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FRESHWATER BIVALVES

# Massive mortality of invasive bivalves as a potential resource subsidy for the adjacent terrestrial food web

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**Abstract** Large-scale mortality of invasive bivalves was observed in the River Danube basin in the autumn of 2011 due to a particularly low water discharge. The aim of this study was to quantify and compare the biomass of invasive and native bivalve die-offs amongst eight different sites and to assess the potential role of invasive bivalve die-offs as a resource subsidy for the adjacent terrestrial food web. Invasive bivalve die-offs dominated half of the study sites and their highest density and biomass were recorded at the warm water effluent. The density and biomass values recorded in this study are amongst the highest values recorded for aquatic ecosystems and show that a habitat affected by heated water can sustain an

extremely high biomass of invasive bivalves. These mortalities highlight invasive bivalves as a major resource subsidy, possibly contributing remarkable amounts of nutrients and energy to the adjacent terrestrial ecosystem. Given the widespread occurrence of these invasive bivalves and the predicted increase in the frequency and intensity of extreme climatic events, the ecological impacts generated by their massive mortalities should be taken into account in other geographical areas as well.

**Keywords** River Danube · *Sinanodonta woodiana* · *Corbicula fluminea* · Invasive species · Climate change · Resource subsidy

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## Introduction

In recent decades, the spread of non-indigenous invasive species in aquatic ecosystems has been highly accelerated, resulting in important changes in ecological processes and functions (Lodge et al., 1998; Ricciardi & MacIsaac, 2000; Kolar & Lodge, 2002; Strayer, 2010). Although many species have been introduced, special attention should be given to those invasive species that dominate the community in terms of density and biomass or carry new attributes to the ecosystem (Simberloff, 2011; Sousa et al., 2011). Invasive bivalves may have a key role in aquatic ecosystems because they can reach high density and biomass influencing primary and secondary production

and the flux of matter and energy, and their ecosystem-engineering activities may alter the structure of the invaded community. All these mechanisms mediated by invasive bivalves can be responsible for important changes in ecosystem functions and services (Vaughn & Hakenkamp, 2001; Sousa et al., 2009).

Due to global climate change, severe weather occurs more frequently than before and the frequency and severity of extreme climatic events are predicted to increase in the future (IPCC, 2007). These events modify biodiversity, including in aquatic areas (Mouthon & Daufresne, 2006), but their significance is still underappreciated. In aquatic ecosystems, both floods and droughts are important drivers of ecological change and some studies have already explored their influence on bivalve assemblages (Hastie et al., 2001; Gagnon et al., 2004; Golladay et al., 2004; Sousa et al., 2012). The high water discharge and increased near-bottom velocity associated with floods can disturb substrates, damaging and dislodging benthic organisms (including bivalves, which live partially or completely buried in the sediments; Strayer, 1999; Hastie et al., 2001). Furthermore, in periods of dry weather, bivalves—because of their low mobility—cannot easily follow decreasing water levels, and thus massive die-offs may occur on the riverbanks due to desiccation (Vaughn & Taylor, 1999; Ilarri et al., 2011).

Early studies quantifying the transport of resources between aquatic and terrestrial ecosystems mainly focussed on the organic and inorganic materials removed from the riverbanks to the aquatic systems (Polis et al., 1997). In recent studies, more attention has been paid to the transport of resources in the opposite direction, from the aquatic towards terrestrial systems. The importance of this research topic becomes especially interesting, when large flows of resources occur, which may have a great impact on food web dynamics (Holt, 2008; Yang et al., 2008). Examples in aquatic systems of these rare episodic events, called resource pulses, include the synchronous emergence of insects, the post-spawning mortality of anadromous fish such as salmonids, and massive die-offs of bivalves (Helfield & Naiman, 2001; Gratton & Vander Zanden, 2009; Sousa et al., 2012).

In this study, the massive mortality of invasive bivalves was observed in the Hungarian section of the River Danube basin during the autumn of 2011, which potentially provides an important resource subsidy for the adjacent terrestrial ecosystem. In the Hungarian

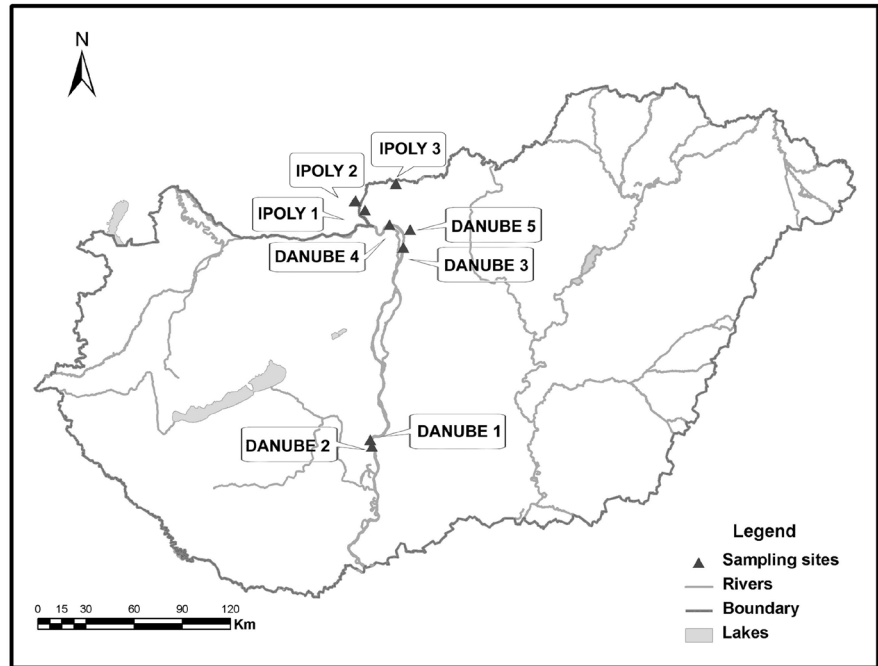
Danube, non-indigenous invasive bivalve species constitute almost 20% of the total number of bivalve species (including Sphaeriidae), and two species (the Chinese pond mussel *Sinanodonta woodiana* (Lea 1834) and the Asian clam *Corbicula fluminea* (Müller, 1774)) dominate the density and biomass of the benthic community (Bódis et al., 2011a). The aim of this study was to quantify and compare the biomass of invasive and native bivalve die-offs amongst eight sites in the River Danube basin subjected to completely different environmental conditions and to assess the role of invasive bivalve die-offs as a potential resource subsidy for the adjacent terrestrial food web. We hypothesised that the biomass of thermophilic invasive bivalve die-offs is significantly higher in a habitat affected by heated water than at other non-disturbed sites and the total biomass of bivalve die-offs at the warm water effluent is amongst the highest values recorded for aquatic ecosystems.

## Materials and methods

Empty shells of bivalves were collected at eight sampling sites along the Hungarian Danube (four sites in the Danube main arm, one site in the Danube side arm and three sites in the River Ipoly, a Danube tributary, Fig. 1). We chose the study sites to represent a wide range of habitats in the Hungarian section of the Danube River basin. The substrate was silt and sand at all study sites. Two sampling sites in the Danube main arm were anthropogenically modified habitats with water temperatures consistently 4–8°C higher than adjacent non-disturbed areas (Bódis et al., 2011a); Danube 1 is located next to the outlet of the cooling water channel of Paks Nuclear Power Plant and Danube 2 is situated 100 m far downstream of the outlet. The study area was surveyed in November 2011, when water discharge was particularly low.

Different sampling methods were used depending on the bivalve density. At sampling sites where the density of bivalves was high (Danube 1 and 2), 5 quadrats with an area of 0.25 m<sup>2</sup> were placed randomly in three positions (0–10, 10–20, 20–30 m from the water edge) due to the stratified arrangement of bivalve shells caused by the changing water levels during the drought period. At Danube 3, we used 5 quadrats to assess the density of small bivalves (*Corbicula*, *Dreissena*) and surveyed an area with 200 m<sup>2</sup> to assess the density of large bivalves

**Fig. 1** The location of sampling sites in the Hungarian Danube River basin



(*Anodonta*, *Unio*, *Pseudanodonta*). At all sites, we measured the total area surveyed and collected all empty shells from the surface of sediment by visual search, identified them to species and measured their size parameters. In the River Danube, two *Corbicula* morphs can be distinguished. The morphology of *Corbicula* morph-2 (CF2) is similar to the characteristics of *C. fluminalis* described from several European ecosystems (rounded triangular shell with a clear asymmetry; robust, slightly rotated shell umbo; presence of numerous and tightly spaced ribs; intensely violet-coloured endostracum in the ventral parts and margins). Nevertheless, according to a recent study (Bódis et al., 2011b), the use of the name '*C. fluminalis*' is probably premature as its phylogenetic relationship with native *C. fluminalis* inhabiting Western Asia and Northern Africa still requires confirmation; so, we use the name *C. morph 2* in this study.

To avoid overestimating bivalve mortality due to shell aggregation from previous periods, we collected entire shells with unharmed periostracum. Fragments of shells and old shells without periostracum were excluded from analyses. In this way, we could eliminate the overestimation of *S. woodiana* mortality due to shell accumulation because the thin and fragile empty shells of *S. woodiana* can be easily damaged

and break into pieces. In addition, most of the collected shells (approximately 60%) still contained portions of bivalve soft tissues, which can indicate whether they died recently during the drought period. Detailed information about the sampling sites and methods are given in Table 1.

To determine the biomass of the studied species, live specimens (78 *S. woodiana*, 100 *C. fluminea*, 120 *C. morph 2*, 35 *A. anatina*, 72 *U. pictorum* and 75 *U. tumidus*) of different sizes were collected and their size parameters and living wet mass (WM) were measured. To assess different biomass values of abundant invasive species, which may have a distinct role in energy and nutrient transport, the dry mass including shell (DM) and ash-free dry mass including shell (AFDM) of *S. woodiana*, *C. fluminea* and *C. morph 2* were also measured. The ash mass can be used as a proxy for the  $\text{CaCO}_3$  content and the AFDM can be used as a proxy for the organic matter content. Biomass was calculated by non-linear regression between shell length (mm) and body mass with shell (g) using Statistica 6.0 (Statsoft Inc., 2001), and we used the following power functions:

$$(1) \quad S. \textit{woodiana}: y \text{ (WM)} = (0.351 * 10^{-3}) x^{2.7987}, \\ y \text{ (DM)} = (0.156 * 10^{-3}) x^{2.7582}, y \text{ (AFDM)} = (0.453 * 10^{-4}) x^{2.5670},$$

**Table 1** Total density and biomass (mean  $\pm$  SD) of the freshwater bivalve die-offs in the Hungarian Danube River basin, with the proportion of each species: *Sinanodonta woodiana* (Sw), *Corbicula fluminea* (Cf), ‘*Corbicula morph*

2’ (Cf2), *Dreissena polymorpha* (Dp), *Dreissena rostriformis bugensis* (Db), *Anodonta anatina* (Aa), *Pseudanodonta complanata* (Pc), *Unio crassus* (Uc), *Unio tumidus* (Ut), *Unio pictorum* (Up)

Site	Danube 1	Danube 2	Danube 3	Danube 4	Danube 5	Ipoly 1	Ipoly 2	Ipoly 3
Latitude	46 34 56.91 N	46 34 54.32 N	47 41 12.26 N	47 49 17.84 N	47 45 13.86 N	47 53 19.32 N	47 55 55.26 N	48 03 56.40 N
Longitude	18 52 20.50 E	18 52 23.07 E	19 07 34.89 E	19 00 57.64 E	19 08 09.65 E	18 45 44.10 E	18 46 18.00 E	19 06 25.56 E
Method	Quadrat	Quadrat	Total + quadrat	Total	Total	Total	Total	Total
Total area (m <sup>2</sup> )	300	300	200	100	200	100	12	30
Density (ind. m <sup>-2</sup> )	530.9 $\pm$ 112.5	944 $\pm$ 407.1	75.7 $\pm$ 48.9	3.9	0.2	0.4	2.1	1.6
Sw (%)	52.8	16.5	2.6	0.8	35.9	2.3	12	93.6
Cf (%)	25.6	32.9	68.7	19	–	–	–	–
Cf2 (%)	9.9	38.8	–	–	–	–	–	–
Dp (%)	0.1	3.7	0.9	1.3	–	–	–	–
Db (%)	–	0.6	–	–	–	–	–	–
Aa (%)	6.8	5.5	0.01	4.9	64.1	13.6	32	4.3
Pc (%)	0.2	0.03	–	0.8	–	–	–	–
Uc (%)	–	0.03	–	0.3	–	47.7	44.0	–
Ut (%)	3.0	1.5	27.7	67.4	–	–	–	–
Up (%)	1.6	0.5	0.04	5.7	–	36.4	12.0	2.1
Biomass (g wet mass m <sup>-2</sup> )	33145.9 $\pm$ 15394.4	22013.8 $\pm$ 14879.2	738.5 $\pm$ 432.5	93.7	27.4	11.7	64.8	324.5
Sw (%)	88.9	68.6	34.9	3.1	70.2	5.9	23.8	98.4
Cf (%)	2.4	9.9	13.8	2.7	–	–	–	–
Cf2 (%)	0.5	6.6	–	–	–	–	–	–
Dp (%)	0.001	0.3	0.02	0.03	–	–	–	–
Db (%)	–	0.03	–	–	–	–	–	–
Aa (%)	4.9	10.6	0.2	9.5	29.8	18.2	34.9	0.9
Pc (%)	0.1	0.04	–	1.0	–	–	–	–
Uc (%)	–	0.02	–	0.2	–	27.7	21.8	–
Ut (%)	1.3	1.4	49.3	66.5	–	–	–	–
Up (%)	1.9	1.7	1.0	16.7	–	48.2	19.4	0.7

Characteristics of sampling sites and method are also given

- (2) *C. fluminea*:  $y$  (WM) =  $0.001432 x^{2.5850}$ ,  $y$  (DM) =  $0.001645 x^{2.3946}$ ,  $y$  (AFDM) =  $(0.185 * 10^{-3}) x^{2.3608}$ ;
- (3) *C. morph* 2:  $y$  (WM) =  $(0.458 * 10^{-3}) x^{3.1355}$ ,  $y$  (DM) =  $(0.306 * 10^{-3}) x^{3.1859}$ ,  $y$  (AFDM) =  $(0.539 * 10^{-3}) x^{1.9835}$ ;
- (4) *A. anatina*:  $y$  (WM) =  $(0.369 * 10^{-3}) x^{2.6723}$ ;
- (5) *U. pictorum*:  $y$  (WM) =  $(0.110 * 10^{-3}) x^{2.9831}$ ;
- (6) *U. tumidus*:  $y$  (WM) =  $(0.149 * 10^{-3}) x^{2.8171}$ .

We estimated the biomass of *D. polymorpha* using the length–mass relationship published by Muskó & Bakó (2005). The biomass of *U. crassus* and *P. complanata* was estimated by the power function used for *U. tumidus* and *A. anatina*, respectively, because these species are endangered and very rare in the Hungarian Danube River basin. Additionally, since their contribution to the total biomass of bivalve die-offs was low, the bias in using the length–mass

relationship of different species has negligible impact on the overall results.

ANOVA was performed to detect possible differences in the shell length of abundant invasive bivalve die-offs according to sampling sites using the R program package (R Development Core Team, 2007).

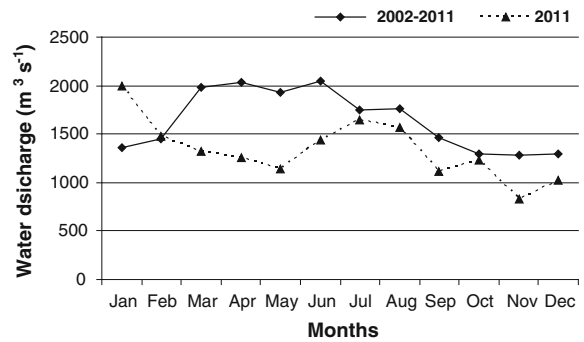
## Results

Ten bivalve species, five invasive bivalves (*S. woodiana*, *C. fluminea*, *C. morph 2*, *D. polymorpha*, *D. bugensis*) and five native bivalves (*A. anatina*, *P. complanata*, *U. crassus*, *U. tumidus*, *U. pictorum*), were found dead on the riverbanks of the Hungarian Danube River basin in November 2011. The massive die-offs of bivalves were probably caused by desiccation due to the very low water in the Hungarian Danube River basin. Data provided by the 'VITUKI' Environmental Protection and Water Management Research Institute showed that the water discharge in the catchment of the Hungarian Danube section was lower during most of the year 2011 than in the previous 10 years, and the water discharge was particularly low in November (Fig. 2).

The density and biomass of dead bivalves varied amongst the different sites (Table 1). Invasive bivalve species dominated half of the study sites and their highest density and biomass were recorded at the outlet of the cooling water channel of Paks Nuclear Power Plant (Danube 1–2; Fig. 3). The density of invasive species at the warm water effluent (Danube 1–2) was 7.6–12.2 times higher, whereas the biomass of invasive species was 6.3–11.2 times higher than the biomass of native species. Amongst the dead invasive bivalves, *S. woodiana*, *C. fluminea* and *C. morph 2* were the most abundant.

*Sinanodonta woodiana* die-offs were recorded at all study sites. The lowest density and biomass values of *S. woodiana* die-offs were recorded in the Danube tributary ( $0.01 \text{ ind. m}^{-2}$ ,  $0.7 \text{ g WM m}^{-2}$ ,  $0.3 \text{ g DM m}^{-2}$  and  $0.03 \text{ g AFDM m}^{-2}$ ), whilst the highest mean ( $\pm$ SD) values were recorded at the cooling water outlet of Paks Nuclear Power Plant reaching a density of  $280.5 \pm 110.6 \text{ ind. m}^{-2}$  and a biomass of  $29467.2 \pm 12181.7 \text{ g WM m}^{-2}$ ,  $10850.0 \pm 4470.9 \text{ g DM m}^{-2}$  and  $1297.4 \pm 527.2 \text{ g AFDM m}^{-2}$  (Tables 1, 2).

*Corbicula* die-offs were not observed in the side arm or the tributary of the River Danube. Despite the small size of *Corbicula*, the biomass of their die-offs was



**Fig. 2** Discharge of the River Danube measured at Vác. The continuous line denotes the mean values of monthly mean water discharge between 2002 and 2011; the dashed line denotes the monthly mean water discharge in 2011. Data provided by the 'VITUKI' Environmental Protection and Water Management Research Institute

high compared to the larger native species. The highest mean ( $\pm$ SD) values of *Corbicula* die-offs were recorded at the warm water outlet reaching a density of  $676.3 \pm 193.9 \text{ ind. m}^{-2}$  and a biomass of  $3662.5 \pm 1782.8 \text{ g WM m}^{-2}$ ,  $2458.8 \pm 1123.0 \text{ g DM m}^{-2}$  and  $189.5 \pm 101.8 \text{ g AFDM m}^{-2}$  (Tables 1, 2).

The ANOVA results detected significant spatial differences in shell length of dead *S. woodiana* ( $P < 0.001$ ) and *C. fluminea* ( $P < 0.001$ ). The highest mortality of *S. woodiana* belonged to the medium size category with a shell length interval of 60–100 mm in the main arm of the Hungarian Danube and at two downstream sites of the tributary River Ipoly, whereas in the side arm of the Hungarian Danube and at the upstream site of the tributary, a major percentage of dead individuals were in the shell length interval of 120–180 mm (Fig. 4). The highest mortality of *C. fluminea* was observed in two different size categories with a shell length interval of 10–14 and 26–34 mm at the warm water effluent, whereas at Danube 3 and at Danube 4, the major percentage of dead individuals belonged to the medium size categories with a shell length interval of 10–18 and 18–26 mm, respectively (Fig. 5). The highest mortality of *C. morph 2* was recorded in the medium size category with a shell length interval of 14–18 mm (Fig. 5).

## Discussion

The massive die-offs of bivalves occurring in the studied area were presumably caused by the extremely



**Fig. 3** Photos showing the large-scale mortality of *Sinanodonta woodiana* at the outlet of the cooling water channel of Paks Nuclear Power Plant

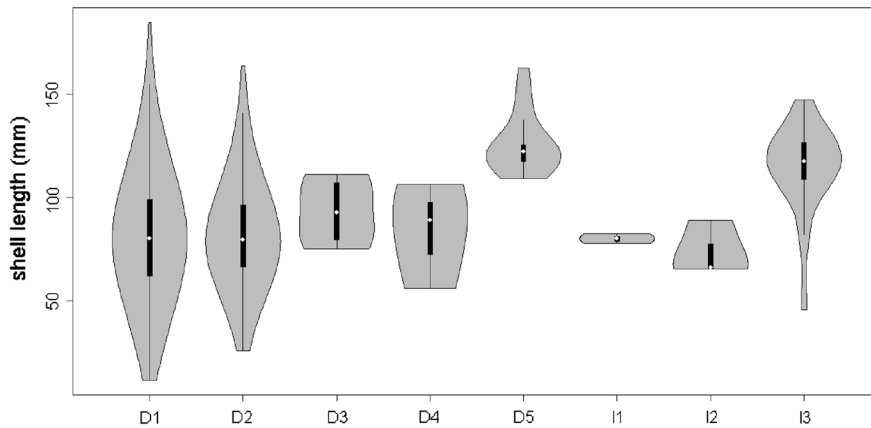
**Table 2** The wet mass (WM), dry mass (DM), and ash-free dry mass (AFDM) (mean  $\pm$  SD) of abundant invasive bivalves: *Sinanodonta woodiana* (Sw), *Corbicula fluminea* (Cf), ‘*Corbicula* morph 2’ (Cf2)

Site	Danube 1	Danube 2	Danube 3	Danube 4	Danube 5	Ipoly 1	Ipoly 2	Ipoly 3
Sw								
WM ( $\text{g m}^{-2}$ )	29467.2 $\pm$ 12181.7	15234.4 $\pm$ 8740.1	388.5 $\pm$ 321.9	2.9	19.2	0.7	15.4	319.2
DM ( $\text{g m}^{-2}$ )	10850.0 $\pm$ 4470.9	5623.0 $\pm$ 3227.5	143.3 $\pm$ 118.2	1.1	7.0	0.3	5.8	116.8
AFDM ( $\text{g m}^{-2}$ )	1297.4 $\pm$ 527.2	679.9 $\pm$ 391.3	17.3 $\pm$ 13.9	0.1	0.8	0.03	0.7	13.6
Cf								
WM ( $\text{g m}^{-2}$ )	779.5 $\pm$ 652.6	2198.3 $\pm$ 2189.0	102.6 $\pm$ 54.5	2.5	–	–	–	–
DM ( $\text{g m}^{-2}$ )	474.6 $\pm$ 387.0	1321.7 $\pm$ 1294.5	69.1 $\pm$ 36.7	1.6	–	–	–	–
AFDM ( $\text{g m}^{-2}$ )	47.7 $\pm$ 38.7	132.6 $\pm$ 129.4	7.1 $\pm$ 3.8	0.2	–	–	–	–
Cf2								
WM ( $\text{g m}^{-2}$ )	177.7 $\pm$ 121.5	1464.2 $\pm$ 1226.2	–	–	–	–	–	–
DM ( $\text{g m}^{-2}$ )	137.5 $\pm$ 94.2	1137.1 $\pm$ 958.3	–	–	–	–	–	–
AFDM ( $\text{g m}^{-2}$ )	7.5 $\pm$ 4.9	56.9 $\pm$ 40.7	–	–	–	–	–	–

low water discharge in the Hungarian Danube River basin since no other stressors of sufficient magnitude to kill bivalves (e.g. pollution) were detected. The whole year of 2011 was extremely dry and much of Central and Eastern Europe experienced major drought conditions in autumn; some countries had their driest November in the last 200 years (NOAA, 2011). The drought led to an extremely low water level in the Danube River basin, especially from South Germany to the Black Sea, causing severe navigational problems.

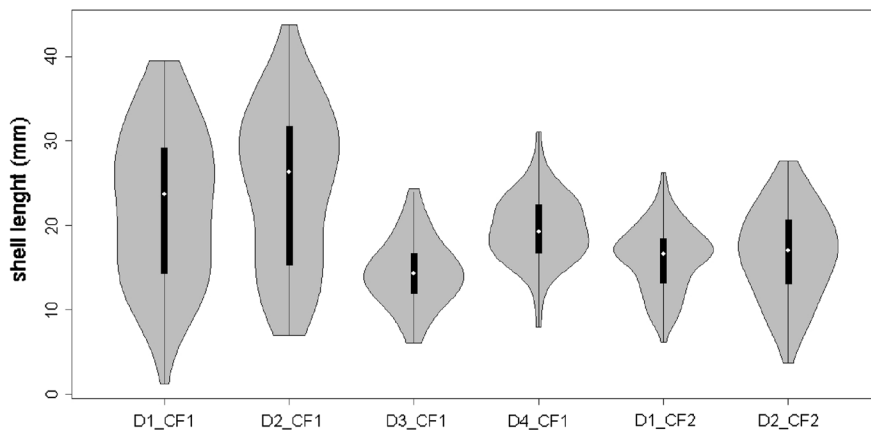
The density and biomass values of bivalve die-offs recorded in this study are amongst the highest values recorded for aquatic ecosystems. Other studies dealing with invasive bivalves also recorded massive mortality due to a response to water level fluctuations (Balogh et al., 2008; Werner & Rothhaupt, 2008). For

example, juvenile specimens of *C. fluminea* (<5 mm) in Lake Constance reached a maximum density of 27,563 ind.  $\text{m}^{-2}$  in December and only 1% of the population survived the harsh condition of low water depth during winter. In addition, *C. fluminea* populations with high density can undergo rapid die-offs during the low flow and high temperature of summer drought (Cherry et al., 2005; Cooper et al., 2005). Although the biomass of bivalve die-offs was not given in these studies, it was probably lower than the ones reported in our study due to the small size of the bivalves. In a recent study, Sousa et al. (2012) also reported high densities and biomass of bivalve die-offs in several Portuguese rivers. These resulted from mortalities occurring after high flood events during the 2009/2010 winter and not from droughts. The highest mean ( $\pm$ SD) value resulting from *C. fluminea*



**Fig. 4** The shell length frequency distribution of *Sinanodonta woodiana* die-offs in the sampling sites (D1—Danube 1, D2—Danube 2, D3—Danube 3, D4—Danube 4, D5—Danube 5, I1—Ipoly 1, I2—Ipoly 2, I3—Ipoly 3). The violin plot is a combination of a symmetrized kernel density plot and a box plot. The shape of violin plot (in grey) represents the density of

data estimated by the kernel method. The wider the shape at a given shell length, the more specimens are associated with that value. The white dot represents the median value, the thick line segment illustrates the inter-quartile range between the first and the third ones, and the thin line represents the range of data without outliers



**Fig. 5** The shell length frequency distribution of *Corbicula* die-offs in the sampling sites (D1—Danube 1, D2—Danube 2, D3—Danube 3, D4—Danube 4). CF1 for *Corbicula fluminea* and CF2 for *Corbicula* morph 2. The violin plot is a combination of a symmetrized kernel density plot and a box plot. The shape of violin plot (in grey) represents the density of data estimated

by kernel method. The wider the shape at a given shell length, the more specimens are associated with that value. The white dot represents the median value, the thick line segment illustrates the inter-quartile range between the first and the third ones, and the thin line represents the range of data without outliers

mortalities was  $10,225 \pm 2,569$  g wet mass  $m^{-2}$ . Maximum values in Portuguese rivers were at least 3 times lower than the maximum values collected in this study, mainly because Portuguese rivers are not colonized by *S. woodiana*, which is a species with a large biomass. Nonetheless, and taking in account that there is a general lack of aquatic studies for comparison, the resulting biomass of these die-offs could only be surpassed by the die-offs of migratory fishes or

carcasses of big mammals (Polis et al., 1997; Wipfli et al., 1998).

This study also provides evidence that a habitat affected by heated water can contribute to the aggregation and an extremely large biomass of thermophilic invasive bivalves. This observation is in agreement with several previous studies, which report that temperature is a major factor affecting the reproduction and growth rates of *Corbicula* and *S.*

*woodiana* (French & Schloesser, 1991; Hornbach, 1992; Cataldo & Boltovskoy, 1999; Kraszewski & Zdanowski, 2001). For example, *S. woodiana* has also found favourable growth conditions in the heated Konin lakes' system (Poland), where it became the dominant species of the benthic community and its biomass exceeded 10 kg wet mass m<sup>-2</sup> (Kraszewski & Zdanowski, 2001). In this study, *Corbicula* and *S. woodiana* unambiguously benefited from the locally heated water. The site at the outlet of the cooling water channel of Paks Nuclear Power Plant can serve as a thermal refuge, providing adequate habitat conditions to survive the harsh conditions of winters when water temperature can drop below 2°C. In fact, warm water effluents can be considered as a hot spot for invasive species native to a warm climate (Gollasch & Nehring, 2006; Galil et al., 2007).

Given the widespread occurrence of the invasive bivalves we studied (*S. woodiana* and *C. fluminea*) and the great density and biomass that they attain in some aquatic ecosystems, the ecological impacts generated by their massive mortalities should be considered in other geographical areas as well. In addition, some endangered native species (*P. complanata* and *U. crassus*) also suffered from the drought conditions and since these species have conservation importance, their die-off events should be incorporated into future management plans (e.g. rapid relocation into the riverbed when these extreme climatic events occur; Sousa et al., 2012).

The recorded mortalities highlight invasive bivalves as a major resource subsidy, possibly contributing remarkable amounts of nutrients and energy to the adjacent terrestrial ecosystem during low water. Although we were not able to find data about the conversion of freshwater bivalve biomass into C, N and P content, there are some assessments for marine bivalve species (e.g. *Mytilus edulis*, Smaal & Vonck, 1997). Using this conversion, the highest summarized dry mass of abundant invasive bivalve die-offs (11,462 g DM m<sup>-2</sup>) recorded in this study can be converted into approximately 4191 g C m<sup>-2</sup>, 893 g N m<sup>-2</sup> and 62 g P m<sup>-2</sup> tissue content. This high quality bivalve carrion can be consumed directly by a great number of species (insects, birds such as crows and ducks, mammals; Bódis, pers. obs.), but probably the major part of this biomass enters the detrital food web driving changes in microbial biomass and nutrient cycles. Additionally, the empty

shells of bivalves can persist for several years after the bivalves die, providing an important source of calcium and habitat for other organisms (Strayer & Malcom, 2007). Overall, the importance of resource subsidies mediated by invasive species can be an interesting topic to explore not only in aquatic ecosystems but also in terrestrial areas (e.g. massive production of fruits and flowers by invasive plants, outbreaks in the population dynamics of invasive small mammals and invertebrates) since they can have strong implications on ecosystem functioning, concentrating nutrients in a small area and potentially affecting primary production and nutrient cycling (Boulêtreau et al., 2011).

The ecological impact of invasive bivalves is probably more remarkable during extreme climatic events such as droughts and floods. Extreme climatic events are projected to increase in frequency and intensity with ongoing climate change, triggering dramatic effects in ecological processes and enhancing biological invasions (Diez et al., 2012). In this study, the drought conditions of 2011 probably intensified the ecological effects of invasive bivalves in the Danube River basin. Furthermore, the massive die-offs of invasive bivalves could have considerable economic impacts as well because the extensive decomposition of bivalve biomass can diminish water quality and the massive accumulation of bivalve shells affects local people and tourists who use the river banks for recreation.

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