Limnologica xxx (xxxx) xxx

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Hydromorphological preferences of freshwater pearl mussel (*Margaritifera margaritifera*) in upland streams of the Bavarian Forest – A case study

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ARTICLE INFO

Keywords:
Freshwater pearl mussel
Margaritifera margaritifera
Hydromorphology
Numerical modelling
Freshwater habitat analysis

ABSTRACT

The freshwater pearl mussel is a highly specialized freshwater bivalve. In four pearl mussel streams located in the Bavarian Forest, hydromorphological microhabitat conditions were investigated in mussel colonized and adjacent non-colonized river stretches to describe hydromorphologic preferences of freshwater pearl mussel. For that purpose, tachymetry, flow velocity and substratum composition were investigated. Hydraulic-numerical models were calculated to predict flow velocities, maximal shear stress and substratum stability under different discharge scenarios. Results indicate that pearl mussels prefer river stretches with certain minimal currents during low flow but at the same time stable substrata even during bankfull discharge. Implications for habitat restoration and release of juvenile mussels from breeding programs are discussed.

1. Introduction

The freshwater pearl mussel (*Margaritifera margaritifera*) is a highly specialized freshwater bivalve. It occurs in clean and oligotrophic silicate rivers and streams of the northern hemisphere (Geist, 2010; Hastie et al., 2000). It has a complex life cycle, which includes a parasitic phase on a host fish, either brown trout (*Salmo trutta*) or Atlantic salmon (*Salmo salar*) (Taeubert et al., 2010; Young and Williams, 1984). After detachment from the host, the juveniles burry into the substratum, where they spend several years before they reappear at the substratum surface, living as filtrators at the interface between substratum and free flowing water (Bauer, 1987).

The freshwater pearl mussel is probably one of the best studied freshwater bivalves and many aspects of their ecological needs are well known. The species depends on a very high water quality with low nutrient and calcium content, e.g. optimal nitrate concentrations are defined to 0.5 mg/L NO_3-N (European Committee for Standardization, 2017). Furthermore, several studies have underlined the central role of substratum quality for freshwater pearl mussel. Especially the juveniles depend on a well sorted, coarse substratum that ensures sufficient flow-through in the interstitial zone. Consequently, the degradation of habitat quality by fine sediments was identified as the main reason of decline, clogging macropores in the interstitial zone, thus reducing flow rates and oxygen supply to juveniles (Denic and Geist, 2015; Geist and Auerswald, 2007; Österling et al., 2010).

At present, in almost all European countries hosting freshwater pearl mussel populations breeding programs are carried out aiming at reinforcement of depleted and overaged populations or reintroduction in habitats, where populations had gone extinct. The selection of an optimal release site is highly important for a successful establishment of juvenile mussels. Several studies on the distribution patterns of different mussel species pointed out the importance of river bed stability and the existence of flow refugia during high flows for mussel bed formation (Allen and Vaughn, 2010; Morales et al., 2006; Sansom et al., 2020; Strayer, 1999). Scheder et al. (2015) demonstrated bed stability in two Austrian freshwater pearl mussel beds. Moorkens and Killeen (2014) demonstrated that characteristics of flow velocity may also be crucial for habitat suitability during low flow.

Despite detailed investigations of substratum composition and physicochemical water quality aspects of freshwater pearl mussel habitats, comparably few studies investigated hydraulic variables like flow velocities, shear stress and their interrelation with substrate composition and stability. Especially, no boundary values have been established so far.

In our study, we investigated hydraulic differences between adjacent colonized and non-colonized areas in five different Central European freshwater pearl mussel river stretches during low flow and modelled bankfull discharge conditions, to increase knowledge on potentially

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https://doi.org/10.1016/j.limno.2022.126034
Received 26 April 2022; Received in revised form 9 September 2022; Accepted 28 September 2022
Available online 14 October 2022

Fig. 1. Map of Germany with localization of the study area indicated by the shaded zone in the south-east.

suitable hydromorphologic conditions for freshwater pearl mussel colonization on the microhabitat scale. Specifically, we hypothesized that freshwater pearl mussels

i) only occur in areas with stable river bed conditions during bankfull discharge.
ii) avoid areas where the portion of fine sediments < 1 mm exceeds 20 % of total sediment, even though the substrate may remain stable during bankfull discharge.
iii) avoid areas with maximal shear stress and flow velocities exceeding 40 N/m^2 and 1.5 m/s, respectively.
iv) avoid areas, where minimal water depth and flow velocities drop below 0.2 m and 0.2 m/s during low flow.

2. Materials and methods

2.1. Study area

The study area is located in the Bavarian Forest in the south-east of Germany close to the borderlines to Austria and the Czech Republic (Fig. 1). All running waters in this area are tributaries to the Danube and many of them host or hosted freshwater pearl mussel populations. Five study stretches in four different streams were selected. Due to the threat of poaching exact locations are not published. All selected streams still host freshwater pearl mussel populations, though they are small and with low or no natural recruitment. The colonized areas of study stretches host 200–500 individuals, with study stretches 1, 2 and 4 even being populated by a few juvenile specimens from natural reproduction.

2.2. Study design

Selection of study stretches aimed at representation of the full range of hydromorphological conditions, in which pearl mussel colonies are found whithin the study area, i.e. small brooks to small rivers with a width of 2–20 m. Furthermore two study stretches exhibited an elongated plain bed situation and two others were located in river bends. All of them comprised a colonized area, which was compared with a directly adjacent non-colonized area. The fifth study stretch was a tail race of a hydropower-plant. There, only a colonized area could be defined due to the complete and comparably even colonization by mussels.

Table 1
Minimal (min), maximal (max) and mean (mean) flow velocities in m/s and water depths in m at colonized and non-colonized areas of the five study stretches.

study stretch	non-colonized			colonized		
	min	max	mean	min	max	mean
	Flow velocity [m/s]					
1	–	–	–	0.8	2.5	1.5
2	0.1	0.9	0.4	0.5	0.8	0.6
3	0.2	0.8	0.3	0.2	0.6	0.3
4	0.3	1.2	0.9	0.2	0.8	0.6
5	0.1	1.3	0.7	0.3	1.1	0.6
	Water depth [m]					
1	-	-	-	0.6	2.5	1.1
2	0.6	1.1	0.8	0.15	0.9	0.5
3	0.3	1.25	0.7	0.6	1.5	0.8
4	0.1	0.9	0.35	0.1	0.9	0.35
5	0.15	0.9	0.4	0.2	0.9	0.4

Field data were collected between 4th–6th October 2016. In all study stretches a detailed tachymetric survey was carried out to get a detailed picture of terrain morphology. Average density of measurements was 0.54 / m^2. Density was adapted to riverbed morphology, i.e. in homogenous areas of study stretches density of data points was lower, but it was increased around structures with an edge length ≥ 0.5 m, such as rocks or large woody debris. Total length of study stretches ranged between 75 and 100 m. At each study stretch, discharge was calculated based on hydrometric flow measurements. Flow velocities were measured with a handheld flow meter (Schiltknecht MiniWater20, Schiltknecht Messtechnik AG, Gossau, Switzerland).

2D-hydraulic-numerical models were calculated with the software HYDRO_AS-2D (Hydrotec, Aachen, Germany). Model transformation and visualization of results was carried out with the software SMS (Aquaveo, Utah, USA). Models were calibrated using data gathered at field surveys with a minimal accuracy of ± 0.05 m, but did not exceed ± 0.02 m. After model calibration, water depth, flow velocities and shear stress were modelled for different discharge scenarios including low water level and bankfull discharge.

Substratum samples were secured separately for colonized and non-colonized areas in each study stretch. Sampling spots were selected to receive representative samples of substratum composition in each area. A tube 0.24 m in diameter was firmly pressed on the substratum to minimize water flow at the sampling spot and thus loss of fine particles. As a first step, coarse particles in the top layer were collected by hand. Finer particles were collected with a small shovel. Substratum was collected to a depth of 0.1 m and a volume of 2.5 L per sampling spot. At the laboratory, substratum samples were processed according to DIN EN ISO 17892–4. Texture lines were calculated.

3. Results

3.1. Hydraulic-numerical models

Models of low flow conditions revealed that mussel occurrence was restricted to areas, which had minimal water depths of 0.2 m and mainly ranged within 0.2–0.4 m. Flow velocities ranged between 0.2 and 0.8 m/s (Table 1). Conditions in adjacent non-colonized areas were more variable with parts of the streambed even falling dry during low

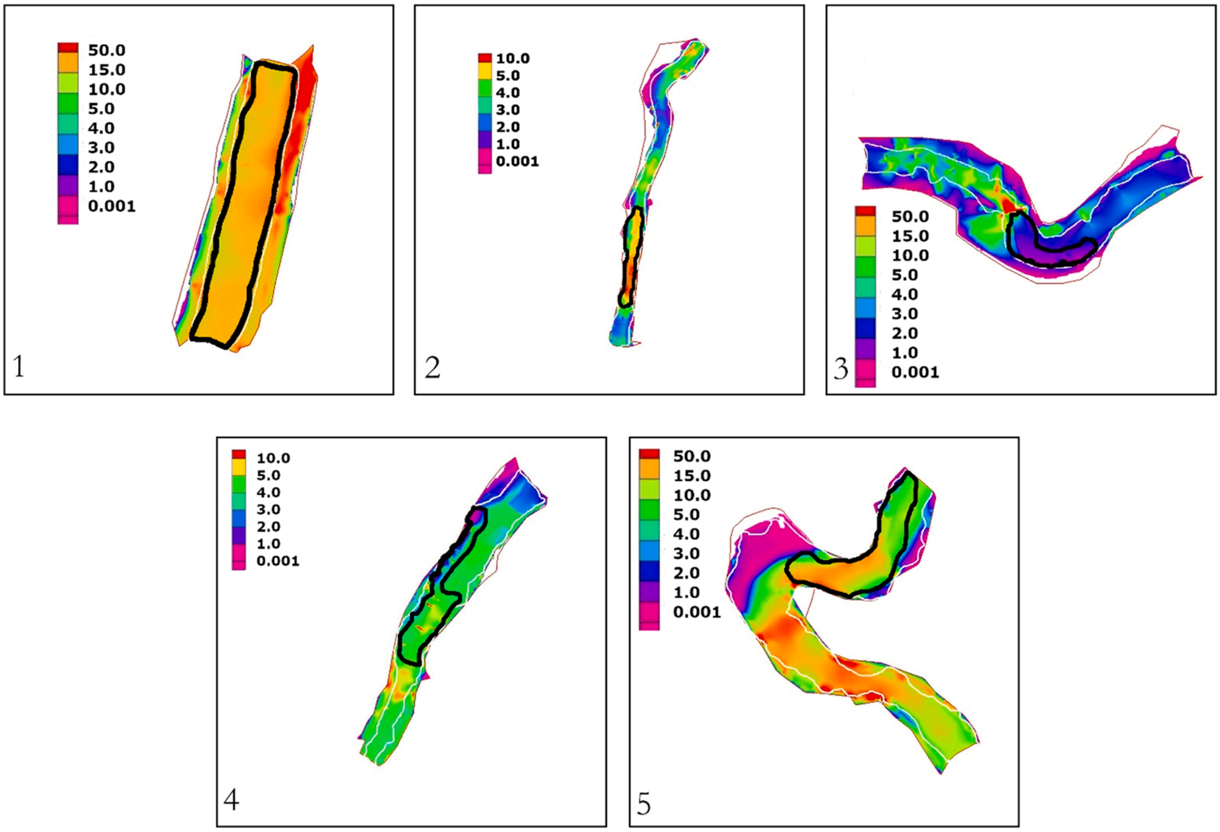

Fig. 2. Maximal shear stress during bankfull discharge in the study stretches 1–5. Black frames indicate mussel colonized areas.

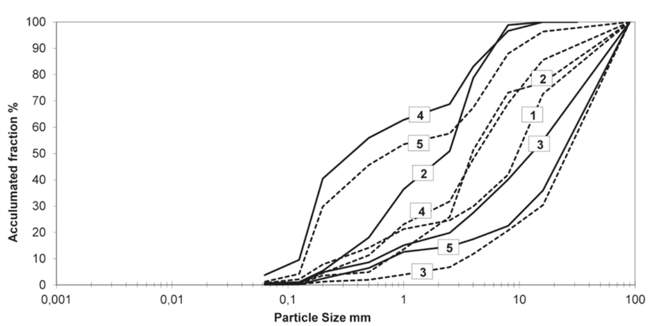

Fig. 3. Grain size distribution at study stretches 1–5 in colonized (dashed lines) and non-colonized areas (solid lines).

flow.

During bankfull discharge, water depths and flow velocities generally increased in both, colonized and non-colonized areas. Again, conditions were more homogenous in colonized areas, where water depths mainly ranged between 0.8 and 1 m. In one study stretch water depth increased to more than 2 m. Flow velocities often stayed below 1 m/s, but could reach a maximum of 2.5 m/s. In non-colonized areas, conditions closely resembled colonized areas. However, variability was a little higher.

Mean shear stress revealed no remarkable differences in colonized and non-colonized areas. Maximal shear stress in colonized areas was always lower than in adjacent non-colonized areas of the same study stretch. The range over all study stretches was 3–30 N/m^2 in colonized versus 12–53 N/m^2 in non-colonized areas (Fig. 2).

3.2. Texture analysis

In colonized areas, fine sediment content of particles < 1 mm ranged between 4 % and 54 %, with two study stretches exceeding a portion of 20 %. At least 10 % of the samples consisted of coarse gravel > 30 mm in diameter except for study stretch 5. With exception of study stretch 5, fine sediment contents were higher and the portion of coarse particles was lower in non-colonized compared to colonized areas. In study stretches 3 and 5, percentage of particles < 1 mm in non-colonized areas was comparable to colonized areas with < 20 % and content of particles > 30 mm was high with 30 % and 40 %, respectively. In three out of four study stretches with adjacent colonized and non-colonized areas, content of fine particles was lower, whereas maximal grain size and content of the fraction > 30 mm were higher in colonized than in non-colonized areas (Fig. 3).

4. Discussion

In our study, we compared hydraulic components and substratum composition in adjacent colonized and non-colonized areas in freshwater pearl mussel streams. We detected a wide range of different substrate compositions, both between adjacent colonized and non-colonized areas but also between study stretches. The same holds true for shear stress, water depths and flow velocities.

Our results confirm the findings of Strayer (1999), Morales et al. (2006) or Allen and Vaughn (2010) that stable mussel colonies successfully establish in flow refugia with substrate stability even during bankfull discharge. In all five study stretches, colonized areas showed a substrate composition that is unlikely to move during shear stress values modelled for bankfull discharge conditions. Scheder et al. (2015) had the same result in two Austrian freshwater pearl mussel rivers. With maximal shear stress values of 4 and 24 N/m^2 Scheder et al. (2015) already made clear that hydraulic conditions at freshwater pearl mussel colonies can strongly vary. In our study, we even found a slightly wider range of 3–30 N/m^2. However, even though maximum shear stress was higher in non-colonized than in colonized areas, indicating substrate movement during elevated discharge, this correlation did not always hold true for the complete investigated area. Consequently, the conclusion of Morales et al. (2006) that mussel distribution is regulated by substratum stability during high flows probably needs to be narrowed, at least in case of the freshwater pearl mussel.

For instance, in study stretch 3, the area upstream from the colonized area can be assumed to remain stable during bankfull discharge judging by shear stress values and substrate composition. Nevertheless, mussels were not found there. One possible explanation may be the finer substrate compared to the colonized area. It may be expected that freshwater pearl mussels prefer substrates with lower amounts of fine sediments. However, the content of particles < 1 mm of 15 % is still below the threshold values defined for good pearl mussel habitats (Geist and Auerswald, 2007). Furthermore, a high fine sediment content does not seem to exclude mussel colonization, at least in case of adult mussels, considering a fine sediment content of 53 % in the colonized area of study stretch 5.

The picture becomes complete, when low flow conditions are considered additionally. Minimal values of water depth and flow velocity defined for suitable habitats are again confirmed by our results and mussels clearly preferred areas with minimal water depths > 0.2 m and flow velocities > 0.2 m/s (Hastie et al., 2000).

Our findings have corroborated the literature values for flow velocity, water depth, substratum composition and shear stress in freshwater pearl mussel habitats. In our approach, we have used these standard parameters to model hydromorphologic conditions on the microhabitat scale during different discharge scenarios demonstrating that for a valid assessment of hydromorphologic habitat suitability, low flow and high flow (bankfull discharge) scenarios both need to be incorporated. Due to the choice of the study stretches, our study is the first to use this modelling approach in habitats of different quality, as study stretches 1, 2, and 4 allowed recent natural recruitment, which is not observed in study stretches 3 and 5. Our data indicate that for adult freshwater pearl mussels substrate stability regardless of substratum structure is enough to allow successful colonization of a river stretch. For successful reproduction and survival of post-parasitic juveniles an additional precondition is a suitable substratum structure with low amount of fine sediments, which is ensured by sufficient currents during low flow conditions. Consequently, our results confirm the studies of Geist and Auerswald (2007) and Moorkens and Killeen (2014), but add another dimension to freshwater pearl mussel habitat assessment.

Furthermore our approach of 2D-hydraulic-numerical models can be a valuable tool in planning of habitat restoration measures and for prediction of optimal release sites for juvenile freshwater pearl mussels from breeding programs. Especially in habitats with very small and impaired populations or for reintroduction of populations gone extinct, choice of the optimal microhabitat for release actions can be challenging and be supported by model calculation in advance of release actions.

However, it is necessary to be aware that our study has a preliminary character due to the restricted sample size and study area. Consequently, conditions may differ in other stream types or regions of the distribution area of the freshwater pearl mussel, which has already been acknowledged in the CEN-standard for the species (European Committee of Standardization, 2017). Furthermore, all Central European pearl mussel habitats are more or less impaired, because of which the colonized areas in our study streams may not represent optimal habitat but rather tolerable conditions. Further application of the method in completely intact habitats and other regions of the distribution area are therefore highly recommendable to corroborate our results and expand knowledge on the range of hydromorphologic conditions enabling freshwater pearl mussel colonization.

CRediT authorship contribution statement

Marco Denic: Conceptualization, Resources, Writing Original draft, review and editing, Visualization, Funding acquisition. Michael Kühneweg: Methodology, Formal analysis, investigation, Data Curation, Writing review and editing, Visualization, Funding acquisition. Thomas Schmidt: Methodology, Resources, Data Curation, Writing review and editing, Visualization, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank Silke Mueller-Stahl for her support during field work.

The study was carried out within the project "ArKoNaVera -Umsetzung regionaler Schutzmaßnahmen und Entwicklung eines neuen überregionalen Artenschutzkonzeptes für die Nationalen Verantwortungsarten: Flussperlmuschel (*Margaritifera margaritifera*) und Malermuschel (*Unio pictorum*)". The project "ArKoNaVera" was funded by the Federal Agency for Nature Conservation with resources from the German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection, by the German Federal Ministry of Education and Research and the Bayerische Naturschutzfonds (grant number 3514 685E13).

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