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Modelling the effects of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river

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Abstract. Self-purification is a key ecosystem service provided by riverine biota that is particularly important in polluted water bodies serving multiple societal uses, but the extent to which self-purification may be influenced by human uses is unknown. We studied a eutrophic lowland river used for drinking water and recreation to identify the maximal sustainable extent of human use. We recorded filtration by mussels and modeled the disturbance to mussels caused by wave action induced from recreational boating. Filtration was significantly affected by shear stress produced from boats down to a depth of 2.7 m. Threshold values for the intensity of wave disturbance ranged from 0.21 N/m² (*Unio tumidus*) to 0.43 N/m² (*Anodonta anatina*) for moderate effects and from 0.02 N/m² (*U. tumidus*) to 0.13 N/m² (*Dreissena polymorpha*) for no effects on filtration. *Anodonta anatina* and *D. polymorpha* showed a significantly lower degree of shell closing and a higher predicted medium-effect shear stress (the shear stress associated with 50% of the maximum shell closing duration) than *U. tumidus* and *Unio pictorum*, which probably results from differences in the species position in and above the sediment. Coupled hydraulic–ecological modeling showed that typical boating activity may reduce self-purification activity by mussels, with the extent of disturbance depending on mussel species, river depth, boating frequency, and cruising speed. Single passages of boats reduced daily mussel filtration rates by 0.02% for muscle-driven boats, 0.45% for yachts, 0.68% for motor boats, and 0.69% for motorized rafting and rowing boats. Depending on total daily boat traffic and hydrological conditions, a reduction in the daily filtration rate by mussel populations within the studied river section was estimated at 6.9%. We conclude that self-purification activity of this lowland river section is not significantly affected by recreational boating, but might be affected by more intense recreational boating under altered river flow conditions.

Key words: ecosystem services, freshwater mussels, wave impact, filtration activity, coupled hydraulic–ecological modeling, shear stress.

Self-purification capacity, such as the ability to remove organic pollution, is a key ecosystem service in rivers (Everard and Powell 2002, Howard and Cuffey 2006). This capacity is particularly important in polluted or eutrophic water bodies serving multiple societal uses and greatly improves opportunities to use the downstream reaches of such rivers (e.g., Heberer et al. 2002, Ho et al. 2003). Water managers rely on the self-purification capacity of rivers to

facilitate multiple uses (Kronvang et al. 1999), which are expected to intensify because of population growth, economic development, and climate change (Pusch and Hoffmann 2000, Meybeck 2003, Tockner et al. 2010). However, few attempts have been made to identify maximum tolerated loads for sustainable use of river ecosystems subjected to multiple uses, and very few investigators have analyzed effects of multiple pressures, such as eutrophication, morphological alterations, and navigation, and the consequences of integrated management approaches (Wechsung et al. 2005, Ducharme et al. 2007, Hofmann et al. 2010). This lack of knowledge is a serious problem because sustainable management should ensure the resilience of

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surface waters, which includes persistence of full self-purification capacity (Rapport et al. 1998).

Ecological effects of human pressures on ecosystems are aggravated when ecosystem resilience already has been impaired (Folke et al. 2004). For instance, in lowland rivers, mussels may contribute a significant proportion of self-purification capacity (Libois and Hallet-Libois 1987, Welker and Walz 1998, Pusch and Hoffmann 2000, Bauer 2001, Pusch et al. 2001), which may efficiently transfer organic matter from the water column to the benthic zone (Howard and Cuffey 2006). This transfer is a critical step for self-purification because most microbial degradation of organic matter in rivers occurs in the sediments (Fischer and Pusch 2001). Thus, any reduction in filtration activity by freshwater mussels is likely to be followed by whole-system effects on the river's ecological status, with corresponding consequences for potential human uses of the water body.

Water bodies used for drinking water often are used for recreational purposes, but the effect of boat traffic on self-purification of such water bodies is unknown. Environmental effects of boat traffic include noise, disturbance of wildlife (Liddle and Scorgie 1980), pollution by fuels and oils (Burgin and Hardiman 2011), and hydromorphological alterations undertaken to facilitate boat traffic (Tacon 1994). Boat-induced wave action is an important pressure that causes resuspension of organic sediments (Beachler and Hill 2003) and disturbs and degrades coastal marine habitats (Bishop 2004, 2007) and littoral zones of inland waters (Gabel et al. 2008, 2011b). Wave action may cause mass detachment of macroinvertebrates if critical levels of shear stress are surpassed (Gabel et al. 2008). Furthermore, the resuspension of sediments can smother or bury benthic organisms (Morgan et al. 1983, Newcombe and MacDonald 1991) or affect dissolved O₂ (DO) concentrations via decomposition of organic particles.

We conducted a field study to analyze how hydraulic disturbance by boating activity might affect self-purification capacity based on the filtration activity of mussels. Our goals were to identify maximum tolerance levels of anthropogenic wave disturbance and to estimate the carrying capacity of a water body for recreational boating.

Methods

Study site

The River Spree is a lowland river in northeastern Germany that is subjected to multiple human uses and is the main source of drinking water for Berlin

(Köhler 1994). We worked along a straight reach of a 20-km river section called Krumme Spree that connects Lake Neuendorfer See and Lake Schwielochsee, near the village of Kossenblatt (lat 52°6'15.35"N, long 14°4'15.83"E). This river reach supports high densities of mussels (Unionidae and *Dreissena polymorpha*; Pusch et al. 2002) and is used heavily for recreational boating during summer. The section was channelized ~100 y ago, so the Krumme Spree channel has a deep, symmetrical trapezoidal cross-section, with a mean width of 25 m and a mean depth of 1.4–2.5 m, depending on discharge level. The mean slope is 0.01%, and the sediments consist mainly of sand with a mean particle size (DC50) of 0.36 ± 0.01 mm. Discharge varied from 0.5–10.4 m³/s during the study period in June and July 2010.

Field measurements and calculation of shear stress

We collected 8 specimens of each of 3 species of unionid freshwater mussels (Swollen River Mussel *Unio tumidus*, Painter's Mussel *Unio pictorum*, and Duck Mussel *Anodonta anatina*), and zebra mussels *Dreissena polymorpha* attached to stones at the same locations. We quantified filtration activity by measuring the gape width between the tips of both shells of each mussel. Gape width is at its maximum during full filtration activity. We used instant adhesive glue to equip mussels at the sampling site with permanent disk magnets (magnet grade = N52, diameter = 5 mm, thickness = 2 mm) near the tip of 1 shell, and a magnetic sensor (radiometric linear Hall-effect sensor A1321; Allegro Microsystems, Worcester, Massachusetts) near the tip of the other shell. We returned the mussels to the river reach. Stress for the mussels was negligible because they were out of the water for handling for <1 min. In laboratory experiments, mussel behavior was not significantly affected by handling or measurement equipment (SL, unpublished data). All individuals began to open their shells for filtration activity shortly after resubmersion.

Magnetic sensor systems with Hall-effects sensors have been used by others to investigate valve movements in bivalves (Wilson et al. 2005, Maire et al. 2007, Robson et al. 2009). The magnetic sensors detect the strength of the magnetic field, which we calibrated against the width of opening at the shell tips (gape width, in mm). Measured voltage was converted to gape width, which was converted to relative values (% shell closing relative to maximum gape width). We calibrated the magnet system in a preliminary laboratory experiment with 3 individuals of each species (sizes were similar to those of the individuals used in the larger experiment). The

calibration was best fit by a linear inverse polynomial equation. We measured gape width at a 1-kHz recording rate averaged to a 1-Hz sampling rate.

We exposed the experimental mussels at various water depths (25, 50, 75, 100, 125, and 180 cm) in the river from 16 to 29 July 2010. We recorded gape width from 1000 to 1600 h each day, the period with most of the boat traffic. We recorded turbidity and dissolved O₂ (DO) with a YSI multiprobe (Yellow Springs Instruments, Yellow Springs, Ohio) installed at the study site at a depth of 1.8 m. We also installed automatic cameras to record boating activity.

During the exposure period, we used a motorboat (8 horsepower [HP]) of the typical size of recreational boats in the study area to produce experimental waves. We ran the boat at various speeds (8, 12, and 18 km/h) and repeated each speed in random order 10 times. We also included waves produced by passing recreational boats. We categorized recreational boats as muscle-driven boats (canoes and kayaks), motor boats (low horsepower open sport boats with outboard motor), yachts (larger boats, including yachts and house boats or barges with inboard motors), and motorized rowing and rafting boats. We measured waves from ≥ 10 passages of boats in each category. We initiated subsequent experimental runs only after turbidity had returned to the predisturbance level and all mussels had fully reopened their shells.

We used an Acoustic Doppler Velocimeter (ADV; Micro ADV 16 MHz, SonTek, San Diego, California) with a recording rate of 50 Hz and the sampling volume positioned 1.5 cm above the river bed to measure bottom orbital velocity (U_w) and wave period (T) near the mussels. In 25-cm-deep water near the shoreline, U_w s created by boat passages were 2.13 ± 0.26 cm/s (SE) (muscle-driven boats), 6.23 ± 0.75 cm/s (motorized rowing and rafting boats), 8.30 ± 0.57 cm/s (yachts), 10.42 ± 2.14 cm/s (motorboats 8 km/h), 14.68 ± 0.63 cm/s (motorboats 10 km/h), 27.19 ± 2.21 cm/s (motorboats 12 km/h), and 30.95 ± 2.51 cm/s (motorboats 18 km/h), which were comparable to values measured by Gabel et al. (2012). We assumed the bottom boundary layer was thinner than the height of the smallest mussel used (cf. Gabel et al. 2008), so our recordings represented the flow velocity acting on the inhalant and exhalant siphons of the mussels.

We obtained wave friction shear stress (τ_w) from U_w of the waves via the wave friction factor (f_w) with the method used by Soulsby (1997) as

$$\tau_w = 0.5 \rho f_w U_w^2$$

where ρ is the density of water and f_w reflects laminar or turbulent flow structure. We calculated the smooth wave friction factor (f_{ws}) as

$$f_{ws} = B R_w^{-N}$$

where coefficients $B = 2$ and $N = 0.5$ for Reynolds numbers (R_w) $\leq 5 \times 10^5$ (laminar flow) or $B = 0.045$ and $N = 0.175$ for $R_w > 5 \times 10^5$ (smooth turbulent flow). We calculated the rough wave friction (f_{wr}) as

$$f_{wr} = 1.39 (A/z_0)^{-0.52}$$

where $A = U_w T / 2\pi$, $z_0 = \text{DC50}/12$, and $R_w = U_w A / \text{kinematic viscosity of water}$. We took f_w as the maximum of f_{ws} and f_{wr} .

Data analyses

We $\sqrt[4]{x}$ -transformed values of τ_w to obtain normal distribution of the data. Relationships between shear stress and duration and % shell closing of all mussel species were best fit by sigmoid regression models. We computed sigmoid regression models and coefficients by minimizing the sum of squared residuals with an iteratively weighted least-squares algorithm to estimate the parameters of the regression model. We used the sigmoid model curves to derive 2 critical levels in the behavioral response of the mussels to increasing shear stress. We defined predicted no-effect shear stress (PNES) as the shear stress at which individuals started closing their shells (10% shell closing). We defined predicted medium-effect shear stress (PMES) as the shear stress associated with 50% of the maximum shell closing duration (inflection point of the sigmoid function of shell closing duration vs τ_w).

We calculated the extent to which mussels were disturbed by boating activity by estimating % reduction of their filtration activity during the 60-s period after boat passage as

Remaining filtration activity =

$$\int_0^{60} \frac{100 - \text{intensity of shell closing}}{60} dt$$

where remaining filtration activity and intensity of shell closing are expressed as percentages. The vertical pattern of shear stress caused by boating and water depth was best fit by polynomial cubic regression models. These models accounted for 2 peaks of shear stress, one near the surface that was generated by surface waves and one near maximum depth that was created by the water jet of the propeller from the boat's motor.

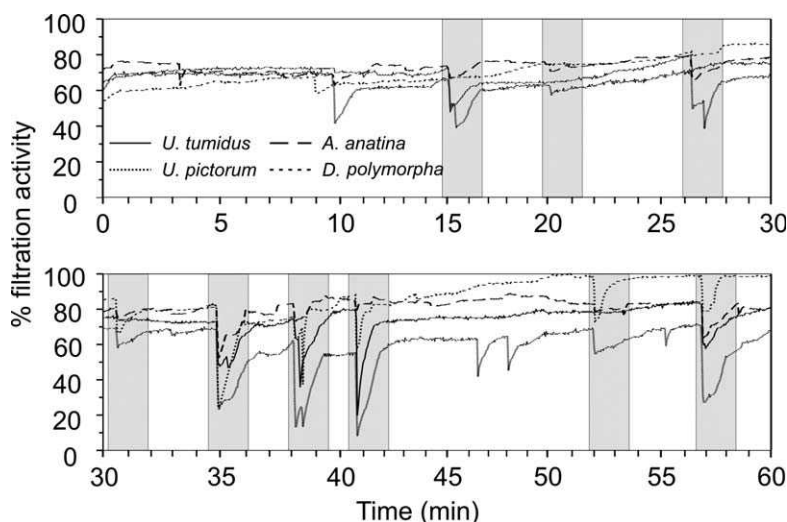


FIG. 1. Percent filtration activity for 1 individual of the 4 mussel species *Anodonta anatina*, *Unio tumidus*, *Unio pictorum*, and *Dreissena polymorpha* over 1 h of investigation. Gray boxes indicate boat passages of different velocities and categories.

We tested for differences in the asymptotic maximum (AMAX), PMES, and PNES of the sigmoid regression models among mussel species as described in Motulsky (1998). We used PASW (version 17.0; SPSS, Chicago, Illinois) and SigmaPlot (version 11.0; Systat Software, Chicago, Illinois) to run all statistical regressions and plots.

Results

Water quality

The river section was heavily loaded with organic particles that consisted primarily of planktonic algae and suspended detritus. Organic seston ranged from 6.22 to 10.57 g/L over the study period (mean \pm SE: 7.94 ± 0.43 g/L). At high water temperatures, microbial degradation of this organic load resulted in low minimum concentrations of DO during early morning hours (range: 2.22–7.78 mg/L, mean \pm SE: 4.06 ± 0.45). For most of the study period, daily minimum DO concentrations were <4 mg/L.

Wave impact on shell closing

All species responded to boat-induced shear stress by partially or fully closing their shells (Fig. 1). Percent filtration activity at times without boat passages when mussels were filtering was estimated as 73 ± 5 (*U. tumidus*), 64 ± 5 (*U. pictorum*), 78 ± 6 (*A. anatina*), and $78 \pm 13\%$ (*D. polymorpha*). Duration and % shell closing gradually increased with higher shear stress produced by boat passages (Fig. 2A–H). All responses were best described by sigmoid regression models (Table 1). *Unio tumidus* had the shortest

AMAX ($\sim 54 \pm 8$ s, $n = 113$; Figs 2B, 3A). This time was longer for *U. pictorum* and *D. polymorpha* ($\sim 77 \pm 7$ s, $n = 123$ and $\sim 92 \pm 12$ s, $n = 97$, respectively; Figs 2C, D, 3A). *Anodonta anatina* had the longest AMAX ($\sim 187 \pm 19$ s, $n = 128$; Figs 2A, 3A). Maximum % shell closing was highest for *U. pictorum* (mean % shell closing = $89 \pm 7\%$; Figs 2G, 3B), followed by similar values for *U. tumidus* ($88 \pm 5\%$; Figs 2F, 3B), and lower values for *D. polymorpha* ($73 \pm 5\%$; Figs 2H, 3B) and *A. anatina* ($68 \pm 7\%$; Figs 2E, 3B). Thus, *A. anatina* had the longest closing duration and lowest % shell closing.

Unio tumidus had the lowest PNES (0.02 ± 0.029 N/m²; Figs 2F, 3C), followed by *A. anatina* (0.05 ± 0.015 N/m²; Figs 2E, 3C), *U. pictorum* (0.10 ± 0.025 N/m²; Figs 2G, 3C), and *D. polymorpha* (0.13 ± 0.043 N/m²; Figs 2H, 3C). *Unio tumidus* had the lowest PMES (0.21 ± 0.029 N/m²; Figs 2B, 3D), followed by *U. pictorum* (0.27 ± 0.025 N/m²; Figs 2C, 3D), *D. polymorpha* (0.38 ± 0.043 N/m²; Figs 2D, 3D), and *A. anatina* (0.43 ± 0.015 N/m²; Figs 2A, 3D).

Shear stress produced by various boat types and speed levels

Vertical patterns of shear stress varied according to boat type (Table 2). Wave disturbance generally decreased with increasing water depth. The vertical pattern was best described by linear regression models for muscle-driven boats and by cubic regression models for all motorized boat categories (Fig. 4A). The cubic regression was not significant for yachts because of the low number of replicates. Therefore, the maximum depth of boat-induced shear stress varied widely among boat categories. Boat-

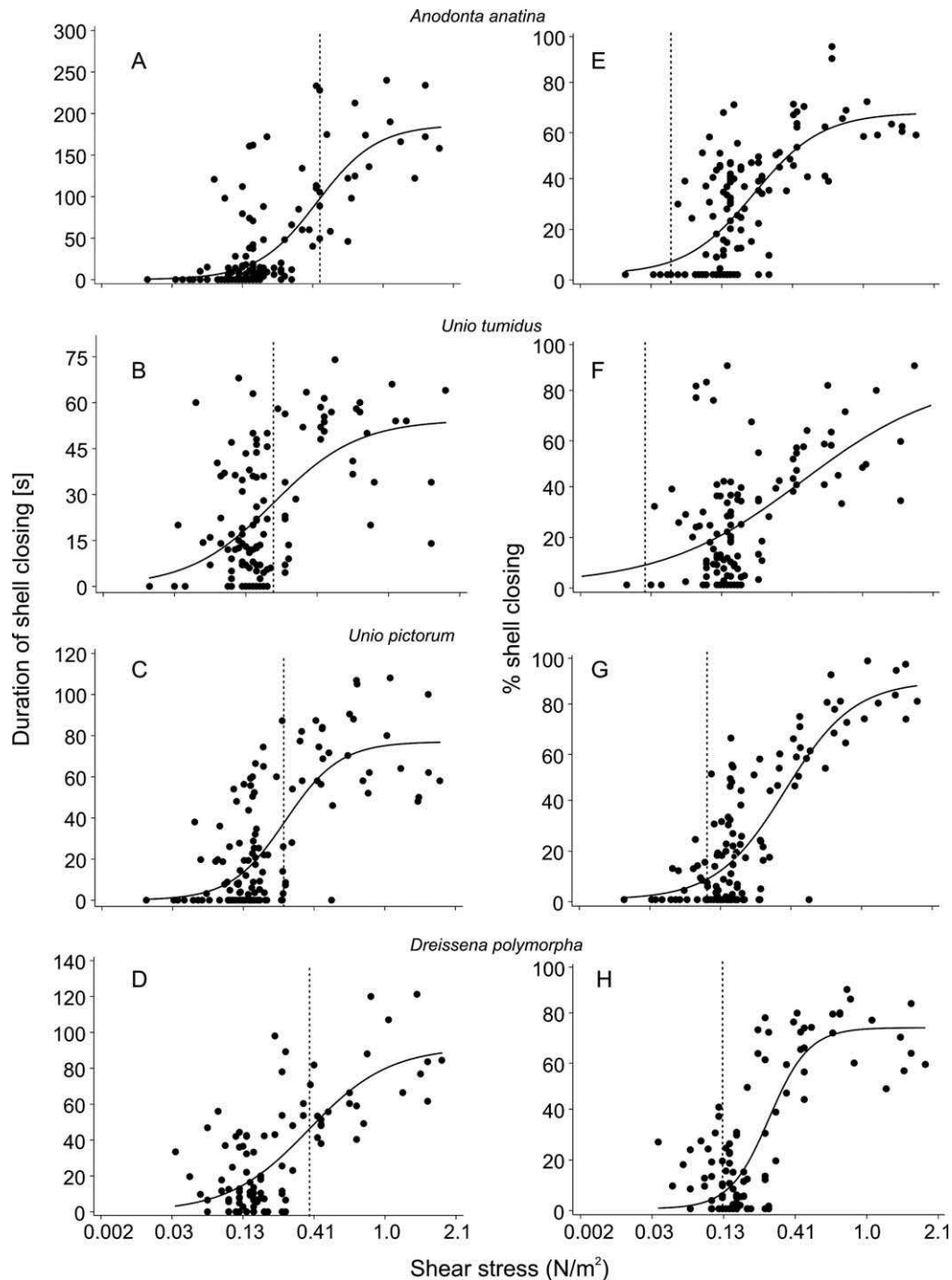


FIG. 2. Duration (A–D) and % shell closing (E–H) as a function of wave-induced shear stress of *Anodonta anatina* (A, E), *Unio tumidus* (B, F), *Unio pictorum* (C, G), and *Dreissena polymorpha* (D, H). Dashed vertical lines in A–D mark the predicted moderate effect shear stress levels (PMES), dashed vertical lines in E–H mark the predicted no-effect shear stress level (PNES).

induced shear stress >PNES occurred to depths ranging from 17 cm (*A. anatina* disturbed by muscle-driven boats) to 270 cm (*U. tumidus* disturbed by yachts) (Table 3). Wave-induced shear stress in the shallow marginal zone more than doubled when motorboat speed increased from low (8 km/h) to

medium (12 km/h) (Fig. 4B). A further increase in motorboat speed to 18 km/h did not produce a further increase in shear stress in the shallow marginal zone, but did produce an increase in deeper parts of the river channel because of the stronger action of the propeller jet (Fig. 4B). At deeper locations,

TABLE 1. Parameters for the best-fitting sigmoid regression models ($f = a/[1 + e^{-(x - x_0)/b}]$) for the dependence of duration and % shell closing on shear stress. The parameters correspond to the asymptotic maximum (AMAX), the slope (b), and the inflection point (x_0) of the respective curves. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Taxon	r^2		AMAX		b		x_0	
	Duration	% closing	Duration	% closing	Duration	% closing	Duration	% closing
<i>Unio tumidus</i>	0.29***	0.30***	54.40	88.39	0.12	0.20	0.68	0.84
<i>Unio pictorum</i>	0.52***	0.68***	77.02	89.33	0.08	0.10	0.72	0.78
<i>Anodonta anatina</i>	0.58***	0.50***	186.54	68.02	0.09	0.10	0.81	0.70
<i>Dreissena polymorpha</i>	0.54***	0.67***	91.75	72.69	0.11	0.06	0.79	0.72

depth of motorboat-induced shear stress >PNES increased 21 cm as speed increased from 12 to 18 km/h.

Spatial extension of disturbance

The depth zones with reduced mussel filtration activity gradually extended downward with increasing motorboat speed (Fig. 5A–D) in shallow marginal

areas affected by surface waves and in the deeper zone affected by the propulsion jet of the boat motor. Open motorboats moving 8 km/h caused reductions of mussel filtration activity to a depth of 50 cm (Fig. 5A), and an increase in boat speed to 18 km/h extended this depth to 90 cm (Fig. 5D). At 18 km/h, the filtration activity of 3 of the 4 species (*A. anatina*, *U. pictorum*, and *D. polymorpha*) stopped completely to a depth of

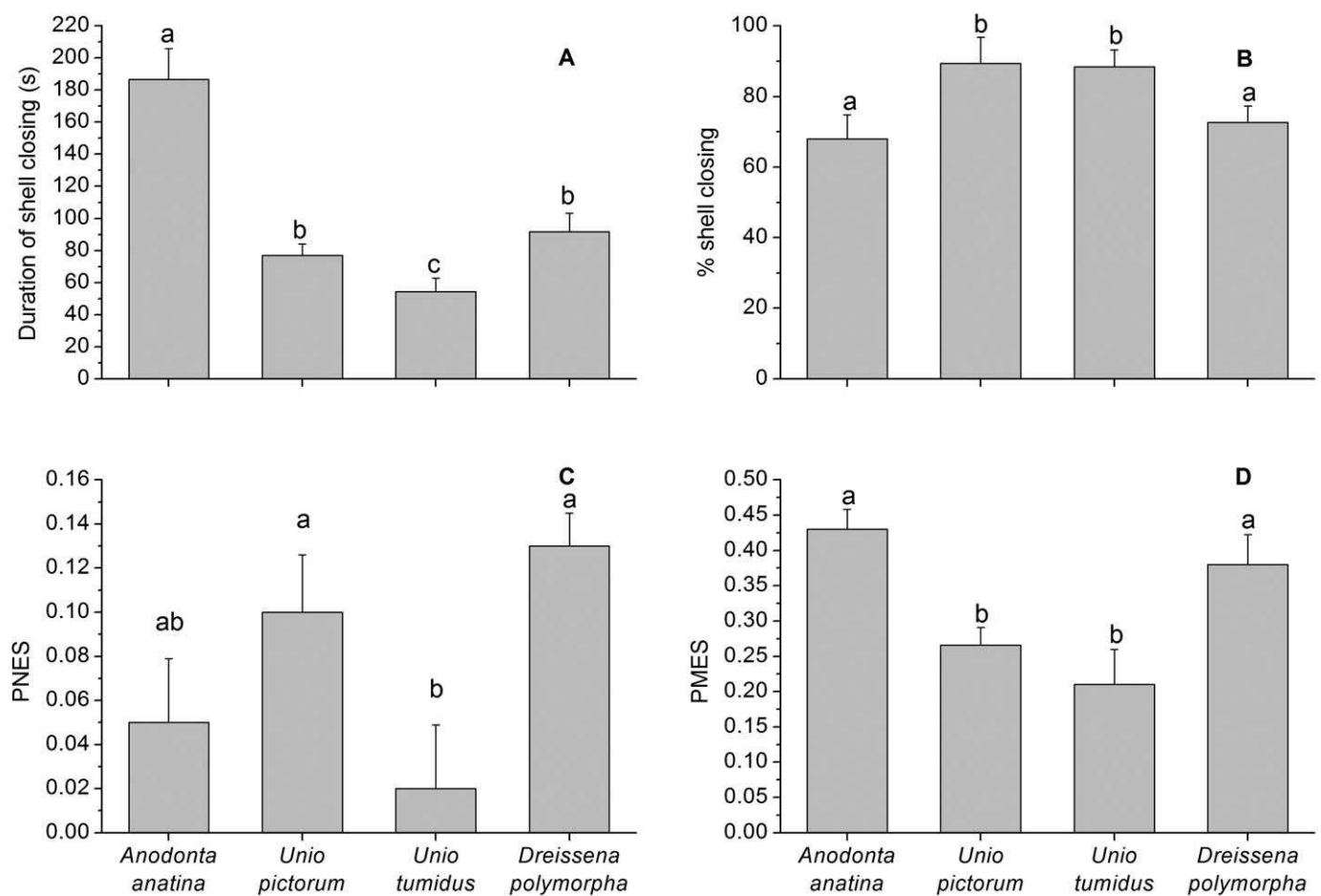


FIG. 3. Mean (+1 SE) duration (A) and % shell closing (B), predicted no-effect shear stress (PNES) (C), and predicted medium-effect shear stress (PMES) (D) for *Anodonta anatina*, *Unio pictorum*, *Unio tumidus*, and *Dreissena polymorpha*. Bars with different letters are significantly different.

TABLE 2. Mean (± 1 SE) shear stress produced by various boat types and speeds at various water depths. Where SE could not be calculated ($n < 3$), calculated values from polynomial cubic regression models are provided with measured means in parentheses.

Type of boat	Shear stress (N/m^2)				
	25 cm	50 cm	75 cm	125 cm	180 cm
Muscle driven boats	0.06 ± 0.010	0.02 ± 0.005	0.001 ± 0.001	0.00 ± 0.000	0.00 ± 0.000
Motorboats (8 km/h)	0.29 ± 0.030	0.09 ± 0.006	0.08 ± 0.007	0.14 ± 0.010	0.13 ± 0.005
Motorboats (10 km/h)	0.49 ± 0.020	0.18 ± 0.030	0.08 ± 0.020	0.20 (0.16)	0.21 (0.14)
Motorboats (12 km/h)	1.27 ± 0.060	0.49 ± 0.020	0.11 ± 0.004	0.19 ± 0.007	0.15 ± 0.005
Motorboats (18 km/h)	1.23 ± 0.070	0.46 ± 0.020	0.30 ± 0.010	0.19 ± 0.008	0.13 ± 0.004
Yachts (10 km/h)	0.89 (0.89)	0.16 ± 0.004	0.03 (0.09)	0.05 ± 0.030	0.15 ± 0.020
Motorized rowing/rafting boats (10 km/h)	0.20 (0.20)	0.12 ± 0.010	0.14 (0.14)	0.27 (0.27)	0.09 ± 0.001

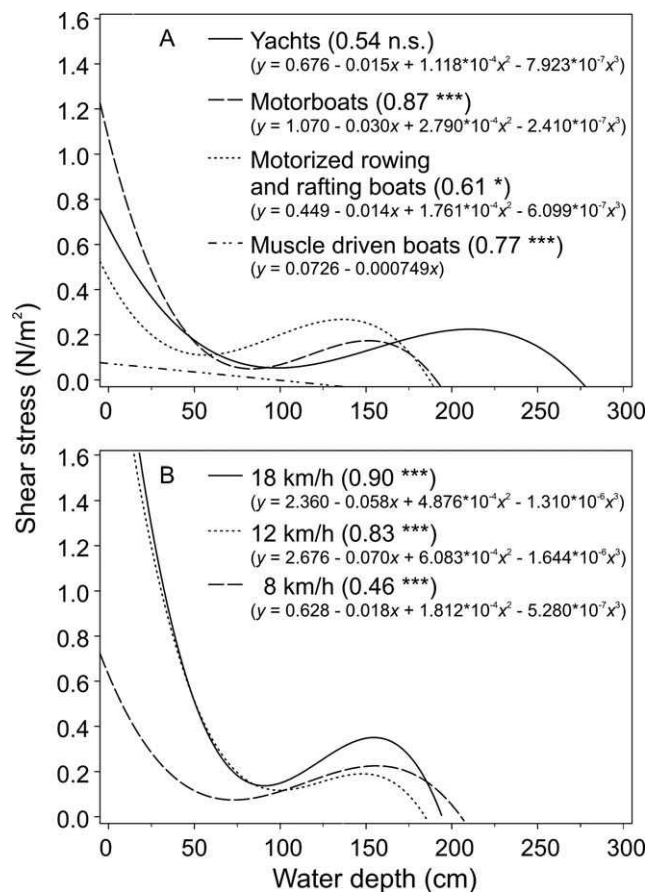


FIG. 4. Polynomial cubic regression models for shear stress measured at 5 water depths for different types of boats (speed of motorized boats = 10 km/h) (A) and for motorboats at 3 speeds (B). For muscle-driven boats, linear regression analysis was done between shear stress and water depth. n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$.

30–50 cm. In deeper water, filtration by all species decreased to a mean of 70% and filtration activity of *A. anatina* decreased to 59% at a depth of ~150 cm when motorboat speed was 18 km/h (Fig. 5D). In contrast, the disturbance level in the intermediate depth zone was mostly stable across all levels of boat speed. *Unio tumidus* appeared to be least affected in the shallow marginal zone and minimally affected in deep water when motorboats passed by with a speed of 18 km/h. *Dreissena polymorpha* in deep water was least affected at all speeds except 18 km/h. *Unio tumidus* was affected most at intermediate water depths, whereas *D. polymorpha* was affected least at these depths.

Influence of boating on filtration activity

We estimated the community filtration rate of the mussel populations at the sampling site as $5.391 \text{ m}^3/\text{h}$ based on estimated filtration rates (Pusch and Hoffmann 2000, Pusch et al. 2001) and population size (Graeber 2007). This estimate indicates that the undisturbed mussel community at our study reach could filter $79,507 \text{ m}^3$ of river water/d. Based on an average discharge rate of $3.13 \text{ m}^3/\text{s}$ ($270,432 \text{ m}^3/\text{d}$) in July 2010, this value corresponds to filtration of 29.3% of the water in this section of the river by mussels. If we apply the spatial disturbance of shear stress to these estimates, single passages of boats would cause a reduction of the community filtration activity by 0.02% (muscle-driven boats), 0.68% (motorboats), 0.45% (yachts), and 0.69% (motorized rafting and rowing boats) at the sampling site (if all motorized boats were navigating at a speed of 10 km/h). Assuming a mean of 35 boats (as counted by automatic cameras, of which 32% were muscle driven) operating during 9 h of daylight (as indicated by the average operation period of the nearby automatic water gates) during a typical weekend

TABLE 3. Maximum water depths at which shear stress above the predicted no-effect shear stress PNES was still detectable according to regression models for *Unio tumidus*, *Anodonta anatina*, *Unio pictorum*, and *Dreissena polymorpha* for various boat types and speeds.

Type of boat	Maximum water depth (cm)			
	<i>U. tumidus</i>	<i>A. anatina</i>	<i>U. pictorum</i>	<i>D. polymorpha</i>
Muscle driven boats	57	17	n. d.	n. d.
Motorboats (8 km/h)	202	200	192	189
Motorboats (10 km/h)	187	185	176	172
Motorboats (12 km/h)	181	179	172	169
Motorboats (18 km/h)	191	190	187	185
Yachts (10 km/h)	270	266	258	253
Motorized rowing/rafting boats (10 km/h)	184	181	176	174

day in July, the reduction in filtration activity would decrease this daily filtration rate by 6.9%, which would reduce the percentage of total river water filtered by mussels to 27.3%.

The effect of boating on the filtration activity of mussels depended strongly on depth (Figs 4A, B, 5A–D), so we calculated the maximum number of motorboats/h that could be present at various water depths until filtration activity of mussels stopped completely (Fig. 6). If the river section is used by 24 to 93 motorboats/h operating at a speed of 10 km/h,

filtration activity by mussels could cease entirely, depending on water depth.

Discussion

Boat-induced increases in shear stress resulted in a highly predictable shell-closing response by mussels. Miller et al. (1999) used magnetic sensors to measure the effects of waves caused by the passage of large work boats or skiffs on mussels and detected shell-closing responses by the North American unionid

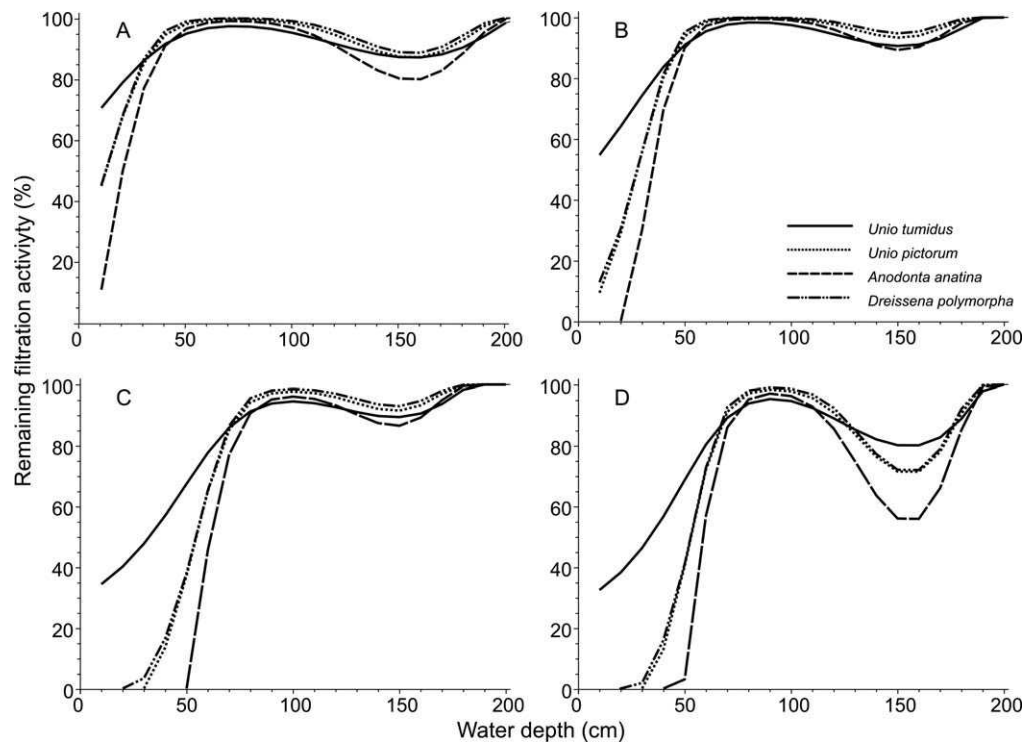


FIG. 5. Remaining filtration activity during the 1-min period after a boat passage vs water depth at locations of experimental *Unio tumidus*, *Unio pictorum*, *Anodonta anatina*, and *Dreissena polymorpha* disturbed by open motorboats navigating at 8 km/h (A), 10 km/h (B), 12 km/h (C), and 18 km/h (D).

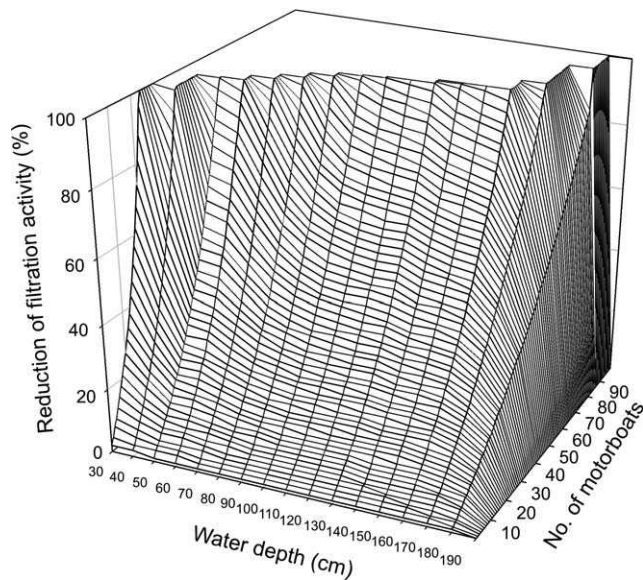


FIG. 6. Mean % reduction of filtration activity in a generalized marginal zone of a water body used for recreational boating during a 1-min period after close boat passage depending on water depth [cm] and the number of open motorboats/h cruising at 10 km/h. Means were calculated across the 4 species *Unio tumidus*, *Unio pictorum*, *Anodonta anatina*, and *Dreissena polymorpha*.

mussel *Amblema plicata*. However, they did not detect a similar response to recreational crafts, even after multiple passages. Based on our results, we assume that the hydraulic effects of recreational boats did not extend to mussels in the depths of the Mississippi River.

In our study, boat passages caused abrupt shell closing that exceeded natural diurnal fluctuations in shell closing by several times. Freshwater mussels can show a diurnal shell-closing pattern with morning and evening peaks (Englund and Heino 1994, 1996). However, we did not observe such a pattern, possibly because an upstream lake provided a consistent supply of seston or because DO concentrations were low during the study period (Vero and Salanki 1969, Morton 1970, Lorenz and Pusch 2012). Shell-closing responses also can be caused by changes in particle size and concentration (Riisgard et al. 2011) and rapid large changes in water temperature (Salanki et al. 1974). Particle concentration was relatively constant during our study period, and water temperature changed only slightly between measurement days. Thus, we conclude that boating activity was the primary variable influencing filtration activity.

Sigmoid response curves to environmental stressors are widely observed (Calow and Forbes 2003). In our study, % shell closing of all 4 species followed a

reproducible sigmoid dose-response curve, and Gabel et al. (2008) observed a similar sigmoid response curve of small benthic invertebrates to wave disturbance. Our sigmoid models explained slightly lower fractions than Gabel's of the total variance (indicated by the r^2 value), especially for *U. tumidus*. The relatively high scatter in response patterns in our study might have been caused by differences in burrowing depths among the unionid species studied. Individuals burrowed deeper in the sediment would experience less wave disturbance than others and, therefore, would show smaller shell-closing responses (discussed further below). Differences in shell position relative to the direction of wave disturbance also could contribute to high variance, especially in *U. tumidus* and *D. polymorpha*.

The sigmoid regression curves facilitated calculation of PMES and PNES thresholds. PMES thresholds discriminated better among species than did PNES thresholds and seem to be more appropriate for detecting differences among mussel species. In contrast, PNES thresholds facilitate identification of conservation requirements for endangered species.

Effect of hydraulic disturbance on freshwater mussel species

The smaller % shell closing and higher PMES for *A. anatina* and *D. polymorpha* compared to *U. tumidus* and *U. pictorum* (Fig. 4A–D) probably were caused by differences in the species' position relative to the sediment surface. Dreissenid mussels live as epifauna attached to hard substrates or to the shells of other mussels. Therefore, *D. polymorpha* might be better adapted to changes in flow or to hydraulic disturbances than endobenthic unionid mussel species, which burrow partially (*A. anatina*) or completely (*U. tumidus*) into the sediment (Mentzen 1926, Arter 1989) so that only the inhalant and exhalant siphons are exposed to the flow occurring near the sediment surface. The partially exposed *A. anatina* had the longest AMAX in our study and, therefore, appears to be less adapted than *D. polymorpha* to hydraulic disturbance. The strong adaptation of the successful invasive species *D. polymorpha* to hydraulic disturbance could be viewed as a preadaptation acquired in its original habitat that suited it for existence in new habitats (Gabel et al. 2011a).

Boating effects on ecosystem services

Freshwater mussels contribute significantly to the self-purification of surface waters, an extremely important ecosystem service (Everard and Powell 2002, Howard and Cuffey 2006). Mussels filter phytoplankton and detrital organic matter from the

water column. In the river section we studied, this benthic–pelagic coupling could lead to removal of most of the phytoplankton in the water column (Welker and Walz 1998). This action improves the ecological status of a water body and increases its utility for other purposes, including recreation and boating (Bockstael et al. 1989). In water bodies that are shallower than the Krumme Spree, boating activities cause significant resuspension of sediments (Beachler and Hill 2003), which can have severe negative effects on mussel filtration activity. The maximum depth of water bodies where outboard motorboats caused resuspension of coarse sandbed material was 1.8 m (Beachler and Hill 2003), which equals the depth measured in our study. However, current boating activity in the Krumme Spree reduces the filtration activity of freshwater mussels by only 6.9% per day, so a severe effect on the self-purification of this river section is not expected.

Management of recreational boating activities

Our modeling approach allows identification of mitigation strategies that might depend on the depth of a given water body or the depth distribution of mussels. Such a model could be used to predict the minimum distance of boat traffic from the shore or maximum boating speed to minimize impacts. We recommend implementation of special restrictions, such as slow no-wake speeds, during times of low flow and low water levels to ensure undiminished ecosystem services. Furthermore, adverse effects of boating might be effectively prevented by restricting access to ecologically vulnerable zones of water bodies to certain vessel types, such as nonmotorized or electric-motor boats, which run at lower speed and often have hulls designed to generate fewer waves. Such restrictions might help protect populations of protected species, water quality, and the resilience of the water body and, thus, enhance its sustainable utility.

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