Horizontal and vertical movements of unionid mussels in a lowland river

Astrid N. Schwalb[1] AND **Martin T. Pusch**[2]

Leibniz-Institut für Gewässerökologie und Binnenfischerei, Müggelseedamm 310, 12587 Berlin, Germany

Abstract. Freshwater mussels are important constituents of freshwater ecosystems, yet much of their basic biology remains to be examined. The behavior of 3 species of unionid mussels (*Unio tumidus*, *Unio pictorum*, and *Anodonta anatina*) was examined in the lowland River Spree (Germany). Mussels were marked individually, and their positions on the sediment surface and depth below the sediment surface were recorded weekly between May and October 2004. The average rate of horizontal movement was 11 ± 15 cm/wk (mean ± 1 SD). The direction of the movements seemed erratic; however, a significant net shoreward displacement of ~17 cm, possibly caused by rising water levels, was observed during the study. A surprisingly high percentage of the mussels (74 ± 7%) was burrowed entirely in the sediment to depths as great as 20 cm during the summer. Smaller mussels and individuals not infested by the zebra mussel, *Dreissena polymorpha*, burrowed deeper in the sediments than larger or infested mussels. Burrowing reduced infestation densities in a laboratory experiment. Significantly more *U. tumidus* individuals were found on the sediment surface during the reproductive period in early summer than in late summer, suggesting that reproductive activity may influence burrowing. Burrowing was significantly related to current velocity (discharge), day length, and water temperature (multiple linear regression, $R^2 = 0.74$, $p < 0.001$), but current velocity appeared to be the dominant factor driving vertical movements ($R^2 = 0.53$, $p < 0.01$). We propose that movement behaviors are important adaptations of unionid mussel populations to the flow and food conditions in rivers. Movement behavior also may help unionids escape predators and control infestation by *D. polymorpha*.

Key words: freshwater mussels, Unionidae, behavior, locomotion, vertical distribution, discharge, sediment, *Unio tumidus*, *Dreissena polymorpha*.

Mussels are an important component of freshwater ecosystems. They constitute up to 90% of benthic invertebrate biomass (Økland 1963, Negus 1966, Pusch et al. 2002) and influence aquatic ecosystems in many ways. As suspension feeders, freshwater mussels are an important link coupling the pelagic and benthic zones because they clear suspended particles from the water column, thereby decreasing phytoplankton biomass (Welker and Walz 1998, Ackerman et al. 2001, Pusch et al. 2001). Freshwater mussels redirect nutrients and organic matter from the pelagic to the benthic food web through biodeposition of feces and pseudofeces. Exposed shells at the sediment surface provide habitat for epizoic and epiphytic organisms and for many invertebrate species, which can reach high densities in mussel beds (Brunke et al. 2002). In addition, mussel burrowing activities cause bioturbation of sediments, which increases the O_2 content of the sediment and influences the release of sediment-borne nutrients to the water column. Burrowing also may protect unionids from infestation by epizoic *Dreissena polymorpha* (Pallas) and remove already attached *D. polymorpha* (Nichols and Wilcox 1997, Burlakova et al. 2000). However, we lack detailed knowledge of these sediment-related processes, and this lack is a significant gap in our understanding of the functional role of unionid mussels in aquatic systems (Vaughn and Hakenkamp 2001).

Mussels traditionally have been viewed as sessile animals, despite the observation of tracks created by unionid mussels moving horizontally on the sediment surface. It was believed that mussels would move only to avoid adverse conditions such as exposure to air during low water levels and cold winter temperatures (Mentzen 1926, Engel 1990). However, studies have suggested a connection between aggregations of mussels and reproduction (e.g., Pichocki 1969, Amyot

[1] Present address: Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada. E-mail: aschwalb@uoguelph.ca

[2] E-mail address: pusch@igb-berlin.de

and Downing 1998). For example, *Anodonta* sp. individuals move closer together during the summer spawning season (Burla et al. 1974). Recent studies have documented seasonal migration in both the vertical (Amyot and Downing 1991, 1997, Balfour and Smock 1995, Watters et al. 2001, Perles et al. 2003) and horizontal directions (Amyot and Downing 1997, 1998). Adults apparently migrate vertically and emerge at the sediment surface during the reproductive period (Balfour and Smock 1995, Watters et al. 2001), whereas juvenile mussels (<3 y) always remain within the sediment (Balfour and Smock 1995). Horizontal movements also might bring animals of the opposite sex closer together during spawning (Amyot and Downing 1998). Aggregations are important for reproduction because the sperm of dioecious species (Wächtler et al. 2001) are released into the water by males and taken up by females. Fertilization of the eggs and development to a parasitic larval stage (glochidium) take place in the suprabranchial chambers of females. Spawning may occur several times per season in European *Unio* species (Hochwald and Bauer 1990), and *Anodonta cygnea* (Linnaeus) specifically releases a portion of glochidia when a potential host fish species is nearby (Bauer 2001). Thus, adult mussels must move to the sediment surface—at least with the posterior part of their valves—for sexual reproduction and larval release into the surface water.

Studies of movements of unionid mussels may provide important clues for understanding their functional role in aquatic ecosystems. Environmental factors, such as temperature and day length, influence seasonal variation in vertical and horizontal movements of unionid mussels (Amyot and Downing 1997, Watters et al. 2001, Perles et al. 2003) and are likely to have the same effects on mussels in both lentic and lotic systems. However, other factors, such as discharge, are specific to lotic systems. Discharge and velocity can be highly variable in streams, exposing mussels to different flow velocities and bottom shear stress, and might affect burrowing behavior (Di Maio and Corkum 1995, Strayer 1999). Most recent studies concerning vertical or horizontal movements of unionids were conducted in lakes (Amyot and Downing 1991, 1997, Saarinen and Taskinen 2003), creeks (Balfour and Smock 1995), or artificial systems (Watters et al. 2001, Perles et al. 2003 [in part]). To the best of our knowledge, no study has examined horizontal movements of unionid mussels in a lowland river. The purposes of our study were to quantify horizontal movements of unionid mussels in the lowland River Spree and to examine how environmental factors influenced the vertical move-

ments of the most abundant species, *Unio tumidus* (Philipsson).

Methods

Study area

Field observations were conducted in the River Spree, a lowland river in northern Germany, that originates in the Lusatian mountains (Saxony, Germany) and flows for 380 km through several shallow lakes to its confluence with the River Havel in Berlin (Welker and Walz 1998). The study reach was part of a 6th-order river section called the Müggelspree, chosen for its high density of unionid mussels (up to 350 ind./m^2; Pusch et al. 2002, this study), which is linked to high seston concentrations and the absence of catastrophic floods. The study site was 45 km east of Berlin, ~400 to 500 m downstream of the Große Tränke weir near the city of Fürstenwalde (lat 52°22′20″N, long 13°59′54″E). As a result of channelization in the early 20th century, the river channel is roughly trapezoidal in profile, with a mean width of 27 m (18–40 m) and water depths ranging between 0.7 and 2.3 m. River discharge varied between 2.5 m^3/s in summer and 21.2 m^3/s in winter 2004. Water depth is strongly influenced by massive macrophyte growth in downstream reaches and, therefore, varies partially independently of discharge. The sediment consists almost exclusively of sand (mean particle size [D_{50}] = 0.42 ± 0.12 mm). In some locations, the sediment contains a hard layer of bog-iron ore, i.e., sand glued together by Fe(III)-hydroxide/oxyhydrate, which is created by precipitation processes when anaerobic ground water entering the river reaches oxygenated river sediments. The Müggelspree is considered eutrophic. Total N concentrations ranged between 0.7 and 1.9 mg/L, total P ranged between 74 and 187 μg/L, and chlorophyll *a* concentrations ranged between 14 and 82 μg/L in 2004. The Müggelspree holds small to moderate populations of otter (*Lutra lutra*) and the nonindigenous species muskrat (*Ondatra zibethicus*) and mink (*Mustela vison*), all of which are potential predators of unionid mussels.

Horizontal and vertical movements

Horizontal and vertical movements of mussels were studied simultaneously in a 3 × 3-m permanently marked study area (area A) >3.5 m from shore. Water depth varied between 0.5 to 1 m (early May) and 1.5 to 2 m (mid-July). Area A was divided into nine 1-m^2 quadrats marked only by short metal stakes, so that mussels could move freely. Mussels on the sediment surface were mapped weekly between 8 May and 4

September and on 2 October 2004. During sampling, a 1-m^2 aluminum frame, subdivided into 25 × 25-cm subquadrats, was placed temporarily over each of the nine 1-m^2 quadrats with the help of a professional SCUBA diver. The grid was used to determine the position of all mussels visible at the sediment surface and was removed after mapping was completed.

All mussels on the sediment surface in area A were labeled individually using numbered plastic labels (Dymo®) that were glued to the posterior part of a valve. Shell length of each mussel was measured (±1 mm) using calipers, species was determined, and individuals were returned to the 25 × 25-cm subquadrat where they were found. On each subsequent sampling date, any unmarked mussels were measured, identified to species, and labeled. The identification numbers of recovered mussels were recorded, and all individuals were returned to their original location. Additional sampling was done on 21 August to determine if labeled mussels had moved from the study area (≤2 m) or had burrowed into the sediment in the study area (1 subquadrat was sampled). On 2 October, all mussels were removed from the sediment to determine the total (labeled and newly encountered individuals) number of mussels within the study area.

The distance traveled by a mussel between encounters was taken as the shortest distance between the centers of the subquadrats in which a mussel was found. The total number of mussels visible on the sediment surface on each sampling date and the total number of individuals within the study area on 2 October were used to calculate the percentages of burrowed mussels during the study period, assuming that the number of mussels in the study area remained constant. The average length of time during which mussels disappeared and were assumed to have burrowed into the substrate was calculated based on data from 35 individuals found in the center 1 × 1-m quadrat of the study area between 8 May and 12 June. This conservative estimate ensured that any disappearance was the result of burrowing rather than of migration from the study area.

Vertical distribution of mussels in the sediment

The vertical distribution of mussels in the sediment was examined in ten 1-m^2 quadrats within a 9 × 3-m area (area B) that was more densely populated than area A. Area B was 5.5 m from shore and ~100 m upstream of area A. Quadrats were chosen randomly within area B; no quadrat was sampled twice. Seven quadrats were sampled in early summer (8 June–7 August 2004) during the reproductive period of the most abundant species (*U. tumidus*), and the 3 remaining quadrats were examined in late summer (28 August–4 September). In quadrats sampled in June, mussels on the sediment surface and burrowed mussels were identified and measured. In quadrats sampled between July and September, the depth of each individual in the sediment (0–5, 5–10, 10–15, or 15–20 cm) was recorded. Unionids were identified to species and measured (shell length), the number of epizoic *D. polymorpha*) per mussel was recorded, and the mussels were returned to the sediment. All mussels found in the upper sediment layer (0–5-cm depth) were defined as epibenthic (surface-dwelling) mussels.

Laboratory experiments

Unio tumidus and *D. polymorpha* were collected in the littoral zone of Lake Dämeritz (lat 52°25′14″N, long 13°43′53″E), which is part of the River Spree. All individuals were transported to the laboratory within 1 h of collection in cooled plastic boxes filled with water and were placed in aerated aquaria or plastic tanks with a sediment layer that allowed mussels to burrow. Experiments were carried out within 1 wk after collecting the mussels. Mussels were fed once a day with dried and ground nettles (Neudorff Ltd., Emmerthal, Germany), which is easily accepted by unionid mussels as food and is commercially available with a constant composition.

Experiment 1 was designed to investigate the influence of mussel size (shell length = body length) on burrowing depth. Twenty large (>6 cm) and 20 small (<5 cm) *U. tumidus* were distributed evenly in a plastic tank (180 L) with their anterior ends placed gently in a 10-cm layer of sandy sediment. The posterior ends of large individuals were marked to permit differentiation from small individuals when they were partially burrowed. The tank was aerated continuously and kept outdoors (temperature 10–20°C). The burrowing depth of all mussels was recorded as the proportion (0–25, 25–75, 75–100, or >100%) of the valve length buried after 24 and 48 h. Differences in the burrowing depth of the 2 groups were examined using a χ^2 test.

Experiment 2 was designed to investigate the influence of *D. polymorpha* infestation on burrowing depth of unionids. Forty *U. tumidus* (6.9 ± 0.6 cm) were distributed among 6 aquaria. Twenty mussels were labeled individually, and *D. polymorpha* were allowed to attach to their valves over a period of 24 to 48 h (cf. Haag et al. 1993), resulting in a mean infestation density of 16 ± 7 (mean ± SD) *D. polymorpha* ind./*U. tumidus* ind. This infestation density was much higher than the mean infestation density found in the field (1 ± 2 *D. polymorpha* ind./*U.*

tumidus ind.; $n = 1803$). All mussels were put in a plastic tank (180 L) as described above. The burrowing depth of all mussels was recorded after 24 and 96 h.

Statistical analyses

χ^2 tests were used to compare differences in the number of mussels at different burrowing depths (experiments 1 and 2) and to compare the number of individuals that moved toward vs away from the shore (River Spree). For all other analyses, the Kolmogorov–Smirnov and Shapiro–Wilk test for smaller sample sizes ($n < 20$) were used to determine whether the data were normally distributed. If data were not normally distributed, nonparametric tests were used (e.g., Spearman rank correlation instead of Pearson correlation). The horizontal distances moved were compared among species with a Kruskal–Wallis test. A Wilcoxon test was used to compare infestation densities of *D. polymorpha* between adjacent depth layers because the data were not independent. Mann–Whitney tests were used to determine whether: 1) the percentage of mussels on the sediment surface differed between early and late summer, and 2) the lengths of burrowed mussels differed between the 0–5-cm sediment layer and deeper layers. Stepwise multiple linear regression analysis was used to examine the relationship between surface densities of mussels and water temperature, day length, discharge, and water level.

Results

Horizontal movements

Densities of unionid mussels in areas A and B ranged from 22 to 289 ind./m². In area B, *U. tumidus* had the highest mean density (156 ± 79 ind./m², mean ± SD), and densities of *Unio pictorum* (Linnaeus) and *Anodonta anatina* (Linnaeus) were lower (18 ± 9 and 11 ± 6 ind./m², respectively).

A total of 759 mussels was labeled. Of these labeled mussels, 544 (72%; *U. tumidus*: $n = 428$, *U. pictorum*: $n = 26$, *A. anatina*: $n = 90$) were encountered at least twice, i.e., recaptured at least once (Table 1), so that the distance they had moved could be calculated. Fourteen labeled mussels were later found dead, but only 4 of those had not been recaptured alive at least once. Mussel movement rate varied between 0 and 226 cm/wk and averaged 11 ± 15 cm/wk ($n = 544$). Approximately 90% of the mussels moved between 0 and 25 cm/wk, and some individuals (19%) always were found in the same 25 × 25-cm subquadrat. No significant differences in the distances moved were found among species (Kruskal–Wallis test, $H = 4.3$, $p > 0.05$, df = 2), size classes ($H = 5.0$, $p > 0.05$, df = 4), or

months ($H = 1.9$, $p > 0.05$, df = 4) because of high variability among individuals. However, mean distance moved increased slightly (from 8 cm to 11 cm/wk or 1.5–2 body lengths) between May and October. Mean movement rate was significantly related to temperature and increased by 0.5 ± 0.07 cm/°C ($R^2 = 0.95$, $p < 0.01$; Fig. 1).

The direction of the horizontal movements of mussels seemed erratic. Mussels frequently turned back in the direction from which they came and crossed subquadrats twice (Fig. 2). However, mean displacement was 17 cm shoreward over the entire study period, and significantly more mussels moved toward the shore than away from the shore ($\chi^2_1 = 38$, $p < 0.01$, $n = 333$). No significant upstream or downstream movement was detected.

Labeled mussels were found as far as 2 m outside the boundary of area A and were found burrowed in the sediment within the study area (based on 1 subquadrat sampled) on 21 August. On average, 40 ± 13% of the mussels found on the surface on one sampling date appeared on the surface within the study area on the subsequent sampling date. Given that 90% of the mussels moved <25 cm/wk, it is likely that ~½ of the mussels burrowed every week. In many cases, mussels disappeared for several weeks (3 ± 2 wk, $n = 35$).

Vertical movements and environmental factors

Mean unionid density on the sediment surface of area A was 17 ± 8 (range = 4–27 ind./m²; Fig. 3A), whereas the estimated percentage of burrowed mussels was 43 ± 26% (range = 20–92%; Fig. 3B). The highest surface densities (>20 ind./m²) were found between early June and mid-August, but these peaks were interrupted by a sharp decline between 10 July and 17 July, when surface density decreased from 24 to 11 ind./m² (Fig. 3A). The lowest surface densities were found in early May and from the end of August to early October (the end of the study period). Many marked mussels (396/759 marked individuals) were found burrowed in the sediment in early October (Fig. 3B).

Discharge varied considerably during the study period (range = 2.5–13.9 m³/s). The greatest flows occurred in May and September (Fig. 3C). Water temperature increased from 15 to 23°C between May and August and decreased again to a low of 13°C in October (Fig. 3D). The sudden decrease in mussel surface density in July (Fig. 3A) was paralleled by an increase in river discharge (from 5.2 to 9.1 m³/s; Fig. 3C), and by a slight decreases in water temperature (from 19.7 to 18.8°C; Fig. 3D) and day length (from 16.5

Table 1.   The number of newly marked and recaptured individuals in area A of the River Spree in 2004, and the frequency of subsequent recaptures for individuals marked on a sampling date.

| Date | No. of individuals | | No. of times a mussel was recaptured | | | | | | | | | | | | | | | |
	Recaptured	Newly marked	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
8 May	0	63	0	5	3	8	12	3	8	10	5	3	3	0	0	2	1
22 May	26	79	11	6	5	9	13	5	12	9	2	4	1	1	0	1	
29 May	72	93	13	11	16	18	12	7	8	4	1	2	1				
5 June	109	87	16	21	16	14	8	4	3	5							
12 June	124	68	8	13	13	8	9	5	9	1	1	0	1				
19 June	136	57	9	12	13	9	6	6	1	1							
26 June	176	64	27	18	4	8	1	3	3								
3 July	192	40	10	11	8	7	3	0	1								
10 July	179	39	15	11	4	4	3	1	1								
17 July	76	20	13	4	2	1	0	0									
24 July	122	30	12	9	6	2	0	1									
7 August	186	39	25	11	2	0	1										
14 August	189	40	25	10	4	1											
21 August	157	21	17	3	1												
28 August	64	9	7	2													
4 September	31	6	3	3													
2 October	31	4[a]	3														
Total		759[a]	211	150	97	89	68	35	46	30	9	9	6	1	0	3	1

[a] Does not include 177 burrowed individuals

to 16.2 h; Fig. 3E). A stepwise multiple linear regression (corrected $R^2 = 0.74$, $p < 0.001$) showed that the dynamics in surface densities of mussels during the study period could be largely explained by discharge (b [slope] $= -1.6 \pm 0.5$ [SE], $p < 0.01$), day length ($b = 2.4 \pm 0.01$, $p < 0.01$), and water temperature ($b = 1.0 \pm 0$, $p < 0.05$) (compare Fig. 3A with Fig. 3C–E). Note that regression results are valid only within the ranges of water temperature (13.5–23.2°C) and day length (12.0–16.8 h) observed during
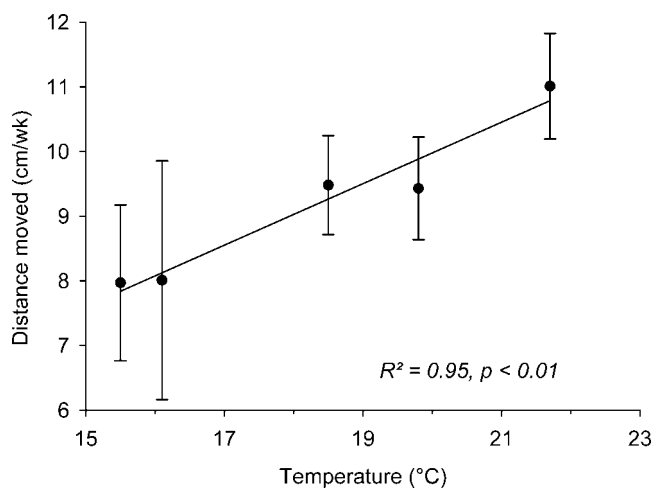

Fig. 1. Linear regression for mean (± 1 SE) distance moved/mo as a function of mean monthly temperature. n = 96 (May), 539 (June), 555 (July), 590 (August), and 62 (September and October).

the study period. Discharge alone explained 53% of the variation in mussel density ($R^2 = 0.53$, $p < 0.01$; Fig. 4), but water level was rejected as an additional predictor because it was correlated with discharge (Spearman r = 0.63, $p < 0.01$; Fig. 3C, F).

Vertical distribution in the sediment

River Spree.—A total of 1803 individuals (1516 *U. tumidus*, 182 *U. pictorum*, 105 *A. anatina*) was found in area B, and 74 ± 7% (range = 61–84% in individual 1-m^2 plots) of the mussels were found completely burrowed. Individuals of all 3 species were found as far as 20 cm below the sediment surface. Most mussels (70 ± 16%) were found within the first 10 cm below the sediment surface. Nearly ½ of the mussels (45 ± 18%; $n = 7$ quadrats) were in the 5–10-cm depth layer, whereas 25 ± 7% were in the 0–5-cm depth layer, 17 ± 8% were in the 10–15-cm depth layer, and 13 ± 12% were in the 15–20-cm depth layer.

The percentage of burrowed *U. tumidus* individuals varied seasonally. In area A, surface densities were highest from June to mid-August (mean = 22 ind./m^2) and lower in May (12 ind./m^2) and from late August to October (9 ind./m^2). In area B, significantly higher percentages were observed on the sediment surface from June to early August (30 ± 8%) than from late August to early September (16 ± 3%) (Mann–Whitney test for small sample size, $U = 6$, $p < 0.05$, $n = 10$).

Vertical distribution varied with size class (Fig. 5). On average, mussels of all species in the 0–5-cm
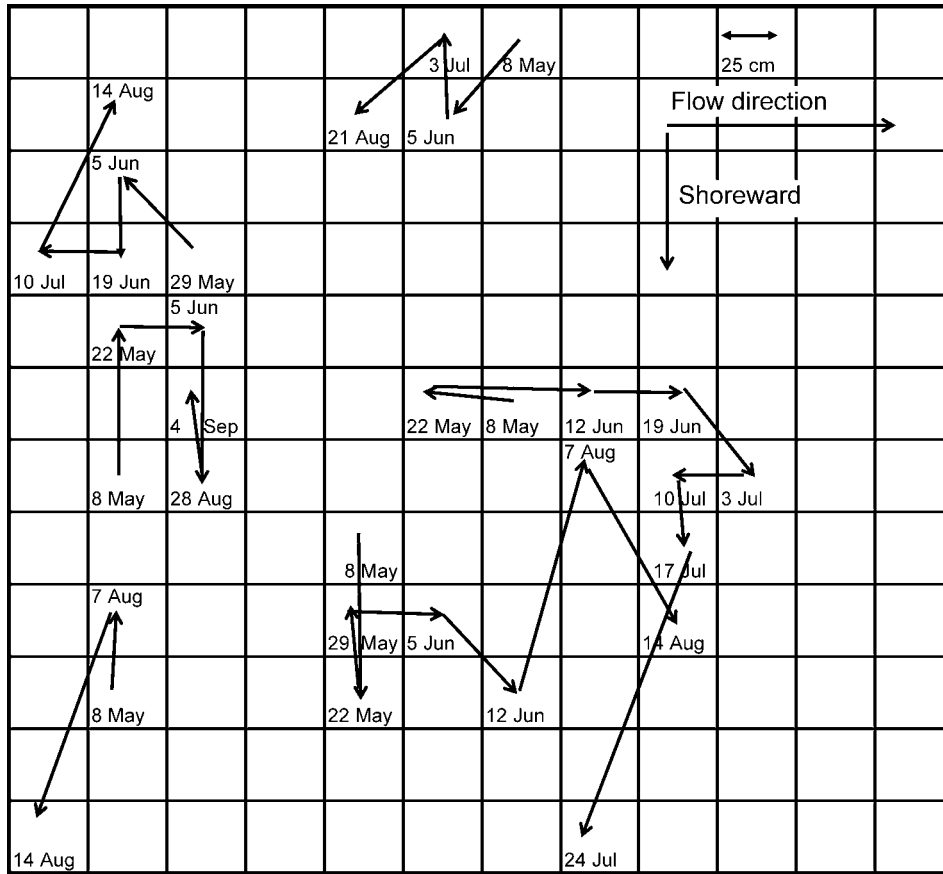
Fig. 2. Examples of movement patterns of 6 individuals (*Unio* sp. and *Anodonta anatina*) during the study period. Changes in positions are shown with the respective recording dates.

sediment layer were ~1 cm larger than mussels in the deeper sediment layers (Mann–Whitney test, $z = 13.6$, $p < 0.01$, $n = 1459$). The percentage of all individuals in the >5-cm size class that was in the 0–5-cm depth layer ($38 \pm 6\%$) was significantly larger than the percentages of all individuals in the <3-cm and 3–5-cm size classes that were in the 0–5-cm depth layer (Wilcoxon test, $z = 2.2$ and 2.4, $p < 0.05$, $n = 7$). No significant differences in the vertical distributions of individuals within size classes were found in the 5–20-cm depth layers (Fig. 5).

Experiment 1.—Burrowing depth differed between mussels in small and large size classes. Large mussels (>6 cm) burrowed deeper than small (<5 cm) mussels. All mussels burrowed $\geq 25\%$ of their valve length after 48 h. Eight large and 0 small mussels burrowed 25–75% of their valve length, 9 large and 8 small individuals burrowed 75–100% of their valve length, and 3 large and 12 small individuals burrowed >100% of their valve length in the sediment. The differences in burrowing depths were significant (after 24 h: $\chi^2_2 = 8.8$, $p = 0.01$; after 48 h: $\chi^2_2 = 13.5$, $p < 0.01$; $n = 40$). Significantly more small than large mussels were

completely burrowed (χ^2 test with continuity correction; after 24 h: $\chi^2_1 = 6.4$, $p = 0.01$; after 48 h: $\chi^2_1 = 6.8$, $p < 0.01$; $n = 40$).

Dreissena polymorpha *infestation density*

River Spree.—*Dreissena polymorpha* infestation density was generally low (*U. tumidus*: mean $= 1 \pm 2$ *D. polymorpha* ind./unionid ind., range $= 0$–15, $n = 1514$; *U. pictorum*: mean $= 1 \pm 1$, range $= 0$–6, $n = 182$; *A. anatina*: mean $= 2 \pm 4$, range $= 0$–26, $n = 105$). Fifty to 66% of the individuals of all 3 species were not infested by zebra mussels. Infestation density tended to be lower on mussels in the 5–20-cm depth layers than on mussels in the 0–5-cm depth layer. Infestation density on *U. tumidus* individuals in the 3.0–4.9-cm and 5.0–6.9-cm size classes was significantly greater in the 0–5-cm depth layer than in the 5–20-cm depth layers (Wilcoxon test, $z = 2.4$ and 2.0, $p < 0.05$, $n = 7$; Fig. 6).

Experiment 2.—Burrowing depth did not differ between mussels with or without epizoic *D. polymorpha* after 24 h and 96 h (χ^2 test with continuity correction, $\chi^2_1 = 1.8$, $p = 0.2$, $n = 40$). However, fewer
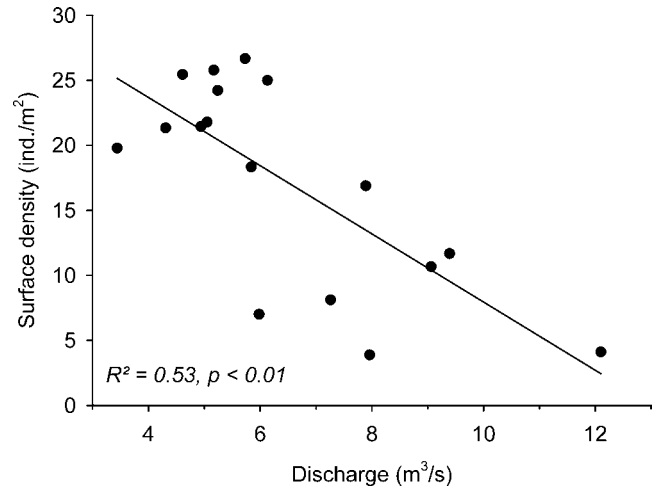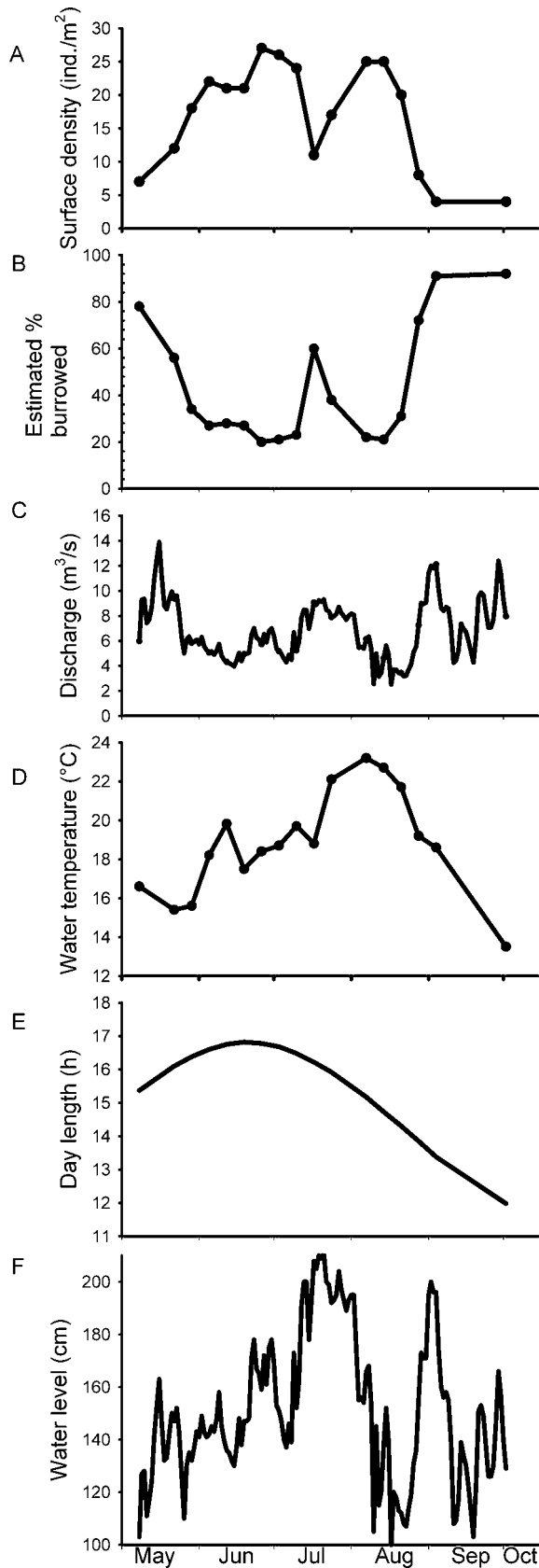
FIG. 4. Linear regression for surface density of unionid mussels and discharge ($y = -2.6x + 34$).

mussels with than without epizoic *D. polymorpha* (4 vs 9 ind.) were completely burrowed after 24 and 96 h. Infestation density was negatively correlated with burrowing depth (Spearman $r = 0.85$, $p < 0.01$), i.e., the lower the infestation density, the deeper unionid mussels were burrowed. Mean infestation density decreased from 16 ± 7 *D. polymorpha* ind./*U. tumidus* ind. at the beginning of the experiment to 9 ± 6 *D. polymorpha* ind./*U. tumidus* ind. at the end of the experiment.

Discussion

Vertical distribution and vertical movements

All mussels found in the 0–5-cm depth layer were defined as epibenthic, but juvenile mussels in this layer probably were burrowed rather than on the sediment surface. Juvenile unionid mussels remain burrowed in the sediment for the first 2 to 4 y of life (e.g., Hochwald and Bauer 1990). Adult mussels also burrow in the sediment (e.g., Amyot and Downing 1991). In particular, high percentages of burrowed adult mussels typically are found during winter months (Amyot and Downing 1991, Balfour and Smock 1995). The estimated percentage of burrowed mussels (juveniles and adults) in area A in the River Spree in the summer was

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FIG. 3. Density of unionid mussels on the sediment surface of area A (A), estimated percentage of burrowed mussels (B), discharge (C), water temperature (D), day length (E), and water level (F) during the study period. The percentage of burrowed mussels was estimated based on surface density and the total number of mussels in area A at the end of the study period.
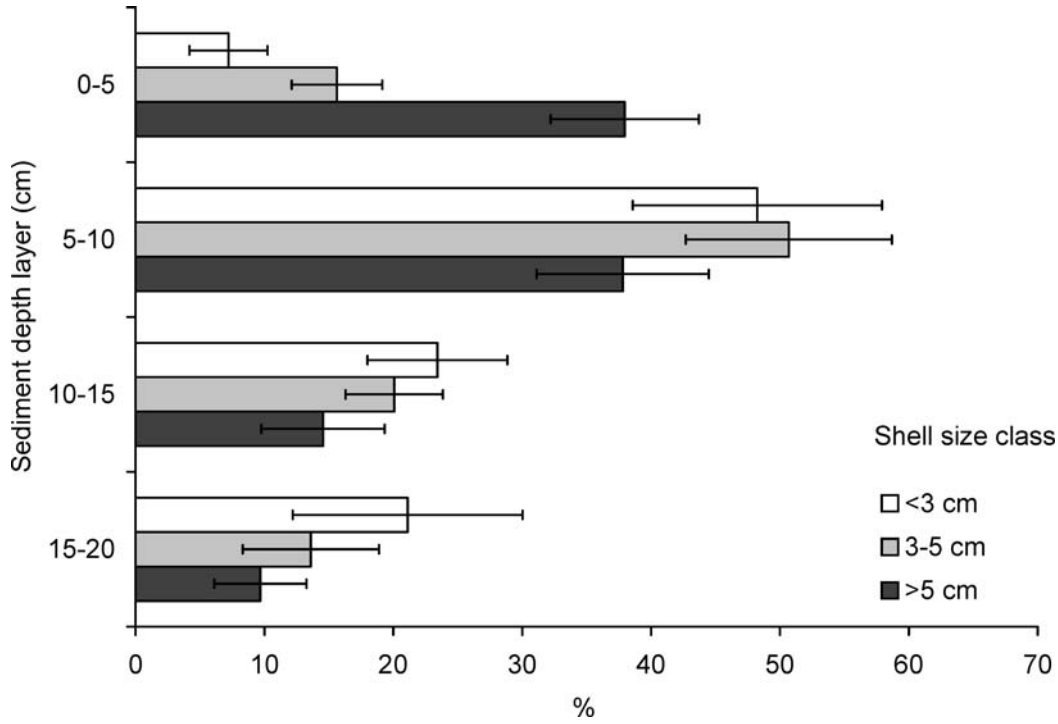
Fig. 5. Vertical distribution of *Unio tumidus* in several shell-length categories. Columns represent the mean (±1 SE, $n = 7$ quadrats) percentages of each size category (relative to the total number of individuals in the size category) found in each sediment depth layer.
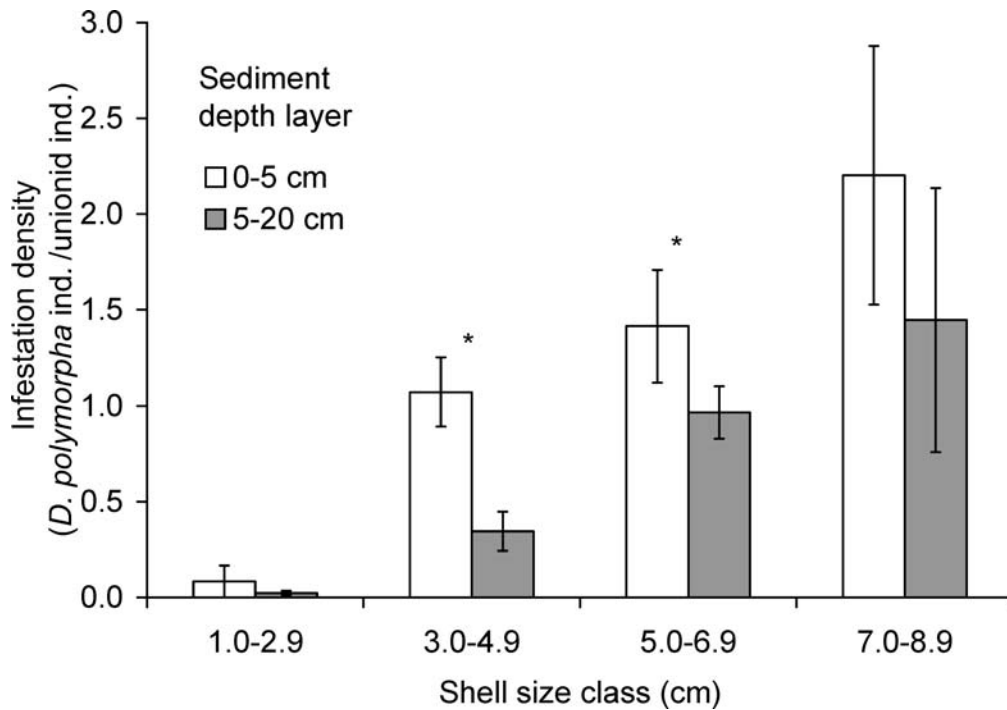

Fig. 6. Mean (±1 SE, $n = 7$) number of epizootic *Dreissena polymorpha/Unio tumidus* individual in shell-size categories in 2 sediment depth layers in the River Spree. * = significant differences between sediment depths (Wilcoxon test, $p < 0.05$, $n = 7$).

$43 \pm 26\%$, and the percentage of burrowed mussels found in area B was $74\% \pm 7\%$. The percentage of burrowed mussels in area B was surprisingly high, but agrees with earlier estimates of $\sim 80\%$ from a different section of the River Spree during the summer (Pusch et al. 2002). Thus, a major part of the unionid population was not visible at the sediment surface, and this result should be considered when planning or implementing conservation strategies (i.e., relocation efforts). Specifically, surveys may strongly underestimate actual population sizes and, thus, may fail to protect endangered or threatened species (cf. Smith et al. 2001).

No mussels were found >20 cm below the sediment surface. A hard layer of Fe(III)-hydroxide/oxyhydrate found in one 1-m^2 plot at ~ 10 cm sediment depth might have prevented mussels from burrowing deeper. However, the lower limit of the mussels' vertical distribution is probably a consequence of low dissolved O_2 (DO) concentration in deeper sediment layers. *Unio crassus* was found as much as 30 to 35 cm below the sediment surface in sediments with relatively high DO concentration (21–25% saturation 30 cm below the sediment surface) in 2 streams in northern Germany (Engel 1990). However, in the Müggelspree, DO decreases to $\sim 30\%$ saturation 7 cm below the sediment surface (Gücker and Fischer 2003) and to 7% saturation 20 to 30 cm below the sediment surface even in mid-channel sediments (ANS, personal observation). The low DO concentration at greater sediment depth in the Müggelspree may also explain the significantly lower infestation density on *U. tumidus* (of sizes 3.0–6.9 cm) in deeper (5–20 cm) sediment layers than in the upper sediment layer (0–5 cm). *Dreissena polymorpha* has poor tolerance for low DO concentrations (Nichols and Wilcox 1997). Other explanations for the lower infestation density of *D. polymorpha* on unionids that are deeper in the sediments are possible (Nichols and Wilcox 1997, Karatayev et al. 1997), but it seems clear that *D. polymorpha* does not strongly affect the unionid population (including their burrowing activity) in the River Spree.

The vertical distribution of unionid mussels differed with mussel size. Significantly more large (>5 cm) than small (<5 cm) individuals were found in the upper sediment layer (0–5-cm depth) in the river, and this pattern was reflected in the higher burrowing activity of small than large mussels in experiment 2. The laboratory results suggest that the differences in the vertical distribution between small and large mussels observed in the field were the result of variations in behavior rather than of passive burial by shifting sediments. The differences in vertical distribution between size classes also may reflect differences between the juvenile stage, which is characterized by permanent burial in sediment, and the adult stage, which is characterized by alternating periods of burrowing and surfacing related to reproduction.

The large number of mussels found in the sediment in early October in area A indicates that, at least at that time, most mussels that were not visible on the sediment surface had burrowed in the sediment rather than moved outside of the study area. This result is in agreement with other studies that have shown that unionid mussels emerge at the sediment surface in spring and burrow again before winter, with the specific timing influenced by local climate conditions (Amyot and Downing 1991, 1997, Balfour and Smock 1995). Vertical movements in the River Spree, as indicated by changes in mussel density on the sediment surface, were influenced by discharge, day length, and water temperature, which together explained 74% of the variation in mussel density. In other studies, water temperature (Amyot and Downing 1997), day length (Perles et al. 2003), or an inseparable combination of these 2 variables (Watters et al. 2001) were listed as the primary factor determining burrowing. Hence, the proximal control of vertical migration is not fully understood.

In the River Spree, water temperature per se was not a proximal factor controlling mussel behavior. However, changes in water temperature appeared to be important because the highest (early June) and the lowest (early September) surface densities of unionids were observed at similar water temperatures (18.2°C and 18.6°C, respectively). In contrast, discharge appeared to be the most important factor affecting burrowing activity. The sudden decrease in surface density associated with high discharge in July is not likely to be explained by any other variable considered in our study. Our observations support the hypothesis that mussels may circumvent dislodgement during extreme flows by burrowing deeper into the sediment (Di Maio and Corkum 1995), and our results suggest that flow velocity may be the dominant factor driving vertical movements of riverine unionid populations.

Horizontal movements

Horizontal movements were detected only if mussels moved from one subquadrat (25×25 cm) to another and, therefore, distance moved was underestimated by the spatial resolution of our observational method. The longest distance moved by a unionid mussel in our study was 226 cm/wk. Thus, unionid mussels are capable of moving long distances (i.e., ~ 40

body lengths) in a relatively short time, a result that agrees with the presence of long tracks that have been observed in the sandy sediment of the River Spree, especially during low water levels in summer (ANS, personal observation). Long tracks also have been observed in several lakes (maximum mean length of crawling tracks = 1.9 ± 2 m; Saarinen and Taskinen 2003). Nevertheless, the mean distance moved within the River Spree population was only 11 cm/wk, and many mussels did not move at all. We are not aware of any comparable data for river-dwelling mussels. However, *Elliptio complanata* moved ~5.6 cm/wk in a 1st-order stream (Balfour and Smock 1995) and 4.2 cm/wk in an oligotrophic lake (Amyot and Downing 1997), whereas *Anodonta* sp. moved between 15 and 45 cm/wk in Lake Zürich (Burla 1971; Table 2). Thus, the horizontal distances moved in the River Spree deviate little from the distances reported for different unionid species in other aquatic systems. However, there are evident differences in the horizontal movement distances among genera, especially when normalized by body length (Table 2). Collectively, these results indicate that unionids can move considerable distances (e.g., 2 body lengths/wk; our study) during the summer months. Little to no movement has been reported in winter (Burla 1971).

The unionid population in the River Spree showed a slight net shoreward movement. The shoreward movement does not appear to have been part of a seasonal horizontal migration, as has been found in other studies (Burla 1971, Engel 1990), because a change in the net direction of the mussels' movements was not noted until the end of the study period. The shoreward movement might have been related to a change in water level. At the beginning of the study (early May), the water level was extremely low. The mussels might have moved toward deeper mid-river areas and returned to the abandoned shallower areas as the water level rose until mid-July. Similar behavior has been observed in *Anodonta grandis* and other species, which migrate on the shore in response to seasonal changes in the water level to avoid prolonged emersion (Mentzen 1926, White [1979] as cited in McMahon 1991).

Mussels moved throughout our study, including during times without major changes in water levels. Such horizontal movements might be related to feeding, e.g., mussels might move to gain greater access to benthic food and to areas that have not been depleted of food. The movement itself could be part of the feeding mechanism (McMahon 1991), e.g., food could be ingested through a focused water current into the anterior portion of unionids, as suggested by Nichols et al. (2005). If a form of pedal feeding occurs

TABLE 2. Compilation of published data on the horizontal movement rates of unionid mussels. BL = body length.

Species	Location	Sampling interval	Mean distance moved (cm/wk)	Mean distance moved (BL/wk)a	Study area	Spatial resolution	No. of individuals	Study
Elliptio complanata	1st-order stream; Virginia, USA	1 mo	5.6[b]	0.4	76 1-m² plots	0.01 m²	84	Balfour and Smock 1995
E. complanata	Oligotrophic lake; Quebec, Canada	1–2 wk	4.2	0.3	40 m²	Exact position	527	Amyot and Downing 1997
Unio pictorum	Lowland river; River Spree, Germany	1–2 wk	13	1.4	9 m²	0.0625 m²	26	This study
U. tumidus	Lowland river; River Spree, Germany	1–2 wk	10	1.3	9 m²	0.0625 m²	428	This study
Anodonta sp.	Mesotrophic lake; Lake Zürich, Switzerland	1 mo	~15–45[c]	1.0–3.1[d]	100 m²	0.25 m²	89[e]	Burla 1971, Burla et al. 1974
Anodonta anatina	Lowland river; River Spree, Germany	1–2 wk	15	1.6	9 m²	0.0625 m²	90	This study

[a] Maximum body length found in literature was used because mean body lengths were not available for all studies
[b] Calculated from mean distance moved/y
[c] Estimated from fig. 9 in Burla (1971)
[d] Calculated based on mean maximum body length of *A. anatina* and *Anodonta cygnea*
[e] 55 of 144 individuals died during the study

in unionids in the River Spree, this mechanism could explain the highly erratic horizontal movements we observed. It might also explain how the unionids were able to meet their nutritional needs even at very low seston concentrations (Pusch et al. 2002).

Biological consequences of movement behaviors

The percentage of the population on the sediment surface increased and, therefore, the surface density of *U. tumidus* population increased during the reproductive period (June to mid-August). Aggregation, which can be caused by mussels moving closer together, can increase reproductive success (Burla et al. 1974, Amyot and Downing 1997). Similar changes in vertical distribution have been observed for unionids in other lotic and lentic systems (Balfour and Smock 1995, Watters et al. 2001).

Unionids in the River Spree burrowed and re-emerged several times during their surface stay in summer. In contrast, *Lampsilis siliquoidea* individuals did not return to the surface in the same year once they were completely burrowed in the sediment (Perles et al. 2003). The pattern of burrowing and return to the surface observed in the River Spree might indicate that separate surface stays are used for egg fertilization and glochidia release, or that multiple clutches of glochidia are produced, as was observed for *U. crassus* (Hochwald and Bauer 1990). Stream conditions might help to disperse sperm, so that the need for aggregation is lower in lotic systems than in lentic systems. During their reproductive period, *U. crassus* individuals were more frequently found in the middle of the stream, where higher flow velocities might have increased fertilization efficiency, than near the banks of the stream (Engel 1990).

Living burrowed within the sediment for long periods may reduce unionids' risks of adverse biological interactions. For example, unionids are preyed on by muskrat, mink, and otter, and empty shells of unionids can be occasionally observed at predator feeding sites (Diggins and Stewart 2000). In addition, *D. polymorpha* cannot colonize unionid shells when the unionids are burrowed, and experiment 2 showed that burrowing reduces the number of epizoic *D. polymorpha* on unionid individuals already infested. However, living burrowed for long periods during summer prevents intake of food resources that are suspended in the water column (Pusch et al. 2001).

In conclusion, we propose that movement behavior is an important adaptation of unionid mussel populations to the flow conditions in rivers. Movement enables unionids to react to the regular disturbances that occur as a result of changing flow conditions and water levels, and movement may help unionids to escape predators and control *D. polymorpha* infestation. Moreover, conditions in the sediment are as important as water quality for the biology and conservation of these organisms because unionids spend most of their lives in the sediment.

Acknowledgements

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