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

E. Bódis[a,*], B. Tóth[a], J. Szekeres[a], P. Borza[a], R. Sousa[b,c]

[a] MTA Centre for Ecological Research, Danube Research Institute, Karolina út 29-31, 1113 Budapest, Hungary
[b] Interdisciplinary Centre of Marine and Environmental Research (CIIMAR/CIMAR), University of Porto, Rua dos Bragas 289, P 4050-123 Porto, Portugal
[c] CBMA – Centre of Molecular and Environmental Biology, Department of Biology, University of Minho, Campus de Gualtar, 4710-057 Braga, Portugal

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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.

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

* Corresponding author. Tel.: +36 1 279 3100.
E-mail address: bodis.erika@okologia.mta.hu (E. Bódis).

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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 Rothaupt, 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.