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Conservation status of two endangered freshwater mussel species in Bavaria, Germany: Habitat quality, threats, and implications for conservation management

Katharina Stoeckl^{1,2} | Marco Denic^{1,3} | Juergen Geist¹ ¹Aquatic Systems Biology Unit, Technical University of Munich, Freising, Germany²Bavarian Academy for Nature Conservation and Landscape Management, Laufen, Germany³Landschaftspflegeverband Passau, Fuerstentzell, Germany**Correspondence**Juergen Geist, Aquatic Systems Biology Unit, Technical University of Munich, Muehlenweg 18-22, D-85354 Freising, Germany.
Email: geist@wzw.tum.de**Funding information**

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Abstract

1. The freshwater pearl mussel (*Margaritifera margaritifera*) and the thick-shelled river mussel (*Unio crassus*) are relatively widespread across Europe, but are strongly declining and are now protected by the European Habitats Directive. In the course of this study, 20 pearl mussel and 14 thick-shelled river mussel streams in Bavaria, Germany, were investigated.
2. The mussel populations were mapped to determine population size and age structure. For the assessment of habitat quality, host fish abundance and physicochemical parameters were investigated, e.g. substratum quality, water chemistry, redox potential, and turbidity. Furthermore, potential risks for the populations such as predation or river maintenance were also recorded and assessed.
3. The average population size and recruitment rates of *M. margaritifera* populations were lower than in *U. crassus* populations, with 3517 (2.2% juveniles) compared with 5566 (41.4% juveniles) individuals, respectively. On average, 22.3% of particles were smaller than 0.85 mm in diameter at *M. margaritifera* sites, whereas the mean proportion of fine particles at *U. crassus* sites was twice as high, at 41.3%. Other parameters such as redox potential or electric conductivity also indicated more favourable habitat conditions in *M. margaritifera* streams. *Unio crassus* seems to be less vulnerable to adverse substratum texture and increased nutrient levels than *M. margaritifera*.
4. The main threats for *U. crassus* were physical habitat destruction, predation by muskrat, or a lack of host fish, whereas *M. margaritifera* mainly suffered from siltation leading to a lack of oxygen supply to the interstitial zone, affecting recruitment. Consequently, conservation strategies need to be species-specific and address stream-specific reasons for decline. As a basis, accurate and comparable monitoring data are necessary, which implies the standardization of monitoring protocols.

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KEYWORDS

European Habitats Directive, habitat, *Margaritifera margaritifera*, population, stream, *Unio crassus*

1 | INTRODUCTION

Freshwater bivalves have colonized diverse habitats worldwide and have adapted to highly diverse habitat conditions (Bogan, 2008); however, they also belong to the most imperilled taxonomic groups worldwide (Lydeard et al., 2004). In particular, unionoid bivalves, which have a complex life cycle including an obligate host-fish stage, are highly vulnerable to habitat alterations, as these can affect the mussels directly as well as their host fish (Taeubert & Geist, 2017). In central Europe, bivalve populations have severely declined over the last decades owing to pollution, physical habitat destruction, and land-use changes (Bauer & Wächtler, 2001; Geist, 2010, 2011; Lopes-Lima et al., 2017). At the same time, bivalves are considered keystone species for the functioning of freshwater ecosystems (Lummer, Auerswald, & Geist, 2016; Vaughn, 2018), as they provide important ecosystem services such as filtration, bioturbation or nutrient allocation (Atkinson, Vaughn, Kenneth, & Cooper, 2013; Vaughn, Gido, & Spooner, 2004; Vaughn & Hakenkamp, 2001).

In European member states, species and habitat types that are considered to be of European importance are protected under the Habitats Directive (Bouchet, Falkner, & Seddon, 1999; Council of the European Communities, 1992). The directive obliges member states to maintain or to reach a favourable conservation status of 200 habitat types and more than 1000 animal and plant species. All habitats and species protected under the Habitats Directive as well as under the Birds Directive (Council of the European Communities, 2010) form the Natura 2000 network of protected areas. Protected species and habitats are defined in Annexes II, IV and V of the Habitats Directive, depending on the means of protection. For example, for species in Annex II, core areas of protection need to be defined ('special areas of conservation'), which are included in the Natura 2000 network. These sites must be managed according to the ecological demands of the target species. Species in Annex IV must be strictly protected not only within but also outside of protected areas, and the exploitation of species in Annex V must not endanger their favourable conservation status. Following Article 17 of the Directive, member states must report to the European Commission on the state of the habitat types and species every 6 years based on the results of monitoring programmes. In most cases, member states have developed national monitoring protocols for species and habitat assessments. As a result, methodologies and data quality can differ widely between the countries. For freshwater pearl mussel (*Margaritifera margaritifera*), the first step to overcome this problem was taken only recently, when a group of international experts from countries with existing populations of this species came together to compile a standard, following the criteria of the European Committee for Standardization (CEN) (Boon et al., 2019). CEN brings together national standardization bodies from

34 European countries for the development of voluntary standards at a European level. The CEN standard for monitoring freshwater pearl mussel streams was developed by experts from 11 countries: Austria, Finland, France, Germany, Ireland, Luxembourg, Norway, Portugal, Spain, Sweden, and the UK. Based on best practice developed and used by those experts, the standard describes approaches that individual countries have adopted for survey, data analysis, and condition assessment, and provides guidance on a consistent approach to monitoring. Among the 44 mollusc species, the freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758) and the thick-shelled river mussel *Unio crassus* (Philipsson, 1778) are listed in the annexes of the Habitats Directive. Both species are relatively widespread throughout Europe but are now strongly declining (European Environment Information and Observation Network (EIONET), 2019a, 2019b): *M. margaritifera* was assessed as Critically Endangered (CR) in the 2011 International Union for Conservation of Nature (IUCN) Global Red List and *U. crassus* was considered Endangered (EN), with large viable populations remaining in northern Europe and Russia. With 46 pearl mussel populations (Denic & Geist, 2017) and with 82 thick-shelled river mussel populations a considerable proportion of German populations occur in the federal state of Bavaria.

This article presents an overview of the population status and habitat conditions in freshwater pearl mussel and thick-shelled river mussel streams in Bavaria and assesses the condition of populations and habitats based on the German assessment criteria within Natura 2000 areas.

2 | METHODS

2.1 | Study area

The study was conducted in 20 *M. margaritifera* and 14 *U. crassus* streams in the state of Bavaria, Germany, between 2012 and 2015. The rivers with *M. margaritifera* included all types of *M. margaritifera* habitats in Bavaria as well as populations in various condition. At a national level, Bavaria holds the majority of German pearl mussel populations. For *U. crassus*, 14 study streams had been selected previously by the Bavarian Environment Agency by random draw for each Bavarian state district from the state database ArtenSchutzKartierung (ASK). As a consequence of a recent illegal pearl fishing event, the names of the mussel rivers are treated as confidential and are not reported here. The natural distribution area of *M. margaritifera* in Bavaria is limited to the Eastern part of the state, which is dominated by siliceous headwater streams (Figure 1). In contrast, *U. crassus* is widely distributed across the state, with the study sites representing all faunal regions that are populated by the species.

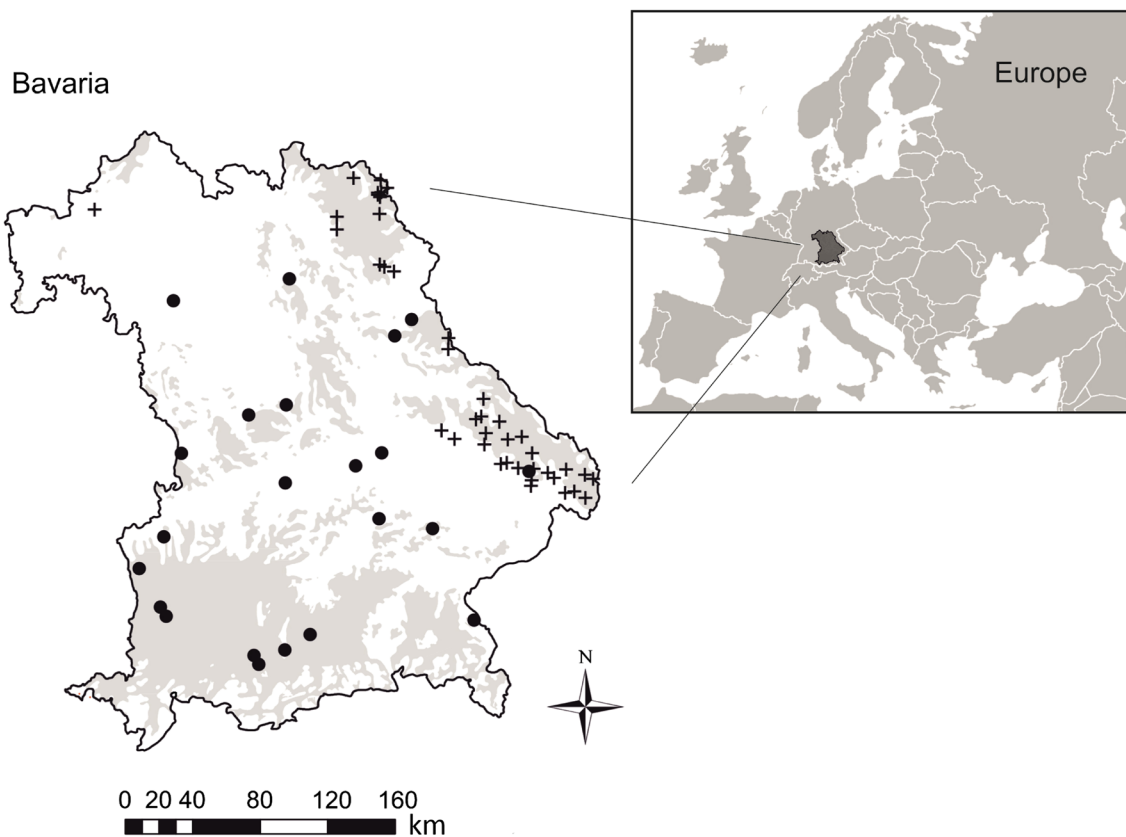


FIGURE 1 Distribution of mussel populations sampled in the study area: • *Unio crassus* populations; + *Margaritifera margaritifera* populations

2.2 | Mussel survey

The survey area covered the colonized area of the mussels in each stream, which was known from previous monitoring programmes, and varied between 0.2 and 18.0 km of river length. For *M. margaritifera*, complete census monitoring was performed where mussel numbers were expected to be smaller than 1000 individuals. In populations of more than 1000 individuals, 5-m cross-channel transects were applied every 100 m to estimate the population size.

For *U. crassus*, a systematic sampling approach (Strayer & Smith, 2003) was applied using cross-channel transects to estimate the population size. According to Christman (2000), systematic sampling provides good spatial coverage and is particularly useful for populations of rare species. The distance between two transects was 80 m and the length of each transect was 20 m. In all streams, visual and tactile searches were performed either by wading in an upstream direction or by snorkelling or scuba diving, drifting downstream, depending on the water depth of each stream.

In areas with at least 10 mussels per metre of stream length, at least 100 mussels were removed from the sediment to determine their length and age. The age of the mussels was assessed: (i) by counting the annual rings in the shells of *U. crassus*; and (ii) by measuring the total length with a caliper in *M. margaritifera* and determining approximate ages from pre-determined age-length relationships. As the shells of *M. margaritifera* grow very slowly and have a dark black colour, age determination by counting the annuli is rarely possible.

Therefore, the length of the mussels was measured to distinguish between juvenile (<65 mm; Hastie, Boon, & Young, 2000) and adult mussels. All live mussels were returned to the river in the approximate locations where they were found. In populations with low numbers (<100), age structure was not determined.

2.3 | Habitat parameters

Physicochemical habitat characteristics were analysed at 290 sites (5–10 sites per stream, depending on the length of the populated stretch). The sites were randomly selected and distributed across the length of each study stream. Electrical conductivity (EC, $\mu\text{S cm}^{-1}$, corrected to 20°C), dissolved oxygen concentration (O_2 , mg L^{-1}), pH value, and temperature (°C) were measured using a handheld Multi 3430 multiparameter meter and a pH 3110 portable pH meter (WTW GmbH, Weilheim, Germany), with one measurement taken per site. Turbidity (NTU) was measured using a turbidity meter (Turb355 T; WTW GmbH).

For water quality analysis, three replicate water samples per stream were collected from free-flowing water. A volume of 50 ml was taken and stored on ice until further processing with ion chromatography (ThermoFisher Scientific, Dreieich, Germany). A mixture of 1.8 mM disodiumcarbonate and 1.7 mM sodiumhydrogencarbonate was used for eluting anions (AG-22 as guard column and AS-22 separation column) and 20 mM methanesulfonic acid for eluting cations

TABLE 1 German assessment scheme for *Unio crassus* streams. The worst score of a single parameter determines the assessment of each subcategory, which are population status, habitat quality, and disturbance

Parameter/category	A	B	C
POPULATION STATUS			
Estimated total population size	>10 000	1000–10 000	<1000
Population density	>50 live ind./m stream length	5–50 live ind./m stream length	<5 live ind./m stream length
Population structure	More than 20% of live individuals are juveniles of up to 5 years of age	Up to 20% of live individuals are juveniles of up to 5 years of age	No live juveniles
HABITAT QUALITY			
Overall habitat quality (expert judgement with explanatory statement)	Well structured, natural streams with clear oxygen-rich water and a strong variation in depth and width	Maintained streams with clear water, near natural ditches; partially strong variation in depth and width	Heavily maintained running waters with no variation in depth and width
Flow velocity	Fast (0.3–1 m s ⁻¹)	Moderate (0.1–0.3 m s ⁻¹)	Slow to stagnant (<0.1 m s ⁻¹)
Structure of substrate and interstitial zone (expert judgement with explanatory statement)	Stable stream bed consisting of sand or fine gravel; well perfused and unclogged interstitial	Stream bed predominantly consisting of sand and fine gravel or silt, but mainly stable; restricted perfusion of interstitial spaces owing to moderate siltation	Very silty substrates; stream bed only partially stable; low perfusion of interstitial spaces owing to strong siltation
NO ₃ or NO ₃ -N concentration in mg L ⁻¹	<8 mg L ⁻¹ NO ₃ or <1.8 mg L ⁻¹ NO ₃ -N	8–10 mg L ⁻¹ NO ₃ or 1.8–2.3 mg L ⁻¹ NO ₃ -N	>10 mg L ⁻¹ NO ₃ or >2.3 mg L ⁻¹ NO ₃ -N
Abundance of potential host fish (expert judgement with explanatory statement, mentioning of fish species)	Numerous potential host fish species with sufficient recruitment	Few host fish species with moderate recruitment	Single host fish species with very low recruitment
DISTURBANCE			
Eutrophication	Not detectable from adjacent areas	Detectable from adjacent areas, e.g. due to eutrophic bank vegetation	Clearly visible from adjacent areas, e.g. wastewater treatments
Substratum mobility, siltation (expert judgement with explanatory statement; description of dimension and causes)	Natural or near-natural	Moderately increased	Strongly increased
Percentage of deciduous/mixed forest and agriculturally unused or extensively used areas in the catchment	>70%	40–70%	<40%
River maintenance	No disturbance	Slight disturbance	Strong disturbance
Predation by neozoa (e.g. muskrat, raccoon, mink, nutria)	No	Moderate (<20 dead shells)	High (>20 dead shells)
Tourism (e.g. boat trips) (expert judgement with explanatory statement)	No detectable disturbance	Moderate disturbance	Strong disturbance

(CG-12 as guard column in line with a CS-12 separation column). The results of NO₃⁻ and ortho-PO₄³⁻ analyses are presented in this article.

Flow velocity was measured with a handheld flow meter (HFA; Höntzsch, Waiblingen, Germany) at 50% water depth. Substratum texture was analysed at three sites per study stream using a box

sampler (Pander, Mueller, & Geist, 2015). This collects the uppermost 10 cm of the substratum; it has a rectangular opening of 16.0 cm × 12.2 cm and a length of 29.3 cm. The box sampler is equipped with an adjustable metal plate on each side to ensure sampling from a well-defined substratum depth. Its use is similar to a bulk-core sampler (Kondolf, 2000). Grain sizes were fractioned with a wet-

TABLE 2 German assessment scheme for *Margaritifera margaritifera* streams. The worst score of a single parameter determines the assessment of each subcategory, which are population status, habitat quality, and disturbance

Parameter/category	A	B	C
POPULATION STATUS			
Estimated total population size	>10 000	1000–10 000	<1000
Age structure and estimated proportion of juvenile mussels	Proportion of juvenile mussels (<10 years) is >20% of all live individuals	Proportion of juvenile mussels (<10 years) is ≤20% of all live individuals	No juvenile mussels found
HABITAT QUALITY			
Overall habitat quality (expert judgement with explanatory statement)	Well structured, natural streams with clear oxygen-rich water and a strong variation in depth and width	Maintained streams with clear water, near-natural ditches; partially strong variation in depth and width	Heavily maintained running waters with no variation in depth and width
Flow velocity	Fast (0.3–1 m s ⁻¹)	Moderate (0.1–0.3 m s ⁻¹)	Slow (< 0.1 m s ⁻¹)
Structure of substrate and interstitial zone (expert judgement with explanatory statement)	Stable substrate consisting of fine gravel to boulders; well perfused and unclogged interstitial zone	Stable stream bed predominantly consisting of fine gravel and pebbles; restricted perfusion of interstitial spaces owing to moderate siltation	Partially stable stream bed consisting of sand and silt; low perfusion of interstitial zone owing to strong siltation
NO ₃ or NO ₃ -N concentration in mg L ⁻¹	Mean value <4.4 mg L ⁻¹ NO ₃ or <1 mg L ⁻¹ NO ₃ -N	Mean value <6.5 mg L ⁻¹ NO ₃ or <1.5 mg L ⁻¹ NO ₃ -N	Mean value >6.5 mg L ⁻¹ NO ₃ or >1.5 mg L ⁻¹ NO ₃ -N
Abundance of potential host fish (expert judgement with explanatory statement, mentioning of fish species)	Natural fish community, all species recruiting	Like A, but single species missing or without recruitment	Unnatural species composition with dominance of single species, occurrence of non-native species and generally low recruitment
DISTURBANCE			
Eutrophication	Not detectable from adjacent areas	Detectable from adjacent areas, e.g. from eutrophic bank vegetation	Clearly visible from adjacent areas, e.g. wastewater treatments
Substratum mobility, siltation (expert judgement with explanatory statement; description of dimension and causes)	Natural or near-natural	Moderately increased	Strongly increased
Percentage of deciduous/mixed forest and agriculturally unused or extensively used areas in the catchment	>90%	50–90%	<50%
River maintenance	No disturbance	Slight disturbance	Strong disturbance
Predation by neozoa (e.g. muskrat, raccoon, mink, nutria)	No		Detectable

sieving tower (Fritsch, Idar-Oberstein, Germany) and different mesh sizes (63.0, 20.0, 6.3, 2.0, and 0.85 mm). The fractions retained on each sieve were dried at 100°C and weighed to the nearest gram. The percentage of each grain fraction was determined, but considering the restricted grab-sample volumes, the largest fraction of >20 mm was generally excluded from further analyses, as suggested by Geist and Auerswald (2007).

Redox potential (Eh) was measured both in the free-flowing water and in the interstitial zone to determine the hydrological exchange of water (and oxygen) between the two compartments. Following the

method described in Geist and Auerswald (2007), the redox potential was first measured in free-flowing water and then at a depth of 10 cm into the substratum. Values above 300 mV imply oxic conditions, whereas values below indicate anoxia (Schlesinger, 1991).

If recent data (less than 2 years old) from State Fish Monitoring by the 'Fachberatung fuer Fischerei – Bezirk Niederbayern' and the 'Fachberatung fuer Fischerei – Bezirk Oberfranken' on fish populations were unavailable, electrofishing was conducted to assess host fish availability and abundance in the streams. Fish populations were sampled with a 1.5-kW portable electrofishing backpack unit

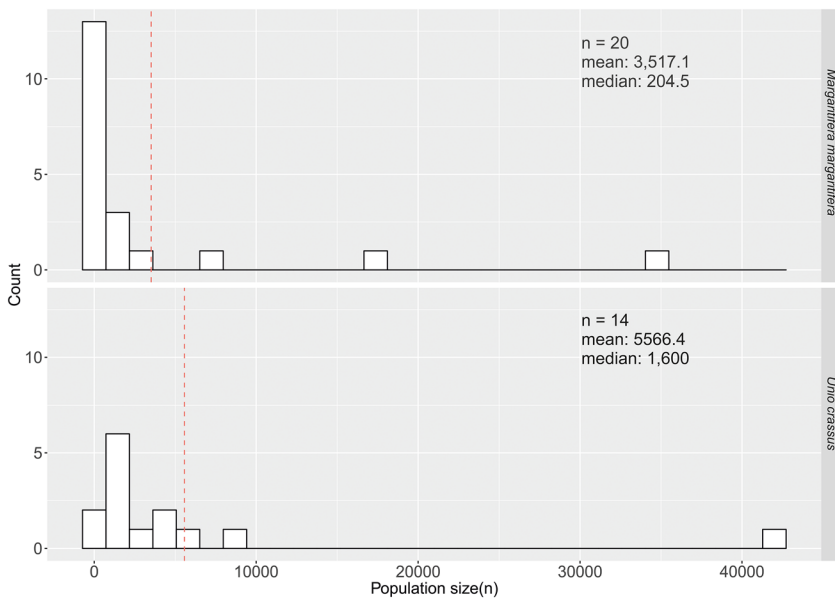


FIGURE 2 Size–frequency distribution for 20 *Margaritifera margaritifera* and 14 *Unio crassus* populations in Bavaria, Germany

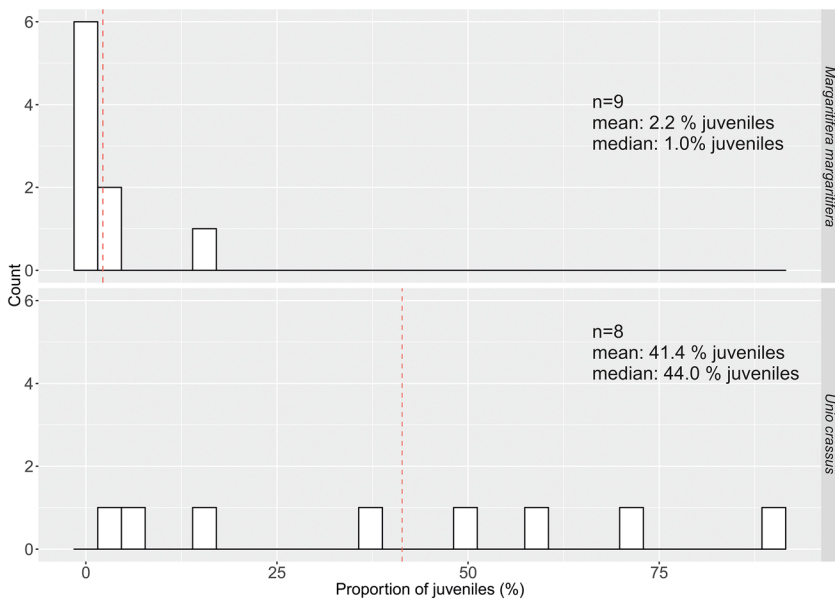


FIGURE 3 Proportion of juveniles: frequency distribution for nine *Margaritifera margaritifera* and eight *Unio crassus* populations in Bavaria, Germany, where the age structure was determined

(FEG 1500; Efko, Leutkirch, Germany), wading in an upstream direction with a single anode following the German standard (Verband Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler (VDFF), 2000). The area covered by electrofishing varied between 5 and 10% of the length of the river stretch that was populated by the mussels. The stunned fish were collected with a dip net and kept in plastic tanks with a permanent oxygen supply. After species determination and length measurements, all fish were released into the same stretch of stream from which they were sampled. Species richness and host fish density were calculated for each stream.

2.4 | Threat assessment

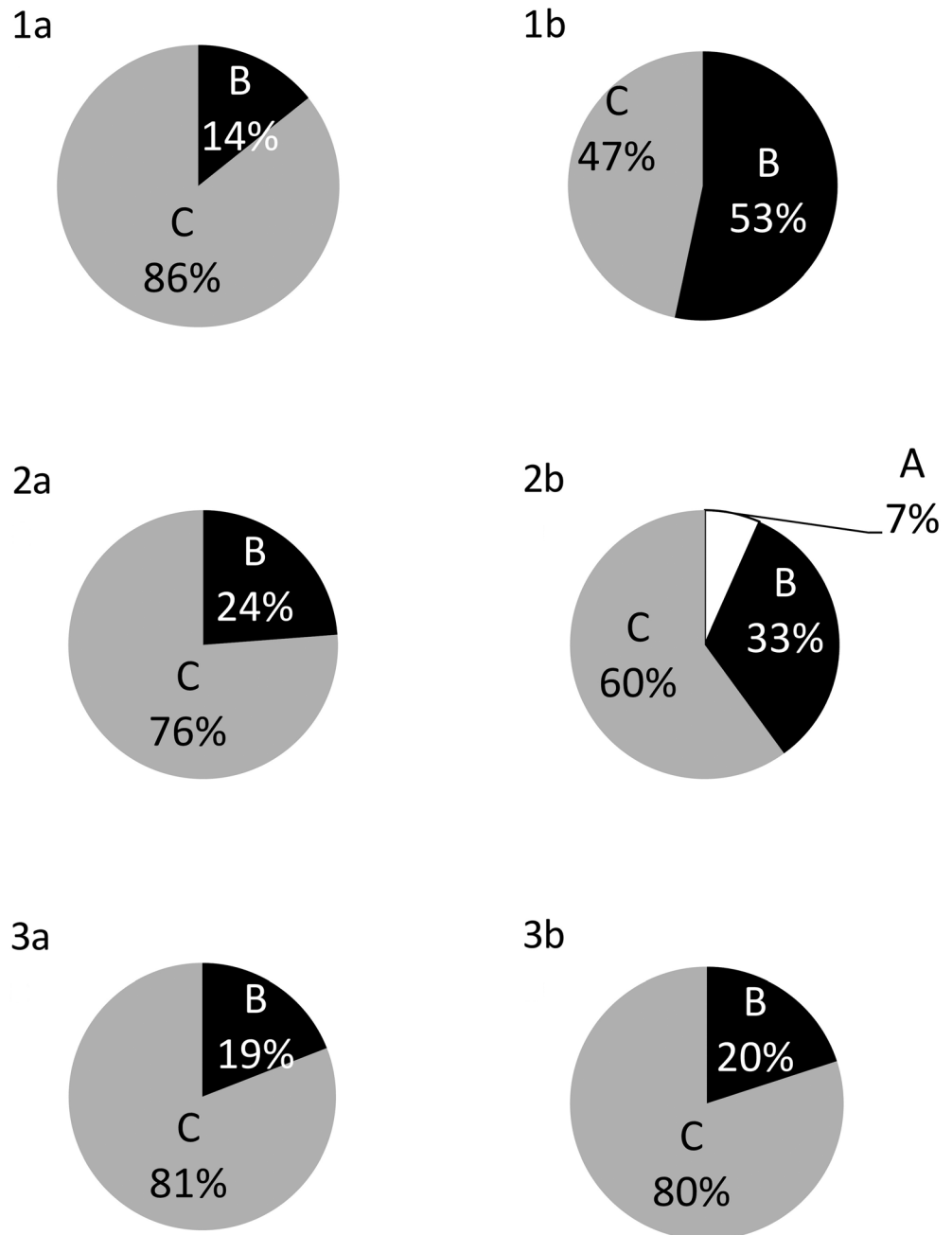
To identify the main threats to mussel populations, a qualitative assessment was conducted in each section between two transects,

evaluating the following criteria: land use in the catchment area, diffuse input, pollution/water quality, indicators of predation, river maintenance, weirs, and pearl fishing. The extent of each threat was categorized in the following three classes: (i) not observed; (ii) weak, but detectable impact; and (iii) severe impact.

2.5 | Data analysis

The monitoring results were used to classify the mussel populations and their habitats. Quantitative and qualitative parameters were recorded in an evaluation matrix (Tables 1 and 2), following the national assessment system (Sachteleben & Fartmann, 2009). Each parameter was categorized as A ('good'), B ('moderate'), or C ('poor'). The worst score of the corresponding subcategories determined the

FIGURE 4 Pie charts categorizing mussel population status, habitat quality, and disturbance, according to Sachteleben and Fartmann (2009), in Bavarian streams with populations of *Margaritifera margaritifera* (1a, population status; 2a, habitat quality; 3a, disturbance) and *Unio crassus* (1b, population status; 2b, habitat quality; 3b, disturbance). Categories: A, good; B, moderate; C, poor



overall assessment of habitat quality and mussel population. Data analyses were carried out with RSTUDIO 1.0.143 (RStudio Team, 2016).

3 | RESULTS

3.1 | Mussel populations

Margaritifera margaritifera population size ranged between <100 and 35 000 individuals (Figure 2). In three streams (15%) with previously known populations, no living individuals were detected. The mean population size of all pearl mussel streams was $3\,517 \pm 8\,500$ individuals (mean \pm standard deviation). In 90% of the *M. margaritifera*

populations, the population size was smaller than 10 000 individuals. Size estimates for *U. crassus* populations ranged between <100 and 40 000 individuals, with an overall mean population size of $5566 \pm 10\,800$ individuals. In 92% of the studied *U. crassus* populations, the population size was smaller than 10 000 individuals.

In nine *M. margaritifera* populations, sufficient numbers of individuals were obtained for the compilation of age profiles. The percentage of juvenile mussels (<65 mm) in the populations was very low (mean 2.2%, Figure 3), indicating that there has been no recruitment for at least 25 years. In contrast, the proportion of juvenile mussels in *U. crassus* populations was considerably higher, with a mean of 41.4%. In one population, the proportion of juvenile mussels exceeded 90%, which results from a lack of adult age classes.

TABLE 3 Fish species composition in *Margaritifera margaritifera* streams with and without mussel recruitment

Study streams	Recruitment (R)						No recruitment (NR)					
	Individuals/100 m ²											
Species												
<i>Salmo trutta fario</i>	3.7	23	12	36	<0.1	2.7	0.4	2.6	133	24	8	
<i>Lota lota</i>	0.9						<0.1					
<i>Squalius cephalus</i>	6.3			1			1.3			<0.1		
<i>Cottus gobio</i>	9.3	10	6.5	11	<0.1	0.7	0.6			11	7.6	
<i>Perca fluviatilis</i>	3.6			1			0.4			0.9		
<i>Leuciscus leuciscus</i>	1.9						0.2			3.1		
<i>Barbatula barbatula</i>							0.1			1.4		
<i>Anguilla anguilla</i>							0.5			<0.1		
<i>Rutilus rutilus</i>	5.9			14			0.8					
<i>Blicca bjoerkna</i>												
<i>Gobio gobio</i>	0.2						1.3			3.9		
Petromyzontiformes	54			0.5			67			0.3		
<i>Alburnoides bipunctatus</i>							2.3			3.1		
<i>Phoxinus phoxinus</i>	27						0.7			63		
<i>Alburnus alburnus</i>							0.9			<0.1		
<i>Chodrostoma nasus</i>												
<i>Pseudorasbora parva</i>							0.1			0.1		
<i>Thymallus thymallus</i>							0.2					
<i>Barbus barbus</i>							<0.1			4.4		
<i>Esox lucius</i>	0.4						0.1					
<i>Abramis brama</i>	0.3						0.2					
<i>Gymnocephalus cernua</i>							<0.1					
<i>Scardinius erythrophthalmus</i>							<0.1					
Number of fish species (n)	11	3	7	3	11	4	8	9	11	3	1	
Proportion of hosts in total fish density (%)	6.2	26.4	33.8	31.7	1.0	62.8	2.4	1.8	34.7	67.8	100.0	

None of the mussel populations investigated was assessed with status A. Instead, small population size and insufficient recruitment resulted in 86% of the *M. margaritifera* populations and 47% of the *U. crassus* populations being assessed with the lowest status class C (Figure 4).

3.2 | Habitat quality

Habitat quality in *M. margaritifera* streams was assessed as moderate (category B) in 24% of the streams and as bad (category C) in 76% of the streams. In the case of *U. crassus*, 7% of the streams were assessed as good, 33% as moderate, and 60% as bad in terms of habitat quality.

Fish species richness was higher in *U. crassus* streams (total number of species, $n = 28$) compared with *M. margaritifera* streams (total number of species, $n = 23$). For both mussel species, overall fish species richness was higher in streams with mussel recruitment

(total number of fish species, $n = 28$ in *U. crassus* streams and $n = 21$ in *M. margaritifera* streams) than in streams without recruitment (total number of fish species, $n = 11$ in *U. crassus* streams and $n = 16$ in *M. margaritifera* streams; Tables 3 and 4). The average fish species richness was similar, with $n = 5.9$ in *M. margaritifera* and $n = 6.4$ in *U. crassus* streams. The mean density of primary hosts of *U. crassus* (*Gasterosteus aculeatus*, *Phoxinus phoxinus*, and *Squalius cephalus*) ranged between 1.0–87.5 ind./100 m². The mean density of brown trout (*Salmo trutta fario*), the only host of *M. margaritifera* occurring in the study streams, ranged between 0.1 and 133.3 ind./100 m².

The percentage of fine sediments of <0.85 mm in size varied considerably between sites and ranged from 1.2 to 99.5% in *M. margaritifera* streams and from 0.2 to 99.7% in *U. crassus* streams. On average, *M. margaritifera* sites contained 22.3% of particles of <0.85 mm in size, whereas the mean proportion of fine particles in *U. crassus* sites was twice as high, at 41.3%. In both species, texture analyses and habitat quality categories

TABLE 3 (Continued)

Study streams													
Species	No recruitment (NR)									Mean density R (Range)	Mean density NR (Range)	Mean density	
	Individuals/100 m ²												
<i>Salmo trutta fario</i>	21	30	0.1	9.1	0.9	5.7	14	13	9.5	26.7 (0.4–133.3)	12.4 (0.1–29.8)	18.3	
<i>Lota lota</i>							0.1	1.5	1.1	0.6 (0.3–0.9)	0.9 (0.1–1.5)	0.8	
<i>Squalius cephalus</i>	1.3		0.6	0.4		3	0.4		5.2	22.0 (1–108.4)	1.8 (0.4–5.2)	11.9	
<i>Cottus gobio</i>	15	3		1.5	0.7	0.3	1.5	5.7		7.0 (0.6–11.2)	5.0 (0.3–15.0)	5.6	
<i>Perca fluviatilis</i>										1.5 (0.4–3.6)	3.6 (3.6–3.6)	1.9	
<i>Leuciscus leuciscus</i>				0.4		0.5			1.6	4.4 (0.2–12.4)	0.8 (0.4–1.6)	2.9	
<i>Barbatula barbatula</i>				<0.1	0.2	2.2	1.8		3.3	14.3 (0.1–54.4)	1.9 (0.2–3.3)	8.1	
<i>Anguilla anguilla</i>					0.2				0.2	0.5 (0.5–0.5)	0.2 (0.2–0.2)	0.3	
<i>Rutilus rutilus</i>									0.2	12.1 (0.8–27.6)	0.2 (0.2–0.2)	9.7	
<i>Blicca bjoerkna</i>									0.2	0.0 (0.0–0.0)	0.2 (0.2–0.2)	0.2	
<i>Gobio gobio</i>			0.4	0.7		7.4			0.6	7.9 (0.2–24.0)	2.3 (0.4–7.4)	5.4	
Petromyzontiformes								2.3		30.3 (0.3–66.7)	2.3 (2.3–2.3)	24.7	
<i>Alburnoides bipunctatus</i>				0.2		3.1				21.5 (2.3–59.2)	1.7 (0.2–3.1)	13.6	
<i>Phoxinus phoxinus</i>				<0.1						24.6 (0.7–63.2)	0.0 (0.0–0.0)	24.6	
<i>Alburnus alburnus</i>						<0.1				0.6 (0.1–0.9)	0.0 (0.0–0.0)	0.6	
<i>Chodrostoma nasus</i>						<0.1				0.0 (0.0–0.0)	0.0 (0.0–0.0)	<0.1	
<i>Pseudorasbora parva</i>			0.1			0.4				0.1 (0.1–0.1)	0.3 (0.1–0.4)	0.2	
<i>Thymallus thymallus</i>				0.1		0.1				0.2 (0.2–0.2)	0.1 (0.1–0.1)	0.1	
<i>Barbus barbus</i>										4.4 (4.4–4.4)	0.0 (0.0–0.0)	4.4	
<i>Esox lucius</i>				<0.1						0.3 (0.1–0.4)	0.0 (0.0–0.0)	0.3	
<i>Abramis brama</i>										0.3 (0.2–0.3)	0.0 (0.0–0.0)	0.3	
<i>Gymnocephalus cernua</i>										0.0 (0.0–0.0)	0.0 (0.0–0.0)	<0.1	
<i>Scardinius erythrophthalmus</i>										0.0 (0.0–0.0)	0.0 (0.0–0.0)	<0.1	
Number of fish species (n)	3	2	4	7	4	10	6	2	9	21	16	23	
Proportion of hosts in total fish density (%)	55.9	90.9	8.3	73.4	45.0	25.0	64.8	69.4	43.4	22.3	53.7	42.2	

corresponded only weakly with each other: for *U. crassus*, for example, samples of habitat category A could contain high quantities of fine sediment, and vice versa (Figure 5).

Physicochemical water quality was often beyond the threshold values defined in the literature for high-quality habitats (Figures 6 and 7). In particular, nutrient-related parameters such as EC, NO₃-N and ortho-PO₄-P concentrations were above or at least close to the limits suggested for intact mussel habitats. For instance, median values for electric conductivity were 200 $\mu\text{S cm}^{-1}$ in *M. margaritifera* streams of category B and 142 $\mu\text{S cm}^{-1}$ in streams of category C, compared with a threshold value of 180 $\mu\text{S cm}^{-1}$ in the literature. Mean ortho-PO₄-P concentrations in *M. margaritifera* habitats were 0.05 and 0.07 mg L⁻¹ (streams in categories B and C). In *U. crassus* streams of categories A and C, the ortho-PO₄-P concentrations remained below detectable levels; in category-B streams the mean ortho-PO₄-P concentration was 0.08 mg L⁻¹.

The median values of turbidity were also twice as high in *M. margaritifera* streams of category B than in streams of category C, with 9.13 NTU compared with 4.36 NTU, respectively. In both categories, values were clearly higher compared with a threshold value of 0.96 NTU for intact habitats. The turbidity values measured in *U. crassus* streams were in a comparable range as the measurements made in *M. margaritifera* streams. The mean pH value in *M. margaritifera* streams was 7.2, and ranged between 6.5 and 7.5, except for one stream, where the pH reached a maximum of 8.1. In *U. crassus* streams, the mean pH was 8.3 and ranged from 7.0 to 9.9. The oxygen content in free-flowing water was generally high, with an average of 10.0 and 9.9 mg L⁻¹ in *M. margaritifera* and *U. crassus* streams, respectively; however, the deltas of redox potentials between free-flowing water and the interstitial zone were more pronounced in *U. crassus* streams, with 229 \pm 97 mV (mean \pm standard deviation), compared with *M. margaritifera* streams (168 \pm 105 mV). Mean flow velocities

TABLE 4 Fish species composition in *Unio crassus* streams with and without mussel recruitment

Study streams	Recruitment (R)							No recruitment (NR)																	
	Individuals/100 m ²							Mean density (Range)																	
Species																			Mean density						
<i>Gasterosteus aculeatus</i>						0.2	2.4	3.4											2.0						
<i>Phoxinus phoxinus</i>						7.3	63.2	2.6	5.1	40.4	40.9	31.4	2.3	8.5	4.6	29.6	24.2	(2.3–63.2)	14.2	(4.6–29.6)	21.4				
<i>Squalius cephalus</i>						2.2	10.3		3.8	1	0.6	53.7	11.7	1.8	11.7	16	10.8	(0.6–53.7)	16.0	(16.0–16.0)	11.3				
<i>Cottus gobio</i>						4	0.6			0.6									1.2	1.7	(0.6–4.0)	1.6			
<i>Perca fluviatilis</i>													1.4		0.9				1.4	(1.4–1.4)	0.9	(0.9–0.9)	1.2		
<i>Leuciscus leuciscus</i>													0.2						1.6	0.2	(0.2–0.2)	1.6	(1.6–1.6)	0.9	
<i>Barbatula barbatula</i>						3	1.4			3.7	7	6	3.5						10.3	4.1	(1.4–7.0)	10.3	(10.3–10.3)	5.0	
<i>Anguilla anguilla</i>												0.3							0.4	(0.3–0.5)	0.0	(0.0–0.0)	0.4		
<i>Rutilus rutilus</i>						0.5								<0.1	0.6				0.6	(0.5–0.6)	0.0	(0.0–0.0)	0.6		
<i>Gobio gobio</i>						0.6	9.8		4.9			22.8	1.7			15.3	8.0	(0.6–22.8)	15.3	(15.3–15.3)	9.2				
<i>Petromyzontiformes</i>							0.3								1.8				0.3	(0.3–0.3)	1.8	(1.8–1.8)	1.1		
<i>Alburnoides bipunctatus</i>						0.1	59.2					9.4	17.8						21.6	(0.1–59.2)	0.0	(0.0–0.0)	21.6		
<i>Lota lota</i>							0.3		0.6	0.3									0.4	(0.3–0.6)	0.0	(0.0–0.0)	0.4		
<i>Alburnus alburnus</i>										5.5		1.3							3.4	(1.3–5.5)	0.0	(0.0–0.0)	3.4		
<i>Chodrostoma nasus</i>														0.1					0.1	(0.1–0.1)	0.0	(0.0–0.0)	0.1		
<i>Pseudorasbora parva</i>											1.5								1.5	(1.5–1.5)	0.0	(0.0–0.0)	1.5		
<i>Thymallus thymallus</i>														0.3					2	(0.3–0.3)	2.0	(2.0–2.0)	1.2		
<i>Barbus barbus</i>							0.7					3.6	4.8						0.1	(0.7–4.8)	0.1	(0.1–0.1)	2.3		
<i>Esox lucius</i>											0.3								0.4	(0.3–0.4)	0.0	(0.0–0.0)	0.4		
<i>Abramis brama</i>																			8.3	(8.3–8.3)	0.0	(0.0–0.0)	8.3		
<i>Cyprinus carpio</i>																			0.1	(0.1–0.1)	3.1	0.2	1.7	(0.2–3.1)	1.1
<i>Salmo trutta fario</i>						3.6	2.6	2		3.4	2	1.1	0.2						2.1	(0.2–3.6)	0.0	(0.0–0.0)	2.1		
<i>Carassius gibelio</i>						0.1													0.1	(0.1–0.1)	0.0	(0.0–0.0)	0.1		
<i>Oncorhynchus mykiss</i>																			0.7	(0.7–0.7)	0.0	(0.0–0.0)	0.7		
<i>Rhodeus amarus</i>																			0.4	(0.4–0.4)	0.0	(0.0–0.0)	0.4		
<i>Silurus glanis</i>										0.3				0.2	0.4				0.3	(0.2–0.4)	0.0	(0.0–0.0)	0.3		
<i>Tinca tinca</i>											0.2								0.2	(0.2–0.2)	0.0	(0.0–0.0)	0.2		
<i>Scardinius erythrophthalmus</i>																			0.3	(0.3–0.3)	0.0	(0.0–0.0)	0.3		
Number of fish species (n)						9	9	3	8	7	3	5	10	10	7	5	2	7	5	28		11		28	
Proportion of hosts in total fish density (%)						44.4	49.8	49.1	57.6	6.2	88.6	79.0	73.2	45.5	7.1	80.7	73.3	42.6	62.6	52.8		59.5		54.3	

ranged between 0.25 and 0.30 m s⁻¹ in all habitat categories of both target species, although minimum and maximum values varied between 0.01 and 1.20 m s⁻¹. The mean total organic carbon (TOC) in *M. margaritifera* streams was 5.1 ± 2.2 mg L⁻¹ in category-B habitats, which decreased to 4.7 ± 1.9 mg L⁻¹ in category-C habitats. In *U. crassus* streams the TOC was higher and increased in habitats from category A to C, with 8.1 ± 2.3, 8.1 ± 3.0, and 11.5 ± 4.6 mg L⁻¹, respectively.

4 | DISCUSSION

In this study, a total of 34 freshwater mussel populations and their habitats were assessed using the national evaluation methodology for species listed in the annexes of the European Habitats Directive. The results showed that both species – the freshwater pearl mussel *M. margaritifera* as well as the thick-shelled river mussel *U. crassus* – have a 'bad' conservation status in the state of Bavaria, which is one of the core areas of their natural distribution in central Europe. Following the criteria of the evaluation protocol, none of the mussel populations was rated to be of good status (A). With the exception of 7% of *U. crassus* habitats, also almost all mussel habitats were rated as being 'poor' (C) or in an 'unfavourable' status (B), with moderate (B) to strong threats (C) in the majority of the streams assessed.

Although the population status of both target species is comparable and both species need to be considered as endangered, there are several pronounced differences regarding the major drivers of their decline and species-specific tolerance against certain threats. Scientific research on the ecological requirements of *M. margaritifera* started in the 1980s and continued to receive great attention compared with other mussel species, eventually resulting in the first European CEN standard to provide guidance on monitoring a single species (Boon et al., 2019). The species has been characterized as a highly specialized inhabitant of oligotrophic gravel-bed streams with high water quality and a low content of fine sediment (Bauer, 1988; Denic & Geist, 2015; Geist, 2010; Geist & Auerswald, 2007; Hastie et al., 2000). The clogging of macropores in the interstitial zone by fine sediments was identified as the main reason for declining populations, resulting in recruitment failure, which is clearly supported by the results of this study. In most of the samples, the proportion of fine sediments exceeded the thresholds of 20% for particles <1 mm and turbidity levels of 0.96 NTU, identified from investigations of intact habitats by Geist and Auerswald (2007) and Österling, Arvidsson, and Greenberg (2010), respectively. At the same time, we observed a strong decline of redox potential from the free-flowing water to the interstitial zone, which leads to a lack of oxygen in juvenile habitats, thus explaining the over-aged pearl mussel populations in the Bavarian study streams. Moreover, some water quality parameters, such as EC or nitrate, were higher in several streams, but as this was also the case in some of the streams with recruitment, these parameters do not seem to have as great an impact as substratum quality.

In contrast to *M. margaritifera*, research activities targeting *U. crassus* were rare until a few years ago. Until then, the habitat needs of both species were assumed to be similar. However, recent studies indicated pronounced differences in their ecological requirements: for example, in their sensitivity to fine sediments or in their general substratum preferences (Denic, Stoeckl, Gum, & Geist, 2014; Inoue, Stoeckl, & Geist, 2017; Stoeckl & Geist, 2016). Thus, in this study, recruitment of *U. crassus* was observed in streams with a maximal proportion of particles <0.85 mm of 99%. It is clear that there is no correlation between substratum structure and recruitment success in the Bavarian study streams (Figure 5). At the same time, even higher deltas of redox potentials were detected between free-flowing water and the interstitial zone in functional *U. crassus* habitats than in non-functional *M. margaritifera* habitats. This may be explained by the shorter post-parasitic phase of *U. crassus* or the lower oxygen demands of juveniles compared with *M. margaritifera*. Furthermore, *U. crassus* does not only exhibit stronger resilience to anthropogenic habitat alteration, but also has a wider ecological range than *M. margaritifera*. For instance, *U. crassus* is not restricted to silicate catchments and also occurs in, and even seems to prefer, limestone streams, which explains the stronger variation in EC and the higher average pH values compared with the results for *M. margaritifera* streams.

Abiotic habitat conditions, especially substratum quality, mainly explain the decline of *M. margaritifera*. The status of *U. crassus* is only weakly correlated with these parameters, however. In many of the Bavarian study streams the host fish abundance appears too low to ensure sufficient recruitment. Particularly in the non-recruiting populations, densities are far below the recommended value of 40 ind./100 m² (Stoeckl, Taeubert, & Geist, 2015). In contrast, host fish abundance is sufficiently high in most of the *M. margaritifera* streams investigated, and higher densities of fish in these situations can even be indicative of eutrophication and poor habitat quality for juvenile mussels (Geist, Porkka, & Kuehn, 2006). An additional threat for *U. crassus* is its occurrence in nutrient-enriched and often heavily modified habitats, or even in man-made ditches located in intensively used catchments (Inoue et al., 2017). The increased nitrogen levels and the frequent observation of intensive agriculture without buffer strips along the streams studied pose a major threat to Bavarian *U. crassus* streams. In some cases, direct disturbances such as dredging were observed, where mussels can be physically harmed. The uniform stream channels with soft and steep banks are often inhabited by the muskrat (*Ondatra zibethicus*). Particularly in winter, when herbal food is scarce, this non-native predator can significantly reduce *U. crassus* populations, which has been observed in recent years by the authors in some of the streams studied.

Despite the critically endangered status of both mussel species and the legal requirement of all European member states to report their conservation status, no consistent methodologies or protocols have been used so far to do this. Thus, monitoring data may not be comparable across the European countries and data quality may vary considerably.

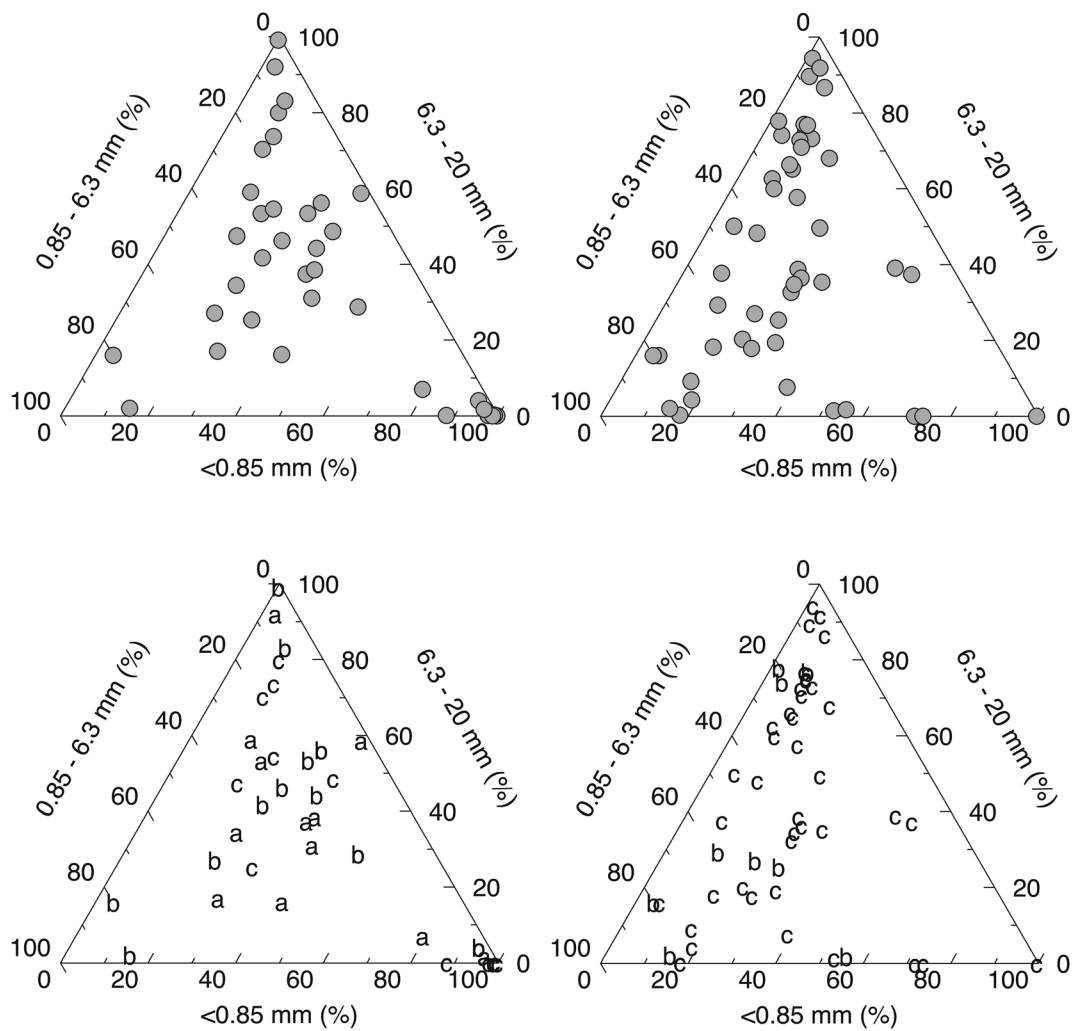


FIGURE 5 Triangle plots of grain size distribution in *Unio crassus* (left) and *Margaritifera margaritifera* streams (right)

Although monitoring results of all species of European interest are available online via the European Environment Information and Observation Network (EIONET) platform, the methods applied for assessing species and their habitats remain unknown. With regard to the importance of data quality and comparability, we strongly suggest that common monitoring methods, such as those described in the CEN standard for *M. margaritifera* (Boon et al., 2019), should be developed. This standard is useful for designing national monitoring programmes in all European member states, because the countries represented by those who wrote the standard include all those in which *M. margaritifera* still occurs in Europe.

The examples of *M. margaritifera* and *U. crassus* clearly show that even species with similar life cycles may have different habitat preferences and resilience against adverse habitat conditions. As a result, deducing the ecological requirements of one species based on another is probably rarely possible, and exact knowledge about ecological needs, population status, genetic structure, and the causes for decline is indispensable for the development of effective conservation strategies. Despite this, there is a lack of such basic

information for the other native European mussel species. With respect to the important ecosystem services that freshwater mussel species provide (Vaughn, 2018) and the continuing loss of biodiversity, it is urgent to gather the missing information on species so far neglected through fieldwork and research. This will allow the design of species-specific conservation actions, as has been achieved for *M. margaritifera*, where several conservation projects around Europe apply a combination of artificial breeding and habitat restoration in prioritized target streams. Unfortunately, the annexes of the European Habitats Directive that list the species for special protection are not updated; hence, monitoring and conservation action for other endangered mussel species that are not listed on the annexes are rarely conducted because of an absence of supporting legislation. This may even result in the decline of tolerant and widely distributed species, with drastic effects on ecosystem functioning and the provision of ecosystem services. Furthermore, the conservation of habitats of those species already protected may also gain from legislative measures. Dobler, Geist, Stoeckl, and Inoue (2019) showed that designated sites such as the special areas of conservation (SACs) selected for mussel

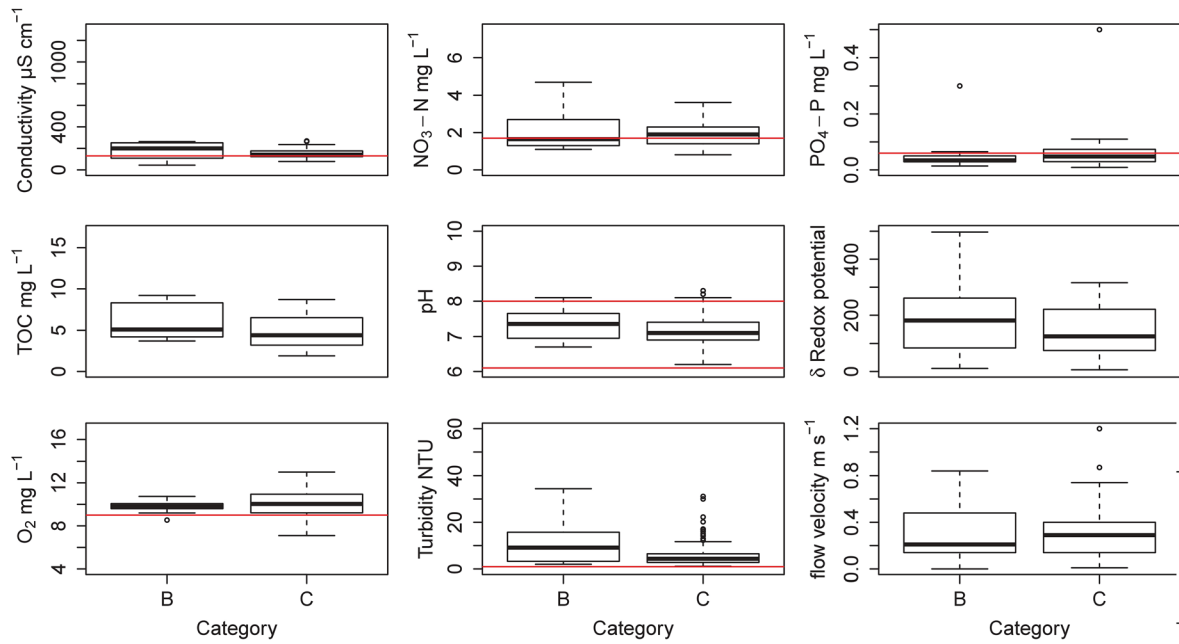


FIGURE 6 Box plots of physicochemical parameters in streams with *Margaritifera margaritifera*. Red lines show threshold values according to the European Committee for Standardization (CEN) standard (DIN EN 16859) defined for the species

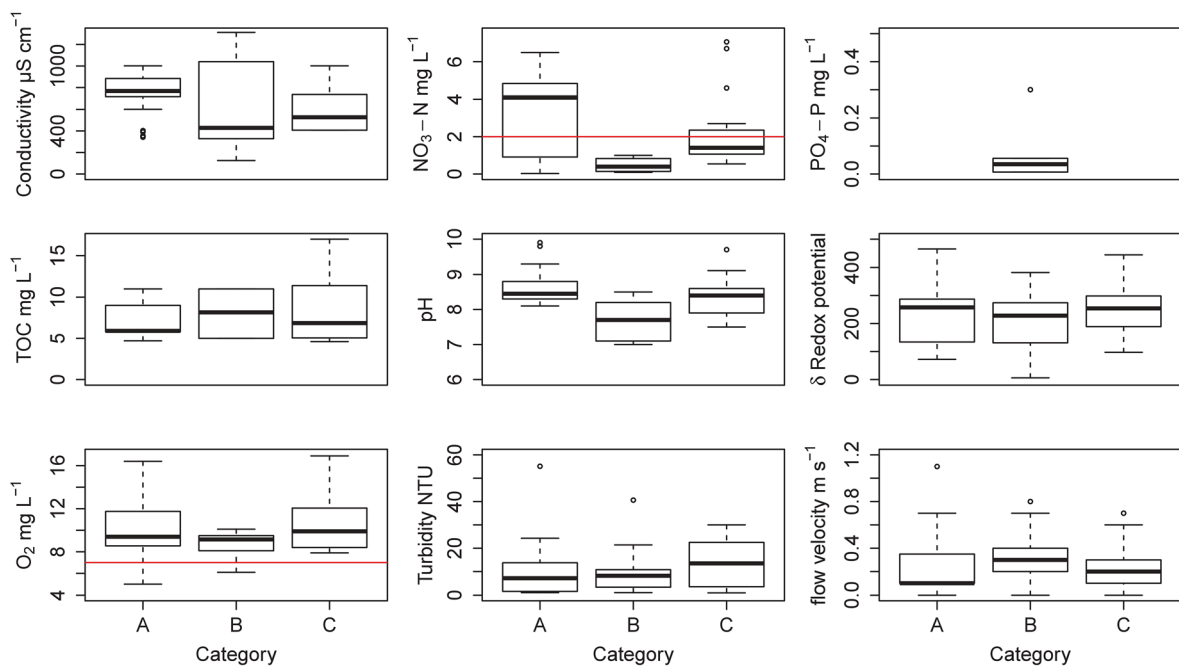


FIGURE 7 Physicochemical parameters in *Unio crassus* streams. Red lines define threshold values according to the 'Leitfaden Bachmuschelschutz' (LfU, 2013)

species in Bavaria are frequently too small to be effective, as in many cases the SACs do not cover the catchment areas of the streams. This means that critical factors such as nutrient and sediment loads originating from the wider catchment cannot be reduced using the legal instruments of the Habitats Directive. The limited capacity of the Natura 2000 network to protect freshwater biodiversity seems to be true for other countries in the European

Union: by assessing the coverage of protected areas on the Iberian Peninsula for more than 90 freshwater species, Hermoso, Filipe, Segurado, and Beja (2015) showed that the current areas of protection fail to provide sufficient coverage of freshwater biodiversity, with less than 20% of the range of species covered on average. We therefore recommend supplementing conservation projects with an expansion of nature reserves, wherever possible.

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ORCID

Juergen Geist  <https://orcid.org/0000-0001-7698-3443>

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