Empty native and invasive bivalve shells as benthic habitat modifiers in a large river

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ABSTRACT

Bivalves are remarkable ecosystem engineers and their long-lasting shells may provide important physical structures for benthic organisms. In the last decades the Danube River has experienced great changes in the bivalve fauna, i.e. several native species have been declining and several invasive species have been introduced. The invasive *Corbicula fluminea* and *Sinanodonta woodiana* are now widespread and produce large amounts of shells. In this study, we investigated empty shells of native (*Anodonta anatina*, *Unio tumidus*) and invasive (*C. fluminea*, *S. woodiana*) bivalves (including their mixtures) as benthic substrates and compared them to clay granules (control), which mimics the natural hard substrates in the Danube River (Hungary). Macroinvertebrate colonization was compared between (i) empty shells and control substrate; (ii) different bivalve species (native and invasive) and (iii) three scenarios (before invasion, and short and long time after invasion) by using a mix of empty shells (native, native plus invasive, and invasive species). In comparison to control treatments the empty shells facilitated the presence of amphipods, caddis larvae and isopods, which contributed to a shift in the trophic structure by decreasing the proportion of gathering collectors while increasing the presence of shredders and predators. Several shell traits such as size, outer-shell surface roughness, hardness, thickness, 3D shape and chemical composition may be important attributes in the habitat modifying effects; however, this study could not disentangle which contribute most for the differences found. Given the capability of invasive *C. fluminea* and *S. woodiana* to accumulate large amounts of empty shells on several sites of the Danube, its habitat modifying effects can be particularly important, especially on the macroinvertebrate community structure. Moreover, these effects may increase in near future due to the predicted more frequent and severe extreme climatic conditions, which have been responsible for massive mortalities in both species.

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Introduction

In the last two decades the concept of ecosystem engineering, i.e. organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (sensu Jones et al., 1994, 1997), has gained prominence in ecological research and the number of studies has increased rapidly (Wright and Jones, 2006). Ecosystem engineers can modify, maintain or create habitats via their own physical structures (autogenic engineering; e.g. coral reefs, shells of bivalves) and via activities that alter the structure of non-living and/or living materials (allogenic engineering; e.g. beavers, bioturbation by bivalves). In theory, and in given circumstances (e.g.

large spatial ranges, high densities, large body size and distinctive behaviour), these species can affect biodiversity (Byers et al., 2006) and ecosystem functions by increasing habitat and biogeochemical heterogeneity (Gutiérrez and Jones, 2006).

Bivalves represent an important group of ecosystem engineers in aquatic ecosystems since they have several attributes that can change the abiotic environment by physically altering structure and ecosystem processes (Gutiérrez et al., 2003; Sousa et al., 2009, 2014). Their most remarkable engineering mechanisms, that may encompass autogenic and allogenic activities, are related to their intensive filtration activity, bioturbation capability and provision of shells (Ilarri et al., 2012; Sousa et al., 2009, 2014; Strayer et al., 1999; Vaughn and Hakenkamp, 2001). Particularly important, but often overlooked, can be the presence of empty bivalve shells that can act as an important physical structure. Shells can accumulate on the bottom of lakes, rivers, estuaries or oceans decreasing the near-bottom current velocity and increasing the microhabitat

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complexity and heterogeneity. The empty shells can also provide appropriate substrate surface for benthic organisms, especially in soft sediments, or serve as shelter against predators or abiotic stress (Gutiérrez et al., 2003; Werner and Rothhaupt, 2007). Some of these shells can persist in the ecosystem for decades, so the legacy of the overall effects may be long lasting (Gutiérrez and Iribarne, 1999; Palacios et al., 2000).

In recent decades several invasive bivalve species, such as zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena bugensis*, Asian clam *Corbicula fluminea*, golden mussel *Limnoperna fortunei* and Chinese pond mussel *Sinanodonta woodiana*, were introduced worldwide and have become widespread and abundant in the invaded ecosystems causing considerable ecological and economic damages (for a review see Sousa et al., 2014). The Danube River is part of an important aquatic invasion corridor in Europe connecting the North Sea and Black Sea via the Rhine–Main–Danube Canal; being an important shipping route it contributes to the accelerated expansion of several non-indigenous aquatic species (Bódis et al., 2012a). Five non-indigenous bivalve species (*C. fluminea*, *C. fluminalis*, *D. bugensis*, *D. polymorpha* and *S. woodiana*) occur along the Hungarian stretch of the Danube River and currently *C. fluminea* and *S. woodiana* dominate the bivalve community attaining a high density (736 ind. m^{-2} and 15 ind. m^{-2}, respectively) (Bódis et al., 2011, 2012b). *S. woodiana* can reach 180–200 mm shell length and individuals can weight 300–400 g; therefore, the 15 ind. m^{-2} density can have major impacts. In addition, due to the predicted more frequent and intensive extreme climatic events, massive die-offs of these invasive species probably will increase in near future resulting in large accumulation of their empty shells. In heavily invaded sites the mean density of empty shells of *Corbicula* and *S. woodiana* can attain 676.3 ± 193.9 ind. m^{-2} and 280.5 ± 110.6 ind. m^{-2}, respectively (Bódis et al., 2014). In the last two decades both species became widespread along the Hungarian stretch of the Danube River and invaded the side-arms and some tributaries, too. The introduction and rapid dispersion of *C. fluminea* was mainly enhanced by river navigation, whereas the spread of *S. woodiana* was triggered by Asian fish transport, since their parasitic glochidium larvae develop on a fish host in a part of their life cycle (Douda et al., 2012).

Ecological effects mediated by shells of some invasive bivalve species have already been demonstrated. Shells of the epibenthic zebra mussel *D. polymorpha* provide excellent habitat and shelter for aquatic organisms. This leads to changes in the macroinvertebrate community structure and decreases the predation efficiency of some benthic fish species (Beekey et al., 2004; Burlakova et al., 2012; Dieterich et al., 2004; Mayer et al., 2001; Ricciardi et al., 1997). Similar results have been described for the golden mussel *L. fortunei* in South America (Sylvester et al., 2007). However, the effects of invasive infaunal bivalves, such as *C. fluminea* and *S. woodiana*, on community structure are less studied (but see Ilarri et al., 2012, 2014 and Werner and Rothhaupt, 2007 for recent studies on *C. fluminea*), despite the fact that these invasive bivalves can dominate the benthic community and large amounts of empty shells can accumulate on certain sites (Bódis et al., 2014; Ilarri et al., 2011; Sousa et al., 2008, 2012). These invasive bivalves can provide new substrates for the invaded ecosystem via the introduction of shells with novel sizes, shapes, and sculpture; thereby altering the quantity and quality of substrates available for the colonization of benthic organisms (Sousa et al., 2009).

Given the possible importance of empty bivalve shells as a physical structure for other benthic organisms the main objectives of this study were to assess the differences in macroinvertebrate colonization as measured by the density, species richness, diversity and functional feeding groups between (i) the empty shells and the control treatment, which mimics the natural hard substrates in the studied area; (ii) different native (*Anodonta anatina*, *Unio tumidus*) and invasive (*S. woodiana*, *C. fluminea*) bivalves and (iii) three scenarios (before invasion, and short and long time after invasion) by using the mix of empty shells of native (*A. anatina*, *U. tumidus*), native plus invasive (*A. anatina*, *U. tumidus*, *S. woodiana*, *C. fluminea*) and invasive (*S. woodiana*, *C. fluminea*) bivalves.

Material and methods

Study area and sampling methods

The study was performed in the main arm of the Danube River. The Danube is the longest river (2857 km in length) in Central-Europe. It receives all the running waters of Hungary in a length of 417 km and has a catchment area of 39,000 km^2 in the country. Its average water discharge is approximately 2200 m^3 s^{-1}. Our study site was located at Göd (1669 river km, 47°40′53.68″N, 19°07′32.84″E) in a depositional zone of the Danube River, where the sediment consists of sand and silt, and the mean annual current velocity is approximately 0.1 m s^{-1}. Detailed description of the environmental characteristics in the study area is available in Bódis et al. (2011).

The experiment was carried out between August and October 2012 on the bottom of the river in the littoral zone at water depth of 150 cm to avoid the possible influence of changes in the water level. This time of the year was chosen because late summer and early fall has the highest abundance of benthic organisms living in the water in their whole life cycle (Nosek et al., 2009). In addition, two months is enough time for the development of a steady macroinvertebrate community on artificial substrates placed on the bottom of the river (Nosek, 2002; Oertel and Nosek, 2006).

To study the effect of empty bivalve shells on macroinvertebrates two native (*A. anatina*, *U. tumidus*) and two invasive (*C. fluminea*, *S. woodiana*) bivalve species and the mix of their shells (native, native plus invasive and invasive species) were used as past, present and future scenarios. We used the mix of native species simulating past conditions where no invasive species were present, the mix of native and invasive species simulating present conditions where native and invasive species co-exist in sympatry, and the mix of invasive species simulating future conditions where we assume that native species will disappear and invasive species will prosper. All the studied species occur frequently and are capable of producing large amounts of empty shells in the Danube River (Bódis et al., 2011, 2014). In addition, clay granules were used as a control substrate, which provides the best artificial surface for the colonization of macroinvertebrates and mimics the natural hard substrates in the studied area (Nosek, 2002; Oertel, 2002). Empty shells from recently dead bivalves from representative size classes were collected and brushed in the laboratory under water to remove contamination. To estimate the surface area the inside and outside of each shell were wrapped in aluminium foil and the foil was weighted; then this was converted to area using a standard area-mass ratio (following Ricciardi et al., 1995). The different treatments with the same surface area (0.45 m^2) were put into bags with mesh size of 10 mm using six replicates. The empty shells were evenly distributed and the number of shells and mean shell size ± SD were the same per replicate: *U. tumidus* (60), 79 ± 9 mm shell length; *A. anatina* (38), 91 ± 9 mm shell length; *S. woodiana* (25), 106 ± 15 mm shell length; *C. fluminea* (200), 26 ± 7 mm shell length; mix native: *U. tumidus* (30), *A. anatina* (20), 86 ± 10 mm shell length; mix native plus invasive: *U. tumidus* (15), *A. anatina* (10), *S. woodiana* (6), *C. fluminea* (50), 52 ± 35 mm shell length; mix invasive: *S. woodiana* (12), *C. fluminea* (100), 35 ± 27 mm shell length.

All samples were collected from the bottom of the river at the beginning of October and put immediately into different boxes.

Some bags were lost during the colonization period and the experiment finished with two replicates for *U. tumidus*, three for *A. anatina*, *S. woodiana* and *C. fluminea* and six for mixed shells. The macrozoobenthos were separated using a series of sieves of various mesh sizes (20 mm, 2360 μm, 710 μm and 250 μm) in the field, and all organisms were fixed in 70% ethanol. In the laboratory, individuals were identified to genus or species level (except oligochaetes and chironomids) and counted. The identification was facilitated by the experts of taxonomic groups and elaborated literature (molluscs: Glöer and Meier-Brook, 1998; Richnovszky and Pintér, 1979; crustaceans: Cărăuşu et al., 1955; Eggers and Martens, 2001; insects: Askew, 2004; Nesemann, 1997; Waringer and Graf, 1997). To assign the functional feeding groups of the recorded macroinvertebrates the classification of each taxon was used and weighted by the density according to Moog (2002), which was processed using the species pool of the Danube River basin and takes into account that certain taxon belongs to more than one functional feeding group.

Data analysis

One-way permutational multivariate analyses of variance (PERMANOVA, type-III) were used to test for differences in univariate measures that include density, number of taxon and Shannon–Wiener diversity indices of the macroinvertebrate community among treatments. The density was expressed by 1 m^2. Overall, differences in the associated community structure were assessed using the treatments as fixed factors (with 8 levels: empty shells of *A. anatina*, *S. woodiana*, *C. fluminea*, *U. tumidus*, clay granules used as control, mix of empty shells of native, native plus invasive and invasive species), which included differences in individual species density. Prior to the one-way PERMANOVA analyses, all variables were normalized and a resemble matrix based on the Euclidean distance was calculated. The PERMANOVAs were run among the eight different levels using all species gathered, the main taxonomic groups (annelids, molluscs, crustaceans, insects) and the feeding groups (active filter-feeders, passive filter-feeders, gathering collectors, grazers, shredders, predators and other feeding types). *p*-Values for the pseudo-*F* ratios were calculated by permutation of raw data through 9999 permutations. When the number of permutations was lower than 150, the Monte Carlo *p*-value was considered. Pairwise comparisons were also performed when appropriate. In addition, to analyze the overall community structure we used multidimensional scaling (MDS) based on the density data of all species gathered. Similarity matrix among treatments was calculated using the normalized Euclidean distance.

Linear regression analysis was used and Pearson's correlation coefficients were calculated to determine the relationship between the shell length and the taxon number, density and Shannon-Wiener diversity. All the analyses were performed with PRIMER v6 with the PERMANOVA+ for PRIMER (Clarke and Gorley, 2006) and with R version 2.6.2. (RDevelopment Core Team, 2007).

Results

Altogether 55 taxa belonging to five main taxonomic groups of benthic macroinvertebrates were collected: flatworms, annelids (oligochaetes, leeches), molluscs (bivalves, gastropods), crustaceans (amphipods, isopods) and insects (caddis larvae, dipterans) (Table 1). Flatworms, contributed to the total of organisms with less than 1%. The percentages of taxonomic groups with more than 1% contribution to the total of organisms differed between treatments. The dominant taxonomic groups, which contributed with more than 10%, were molluscs (40.0%), crustaceans (30.6%) and insects (22.3%) (Fig. 1). On a lower taxonomic level six taxonomic groups
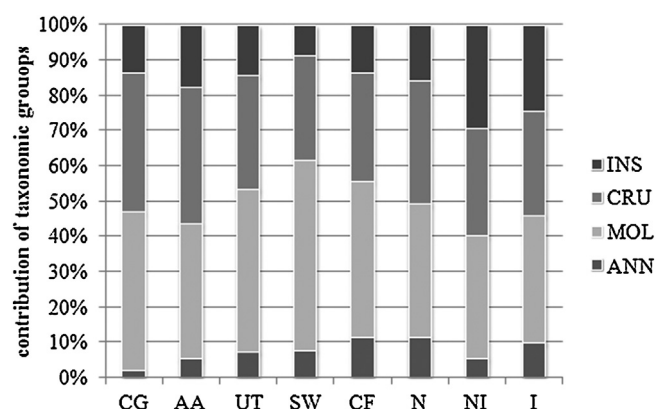

Fig. 1. Percentage contribution of the main taxonomic groups (ANN – Annelida, MOL – Mollusca, CRU – Crustacea, INS – Insecta) according to treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive).
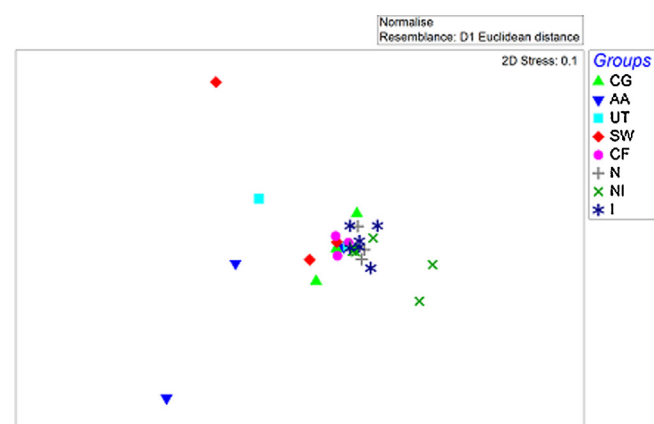

Fig. 2. Results of NMDS ordination based on overall community structure. Treatments: CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive.

contributed with more than 5%: amphipods (28.3%), bivalves (23.2%), gastropods (18.6%), caddis larvae (17.1%), oligochaetes (6.9%), and isopods (5.3%). Dipterans (mainly chironomids), leeches and flatworms were found in very low density. The five most abundant taxa were *C. fluminea* (20%), *Hydropsyche bulgaromanorum* (9.9%), *Chelicorophium curvispinum* (7.7%), *Lithoglyphus naticoides* (6.9%) and oligochaetes (6.7%) (Table 1).

The PERMANOVA analysis showed significant differences in overall community structure (pseudo $F = 1.701$, df = 7, $p < 0.01$). In pairwise comparisons *A. anatina* differed significantly from the mix of shells (*A. anatina*-mix native: $t = 1.805$, $p < 0.05$; *A. anatina*-mix native plus invasive: $t = 1.690$, $p < 0.05$; *A. anatina*-mix invasive: $t = 1.681$, $p < 0.05$). The MDS ordination including all the recorded taxa revealed a different community structure associated with larger shells of unionids (Fig. 2).

If we compare the main taxonomic groups of macroinvertebrates significant differences were found in annelids (pseudo $F = 2.154$, df = 7, $p < 0.05$), molluscs (pseudo $F = 1.817$, df = 7, $p < 0.01$) and crustaceans (pseudo $F = 1.860$, df = 7, $p < 0.05$) (Fig. 3a–c), but no significant differences were detected in insects (Fig. 3d). Pairwise comparisons indicated that the density of annelids was significantly lower on control substrates, than on *A. anatina* ($t = 6.549$, $p < 0.01$), mix native ($t = 2.593$, $p < 0.05$) and *C. fluminea* ($t = 2.828$, $p < 0.05$); and it was significantly higher on *A. anatina* than on *C. fluminea* ($t = 4.608$, $p < 0.01$). The density of molluscs was significantly higher on *A. anatina* and *S. woodiana* than on mixed shells

Table 1
Mean (±SD) density (ind. m^{-2}) of recorded taxa per treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – native species, NI – native and invasive species, I – invasive species).

	CG	AA	UT	SW	CF	N	NI	I
Platyhelminthes								
Polycelis sp.	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Annelida								
Erpobdella octoculata	0.0 ± 0.0	0.0 ± 0.0	2.2 ± 3.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Helobdella stagnalis	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 1.6	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Oligochaeta	1.5 ± 2.6	21.5 ± 4.6	15.6 ± 3.1	20.7 ± 18.0	7.4 ± 2.6	33.3 ± 20.5	19.4 ± 21.5	25.0 ± 17.0
Mollusca								
Acroloxus lacustris	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.73 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ancylus fluviatilis	0.0 ± 0.0	1.5 ± 1.3	1.1 ± 1.6	1.5 ± 1.3	0.7 ± 1.3	0.0 ± 0.0	0.5 ± 1.1	0.9 ± 2.3
Anodonta anatina	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.5 ± 1.1	0.0 ± 0.0	0.0 ± 0.0
Bithynia tentaculata	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.5 ± 1.1	0.0 ± 0.0
Borysthenia naticina	0.7 ± 1.3	3.0 ± 3.4	1.1 ± 1.6	1.5 ± 2.6	2.2 ± 3.8	0.5 ± 1.1	0.0 ± 0.0	0.0 ± 0.0
Corbicula fluminea	11.9 ± 3.4	48.2 ± 42.7	26.7 ± 28.3	34.8 ± 24.5	11.1 ± 9.7	84.7 ± 43.6	108.8 ± 26.4	69.9 ± 19.1
Dreissena polymorpha	4.4 ± 0.0	5.9 ± 5.6	1.1 ± 1.6	3.0 ± 3.4	2.2 ± 3.8	0.0 ± 0.0	0.9 ± 2.3	0.5 ± 1.1
Esperiana daudebartii	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Esperiana esperi	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1	0.0 ± 0.0
Galba truncatula	0.0 ± 0.0	1.5 ± 2.6	0.0 ± 0.0	1.5 ± 2.6	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Haitia acuta	0.0 ± 0.0	0.7 ± 1.3	2.2 ± 3.1	2.2 ± 3.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Lithoglyphus naticoides	30.4 ± 19.2	42.2 ± 32.9	41.1 ± 51.9	48.1 ± 38.8	17.8 ± 7.7	7.9 ± 4.5	9.3 ± 12.0	12.0 ± 6.5
Musculium lacustre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.5 ± 1.1	0.0 ± 0.0	0.0 ± 0.0
Pisidium amnicum	1.5 ± 2.6	3.0 ± 1.3	2.2 ± 0.0	2.2 ± 2.2	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pisidium casertanum	0.0 ± 0.0	2.2 ± 2.2	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pisidium henslowanum	0.0 ± 0.0	4.4 ± 2.2	0.0 ± 0.0	5.2 ± 3.4	0.0 ± 0.0	0.5 ± 1.1	0.5 ± 1.1	0.0 ± 0.0
Pisidium moitessierianum	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.7 ± 4.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pisidium subtruncatum	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	0.5 ± 1.1	0.0 ± 0.0	0.5 ± 1.1
Pisidium supinum	2.2 ± 2.2	6.7 ± 0.0	5.6 ± 7.9	6.7 ± 5.9	3.0 ± 2.6	0.5 ± 1.1	0.0 ± 0.0	0.5 ± 1.1
Potamopyrgus antipodarum	0.0 ± 0.0	12.6 ± 16.4	4.4 ± 6.3	4.4 ± 3.8	2.2 ± 2.2	0.5 ± 1.1	1.4 ± 3.4	1.4 ± 1.5
Radix balthica	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Sphaerium rivicola	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 2.3
Sphaerium solidum	5.9 ± 3.4	8.1 ± 1.3	7.8 ± 4.7	3.7 ± 3.4	4.4 ± 2.2	5.6 ± 3.9	4.2 ± 2.9	3.2 ± 1.1
Theodoxus danubialis	2.2 ± 2.2	1.5 ± 2.6	2.2 ± 3.1	3.7 ± 1.3	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Theodoxus fluviatilis	11.1 ± 8.9	15.6 ± 21.4	25.6 ± 36.1	25.9 ± 19.2	7.4 ± 5.6	9.3 ± 9.6	4.6 ± 5.2	3.2 ± 3.2
Unio tumidus	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Viviparus acerosus	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Crustacea								
Chelicorophium curvispinum	42.2 ± 49.6	85.9 ± 75.6	43.3 ± 58.1	53.3 ± 61.7	25.9 ± 41.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Chelicorophium robustum	1.5 ± 2.6	0.7 ± 1.3	3.3 ± 4.7	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Chelicorophium sowinskyi	0.0 ± 0.0	2.2 ± 3.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Chelicorophium sp.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	13.9 ± 11.7	26.9 ± 13.2	12.3 ± 11.3
Dikerogammarus bispinosus	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	44.4 ± 46.2	34.7 ± 19.0	20.4 ± 11.5
Dikerogammarus haemobaphes	24.4 ± 33.2	25.2 ± 14.8	25.6 ± 36.1	10.4 ± 10.0	13.3 ± 19.2	12.5 ± 10.9	9.7 ± 8.0	7.9 ± 7.7
Dikerogammarus villosus	14.8 ± 17.0	20.0 ± 10.2	16.7 ± 17.3	17.0 ± 6.8	11.9 ± 12.8	12.5 ± 15.4	6.9 ± 5.8	6.0 ± 4.5
Echinogammarus ischnus	25.9 ± 18.6	32.6 ± 39.5	20.0 ± 9.4	20.0 ± 19.8	14.8 ± 19.9	3.2 ± 6.7	8.3 ± 9.1	4.6 ± 5.5
Echinogammarus trichiatus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 2.3	0.9 ± 1.4
Jaera istri	5.9 ± 6.8	45.2 ± 39.1	20.0 ± 28.3	17.8 ± 20.4	3.7 ± 6.4	3.7 ± 4.9	7.4 ± 7.6	4.6 ± 3.8
Obesogammarus obesus	3.0 ± 5.1	29.6 ± 24.0	6.7 ± 9.4	23.7 ± 20.5	1.5 ± 2.6	12.5 ± 8.9	19.0 ± 16.8	18.5 ± 14.8
Insecta								
Brachycentrus subnubilus	0.7 ± 1.3	7.4 ± 7.8	1.1 ± 1.6	3.0 ± 1.3	2.2 ± 3.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Hydropsyche bulgaromanorum	20.0 ± 22.6	20.7 ± 12.2	26.7 ± 25.1	14.8 ± 11.0	11.1 ± 9.7	24.5 ± 15.8	52.3 ± 39.8	42.1 ± 31.8
Hydropsyche contubernalis	2.2 ± 2.2	28.9 ± 40.8	7.8 ± 11.0	1.5 ± 2.6	3.0 ± 3.4	9.7 ± 6.5	31.0 ± 32.5	7.4 ± 4.9
Hydropsyche ornatula	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1	0.9 ± 2.3
Hydropsyche sp. juvenilis	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	12.5 ± 12.8	23.6 ± 18.7	11.1 ± 12.5
Ephemera danica	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 1.4	0.0 ± 0.0
Heptagenia flava	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 1.4	0.0 ± 0.0
Gomphus vulgatissimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1
Gomphus flavipes	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1
Chironomidae	0.0 ± 0.0	3.7 ± 4.6	1.1 ± 1.6	2.2 ± 3.8	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1
Ceratopogonidae	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.1	0.0 ± 0.0
Diptera pupa	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Limoniidae	0.0 ± 0.0	0.7 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

(*A. anatina*-mix native: $t = 1.816$, $p < 0.05$; *A. anatina*-mix native plus invasive: $t = 1.874$, $p < 0.05$; *A. anatina*-mix invasive: $t = 1.855$, $p < 0.05$; *S. woodiana*-mix native plus invasive: $t = 1.843$, $p < 0.05$; *S. woodiana*-mix invasive: $t = 1.817$, $p < 0.05$). The density of crustaceans was also significantly higher on *A. anatina* than on mixed shells (*A. anatina*-mix native: $t = 1.848$, $p < 0.05$; *A. anatina*-mix native plus invasive: $t = 1.901$, $p < 0.05$; *A. anatina*-mix invasive: $t = 1.966$, $p < 0.05$).

The proportion of functional feeding groups differed with treatments and was dominated by active filter-feeders (44.5%), gathering collectors (21.3%) and grazers (11.5%). Other groups were represented by lower values: predators (7.4%), shredders (7.4%), other feeders (5.0%) and passive filter-feeders (2.9%) (Fig. 4). On the level of functional feeding groups significant differences in all groups were found: active filter-feeders (pseudo $F = 2.567$, df = 7, $p < 0.001$), passive filter-feeders (pseudo $F = 2.621$, df = 7, $p < 0.05$), gathering collectors (pseudo $F = 1.827$, df = 7, $p < 0.01$), grazers (pseudo $F = 1.943$, df = 7, $p < 0.01$), shredders (pseudo $F = 2.365$, df = 7, $p < 0.01$), predators (pseudo $F = 2.124$, df = 7, $p < 0.01$) and other feeding types (pseudo $F = 2.124$, df = 7, $p < 0.01$). These significant differences were due to the distinct colonization of individual and mixed shells (Table 2, Fig. 5).
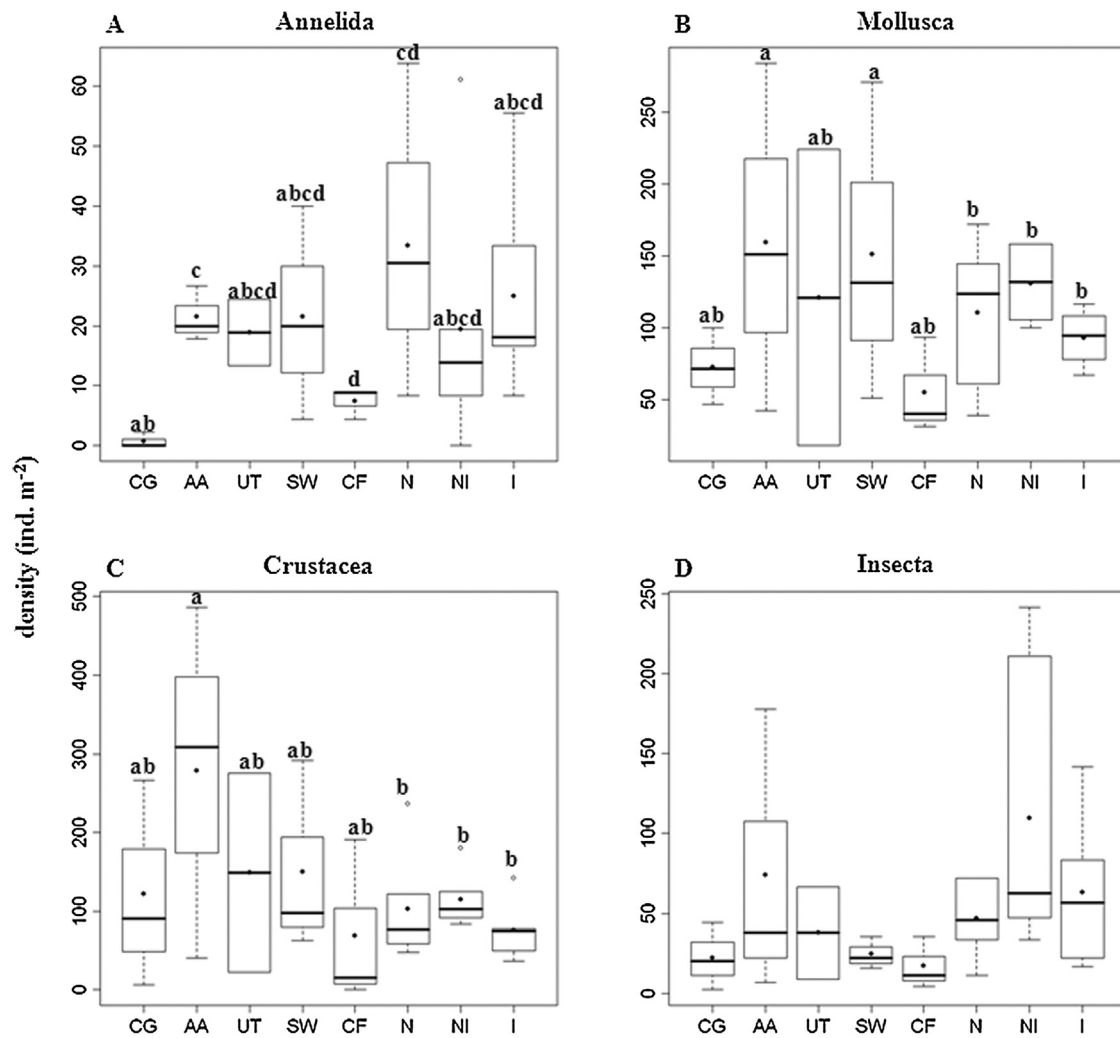
Fig. 3. The density of the main taxonomic groups (Annelida (a), Mollusca (b), Crustacea (c), Insecta (d)) according to treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive). Box plots represent the lower and upper quartiles, the minimum and maximum values. Median and mean values are indicated by bold horizontal lines and dots, respectively. Statistically significant differences between treatments are represented by different letters.

The richness and Shannon-Wiener diversity were higher on *A. anatina* and *S. woodiana* shells, than on other treatments, and the density was higher on *A. anatina* and *S. woodiana* shells and on mix of native shells than on *C. fluminea* shells and on control substrate (Fig. 6a–c). However, statistically significant differences were

detected only in the case of Shannon–Wiener diversity (pseudo $F = 3.786$, df = 7, $p < 0.01$ (Fig. 6c). Pairwise comparisons showed that the diversity was higher on *A. anatina* and *S. woodiana* than on all types of mixed shells (*A. anatina*-mix native: $t = 3.995$, $p < 0.01$; *A. anatina*-mix native plus invasive: $t = 3.568$, $p < 0.01$;

Table 2
Pairwise comparisons of treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive) per functional feeding groups (AFIL – active filter-feeders, PFIL – passive filter-feeders, GCOL – gathering collectors, GRA – grazers, SCH – shredders, PRE – predators, OTH – other feeders), where significant differences were found.

| AFIL		PFIL	GCOL	GRA	SCH	PRE	OTH
CG-N	$p < 0.05, t = 1.791$	$p < 0.05, t = 2.481$	$p < 0.05, t = 1.719$	–	–	$p < 0.05, t = 1.660$	$p < 0.05, t = 1.660$
CG-NI	$p < 0.05, t = 1.865$	$p < 0.05, t = 2.078$	$p < 0.05, t = 1.961$	–	$p < 0.05, t = 1.904$	$p < 0.05, t = 1.750$	$p < 0.05, t = 1.750$
CG-I	$p < 0.05, t = 1.744$	$p < 0.05, t = 2.376$	–	–	$p < 0.05, t = 1.861$	$p < 0.05, t = 1.713$	$p < 0.05, t = 1.713$
AA-N	$p < 0.01, t = 2.407$	–	$p < 0.05, t = 1.721$	$p < 0.05, t = 1.998$	$p < 0.05, t = 1.962$	$p < 0.05, t = 2.007$	$p < 0.05, t = 2.007$
AA-NI	$p < 0.01, t = 2.353$	–	$p < 0.05, t = 1.803$	$p < 0.05, t = 1.923$	$p < 0.05, t = 2.260$	$p < 0.05, t = 2.084$	$p < 0.05, t = 2.084$
AA-I	$p < 0.01, t = 2.419$	–	$p < 0.05, t = 1.954$	$p < 0.05, t = 2.016$	$p < 0.05, t = 2.299$	$p < 0.05, t = 2.111$	$p < 0.05, t = 2.111$
UT-N	$p < 0.05, t = 1.814$	$p < 0.05, t = 2.980$	–	–	–	–	–
UT-NI	$p < 0.05, t = 1.825$	$p < 0.05, t = 2.555$	–	–	$p < 0.05, t = 1.821$	–	–
UT-I	–	$p < 0.05, t = 2.908$	–	–	$p < 0.05, t = 1.854$	–	–
SW-N	$p < 0.05, t = 1.778$	$p < 0.05, t = 2.909$	–	$p < 0.05, t = 1.890$	$p < 0.05, t = 1.894$	$p < 0.05, t = 1.782$	$p < 0.05, t = 1.782$
SW-NI	$p < 0.05, t = 1.992$	$p < 0.05, t = 2.376$	–	$p < 0.05, t = 1.775$	$p < 0.01, t = 2.424$	$p < 0.05, t = 1.896$	$p < 0.05, t = 1.896$
SW-I	$p < 0.05, t = 1.845$	$p < 0.05, t = 2.812$	$p < 0.05, t = 1.752$	$p < 0.05, t = 1.914$	$p < 0.01, t = 2.503$	$p < 0.05, t = 1.875$	$p < 0.05, t = 1.875$
CF-N	$p < 0.05, t = 1.662$	–	–	–	–	–	–
CF-NI	$p < 0.05, t = 1.727$	–	–	–	$p < 0.05, t = 1.899$	–	$p < 0.05, t = 1.620$
CF-I	–	–	$p < 0.05, t = 1.778$	–	$p < 0.05, t = 1.845$	–	–
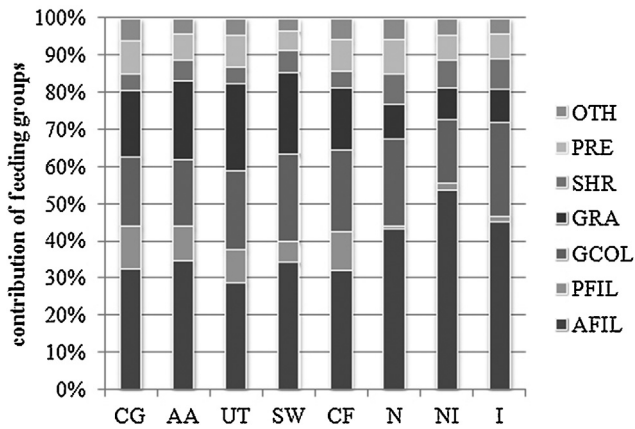
Fig. 4. Percentage contribution of the main functional feeding groups (AFIL – active filter-feeders, PFIL – passive filter-feeders, GCOL – gathering collectors, GRA – grazers, SCH – shredders, PRE – predators, OTH – other feeders) of macroinvertebrates according to treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive).

A. anatina-mix invasive: $t = 2.940$, $p < 0.05$; *S. woodiana*-mix native: $t = 3.432$, $p < 0.01$; *S. woodiana*-mix native plus invasive: $t = 3.043$, $p < 0.05$; *S. woodiana*-mix invasive: $t = 2.527$, $p < 0.05$) and the control substrate and *C. fluminea* differed from two types of mixed shells (control substrate-mix native: $t = 3.298$, $p < 0.05$; control substrate-mix native plus invasive: $t = 2.487$, $p < 0.05$; *C. fluminea*-mix native: $t = 4.650$, $p < 0.01$; *C. fluminea*-mix native plus invasive: $t = 4.052$, $p < 0.01$).

No relationship was found between shell size and taxon number, density and Shannon-Wiener diversity (Pearson's correlation, Linear Regression, $r = 0.307$, $R^2 = 0.061$, $p = 0.105$; $r = 0.298$, $R^2 = 0.055$, $p = 0.117$; $r = 0.245$, $R^2 = 0.025$, $p = 0.200$, respectively).

Discussion

Our results showed that the empty shells of the studied bivalve species provided suitable habitat and refuges for most of the benthic organisms, especially for molluscs, crustaceans and insects. In the same vein, the individual empty shells were colonized in a different way than the control substrate (clay granules), which mimics the natural hard substrates in the studied area. In fact, the studied empty bivalve shells generated a great diversity of microhabitats allowing the colonization by numerous taxa otherwise not represented or only found in low density in the natural substrates of the studied watercourse characterized by silt and sandy bottoms. In comparison with an earlier study by Nosek et al. (2009), that reported data from the same sampling site, we conclude that the empty bivalve shells attracted macroinvertebrate fauna, which was different from the natural macroinvertebrate community composition. For example, in our study the dominant taxonomic groups were amphipods (28%), bivalves (23%), gastropods (19%), caddis larvae (17%), and oligochaetes and isopods contributed to more than 5% of the total fauna, while Nosek et al. (2009) demonstrated that in the depositional littoral zone of the Danube River the community was composed mainly of bivalves (39%), chironomids (34%), gastropods (10%) and oligochaetes (11%). Amphipods, caddis larvae and isopods were found only in low density (<2%). In summary, the modification of the macroinvertebrate community structure by empty bivalve shells on bottom texture of silt and sand was marked by an increase in amphipods, caddis larvae, isopods and gastropods, and a decrease in bivalves, chironomids and oligochaetes (i.e. the empty shells facilitate mainly the epifaunal and inhibit the presence of infaunal elements).

Certain taxonomic groups may be favoured by empty shells by different reasons. Shells can assure hard substrate in an otherwise unstructured area, or afford interstitial spaces as refuges from predators or abiotic disturbances such as water flow changes by its structural complexity, and direct and indirect trophic interactions can turn up due to the appearance of several species (reviewed in Gutiérrez et al., 2003; Karatayev et al., 2002; Stewart et al., 1998). Amphipods and caddis larvae likely find refuges among the empty bivalve shells, while gastropods, leeches and flatworms found attachment sites with the presence of hard substrate, and the altered trophic conditions.

The accumulation of empty bivalve shells probably contributes to a considerable shift in the trophic structure of the studied benthic community. In our study the dominant functional feeding guilds on empty bivalve shells were active filter-feeders (45%), gathering collectors (21%) and grazers (12%), while shredders and predators contributed to more than 5% of the total fauna. Nosek et al. (2009) mainly reported active filter-feeders (46%), gathering collectors (34%) and grazers (11%) in the depositional areas of the Danube River, while the other feeding groups contributed to less than 5%. Hence, the accumulation of empty bivalve shells on siltier and sandier sediments seems to be able to transform the composition of feeding groups by decreasing the proportion of gathering collectors and increasing the proportion of shredders and predators.

Overall, our findings follow results that have been described in several studies dealing with the complex facilitative effect of living bivalves, especially epibenthic species (Borthagaray and Carranza, 2007; Burlakova et al., 2012; Zaiko et al., 2009), but little attention has been paid for the habitat modifying effect of empty bivalve shells. In theory, the living bivalves have a more powerful effect on the ecosystem since they have both autogenic and allogenic ecosystem engineering mechanisms. Some studies reported that the impact of living bivalves (for example zebra mussels) on benthic communities was more pronounced than the effect of shells (Stewart et al., 1998; Zaiko et al., 2009). In fact, these studies found a continuous shift in species composition, abundance and biomass along the gradient 'bare substrate-empty shells-live zebra mussels', which indicated that empty shells have also a considerable importance in modifying the structure of benthic communities. In addition, studies carried out in marine ecosystems also showed that the physical structure of bivalves largely contribute to their overall effects on other organisms (Palomo et al., 2007).

Interestingly, in our study differences in macroinvertebrate colonization were detected between different bivalve species and the individual and mixed shells. Our results showed that the individual larger shelled unionids *A. anatina* and *S. woodiana* attracted a denser and more diverse macroinvertebrate community than the smaller shelled *C. fluminea* and the mixed shells of different sizes. These results suggest that the shell size may play an important role in determining the macroinvertebrate composition. In fact, the shell size can increase the shell cavity and space available for shelter, and thus larger shells can act as a surface for settlement and a refuge area multiplying the likelihood of a denser and more diverse benthic community. This may be particularly important in rivers with sand or silt bottoms and few hard substrates, as unionids provide a large amount of stable hard substrate for associated organisms (Beckett et al., 1996). However, in our study no significant relationship was established between shell size and richness, density and diversity. Indeed, other shell traits such as outer-shell surface roughness, shell hardness, thickness, 3D shape and chemical composition may be different between species and these aspects could also have influenced the associated fauna; future studies have to be conducted in order to disentangle the importance of these shell traits.
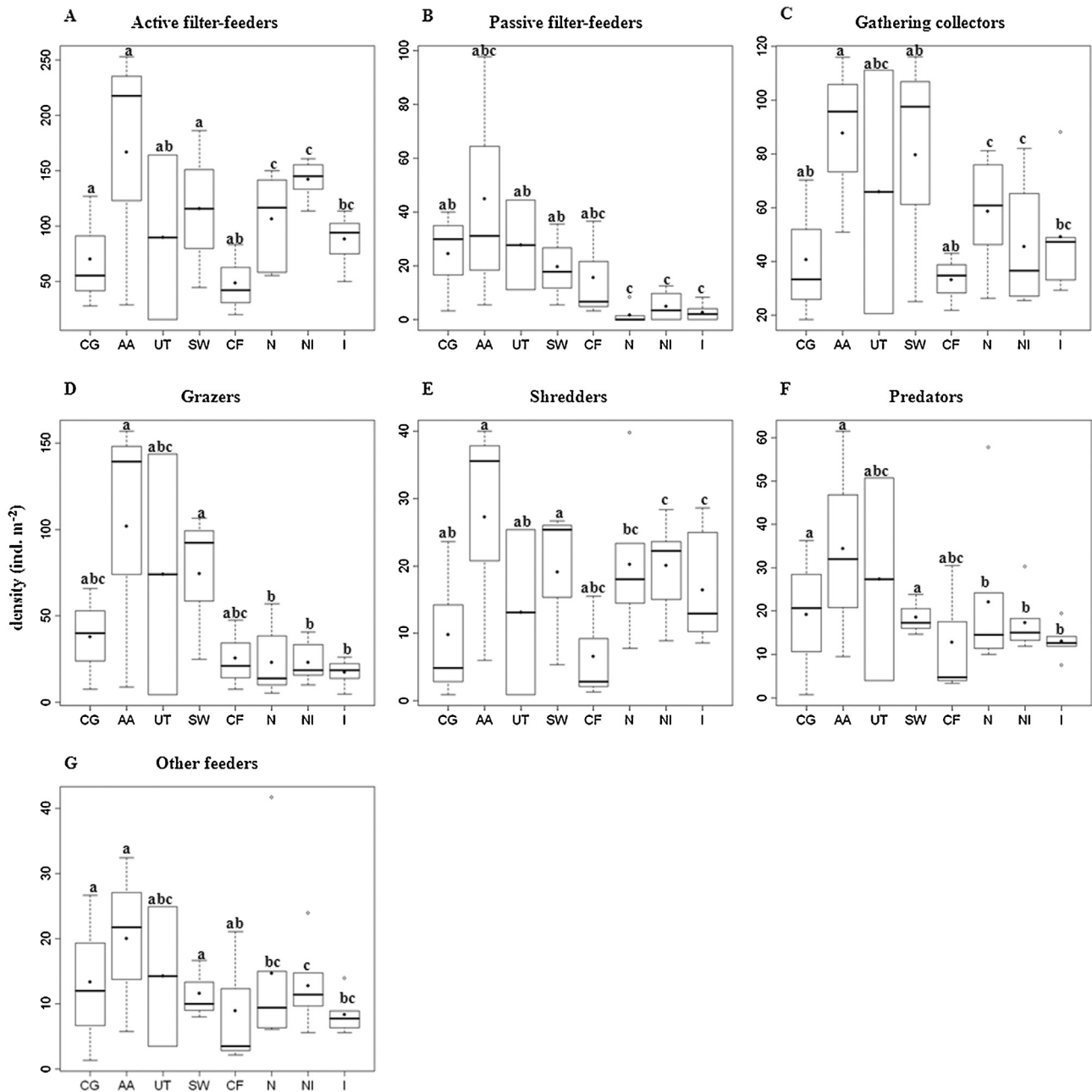
Fig. 5. The density of the main functional feeding groups (active filter-feeders (a), passive filter-feeders (b), gathering collectors (c), grazers (d), shredders (e), predators (f), other feeders (g)) according to treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive). Box plots represent the lower and upper quartiles, the minimum and maximum values. Median and mean values are indicated by bold horizontal lines and dots, respectively. Statistically significant differences between treatments are represented by different letters.

Anthropogenic disturbances can strongly modify communities by removing native engineers through habitat degradation and introducing invasive engineers, which may have unforeseen consequences. Bouma et al. (2009) suggested that the local biodiversity effects of invasive ecosystem engineers will depend on the engineering strength (i.e. the number of habitats it can invade and the extent of modification) of the invasive species. In the Danube River, both *C. fluminea* and *S. woodiana* are widespread and capable of producing large amounts of empty shells due to their massive mortality during extreme climatic events (Bódis et al., 2014). Given the widespread distribution, high density and the relatively long-term persistence of their empty shells, their habitat modifying effects can be particularly important.

In conclusion, our study clearly showed that the empty shells of bivalves can induce changes in the benthic community in a large river such as the Danube. The accumulation of empty shells can facilitate the presence of amphipods, caddis larvae and isopods, which contributed to a shift in the trophic structure by decreasing the proportion of gathering collectors while increasing the presence of shredders and predators.

However, in order to assess the overall and long-term effects of empty bivalve shells on benthic communities, it is important to consider shell persistence and decay rates, and the colonization process of other benthic organisms, such as benthic algae, which may prefer other attributes of empty shells as substrate, and may trigger considerable changes in trophic structure.
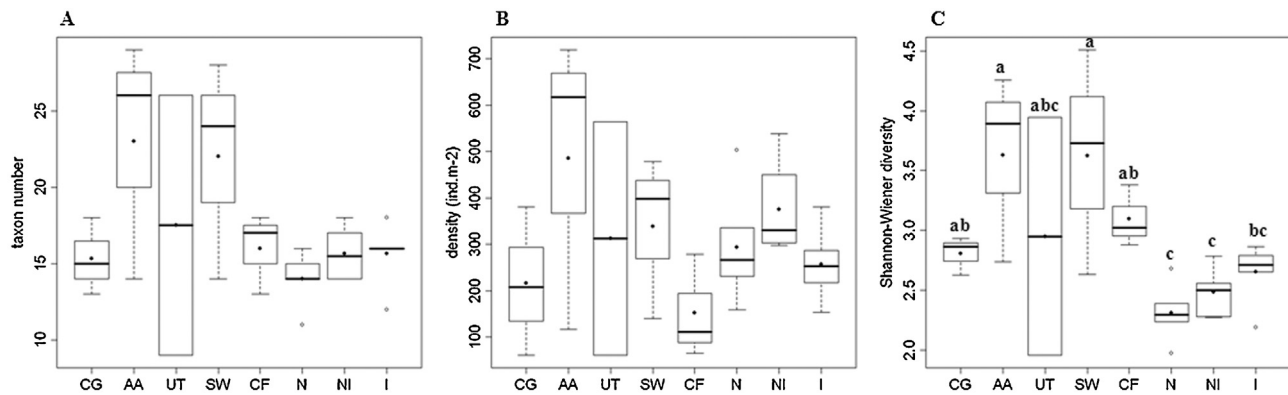
Fig. 6. Taxon number (a), density (b) and Shannon–Wiener diversity (c) according to treatments (CG – clay granules, AA – *Anodonta anatina*, UT – *Unio tumidus*, SW – *Sinanodonta woodiana*, CF – *Corbicula fluminea*, N – mix native, NI – mix native plus invasive, I – mix invasive). Box plots represent the lower and upper quartiles, the minimum and maximum values. Median and mean values are indicated by bold horizontal lines and dots, respectively. Statistically significant differences between treatments are represented by different letters.

Acknowledgements

References

Askew, R.R., 2004. The Dragonflies of Europe. Harley Books, Colchester.

Beckett, D.C., Green, B.W., Thomas, S.A., Miller, A.C., 1996. Epizoic invertebrate communities on upper Mississippi River unionid bivalves. Am. Midl. Nat. 135, 102–114.

Beekey, M.A., McCabe, D.J., Marsden, J.E., 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. Oecologia 141, 164–170.

Borthagaray, A.I., Carranza, A., 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. Acta Oecol. 31, 243–250.

Bouma, T.J., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgoland Mar. Res. 63, 95–106.

Bódis, E., Nosek, J., Oertel, N., Tóth, B., Hornung, E., Sousa, R., 2011. Spatial distribution of bivalves in relation to environmental conditions (middle Danube catchment, Hungary). Community Ecol. 12 (2), 210–219.

Bódis, E., Borza, P., Potyó, I., Puky, M., Weipert, A., Guti, G., 2012a. Invasive mollusc, crustacean, fish and reptile species along the Hungarian section of the River Danube and some connected waters. Acta Zool. Acad. Sci. Hung. 58 (Suppl. 1), 29–45.

Bódis, E., Sipkay Cs Tóth, B., Oertel, N., Nosek, J., Hornung, E., 2012b. Spatial and temporal variation in biomass and size structure of Corbicula fluminea in Middle Danube catchment, Hungary. Biologia (Bratisl.) 67 (4), 739–750.

Bódis, E., Tóth, B., Sousa, R., 2014. Massive mortality of invasive bivalves as a potential resource subsidy for the adjacent terrestrial food web. Hydrobiologia 735, 253–262.

Burlakova, L.E., Karatayev, A.Z., Karatayev, A.V., 2012. Invasive mussels induce community changes by increasing habitat complexity. Hydrobiologia 685, 121–134.

Byers, J.E., Cuddington, K., Jones, C.G., Hastings, A., Lambrinos, J.G., Crooks, J.A., Wilson, W.G., 2006. Using ecosystem engineers to restore ecological systems. Trends Ecol. Evol. 21 (9), 493–500.

Cărăuşu, S., Dobreanu, E., Manolache, C., 1955. Amphipoda forme salmastre şi de apă dulce (Freshwater and brackish water Amphipoda). Fauna Republicii populare Romîne, vol. 4, 4. Editura Academiei Republicii Populare Romîne, Bucureşti.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Dieterich, A., Mörtl, M., Eckmann, R., 2004. The effects of zebra mussels (Dreissena polymorpha) on the foraging success of Eurasian perch (Perca fluviatilis) and ruffe (Gymnocephalus cernuus). Int. Rev. Hydrobiol. 89, 229–237.

Douda, K., Vrtilek, M., Slavik, O., Reichard, M., 2012. The role of host specificity in explaining the invasion success of the freshwater mussel Anodonta woodiana in Europe. Biol. Invasions 14, 127–137.

Eggers, T.O., Martens, A., 2001. Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42, 1–68.

Glöer, P., Meier-Brook, C., 1998. Süsswassermollusken, 12 Aufl. Deutscher Jugendbund für Naturbeobachtung, Hamburg.

Gutiérrez, J.L., Iribarne, O.O., 1999. Role of Holocene beds of the stout razor clam Tagelus plebeius in structuring present benthic communities. Mar. Ecol. Prog. Ser. 185, 213–228.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Gutiérrez, J.L., Jones, C.G., 2006. Physical ecosystem engineers as agents of biogeochemical heterogeneity. BioScience 56, 227–236.

Ilarri, M., Antunes, C., Guilhermino, L., Sousa, R., 2011. Massive mortality of the Asian clam Corbicula fluminea in a highly invaded area. Biol. Invasions 13, 277–280.

Ilarri, M., Freitas, F., Costa-Dias, S., Antunes, C., Guilhermino, L., Sousa, R., 2012. Associated macrozoobenthos with the invasive Asian clam Corbicula fluminea. J. Sea Res. 72, 113–120.

Ilarri, M.I., Souza, A.T., Antunes, C., Guilhermino, L., Sousa, R., 2014. Influence of the Asian clam Corbicula fluminea (Bivalvia: Corbiculidae) on estuarine epibenthic assemblages. Estuarine Coastal Shelf Sci. 143, 12–19.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78 (7), 1946–1957.

Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In: Leppakoski, E., Gollach, S., Olenin, S. (Eds.), Invasive Aquatic Species of Europe: Distribution, Impacts and Management. Kluwer Academic Publishers, Dordrecht.

Mayer, C.M., Rudstam, L.G., Mills, E.L., Cardiff, S.G., Bloom, C.A., 2001. Zebra mussels (Dreissena polymorpha), habitat alteration, and yellow perch (Perca flavescens) foraging: system-wide effects and behavioural mechanisms. Can. J. Fish. Aquat. Sci. 58, 2459–2467.

Moog, O., 2002. Fauna Aquatica Austriaca, 2002 ed. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Vienna.

Nesemann, H., 1997. Egel und Krebsegel Österreichs. Sonderheft der Ersten Vorarlberger Malakologischen Gesellschaft, Rankweil.

Nosek, J.N., 2002. Macroinvertebrate studies at the Hungarian Danube section. 4. The colonization dynamics of macroinvertebrates of different substrates. Limnological Reports [Proceedings of the International Association for Danube Research], vol. 34. Editura Academia Romana, Bucharest, pp. 317–326.

Nosek, J., Oertel, N., Bódis, E., Tóth, B., 2009. A bentikus szervesanyag és a makrogerinctelen társulások tér- és időbeli változása a Duna Kismaros (1688 fkm) és Göd (1668 fkm) közötti szakaszán (Spatial and temporal changes of benthic organic matter and macroinvertebrate communities in the Kismaros (1688 rkm)-Göd (1668 rkm) section of the River Danube). Acta Biol. Debrecina Suppl. Oecol. Hung. 20, 165–179.

Oertel, N., 2002. Macroinvertebrate studies at the Hungarian Danube section. 3. Artificial substrate as a tool to study macroinvertebrate colonization. Limnological Reports [Proceedings of the International Association for Danube Research], vol. 34. Editura Academia Romana, Bucharest, pp. 327–336.

Oertel, N., Nosek, J.N., 2006. Sampling of macroinvertebrates by artificial substrates in the River Danube Hungary. Verhandlungen Internationale Vereinigung Für Theoretische und Angewandte Limnologie 29 (Part 4), 1762–1766.

Palacios, R., Armstrong, D.A., Orensanz, J., 2000. Fate and legacy of an invasion: extinct and extant populations of the soft-shell clam (Mya arenaria) in Grays Harbor (Washington). Aquat. Conserv. 10, 279–303.

Palomo, M.G., People, J., Underwood, A.J., Chapman, M.G., 2007. Separating the effects of physical and biological aspects of mussel-beds on their associated assemblages. Mar. Ecol. Prog. Ser. 344, 131–142.

R Development Core team, 2007. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org

Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Can. J. Fish. Aquat. Sci. 52, 1449–1461.

Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can. J. Fish. Aquat. Sci. 54, 2596–2608.

Richnovszky, A., Pintér, L., 1979. A vízicsigák és kagylók (Mollusca) kishatározója. In: Felföldy, L. (Ed.), Vízügyi Hidrológia 6. VIZDOK, Budapest.

Sousa, R., Nogueira, A.J.A., Gaspar, M., Antunes, C., Guilhermino, L., 2008. Growth and extremely high production of the non-indigenous invasive species *Corbicula fluminea* (Müller, 1774): possible implications for ecosystem functioning. Estuarine Coastal Shelf Sci. 80, 289–295.

Sousa, R., Gutiérrez, J.L., Aldridge, D.C., 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biol. Invasions 11, 2367–2385.

Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J., Guilhermino, L., 2012. Massive die-offs of freshwater bivalves as resource pulses. Ann. Limnol. – Int. J. Limnol. 48, 105–112.

Sousa, R., Novais, A., Costa, R., Strayer, D.L., 2014. Invasive bivalves in fresh waters: impacts from individuals to ecosystems and possible control strategies. Hydrobiologia 735, 233–251.

Stewart, T.W., Miner, J.G., Lowe, R.L., 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. J. N. Am. Benthol. Soc. 17, 81–94.

Strayer, D.L., Caraco, N.F., Cole, J.J., Findlay, S., Pace, M.L., 1999. Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. BioScience 49, 19–27.

Sylvester, F., Boltovskoy, D., Cataldo, D., 2007. The invasive bivalve *Limnoperna fortunei* enhances benthic invertebrate densities in South American floodplain rivers. Hydrobiologia 589, 15–27.

Vaughn, C.C., Hakenkamp, C.C., 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biol. 46, 1431–1446.

Waringer, J., Graf, W., 1997. Atlas der Östereichischen Köcherfliegenlarven. Facultas Universitätsverlag, Wien.

Werner, S., Rothhaupt, K.O., 2007. Effects of the invasive bivalve *Corbicula fluminea* on settling juveniles and other benthic taxa. J. N. Am. Benthol. Soc. 26 (4), 673–680.

Wright, J.P., Jones, C.G., 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56 (3), 203–209.

Zaiko, A., Daunys, D., Olenin, S., 2009. Habitat engineering by the invasive zebra mussel *Dreissena polymorpha* (Pallas) in a boreal coastal lagoon: impact on biodiversity. Helgoland Mar. Res. 63, 85–94.