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Contrasting decay rates of freshwater bivalves' shells: Aquatic versus terrestrial habitats

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ABSTRACT

Freshwater flow regimes are particularly vulnerable to global climate change with changes to the volume and regime of water contributing to global declines in freshwater biodiversity. Droughts or floods can cause massive mortalities of freshwater bivalves, facilitating the accumulation of shells in the aquatic but also in adjacent terrestrial habitats. In order to fully understand the long term impact of these massive mortality events, it is important to assess how bivalve shells persist in the environment. Given that, the present study aimed at studying the shell decays of four different bivalve species (*Anodonta anatina*, *Corbicula fluminea*, *Potomida littoralis* and *Unio delphinus*) in aquatic (i.e. river) versus terrestrial (i.e. sand soil) habitats. Shell decay rates were significantly different among species and habitats. In the aquatic habitat the shell decay rates varied among species, with the native species *A. anatina*, which have the largest and thinnest shell, showing the highest decay rate. Alternatively, in the terrestrial habitat the shell decay rates were more even among species and not related to a particular shell feature or morphology, with the native *U. delphinus* showing the fastest decay. The shell decay rates were 6 to 12 times higher in aquatic than in the terrestrial habitat. These results suggest that bivalve shells can persist for long periods of time on both habitats (but mainly in terrestrial), which may perhaps trigger significant changes on the ecosystem structure and functioning.

Introduction

Rivers by being highly fragmented in a predominantly terrestrial landscape facilitate the exchange of resources between the terrestrial and aquatic habitats; these subsidies can have important implications in terms of productivity and ecosystems processes for both habitats (Polis et al., 1997). In recent decades many studies called the attention for the movement of nutrients, detritus, prey and consumers between the land-water interfaces (Norlin, 1967; Hunt, 1975; Siegfried, 1981; Wetzel, 1990; Polis and Hurd, 1996; Polis et al., 1997). Nevertheless, a large proportion of studies focus on subsidies from terrestrial to aquatic ecosystems, primarily the importance of leaf litter resources and their use, maintenance or recycling on food-webs (Gessner et al., 1999; Lecerf et al., 2007). Subsidies in the opposite direction (aquatic to terrestrial) are not as well studied (neither receiving the same amount of attention when compared to leaf litter); most of the studies addressing this topic focused in the fundamental importance of emergent insects from the aquatic to adjacent terrestrial ecosystems, emphasizing their ecological significance for the riparian communities (Kato et al., 2003; Nakano and Murakami, 2001; Baxter et al., 2005).

One mechanism which can facilitate subsidies from aquatic to terrestrial are major floods or droughts, which can contribute to massive mortalities of freshwater bivalves (Hastie et al., 2001; Sousa et al., 2012; Bódis et al., 2014a), facilitating the accumulation of dead animals both in the aquatic and in the adjacent terrestrial ecosystems. Some studies have already showed that the biomass resulting from these die-offs may be massive (reaching dozens of kg per m^2; Sousa et al., 2012; Bódis et al., 2014a), with part of this carrion being consumed by higher trophic levels and the other part entering the detritus food-web (Ilarri et al., 2011; Sousa et al., 2012, 2014). Since extreme climatic events, such as floods, droughts and heat waves are expected to occur more often in the near future in response to temperature and precipitation regime shifts (Daufresne et al., 2003; Mouthon and Daufresne, 2006; Poff and Zimmerman, 2010) the frequency of these bivalve die-offs may also increase in

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the future (Sousa et al., 2012). However, to date very few studies assessed the longer term impacts of these mortality events. Unlike soft tissue, which quickly decompose down, shells may persist for longer periods of time (Gutiérrez et al., 2003; Mincy, 2012). The input of shells can lead to profound consequences at different ecological levels, from individuals to ecosystems (e.g. Gutiérrez et al., 2003; Strayer and Malcom, 2007), given that the physical structure of shells can provide habitat to a myriad of organisms (Werner and Rothhaupt, 2008) and play an important role in the carbon cycling (Gutiérrez et al., 2003; Sousa et al., 2009).

The newly emerging conditions resulting from these extreme climatic events represent a new challenge in ecology. Until now, just a few studies attempted to investigate the influence of extreme climatic events on bivalve species (but see Sousa et al., 2008; Ilarri et al., 2011; Sousa et al., 2012; Bódis et al., 2014a). Furthermore, these studies only quantified the density and biomass resulting from these mortality events, not assessing the possible fate of shells provided by these species on the aquatic and adjacent terrestrial habitats, which may be of particular importance considering that bivalve shells can persist for several years (Palacios et al., 2000; Strayer and Malcom, 2007). In this context, it is important to assess shell persistence in different habitats (aquatic vs. terrestrial). For this, the present study aimed at: (a) examining if different bivalve species (*Anodonta anatina*, *Corbicula fluminea*, *Potomida littoralis* and *Unio delphinus*) have different shell decay rates; and (b) comparing the shell decay rates of the selected bivalve species between the aquatic and terrestrial habitats. Due to differences in shell structure, size and robustness we hypothesized interspecific differences both in aquatic and terrestrial habitats with species with hard and larger shells being more resistant to decay. In the same vein and due to completely different abiotic conditions between the aquatic and terrestrial habitats we hypothesized much larger decay rates in aquatic habitats mainly due to influence of the current velocity.

Material and methods

Study area

The experiment was conducted in the River Minho (NW of the Iberian Peninsula). This river originates in the Serra de Meira, (Spain), with most of its hydrological basin (95%) located in Spain and approximately 5% in Portugal. It has a length of 310 km and a maximum width of two km near the mouth, flowing NNE-SSW into the Atlantic Ocean. The study was performed near the city of Monção (Portugal), nearly 40 km from the river mouth. The study area selected for the assessment of the decaying rates in aquatic habitats was located near the margins (42°04′36.81″N, 8°31′00.25″W). This area has a high density of the Asian clam *C. fluminea*, with more than 2000 ind m^{-2}, being also colonized by the native species *A. anatina*, *P. littoralis, U. delphinus* and several species from the *Pisidium* genus. These native species have very low densities (less than 1 ind m^{-2}) (Sousa et al., 2005). In this area the current velocity varied from moderate (summer and fall conditions) to strong (winter and spring conditions) throughout the year, with variations also occurring in a daily basis due to operations of a dam located 30 km upstream. Furthermore, it is a very shallow area (no more than 1 m depth during summer) with permanent freshwater conditions and colonized by sparse submerged vegetation (Fig. 1a). The study area selected to assess decay rates in terrestrial habitats was located 250 m inland from the River Minho margin (42°04′28.12″N, 8°31′29.14″W) and 1 km downstream from the area used to evaluate the shell decay underwater. This area is characterized by sandy sediments and by the dominance of extensive forest areas formed mainly by acacia, pine, eucalyptus and oak trees (authors personal observation). This area was chosen because during the great flood of 2001 large quantities of bivalves were washed away from the main river channel and were deposited in this site. After more than 12 years shells of the selected species still persist in the area (Fig. 1b).

Field observations

The densities of empty shells in the aquatic habitat were assessed through a Van Veen grab and in the terrestrial habitat through a quadrat; both sampling devices had an area of 0.05 m^2. Six replicates were taken for each habitat.

Experimental design and laboratory procedures

To study the bivalve's shell decays in aquatic and terrestrial habitats, empty shells that were intact (i.e. of recently dead organisms) of four species were used, namely *A. anatina*, *C. fluminea*, *P. littoralis* and *U. delphinus*. Shells not connected at the hinge of the four bivalve species were manually cleaned, in order to remove any traces of soft tissue, dried for 48 h at 50 °C, weighed, and measured to the nearest 0.1 mm before placing in individual, sealed nylon net bags with 10 mm of mesh size. Each bag had only a single shell. To test the shell decays in the aquatic habitat, a total of 64 net bags (16 per species) were tied with a string in a stake and placed underwater (ca. 70 cm below the lowest water level) about ten meters away from the river margin. The same procedure was used for the terrestrial habitat; however, in this case the stake was placed on land being shells deposited in the sediment surface. Shells remained for 12 months (from July 2012 to July 2013) in both aquatic and terrestrial conditions, in order to experience the environmental pressure of an entire year cycle. At the end of the experiment, the shells were dried (following the same procedure described previously), measured and weighted. The methodology used in the present study did not distinguish the decay rates of the mineral versus organic contents separately.

Data analysis

The instantaneous rate of shell loss (k, year^{-1}) was calculated following the method developed by Strayer and Malcom (2007) as:

$$k = \left(\frac{1}{t}\right)\left[\ln\left(\frac{\text{mass final}}{\text{mass initial}}\right)\right]$$

where t is the length of time (in years) that the shells were in water or land. The instantaneous rate of shell loss was selected to facilitate comparison of results to other studies.

Permutational Multivariate Analysis of Variance (PERMANOVA) was carried out to compare the shell decay rates of bivalve species in two different habitats (aquatic and terrestrial). This method analyzes the variance of multivariate data explained by a set of explanatory factors on the basis of any chosen measure of distance or dissimilarity, thereby allowing for a wide range of empirical data distributions (Anderson, 2001). The shell decay and the percentage of shell decay per year, and the instantaneous rate of shell loss were statistically tested using a two-way PERMANOVA (type-III), with treatment (four levels: *Anodonta*, *Potomida*, *Unio*, *Corbicula*) and habitat (two levels: aquatic and terrestrial) as fixed factors. Prior to the two-way PERMANOVA analyses, all variables were always normalised without data transformation and a resemble matrix based on the Euclidean distances was calculated.

In all PERMANOVA tests, the statistical significance of variance ($\alpha = 0.05$) was tested using 9999 permutations of residuals within a reduced model. When the number of unique permutations was lower than 150, the Monte Carlo p-value was considered. Pairwise comparisons were also performed for all PERMANOVA tests.

Fig. 1. The selected areas for the study in the River Minho, NW Iberian Peninsula. (a) study area in the aquatic habitat; (b) study area in the terrestrial habitat.

To assess the relative contributions of the size of the shells to each habitat (e.g. aquatic and terrestrial), a distance-based linear modeling (DistLM) was also carried out. DistLM makes it possible to test the significance ($\alpha = 0.05$) of explanatory variables for a multivariate response variable in the form of a resemblance matrix (Anderson et al., 2008). For the model used on the DistLM, the AIC (Akaike Information Criterion) was selected, and the analyses were based on the Euclidean distance resemblance after the normalisation of the data.

PRIMER analytical software (vers. 6.1.6, PRIMER-E Ltd, Plymouth, U.K.) with PERMANOVA + 1.0.1 add-on (Anderson et al., 2008) was used for all statistical tests.

The extrapolation of the number of years necessary to calculate the total shell disintegration was performed considering the instantaneous rate of shell loss (k, year^{-1}).

Spearman correlations were performed with the shell decay and shell size for each species in both habitats. All the correlations were performed using R software (R Development Core Team, 2009).

Results

Field observations

In the aquatic habitat the mean density of empty shells was of 1908.4 ± 823.50 ind. m^2; in this area all the shells belong to *C. fluminea*. In the terrestrial habitat the mean density of empty shells resulting from the 2001 flood deposits were of 2367.5 ± 1023.90 ind. m^2; more than 99% of the shells belong to *C. fluminea* and the remaining percentage to *A. anatina*, *P. littoralis* and *U. delphinus*.

Shell decay rates – Aquatic versus terrestrial habitat

Underwater *A. anatina* was the species that exhibited the highest percentage of shell decay per year (52.0%), followed by *U. delphinus* (24.7%), *C. fluminea* (23.3%) and *P. littoralis* (13.6%) (Fig. 2a). Inland *U. delphinus* (2.4%) was the species that exhibited the highest percentage of shell decay per year, followed by *C. fluminea* (2.1%), *A. anatina* (2.1%) and *P. littoralis* (1.8%) (Fig. 2b). Shell decay was significantly different among species (Pseudo-F = 73.05; p < 0.001), habitat (Pseudo-F = 739.52; p < 0.001) and in the interaction species x habitat (Pseudo-F = 71.90; p < 0.001). The shell decay per year and the instantaneous rate of shell loss were also significantly different among species and habitat (Table 1). The total time for the disintegration of the studied species suggests that the most resistant shells underwater were those from *P. littoralis*, *C. fluminea*, *U. delphinus* and *A. anatina*, respectively. On the other hand, inland, the total time disintegration were more even, with *P. littoralis* being the most resistant species followed by *A. anatina*, *C. fluminea* and *U. delphinus* (Table 2). The total percentage of shell decay per year in the aquatic habitat (22.5%) was much higher than in the terrestrial habitat (1.9%).

Effect of shell size on decay rates

In the aquatic and terrestrial habitats *A. anatina* (underwater mean shell size: 82.61 ± 15.24 mm; inland mean shell size: 81.49 ± 10.68 mm) was the species with the highest size, followed by *P. littoralis* (underwater mean shell size: 70.37 ± 6.91 mm; inland mean shell size: 57.76 ± 5.54 mm), *U. delphinus* (underwater mean shell size: 57.52 ± 8.04 mm; inland mean shell size: 49.21 ± 7.17 mm) and *C. fluminea* (underwater mean shell size: 30.92 ± 4.57 mm; inland mean shell size: 24.17 ± 5.39 mm). The size of the shells seems to have influenced the bivalve shell decay rates, with significant correlations being observed (Fig. 3); however, this influence was higher in the aquatic habitat, with the size of the shells explaining 25.10% (AIC = 53.19, SS-trace = 45.94, Pseudo-F = 20.11, p < 0.01) of the variance, and in the terrestrial habitat just 18.21% (AIC = 124.16, SS-trace = 73.23, Pseudo-F = 29.63, p < 0.01).

Discussion

The findings of the present study suggest that the shell decays varied among bivalve species and habitats. The observed interspecific differences are probably due to structural and morphological features of the bivalve shells. The selected species have remarkable differences in size and shell robustness. In relation to size, *A. anatina* is the largest species followed by *P. littoralis*, *U delphinus* and *C. fluminea*. Shell robustness is also highly different, with *P. littoralis* showing a robust, thick and hard shell, while *C. fluminea* have a slightly less hard and thinner shell. Alternatively, *A. anatina* has the most thin and fragile shell; *U. delphinus* shell is also thin and delicate although not as much as *A. anatina*. Both size and robustness may play an important role in the shell decay process (Strayer and Malcom, 2007; Pearce, 2008). Larger shells by having a smaller surface area to mass ratio are expected to lose mass more slowly than smaller ones, given that shells

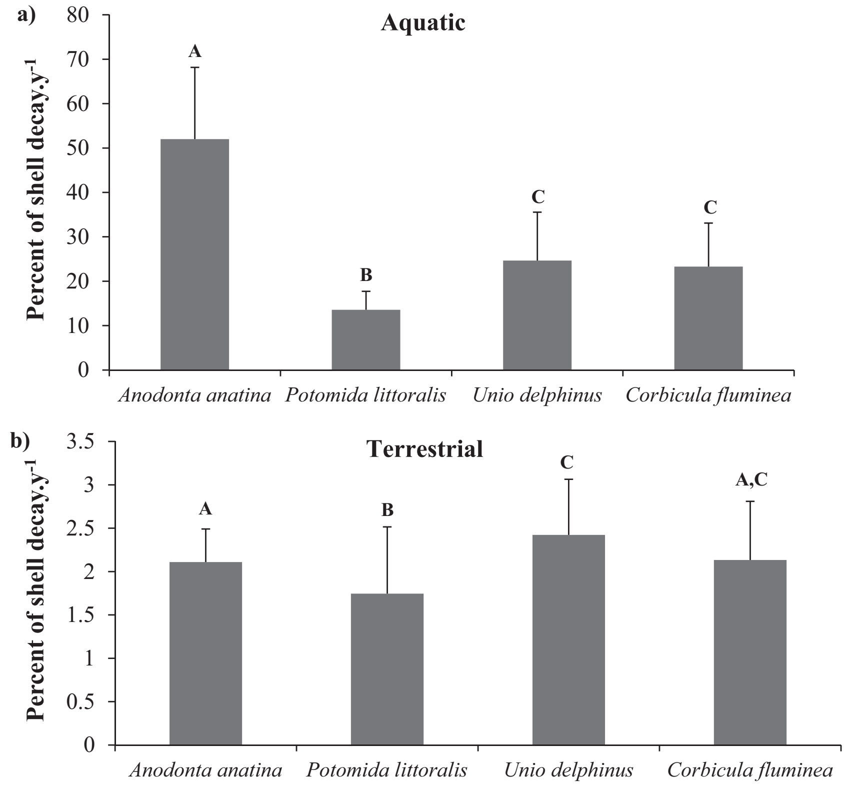

Fig. 2. Mean (±SD) values of the percent of shell decay per year for the different species in aquatic (a) and terrestrial habitats (b). Different letters indicate significant differences among treatments.

with a high surface area to mass ratio dissolve faster (Claassen, 1998). In addition, intrinsic factors such as $CaCO_3$, crystal size and mineralogy, chemical composition and organic matter of the shell may be different among species and this situation may also contribute for the distinct results obtained (Strayer and Malcom, 2007).

When comparing the decays within the different habitats, underwater the species with the thinnest shells (*A. anatina* and *U. delphinus*) exhibited the highest decay rate, suggesting that shell robustness, rather than the surface area, is the controlling factor in shell decay rate. Indeed, earlier studies emphasized that physical and chemical influence is higher in thin-shelled species (Evans,

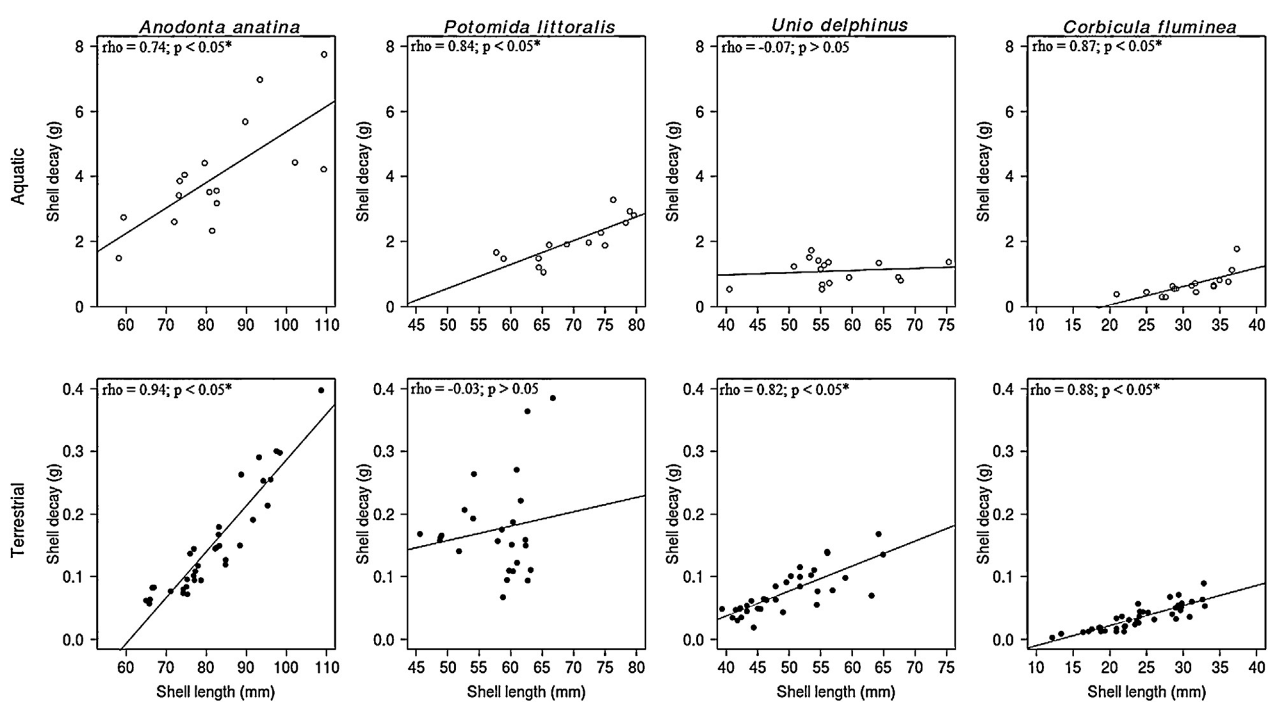

Fig. 3. Spearman's correlation results of the relation between the shell length and shell decay per year for the different species in aquatic and terrestrial habitats.

Table 1
Mean (±SD) values of shell decay (g) per year and instantaneous rate of shell loss ($-k$) and two-way PERMANOVA test results of the shell decay and instantaneous rate of shell loss comparison between the aquatic and terrestrial habitats. $^{**}p < 0.001$. Different letters indicate significant differences among treatments. Upper case letters refers to comparisons among species, while lower case letters refers to comparisons among habitats.

Species	Two-way PERMANOVA									
	Shell decay per year					$-k$				
	Aquatic	Terrestrial	Species	Habitat	Species × habitat	Aquatic	Terrestrial	Species	Habitat	Species × habitat
Anodonta anatina	$4.01 \pm 1.63^{A,a}$	$0.15 \pm 0.09^{A,b}$	Pseudo-F = 98.18^{**}	Pseudo-F = 531.92^{**}	Pseudo-F = 86.20^{**}	$0.90 \pm 0.45^{A,a}$	$0.02 \pm 0.005^{A,b}$	Pseudo-F = 58.18^{**}	Pseudo-F = 303.95^{**}	Pseudo-F = 57.95^{**}
Potomida littoralis	$2.03 \pm 0.67^{B,a}$	$0.18 \pm 0.07^{A,b}$				$0.15 \pm 0.05^{B,a}$	$0.02 \pm 0.01^{B,b}$			
Unio delphinus	$1.09 \pm 0.37^{C,a}$	$0.07 \pm 0.04^{B,b}$				$0.30 \pm 0.16^{C,a}$	$0.03 \pm 0.009^{C,b}$			
Corbicula fluminea	$0.67 \pm 0.36^{D,a}$	$0.04 \pm 0.02^{C,b}$				$0.28 \pm 0.17^{C,a}$	$0.02 \pm 0.01^{AC,b}$			

Table 2
Extrapolation of the number of years necessary for the total shell disintegration of four freshwater bivalve species from the River Minho (NW Iberian Peninsula), when allocated on aquatic and terrestrial habitats.

Total time (years)		
Species	Aquatic habitat	Terrestrial habitat
Anodonta anatina	1.1	40.9
Potomida littoralis	6.7	56.7
Unio delphinus	3.3	34.4
Corbicula fluminea	3.5	39.7

1972). On the other hand, inland, shell decay rates were more even among species, and were not related to a particular feature, not following any clear pattern. *U. delphinus* was the species with the highest decay rates and it has not the smallest nor the thickest shell among the studied species. This finding is different from previous studies performed inland (i.e. Menez, 2002; Pearce, 2008) that identified that the decays in larger shells are slower when compared to small ones.

Overall, the decay rates of bivalve shells in the terrestrial habitat were much lower (from 6 to 12 times) than in the aquatic habitat. In fact, the shell dissolution rates are expected to vary between habitats. Strayer and Malcom (2007) suggest that the dissolution rates are correlated with the chemistry and water movement of the environment (Strayer and Malcom, 2007). In this case both habitats are subjected to low pH values, with the terrestrial varying from acid to very acid (pH between 4.6 and 4.8) (Nunes et al., 2010) whereas in the aquatic is slightly acidic (pH between 6.5 and 7; Sousa et al., 2005, 2007). The lower pH values increases the speed of shell decomposition (Reitz and Wing, 1999; Strayer and Malcom, 2007; Pearce, 2008). However, in the present study the presence of water associated to its current velocity seems to have been the main factor for the contrasting rates observed in aquatic and terrestrial habitats. Since the shells in the aquatic habitat were always underwater, much higher decaying rates were expected when compared to the terrestrial habitat that only during rainfall conditions was subjected to this form of weathering. Furthermore, the study area in the River Minho is subject to lotic conditions, with the current velocity varying from moderate (summer and early autumn) to very high (winter and early spring).

Several invertebrate and fish species use the shell structure as hard substrata ready for colonization (Buchman et al., 2007; Rabaoui et al., 2009; Bódis et al., 2014b). The empty shells act as a refuge from predators and/or unfavorable environmental conditions, and to avoid the detrimental effects of inter- and intraspecific competition (Gutiérrez et al., 2003). The bivalve species by having highly variable rates of shell production and decay, both in the aquatic and terrestrial habitats, probably influence each habitat differently. Underwater, the high amount of shell production and also the high decaying rates turn the shell influence over other organisms constant but with each individual shell being relatively quickly disintegrated and the minerals contained in the shells becoming available to the environment rapidly. However, these decay rates can be highly context dependent because aquatic ecosystems are subjected to different abiotic conditions (lentic to lotic conditions, concentrations of calcium carbonate, pH), which may be responsible for completely different values than the ones reported in the present study. On the other hand, on land, bivalve shell input is sporadic and the decay rates were much slower, meaning that shells will enter the terrestrial habitat erratically and probably will persist in the environment for longer, thus creating a relatively long-lasting habitat that is highly different from the normal conditions. This new habitat in the terrestrial system may perhaps change the structure of terrestrial macrofauna, and due to its persistence its effects can be significant; however, these possible changes in the terrestrial macrofauna where never assessed and further discussion remains speculative. In the same vein, bivalve shells may contribute with significant quantities of calcium, which may influence biogechemical cycles. Future studies involving the decay rates, including Ca^{2+} measurements, should be performed to better understand the complete process encompassing the $CaCO_3$ fraction of the shell in these habitats.

The introduction and the following accumulation of bivalves shells act as a resource subsidy (i.e. the movement of prey, nutrients, or energy) (Nowlin et al., 2007). In the River Minho bed the accumulation of empty shells underwater is continuous throughout the year; however, the exportation of these empty shells to the terrestrial habitat occurs only during extreme climatic events like floods and in this particularly case it can be considered an allochthonous resource subsidy. An increase on the frequency of extreme climatic events, such as droughts and floods are expected for Southwestern Europe according to the IPPC predictions (IPCC, 2007). Therefore, massive bivalve die-offs (Ilarri et al., 2011; Sousa et al., 2012) will probably occur more frequently. Tied to this, probably there will be an increase in the accumulation of climatically driven resources, such as bivalve shells. Simultaneous to the increase of shells availability severe alterations in the community structure of the River Minho can be expected, considering that specific groups of macroinvertebrates (Ilarri et al., 2012) and fish species (Ilarri et al., 2014; Souza et al., 2014) were influenced by the presence of *C. fluminea* (i.e. live, and dead individuals represented by empty shells) on the river bed. Since the ecological consequences resulting from the exportation of shells to land is poorly understood and the likelihood of new occurrences of climatic extremes is acknowledge, further studies dealing with these issues are necessary in order to better understand the role played by bivalve shells in adjacent terrestrial ecosystems.

To date few studies were performed involving shell decay rates. In most of the cases the studies focused on rates of shell production, with almost no work focusing in rates of shell decay. Dissolution of shells has been best studied in marine environments, with few existing data for freshwater shells (Cadeé, 1999). This make difficult to compare our results with other studies. When comparing our results, the shell decay rate observed for *C. fluminea* in the aquatic habitat (23.3%) was very similar to the observed (26.6%) by Mincy (2012) in Charleys Branch stream (United States of America), an area with comparable pH values (varied from 4.56 to 8.5). However, Mincy (2012) observed reduced rates for the mussel *Villosa iris* (1.7%), compared to the decay rates observed in the present study. In the terrestrial habitat, the percentage of shell loss observed in the present study were much reduced (varied from 1.8% to 2.4%) to the observed by Pearce (2008) that detected an average of 6.4% to 10.2% of decay rate per year for snails in two different areas with very similar pH values (4.5) to our study area. However, gastropods and bivalves may have different decay rates. Overall, these comparisons suggest that the results can be highly context dependent and vary according to biotic and abiotic conditions. In this context, future studies should be performed in order to better understand the process involved in shell decomposition rates in different environments.

Conclusion

Through field experiments the results of the present study suggest that the shell decay rates varied among species and habitats. In the aquatic habitat the determinant feature for a lower decay rate was the shell robustness, while inland, the shell decay rates were more even among species, and not related to a particular feature. Furthermore, the shell decay rates in the terrestrial habitat were much lower (from 6 to 12 times) than in the aquatic habitat. The results of the present study also suggest that the influence of freshwater bivalve species (i.e. native and invasive) on aquatic and terrestrial habitats can persist for long periods of time.

As the frequency of extreme climatic events and the introduction of invasive bivalve species are expected to increase in the future, further studies addressing shell decay rates are necessary for a complete understanding of bivalve impacts and legacies in the aquatic and terrestrial environments.

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