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Mortality, movement and behaviour of native mussels during a planned water-level drawdown in the Upper Mississippi River

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SUMMARY

1. Managers in the Upper Mississippi River (UMR) are using reductions in the River's water levels during summer to mimic historical water regimes and rehabilitate habitats for vegetation and other species. Concerns for the unintended effects of these actions on mussel populations threatened to halt these projects.

2. Our objective was to characterise the survival and movement of two mussel species in the UMR associated with a water level drawdown. During 2009 (no drawdown) and 2010 (0.3 m summer drawdown), we glued passive integrated transponder tags to 10 *Amblema plicata* and 10 *Lampsilis cardium* at each of 11 sites. Five sites were in shallow areas expected to be minimally affected by the drawdown (reference sites), and six sites were in shallow areas expected to be directly affected by the drawdown (treatment sites). About equal numbers of sites within both the reference and treatment areas had low and high slopes. Tagged mussels were randomly allocated across sites (within years).

3. Recovery of tagged mussels was >88% in 2009 and 2010. Mortality was similar and low (mean, *c.* 5% in both species) among reference sites but was variable and relatively high (means, *c.* 27% in *L. cardium* and *c.* 52% in *A. plicata*) among treatment sites; variation in mortality among treatment sites appeared related to slope.

4. The study found evidence of drawdown associations with net horizontal movements in *A. plicata* but not *L. cardium*. Weekly horizontal movements in both species were significantly correlated with changes in water elevation. We observed significant slope associations related to the drawdown for mortality and net horizontal movement in *A. plicata*.

5. There were strong species-specific differences in the effects of the drawdown on mortality, vertical movement and horizontal movement. These results suggest that *A. plicata* responded to the drawdown by vertical movement into the substratum, whereas *L. cardium* responded by horizontal movement to deeper water. No directionality of movement was observed in either species.

6. Collectively, these data suggest that drawdowns can influence the mortality, movement and behaviour of mussels in the UMR. However, more information on spatial and temporal distributions of mussels is needed to better understand the magnitude of these effects. Results from this study are being used by resource managers to better evaluate the effects of this management tool on native mussel assemblages.

Keywords: behaviour, mortality, movement, native mussels, water level

Introduction

Water level reductions (drawdowns) and subsequent reflooding have been used to enhance aquatic habitats in many managed freshwater systems (Abrahams, 2006). Resource managers use drawdowns in regulated reaches of the Upper Mississippi River (UMR) to mimic historical, pre-impoundment conditions during summer low flows, and rehabilitate habitats for vegetation and certain desirable fauna (Kenow & Lyon, 2009). However,

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drawdowns may have unintended adverse effects on native mussel populations. Recent systematic surveys of mussels in three large reaches of the UMR found considerable mussel populations including a small, but significant fraction that resides in shallow water (Newton *et al.*, 2011) – the area presumed to be most affected by a drawdown. Lacking definitive data on mortality in the shallow waters, scientists assumed that mortality in the dewatered zone was 100%. However, it is likely that some of these mussels are able to migrate out of the drawdown zone and reach deeper water (especially in highly sloped areas) and some may survive by burrowing into the substratum.

Little is known about the movement behaviour of mussels and its ecological significance, but movement behaviour of animals is often an important adaptation for responding to changing environmental conditions and disturbances and fulfilling life history requirements (Haag, 2012). For native mussels inhabiting rivers, movement behaviour might be particularly important for responding to disturbances that occur as a result of changing flow conditions and water levels. Some species of mussels may move seasonally into aggregations to enhance reproduction (Amyot & Downing, 1998; Watters, O'Dee & Chordas, 2001). Vertical movement or burrowing may help mussels escape predation, control zebra mussel infestation (Nichols & Wilcox, 1997; Burlakova, Karateyev & Padilla, 2000), avoid extreme temperatures and reduce dislodgement and transport to unsuitable conditions (Schwalb & Pusch, 2007).

Most of the prior research on movement patterns in mussels has been conducted in lakes (e.g. Amyot & Downing, 1997, 1998; Cyr, 2008, 2009), whereas natural movements of mussels in large rivers are largely unstudied. Schwalb & Pusch (2007) evaluated movement of three species in the River Spree in Germany and found mussels typically moved little horizontally (mean *c.* 11 cm week^{-1}) from May to October, and most (70%) were found completely buried in sediment. However, mussels in their study were restricted within 3 m × 3 m corrals, potentially altering natural movement behaviour. Until recently, studies of movement and survival of mussels in natural systems were constrained due to the difficulty of relocating individual mussels. However, Kurth *et al.* (2007) marked mussels with passive integrated transponder tags (PIT tags) in the Sebasticock River, River, ME, U.S.A., and successfully relocated them after 21 months. The recapture rate of mussels with PIT tags was twofold greater than the recapture rate using visual searches alone. Because PIT tag codes can be read at short distances, this technology provides an opportunity for repeated relocation and identification of individual mussels without disturbance.

Movement behaviour of mussels is often species-specific (Allen & Vaughn, 2009; Daniel & Brown, 2014). Differences in shell geometry among species might influence movement because shell form has been shown to be closely related to locomotor function (Watters, 1994). North American mussels have been categorised into five tribes that differ greatly in behaviour and life history, and some of these traits may influence movement of mussels. For example, prior research suggests that Lampsilini mussels are more active than Amblemini mussels (Haag *et al.*, 1993; Waller, Gutreuter & Rach, 1999). Also, Amblemini mussels close their valves tightly and are probably better at conserving water than Lampsilini mussels (WIDNR *et al.*, 2006). This might be one reason an observational study of mortality of native mussels associated with water level drawdown in Pool 5 of the UMR suggested that Amblemini mussels had higher survival rates than Lampsilini mussels (WIDNR *et al.*, 2006).

Movement of mussels may also be influenced by physicochemical variables. Movement of mussels in the River Spree was associated with discharge, water temperature, day length and water level (Schwalb & Pusch, 2007). The lower limit of a mussel's vertical distribution may be limited by low dissolved oxygen concentrations and sediment temperatures (Haag, 2012). Slope of the sediment surface may also be important in predicting survival of mussels as water levels recede during a drawdown (WIDNR *et al.*, 2006). Highly sloped surfaces might cue directional movement and provide easier access to deeper water than unsloped surfaces. Our objective was to characterise the effects of water level drawdown on the mortality, movement and behaviour of two common mussel species (*Amblema plicata* and *Lampsilis cardium*) across low and high slope sites in a regulated reach (Navigation Pool 6) of the UMR during 2009 and 2010. We hypothesised that: (i) mortality associated with the planned drawdown would be greater at treatment than at reference sites; (ii) mortality associated with the planned drawdown would be greater at sites with relatively low slope; (iii) *A. plicata* would respond to the drawdown by burrowing, whereas *L. cardium* would respond by horizontal movement; and (iv) mussels would respond to the drawdown by more directed horizontal movement to deep water at sites with high slopes than at sites with low slopes.

Methods

The UMR stretches from St. Paul, MN, to Cairo, IL (U.S.A.), and contains 29 locks and dams designed to facilitate commercial navigation. A navigation pool is defined as the reach between two consecutive locks and dams, and the pools are numbered from north to south. The year prior to the drawdown (2009), we set up a before-after-control-impact (BACI) experiment by placing tagged mussels at sites in the upper (reference) and lower (treatment) areas of the pool to evaluate the effects of the drawdown on mortality and movement of mussels. The drawdown in 2010 was predicted to result in a 0.3 m reduction in the lower pool, *c.* 0.2 m reduction in mid-pool and no appreciable reduction in the upper pool. Water levels were lowered *c.* 5 cm day^{-1} until the desired elevation was reached (this took *c.* 14 days) and then water levels remained low for 56 days. The drawdown exposed *c.* 73 ha in the lower part of the pool.

We chose six high slope and six low slope sites (Fig. 1) from a random selection of points along the shore in the channel border of Pool 6. Substratum at all sites was predominantly sand. Slope was estimated from the water depth at 2 m from the shoreline at the time of site selection – low slope sites measured 11–16 cm (6–8%); high slope sites measured 18–23 cm (9–12%). Sites 1, 4, 6, 9, 10 and 12 had low slopes; sites 2, 3, 5, 8 and 11 had high slopes. The reference sites (sites 8–12) were located just downstream from Lock and Dam 5a – an area that presumably would not be affected by the drawdown. One reference site was disturbed by barge fleeting during 2009 and was subsequently abandoned and the data discarded. The treatment sites (sites 1–6) were located just upstream of Lock and Dam 6 – an area that presumably would be most affected by the drawdown. All sites except site 1 contained resident mussels. At each site in 2009, four 12.5-mm PVC stakes were driven into the sediment to establish reference points at the corners of a 3 m × 2 m experimental grid (Fig. 1). In 2010, the experimental grid was enlarged to 4 m × 2 m to reduce trilateration errors at larger distances.

Because movement of mussels may be influenced by sediment temperatures, we continuously recorded temperature by placing three iButtons® (Alpha Mach Inc., Mont-St-Hilaire, QC, Canada) on wooden stakes near each of the four PVC stakes. These recorded hourly temperatures at sediment depths of 5, 10 and 20 cm from 10 June until 6 November, 2009. Each iButton® was coated with rubber sealant (tool handle dip) and then vacuum sealed in plastic for waterproofing. To measure water temperatures near the sediment–water interface, we also placed an iButton® at stake 2 at sites 1, 4, 6, 9 and 12. Because most of the mussels moved out of the experimental grid within about 3 weeks in 2009, the sediment temperature data may not be representative of where the mussels were residing. Thus, in 2010, the iButtons® were placed in a line perpendicular to the experiment grid at distances that approximated the spatial array of mussels in 2009. For example, iButtons® at site 3 were placed at 0, 2.5, 5.0 and 7.5 m from the experimental grid. To compare between years, one iButton® was placed in a similar location at each site in 2009 and 2010. Unfortunately, technical errors led to the loss of hourly temperature data from three reference sites in 2010.

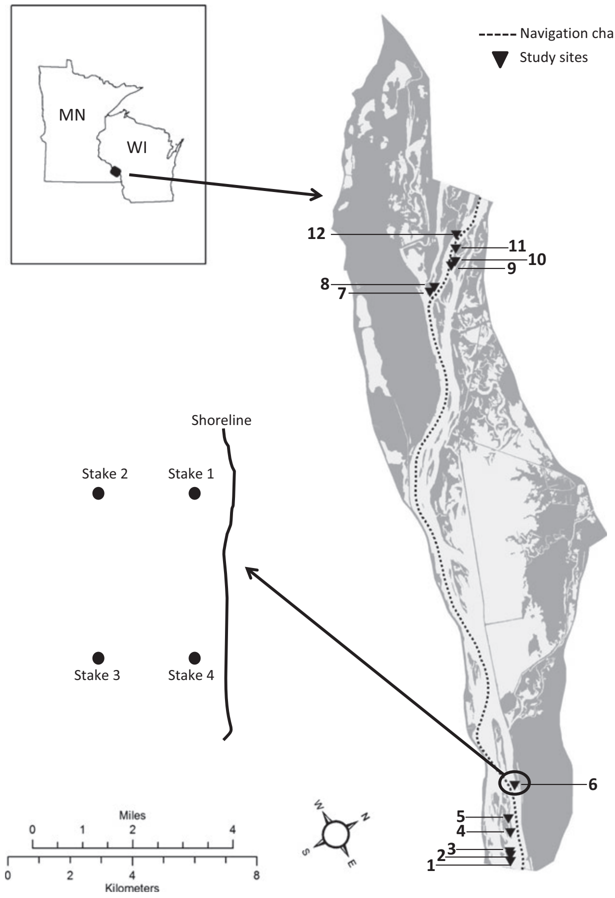

Fig. 1 Map of Pool 6 of the Upper Mississippi River (U.S.A.) showing locations of 12 sites where the movement of two species of native mussels was followed during 2009 and 2010. The inset shows the experimental grid (3 m × 2 m in 2009, 4 m × 2 m in 2010) used to identify sites. Stake 1 was placed upstream on the shoreline, and stake 4 was placed downstream on the shoreline. Site 7 was abandoned in mid-2009 due to barge fleeting.

We obtained 110 *A. plicata* and 110 *L. cardium* mussels from several sites in Pool 6 in June of 2009 and 2010; mussels were pooled and randomly distributed among study sites. Shell length, sex (*L. cardium* only) and gravidity (*L. cardium* only) were measured. Mean initial lengths of mussels for both species were similar between reference and treatment sites (77.6 and 78.6 mm in *A. plicata* and 109.6 and 110.0 mm in *L. cardium*, respectively) across years. In both years, *c.* 60% of the *L. cardium* were male. The proportions of *L. cardium* females that were gravid at the start of the study were 0.60 in 2009 and 0.25 in 2010. Mussel shells were scrubbed to remove existing zebra mussels. A 20- (2009) or 23- (2010) mm PIT tag (Biomark, Boise, ID, U.S.A.) was attached near the umbo of each mussel using superglue. One end of a 36-cm piece of buoyant fishing line was glued near the posterior edge of each shell to facilitate relocation and to estimate vertical depth of buried mussels. It took *c.* 4 min to process each mussel, from scrubbing to placement in the experimental grid. Ten *A. plicata* and 10 *L. cardium* were placed at random locations in the 0–0.3 m depth contour of each experimental grid in June of each year.

Mussels were located about weekly from June to November 2009 and from June to September 2010. A PIT tag reader with an 18-cm loop antenna was used to find the general area of each mussel, and then, a view bucket (*c.* 20 cm × 51 cm PVC pipe with clear Plexiglas attached to one end) was used to visually confirm the precise location of each mussel. Precise location of some mussels using the view bucket was not possible (e.g. due to deep water), so in these cases, mussel position was estimated solely based on detection with the PIT tag reader. However, location errors in those cases would still be expected to be modest because preliminary experiments showed that PIT tags could be relocated within <30 cm using the PIT tag reader alone (and to a depth of at least 20 cm). Once a mussel was found, a PVC stake was temporarily placed in the substratum to mark its position. Each time a mussel was found we measured (i) its horizontal distance from the three reference PVC stakes marking the site with a tape measure, (ii) water depth and (iii) its burial depth estimated from the length of exposed fishing line. When possible, mussels were observed with the view bucket to ascertain their status as alive or dead based on siphoning activity (alive) or if the valves were far apart (dead). Mussels were not removed from the substratum for inspection during the course of the experiment because handling might influence movement. However, in October 2009 and September 2010, survival of all mussels was evaluated by removing them from the substratum for examination. Any mussels that were alive after the last tracking date were replaced into the river.

Water temperature and dissolved oxygen (DO) concentrations were measured at mid-water column on the river and shore side of the experimental grid on each sampling day. In September 2009, we also obtained six surficial sediment samples at each site with an Ekman dredge in the area where mussels were residing to estimate moisture content (APHA, 1995), organic content (APHA, 1995), bulk density (Hakanson & Jansson, 1983) and particle size (Guy, 1977). Sediment characteristics were generally similar among sites. Percentage moisture ranged from 19 to 27%, bulk density ranged from 1.4 to 1.6 g cm^{-3}, and % organic content ranged from 0.4 to 0.9% among sites. The median particle size (Steuer, Newton & Zigler, 2008) ranged from 0.2 mm at site 6 to 0.4 mm at site 8, which indicates all sites were predominately sand.

For each site and year, mortality was calculated as the number of mussels found to be dead at the end of each year divided by the corresponding number of non-missing (live or dead) mussels at the end of the year; we address whether the probability of a mussel being missing was a function of the study design in the results. Mussel location and horizontal movement was analysed using ArcGIS (ESRI, Redlands, CA, U.S.A.) using an artificial coordinate system with the downstream, west-most stake (stake 3; Fig. 1) referenced as the origin (0 east, 0 north). The position of each mussel was estimated by trilateration using measurements to the three reference stakes. Position errors due to field measurements were evaluated based on trilateration error surfaces. We estimated that 80–86% of the locations had error polygons of ≤300 cm^2 (i.e. equivalent to *c.* 10-cm radius circle) in 2009 and 2010 and 96–98% were ≤600 cm^2 (i.e. equivalent to *c.* 20-cm radius circle). The distance a mussel moved was calculated in two ways. Net movement was calculated as the straight line distance between a mussels' initial and final position for each year for individuals found alive at the end of the year, had moved >1 m over this interval and were found on consecutive weeks. Weekly movement was calculated for those mussels found alive on consecutive weeks. The net angle of movement, an indication of whether mussels moved upstream or downstream, was estimated by calculating the angle between a mussels' initial and final position for each year for individuals found alive at the end of the year. Note that, for both net movement and net angle of movement, 'initial' position was defined as the position at week 2 because the first (placement) location was artificial and handling might have altered mussel behaviours. Evaluation of short-term behaviour of mussels was beyond the scope of the study, but we assessed overall patterns in weekly movement and the burrowing behaviour (minimum depth during each year) by examining graphical plots.

We evaluated drawdown associations with mortality, net distance moved and net angle moved using a BACI experimental design; 2009 was treated as the 'before' year and 2010 the 'after' year; the upper pool was treated as the 'control (reference)' area and the lower pool the 'impact (treatment)' area. Mortality was modelled using logistic regression; likelihood and AICc values (small sample variant of the Akaike information criterion; Hurvich & Tsai, 1989) reflected explicit adjustment for site–year interaction effects, while quantitative estimates of BACI and slope associations represented averages over those site–year effects. Variation at the site scale in excess of that assumed under a binomial assumption (given adjustment for site × year effects) was estimated as essentially zero for both species and so was ignored. Inferences on drawdown associations were evaluated by comparing models with and without a year × reference–treatment interaction term using the AICc. Lower AICc values indicate greater support for the given models (Burnham & Anderson, 2002). In the context of this study, the odds ratio represents the odds of dying as a result of the drawdown at a treatment site, relative to the odds of dying as a result of the drawdown at a reference site. BACI associations were adjusted for slope associations (averaged over sites and years) and vice versa. Missing data patterns were not clearly associated with the BACI component of the study design. This conclusion was based on evaluating BACI effects on counts of missing mussels (AICc values were >3 units larger for both species when missing data were modelled as a function of the full BACI design), as well as on visual inspection of missing data patterns. Accordingly, we presumed the missing mortality data were missing at random. The movement model for *A. plicata* incorporated an indicator term that adjusted for an unusually large movement by one mussel. This mussel moved 25 m, or 150% more than any other mussel was estimated to have moved. Adjusting for this outlier did not qualitatively change model inferences. All models of mortality data were fitted using SAS' generalised linear mixed modelling procedure (PROC GLIMMIX; SAS, 2009).

The analysis of net angle and net distance data followed that of the mortality data with the following exceptions. First, angular and distance data were modelled using linear regression (site and site × year effects were treated as random). Second, slope and BACI terms were allowed to fully cross. Akaike information criterion and −2 log likelihood values were estimated under full maximum likelihood, while point estimates with confidence intervals were estimated under restricted maximum likelihood (REML); we used REML because it provides better variance component estimation under small sample sizes (McCullagh & Nelder, 1989). Models of angles and distances moved were fitted using SAS' generalised linear mixed modelling procedure (PROC GLIMMIX; SAS Institute, 2009).

Linear models are not generally recommended for the analysis of angular data (Fisher, 1993). Consider, for example, that 180° represents a poor estimate of the mean of 2° and 358°. Despite this, we used linear models for analysis of the angular data because a circular statistical method has not, to our knowledge, been developed for a two-factor-with-interaction study design. However, the use of linear models appeared reasonable for the current study's angular data because angles were concentrated not only within site × year clusters (mean and median resultant radians, r, for the clusters were 0.84 and 0.87, respectively, with smallest $r = 0.63$) but also across clusters (range of the sample cluster means = 1.5 r). For statistical models purposes, we avoided angles near 0° by rotating angles such that their means centred near 180° (note that our graphical displays make use of non-transformed angular data). We evaluated the analysis of angular data under linear rather than circular assumptions by performing a one-way ANOVA under both circular and linear assumptions (using the circanova SAS macro available at http://statweb.calpoly.edu/ulund/ and SAS' linear modelling procedure, respectively; SAS Institute, 2009). The results suggested comparable conclusions from the two methods ($F_{3,167} = 0.37$ and $F_{3,165} = 0.54$, $P = 0.77$ and $P = 0.66$, for *A. plicata* and *L. cardium,* respectively).

Results

Adequate flows were maintained during the Pool 6 drawdown such that there was little evidence of an effect of the drawdown on mean water temperature or DO (Table 1; not shown is that weekly measures of DO and water temperature were similar among sites). However, the complete temperature data sets from eight sites in 2009 and 2010 suggest a strong effect of the drawdown on substratum temperature. At treatment site 6, for example, average nearshore substratum temperatures during the drawdown appeared only slightly elevated relative to those in 2009 (Fig. 2d,e). However, daily ranges were much higher in 2010 than in 2009. As expected, mean substratum temperature and its

Table 1 Mean dissolved oxygen concentration and temperature measured at mid-water column on the nearshore and offshore side of the experimental grid at 11 sites in the Upper Mississippi River (U.S.A.) during 14 June to 18 September in 2009 (no drawdown) and 2010 (0.3 m summer drawdown); ranges in parentheses. Sites 1–6 were treatment sites and sites 8–12 were reference sites

	Dissolved oxygen (mg L^{-1})		Temperature (°C)	
Site	2009	2010	2009	2010
1	9.0 (2.3, 20.0)	8.0 (3.9, 20.0)	23.5 (20.0, 28.0)	25.5 (15.6, 35.5)
2	7.7 (5.3, 9.9)	6.9 (5.6, 8.7)	24.1 (21.5, 27.5)	24.6 (20.7, 27.4)
3	8.1 (5.7, 10.6)	7.4 (6.2, 10.7)	23.8 (21.0, 26.0)	24.7 (19.3, 27.2)
4	13.0 (4.8, 18.0)	8.9 (6.9, 11.5)	25.3 (21.0, 29.0)	25.0 (21.1, 29.1)
5	8.0 (4.8, 10.7)	7.7 (6.0, 9.0)	23.3 (21.5, 25.0)	24.8 (19.3, 28.5)
6	7.9 (5.0, 13.4)	6.5 (4.1, 8.4)	23.2 (21.0, 25.0)	24.0 (18.4, 26.5)
8	8.1 (6.2, 10.4)	7.1 (6.0, 9.1)	23.6 (20.5, 26.5)	24.3 (20.0, 29.2)
9	9.5 (6.8, 11.4)	7.3 (5.7, 9.9)	23.9 (21.0, 27.0)	24.9 (21.6, 30.9)
10	9.3 (7.2, 14.0)	7.3 (5.3, 9.3)	24.3 (21.0, 27.3)	24.8 (21.5, 28.6)
11	7.3 (5.6, 9.0)	7.2 (5.5, 8.8)	23.6 (22.0, 26.0)	24.6 (21.3, 28.0)
12	7.7 (5.3, 9.4)	6.8 (4.8, 8.5)	24.1 (21.5, 26.5)	24.0 (20.0, 27.5)
Overall mean	8.7	7.4	23.9	24.7

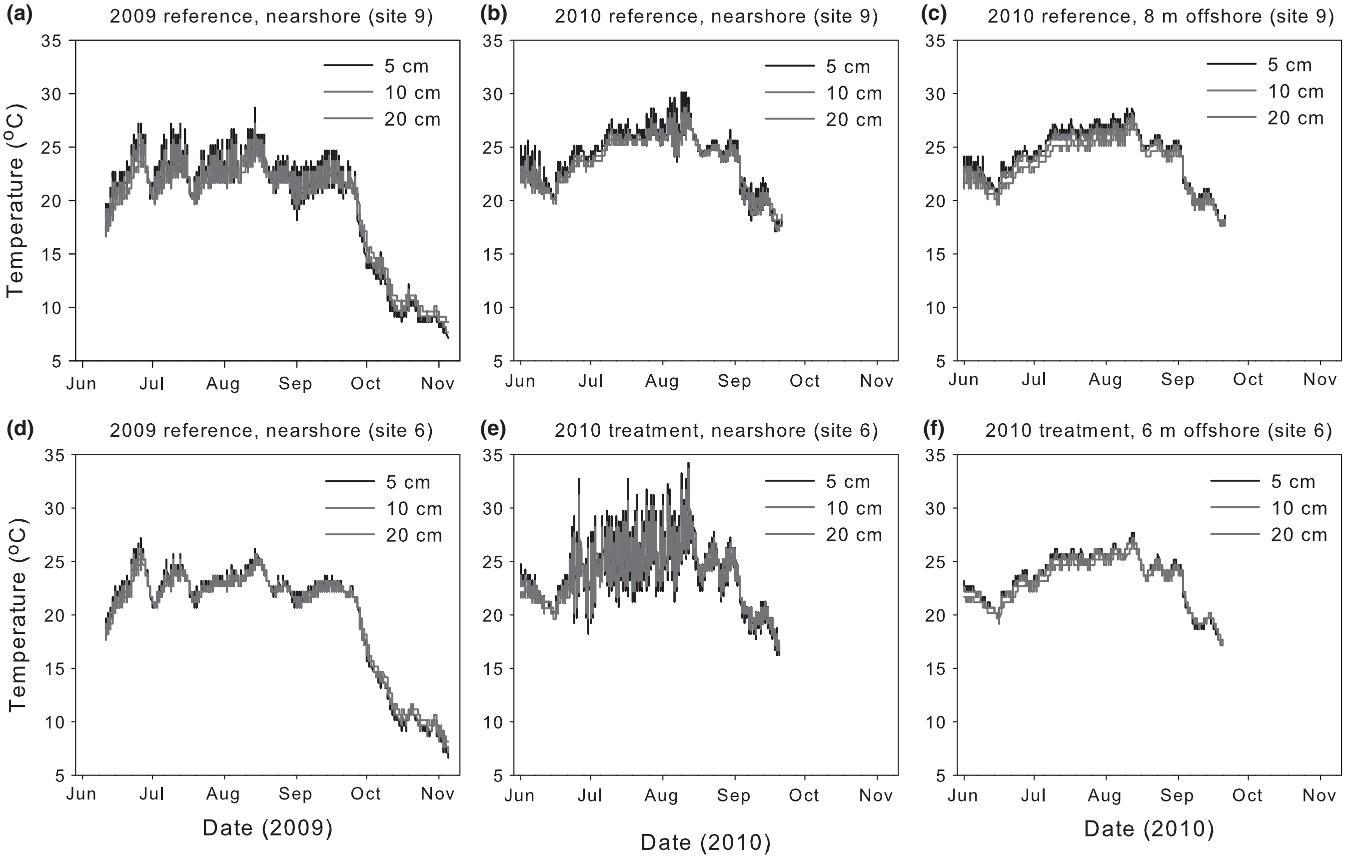

Fig. 2 Substratum temperature at 5, 10 and 20 cm below the sediment–water interface at one reference (site 9) and one treatment (site 6) site during 2009 (no drawdown) and 2010 (0.3 m summer drawdown).

variation was much lower 6–8 m offshore (e.g. Fig. 2c,f). In contrast, nearshore substratum temperature at reference site 9 was slightly lower and less variable in 2010 (Fig. 2b) than in 2009 (Fig. 2a), presumably due to the high water levels experienced in 2010.

We did not measure the width of the dewatered zone at each site as the drawdown was occurring. However, we estimated these zones after the fact by overlaying estimates of the dewatered area (obtained from aerial photography) on light detection and ranging data obtained on 27 July 2010. Estimates of the width of the dewatered area were 5 m at site 6, 9 m at site 1 and 16 m at site 4; the width of the dewatered area at all other sites was zero. These data suggest that of the six treatment sites, sites 1 and 4 appeared to be most affected by the drawdown, which concurred with qualitative field observations during the study. Thus, sites 1 and 4 were shallower than the other treatment sites for a considerable distance from shore, and water receded quickly from these sites and left large areas of exposed substratum.

The total number of observations of tagged mussels was 6179 during the study. In 2009, each site was visited *c.* 18 times from June to November. In 2010, the reference sites were visited eight times and the treatment sites were visited *c.* 13 times from June to September. The number of visits to the reference sites in 2010 was relatively low because high water in the upper portion of the pool prevented wading and relocation of mussels during mid to late summer. Of the 440 tagged mussels, 417 were recovered either alive or dead. The 23 unrecovered mussels (5%) were roughly equally distributed among species, years, treatments and slopes. Specifically, recovery averaged 98% in *A. plicata* and 94% in *L. cardium* in 2009 and 93% in *A. plicata* and 95% in *L. cardium* in 2010. We only encountered two broken PIT tags during the course of the study.

Drawdown associations with mussel mortality were unclear. Estimates of odds ratios were larger for both species in the treatment area than in the reference area, suggesting a negative drawdown effect (Table 2). However, only the confidence interval (CI) for the questionably large estimate for *A. plicata* in the treatment area excluded the null value of one, suggesting weak support for drawdown-associated mortality. Of greater relevance for this study are the ratios of the reference and treatment odds ratios. Estimates of these ratios were, as expected, <1, indicating support for drawdown-related mortality; however, because CIs included the null value of one, this support is relatively weak. These patterns are mirrored in estimates of mortality proportions (Fig. 3) and model statistics. Specifically, models that assumed a drawdown-mortality association ('full model', Table 3) had no better (*A. plicata*) to slightly less (*L. cardium*) support based on AICc values, than did

Table 2 Estimated odds of mortality for two mussel species (*Amblema plicata* and *Lampsilis cardium*) at reference and treatment sites and across low and high slope sites in 2010 (0.3 m summer drawdown), relative to those in 2009 (no drawdown), in Pool 6 of the Upper Mississippi River (U.S.A.). Data limitations precluded direct estimation of treatment*year*slope effects

Species	Site type	Odd ratio estimate (95% confidence interval)*
Averaged over low and high slope sites		
A. plicata	Reference	2.00 (0.05–87.64)
A. plicata	Treatment	112.39 (3.85–3278.82)
A. plicata	Reference : treatment	0.02 (0.00–2.83)
L. cardium	Reference	1.87 (0.19–18.18)
L. cardium	Treatment	3.92 (0.70–22.00)
L. cardium	Reference : treatment	0.48 (0.03–8.26)
Averaged over reference and treatment sites and years		
A. plicata	High slope	0.07 (0.01–0.55)
L. cardium	High slope	0.32 (0.07–1.43)

*See Methods section for a study-specific interpretation of odds ratios.

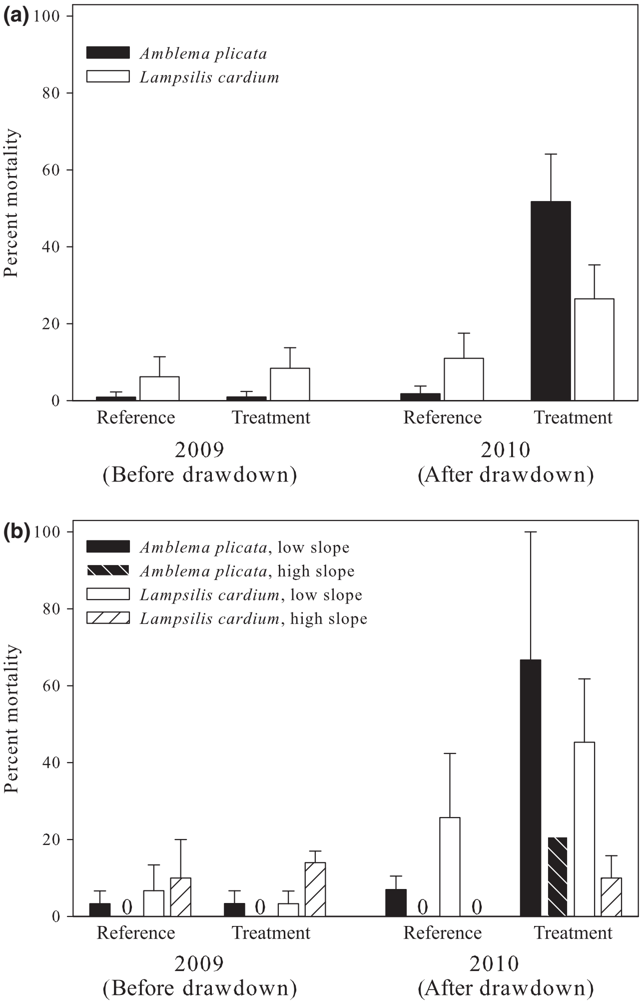

Fig. 3 Mean percentage mortality ± 1 SE in two species of native mussels during a water level reduction experiment in Pool 6 of the Upper Mississippi River (U.S.A.) in 2009 and 2010. Data (a) summarised across treatments (*n* = 5 sites for 2009 & 2010 reference; *n* = 6 sites for 2009 reference and 2010 treatment); (b) summarised across treatments and slope (*n* = 3 sites except for high slope reference where *n* = 2 sites).

Table 3 Model criteria (small sample variant, Akaike's information criterion, AICc) from candidate models of mortality, net distance moved and net angle moved by *Amblema plicata* and *Lampsilis cardium* during a planned water level drawdown in Pool 6 of the Upper Mississippi River (U.S.A.). An asterisk suggests support for drawdown or slope associations (based on a difference of >2 AICc units when the assumption of the given association is removed from the full model)

	A. plicata			*L. cardium*		
Model description	−2 log likelihood	*k*	AICc	−2 log likelihood	*k*	AICc
Mortality						
Full	40.2	6	57.8	63.2	6	80.8
Full, less drawdown association	43.3	5	57.1	63.5	5	77.2
Full, less slope association	46.8	5	60.5*	65.4	5	79.2
Intercept only	56.2	2	60.9	69.0	2	73.6
Net distance moved						
Full	631.3	13	659.6	778.7	13	807.1
Full, less drawdown association	641.7	10	663.1*	780.5	12	806.5
Full, less slope association	655.5	8	672.4*	786.9	10	808.3
Intercept only	663.8	5	674.1	790.7	7	805.4
Net angle moved						
Full	1694.6	12	1720.6	1722.8	11	1746.5
Full, less drawdown association	1697.0	10	1718.3	1722.9	9	1742.0
Full, less slope association	1699.1	8	1716.0	1725.3	7	1739.9
Intercept only	1700.5	5	1710.8	1727.5	4	1735.7

k varies by outcome because the number of variance components (including measurement-scale components, which might differ by before–after × reference–treatment combination) varied by outcome. The full models contain before–after, reference–treatment, before–after × reference–treatment interaction, and one or more slope terms. The full, less drawdown association models assumed an absence of drawdown effects by omitting before-after × reference–treatment interaction term from the full model.

those that ignored that assumption ('full, less drawdown association'). Higher slopes were not clearly associated with *L. cardium* mortality, but were associated with decreased mortality for *A. plicata* (averaged over year × reference–treatment area combinations; Tables 2–3, Fig. 3). In fact, the point estimate of the odds of an *A. plicata* dying at high slope sites was 93% lower than the corresponding odds at low slope sites (i.e. 100 (1 − 0.07)%; Table 2).

Across both years, *c.* 18% of the mussels were completely buried in river sediments. Interestingly, 37 mussels burrowed at least 0.5 cm in both years (12 *A. plicata* and 25 *L. cardium* in 2009 and 27 *A. plicata* and 10 *L. cardium* in 2010). In 2009, 83% of the *A. plicata* and 100% of the *L. cardium* had buried ≤5 cm. In 2010, 78% of the *A. plicata* and 50% of the *L. cardium* had buried ≤5 cm. However, there appeared to be a species-specific pattern to the vertical movement of mussels. During 2009, most (68%) of the buried mussels were *L. cardium*, but in 2010, most (73%) of the buried mussels were *A. plicata*. The maximum a mussel buried was 6 cm in 2009 (*A. plicata*) and 25 cm in 2010 (*L. cardium*).

Drawdown associations with net horizontal movement were evident for *A. plicata*, but not for *L. cardium*. Differences in mean movement across years did not differ significantly among reference and treatment areas for *L. cardium* (mean = −0.3, CI = −2.7 to 2.0 m, Fig. 4a). By contrast, the corresponding differences in mean movement by *A. plicata* were smaller in the reference area (by 2.4 m, CI = 0.3 to 4.4 m, Fig. 4a). These inferences are also seen in the AICc model statistics (i.e. the AICc statistic was smaller – 'better' – by 3.5 units for *A. plicata* but nearly identical for *L. cardium* when drawdown associations were modelled; middle panel, Table 3). Slope associations with movement were also seen for *A. plicata* but not for *L. cardium* (i.e. when slope associations were modelled, AICc values were smaller by 12.8 units for *A. plicata* and by only 1.2 units for *L. cardium*; Table 3). Mean movements by *A. plicata* and possibly by *L. cardium*, averaged over years and reference–treatment areas, appeared shorter on high slopes (1.3 m, 0.2 to 2.5 m and 1.4 m, −0.9 to 3.7 m, respectively; Fig. 4b). The estimated mean movement difference for *A. plicata* changed only modestly when adjusted for the outlier mentioned in the methods (i.e. to 1.1 m, −0.3 to 2.4 m).

Mean horizontal weekly movement was variable between years and species, and between low and high slope sites. In 2009, the mean weekly horizontal movement was similar between species, but was highly variable between low and high slope sites. Mean movement per mussel varied from 0 to 12 m week^{-1} at the low slope sites, but only from 0 to 5 m week^{-1} at the high slope sites in 2009 (Fig. 5). In 2010, the range of mussel movement was greater at the treatment sites (0–

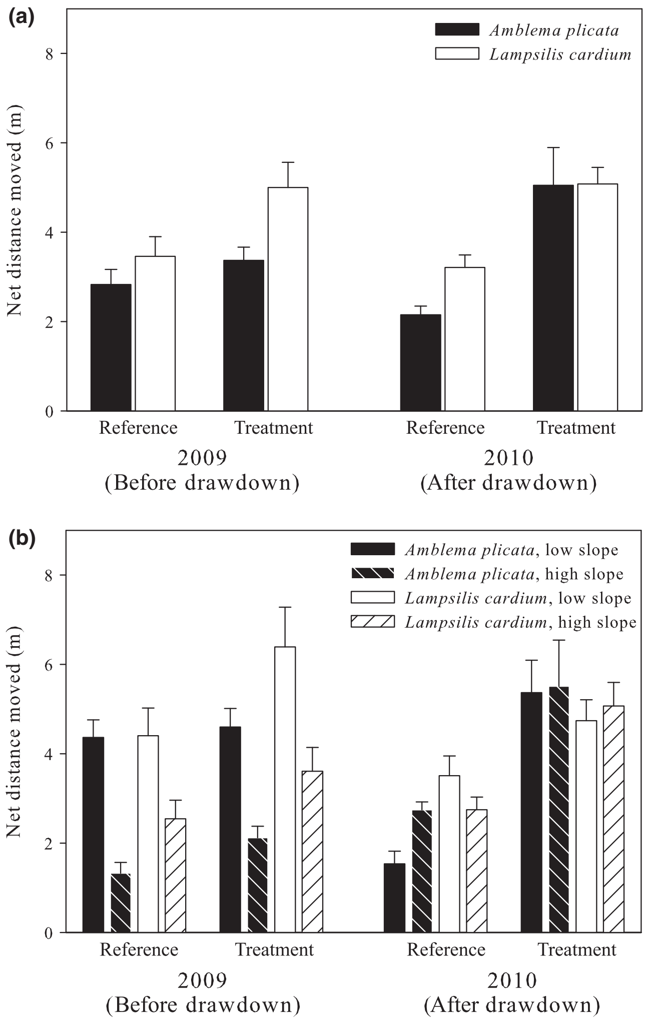

Fig. 4 Estimated net movement (m) ± 1 SE in two species of native mussels during a planned water level reduction in Pool 6 of the Upper Mississippi River (U.S.A.) in 2009 and 2010. Data (a) summarised across treatments (n = 5 sites for 2009 & 2010 reference; n = 6 sites for 2009 reference and 2010 treatment); (b) summarised across treatments and slope (n = 3 sites except for high slope reference where n = 2 sites).

15 m week^{-1}) than at the reference sites (0–4 m week^{-1}) and the magnitude of this association was greater for *L. cardium*. There also appeared to be a temporal pattern to movement, although this was not formally evaluated. For example, these data suggest a larger range of movement in June at all sites, but especially in low slope areas. This could be due to the effects of artificially placing mussels in shallow water at the beginning of the study, but the higher range of movement continues for a significant period of time (into July) and could be related to natural movement patterns. Also, there is substantial evidence of higher movement for both species at treatment sites, compared to reference sites, during the onset of the drawdown (Fig. 5) in 2010; the range of movement was especially high at low slope sites. By mid-July 2010, movement at treatment sites declined to levels similar to those observed in 2009, but movement at reference sites could not be evaluated due to high water. The timing of movement was coincident with the initiation of the drawdown. Patterns in mussel movement appeared associated with the change in water elevation in 2010 when elevations varied substantially during the summer, but not in 2009 when elevation changed little (Fig. 6).

Most mussels, regardless of species, slope or treatment, moved offshore into deeper water at net angles of *c.* 100° from shoreline. Net angle of horizontal movement from reference sites in 2009 and 2010 varied from 88 to 112° in *A. plicata* and from 97 to 123° in *L. cardium* (Fig. 7a). The drawdown did not clearly influence the angle of movement in either species. Specifically, AICc values were larger by 2.3 units (*A. plicata*) and 4.5 units (*L. cardium*) when a drawdown association on angle of movement was modelled (lower panel, Table 3). The mean difference in angular movement related to the drawdown would correspond to mean movement differences in 2010 relative to 2009 at the treatment sites less the corresponding difference across reference sites. Estimates of these differences were not clearly different for either *A. plicata* (9 m, −24 to 43 m) or *L. cardium* (2 m, −24 to 28 m). Slope was also not clearly associated with net angular movement for either species; mean differences between angles of movement on high and low slope sites appeared biologically unimportant for both *A. plicata* (3°, −14 to 20°) and *L. cardium* (−8°, −33 to 17°). Further, data yielded greater support for movement models that ignored slope (i.e. AICc values were larger by 4.6 units for *A. plicata* and 6.6 units for *L. cardium* when slope terms were modelled, Table 3).

Discussion

Rivers and other flowing waters have water levels that naturally fluctuate based on short-term, seasonal, annual or longer hydrologic patterns. Regulation by dams and other structures can dramatically alter patterns in discharge and water level. Flooding is largely uncontrolled in the UMR, but regulation has effectively eliminated the historical pattern of lowered water levels during summer (Gaugush & Johnson, 2008). Drawdowns are intended to partly restore summer patterns of low water levels, but commercial traffic and other uses presently constrain drawdowns to modest levels (typically <0.5 m at the downstream dam) compared to historical condi-

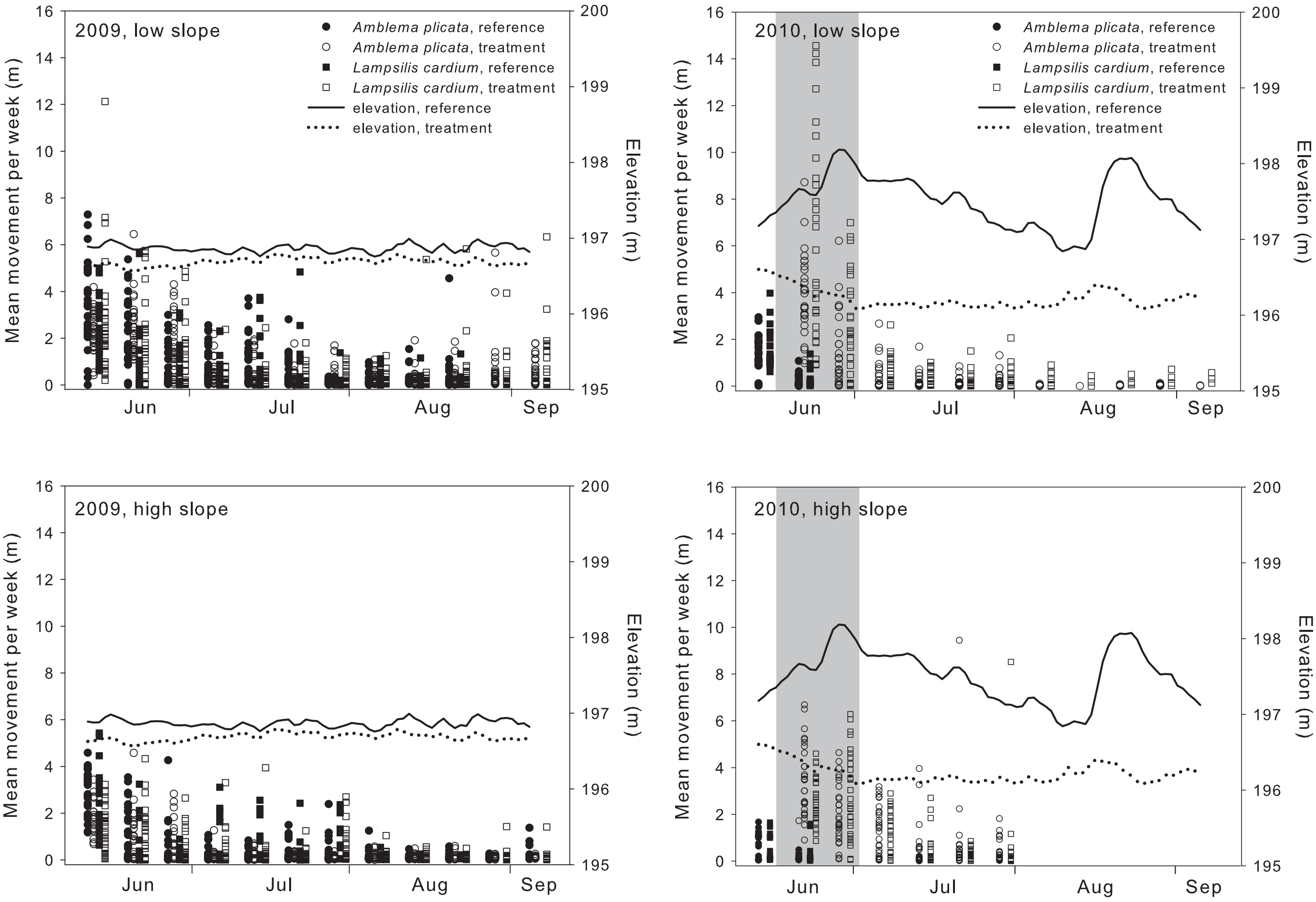

Fig. 5 Relationship between water elevation and weekly movement of two species of native mussels across low and high slope sites during a water level reduction in Pool 6 of the Upper Mississippi River (U.S.A.) during 2009 (no drawdown) and 2010 (0.3 m summer drawdown). The drawdown was initiated on 18 June 2010 and the full 0.3 m water level reduction was achieved on 1 July 2010 (denoted by grey shading). Note data at reference sites are missing after mid-June 2010 because high water prevented observation of mussels at those sites and there is no data after July in the 2010 high slope graphic because there were no mussels found alive on consecutive weeks.

tions. Although there have been numerous reports of the effects of droughts on native mussel assemblages (e.g. Golladay *et al.*, 2004; Haag & Warren, 2008; Allen *et al.*, 2013), a drawdown (as defined on the UMR) is more akin to summer low flow conditions than to drought. Unlike droughts, drawdowns in the UMR typically maintain adequate flows, have minimal effects on water quality and dewater a minor proportion of the aquatic area.

Although the average mortality at treatment sites was substantial (27% in *L. cardium*, 52% in *A. plicata*) and the odds ratio at treatment sites was suggestive of a drawdown effect, our results did not clearly associate the drawdown with mortality of either species. This ambiguity was probably related to the large variation in mortality among sites within the reference or treatment groups. For example, the mean percentage mortality in *A. plicata* at the treatment sites in 2010 was 52% but varied from 0 to 100%. Interestingly, sites with 100% mortality (sites 1 and 4) had the largest estimated dewatered area. Site 1 also had no mussels at the start of the study which may explain the high mortality. In hindsight, our decision to characterise site-to-site variation in topography by slope estimates in only the shallowest area (0–2 m from shore) was inadequate; most mussels quickly vacated this area. However, a companion study showed a strong effect of the Pool 6 drawdown on estimated mortality of *A. plicata* and Lampsilines (primarily *L. cardium*) restricted to 0.25 m^2 corrals. Total mortality over the 9 week drawdown in dewatered corrals was 38% in *A. plicata* and 82% in Lampsilines, compared to <3% mortality in reference corrals in deeper water (MNDNR, 2011). The apparent differences in results in the treatment area between the two studies suggest the importance of species-specific behaviour, especially the protective effect of movement into deeper water.

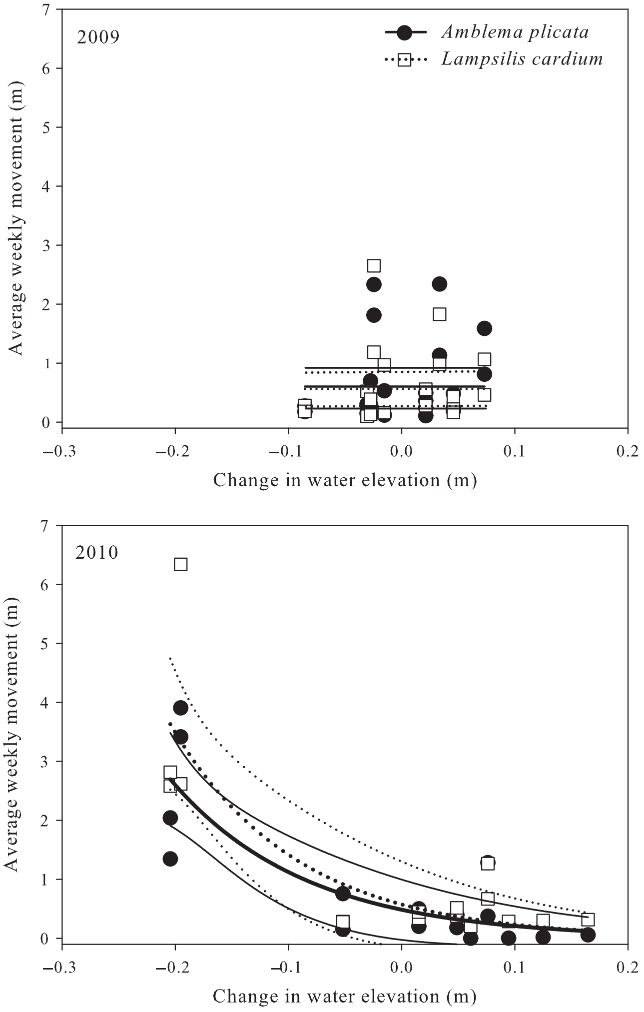

Fig. 6 Average weekly movement (and 95% confidence bands) of two species of native mussels and water elevation by study year and slope category during a planned water level reduction in Pool 6 of the Upper Mississippi River (U.S.A.) during 2010 (0.3 m summer drawdown).

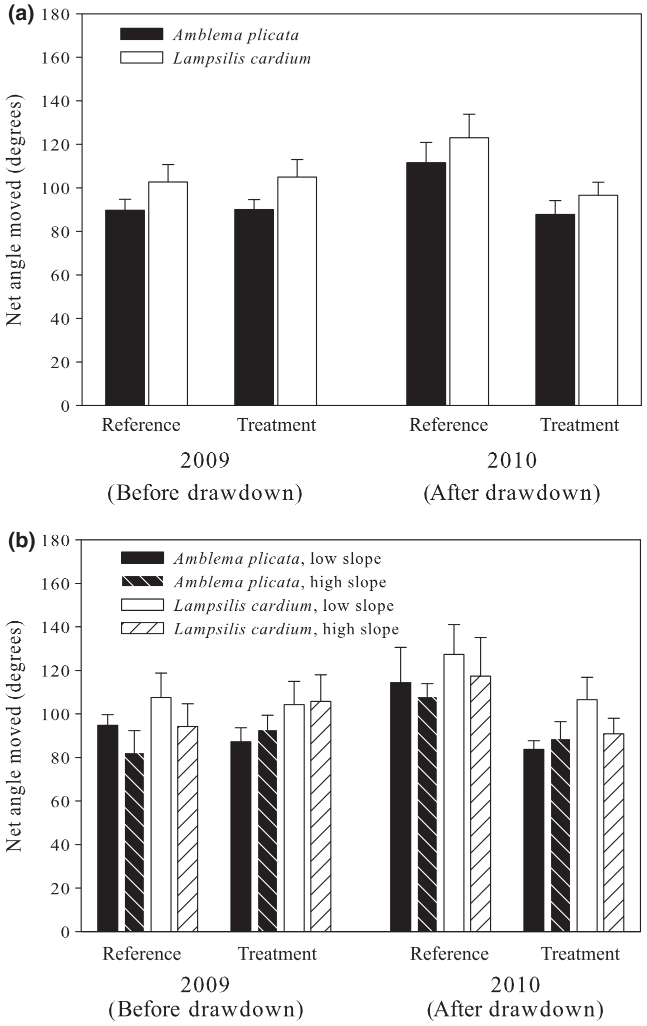

Fig. 7 Estimated net angle (°) ± 1 SE in two species of native mussels during a water level reduction in Pool 6 of the Upper Mississippi River (U.S.A.) in 2009 and 2010; (a) summarised across treatments (n = 5 for 2009 and 2010 reference sites and n = 6 for 2009 reference and 2010 treatment sites); (b) summarised across treatments and slope (n = 3 for all treatment and slope combinations except for high slope reference sites where n = 2).

We observed significant slope associations related to the drawdown for mortality of *A. plicata* and possibly of *L. cardium*. The substantial protective effect of slope corroborates observations that mortality of mussels appeared higher on low slope areas than on high slope areas during a 2005 drawdown of Pool 5 of the UMR (WIDNR *et al.*, 2006). Similarly, the risk of mortality of *A. neislerii* in the Apalachicola River, GA (U.S.A.), during a drought declined as slope increased such that mussels at sites with a mean slope of <20% were at much higher risk of mortality than were those at sites with higher slopes (Kaeser & Herrington, 2011). We hypothesised that highly sloped surfaces might cue directional movement of mussels and provide easier access to deeper water than unsloped surfaces. However, given that horizontal movement was directional regardless of the degree of slope, this hypothesis was not supported.

Higher and more variable sediment temperatures in dewatered areas, which was as high as 31–34 °C at one treatment site in this study, may have contributed to mortality. Laboratory studies with juvenile mussels suggest that many species already reside near their upper thermal tolerance (Pandolfo *et al.*, 2010), and substantial mortality has been observed at 25–30 °C (Ganser, Newton & Haro, 2013). Galbraith, Spooner & Vaughn (2010) observed differences in species tolerance to drought conditions such that thermally tolerant species were more likely to survive drought conditions than were thermally sensitive species. Alternatively, Haag & Warren (2008) reported that all mussel species in seven streams in AL and MS were similarly affected by a drought and hypothesised that the probability of surviving the drought was a function of pre-drought abundance and not due to relative differences in drought tolerance among species.

Although burrowing can be an important behaviour in mussels, little is known about this behaviour, especially in rivers. Mussels that become emersed or subjected to high temperatures in shallow water due to drought or drawdown may seek a thermal refuge by burrowing because sediment temperatures generally cool with depth (Fig. 2). Only 18% of the mussels burrowed entirely in our study, but many mussels moved horizontally to deeper water. A separate corral experiment conducted during the 2010 drawdown in the UMR found that about 38% of Amblemine and Lampsiline mussels that were denied opportunity for horizontal movement were buried after 9 weeks (MNDNR, 2011). Thus, burial into cooler river sediments can be a behavioural response to reduce the short-term effects of a drawdown on mussels. However, burrowing behaviour has been shown to vary widely among species (Smith *et al*., 2000).

We observed species-specific patterns in burial depth in response to the drawdown. In the reference year, most of the burrowed mussels were *L. cardium* and in the drawdown year, most of the burrowed mussels were *A. plicata*. This observation supports our anecdotal observations in other UMR reaches that *A. plicata* tend to be found with much of their shell above the sediment–water interface, whereas *L. cardium* are generally burrowed a few cm into the substratum during summer. We hypothesise that the temporal change in burial depth is a direct response to the drawdown because *A. plicata* at the treatment sites generally moved less than *L. cardium*. Thus, patterns in the proportion of buried mussels are consistent with our hypothesis that *A. plicata* would respond to the drawdown by burrowing. The ability of *A. plicata* to close its valves tightly (unlike *L. cardium*) may have allowed individuals of this species to seal in moisture and avoid high water temperatures. However, this was only a marginally effective survival strategy for *A. plicata* in the corral study by the MNDNR (2011), because mortality was only 16–18% up through week 5, but was 59% by week 9. Without the ability to move to deeper water, most *A. plicata* perished. In contrast, only 7% of tagged *A. neislerii* survived >6 days following a drought in the Apalachicola River, GA (Kaeser & Herrington, 2011). Because we did not retrieve burrowed mussels from the sediments until the end of each year, we do not know when the burrowed mussels died. However, many of the burrowed *A. plicata* still contained tissue at the end of the drawdown, suggesting they had died recently. This might indicate modestly shorter drawdowns could reduce mortality in *A. plicata*.

Few studies have evaluated horizontal movement of mussels, especially in rivers. Some of the early research suggested that mussels were largely sedentary. For example, 85% of mussels tagged by Isley (1914) were recovered after 1 year in the same position. More recent work has indicated that most movement in mussels is modest, but some individuals undertake greater movement. The average movement of *Elliptio complanata* in a headwater stream in VA (U.S.A.) was 3 m in 1 year, but a few individuals moved up to 46 m (Balfour & Smock, 1985). In our study, the average net horizontal movement, averaged over both species at reference sites, was 3 m but some individuals moved up to 15 m over *c.* 3.5 months. Larger movements may be prompted by stress, changes in environmental conditions (e.g. droughts) or physical conditions (e.g. substratum type). Some species track water levels closely, moving shoreward during high water and retreating to deeper water as water levels recede (Gagnon *et al*., 2004; Allen & Vaughn, 2009; Gough, Gascho Landis & Stoeckel, 2012). This behaviour presumably reduces mortality (Haag & Warren, 2008) because it may allow mussels to avoid emersion during times of receding water levels.

The drawdown significantly influenced the net distance that *A. plicata* moved such that movement was greater at treatment sites relative to reference sites after adjusting for year effects. This may be an artefact of the analysis, however, because net distance was estimated only for individuals that remained alive at the end of each year. Thus, the 52% of *A. plicata* that died at treatment sites, and presumably moved little, were not included in the analysis. Interestingly, during 2009 reference and treatment periods and 2010 reference periods, movement of *L. cardium* was greater than that of *A. plicata*. This finding is congruent with those from laboratory studies that suggest that *L. cardium* is more active than *A. plicata* (Waller *et al*., 1999; Allen & Vaughn, 2009). Our models provided evidence that *A. plicata* moved more on low slope sites than on high slope sites. We offer two hypotheses that might account for the influence of slope on horizontal movement. First, in addition to differing conditions at the treatment sites in 2010 due to the drawdown, the conditions in the reference sites were also quite different in 2010 due to flooding in the upper reaches of Pool 6. If shallow water is an important factor stimulating mussel movement, higher water levels in 2010 might have resulted in less movement, especially at low slope sites. Second, the similarity in net movement at high and low slope treatment sites in 2010 might be partly due to mortality. More mussels may have died at low slope treatment sites than high slope treatment sites. Because net movement was only computed for mussels that survived the entire experiment, slower moving mussels at low slope sites might have been more likely to die leaving only mussels that survived by moving larger distances into deeper water.

Both species of mussels moved considerable horizontal distances on a weekly basis. However, the range of weekly movement at treatment sites was greater for *L. cardium* (up to 14.6 m) than for *A. plicata* (up to 8.7 m). This supports our hypothesis that *L. cardium* would respond to the drawdown by horizontal movement. Similarly, Daniel & Brown (2014) found that Lampsilini mussels had faster rates of movement and were better at tracking receding water levels than were Amblemini mussels. Movement was more variable on low slope (0–15 m) than high slope (0–9 m) especially during the first 2 weeks after the drawdown was initiated, as mussels presumably searched for deeper water as sites were dewatered. The greater movement of mussels in this study at the treatment sites, relative to the reference sites, during the drawdown and the strong correlation between the rate of movement and the change in water elevation suggest that receding water levels were a trigger for mussel movement.

Mussels did not appear to exhibit directionality of net movement in response to the drawdown. Regardless of species, slope, or treatment, mussels moved, over the course of each year, about perpendicular to shore to reach deeper water. Mussel movement is often regarded as random (e.g. Schwalb & Pusch, 2007); however, our data suggest that movement over the long term may in fact be strongly directional in some instances. Directional movement may be needed to avoid shallow water during certain environmental conditions. In any case, when properly motivated, movement appears non-random. However, our observations did not support the hypothesis that mussels would have more directed horizontal movement on high slope sites compared to low slope sites.

There is a considerable research on the ecology and management of biota in large rivers, but relatively little work on the effects of drawdowns and other water level management strategies despite increasing recognition as a conservation tool (Theiling, 1995; Abrahams, 2006). While beneficial to aquatic vegetation (Kenow & Lyon, 2009), our results suggest drawdowns can have adverse effects on native mussels in shallow water. Unfortunately, we know little about spatial and temporal patterns in mussel distributions in large rivers. These types of data are needed to better understand the potential effects of drawdowns on native mussel assemblages. Because drawdowns, as practiced in the UMR, are relatively modest and applied infrequently (for a given reach), they may be less consequential to overall mussel populations than historical (pre-impoundment) drops in water levels during summer low flows and droughts. Nonetheless, managers face difficult questions about incidental mortality of at-risk mussel populations. In the UMR, 28 of 50 species in the historical record now have a conservation listing in one or more states. Presence of one or more of these species in shallow areas affected by a proposed drawdown can greatly complicate such a management action. Our study shows that site-specific conditions, especially slope, may be an important determinant of local mussel mortality and should be considered when evaluating potential effects of proposed drawdowns in a given reach. Species-specific behaviours regarding movement and burrowing also appear to be important and might influence drawdown outcomes for mussels. Drawdown parameters such as rapidity of the initial drawdown and drawdown length should be investigated as a means to reduce mussel mortality. Recognition and assessments of the linkages between water elevation and behavioural responses of native mussels are needed to evaluate the effects of this management tool on native mussel assemblages in the UMR and other systems.

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