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ORIGINAL PAPER

Filtration activity of invasive mussel species under wave disturbance conditions

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Abstract Self-purification is one of the most important ecosystem functions of rivers. Multiple human activities regularly impact this ecosystem service, consequently altering river morphology, hydrology, and the composition of biotic assemblages that contribute to self-purification. However, little quantitative information is available about the importance of such impacts. Hence, we tested how invasive mussel species contribute to self-purification under disturbed riverine conditions. In laboratory experiments, invasive mussel species equipped with magnetic sensors that recorded filtration activity were exposed to artificial waves of varying intensity that simulated the hydraulic effects of inland navigation. Our results suggest that invasive mussel species are more resistant to wave disturbance compared to native species, as estimated threshold values for initiating shell closure are very high (*Dreissena rostriformis bugensis*) or the duration (*Corbicula fluminea*) and degree of shell closing (*D. rostriformis bugensis*, *C. fluminea*) very low. Also we demonstrated that the invasive species *D. rostriformis bugensis* and *C. fluminea* continued filtering during wave impact, whereas *Dreissena polymorpha* did not behave significantly differently than previously studied native mussel species, based on the studied susceptibility parameters. Thus, *D. rostriformis bugensis* and *C. fluminea* appear to be pre-adapted to hydraulic or morphological disturbance, and may compensate against other losses regarding this important ecosystem function in rivers that are intensively used for inland navigation. However, as the dominance of invasive species in river systems may disrupt natural food webs, this compensation of filter-feeding activity may be accompanied by the loss of other ecosystem functions.

Keywords Benthic invertebrates · Ecosystem functioning · Hydraulic disturbance · Navigation · Recreational boating · Self-purification

Introduction

Human civilization depends, to a certain extent, on ecosystem services provided by rivers; however, these services are often overused (Costanza et al. 1997; Everard and Powell 2002; Kareiva et al. 2007). Among other functions, many river systems worldwide are intensively used for inland navigation and boating activities (Food and Agriculture Organization of the United Nations 2008). Worldwide, 671,886 km of waterways exist for inland navigation (Central Intelligence Agency 2011), many of which use natural

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rivers and lakes. As many inland waterways are connected to other river systems by canals, inland navigation facilitates or accelerates the spread of invasive invertebrate species to new biogeographic regions. Thereby, species may be actively translocated as a result of being attached to the hull of boats or within the ballast water, or may spread independently along newly built waterways, as documented for the Danube-Main Canal (Leuven et al. 2009; Mills et al. 1993; Pusch et al. 2009). As a consequence, invasive species arriving from various biogeographical regions meet habitat conditions in other river systems that have been modified by humans in many aspects (Tockner et al. 2010, 2011). This situation often enables non-native species to successfully establish novel ecological niches, and build up large populations (Darrigran 2002). As rivers subjected to multiple human pressures only offer suboptimal habitat conditions to native species, invasive species often replace native species (Byers 2002). Thereby, some invasive species may also benefit from pre-adaptations acquired from their original natural habitats, which result in gaining a superior competitive position relative to native species (Correa and Gross 2008; Gabel et al. 2011a). Yet there is still a tremendous lack of knowledge on the mechanisms how non-native species become successful colonizers especially in waterways, and both theories of pre-adaptations as well as of rapid adaptive changes are supported in literature (Alford et al. 2009; Correa and Gross 2008; Gabel et al. 2011a; Henery et al. 2010).

Given the profound alterations in the physical and biotic structure of major inland waters described above, there is also a high probability of changes in key ecosystem services, such as self-purification capacity, which includes the removal of organic matter from the water column (Pusch and Hoffmann 2000; Tockner et al. 2011). Recent publications have demonstrated that waves induced by navigation and boating may cause significant hydraulic disturbances to benthic invertebrates and fish (Bishop and Chapman 2004; Gabel et al. 2008, 2011b), which may also affect the filtration activity of mussel populations (Lorenz et al. 2013; Payne et al. 1999; Widdows et al. 1979).

As freshwater mussels are primary consumers of phytoplankton and seston in aquatic habitats, this group supplies significant food resources to the benthic food web (Howard and Cuffey 2006), in addition to significantly contributing to the self-purification of running waters. Thus, mussels may significantly improve water quality, particularly in eutrophicated surface waters (Welker and Walz 1998). Consequently, anthropogenic impacts on the filtration activity of freshwater mussels are likely to affect the productivity of the benthic food web and decrease ecosystem resilience, in addition to increasing the eutrophication of aquatic ecosystems. However, in the case river when systems have been colonized by invasive mussel species, the filtration rate of the benthic community may be even increased, as their filtration capacities and rates are typically higher compared to native species (Atkinson et al. 2011; Leff et al. 1990; Weitere et al. 2008). Aside from the greater capacity to compete for food (Strayer and Smith 1996), invasive species may exhibit other biological characteristics that better fit the habitat conditions of altered river systems, such as substrate preference (as for *Dreissena* spp.), temperature preference, or mechanical resistance (as for *Corbicula* spp.) (Tockner et al. 2011). However, there is limited information clarifying which of these multiple modes of anthropogenic disturbance is the most decisive for a given species, or how these modes favor specific invasive species (e.g. Gabel et al. 2011a).

We conducted a laboratory study to test whether wave disturbance, which represents an anthropogenic disturbance typical to large rivers, affects the filtration activity of three invasive mussel species. The results were discussed with similar data obtained from a previous study on native mussel species (Lorenz et al. 2013). We hypothesized that invasive mussels exhibit pre-adaptations to hydraulic disturbance, and are more likely to perform better under wave disturbance than native mussel species. This hypothesis would be supported by obtaining a consistent difference for both wave sensitivity and shell closing behavior between native and invasive species. We predicted that invasive mussel species are less susceptible to ship-induced waves, and that filtration activity is higher under disturbed conditions.

Material and methods

Experimental settings

We obtained 15 individuals of three invasive mussel species in Germany; specifically (1) the Asian clam

Corbicula fluminea MÜLLER 1774 from Rhine River, (2) the quagga mussel *Dreissena rostriformis bugensis* ANDRUSOV 1897 from Main River, and (3) the zebra mussel *Dreissena polymorpha* PALLAS 1771 from the Spree River. The mussels were acclimatized in separate aerated laboratory aquaria to a water temperature of 18 °C. After acclimatization, five individuals of the two *Dreissena* species were placed on ceramic tiles inside the respective aquaria, and were kept for another 2 weeks at 18 °C in a climate chamber. After all individuals used byssus threads to attach to the tiles, each mussel was equipped with a magnetic sensor (radiometric linear Hall-effect sensor A1321, Allegro Microsystems Inc., Worcester, MA, USA) on one shell, and a disc magnet (magnet grade N48, diameter 2 mm, thickness 2 mm) on the other shell. This equipment was used to record shell gape as a parameter of filtration activity (Hopkins 1933). Subsequently, one tile with five individuals was placed on the sediment inside an experimental wave tank that had three replicate flumes (Fig. 1). For *C. fluminea*, five magnet and sensor equipped individuals were transferred to each replicate section, and individuals were allowed to burrow into the sediment before the experiment. The wave tank was filled with aerated unchlorinated tap water, with a similar temperature of 18 °C. The sediment bed consisted of a 10 cm layer of silica sand, with a grain size of 0.2–0.63 mm. All three species were kept inside this wave tank for an additional 24 h. During all time in laboratory aquaria, individuals were fed with dried *Spirulina* sp. algae (food concentration 10 mg L^{-1}).

After all individuals exhibited filtration activity, waves of different intensity (5, 8, 11, 14, 17, 21, and 24 cm s^{-1}) were produced with a wave paddle driven by a car windshield wiper motor in random order to avoid individual mussels becoming acclimated to the waves. Each type of wave intensity was repeated three times. Data were recorded and processed using our own software written in LabVIEW (National Instruments, Germany). Shell gape was calibrated against voltage (mV), and the measured voltage data (x) was then converted into gape opening (in mm) by using the following linear inverse (x) polynomial equation (Lorenz et al. 2013):

$$\text{Distance} = a + \frac{b}{x} + \frac{c}{x^2} + \frac{d}{x^3} + \frac{e}{x^4} + \frac{f}{x^5} \tag{1}$$

Afterwards, data were converted into relative values (percentage of maximum gape opening).

Calculation of shear stress

The bottom flow velocity that was associated with experimental waves was recorded using an Acoustic Doppler Velocimeter (ADV, Micro ADV 16 MHz, Sontek, San Diego, CA, USA), at a rate of 50 Hz. The ADV was placed in the middle section of each wave tank flume, using the same technical set-up as in previous experiments (Gabel et al. 2011a). The three flumes of the wave tank showed no significant differences in orbital velocities (Gabel et al. 2011a). The sampling volume of the ADV probe head was adjusted to 1 cm above the sediment bed. As ADV measurements in clear tap water tend to be subject to high backscatter, one drop of *Lycopodium clavatum* spore suspension was added directly over the probe head before creating each wave to enhance particle concentration, and hence reduce backscatter. Using the bottom orbital velocity U_w and the wave friction factor f_w, wave friction shear stress τ_w was calculated for each wave that was produced, as:

$$\tau_w = \frac{1}{2} \times \rho \times f_w \times U_w^2 \tag{2}$$

(see Soulsby (1997) for detailed description).

Data analysis

The recorded shear stress values were double-square-root transformed to obtain a normal distribution, while the other data were left untransformed. Sigmoid regression models of the type:

$$f = \frac{a}{1 + e^{\frac{-(x - x_0)}{b}}} \tag{3}$$

were calculated for the relationship between shear stress (x) and the duration of shell closure and the degree of shell closure (percent reduction of maximum shell gape) as functions of x. This type of sigmoid regression model explained the highest proportion of mussel response pattern with rising shear stress levels. In the relationships of shear stress versus shell closure duration, the inflection point of the curves (x_0) was determined and re-transformed to an unpotentiated scale. The inflection point x_0 was defined as a threshold value separating tolerable and severe impacts on filtration activity, representing a predicted moderate value for the effect of shear stress, PMES (Lorenz et al. 2013). Accordingly, shear stress levels above this threshold produced less shell gape in all

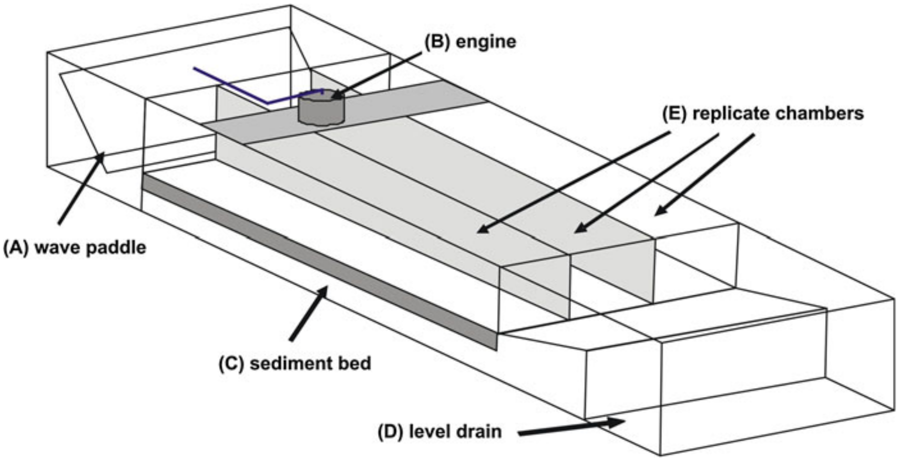

Fig. 1 Experimental wave tank that was used to produce waves of different intensity. The tank consisted of *a* a wave paddle, *b* an engine, *c* a sediment bed, *d* a level drain, and *e* three replicate chambers

experimental specimens, whereas some specimens were not affected below this threshold. The starting point of any shell closing behavior was defined as the value where 10 % of the maximum closing intensity is reached (Lorenz et al. 2013). The value was re-transformed to an unpotentiated scale, and considered as the predicted no-effect shear stress level (PNES).

We tested for differences in the parameter ‘a’ (asymptotic maximum), PMES, and PNES between the three invasive species using unpaired *t* tests as described in Motulsky (1998). As the biotic and abiotic conditions (water temperature, turbidity, dissolved oxygen, food concentration) of this laboratory experiment were highly comparable to the experimental conditions in a previous field experiment (Lorenz et al. 2013), we statistically compared sigmoid regression models for *D. polymorpha* from both studies. Thereby, we tested differences in the regression parameters ‘a’ (asymptotic maximum), ‘b’ (slope), and ‘x_0’ (PMES) between field versus laboratory approaches using unpaired *t* tests as described in Motulsky (1998). All statistical regressions and plots were performed using PASW (version 17.0, SPSS Inc., Chicago, IL, USA) and SigmaPlot (version 11.0, Systat Software Inc., Chicago, IL, USA).

Results

Degree and duration of shell closing

According to the sigmoid regression analysis (Table 1), the longest average closing duration was shown by *D. polymorpha* (a = 92 s), followed by *D. rostriformis bugensis* (87 s) and *C. fluminea* (20 s) (Fig. 2). Duration of shell closing did not differ significantly between both *Dreissena* species (df = 21, $p = 0.87$) but was significantly lower in *C. fluminea* than in *D. rostriformis bugensis* and *D. polymorpha* (df = 21, $p < 0.0001$ and $p < 0.0001$, respectively). The average degree of closing after

Table 1 Parameters of sigmoid regressions [$f = a/(1 + \exp(-(x - x_0)/b))$] between the duration of shell closing (s) and shear stress (N m^{-2}), and the degree of shell closing (%) and shear stress (N m^{-2})

	a		b		x_0	
	Duration	Degree	Duration	Degree	Duration	Degree
D. polymorpha (0.31***/0.59***)	91.65	67.54	0.11	0.04	0.73	0.77
D. rostriformis bugensis (0.74***/0.59***)	86.77	38.84	0.03	0.10	0.83	0.74
C. fluminea (0.69***/0.65***)	19.86	40.18	0.06	0.05	0.61	0.57

For each test, the r^2 value and the corresponding significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) are provided (duration/degree) wave disturbance was greatest in *D. polymorpha* (68 %), followed by *C. fluminea* (40 %) and *D. rostriformis bugensis* (39 %) (Fig. 2). Degree of shell closing did not differ significantly between *D. rostriformis bugensis* and *C. fluminea* (df = 21, $p = 0.77$) but was significantly higher in *D. polymorpha* than in *D. rostriformis bugensis* and *C. fluminea* (df = 21, $p < 0.0001$ and $p < 0.0001$, respectively).

Threshold values for the inhibition of filtration activity

Predicted moderate effect shear stress (PMES) values were higher in *D. rostriformis bugensis* (0.47 N m^{-2}) and *D. polymorpha* (0.38 N m^{-2}) compared to *C. fluminea* (0.14 N m^{-2}) (Fig. 3). PMES values did not differ significantly between both *Dreissena* species (df = 21, $p = 0.36$) and between *D. polymorpha* and *C. fluminea* (df = 21, $p = 0.46$), but was significantly higher in *D. rostriformis bugensis* than in *C. fluminea* (df = 21, $p < 0.001$). Similarly, the predicted no-effect shear stress (PNES) value was higher in *D. rostriformis bugensis* (0.24 N m^{-2}) compared to *D. polymorpha* (0.13 N m^{-2}) and *C. fluminea* (0.04 N m^{-2}) (Fig. 3). PNES values did not differ significantly between *D. polymorpha* and *C. fluminea* (df = 21, $p < 0.01$), but was significantly higher in *D. rostriformis bugensis* than in *C. fluminea* and *D. polymorpha* (df = 21, $p < 0.0001$ and $p < 0.001$, respectively).

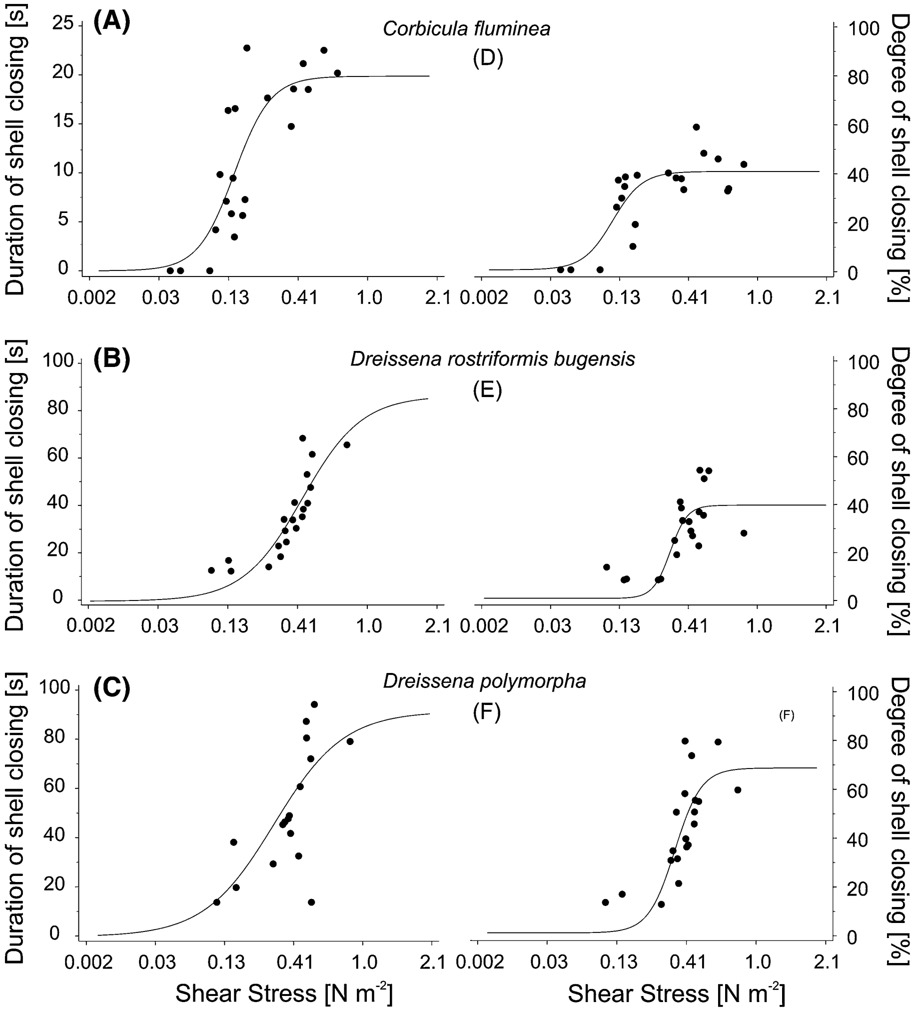

Fig. 2 Duration (**a**–**c**) and degree (**d**–**f**) of shell closing as functions of shear stress (N m^{-2}) caused by experimental waves of different intensity in the three invasive mussel species *C. fluminea*, *D. rostriformis bugensis*, and *D. polymorpha*

Comparison of field and laboratory studies

The shell closing behavior of *D. polymorpha* followed similar sigmoidal patterns under both field and laboratory conditions (Fig. 4). Respective regressions did not significantly differ between field or laboratory data for the relationship of shear stress and shell closing duration [unpaired *t* test, $df = 114$, $p = 0.99$ (a), $p = 0.85$ (b), $p = 0.92$ (x_0)], or the relationship of shear stress and shell closing degree [unpaired *t* test, $df = 112$, $p = 0.45$ (a), $p = 0.94$ (b), $p = 0.81$ (x_0)].

Discussion

To date, few studies have attempted to link the success of invasive species in newly colonized river systems to the specific habitat conditions that are available, which might reflect the respective biological or ecological traits of particular invasive species (Bij de Vaate et al. 2002; Devin and Beisel 2007; Ricciardi and Rasmussen 1998). In river systems subjected to strong or multiple human pressures, habitat conditions become suboptimal for native species, consequently favoring the establishment of invasive species. Thereby, the successful establishment of invasive species is not only governed by physical habitat conditions, but also by interspecific interactions. Invasive species have been shown to cause a decline in the abundance of native species, such as through competition for food sources (Strayer and Smith 1996). This exploitative competition may even occur among invasive species, as exemplified by the spread of the quagga mussel *D. rostriformis bugensis*, which caused a decline in the abundance of *D. polymorpha* (Zhulidov et al. 2010).

Our results indicate that, besides alterations to river hydrology, temperature, water quality, and channel morphology (Rahel and Olden 2008), higher filtration activity under wave exposure provides an additional mechanism to explain the success of invasive species in fresh water habitats used for inland navigation. In our studies, experimentally created waves consisted the primary variable influencing filtration activity (but see e.g. Moore 1977; Riisgard et al. 2011; or Salanki et al. 1974 for further variables influencing filtration). As invasive invertebrates, such as mussels, in freshwater habitats are mainly spread by ships via navigation channels (Leuven et al. 2009), the benefits of transportation to novel habitats might be twofold. First, their spread is accelerated by the anthropogenic disturbances (Byers 2002), such as ship traffic, and second, they are less susceptible to strong exposure from disturbance by ship-induced waves.

A comparison of our results with variables representing the susceptibility to wave stress from former field experiments of native mussel species (Lorenz et al. 2013) revealed some differences in the shell closing behavior of native versus invasive mussel species. The invasive species *D. polymorpha* studied both under laboratory and field conditions showed no significant difference in its shell closing behavior, suggesting that available data of native and invasive species were comparable as well between both setups. In summary, the native species investigated in the previous study showed relatively low PNES values in combination with either the highest duration of shell closing (*A. anatina*) or the highest degree of shell closing (*U. tumidus* and *U. pictorum*) (Fig. 3). Thus, we conclude that native mussel species seem to be more susceptible to wave disturbance than invasive species. To demonstrate how this varying susceptibility to wave action could influence filtration, we calculated the remaining filtration activity for each mussel species according to Eq. 2 from Lorenz et al. (2013) (general assumption: single motorboat passages with a speed of 18 km h^{-1}, mussels located at a water depth of 1.5 m). Thereby, the native species would show a remaining filtration activity of 80 % (*U. tumidus*), 71 % (*U. pictorum*), and 56 % (*A. anatina*), while the remaining filtration activities of invasive species would be 72 % (*D. polymorpha*), 88 % (*C. fluminea*), and 98 % (*D. rostriformis bugensis*) compared to undisturbed conditions. In comparison, this means an average reduction in filtration activity of 31 % for the studied native species, but just 14 % for invasive species. In contrast to *D. rostriformis bugensis* and *C. fluminea*, *D. polymorpha* differs not seriously from native species in any of the studied susceptibility parameters. Thus, the colonization success of this species (Aldridge et al. 2004; Johnson and Carlton 1996; Johnson and Padilla 1996) cannot be explained (at least for Europe) by invasive species exhibiting lower susceptibility to wave disturbance compared to native species.

We demonstrated that *D. rostriformis bugensis* and *C. fluminea* continue to filter under wave impacts, which would provide a crucial competitive advantage in fresh waters used intensively for navigation.

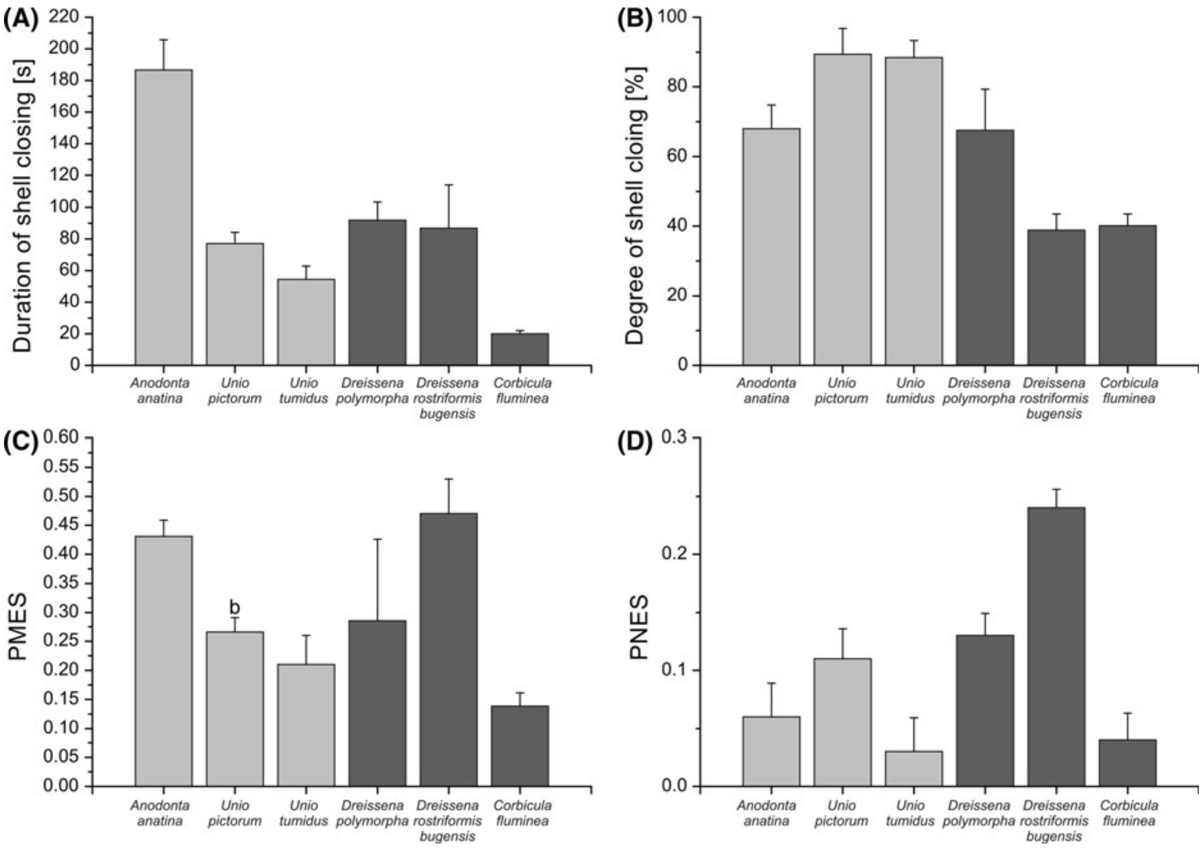

Fig. 3 **a** Duration (in s) and **b** degree (in %) of shell closing as functions of shear stress (N m^{-2}), and respective **c** PMES and **d** PNES threshold values for the native (*three left species*) and invasive (*three right species*) mussel species that were studied. The results for the native species were obtained from Lorenz et al. (2013)

Although both species exhibited similar degrees of shell closing at higher shear stress levels, they exhibited different sensitivity toward this stressor. For instance, *D. rostriformis bugensis* was the most stress–resistant species, with a minimal degree of shell closing, and maximal PNES and PMES values. Hence, *D. rostriformis bugensis* seems to be adapted to perform significant filtration activity even in habitats with high hydraulic disturbance. In comparison, while *C. fluminea* also showed a minimal degree of shell closing, which was even accompanied by a minimal duration of shell closing, this species exhibited minimal PMES and second minimal PNES values among the studied species. This ‘opportunistic’ pattern to exhibit a minimally sensitive response to hydraulic disturbance may represent an adaptation to life in hydraulically sheltered interstitial spaces within the sediments of fast-flowing rivers (McMahon 1999). In such habitats, disturbance may be mainly produced by relatively coarse particles transported along the river bottom, which pass by quickly. The ingestion of such particles may therefore be avoided by mussels, even by the short and incomplete closure of shells. During the experiments, we observed that *C. fluminea* individuals exhibited burrowing behavior in response to wave stress, which is a behavioral pattern that has not been previously observed in burrowing unionid species (Lorenz et al. 2013). Thereby, individuals escaped wave disturbances by burrowing into the sediment immediately after the passage of the first wave, leaving just their inhalant and exhalant siphons protruding from the sediment. In other cases, the mussels burrowed completely, without the siphon protruding but the shells remained open. This behavior

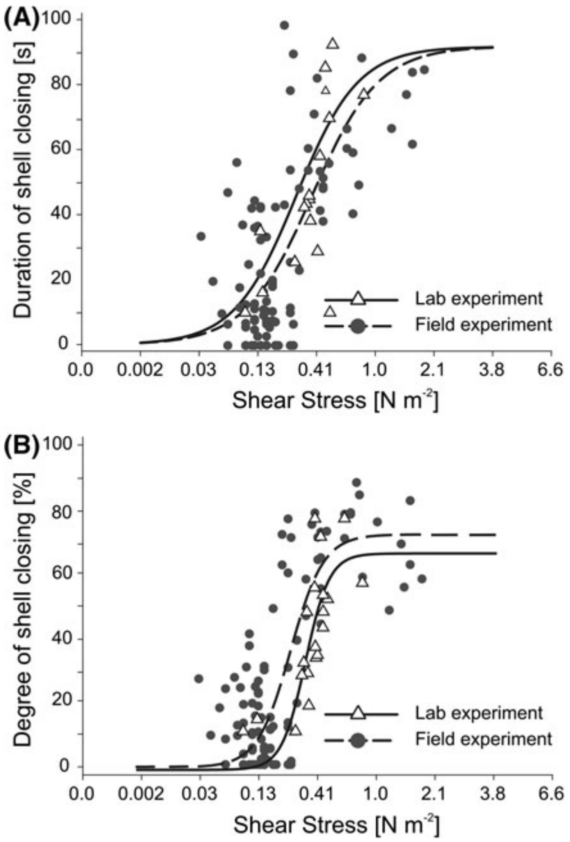

Fig. 4 **a** Duration (in s) of shell closing and **b** degree (in %) of shell closing as functions of shear stress caused by experimental waves of different intensity in *D. polymorpha* in field (*dashed lines*, n = 105) and laboratory (*solid lines*, n = 21) experiments

supports the assumption that filter feeding may not consist the only foraging strategy for *C. fluminea*, as additional pedal feeding has been described for this species (Reid et al. 1992).

The underlying mechanism that causes low susceptibility may be based on a pre-adaptation that some invasive species may have acquired through evolution in their original biogeographical region (Correa and Gross 2008), or may reflect adaptive changes in their behavior in newly colonized habitats (Alford et al. 2009), or a combination of the two (Henery et al. 2010). In the case of *C. fluminea*, the minimal sensitive response to wave disturbance may be the result of a pre-adaptation acquired in the hydraulic disturbed environments of its native range. Its rapid burrowing response to wave stress may be seen as an adaptive behavior that has developed under even more disturbed conditions. Thus, this species reflects a high degree of behavioral flexibility, which represents a recently suggested explanation for invasion success in novel environments (Sol 2007). Therefore, our results support the hypothesis that the high invasion success of non-native species might be based on the interaction of pre-adaptations and rapid adaptive changes (Henery et al. 2010).

Human impacts on aquatic ecosystems, including wave disturbance by navigation, often result in dramatic and well-known reductions in population size or species richness of autochthonous biota (Tockner et al. 2010), whereas the detailed effects on key ecosystem services remain poorly documented (Chapin et al. 2000) despite their common acceptance (Binimelis et al. 2007). Threats to the supply of clean water by *D. polymorpha* consists one of the few well documented impacts causing risks on regulating ecosystem services (Charles and Dukes 2007). The estimated damage of this invasion has been estimated at 5 billion US$ solely in the United States (Pimentel 2005). Even though this economic loss is dramatic, the ecological assessment of fresh water habitats currently is mostly based on the composition of biotic assemblages, while the status of ecosystem functioning is rarely assessed. The important self-purification mechanism in rivers that is provided by the transport of organic matter from the water column to the benthic food web by the filtration activity of freshwater mussels (Howard and Cuffey 2006; Pusch et al. 2001) is a major process contributing to high water quality (Tockner et al. 2011). Consequently, a reduction in the filtration activity of freshwater mussels by ship waves will result in the loss of the capacity for the self-purification of surface waters and, thus, directly affect the provision of important ecosystem services. The lower susceptibility of invasive mussel species to wave disturbance indicates that the detrimental effects of ship waves may be compensated by the presence of less susceptible invasive mussel species within this community. The impact of those species might thus be valued both positively (as for water filtration, e.g. pointed out for *D. polymorpha* by Minchin et al. (2002)) and negatively (as on species composition), adding another controversy to the ongoing debate on the perception of invasive species impact on contrasting levels of examination (Binimelis et al. 2007).

As climate change will result in lower minimum water levels of many surface waters, the impact of boat generated waves on mussels is likely to increase (Lorenz et al. 2013). In parallel, the invasion of non-native mussel species, which are also favored by climate change (Rahel and Olden 2008) may ensure that an important component of self-purification in freshwater ecosystems is retained, despite the negative effects of climate change and high boating activities. Accordingly, the ecological carrying capacity of inland waters for boating, as calculated by Lorenz and Pusch (2012), might also benefit from the introduction of mussel species that are less susceptible to the impacts of ship-induced waves. However, as the dominance of invasive species in river systems may disrupt natural food webs, such compensation of filter-feeding activity may be accompanied by important losses in other ecosystem functions, which require identification.

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