Freshwater mollusc assemblages and habitat associations in the Danube River drainage, Hungary

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ABSTRACT

1. Native freshwater mollusc diversity has been declining over the past decades. For developing efficient conservation management plans for molluscs, it is especially important to identify areas with high native biodiversity.

2. The River Danube is one of the most important freshwater ecosystems in Europe and should receive special attention. The main objective of this work was to characterize the composition, diversity and conservation status of freshwater molluscs occurring in the Hungarian Danube River Drainage in five river habitat types (main channel of the Rivers Danube and Tisza, side channels of River Danube, tributaries of Rivers Danube and Tisza).

3. In total, 53 mollusc species were identified including 10 invasive species and 12 species of conservation concern. The main determining factors of mollusc composition were sediment characteristics, current velocity and oxygen content. Nitrate–nitrogen, ammonium–nitrogen, and calcium content also play a key role.

4. Overall, density, species richness and diversity showed significant differences between habitat types. The highest diversity values were detected in the side channels, but the highest proportion of threatened species was observed in the tributaries. The highest number and proportion of invasive species was detected in the main channel of the Danube. Most of the recorded invasive species were previously documented in side channels and the adjacent wetlands, but did not invade the tributaries.

5. Tributaries may provide refuges for native molluscs and could be considered as 'source' populations, which may be critically important in the regional maintenance of threatened species. Tributaries are still less disturbed and less invaded; and should be given priority in future conservation management plans.
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INTRODUCTION

Global freshwater biodiversity is experiencing far greater declines than terrestrial or marine ecosystems (McAllister *et al.*, 1997; Dudgeon *et al.*, 2006; Strayer and Dudgeon, 2010). For example, future extinction rates of freshwater faunal species in North America are predicted to be five times higher than for terrestrial fauna (Ricciardi and Rasmussen, 1999). Freshwater ecosystems are extremely threatened and their conservation is very difficult since they have high levels of endemism owing to natural isolation, catchment division and presence of saltwater barriers which impair re-colonization. In addition, they have a special landscape position as receivers being affected by all the changes and disturbances from adjacent terrestrial areas (Carpenter *et al.*, 2011). Moreover, rivers are open, directional systems, and many species migrate longitudinally or laterally by using different habitats during their life cycle, which may be significantly altered by human activities and makes the implementation of management and conservation measures especially difficult (Dudgeon *et al.*, 2006). Therefore, if freshwater species, declines continue at current rates, and the human demands for water remain constant, the opportunity to conserve freshwater biodiversity may disappear (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010).

All organisms are ultimately affected by human perturbations but freshwater molluscs are especially sensitive to anthropogenic and climatic disturbances (e.g. habitat loss and degradation, pollution, introduction of invasive species, floods, droughts), and species loss has accelerated over the past decades (Régnier *et al.*, 2009). Moreover, freshwater bivalves belonging to the family Unionidae are considered one of the most endangered groups of animals, and many populations are regionally or globally in decline (Bogan, 1993; Lydeard *et al.*, 2004; Burlakova *et al.*, 2011a, b; Lopes-Lima *et al.*, 2014). Since freshwater molluscs are involved in several key ecosystem functions and services (Rosemond *et al.*, 1993; Strayer *et al.*, 1999; Vaughn and Hakenkamp, 2001; Gutiérrez *et al.*, 2003; Spooner and Vaughn, 2008; Spooner *et al.*, 2012; Strayer, 2014; Tolley-Jordan *et al.*, 2015) their continued decline can result in cascading effects that may alter the whole ecosystem. Despite their central ecological role, studies dealing with their distribution and diversity patterns in large river systems are insufficient.

Although many freshwater ecosystems have undergone declines in native diversity they have also experienced the introduction of many invasive species (Sousa *et al.*, 2014). The River Danube, one of the most important shipping routes in Europe, is a good example (Bódis *et al.*, 2012a). Some invasive mollusc species deserve special attention since they can dominate the benthic community in density and biomass triggering significant changes in the structure and functioning of freshwater ecosystems (Strayer *et al.*, 1999; Sousa *et al.*, 2009, 2011, 2014). In the Danube River Basin the Asian clam, *Corbicula fluminea* and the Chinese pond mussel, *Sinanodonta woodiana* became dominant in a short period of time and may impair the conservation of native molluscs (Bódis *et al.*, 2011, 2012a, b, 2014a, b).

If conservation priorities are to be set, and efficient conservation management plans put in place it is important to monitor the distribution and diversity of freshwater molluscs regularly and follow up the changes in the range and population size of threatened and invasive species. The River Danube is one of the most important freshwater ecosystems in Europe and should receive special attention. The main objectives of this work were to characterize the composition, diversity and conservation status of freshwater molluscs in the Hungarian Danube River Drainage, in five different habitat types (main channel of the rivers Danube and Tisza, side channels of the Danube, tributaries of the rivers Danube and Tisza) and to determine the principal environmental variables influencing the composition of the mollusc assemblages. This information may provide reference data to assess future changes to the molluscan assemblages and to guide the management measures that need to be applied to the conservation of key native species or problematic invasive species.

MATERIAL AND METHODS

Study area

The Danube is the longest river (2857 km) in Central Europe. It has a catchment area of

$817\,000\,km^2$ ($39\,000\,km^2$ in Hungary) and receives all of the running waters of Hungary in a length of 417 km. Its average annual discharge is approximately $2350\,m^3\,s^{-1}$ at Budapest (Tőry, 1952). The River Tisza is one of the main rivers in Central Europe, and has the largest catchment and length among the Danube tributaries. The Tisza drains an area of ~157 135 km² (47 000 km² in Hungary) and has a length of 966 km. With an average annual discharge of $820\,m^3\,s^{-1}$ at Szeged, its contribution to the Danube is about 13% (Alföldi and Schweitzer, 2003). The River Rába is a tributary of the Danube comprising a total basin area of 10 113 km², a length of 283 km and an average annual discharge of $27\,m^3\,s^{-1}$ at Győr. The River Ipoly is the largest tributary on the left side of the Hungarian Danube section with a length of 212 km, a catchment area of 5108 km² (143 km, 1518 km² in Hungary) and an average annual discharge of $21\,m^3\,s^{-1}$. The River Bodrog is a tributary of the River Tisza and has a length of 65 km (15 km in Slovakia, 50 km in Hungary). Its catchment area is 13 579 km² (972 km² in Hungary) and its average annual discharge is $115\,m^3\,s^{-1}$.

Three side channels connected with the Danube were also investigated. The Mosoni-Danube, the longest side channel with a length of 121.5 km in Hungary, is located in the wetland of Szigetköz. In general, the Szigetköz has a very high conservation value and is usually considered a pristine area. However, hydrological changes caused by the Gabcikovo hydropower plant have affected the faunal assemblages (Nosek *et al.* 2007; Bódis *et al.* 2008). The Ráckevei-(Soroksári)-Danube has a length of 57.3 km, and has a regulated water discharge through the Kvassay water-gate with anthropogenically disturbed habitats. The side channel at Göd is short, and during low water levels in the Danube (approximately 125 cm at Vác) its northern connection with the main channel is interrupted so that for 45% of the year the water flow ceases in the side channel.

Sampling methods

Sampling sites (35 in total) were located in the main channel of the River Danube (D1-6); in the side channels of the River Danube: Mosoni-Danube (MD1-3), Göd (SD1), Ráckevei-(Soroksári)-Danube (SD2-3); in the tributaries of the River Danube: River Rába (R1-3), River Ipoly (I1-8); in the main channel of the River Tisza (T1-6); and in the tributary of the River Tisza: River Bodrog (B1-6) (Figure 1). The sampling sites of the Danube were
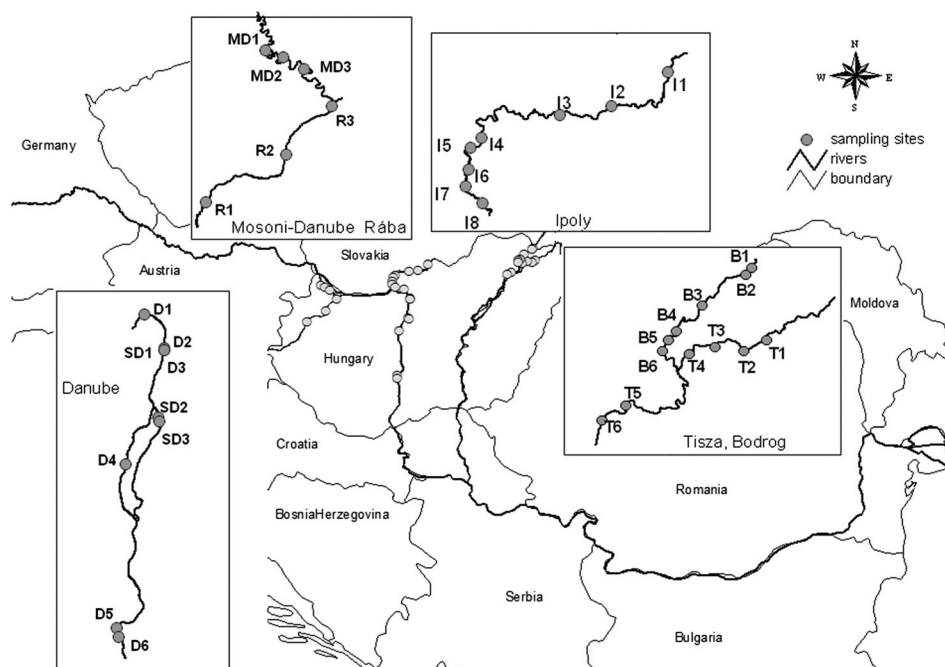

Figure 1. Map of sampling sites.

chosen based on previous studies (Bódis *et al.*, 2008; Nosek and Oertel, 2008) to represent both depositive and erosional parts of the main channel upstream and downstream to Budapest and the different types of side channels. The sampling sites in the tributaries were evenly distributed throughout the length of the rivers.

Quantitative samples of bottom sediment were collected in the main and side channels of the Danube seasonally in 2007 and 2008, and in the River Tisza and the tributaries (River Rába, River Ipoly, River Bodrog) in 2011 and 2012. A hand net was used, 25 cm wide and with a mesh size of 500 μm. At each sampling site four replicates with an area of 0.5 m^2 were taken randomly within a longitudinal section of 10–15 m. To assess the density of large unionids in the River Tisza and tributaries, where large populations were detected, 15 randomly placed 0.25 m^2 quadrats were searched visually in the littoral zone at a water depth of 1m. Samples were fixed *in situ* in 70% Patosolv solution and in the laboratory animals were identified and preserved in 70% ethanol. Nomenclature follows the Checklist of the European Continental Mollusca (Falkner *et al.*, 2001) and the catalogue of Fehér and Gubányi (2001) that reflects the Hungarian situation. Conservation status of species in Hungary was assigned with reference to the work of Fehér *et al.* (2006) and in Europe with reference to the IUCN Red List (IUCN, 2001) and the DAISIE database.

In the River Tisza and tributaries, where the substrate and water flow were relatively homogeneous, environmental variables were measured only from the water column (conductivity, pH, dissolved oxygen, chlorophyll-a, Ca, NO$_3$-N, NH$_4$-N, PO$_4$-P). In the main and side channels of the Danube, where the environment was heterogeneous in terms of substrate and water flow, included a diverse range of habitats, environmental variables were measured seasonally. Sediment samples were collected to assess granulometry using the following fractions of sediment: coarse (C, 2360 > 750 μm), fine (F, 750 > 250 μm), very fine (V, 250 > 63 μm) and ultra fine (U, 63 > 0.45 μm) and benthic organic matter (BOM) content of the sediment was measured according to the fractions of sediment (CBOM,

FBOM, VBOM, UBOM)). In the water column measurements were made of temperature, conductivity, redox potential, pH, dissolved oxygen, chlorophyll-a and current velocity. A detailed description of the methods and environmental parameters measured are presented in Bódis *et al.*, 2011, 2012b. In order to characterize the habitat types and compare the sampling sites the environmental data set of the National Inspectorate for Environment was used, which is based on monthly sampling.

Data analysis

One-way nonparametric multivariate analyses of variance (one-way NPMANOVA) were performed using the PAST program package (Hammer *et al.*, 2001) to test for differences in univariate measures (density, species richness and Shannon–Wiener diversity) of the mollusc assemblages among habitat types. Overall, differences in the associated assemblage structure were assessed using the habitat types as fixed factors (with five levels: main channel of River Danube, side channel of River Danube, tributary of River Danube, River Tisza, tributary of River Tisza), which included differences in individual species density. Before the one-way NPMANOVA analyses, all variables were normalized and a similarity matrix based on the Bray–Curtis coefficient was calculated. The NPMANOVAs were run among the five different levels using all species collected. *P*-values for the pseudo-*F* ratios were calculated by permutation of raw data through 9999 permutations. Pairwise comparisons were also performed when appropriate. In addition, a SIMilarity PERcentages procedure (SIMPER) was used to assess the species contributing most to similarities within communities defined by the five main habitat types. In order to establish correlations between biotic and environmental data BIOENV analysis was performed using the Spearman coefficient. BIOENV analysis was done separately with only water chemistry data for all sites, and both water chemistry and sediment data only for sites in the main and side channels of the Danube. SIMPER and BIOENV analyses were performed using PRIMER v5 (Clarke and Warwick, 2001).

To relate the species composition to environmental variables Redundancy Analysis (RDA) was performed using the software CaNOCO, version 4.5 (Ter Braak and Smilauer, 2002). Redundancy Analysis was done both for water chemistry and sediment characteristics in the main and side channels of the Danube. The length of the ordination gradient was tested by Detrended Correspondence Analysis (DCA). The gradient length of the DCA axis (tributaries: first axis: 2.773, 2. axis: 3.722, 3–4. axis: < 2; Danube: first axis: 2.857, 2–4. axis: < 2) suggested that the use of RDA is suitable for the data set. The most significant environmental variables were selected using the stepwise 'forward' selection procedure. An unrestricted random Monte Carlo permutation test was used to determine the significant abiotic effects and to verify the significance of the model.

RESULTS

In total 53 mollusc species and one bivalve variety (21 bivalves and 32 gastropods) were identified including 10 invasive species and 12 species of conservation concern (Table 1). Based on the cumulative species list, the five most widespread mollusc species were *Unio tumidus* (80%), *Pisidium amnicum* (74.3%), *Lithoglyphus naticoides* (74.3%), *Unio crassus* (71.4%), and *Pisidium henslowanum* (65.7%). On the basis of relative abundances (number of individuals of the given species/total number of individuals) the five most abundant mollusc species were *L. naticoides* (38.5%), *P. amnicum* (9.1%), *Pisidium subtruncatum* (6.9%), *Borysthenia naticina* (5.0%) and *Valvata piscinalis* (3.8%, Table 1).

The contribution of endangered and rare species to the total density was highest in the tributaries of the Danube and in the main channel of the Tisza (~30%), and it was lowest in the main channel of the Danube (less than 10%, Figure 2). The contribution of invasive species to the total density was highest in the main channel of the Danube and the Tisza (~20%), and it was lowest in the tributaries (less than 10%, Figure 2).

Overall composition of the mollusc assemblages showed significant differences between habitat types ($P < 0.0001$, F = 3.28). The density ($P < 0.01$, F = 3.91), number of species ($P < 0.0001$, F = 12.80) and Shannon–Wiener diversity ($P < 0.01$, F = 4.47) also showed significant differences between habitat types (Figure 3). In pairwise comparisons, the overall composition and the number of species in almost every habitat differed from each other (Table 2), whereas the differences in density were caused mainly by the low values detected in the main channel of the Tisza, and the differences in the Shannon–Wiener diversity were caused mainly by the high values detected in the side channel of the Danube (Table 2, Figure 3).

In the main channel of the Tisza the average density, species richness, and Shannon diversity were 23.6 ind. m^{-2}, 7.2, and 2.2, respectively. The assemblage was characterized by *U. crassus, U tumidus, Theodoxus fluviatilis, Unio pictorum, L. naticoides, Viviparus contectus* and *P. amnicum* (Table 3).

In the tributary of the River Tisza (River Bodrog) the average density, species richness and Shannon diversity were 121.2 ind. m^{-2}, 11.0 and 2.3, respectively. The assemblage was characterized by *L. naticoides, P. amnicum, U. tumidus, U. crassus, B. naticina, Haitia acuta, T. fluviatilis* and *U. pictorum* (Table 3).

In the side channels of the River Danube the average density, species richness, and Shannon diversity were 147.3 ind. m^{-2}, 26.2 and 5.4, respectively. The assemblage was mainly characterized by *P. subtruncatum, L. naticoides, P. henslowanum, Pisidium casertanum, Viviparus piscinalis, Bythinia tentaculata, P. amnicum, U. tumidus, Gyraulus albus* and *H. acuta* (Table 3).

In the tributaries of the River Danube (rivers Ipoly and Rába) the average density, species richness and Shannon diversity were 71.8 ind. m^{-2}, 10.9 and 2.9, respectively. The assemblage was characterized by *P. henslowanum, U. crassus, P. amnicum, Sphaerium corneum, P. nitidum, U. tumidus, U. pictorum, P. subtruncatum, Anodonta anatina, L. naticoides, Sphaerium rivicola* and *Pisidium supinum* (Table 3).

In the main channel of the Danube the average density, species richness and Shannon diversity were 300.8 ind. m^{-2}, 20.8 and 3.7, respectively.

Table 1. Conservation status, frequency of occurrence and relative abundance of recorded freshwater bivalves and gastropods in different habitat types

Species	Codes	Conservation status		Frequency of occurrence (%)						Relative abundance (%)					
		Hungary	Europe	All sites	Danube main channel	Danube side channels	Danube tributaries	Tisza main channel	Tisza tributaries	All sites	Danube main channel	Danube side channels	Danube tributaries	Tisza main channel	Tisza tributaries
Bivalvia															
Pseudanodonta complanata	Pco	E	VU	20.0	16.7	50.0	18.2	0.0	16.7	0.1	0.1	0.4	0.3	0.0	0.8
Unio crassus	Uc	E	EN	71.4	0.0	33.3	100.0	100.0	100.0	1.3	0.0	0.6	4.2	20.6	11.6
Pisidium amnicum	Pam	R	–	74.3	66.7	83.3	72.7	50.0	100.0	9.1	11.4	7.8	34.0	16.6	47.8
Sphaerium rivicola Sr	R	VU	34.3	50.0	33.3	36.4	33.3	16.7	0.8	3.2	1.0	1.0	16.6	1.0	0.0
Sphaerium solidum	Ss	R	NT	25.7	83.3	16.7	27.3	0.0	0.0	3.5	8.6	0.4	14.3	0.0	0.0
Anodonta anatina	Aa	F	LC	48.6	66.7	83.3	45.5	33.3	16.7	0.5	0.9	0.8	1.7	2.3	0.5
Musculium lacustre	Ml	F	LC	20.0	33.3	83.3	0.0	0.0	0.0	0.4	0.4	4.3	0.0	0.0	0.0
Pisidium casertanum	Pca	F	LC	34.3	50.0	100.0	27.3	0.0	0.0	0.6	0.2	4.8	0.9	0.0	0.0
Pisidium cas. var. ponderosum	Pcp	F	–	5.7	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Pisidium henslowanum	Ph	F	LC	65.7	100.0	100.0	90.9	0.0	16.7	3.6	6.2	9.4	11.5	0.0	2.0
Pisidium moitessierianum	Pm	F	–	40.0	33.3	66.7	36.4	0.0	66.7	0.8	5.2	2.0	0.4	0.0	5.1
Pisidium nitidum	Pn	F	–	37.1	33.3	66.7	63.6	0.0	0.0	1.8	0.7	3.5	7.6	0.0	0.0
Pisidium subtruncatum	Psb	F	LC	51.4	66.7	100.0	54.5	0.0	33.3	6.9	6.1	45.1	12.3	0.0	5.1
Pisidium supinum	Psp	F	LC	40.0	100.0	66.7	36.4	0.0	0.0	2.6	17.1	6.0	2.7	0.0	0.0
Sphaerium corneum	Sc	F	LC	40.0	50.0	66.7	63.6	0.0	0.0	0.7	0.5	1.9	2.5	0.0	0.0
Unio pictorum	Up	F	LC	62.9	33.3	66.7	63.6	83.3	66.7	0.8	0.2	1.5	2.7	8.8	3.2
Unio tumidus	Ut	F	LC	80.0	66.7	83.3	63.6	100.0	100.0	1.2	1.4	2.3	1.1	25.8	23.0
Corbicula fluminea	Cf	I	AW	40.0	100.0	66.7	18.2	33.3	0.0	3.7	28.4	5.3	2.4	7.5	0.0
Corbicula fluminalis	Cf2	I	–	5.7	33.3	0.0	0.0	0.0	0.0	0.5	5.8	0.0	0.0	0.0	0.0
Dreissena polymorpha	Dp	I	AW	22.9	83.3	50.0	0.0	0.0	0.0	0.2	0.4	1.9	0.0	0.0	0.0
Dreissena rostriformis bugensis	Db	I	–	2.9	16.7	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Sinanodonta woodiana	Sw	I	–	22.9	33.3	50.0	18.2	16.7	0.0	0.4	2.9	0.5	0.5	1.8	0.0
Gastropoda															
Anisus vorticulus	Av	E	NT	5.7	0.0	33.3	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0
Borysthenia naticina	Bn	E	LC	45.7	100.0	50.0	0.0	33.3	83.3	5.0	12.6	1.3	0.0	15.8	6.7
Esperiana daudebartii	Ed	E	LC	14.3	50.0	33.3	0.0	0.0	0.0	0.8	0.5	5.5	0.0	0.0	0.0
Esperiana esperi	Ee	E	LC	25.7	83.3	66.7	0.0	0.0	0.0	0.3	0.4	1.7	0.0	0.0	0.0
Theodoxus danubialis	Td	E	–	14.3	66.7	16.7	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Bathyomphalus contortus	Bc	R	LC	5.7	0.0	33.3	0.0	0.0	0.0	0.1	0.0	0.6	0.0	0.0	0.0
Physa fontinalis	Pf	R	LC	25.7	16.7	50.0	27.3	0.0	33.3	0.3	0.0	1.5	2.0	0.0	0.5
Acroloxus lacustris	Al	R/F	LC	11.4	0.0	66.7	0.0	0.0	0.0	1.7	0.0	13.4	0.0	0.0	0.0
Anisus spirorbis	As	R/F	–	11.4	0.0	0.0	9.1	33.3	16.7	0.1	0.0	0.0	0.7	1.4	0.1
Ancylus fluviatilis	Af	F	LC	17.1	50.0	33.3	9.1	0.0	0.0	0.1	0.2	0.3	0.7	0.0	0.0
Anisus vortex	Av	F	–	11.4	0.0	50.0	9.1	0.0	0.0	0.3	0.0	2.4	0.7	0.0	0.0
Bithynia tentaculata	Bt	F	LC	31.4	50.0	83.3	18.2	0.0	16.7	1.3	0.3	8.9	2.0	0.0	0.4
Galba truncatula	Gt	F	LC	20.0	16.7	16.7	27.3	0.0	33.3	0.2	0.0	0.1	4.7	0.0	0.2
Gyraulus albus	Ga	F	LC	25.7	16.7	83.3	27.3	0.0	0.0	1.0	0.0	7.5	2.0	0.0	0.0
Gyraulus crista	Gc	F	LC	2.9	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hippeutis complanatus	Hc	F	LC	8.6	0.0	50.0	0.0	0.0	0.0	0.2	0.0	1.4	0.0	0.0	0.6
Lymnea stagnalis	Ls	F	–	14.3	33.3	33.3	0.0	0.0	16.7	0.2	0.1	0.3	0.0	0.0	0.6
Lythoglyphus naticoides	Ln	F	LC	74.3	100.0	100.0	45.5	50.0	100.0	38.5	75.5	16.1	74.0	54.8	83.0
Planorbarius corneus	Pc	F	LC	8.6	0.0	0.0	0.0	16.7	33.3	0.1	0.0	0.0	0.0	0.7	0.2
Radix auricularia	Ra	F	LC	5.7	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0

(Continues)

Table 1. (Continued)

Species	Conservation status			Frequency of occurrence (%)						Relative abundance (%)					
	Codes	Hungary	Europe	All sites	Danube main channel	Danube side channels	Danube tributaries	Tisza main channel	Tisza tributaries	All sites	Danube main channel	Danube side channels	Danube tributaries	Tisza main channel	Tisza tributaries
Radix labiata	Rl	F	–	22.9	66.7	33.3	18.2	0.0	0.0	0.2	0.2	0.3	2.0	0.0	0.0
Radix balthica	Rb	F	LC	11.4	33.3	33.3	0.0	0.0	0.0	0.1	0.1	0.5	0.0	0.0	0.0
Segmentina nitida	Sn	F	–	8.6	0.0	0.0	27.3	0.0	0.0	0.1	0.0	0.0	2.7	0.0	0.0
Valvata cristata	Vc	F	LC	2.9	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Valvata piscinalis	Vp	F	LC	22.9	16.7	83.3	9.1	0.0	16.7	3.8	0.1	28.2	3.3	0.0	0.2
Viviparus acerosus	Va	F	LC	25.7	50.0	50.0	9.1	0.0	33.3	1.7	4.2	1.7	3.3	0.0	1.6
Viviparus contectus	Vc	F	LC	22.9	0.0	16.7	9.1	50.0	50.0	0.5	0.0	0.1	1.3	8.9	1.3
Ferrissia wautieri	Fw	I	–	2.9	0.0	16.7	0.0	33.3	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Haitia acuta	Ha	I	–	34.3	16.7	83.3	0.0	0.0	66.7	0.8	0.2	2.6	0.0	2.1	2.4
Melanoides tuberculatus	Mt	I	–	2.9	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Potamopyrgus antipodarum	Pa	I	–	31.4	100.0	83.3	0.0	0.0	0.0	0.6	0.4	3.9	0.0	0.0	0.0
Theodoxus fluviatilis	Tf	I	–	48.6	100.0	50.0	0.0	66.7	66.7	2.3	5.2	0.4	0.0	16.4	2.6

E – endangered, R – rare, F – frequent; I – invasive, AW – among the 100 worst invasive species in Europe, EN – endangered, VU – vulnerable, NT – near threatened, LC – least concern.
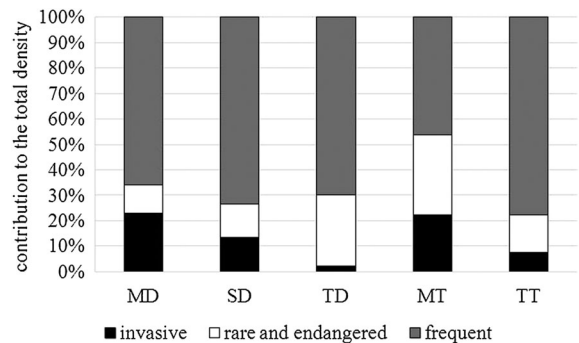Conservation status in Europe was assigned according to the IUCN Red List categories (IUCN, 2001).

Figure 2. Percentage contribution of invasive, rare and frequent species to the total density according to habitat types (MD - Danube main channel, SD - Danube side channels, TD - Danube tributaries, MT - Tisza main channel, TT - Tisza tributaries).

The assemblage was mainly characterized by *L. naticoides*, *C. fluminea*, *T. fluviatilis*, *B. tentaculata*, *P. supinum*, *P. henslowanum*, *Sphaerium solidum*, *Potamopyrgus antipodarum*, *Dreissena polymorpha* and *Esperiana esperi* (Table 3).

Significant differences in environmental parameters were not detected between the habitat types, but the highest conductivity, PO_4-P, NH_4-N, and NO_3-N content were observed in the tributaries of the Danube, the calcium content in the Tisza was half that of the Danube, and the pH and chlorophyll content was lowest in the tributary of the River Tisza (Table 4).

The BIOENV analysis based on the environmental variables measured only in the water column showed that the strongest explanatory factors with the highest correlation values were the NO_3-N, NH_4-N, oxygen and calcium content. On the other hand, on the basis of environmental variables measured both in the water column and in the sediment the strongest explanatory factors were the sedimenthological characteristics (coarse fraction of sediment, organic matter content of coarse and very fine fractions), the current velocity and the oxygen content (Table 5).

Based on the redundancy analyses (RDA) four of 17 environmental variables (coarse and fine fractions of sediment, organic matter content of ultra fine fraction and current velocity) were found to have a significant influence on the composition of the mollusc assemblages (Table 6, Figure 4). For the first and second axis the eigenvalues, the species–environment correlation,
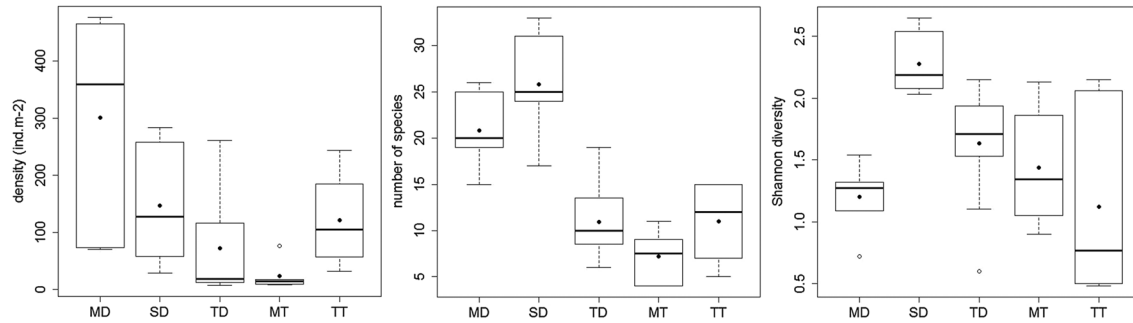
Figure 3. Density, number of species and Shannon diversity of molluscs according to habitat types (MD - Danube main channel, SD - Danube side channels, TD - Danube tributaries, MT - Tisza main channel, TT - Tisza tributaries).

Table 2. Pairwise comparisons of overall structure, density, number of species and Shannon diversity of mollusc assemblages in the Hungarian Danube River Drainage among habitat types (MD - Danube main channel, SD - Danube side channels, TD - Danube tributaries, MT - Tisza main channel, TT - Tisza tributaries). Only significant differences are shown

	Overall structure	Density	Number of species	Shannon diversity
	$P < 0.001$	$P < 0.01$	$P < 0.0001$	$P < 0.01$
MD-SD	$P < 0.01$	–	–	$P < 0.01$
MD-TD	$P < 0.001$	$P < 0.05$	$P < 0.001$	–
MD-MT	$P < 0.01$	$P < 0.01$	$P < 0.01$	–
MD-TT	–	–	$P < 0.01$	–
SD-TD	$P < 0.05$	–	$P < 0.001$	$P < 0.01$
SD-MT	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
SD-TT	$P < 0.01$	–	$P < 0.01$	$P < 0.01$
TD-MT	$P < 0.01$	–	$P < 0.05$	–
TD-TT	$P < 0.001$	–	–	–
MT-TT	$P < 0.05$	$P < 0.01$	–	–

the cumulative percentage variance of species data and the cumulative percentage variance of the species–environment relationship were 0.925 and 0.017; 0.993 and 0.884; 92.50 and 94.20; 97.00 and 98.80, respectively. Eigenvalues of RDA axes were significant when tested with Monte Carlo permutations ($P < 0.05$). The first axis reflects the distribution of species in response to the sediment characteristics and organic matter content, while the second axis indicates the current velocity. The species located at the positive end of axis 1 (*P. amnicum*, *Pisidium moitessierianum*, *P. henslowanum*, *S. rivicola*, *S. solidum*, *L. naticoides*, *B. naticina*, *Theodoxus danubialis* and *Radix balthica*) preferred the ultrafine sediment fraction with high organic matter content. The species located towards the positive end of axis 2 (*D. polymorpha*, *Dreissena bugensis*, *Ferrissia wauteri*, *Ancylus fluviatilis*, *E. esperi*, *Esperiana daudebartii*, *Galba truncatula*, *C. fluminea* and *P. supinum*) were present preferentially in sites with high current velocity.

DISCUSSION

This study confirms the presence of diverse freshwater mollusc assemblages in the Hungarian Danube River Drainage and significant differences were detected among the distinct river habitat types. The highest di versity values were found in the side channels of the Danube, whereas the highest proportion of threatened species that contributed to the total density was observed in the tributaries of the Danube and Tisza. These results show that the low water flow, or almost lentic environment with a rich macrophyte community in side channels, provide an ideal habitat for high mollusc species richness and diversity. At the same time, invasive species are already present in the side channels and thus only the tributaries can provide effective refuge for threatened species.

Taking into consideration the relationship between freshwater mollusc species and environmental variables in a heterogeneous environment, which is characterized

Table 3. Average similarities for the mollusc groups defined by habitat types (MD - Danube main channel, SD - Danube side channels, TD - Danube tributaries, MT - Tisza main channel, TT - Tisza tributaries). Only species that altogether contribute with more than 90% total similarity are included

	MT	TT	TD	SD	MD
Unio crassus	28.81	11.61	15.22	–	–
Unio tumidus	25.30	12.46	5.75	4.32	2.05
Theodoxus fluviatilis	13.03	4.77	–	–	10.29
Unio pictorum	8.30	4.12	5.55	1.67	–
Lithoglyphus naticoides	6.04	27.83	4.16	9.42	19.56
Viviparus contectus	5.70	–	–	–	–
Pisidium amnicum	3.70	16.23	9.50	4.34	3.07
Borysthenia naticina	–	9.28	–	–	9.64
Haitia acuta	–	4.83	–	3.69	–
Pisidium henslowanum	–	–	18.69	7.82	5.31
Sphaerium corneum	–	–	8.74	1.80	–
Pisidium nitidum	–	–	8.41	2.54	–
Pisidium subtruncatum	–	–	5.49	10.27	2.95
Anodonta anatina	–	–	4.95	3.24	–
Sphaerium rivicola	–	–	2.11	–	–
Pisidium supinum	–	–	2.05	3.16	5.70
Pisidium casertanum	–	–	–	6.56	–
Valvata piscinalis	–	–	–	6.02	–
Bithynia tentaculata	–	–	–	5.32	–
Gyraulus albus	–	–	–	3.78	–
Musculium lacustre	–	–	–	3.54	–
Potamopyrgus antipodarum	–	–	–	3.03	4.03
Acroloxus lacustris	–	–	–	2.94	–
Corbicula fluminea	–	–	–	2.29	10.43
Pisidium moitessierianum	–	–	–	1.82	–
Esperiana esperi	–	–	–	1.34	3.39
Anisus vortex	–	–	–	1.26	–
Sphaerium solidum	–	–	–	–	4.80
Dreissena polymorpha	–	–	–	–	3.43
Theodoxus danubialis	–	–	–	–	2.03
Radix labiata	–	–	–	–	1.69
Viviparus acerosus	–	–	–	–	1.67

Table 5. Combination of environmental variables giving the highest correlations (Spearman rank correlation) between biotic and environmental matrices using BIOENV analysis

Environmental variables	Correlation
Water chemistry	
NH_4-N, NO_3-N	0.439
NO_3-N	0.434
O_2, NO_3-N, Ca	0.371
O_2, NH_4-N, NO_3-N, Ca	0.358
O_2, Ca	0.341
Water chemistry and sediment characteristics	
CBOM, VBOM	0.462
CBOM, VBOM, O_2	0.451
CBOM, VBOM, velocity	0.447
CBOM, VBOM, velocity, O_2	0.443
CBOM, VBOM, C	0.440

CBOM – coarse benthic organic matter.
VBOM – very fine benthic organic matter

et al., 2005, 2007; Eedy and Giberson, 2007; Gangloff and Feminella, 2007; Miserendino, 2009; Pérez-Quintero, 2012; Jurkiewicz-Karnkowska and Karnkowski, 2013). In addition, other environmental factors such as NO_3-N, NH_4-N, oxygen and calcium content of the water column were also important for determining the mollusc composition in this study. These results are consistent with several studies, which revealed that the high nitrate–nitrogen content exerts a negative impact on mollusc species richness and diversity, whereas the high oxygen and calcium content are essential for diverse and rich mollusc assemblages (Horsák and Hájek, 2003; Douda, 2007, 2009; Jurkiewicz-Karnkowska and Karnkowski, 2013). The majority of mollusc species preferred the low current velocity and sediments rich in organic matter, but some species are adapted to high water flow and coarse sediment fractions. In general, the successful invasive species (*C. fluminea*, *D. polymorpha*, *D. bugensis* and *T. fluviatilis*) can

by variable substrate types and water flow conditions, that the main determining factors are the fractions and organic matter content of sediment, and the current velocity. These results are in accordance with previous studies, which showed that the habitat structure, heterogeneity and complexity are the most important factors affecting the composition of the mollusc assemblages (Sousa

Table 4. Average ($\pm$SD) values of environmental variables of the water column according to habitat types (MD - Danube main channel, SD - Danube side channels, TD - Danube tributaries, MT - Tisza main channel, TT - Tisza tributaries)

	MD	SD	TD	MT	TT
Conductivity (μS cm^{-1})	390.9 $\pm$ 45.6	400.6 $\pm$ 67.6	526.9 $\pm$ 142.4	406.6 $\pm$ 101.5	358.4 $\pm$ 74.5
pH	8.3 $\pm$ 0.2	8.1 $\pm$ 0.1	7.7 $\pm$ 0.2	8.3 $\pm$ 0.3	5.8 $\pm$ 0.2
O_2(%)	87.4 $\pm$ 15.5	87.1 $\pm$ 14.0	79.6 $\pm$ 20.5	88.5 $\pm$ 16.3	82.2 $\pm$ 17.2
Ca^{2+}(mg L^{-1})	47.3 $\pm$ 5.0	45.6 $\pm$ .0.3	52.6 $\pm$ 7.8	24.3 $\pm$ 1.9	24.0 $\pm$ 0.7
PO_4-P (μg L^{-1})	47.6 $\pm$ 27.7	16.8 $\pm$ 7.0	105.4 $\pm$ 116.5	25.4 $\pm$ 23.4	73.2 $\pm$ 31.7
NO_3-N (mg L^{-1})	1.85 $\pm$ 0.59	1.77 $\pm$ 0.72	2.43 $\pm$ 1.17	0.94 $\pm$ 0.42	1.16 $\pm$ 0.32
NH_4-N (mg L^{-1})	0.04 $\pm$ 0.03	0.06 $\pm$ 0.03	0.20 $\pm$ 0.31	0.13 $\pm$ 0.10	0.17 $\pm$ 0.18
chl-a (μg L^{-1})	17.5 $\pm$ 20.1	15.8 $\pm$ 13.9	7.1 $\pm$ 14.1	8.4 $\pm$ 17.2	3.5 $\pm$ 2.7

Table 6. Significant environmental variables defined by a Monte Carlo permutation test (999 permutations) in a forward selection procedure

Environmental variable	Code	Variance (%)	Cumulative variance	P-value	F-value
coarse benthic organic matter	C	43.4	0.434	0.032	5.358
velocity	velo	37.2	0.806	0.008	11.508
fine benthic organic matter	F	9.4	0.900	0.024	4.672
ultra fine benthic organic matter	UBOM	1.2	0.954	0.012	4.646
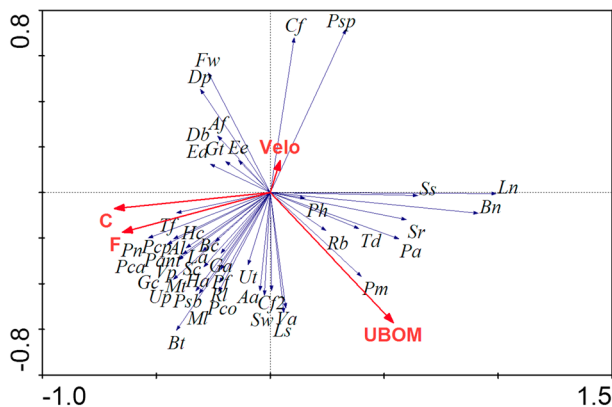
Figure 4. Redundancy analysis (RDA) of mollusc species, environmental variables and sampling sites. For codes of species see Table 1. For codes of environmental variables: see Table 6.

colonize habitats with variable conditions owing to their wider ecological tolerance and special adaptive abilities, whereas threatened species prefer less disturbed habitats because of their narrower ecological tolerance and sensitivity to human activites.

Although several of the species recorded are seriously threatened in Europe, only their distributions have been studied thoroughly (Varga and Csányi, 1997; Varga et al., 1998–1999; Varga and Uherkovich, 2002; Juhász et al., 2004, 2009; Bódis, 2008; Kovács et al., 2011, Horvai et al., 2012). Indeed, there is a general lack of data concerning basic ecological characteristics such as density, biomass and biotic and abiotic requirements for each species and the Hungarian Danube River Drainage is no exception. This kind of information is also lacking worldwide (Jones and Byrne, 2014; Lopes-Lima et al., 2014) although it should be the basis of effective conservation efforts.

The depressed river mussel (Pseudanodonta complanata) and the thick-shelled river mussel (U. crassus) are threatened and classified as 'Vulnerable' and 'Endangered', respectively, by the IUCN Red List (IUCN, 2014). These species are also protected by national legislation in Hungary. Furthermore, U. crassus is listed in the Habitats Directive of the European Union (Annexes II and IV). A high density of U. crassus was recorded in the River Tisza and in the tributaries studied (for example in the River Ipoly–17.9 ind. m^{-2}), but in the Danube this species had almost disappeared (recently only a few individuals have been found sporadically; Bódis, personal observation). Pseudanodonta complanata is found to be threatened in the Hungarian Danube River Drainage, since only a few individuals were detected in the water systems studied. Sphaerium rivicola and S. solidum are classified in the IUCN Red List as 'Vulnerable' and 'Near Threatened', respectively (IUCN, 2014). However, in the present study they were relatively frequent and S. solidum had high densities at certain sites. Anisus vorticulus has been listed in the EC Habitats Directive since 2004 (Annexes II and IV) and has been classified as 'Near Threatened' in the latest European assessment (IUCN, 2014). However, there is a lack of information across the eastern extent of its distribution and in the rivers studied only a few individuals were recorded in the Mosoni-Danube.

In addition to the species already mentioned, others are endangered in Hungary and protected by national legislation. Among these, E. daudebartii, E. esperi and T. danubialis were recorded only in the main and side channel of the Danube. Among species registered as rare in Hungary Bathyomphalus contortus occurred only in the side channel of the Danube, always with low density. However, other endangered (B. naticina) or rare species (P. aminicum, Physa fontinalis) still have some large populations, mainly in tributaries. Although some species important for

conservation, such as *Theodoxus transversalis* and *Valvata macrostoma*, were not recorded during this study, their presence in the Hungarian Danube River Drainage has been noted previously (Pintér and Suara, 2004; Kovács *et al*., 2011; Fehér *et al*., 2012).

Freshwater molluscs are threatened by human and climatic disturbances such as habitat loss, degradation and fragmentation, pollution, overexploitation, introduction of invasive species, droughts, and floods. The outcomes of these disturbances are responsible for alterations to channel characteristics, sedimentation processes, chemical composition, flow regime, habitat availability, and temperature and may modify important biotic interactions, which all have serious consequences for freshwater biota (Allan and Flecker, 1993; Mueller *et al*., 2011). In addition, these changes can affect fish species that serve as host organisms and vectors for the dispersal of freshwater mussels (Geist and Kuehn, 2005). The above-mentioned perturbations have a significant adverse effect both on bivalves (Layzer *et al*., 1993; Williams *et al*., 1993; Vaughn and Taylor, 1999; Aldridge, 2000; Poole and Downing, 2004; Newton *et al*., 2008; Babko and Kuzmina, 2009) and gastropods (Bogan, 2006; Tolley-Jordan *et al*., 2015) worldwide, and the Hungarian Danube River Drainage is no exception.

The rapid spread of invasive species is another threat to native molluscs and in the long term may contribute to the homogenization of the mollusc assemblages present in the Hungarian Danube River Drainage. The highest occurrence and density of invasive mollusc species were detected in the main channel of the Danube. Some of the invasive species recorded have already spread to the side channels and the adjacent wetland areas (Bódis *et al*., 2008), but most of them were not present in the tributaries surveyed. In the smaller rivers invasive species are restricted to areas close to the confluence with the rivers Danube and Tisza. However, *C. fluminea* and *S. woodiana* extended their range rapidly along the larger tributaries of the Danube in Bulgaria and the average dispersal rate of *C. fluminea* in the upstream direction was estimated to range between 5 and 8 km per year (Hubenov *et al*.,

2013). Some human activities such as fishing, fish stocking, recreational activities, and sand and gravel extraction may facilitate the establishment and spread of invasive species, and these activities deserve special attention. For example, a small population of *S. woodiana* was found in the River Ipoly, far from the confluence with the Danube, probably because of fish stocking activities. In addition, warm-water effluents can contribute to the aggregation of an extremely large biomass of thermophilic species, and serve as a thermal refuge for invasive species native to a warm climate and as a source of individuals for adjacent areas (Gollasch and Nehring, 2006; Galil *et al*., 2007). An extremely high density of *C. fluminea*, *C. fluminalis* and *S. woodiana* was observed at the outlet of the cooling water channel of Paks Nuclear Power Plant, which is an artificially modified habitat with water temperatures consistently 4–8 °C higher than adjacent non-disturbed areas (Bódis *et al*., 2011).

Some of the invasive species, such as *C. fluminea*, *S. woodiana* and *T. fluviatilis* were widespread and abundant throughout the Hungarian Danube and Tisza and they may have adverse impacts on native fauna. For example, *C. fluminea* may compete with native bivalves owing to its high filtration ability (Strayer *et al*., 1999). At those sites in the River Danube where it attained high densities (736 ind. m^{-2}), the population of rare species (*S. rivicola* and *P. amnicum*) declined or disappeared (Bódis *et al*., 2011, 2012b). *Theodoxus fluviatilis*, which is abundant in the main channel of the Danube, may also have a negative impact on native *Theodoxus* species (*T. danubialis* and *T. transversalis*), since these species have become very rare or have almost completely disappeared in the Danube (Fehér *et al*., 2012; Pavlova *et al*., 2013). *Sinanodonta woodiana* is a broad host generalist; its parasitic larval glochidia can develop both on native and invasive fish hosts in contrast to the native unionids, which are considered to have a limited number of host fish species (Douda *et al*., 2012a, b). Therefore, *S. woodiana* may decrease the chances for native unionids to find appropriate host organisms. Overall, the River Danube is an important invasion corridor contributing to the rapid spread of invasive species (Bódis *et al*.,

2012a), which may adversely affect several native mollusc species. However, most of these negative impacts are still speculative and further studies are needed to assess their real effects on native molluscs.

In conclusion, in the main channel of the Danube the presence of invasive species is high, while the occurrence of threatened native species is very low. In the side channels and the River Tisza the proportion of invasive and threatened native species is similar, but in future this ratio may shift towards invasive species, which may result in biodiversity loss and homogenization of the mollusc assemblages. Fortunately in the tributaries and some parts of the wetland areas the mollusc assemblages are still unharmed and several endangered species (for example *U. crassus* and *T. transversalis*) can still find suitable conditions (Juhász *et al.*, 2009; Kovács *et al.*, 2011; Fehér *et al.*, 2012). Although species richness and diversity was highest in side channels, the proportion of threatened species was highest in tributaries. Tributaries may provide valuable habitats for threatened species and could be considered as 'source' populations that are critically important in the regional maintenance of threatened species. Based on some studies, the number of 'source' populations in a given area is a more relevant ecological criterion than species richness in the assessment of conservation value (Angermeier and Winston, 1997; Jurkiewicz-Karnkowska and Karnkowski, 2013). Consequently the protection and risk assessment of catchments connected with the River Danube are especially important and deserve conservation attention.

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