i>	SL	SD	<i>N</i>	SL	SD	<i>N</i>	SL	SD	<i>N</i>	SL	SD
Bighead goby	31	72.1	8.4	50	73.7	10.4	33	75.6	14.2	50	73.3	14.2
Round goby	32	73.1	8.8	40	72.9	6.8	28	69.4	7.9	58	70.2	5.7

significant difference in standard length between those from the native and non-native ranges within a species (*t*-tests,  $P > 0.05$ ) (Table 1). Preliminary analysis demonstrated no significant inter-annual variability in gut contents of the two species. Therefore, specimens collected in 2005 and 2006 (approximately equal numbers per year) were pooled. Their gut containing prey items was removed and weighed to the nearest 0.001 g. The prey items were then removed and the empty gut tissue was re-weighed. Prey items were then grouped according to taxa. Individual gut contents were typically markedly dominated by one or a few taxa groups and some of the prey types occurred in amounts too small for reliable weighing. Therefore the per cent contribution of all taxa groups to the entire gut content (100%) was visually estimated (Marrero & Lopez-Rojas 1995; McMahon et al. 2005). Since relative interpopulation differences were tested, all samples were analysed by the same person. Costello's graphical method modified according to Amundsen et al. (1996) was applied to visualise the diet patterns of native and non-native *Neogobius* populations. In Costello's plots, individual prey items are expressed as points distributed along two diagonal axes of the diagram [Fig. 2(a,b)]. The percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper end and rare prey at the lower end. The second diagonal represents niche width contribution and prey points positioned in either the upper left or the lower right corner are indicative of different feeding strategies. Prey items positioned in the upper left were consumed by a few individuals but in high quantities (representing specialisation) whereas prey items in the lower right corner were consumed by most individuals but in low quantities.

Prey selectivity in the laboratory

Despite the fact that molluscs (especially bivalves) are considered to be a preferred prey for round goby

(Ghedotti et al. 1995; Charlebois et al. 1997; Ray & Corkum 1997; French & Jude 2001; Pinchuk et al. 2003a), they were rarely consumed in the sampled area of the non-native range. Although the molluscs were recorded frequently here (see Results), we did not perform quantitative estimate of their abundance and thus we were not able to decide whether the low-mollusc consumption rate reflected their (possibly) low availability in the environment or the predator avoidance.

Therefore, a laboratory test was performed to test the prey preferences of round goby. We hypothesised that the low molluscs' consumption was caused by prey selectivity. We allowed the experimental round gobies to choose between two prey items – the zebra mussel and an amphipod *Gammarus roeselii* Gervais, 1835. In October 2007, experimental fish were captured in the (non-native) Slovak stretch of the Danube River (r. km 1846) by hook and line sampling, 1 week prior to the experiment. Fish were acclimatised in a series of 170l aquariums and fed frozen fish meat and chironomid larvae once per day, except for the 24 h starving prior to the experiment. Zebra mussels were collected 3 days prior to the experiment. Amphipods were collected in the Svitava River, Czech Republic, 2 days prior to the experiment.

The experiment was run during daylight at water temperatures between 15 and 16 °C. Fifteen replicates were conducted. For each replicate, a 20l aerated aquarium was filled with clear, dechlorinated water. Three ceramic caves, six to seven rocks of 5–8 cm in diameter, and a cluster of 10 zebra mussels larger than 20 mm were provided to mimic the interstitial-rich natural environment of the non-native populations (Polačik et al. 2008). In each replicate, an individual round goby (standard length range 71–83 mm, mean = 76.2 mm, SD = 4.6) was placed in one half of the tank and allowed to acclimate to aquarium conditions for 30 min. The second half of the tank was separated by a transparent plastic slide and 20 live amphipods and 30 zebra mussels were introduced there at the time of fish introduction into the first

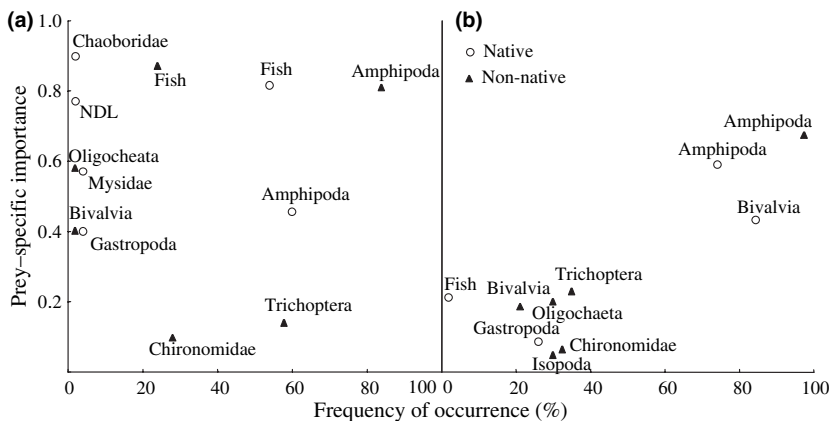


Fig. 2. The diet patterns of (a) bighead goby and (b) round goby. NDL, nonchironomid benthic Diptera larvae. The prey items of low prey-specific importance (<0.2) and consumed with low frequency (<20%) were omitted from the plots for clarity.

compartment. A mean of 72% experimental zebra mussels (out of 30 mussels per replicate,  $SD = 5.8$ ) were attached to a small pebble to simulate the way they occur naturally. The mean size of amphipods within a replicate varied between 6.5 mm and 8.1 mm with a total range 3.2–12.6 mm. The mean size of zebra mussels within a replicate varied between 7.9 mm and 9.3 mm, with a total range 2.7–13.7 mm.

After the acclimation period, the plastic slide was removed and the fish was allowed to feed for 1 h. Subsequently the fish was killed and specimens of both prey types in the gut were counted and measured. This procedure was necessary because in pilot trials, the sum of the consumed amphipods together with living amphipods retrieved from the tank after the trial reached in some cases only 90% of the introduced specimens. Amphipods remained hidden in the mussel clusters and were difficult to find and therefore estimating the amount of each prey taxa consumed depended on gut content analysis.

Because the experiment yielded very low consumption of zebra mussels (see Results) and following the fact that no zebra mussels were found in the guts of 20 round gobies collected together in the field along with the experimental fish (despite the stable occurrence of zebra mussels at the collecting site, Nagy 2006), a second experiment was conducted to confirm whether the experimental round goby population was even capable of preying on zebra mussels. Another 15 experimental replicates were performed with the same tank setup and conditions, but with 30 zebra mussels as the only prey item available (mean mussel length varied within a trial from 8.4 to 10.7 mm, 72%,  $SD = 8.82$  mussels were attached).

The percentage of consumed amphipods and zebra mussels was compared using a paired Wilcoxon test. Differences in percentage of consumed zebra mussel individuals between the two experiments were compared using the Mann–Whitney  $U$ -test. Binomial generalised linear model (GLM-b, logit link) was used to test whether fish size and size of prey (amphipods in the first experiment, zebra mussels in the second experiment) affected consumption. All data were analysed using software STATISTICA for Windows 8.0 Statsoft Inc., Tulsa, Oklahoma, U.S.A. and R 2.0.1.

## Results

### Food resources in the field

Significantly higher mean biomass of macrozoobenthos was recorded in the Austrian stretch ( $t$ -test,  $P < 0.05$ , Fig. 3) and in both sampled stretches, nonmollusc macrozoobenthos was strongly dominated by amphipods (*Corophium* sp., *Dikerogammarus* sp., *Gammarus* sp.), followed by chironomids (Chironom-

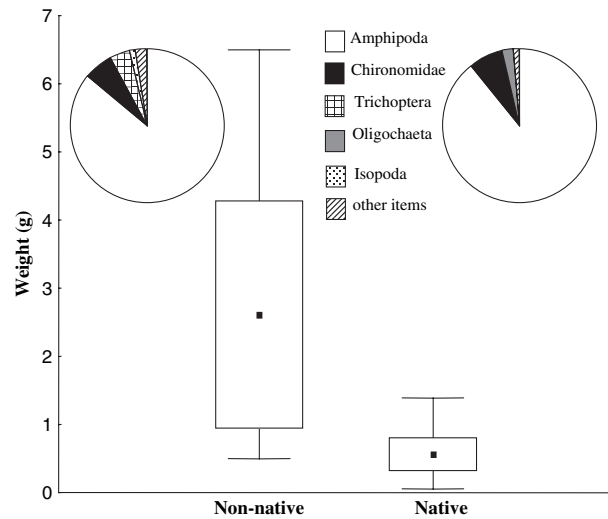


Fig. 3. The taxonomical composition of nonmollusc macrozoobenthos (pie plots) and mean weight of macrozoobenthos samples (box-whisker plots) in the two sampled Danube stretches. The centre points represent mean, the boxes denote 95% confidence intervals and the whiskers denote range.

idae). Oligochaetes (Oligochaeta) in the native range and caddisflies in the non-native range (Trichoptera, represented mainly by noncased families Hydropsychidae and Psychomyiidae) together with isopods (*Jaera sarsi*) constituted much smaller proportion of the benthos (Fig. 3). Other macrozoobenthos taxa (nonchironomid benthic Diptera larvae, Nematoda, Hirundinella, Turbellaria, Coleoptera larvae, Ephemeroptera, Hydrachnida, Ostracoda) comprised together less than 3% of macrozoobenthos (Fig. 3).

Molluscs (mostly zebra mussel, *Corbicula* sp. and *Lithoglyphus* sp.) were recorded frequently in both ranges – they were documented at 96% and 71% of sites sampled in the Bulgarian and Austrian stretch, respectively.

### Condition coefficient, growth rate and diet patterns

Fulton's condition coefficient was significantly higher in the upper Danube in both goby species ( $t$ -tests,  $P < 0.05$ , Fig. 4).

Scale circuli spacing, represented by the GRI, was denser (indicating slower growth) in the examined native populations of the bighead goby (mean  $GRI \pm SD$  of native population  $21.11 \pm 1.76$ , non-native  $18.63 \pm 1.84$ ; ANCOVA,  $P < 0.001$ ). The same result was found in the round goby (native  $20.36 \pm 2.28$ , non-native  $16.46 \pm 1.35$ ; ANCOVA,  $P < 0.001$ ). The GRI value was not significantly affected by fish standard length (ANCOVA  $P > 0.05$ ).

The diet patterns of the bighead and round goby differed between the examined native and non-native populations. The non-native population of the bighead

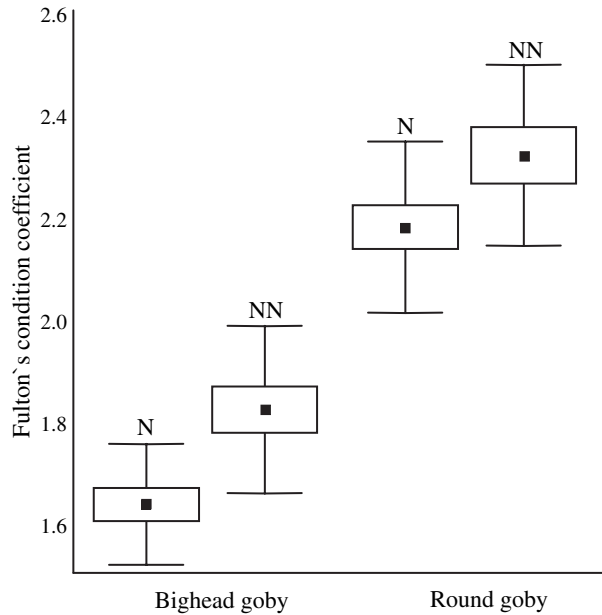


Fig. 4. The mean Fulton's condition coefficient (centre points) of the native (N) and non-native (NN) populations of the bighead and round goby. The boxes denote 95% confidence intervals and the whiskers denote standard deviation.

goby was characterised by a clear dominance of amphipods as the most important prey item. Fish were consumed rarely. By contrast, the diet of the native population was largely based on two prey taxons – fish and amphipods [Fig. 2(a)].

Similarly to the bighead goby, the non-native round gobies heavily utilised the amphipods as the very dominant prey with other prey items being of notably lower importance. Contrary, the native population of the round goby preyed to a similar extent on two important preys – bivalves and amphipods [Fig. 2(b)].

#### Prey selectivity in the laboratory

In the presence of both prey items, amphipods were found in large abundance in the guts of round gobies. Zebra mussels, however, were not consumed (Fig. 5) and hence the preference towards amphipods was very significant (Wilcoxon paired test,  $P < 0.001$ ). The number of consumed amphipods increased with fish standard length and bigger amphipods were preferred over smaller amphipods (GLM-b, both  $P < 0.01$ ).

In the second experiment where zebra mussels were the only prey available, fish significantly increased their total consumption of zebra mussels as compared to the setup where amphipods were also available (Mann–Whitney  $U$ -test,  $P < 0.001$ , Fig. 5). After the experiment, no empty or crushed uneaten shells were found in experimental tanks. During the dissections, in the fish guts the shells were found intact or sometimes

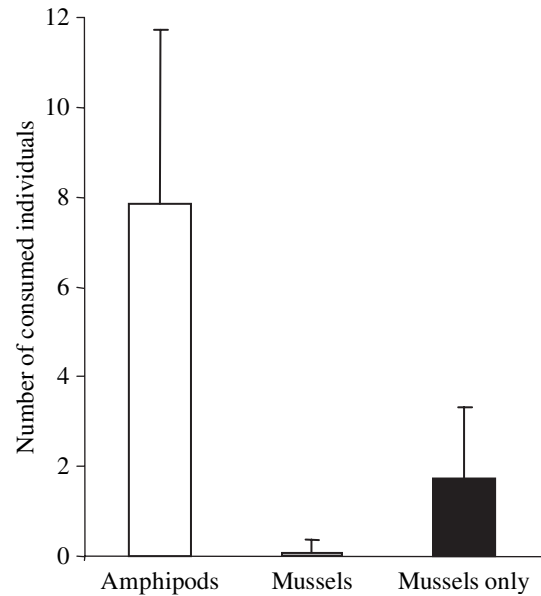


Fig. 5. The mean number (with standard deviation) of amphipods and zebra mussels consumed by round goby in the presence of both prey items and in the presence of zebra mussels only.

partly crushed. Fish size did not significantly influence zebra mussel consumption, but fish preferred mussels of smaller size (GLM-b,  $P > 0.05$ , and  $P < 0.01$ , respectively).

## Discussion

### Condition coefficient and growth rate

Differences in growth rates and Fulton's condition coefficient confirmed our hypothesis of better nutritional status of the examined non-native bighead and round goby populations.

Growth rate and Fulton's condition coefficient used in this study were suitable measures of food availability and/or quality (Lankford & Targett 1997; Muller-Feuga 1999; Rennie & Verdon 2008). In a previous study, two lines of evidence gave rise to the hypothesis that increased food availability is a factor facilitating successful invasion: first, higher *Neogobius* spp. density and second, larger mean body sizes of bighead and round gobies in the non-native range (Polačik et al. 2008). However, genus density or body size may be under significant influences of many ecological factors, e.g., predation (see e.g., Begon et al. 1990) which were not investigated and thus further evidence was necessary.

### Food resources in the field

Markedly higher biomass of nonmollusc macrozoobenthos (dominated by amphipods) recorded in the

upper Danube corresponds to the findings of better condition status of non-native goby populations. Despite the general scarcity of studies simultaneously evaluating abundance of benthic organisms along the longitudinal profile of the Danube River, the overall macrozoobenthos abundance appears to decrease in a downstream direction (Literáthy et al. 2002). Consistent with our data, the quantity of amphipods, which contributed substantially to the weight of benthos samples in both stretches (Fig. 3), was particularly low in the Bulgarian–Romanian section of the Danube (Popescu-Marinescu et al. 2001). Holčík et al. (2003) suggested the contrary viewpoint that the food availability in the Danube decreases along downstream-upstream gradient. They proposed this conclusion based on faster growth rates of downstream monkey goby populations (though actually from brackish or marine environments). It should be noted, however, that brackish or marine environments differ from freshwaters in other important aspects and cannot be described as a simple downstream-upstream gradient (Pinchuk et al. 2003b).

Based on their frequency of occurrence, molluscs (mainly the invasive and exotic zebra mussels and *Corbicula* sp.) can be regarded as widely available prey in both areas of the bighead and round goby distribution (Literáthy et al. 2002; this study), though especially *Corbicula* sp. seems to reach relatively higher abundances in the lower Danube (Literáthy et al. 2002).

#### Diet patterns in the field

Amphipods clearly dominated the diet of both species in the upper Danube with no other prey of similar importance [Fig. 2(a,b)]. Amphipods are relatively hard-bodied organisms (i.e., less preferred prey by benthiphagous fish than soft bodied taxa, but more preferred than e.g., molluscs, Fullerton et al. 1998). On the other hand, amphipods are also characterised by their relatively large size. This, in combination with their high availability in the upper Danube, is likely to make amphipods a profitable prey in terms of long-term energetic intake/output ratio, as supported by the superior condition of the Austrian populations (see Lankford & Targett 1997).

Bighead gobies are the most distinct fish predators among the Danubian gobies (Vasileva & Vasilev 2003) but when they had an opportunity to utilise rich invertebrate food supply in the non-native range, fish were rarely consumed [Fig. 2(a)] (Borza et al. 2009). Although fish may be a more valuable prey due to their higher nutritional value (Elliott & Hurley 2000), they are much less abundant than invertebrates due to their higher position at the trophic level. In other words, there are increased energy costs linked to

obtaining this prey type. Given the slower growth rate and lower Fulton's condition coefficient in the native bighead gobies, we explain higher consumption of fish by bighead goby in the native range as a consequence of lower availability of profitable invertebrate prey rather than opportunistic use of more nutritious prey.

Round gobies consumed molluscs frequently and in large amounts in their native range, but this prey, albeit available, was of low importance in the upper Danube [Fig. 2(b)]. These results contradict the commonly accepted view of the round goby as a distinct molluscivore. Based on gut contents analysis and single-prey laboratory experiments, most authors have regarded round goby as a species with clear preference towards molluscs as prey, especially bivalves such as zebra mussels (e.g., Ghedotti et al. 1995; Charlebois et al. 1997; Ray & Corkum 1997; French & Jude 2001; Pinchuk et al. 2003a). Ray & Corkum (1997) even pointed out that regurgitation of shells and shell fragments may lead to further underestimation of the mussels' importance in the round goby diet. The opposite view that a large proportion of bivalves in the round goby diet may not reflect preference but rather be a consequence of low encounters with alternative prey was proposed via experimental work of Diggins et al. (2002). Using stable isotopes, Barton et al. (2005), revealed that mussel shells passed the digestive tract more slowly than soft prey and so the relative importance of bivalves is rather overestimated than underestimated.

In both direct and indirect manner, data from this study clearly support the view that zebra mussels are not the preferred prey of the round goby when other (softer) preys are available. Our indirect support comes from the fact that the round goby population with low-mollusc diet (non-native) was in better condition and grew faster than the native, high-mollusc diet population. Our direct support comes from our laboratory evidence (see below).

#### Prey selectivity in the laboratory

We found direct support via laboratory experiments of the upper Danube round goby clearly preferring amphipods over zebra mussels. Therefore, the low consumption of mussels in the upper Danube is likely to be a consequence of selective predation. It is not the availability of mussels but the availability of other prey that plays a decisive role. The consumption of zebra mussels in treatments with amphipods absent demonstrated that the experimental round goby population was capable of preying on zebra mussels. Most studies on feeding habits of the round goby found either large proportions of molluscs in the round goby diet (e.g., Great Lakes - Ray & Corkum 1997; Baltic Sea - Skóra & Rzeznik 2001; lower Danube - Simonovič

et al. 2001) or attributed their absence to their lack in the environment (Copp et al. 2008). Only a few studies admitted the possibility of selective preferential predation on nonmollusc prey types in cases when both prey types were available (Diggins et al. 2002; Barton et al. 2005; Bauer et al. 2007).

As the consumption of molluscs by the round goby is influenced by availability of nonmollusc prey, alternative prey availability is important for interpreting diet analyses of this species. Despite of that it appears to be surprisingly overlooked. For example, there is growing knowledge about the drastic decrease of nonmollusc macrozoobenthos biomass in the Great Lakes (e.g., Hondorp et al. 2005; Nalepa et al. 2007, 2009). The nonmollusc macrozoobenthos decrease may in fact significantly constrain the opportunities for nonmollusc prey selection by the round goby. However, this is hardly considered in the round goby diet studies originating in the Great Lakes area.

The important question remains why the round goby avoids molluscs. During our dissections, open shells having sharp edges or even completely intact zebra mussels and *Corbicula* sp. (which have very thick valves) were recovered from the gut. In some individuals the gut tissue appeared to be tightly stretched to an abnormal extent around bivalve shells. Therefore, we believe three possibilities may be of importance for gobies preying on bivalves (and molluscs in general): (i) there may be a risk of shells damaging the gut tissue (Stein & Kitchell 1975), (ii) fish may obtain lower amounts of nutrients given restricted access to soft tissues in shell-protected food (Ray & Corkum 1997; Cantanhêde et al. 2008) and (iii) fish may pay higher energetic costs in terms of handling the attached (zebra mussel) or buried (*Corbicula* sp.) prey (Stein & Kitchell 1975; Djuricich & Janssen 2001).

In summary, the non-native bighead and round goby encountered and exploited the superior food base found in the upper Danube which was reflected in their better condition and faster growth rate. The upper Danube populations of both species fed chiefly on readily available amphipods, whereas the native populations of the bighead and round goby, characterised by lower availability of nonmollusc macrozoobenthos, additionally utilised fish and bivalves, respectively. Zebra mussels were rarely consumed prey of round goby when amphipods were abundant in the environment.

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