

Biotic Typology of the Danube River Based on Distribution of Mollusc Fauna as Revealed by the Second Joint Danube Survey (2007)

Jelena Tomović¹, Momir Paunović¹, Ana Atanacković¹, Vanja Marković¹, Zoran Gačić², Bela Csányi³, Vladica Simić⁴

¹Institute for Biological Research 'Siniša Stanković', University of Belgrade, 11000 Belgrade, Serbia; E-mail: simic@kg.ac.rs

²Institute for Multidisciplinary Research, University of Belgrade, 11060 Belgrade, Serbia

³Danube Research Institute, Centre for Ecological Research, MTA (Hungarian Academy Of Sciences), Göd, H-2131, Hungary

⁴Institute of Biology and Ecology, Faculty of Science, University of Kragujevac, 34000 Kragujevac, Serbia

Abstract: The aim of this study is to present the distribution of aquatic molluscs along a 2600 km long stretch of the Danube River based on information obtained during the Second Joint Danube Survey (JDS2) in 2007. The collected data are used to validate the abiotic typology of the Danube River and to determine the extent of variations in mollusc richness and composition that can be explained by the basic habitat characteristics of the sites. The examination of the distribution of mollusc fauna reveals differences between the three main sectors of the river, the Upper, Middle and Lower Danube. The Iron Gate Section was identified as the boundary between the Middle and Lower Danube. A total of 42 aquatic mollusc species-group taxa of 14 families are detected within the study area. The Middle and Upper sectors are characterised by higher species richness and diversity as compared to the Lower Danube.

Keywords: Aquatic molluscs, river section type, Danube River

Introduction

The aim of the present study is to divide the Danube River into sectors as a framework for the identification of water bodies, the main sub-objects of the water management as stated in the requirements of the EU Water Framework Directive (WFD 2000), based on the distribution of mollusc fauna.

A series of localities was sampled along the entire length of the Danube River during the Second Joint Danube Survey (JDS 2) in 2007. The Survey provided comparable data on the composition of mollusc fauna of this complex river system. This fact illustrates the necessity for an effective sectioning (typology) that should reflect the natural state in order to define efficacious management. Namely, the WFD (2000) requires the design of specific monitoring and assessment system, which implies necessity of using specific metrics and threshold values for

each water type/ group of types, in order to assess properly the ecological status.

The main characteristics of the Danube River Basin are presented in LÁSZLÓFFY (1965), LITERÁTHY *et al.* (2002), ROBERT *et al.* (2003), and TUBIĆ *et al.* (2013). The Danube River is the second largest European river (length of 2857 km and catchments size of 801 463 km²) and more than 80 million people, residing in 19 countries, share the Danube River catchment area, making it the world's most international river basin.

Until the end of the 19th century, the Danube River possessed a natural dynamics, exhibiting a huge capacity for self-purification and constant changes of its course (TUBIĆ *et al.* 2013). The steady degradation of the Danube's environment has destroyed over 80% of its wetlands, floodplains and floodplain forests (TUBIĆ *et al.* 2013) and consequently much of its biodiversity.

A precise typology has been considered by the Water Framework Directive (WFD 2000) to be an important aspect of effective water management and monitoring of the ecological status.

Based on the catchment geology, described by several authors (LÁSZLÓFFY 1965, LITERÁTHY *et al.* 2002, ROBERT *et al.* 2003), the Danube River can be divided into three sub-regions: the Upper, Middle and Lower Danube.

The Upper Basin, which has an area of 132,000 km², extends from the source tributaries in the Black Forest (Germany) to the Devin Gate (Slovak Republic). The Middle Basin, with an area of 445,000 km², is the largest sub-region. It includes the part from the Devin Gate (Slovakia/ Austria) to the Iron Gate Dams (Serbia/ Romania). The Lower Danube Basin, with an area of 241,000 km², extends from the Iron Gate to Sulina (the Black Sea Mouth of the Danube River) and includes the very large river delta.

A division based on the river slope has generated six sections (LÁSZLÓFFY 1965). Nine distinct reaches have been characterised considering specific geomorphological landscape features, as well as anthropogenic impacts (LITERÁTHY *et al.* 2002), while ROBERT *et al.* (2003) have divided the Danube River into ten section types.

Molluscs constitute one of the largest invertebrate phyla with regard to the number of identified species and relative abundance, especially in large lowland rivers (JAKOVČEV 1987, 1988, ARAMBAŠIĆ 1994, SIMIĆ *et al.* 1997, SIMIĆ, SIMIĆ 2004, GOMES *et al.* 2004, PAUNOVIĆ *et al.* 2005, 2007a, TUBIĆ *et al.* 2013). The Gastropoda and Bivalvia are best represented in benthic systems and the species belonging to these classes have been used to characterise benthic associations (DIAZ, PUYANA 1994).

While several studies have been carried out on the benthic communities of the Danube River basin, the spatial patterns displayed by benthic communities and identification of the factors responsible for the observed patterns have not been investigated fully (SIMIĆ *et al.* 1997, MOOG 2002, SIMIĆ, SIMIĆ 2004, LORENZ, HERING 2004, PAUNOVIĆ *et al.* 2005, 2007a, TOMOVIĆ *et al.* 2010, BÓDIS *et al.* 2011, TUBIĆ *et al.* 2013).

Considering the actual stretch that was covered by the present investigation, the results of this study should contribute to a more accurate sectioning of a large lowland river such as the Danube River.

Material and Methods

Study area and sampling

Sampling was performed at 96 sites along 2600 km of the Danube River (Table 1, Fig. 1) from

13 August to 26 September 2007. Out of the total number of sites, 24 sampling points were positioned in the mouth section of the main tributaries or side arms. The samples were collected by a hand net with mesh size of 500 µm (EN 27828:1994), benthological dredge, scratching from hard substrates, and by free diving (up to a depth of 5 m).

The essential habitat characteristics of the sites: type of river channel, the level of hydromorphological degradation, the predominant substrate, habitat diversity, and the data about surface flow velocity were collected during the survey (LIŠKA *et al.* 2008).

Data analysis

The basic community characteristics (saprobic condition, current preference, preference to bottom substrate type, general river zonation and feeding types) were calculated using Asterics software (AQEM 2002). The autecological data were taken from AQEM (2002) and NESEMANN, REISCHÜTZ (2002a,b).

In order to analyse the differences between the sites and sections, frequency analyses for each species were performed. The following scale was used to evaluate constancy: $F_1=0-0.25$ – accidental species; $F_1=0.25-0.50$ – accessory taxa; $F_1=0.50-0.75$ – constant; and $F_1=0.75-1$ – euconstant.

The Correspondence Analysis (PIELOU 1984) was performed in order to analyse the mollusc distribution. The software package Statistica 6 for Windows was used for statistical processing of the data and graphic visualisation. To downweight large numbers and ensure normal distributed values, the statistical analysis was performed on transformed logarithmic individual abundance values. Adding the number 1 was performed before transformation of the abundance values on each number.

The basic abiotic typology of the Danube River served as a framework for the analyses (ROBERT *et al.* 2003). The typology of the Danube River according to ROBERT *et al.* (2003) comprises ten sections: Upper course of the Danube, Western Alpine Foothills Danube, Eastern Alpine Foothills Danube, Lower Alpine Foothills Danube, Hungarian Danube Bend, Pannonian Plain Danube, Iron Gate Danube, Western Pontic Danube, Eastern Wallachian Danube and Danube Delta. The aim was to validate this division of the river into ten section types, based on the distribution of molluscs which served as a parameter that could provide more precise sectioning of the Danube River.

Results

During our investigation, molluscs were found to be one of the principal components of the macroinver-

Table 1. Sampling sites along the Danube River studied by the Second Joint Danube Survey (JDS2), 2007

JDS2	Site	rkm	JDS2	Site	rkm
1	Upstream Iller	2600	49	Tisa (rkm 1.0)	1215
2	Kelheim – gauging station	2415	50	Downstream Tisa/ Upstream Sava (Belegis)	1200
3	Geisling Power Plant	2354	51	Sava (rkm 7.0)	1170
4	Deggendorf	2285	52	Upstream Pancevo/ Downstream Sava	1159
5	Niederalteich	2278	53	Downstream Pancevo	1151
6	Inn, rkm 4.2	2225	54	Grocka	1132
7	Jochenstein	2204	55	Upstream Velika Morava	1107
8	Upstream dam Abwinden-Asten	2120	56	Velika Morava	1103
9	Upstream dam Ybbs-Persenbeug	2061	57	Downstream Velika Morava	1097
10	Oberloiben	2008	58	Starapalanka – Ram	1077
11	Upstream dam Greifenstein	1950	59	Banatska Palanka/ Bazias	1071
12	Klosterneuburg	1942	60	Irongate Reservoir (Golubac/ Koronin)	1040
13	Wildungsmauer	1895	61	Donji Milanovac	991
14	Upstream Morava (Hainburg)	1881	62	Irongate Reservoir (Tekija/ Orsova)	954
15	Morava (rkm 0.08)	1880	63	Vrbica/ Simijan	926
16	Bratislava	1869	64	Iron Gate II	865
17	Gabčikovo Reservoir	1852	65	Upstream Timok (Rudujevac/ Gruia)	849
18	Medvedov/ Medve	1806	66	Timok (rkm 0.2)	845
19	Moson Danube Arm – end (rkm 0.1)	1794	67	Pristol/ Novo Selo Harbour	834
20	Komarno/ Komarom	1768	68	Calafat	795
21	Vah (rkm 0.8)	1766	69	Downstream Kozloduy	685
22	Iza/ Szony	1761	70	Upstream Iskar (Bajkal)	640
23	Sturovo/ Esztergom	1719	71	Iskar (rkm 0.3)	637
24	Hron (rkm 0.5)	1716	72	Downstream Iskar	629
25	Ipoly (rkm 0.7)	1708	73	Upstream Olt	606
26	Szob	1707	74	Olt (rkm 0.4)	605
27	Upstream end of Szentendre Island	1692	75	Downstream Olt	602
28	Upstream end of Szentendre Island (arm)	1692	76	Downstream Turnu-Magurele/ Nikopol	579
29	Budapest upstream	1659	77	Downstream Zimnicea/ Svishtov	550
30	Budapest (old Danube) end of S.arm	1658	78	Yantra (rkm 1.0)	537
31	Rackeve-Soroksar Danube Arm - start	1642	79	Downstream Yantra	532
32	Budapest downstream	1632	80	Upstream Ruse	500
33	Adony/ Lórév	1605	81	Russenski Lom	498
34	Rackeve-Soroksar Danube Arm - end	1586	82	Downstream Ruse/ Giurgiu	488
35	Dunafoldvar	1560	83	Upstream Arges	434
36	Paks	1533	84	Arges	432
37	Sio (rkm 1.0)	1497	85	Downstream Arges, Oltenita	429
38	Baja	1481	86	Chiciu/ Silistra	378
39	Hercegszanto	1434	87	Upstream Cernavoda	295
40	Batina	1424	88	Giurgeni	235
41	Upstream Drava	1384	89	Braila	167
42	Drava (rkm 1.4)	1379	90	Siret (rkm 1.0)	154
43	Downstream Drava (Erdut/ Bogojevo)	1367	91	Prut (rkm 1.0)	135
44	Dalj	1355	92	Reni	130
45	Ilok/ Backa Palanka	1300	93	Vilkova - Chilia arm/ Kilia arm	18
46	Upstream Novi-Sad	1262	94	Bystroe canal (to be confirmed)	8
47	Downstream Novi-Sad	1252	95	Sulina - Sulina arm	0
48	Upstream Tisa (Stari Slankamen)	1216	96	Sf. Gheorghe - Sf. Gheorghe arm	0

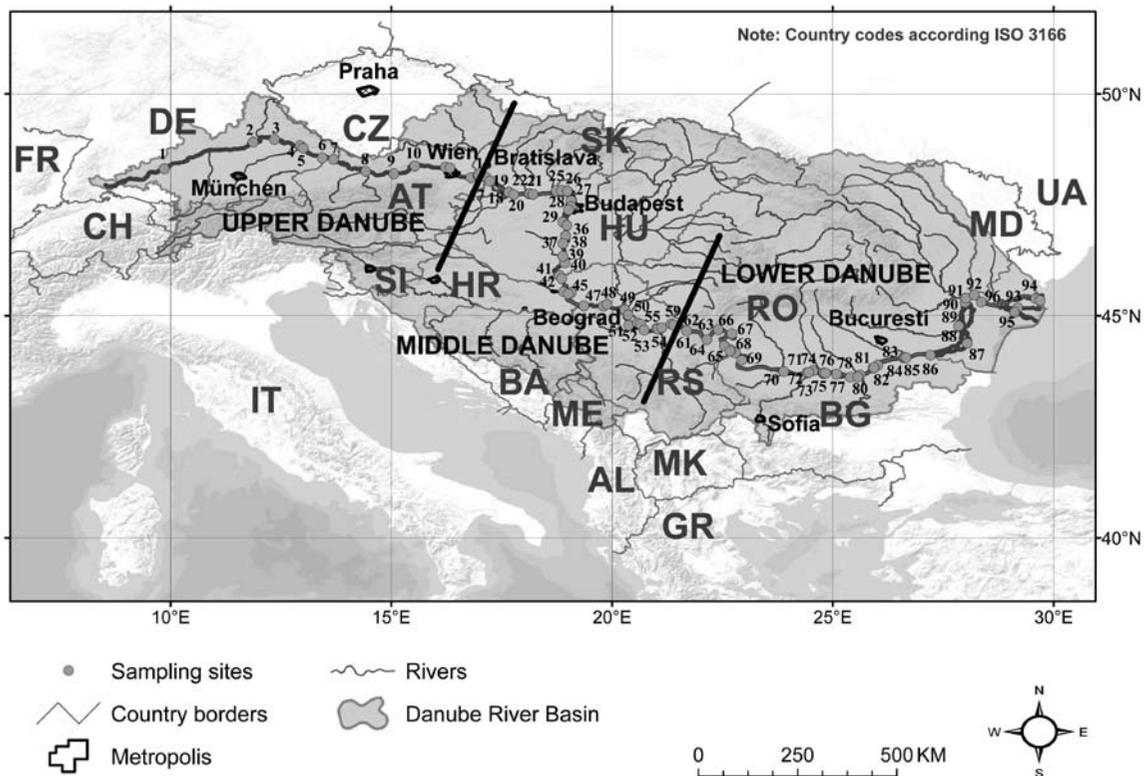


Fig. 1. Sampling location within the study area

tebrate communities with regard to species richness (19%) and relative abundance (35.7%). A total of 42 aquatic mollusc species-group taxa of 14 families were detected in the area of investigation. A total of 21 species, belonging to 10 families of gastropods and 21 taxa belonging to four families of bivalves was recorded (Table 2).

According to the ecological classification of taxa with regard to the saprobic conditions (saprobic valence) of NESEMAN, REISCHÜTZ (2002a, b), a majority of 47.25% of the registered species belonged to the beta-mesosaprobic, while 15.89% of the taxa could be characterised as an alpha-mesosaprobic group (the species tolerant of moderate organic loading). The species adapted to high organic loading (poly-saprobic) were represented by only 0.1% of the total number of taxa. The percentage participation of the species classified as sensitive to organic pollution (xeno-saprobic and oligo-saprobic taxa) was 4.1%. For the remaining species (27.7%) there were no available data about saprobic tolerance.

The majority of the recorded taxa (43.32%) were characteristic of bottom substrate types typical for large lowland rivers (the observed substrate types were pelal, psammal and argillal). The argillophilous taxa contributed to 9.69% of the total number of recorded mollusc species, while the taxa with preferences for psammal and pelal macrohabitats contrib-

uted to 16.93% and 16.7, respectively. The lithophilous species that prefer larger fraction of the substrate (>2cm) were represented by 13.1%, while taxa characterised as phytophilous participated with 2.83% of the total number of the identified species. For the remaining species there was not enough information about their microhabitat preference (AQEM 2002).

According to classification with regard to the longitudinal zonation, the greatest part of the recorded taxa (75.5%) were potamal species (characteristic of the lower stretches of the river). A smaller number (5.8%) of species was confined to the upper stretch of the river (rhithral species).

In respect of the current preferences of mollusc species, the majority of the identified species was characteristic of slow-flowing streams and lentic zones (rheo- to limnophilous taxa – RL–41.81% of the total number of the recorded species). The recorded community was characterised by small numbers of species, distinguished as limno- to rheophilous taxa (Type LR–1.50%), *i.e.* taxa that prefer standing waters. A significant number of species (12%) was apparently indifferent to the prevailing current conditions, while 31.56% of the taxa could not be classified with regard to the prevailing preference due to a lack of relevant data (AQEM 2002).

Concerning the prevalent feeding types, the highest proportion of molluscs were gatherers and

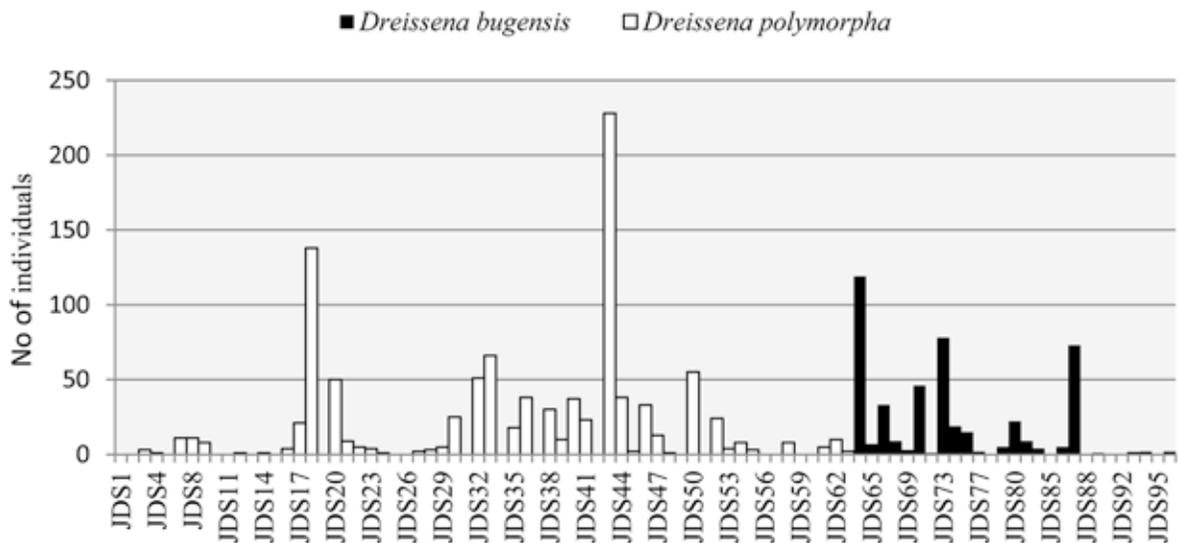


Fig. 2a. Distribution of *Dreissena polymorpha* and *Dreissena bugensis* along the Danube River

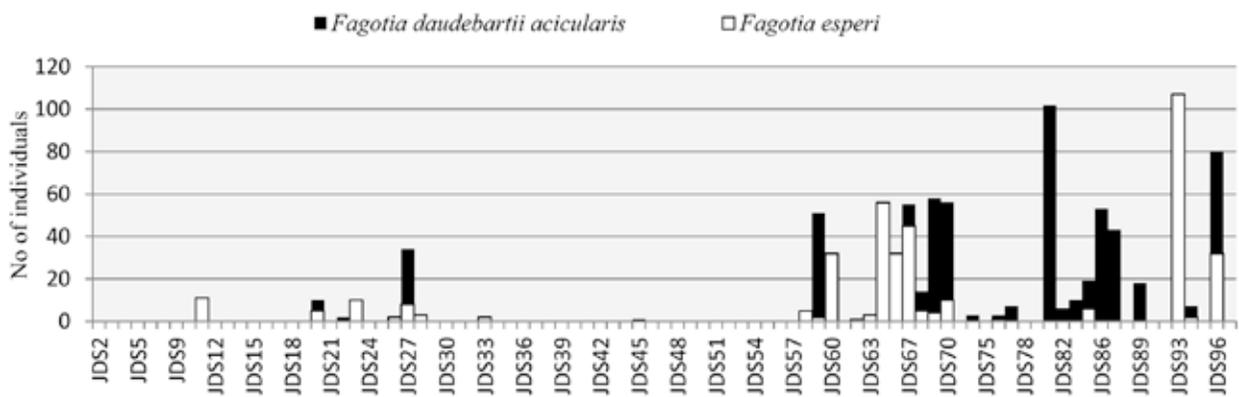


Fig. 2b. Distribution of *Fagotia daudebartii acicularis* and *Fagotia esperi* along the Danube River

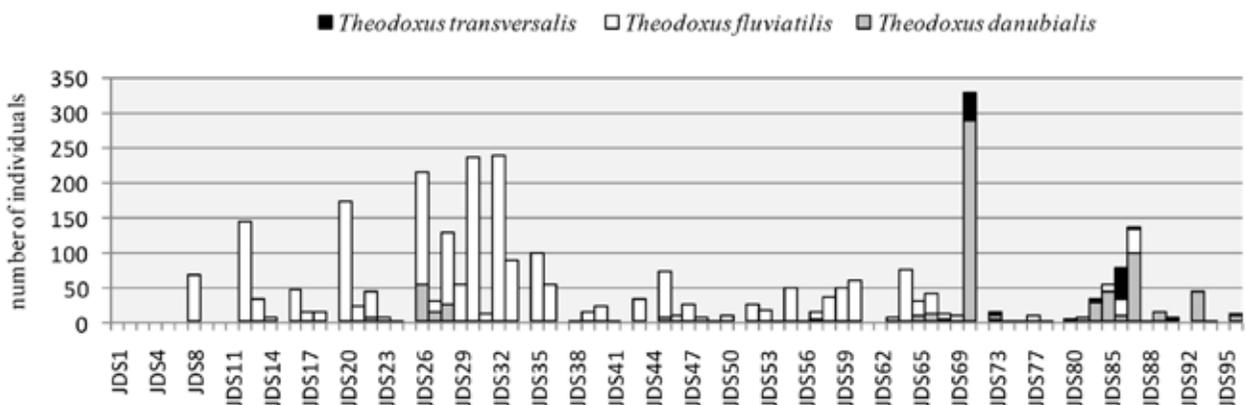


Fig. 2c. Distribution of *Theodoxus danubialis*, *Theodoxus fluviatilis* and *Theodoxus transversalis* along the Danube River

collectors (27.86%). The proportion of the active filter-feeding organisms was 22.93%, while the grazers and scrapers participated with 21.05% species in the total mollusc community. For 24.15% of detected taxa, data about the feeding types were not available.

When the Danube sections were compared in terms of taxa richness, the Hungarian Danube Bend (middle stretch) section with 30 recorded taxa, clearly stood out as significant with regard to biodiversity. Considerable taxa richness was detected in the Lower Alpine Foothills Danube section (the upper

stretch) and in the Pannonian Plain Danube section (the middle stretch), with 27 taxa each, as well as in the Western Pontic Danube section (the lower stretch), with 20 taxa; the number of taxa in the other sections was lower.

The analysis of the faunistic composition revealed that the main members of the mollusc community with regard to relative abundance were the gastropods *Lithoglyphus naticoides* (37.5%) and *Theodoxus fluviatilis* (7.5%) as well as the bivalves *Corbicula fuminea* (25.5%) and *Dreissena polymorpha* (3.3%). The percentage participation of other taxa was significantly lower.

According to the frequency analyses (occurrence of taxa in all samples/ at sampling sites), two euconstant taxa were recorded – *C. fuminea* and *L. naticoides* ($F_1=0.79-0.87$). *Unio tumidus* and *T. fluviatilis* were constant taxa ($F_1=0.54-0.65$). Four gastropods (*Fagotia esperi*, *Fagotia daudebartii acicularis*, *Theodoxus danubialis*, and *Viviparus acerosus*) and six bivalve species (*Anodonta anatina*, *Pisidium supinum*, *Sinanodonta woodiana*, *Sphaerium rivicola*, *Unio pictorum* and *Dreissena polymorpha*) could be considered as accessory ($F_1=0.25-0.48$). The frequencies of the remaining taxa were very low (F_1 ranged 0.01-0.23).

Two invasive species of Asian clams were detected in the area of investigation. The first of them, *Corbicula fluminalis*, was extremely rare and occurred only at three sampling sites: JDS 5 (2278 rkm), JDS 11 (1950 rkm) and JDS 38 (1481 rkm) from the Upper and Middle Danube, according to the classification of LÁSZLÓFFY (1965). This finding is in striking contrast with another species, *C. fuminea*, which was found in dense populations in many sections.

Unio pictorum and *U. tumidus* were the most common large mussel taxa in the investigated area. *U. pictorum* was identified already in the uppermost section of the Danube River and both species attained very high abundance in the Hungarian-Slovakian section up to the Iron Gate I Reservoir (Golubac/Koronin).

A stable population density of the invasive species *Sinanodonta woodiana* was observed between the Middle Danube and the Danube Delta, with the largest population density in the stretch from Hungary to the Drava confluence. *A. anatina* was rarely observed in the upper sections and was abundant in the stretch from the Gabčikovo Reservoir (JDS17) to the Drava confluence.

Two introduced dreissenid species were detected in the Danube River. *D. polymorpha* was one of the most abundant species in the Upper and Middle

Danube, while the new invader *Dreissena bugensis* was detected in the section between the Iron Gate II (JDS64) and the Delta – JDS96 (Fig. 2a).

Based on our data, all species of the genus *Pisidium* (7 species) were observed to populate the section between Kelheim (JDS 2; 2415 rkm) and Paks (JDS 37; 1497 rkm). Among them, only *P. amnicum* was detected in the downstream part of the river until 1132 rkm (site JDS54), with low abundance.

While occasionally occurring in the Middle Stretch, *F. daudebartii acicularis* and *F. esperi* were more frequent and abundant in the Lower Sector and the Danube Delta (Fig. 2b).

The highest population density of *T. fluviatilis* was detected in the Upper and Middle Sectors of the Danube River, according to the classification of LÁSZLÓFFY (1965). Peaks in the population density were detected in the Austrian, Slovakian and Hungarian Sections (Fig. 2c).

T. danubialis had a stable population in the Slovakian-Hungarian Danube. It was also recorded in the Serbian stretch. Downstream of the Iron Gate II it was one of the most frequent species in the Lower Stretch (Fig. 2c). *Theodoxus transversalis* (Fig. 2c) was detected in a very restricted section and only in the Lower Danube (JDS70-86).

The distribution of the sampling sites in a bi-dimensional space generated by the correspondence analyses (PIELOU 1984) is presented in Fig. 3. The Upper course of the Danube River (Section 1) contains only one locality (the source of the Danube River) and it is completely different from the other Danube Sections. In order to present more clearly the distribution of molluscs along the Danube, Section 1 was excluded from the analysis. The correspondence analysis clearly shows changes in mollusc communities along the watercourse. The sites along the Upper Danube are situated in the upper right area of the diagram. The sites that belong to the Middle Sector are grouped around zero position. The Lower Danube sites are located on the left side of the diagram (classification according to LÁSZLÓFFY 1965). The greatest dispersion was observed between the sampling sites in the Upper Danube Sector (the sampling sites at the Alpine Foothills Danube and the Lower Alpine Foothills Sections). Moreover, based on the resulting diagram, smaller differences were detected between the sites of the Middle Danube and Lower Danube Sector. In the Middle Danube, most of the species were found in the Hungarian Danube Bend and were also presented in the Pannonian Plain Danube. The positioning of the sampling sites on the graph (Fig. 3) revealed some similarities in the composition of mollusc fauna among the samples from

Table 2. List of identified molluscs taxa from the Danube River in the frames of the Second Joint Danube Survey (JDS2), 2007

GASTROPODA	<i>Viviparus acerosus</i> (Bourguignat, 1862)
ACROLOXIDAE	<i>Viviparus viviparus</i> (Linnaeus, 1758)
<i>Acroloxus lacustris</i> (Linnaeus, 1758)	<i>Viviparus</i> sp.
PLANORBIDAE	BIVALVIA
<i>Ancylus fluviatilis</i> O. F. Müller, 1774	CORBICULIDAE
<i>Gyraulus albus</i> (O. F. Müller, 1774)	<i>Corbicula fluminalis</i> (O. F. Müller, 1774)
<i>Planorbis carinatus</i> O. F. Müller, 1774	<i>Corbicula fluminea</i> (O. F. Müller, 1774)
BITHYNIIDAE	DREISSENIDAE
<i>Bithynia tentaculata</i> (Linnaeus, 1758)	<i>Dreissena bugensis</i> (Andrusov, 1897)
VALVATIDAE	<i>Dreissena polymorpha</i> (Pallas, 1771)
<i>Borysthenia naticina</i> (Menke, 1845)	SPHAERIIDAE
<i>Valvata piscinalis piscinalis</i> (O. F. Müller, 1774)	<i>Musculium lacustre</i> (O. F. Müller, 1774)
MELANOPSIDAE	<i>Pisidium amnicum</i> (O. F. Müller, 1774)
<i>Fagotia daudebartii acicularis</i> (A. Férussac, 1823)	<i>Pisidium casertanum</i> var. <i>ponderosum</i> (Stelfox, 1918)
<i>Fagotia esperi</i> (A. Férussac, 1823)	<i>Pisidium henslowanum</i> (Sheppard, 1823)
<i>Amphimelania holandrii</i> (Pfeiffer, 1828)	<i>Pisidium moitessierianum</i> Paladilhe, 1866
HYDROBIIDAE	<i>Pisidium nitidum</i> Jenyns, 1832
<i>Lithoglyphus naticoides</i> (C. Pfeiffer, 1828)	<i>Pisidium subtruncatum</i> Malm, 1855
<i>Potamopyrgus antipodarum</i> (Gray, 1843)	<i>Pisidium supinum</i> A. Schmidt, 1851
PHYSIDAE	<i>Sphaerium corneum</i> (Linnaeus, 1758)
<i>Physa fontinalis</i> (Linnaeus, 1758)	<i>Sphaerium rivicola</i> (Lamarck, 1818)
<i>Haitia acuta</i> (Draparnaud, 1805)	<i>Sphaerium solidum</i> (Normand, 1844)
LYMNAEIDAE	UNIONIDAE
<i>Radix balthica</i> (Linnaeus, 1758)	<i>Pseudanodonta complanata</i> (Rossmässler, 1835)
NERITIDAE	<i>Sinanodonta woodiana</i> (Lea, 1834)
<i>Theodoxus danubialis</i> (Pfeiffer, 1828)	<i>Anodonta anatina</i> (Linnaeus, 1758)
<i>Theodoxus fluviatilis</i> (Linnaeus, 1758)	<i>Unio crassus</i> Philipsson, 1788
<i>Theodoxus transversalis</i> (Pfeiffer, 1828)	<i>Unio pictorum</i> (Linnaeus, 1758)
VIVIPARIDAE	<i>Unio tumidus</i> Philipsson, 1788

the Lower Danube (Western Pontic Danube, Eastern Wallachian Danube) and the Danube Delta.

The Iron Gate area could be considered as an intermediary zone between the Middle and Lower Danube.

The characteristic locations of the samples on the diagram are mainly a result of both a shift in the principal components of mollusc communities (the euconstant, constant and abundant species described above) and the absence of certain species in particular stretches of the river.

In the Upper Danube, 28 taxa were identified. The stretch was typified by the presence of taxa that were not identified in other sectors, such as *Ancylus fluviatilis*, *Gyraulus albus* and *Planorbis carinatus*. The dominant taxa in the Upper Sector with regard to frequency and abundance were the invasive snail species *Potamopyrgus antipodarum* (F= 0.71, 31.9%) and *L. naticoides* (F=0.71, 15.8%).

The greatest species richness (36 taxa) was observed in the Middle Sector. In terms of abundance,

the most dominant species were *L. naticoides* (43.9%) and *T. fluviatilis* (12.2%), with frequencies of occurrence of F=0.9 and F=0.8, respectively. Two characteristic species that occurred only in the Middle Sector were *Acroloxus lacustris* and *Unio crassus*. A single finding of *Unio crassus* at three sampling sites (JDS 21, 23 and 25 – the Middle Danube) is worth mentioning. According to the IUCN classification, this species is considered endangered in Europe (VAN DAMM 2011a) and is included in the European Union list of species of special community interest (92/43/EEC).

It is also worth mentioning the occasional occurrence of *Pseudanodonta complanata* in the Middle and Lower sections of the Danube River. This species is endangered in many countries and included as a vulnerable species in the IUCN Red List (VAN DAMM 2011b).

In the Lower Danube, 26 mollusc taxa were identified. Three distinct species identified in the Lower reach and found only in this sector were *Amphimelania holandrii*, *T. transversalis* and *D. bu-*

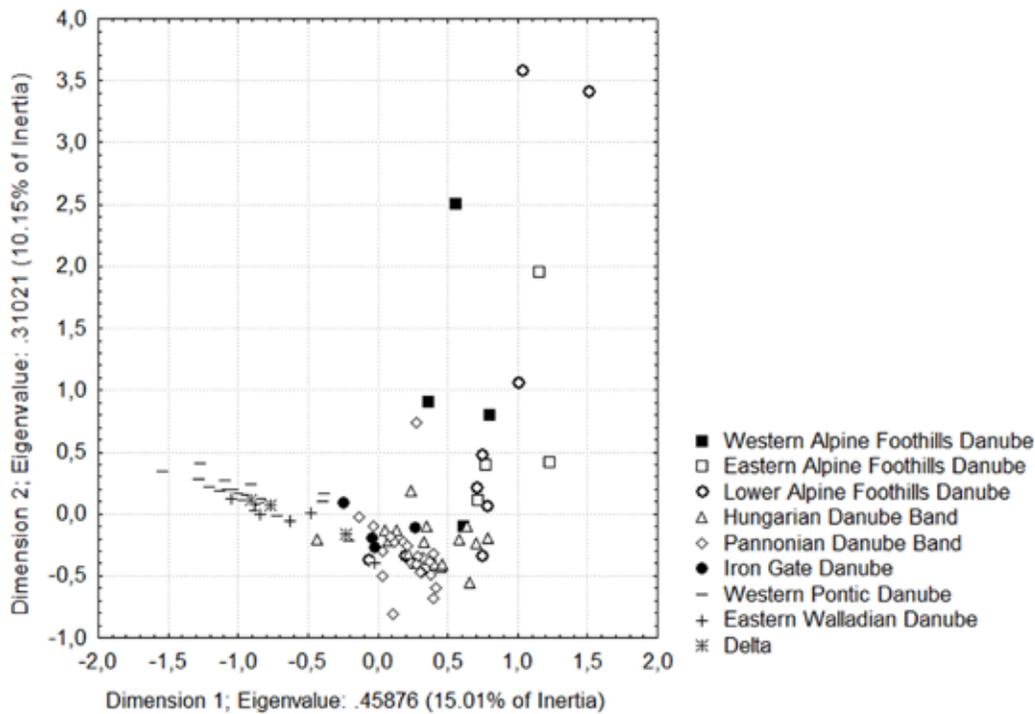


Fig 3. Correspondence analysis of mollusc community

gensis. The most dominant taxa in regard to relative abundance were *L. naticoides* (33.9%) and *C. fluminea* (43.6%), which were also observed as dominant species with respect to frequency ($F=0.94$). Aside from the most frequent mussel species in the Lower sector, a high frequency was determined for the snail *T. danubialis* ($F=0.68$).

Discussion

In general, the recorded mollusc fauna described along the Danube River is characteristic of the large potamon types of rivers in the Danube Basin (PAUNOVIĆ *et al.* 2008, 2012, TOMOVIĆ *et al.* 2012, 2013, TUBIĆ *et al.* 2013). This result confirmed that the major part of the investigated stretch is a typical potamon river type. A shift in the distribution patterns in the mollusc communities correlated highly with changes in the complex of environmental parameters, such as the dominant type of river bed and current velocity.

The Danube River belongs to the Southern Invasive Corridor (the Black Sea-Danube-Main/Danube Channel-Main-Rhine-North Sea waterway), being one of the four most important European routes of spread of invasive species (GALIL *et al.* 2007). The river is exposed to intensive colonisation by aquatic invasive species throughout the Danube Basin. The dispersal of certain non-indigenous mollusc species in the Danube River has been discussed by several authors (PAUNOVIĆ *et al.* 2006, 2007b,

SON 2007, RAKOVIĆ *et al.* 2013, BÓDIS *et al.* 2012a, b, 2014.). Based on our results, several mollusc species were identified as the most prominent mollusc invaders in the Danube River. These were five species of Bivalvia (*C. fluminea*, *C. fluminalis*, *D. polymorpha*, *D. bugensis* and *S. woodiana*), and one gastropod species (*P. antipodarum*). The latter was the predominant species, with huge population size, inhabiting the stretch from the Geisling Power Plant (2354 rkm) to the Gabčíkovo Reservoir (1852 rkm), with occasional occurrence up to Paks (1533 rkm).

The distribution of the mollusc fauna clearly revealed the differences between the three main stretches of the river. Based on the results of the correspondence analysis supported by the total mollusc data set, three sector types of the Danube River with one transitional zone might be distinguished. The sites that are in the transitional zone (JDS59, JDS60, JDS61, and JDS62) were not clearly positioned along one stretch. The Iron Gate Section has been identified as the boundary between the Middle and Lower Danube with respect to the hydro-morphological conditions and concentration of natural differences between the sectors situated upstream and downstream (ROBERT *et al.* 2003, TUBIĆ *et al.* 2013). The analysis of the composition of the macroinvertebrate community in the sector upstream of the Iron Gate (km 1083-1071) revealed a similar situation. In this sense, the Iron Gate was indicated as the border zone between the Middle and Lower Danube (PAUNOVIĆ

et al. 2005). We pointed out previously that the sector concerned is influenced both by the downstream sector (the Lower Danube) and the upstream zone (the Middle Danube). This case confirms the concept of a gradual longitudinal change as described by STANKOVIĆ (1960) and later discussed in the River Continuum concept by VANNOTE *et al.* (1980).

The separation into a larger number of stretches by abiotic typology (ROBERT *et al.* 2003) was not confirmed in our study. This was probably because of the ecological plasticity in a significant number of the recorded species (MOOG 2002) and the hydrological pressures that can significantly change the natural distribution of taxa and the structure of communities. The intensity of hydromorphological pressure, which was most pronounced in the Upper Sector and the Iron Gate stretch, is illustrated by the fact that along the main course of the Danube River, 69 dams were built and that 30% of the Danube's total length was affected by changes in the sediment transport, flow velocity and the groundwater regime (SOMMERWERK *et al.* 2009). According to ELLIS (1942), an impounded river exhibits silt accumulation, loss of shallow water habitats, stagnation, accumulation of pollutants and depletion of nutrients. The changes in mollusc communities caused by hydromorphological modifications are complex and range from a reduction in species numbers and their replacement with other species to exchanges of abundant taxa with non-indigenous taxa.

A considerable amount of data collected in the course of JDS2 illustrates the longitudinal distribution of mollusc taxa in the Danube River. These results form a very important part of the second detailed international Danube survey program that is aimed at describing the basic faunal composition of this river. In general, the Mollusca (Gastropoda, Bivalvia) contribute to the most characteristic taxonomic group, which inhabits the near-littoral zone of the Danube River. Mollusc taxa are one of the principal components of the macrozoobenthos communities at any of the sampling sites in the Upper, Middle and Lower Sections of the river (GRAF *et al.* 2008).

Our results are in agreement with authors who investigated the Danube River or other large European rivers in that the molluscs are one of the main groups of animal communities in large lowland rivers that could clearly demonstrate the river typology (PAUNOVIĆ *et al.* 2008, TUBIĆ *et al.* 2013).

The composition and spatial heterogeneity of the bottom substrate exerts the most important influence on the structure and composition of mollusc communities, as well as their diversity and abundance in different lentic waters (*e.g.* HARMAN 1972, BAILEY 1988, ŠPORKA

and NAGY 1998, WEIGAND, STADLER 2000, LEWIN 2006). Previous studies (HAUKIOJA, HAKALA 1974, LEWANDOWSKI, STANCZYKOWSKA 1975) and our results demonstrate that molluscs prefer free flowing stretches of rivers and that they attain high abundance in shallow waters in the littoral part, with a relatively few species capable of colonising impoundment depths.

The findings presented herein document the patterns of species composition and diversity in relation to the substrate type. The malacocoenoses in the habitats of the Middle and Upper Danube were characterised by higher species richness and diversity as compared to the sites in the Lower Danube. Considering the variation among the dominant sediment types in the particular stretches of the Danube River, this could be the main reason for the observed differences. The Upper Danube is characterised by reaches of the Alpine river type. The transitional zone between the Alpine and lowland river types is situated between the Gabčíkovo Reservoir (river km 1816) and Budapest (upstream the city, river km 1659). This sector is characterised by a preponderance of coarse (20-63 mm) and medium gravel (6.3-20 mm). The Middle Sector is distinguished by a higher proportion of habitats with fine and medium gravel (2-6.3 mm and 6.3-20 mm, respectively) and silt (<0.63 mm), while the Lower stretch is predominantly characterised by sand (0.63-2 mm) and silt (<0.63 mm), with significant amounts of organic material.

Concerning the longitudinal zonation, the majority of the recorded species is typical of the lower stretches of the river (potamal species). The recorded assemblages were characterised by a predominance of taxa that prefer slow-flowing streams and lentic zones (rheo- and limnophilous taxa), as well as by species that prefer fine-grained substrates.

It seems that the characteristics of the habitat type in the study area are one of the most important environmental factors that influence the composition of mollusc communities and their species richness in this large lowland river.

Acknowledgements: The material was collected during the Joint Danube Survey 2 and the Secretariat General of the International Commission for the Protection of the Danube River coordinated the investigation. We would like to express our gratitude to all of the participants in the JDS 2 expedition, especially Patrick Leitner and Wolfram Graf. We are thankful to Dr. Erika Bódis for her work on the taxonomical determination of the Pisidium taxa of the JDS2 samples. The preparation of the manuscript was supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia, Project No. 173025. We also express our thanks to Dr. Goran Poznanovic for his constructive comments during preparation of the manuscript, as well as to anonymous referees for constructive suggestions for improving the manuscript.

References

- AQEM 2002. Manual for the application of the AQEM system: A comprehensive method to assess European streams using benthic macroinvertebrates, developed for the purpose of the Water Framework Directive. Contract No: EVK1-CT1999-00027.
- ARAMBAŠIĆ M. 1994. Composition and structure of mollusc fauna of the Yugoslav part of the Danube and saprobity estimation. 124-130. In: JANKOVIĆ D., M. JOVIČIĆ (Eds.), The Danube in Yugoslavia - Contamination, Protection and Exploitation. Publ. Institute for Biological Research 'Siniša Stanković', Institute for Development of Water Resources "Jaroslav Černi", Commission of the European Communities, Brussels, Belgium, Belgrade.
- BAILEY R. C. 1988. Correlations between species richness and exposure: Freshwater molluscs and macrophytes. – *Hydrobiologia*, **162**: 183–191.
- BÓDIS E., J. NOSEK, N. OERTEL, B. TÓTH, E. HORNING and R. SOUSA 2011. Spatial distribution of bivalves in relation to environmental conditions (Middle Danube catchment, Hungary). – *Community Ecology*, **12** (2): 210-219.
- BÓDIS E., Cs. SÍPKAY, B. TÓTH, N. OERTEL, J. NOSEK and E. HORNING 2012a. Spatial and temporal variation in biomass and size structure of *Corbicula fluminea* in Middle Danube catchment, Hungary. – *Biologia Bratislava*, **67**(4): 739-750.
- BÓDIS E., P. BORZA, I. POTYÓ, M. PUKY, A. WEIPERT and G. GUTI 2012b. Invasive mollusc, crustacean, fish and reptile species along the Hungarian section of the River Danube and some connected waters. – *Acta Zoologica Academiae Scientiarum Hungaricae*, **58** (Supplement 1): 29-45.
- BÓDIS E., B. TÓTH and R. SOUSA 2014. Massive mortality of invasive bivalves as a potential resource subsidy for the adjacent terrestrial food web. – *Hydrobiologia*, **735**: 253-262.
- DÍAZ J. M., M. PUYANA 1994. Moluscos del Caribe Colombiano. Un catálogo ilustrado. COLCIENCIAS, Fundación Natura e INVEMAR, Bogotá. 367 pp.
- EEC 92/43 - Council Directive of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.
- ELLIS M. M. 1942. Fresh-water impoundments. Transactions of the American Fisheries Society, 71st Annual Meeting, 80-93.
- EN 27828:1994, ISO 7828-1985. Water quality. Methods for biological testing. Methods of biological sampling: guidance on handnet sampling of aquatic benthic macroinvertebrates.
- GALIL B. S., S. NEHRING and V. E. PANOV 2007. Waterways as invasion highways – Impact of climate change and globalisation. In: NENTWIG W. (Ed.), – *Biological Invasions*. Ecological Studies Nr. 193, Springer, Berlin: 59–74.
- GOMES M. A., R. NOVELLI, I. R. ZALMON and C. M. Souza 2004. Malacological assemblages in sediments of eastern Brazilian continental shelf, coordinates 108 and 208 S, between Bahia and Espírito Santo State. – *Bios*, **12**: 11–24.
- GRAF W., B. CSÁNYI, B. LEITNER, M. PAUNOVIC, G. CHIRIAC, I. STUBAUER, T. OFENBÖCK and F. WAGNER 2008. Macroinvertebrates. In: LIŠKA I., F. WAGNER, J. SLOBODNÍK (Eds.): Joint Danube Survey. Final Scientific Report. 41-53; ICPDR – International Commission for the Protection of the Danube River, Wien.
- HARMAN W. N. 1972. Benthic substrates: their effect on fresh-water Mollusca. – *Ecology* **53**: 271-277.
- HAUKIOJA E., T. HAKALA 1974. Vertical distribution of freshwater mussels (Pelecypoda, Unionidae) in southwestern Finland. – *Annales Zoologici Fennici*, **11**: 127-130.
- JAKOVČEV D. 1988. Zustand der Benthofauna der Flusses Sava im Region Belgrad. - 27. Arbeitstagung der IAD, SIL, Limnologische Berichte Donau 1988, 259-263, Mamaia, Rumänien.
- JAKOVCEV D. 1987. Die Saprobologische Analyse der Donau im Belgrader Gebeit Anhand der Boden Fauna. 26. Arbeitstagung der IAD, SIL, Passau, Deutschland, Wissenschaftliche Referate, 529-532.
- LÁSZLÓFFY W. 1965. Die Hydrographie der Donau. Der Fluß als Lebensraum. In Liepolt, R. (ed.), Limnologie der Donau – Eine monographische Darstellung. II. Kapitel. Stuttgart (Schweizerbart): 16-57.
- LEWANDOWSKI K., A. Stanczykowska 1975. The occurrence and role of bivalves of the family Unionidae in Mikolajskie Lake. – *Ekologia Polska*, **23**: 317-334.
- LEWIN I. 2006. The gastropod communities in the lowland rivers of agricultural areas – their biodiversity and bioindicative value in the Ciechanowska Upland, Central Poland. – *Malacologia*, **49**: 7–23.
- LIŠKA I., F. WAGNER and J. SLOBODNIK 2008. Joint Danube Survey - Final Report ICPDR - International Commission for the Protection of The Danube River: 235.
- LITERÁTHY P., V. KOLLER-KREIMEL and I. LIŠKA 2002. Joint Danube Survey. Technical Report of the International Commission for the Protection of the Danube River, 261 pp.
- LORENZ A., C. K. FELD and D. HERING 2004. Typology of streams in Germany based on benthic invertebrates: Ecoregions, zonation, geology and substrate. – *Limnologica*, **34**: 390-397.
- MOOG O. 2002. Fauna Aquatica Austriaca. Katalog zur autecologischen Erfassung. Aquatischer Organismen Österreichs. Teil II B, Metazoa, Saprobielle Valenzen.
- NESEMANN H., P. REISCHÜTZ 2002a. Mollusca: Gastropoda – part III, 19 pp. – In Moog O. (Ed) 2002. Fauna Aquatica Austriaca, Edition 2002. Wasserwirtschaftskataster, Bundesministerium für Land- and Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.
- NESEMANN H., P. REISCHÜTZ 2002b. Mollusca: Bivalvia – part III, 10 pp. – In: MOOG O. (Ed.) 2002. Fauna Aquatica Austriaca, Edition 2002. Wasserwirtschaftskataster, Bundesministerium für Land- and Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.
- PAUNOVIĆ M., V. SIMIĆ, D. JAKOVČEV-TODOROVIĆ and B. STOJANOVIĆ 2005. Results on macroinvertebrate community investigation in the Danube River in the sector upstream the Iron Gate (1083-1071 km). – *Archiv of Biological Sciences*, **57**: 57–63.
- PAUNOVIĆ M., B. CSÁNYI, V. SIMIĆ, B. STOJANOVIĆ and P. ČAKIĆ (2006). Distribution of *Anodonta (Sinanodonta) woodiana* (Lea, 1834) in inland waters of Serbia. – *Aquatic Invasions*, **1**: 154-160.
- PAUNOVIĆ M., D. JAKOVČEV-TODOROVIĆ, V. SIMIĆ, B. STOJANOVIĆ and P. ČAKIĆ 2007a. Macroinvertebrates along the Serbian section of the Danube River (stream km 1429-925). – *Biologia*, **62**: 1-9.
- PAUNOVIĆ M., B. CSÁNYI, S. KNEZEVIĆ, V. SIMIĆ, D. NENADIĆ, D. JAKOVČEV-TODOROVIĆ, B. STOJANOVIĆ and P. ČAKIĆ 2007b. Distribution of Asian clams *Corbicula fluminea* (Müller, 1774) and *C. fluminalis* (Müller, 1774) in Serbia. – *Aquatic Invasions* **2** (2): 99-106.

- PAUNOVIĆ M., S. BORKOVIĆ, S. PAVLOVIĆ, Z. SAIČIĆ and P. ČAKIĆ 2008. Results of the 2006 Sava survey – aquatic macroinvertebrates. – *Archive of Biological Sciences*, **60**: 265-270.
- PAUNOVIĆ M., J. TOMOVIĆ, S. KOVAČEVIĆ, K. ZORIĆ, K. ŽGANEC, V. SIMIĆ, A. ATANACKOVIĆ, V. MARKOVIĆ, M. KRAČUN, S. HUDINA, J. LAJTNER, S. GOTTSTEIN and A. LUCIĆ 2012. Macroinvertebrates of the Natural Substrate of the Sava River – Preliminary Results. – *Water Research and Management*, **2** (4): 32-39.
- PIELOU E. C. 1984. The Interpretation of Ecological Data - A Primer on Classification and Ordination. A Wiley-Interscience Publication, John Wiley & Sons, New York, Chichester, Brisbane, Toronto, Singapore, 265 pp.
- ROBERT S., S. BIRK and M. SOMMERHÄUSER 2003. Typology of the Danube River – part 1: top-down approach. In UNDP/GEF Danube Regional Project, Activity 1.1.6, Typology of Surface Waters and Definition of Reference Conditions for the Danube River. – Final report, 51–59.
- RAKOVIĆ M., N. POPOVIĆ, V. KALAFATIĆ and V. MARTINOVIĆ-VITANOVIĆ 2013. Spreading of *Dreissena rostriformis bugensis* (Andrusov, 1897) in the Danube River (Serbia). – *Acta Zoologica Bulgarica*, **65** (3): 349-358.
- SIMIĆ, S., A. OSTOJIĆ, V. SIMIĆ and D. JANKOVIĆ 1997. Promene u strukturi planktona i bentosa na delu toka Dunava od Velikog Gradišta do Prahova tokom letnjeg aspekta. – *Ekologija*, **32**: 65-80. (In Serbian)
- SIMIĆ, V., S. SIMIĆ (2004). Macroinvertebrates and fishes in the part of the Danube River flowing through the Iron Gate National Park and possibilities of their protection under *in situ* and *ex situ* conditions. – *Archive of Biological Sciences*, **56**: 53-57.
- SOMMERWERK, N., C. BAUMGARTNER, J. BLOESCH, T. HEIN, A. OSTOJIĆ, M. PAUNOVIĆ, M. SCHNEIDER-JAKOBY, R. SIBER and K. TOCKNER 2009. The Danube River Basin, Part 3, pp. 59-113. – In: TOCKNER K., U. UEHLINGER and C. T. ROBINSON (Eds.), Rivers of Europe. Academic Press, San Diego.
- SON O. M. 2007. Native range of the zebra mussel and quagga mussel and new data on their invasions within the Ponto-Caspian Region. – *Aquatic Invasions*, **2** (3): 174-184.
- ŠPORKA F., S. NAGY 1998. The macrozoobenthos of parapotamon-type side arms of the Danube River in Slovakia and its response to flowing conditions. – *Biologia*, **53**: 633-643.
- STANKOVIĆ S. 1962. Ekologija životinja. Univerzitet u Beogradu i Zavod za izdavanje udžbenika SR Srbije, Beograd. 432. (In Serbian)
- TUBIĆ B., V. SIMIĆ, K. ZORIĆ, Z. GAČIĆ, A. ATANACKOVIĆ, B. CSÁNYI and M. PAUNOVIĆ 2013. Stream section types of the Danube River in Serbia according to the distribution of macroinvertebrates. – *Biologia*, **68** (2): 294-302.
- TOMOVIĆ J., J. VRANKOVIĆ, K. ZORIĆ, S. BORKOVIĆ MITIĆ, S. PAVLOVIĆ, Z. SAIČIĆ and M. PAUNOVIĆ 2010. Chapter 12 Malakofauna of the Serbian stretch of the Danube River and studied tributaries (the Tisa, Sava and Velika Morava). Pp. 207-224. – In: PAUNOVIĆ M., P. SIMONOVIĆ, V. SIMIĆ and S. SIMIĆ (Eds.). Danube in Serbia – Joint Danube survey 2. Ministry of Agriculture, Forestry and Water Management – Directorate for Water, University of Kragujevac, Faculty of Science, Institute for Biology and Ecology, University of Belgrade, Institute for Biological Research 'Siniša Stanković', Belgrade.
- TOMOVIĆ J., K. ZORIĆ, M., KRAČUN, V. MARKOVIĆ, B. VASILJEVIĆ, V. SIMIĆ and M. PAUNOVIĆ 2012. Freshwater Mussels of the Velika Morava River. – *Water Research and Management* **2** (4): 51-55.
- TOMOVIĆ J., V. Simić, B. Tubić, K. Zorić, M. Kračun, V. Marković and M. Paunović 2013. Freshwater mussels of the Serbian stretch of the Tisa River. – *Water Research and Management*, **3** (1): 35-40.
- VAN DAMME D. 2011a. *Unio crassus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Accessed 09 March 2014.
- VAN DAMME, D. 2011b. *Pseudanodonta complanata*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Downloaded on **27 July 2014**.
- VANNOTE R. L., G. W. Minshall, K. W. Cummings, J. R. Sedell and C. E. Cushing 1980. The River Continuum Concept. – *Canadian Journal of Fisheries and Aquatic Sciences*, **37**: 130-137.
- WEIGAND E., F. STADLER 2000. Die aquatischen Mollusken der Regelsbrunner Au. Abh. – *Zoologisch-Botanische Gesellschaft in Österreich*, **31**: 99–124.
- WFD 2000. Water Framework Directive - Directive of European Parliament and of the Council 2000/60/EC – Establishing a Framework for Community Action in the Field of Water Policy.

Received: 02.05.2014

Accepted: 22.08.2014

