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APPLIED ISSUE

Habitat persistence for sedentary organisms in managed rivers: the case for the federally endangered dwarf wedgemussel (*Alasmidonta heterodon*) in the Delaware River

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SUMMARY

1. To manage the environmental flow requirements of sedentary taxa, such as mussels and aquatic insects with fixed retreats, we need a measure of habitat availability over a variety of flows (i.e. a measure of persistent habitat). Habitat suitability measures in current environmental flow assessments are measured on a 'flow by flow' basis and thus are not appropriate for these taxa. Here, we present a novel measure of persistent habitat suitability for the dwarf wedgemussel (*Alasmidonta heterodon*), listed as federally endangered in the U.S.A., in three reaches of the Delaware River.
2. We used a two-dimensional hydrodynamic model to quantify suitable habitat over a range of flows based on modelled depth, velocity, Froude number, shear velocity and shear stress at three scales (individual mussel, mussel bed and reach). Baseline potentially persistent habitat was quantified as the sum of pixels that met all thresholds identified for these variables for flows ≥40 $m^3 s^{-1}$, and we calculated the loss of persistently suitable habitat by sequentially summing suitable habitat estimates at lower flows. We estimated the proportion of mussel beds exposed at each flow and the amount of change in the size of the mussel bed for one reach.
3. For two reaches, mussel beds occupied areas with lower velocity, shear velocity, shear stress and Froude number than the reach average at all flows. In the third reach, this was true only at higher flows. Together, these results indicate that beds were possible refuge areas from the effects of these hydrological parameters. Two reaches showed an increase in the amount of exposed mussel beds with decreasing flow.
4. Baseline potentially persistent habitat was less than half the areal extent of potentially suitable habitat, and it decreased with decreasing flow. Actually identified beds and modelled persistent habitat showed good spatial overlap, but identified beds occupied only a portion of the total modelled persistent habitat, indicating either that additional suitable habitat is available or the need to improve habitat criteria. At one site, persistent beds (beds where mussels were routinely collected) were located at sites with stable substratum, whereas marginal beds (beds where mussels were infrequently collected or that were lost following a large flood event) were located in scoured areas.
5. Taken together, these model results support a multifaceted approach, which incorporates the effects of low and high flow stressors, to quantify habitat suitability for mussels and other sedentary taxa. Models of persistent habitat can provide a more holistic environmental flow assessment of rivers.

Keywords: benthic, hydrology, metapopulation, river management, two-dimensional hydrodynamic model, Unionidae

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Introduction

In rivers, hydrology is considered the 'master variable' that governs many instream processes including population persistence and community structure (Poff *et al.*, 1997). The hydrological regime of most rivers is naturally variable, typically experiencing periods of high and low flows in a relatively short period of time. The riverine biota has evolved (e.g. timing of migration and spawning) in response to these regimes (Hynes, 1970; Resh & Rosenberg, 1984; Bunn & Arthington, 2002). However, the flow regime of most rivers has been greatly altered by humans (Dynesius & Nilsson, 1994; Norris *et al.*, 2007), which has led to a disruption of these natural cycles. For freshwater mussels, hydrological alteration has made them one of the most imperilled groups of biota in the world (Williams *et al.*, 1993; Lydeard *et al.*, 2004; Strayer *et al.*, 2004).

Freshwater mussels have several characteristics that make them susceptible to managed flows (Cummings & Graf, 2010). First, although mussels can move (Balfour & Smock, 1995), they are largely sedentary and are unable to shift rapidly from unsuitable habitat during low or high flows. Thus, rapid dewatering in managed systems can strand them in isolated pools with low dissolved oxygen concentration and high temperature, or they may dry out (Haag & Warren, 2008; Galbraith, Spooner & Vaughn, 2010, 2010). Second, mussels are generally long-lived (>30 years) and thus experience a wide range of hydrological disturbances during their life time. Third, mussels generally reach sexual maturity only after several years (Cummings & Graf, 2010). Together, longevity and delayed reproduction may amplify the inability of mussels to recolonise rapidly following a disturbance. Fourth, mussels have a complex life history, including a glochidium larva (Barnhart, Haag & Roston, 2008; Cummings & Graf, 2010), that normally is parasitic on a fish host. This host may also be affected by the managed flows, and this may compound the effects of altered flow on mussels.

The biotic characteristics of mussels make it difficult to manage flows for their conservation. Conventional environmental flow assessments (EFAs) quantify available habitat at discrete flows, independently of each other, assuming that the focal taxa (usually fish) can disperse into created habitat and out of inhospitable areas (Bovee *et al.*, 1998; Tharme, 2003). Even EFAs modified for less mobile taxa (e.g. benthic macroinvertebrates) usually have focussed on a particular flow (Gore, Layzer & Mead, 2001). Although appropriate for mobile animals, such techniques are inappropriate for sedentary taxa like mussels that require suitable flow conditions at a particular point, continuously. For these taxa, we need a measure of habitat that quantifies habitat suitability under the range of possible flows experienced over their entire life cycle or for key components of their life cycle (i.e. a measure of 'persistently suitable habitat'). However, persistent habitat is rarely examined, probably due to the difficulty in its estimation and because most river management scenarios are based on mobile species (i.e. fish), which often do not require such a measure.

Here, we used a two-dimensional hydrodynamic flow model to quantify the persistence of suitable habitat for adults of the endangered dwarf wedgemussel (*Alasmidonta heterodon* Lea, 1830) over a variety of flow scenarios in the Delaware River, U.S.A. This is a small (maximum length ≤45 mm) mussel (Bivalvia: Unionidae) inhabiting small streams to large rivers with a variety of substrata. Historically, it occupied a range of coastal catchments from North Carolina to New Brunswick (Nedeau, 2008). *Alasmidonta heterodon* has a relatively short life span (<12 year), low fecundity and population density, and high host specificity to fish with low dispersal ability (mainly the tessellated darter, *Etheostoma olmstedi* Storer, 1842) (Michaelson & Neves, 1995; McLain & Ross, 2005; Nedeau, 2008). The upper section of the Delaware River, although free-flowing for the majority of its mainstem, is heavily regulated by three dams that are designed for water supply. Because of the flow regulation associated with the operation of these dams, the river experiences frequent episodes of below median flows. To provide resource managers with data that would enable them to manage the Delaware River more effectively for the protection of *A. heterodon*, we quantified habitat suitability (persistence) under a variety of flow scenarios at three reaches with populations of the mussel. We quantified hydrological parameters identified previously as governing mussel populations (depth, velocity, shear stress; Layzer & Madison, 1995; Steuer, Newton & Zigler, 2008; Daraio, Weber & Newton, 2010; Fulton *et al.*, 2010) using a two-dimensional hydrodynamic model at three scales (individual mussels, mussel bed, reach). We next modelled the amount of habitat at different flows. Finally, we evaluated how bed instability may have affected the population at one site by comparing bed topography from 2005 and 2010. We hypothesised that *A. heterodon* would occupy the habitat non-randomly within the reach and that this habitat would provide a refuge from hydrological stress during low and high flows (Strayer, 1999; Howard & Cuffey, 2003; Gangloff & Feminella, 2007).

Methods

Study area

The Delaware River is located in the mid-Atlantic region of the U.S.A, flows in a southerly direction separating the states of New York and New Jersey from Pennsylvania, empties into the Delaware Bay and drains an area of 33 061 km^2 (Fig. 1). The length of river from the confluence of the East and West Branches of the Delaware River at Hancock, NY to the Delaware Bay is 533 km. We selected three reaches (DEL1, DEL2 and DEL3) between the cities of Callicoon, NY and Hancock, NY that an initial freshwater mussel survey in 2000 (Lellis, 2001) identified as containing *A. heterodon* populations. Subsequent surveys (2002, 2006, 2008, 2010, W. Lellis, unpubl. data) confirmed these sites as having persistent occupation over a 10-year period. Substratum in the reaches was mainly large cobbles and boulders with sporadic patches of gravel and sand. Reaches were long enough (4.2, 3.3 and 3.0 km) to encompass several run, pool and riffle habitats.

The Delaware River provides water for nearly 17 million people. To facilitate these needs, three dams were constructed in the mid 1900s. Two of them, the Cannonsville and Downsville Dams (located on the west and east branches of the Delaware River, respectively) are upstream of the survey sites (Fig. 1). The third (Neversink) is located on a separate tributary that flows into the Delaware main stem downstream of our sites. These dams are currently operated on a Flexible Flow Management Programme (FFMP), which was initiated in 2007, and is designed to provide a more natural flow regime and to enable more adaptive means of operation of the three dams. It addresses competing needs, including water supplies for human use, drought management, flood mitigation, protection of cold water fisheries, habitat needs of the mainstem river, estuary and bay, and salinity repulsion. The Upper Delaware River is also currently managed using a minimum basic flow rate (during normal storage conditions) of 49.6 $m^3 s^{-1}$ (1750 $ft^3 s^{-1}$) at the USGS stream gauge at Montague, New Jersey (USGS Gauge number 01438500), which is downstream of our study sites and all three dams (Fig. 1). An understanding of how these management practices affect *A. heterodon* populations in the

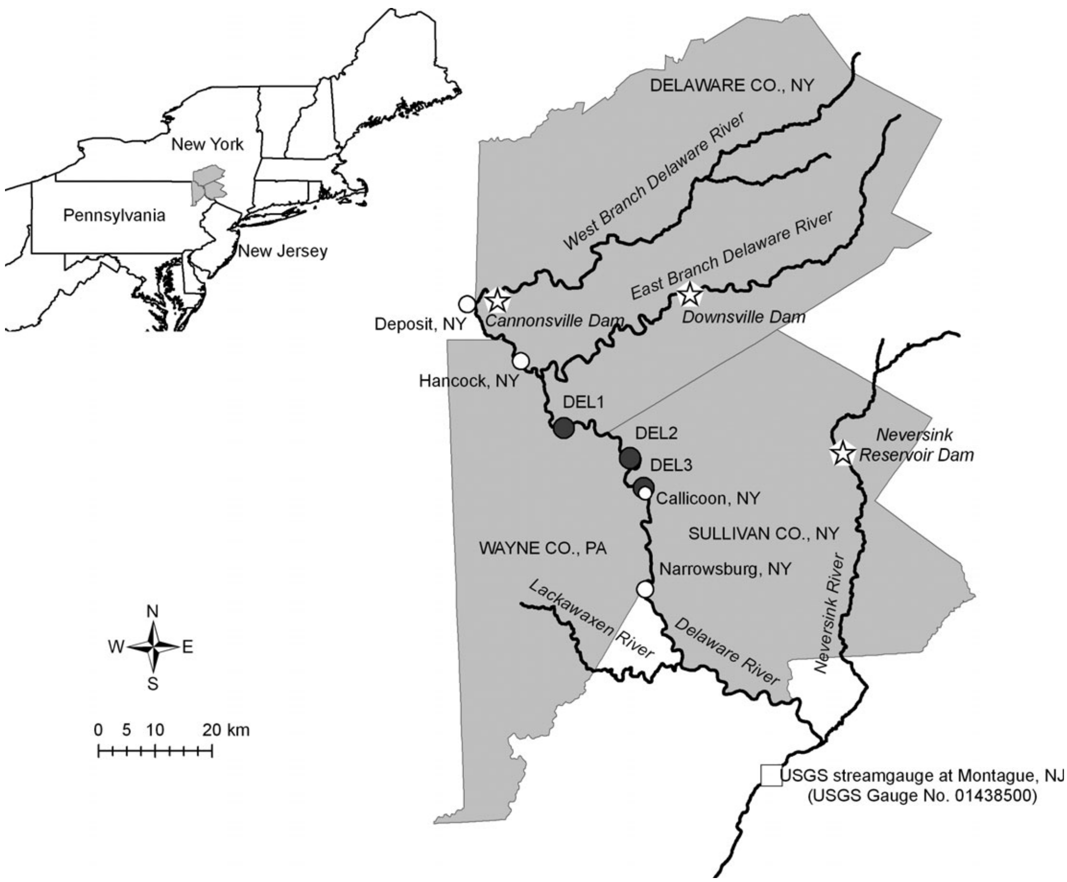

Fig. 1 Map displaying study area (between the cities of Hancock, NY and Callicoon, NY) and the three dams on the upper section of the Delaware River. DEL1, DEL2 and DEL3 (•) indicate study reaches. Inset shows study location in relation to the north-eastern U.S.A.

Table 1 Summary hydrological statistics for USGS stream gauge at Callicoon, NY (USGS Gauge number 01427510, data from 27 June 1975 to 13 December 2010)

Statistic	Discharge ($m^3\ s^{-1}$)			Number of events above
	DEL1*	DEL2*	DEL3	
Max	3056.8	3488.4	3596.2	
Min	7.5	8.6	8.8	
Mean	70.6	80.6	83.1	
Median	36.6	41.8	43.0	
Stdev	102.9	117.4	121.0	
5th percentile	17.3	19.7	20.3	12 282
10th percentile	20.0	22.8	23.5	11 632
20th percentile	24.1	27.5	28.3	10 277
25th percentile	26.2	29.9	30.9	9666
30th percentile	27.9	31.9	32.8	8987
40th percentile	31.5	36.0	37.1	7685
50th percentile	36.6	41.8	43.0	6425
60th percentile	46.9	53.5	55.2	5172
70th percentile	64.7	73.9	76.2	3874
75th percentile	78.2	89.3	92.0	3222
80th percentile	96.3	109.9	113.3	2559
90th percentile	154.8	176.6	182.1	1291
95th percentile	223.5	255.0	262.9	647
100th percentile	3056.8	3488.4	3596.2	0

*Values estimated either by distance weighting (DEL2) or by site:site gauge relationship by use of a gauge close to DEL1 that had short-term data.

mainstem is hindered by lack of information on their habitat requirements.

The long-term (35 year) median flow of the river at the Callicoon USGS stream gauge (USGS Gauge number 01427510) is 43.0 $m^3\ s^{-1}$, with a minimum flow of 8.8 $m^3\ s^{-1}$ and a maximum of 3600 $m^3\ s^{-1}$ (Table 1) and the river regularly experiences low and high flow events (Supporting Information, Figure S1). Management of the river sometimes results in highly variable hydrological conditions. For example, during our September/October 2010 sampling, discharge at the Callicoon gauge reached a low of 14.6 $m^3\ s^{-1}$ on 28 September at 11:00 but, following a rain event, reached 1806.6 $m^3\ s^{-1}$ on 1 October at 14:15. These rapid hydrological changes expose large amounts of bed at the lower flows and create potentially hydrologically inhabitable areas at flood flows and may strongly affect sedentary taxa such as *A. heterodon*.

Bed topography

A detailed bathymetric survey was conducted for each reach between August and October 2010. Site surveys were conducted using a combination of real-time kinematic (RTK) survey-grade GPS equipment (for wadeable areas with strong GPS signals, Trimble 5800 rover with model 5700 base station), an optical 3-s total station (for locations where GPS signals were not strong, Leica TC800), and using echosounding with sonar and Acoustic Doppler Current Profiler equipment (for deep, unwadeable sections, Biosonics DT4000 and DE-X). LIght Detection And Ranging (LIDAR) was used to provide elevation data for areas on banks that were inaccessible or not sampled effectively with site surveys. Raw elevations from each of the methods were standardised and compiled into a single preliminary bed file and quality assured/quality controlled following the procedures in Bovee *et al.* (2007). At each point surveyed, a visual estimate of median particle size using the Wentworth scale was recorded for later use in the hydrodynamic model.

2-D hydrodynamic model

We used the River2D model (Steffler & Blackburn, 2002) for all hydraulic simulations. River2D is a two-dimensional, depth averaged, finite-element hydrodynamic model (Steffler & Blackburn, 2002) and has been often used in modelling hydrological attributes and fish habitat (Bovee *et al*., 2007) under varying flow scenarios. The River2D modelling process involves several steps. First, the preliminary bed file compiled above needs to be refined by deleting erroneous points and adding breaklines to enable smoother triangulation of elevation data (Bovee *et al*., 2007). We performed this process using the River2D_bed editor (Steffler, 2002). Each point in the bed file requires an estimate of roughness (an indicator of flow resistance). We assigned a default roughness value of 0.1 to all particle sizes that were pebbles (16–64 mm) or smaller; for all other larger sizes, roughness was estimated as $1.5 \times d_{50}/1000$, where d_{50} is the diameter of the 50th percentile particle. Next, River2D requires a computational mesh to calculate water depth and velocity. We created our meshes using River2D_mesh (Waddle & Steffler, 2002). Model performance improves with mesh density; however, processing time increases exponentially with mesh density, and thus, there is a trade-off in constructing meshes to achieve optimal performance. We optimised mesh density and computational burden by decreasing mesh density in uniform areas (e.g. large flat pools) and increasing mesh density in areas with abrupt transitions (shallow areas, boulders and banks; Bovee *et al*., 2007). The number of nodes in a mesh varied for each site by flow but was *c*. 21 700 for DEL1, 17 700 for DEL2 and 15 000 for DEL3.

River2D needs inflow boundary discharge and water surface elevations (WSE) along the modelled reach and at outflow boundaries. Two sites were located close to USGS stream gauges (DEL1, Lordville gauge, USGS Gauge number 01427207 and DEL3, Callicoon gauge, USGS Gauge number 01427510). Boundary conditions (discharge, WSE) were defined using rating curves developed from these gauges. DEL2 was located between the other two sites, and we used distance weighting and the two above rating curves to estimate boundary conditions for this site. Next, River2D model runs need to be calibrated. Fortuitously, our surveys occurred during a large storm event, which allowed us to calibrate our models by measuring WSE at four–five locations in each reach for four–five discharge levels (Table S1). The initial River2D run WSE was adjusted by increasing or decreasing the spatially explicit roughness estimates by a constant until modelled and observed WSE were within ±5 cm. Finally, we ran a suite of models of simulated flows that: (i) covered the range of flow conditions experienced at each site (Table 1), (ii) focussed on low flow events (<20 $m^3 s^{-1}$), (iii) and included several flood events (>100 $m^3 s^{-1}$); in all we ran ~35 flow events for each reach (Table S1). For each flow, River2D calculates average depth (D), velocity (V), Froude number (Fr) and shear velocity (V_*). We also calculated shear stress as $\rho(V_*)^2$, where ρ is the density of water (998.2 kg m^{-3}), and Reynolds number as $R_e = \frac{VD}{v}$, where v is kinematic viscosity (1.006×10^{-6} $m^2 s^{-1}$; Gordon *et al.*, 2004) because these two parameters have been shown by modelling predictions to be strong drivers of mussel bed formation (Steuer *et al.*, 2008; Daraio *et al.*, 2010; Fulton *et al.*, 2010).

Data analysis

Hydrological conditions. We summarised each hydrological parameter at three scales: individual mussel GPS locations from all surveys (+3 m buffer for GPS resolution), mussel beds (estimated by a convex hull of mussel GPS points + 3 m buffer), and for the entire surveyed reach (to estimate an amount of potentially suitable habitat). We used the curves from these analyses to identify upper and lower thresholds of the parameters that *A. heterodon* and mussel beds experienced over all flow scenarios. For example, the highest shear stress that a mussel experienced was 47.3 N m^{-2} and occurred at a modelled flow of 3600 $m^3 s^{-1}$ at DEL3. To test whether hydrological conditions near mussels were different from random locations, we generated 1000 random points throughout the surveyed reach and calculated mean and 95% confidence limits for each hydrological parameter at these random points. We considered mussels were located in non-random habitat if the 95% confidence limits of the habitat at the mussel location did not overlap the 95% confidence limits of these random points.

Habitat and mussel exposure. Alasmidonta heterodon is sensitive to drying (H. Galbraith, USGS, unpubl. data), so we calculated the amount of habitat within the mussel bed that would go dry at each flow (% bed exposed). As a conservative measure to account for the possibility of a larger bed than identified by surveys, we also calculated the amount of dry habitat in an extended mussel bed (calculated as the bank to bank area from the upstream/downstream limits of the mussel locations). We used piecewise (or segmented) regression on the % bed exposed versus flow relationship to identify changes in slopes that may indicate a 'threshold'. Piecewise regression was conducted using the segmented function in the segmented package (Muggeo, 2011) in R (R Development Core Team, 2011). This function updates a linear model by adding one or more segmented relationships that are based on predefined break points in the linear slope. We predefined our break points using the davies.test function in the segmented package.

Potentially suitable habitat, persistent habitat and bed stability. We first calculated the amount of habitat within the entire reach available to the mussels as the area in which all predicted hydrological parameters were within the range experienced by existing individual mussel. We did this by using the habitat thresholds identified above to label a habitat patch (1 m^2 pixel) as suitable (assigned a 1) or unsuitable (assigned a 0 if any habitat parameter was not satisfied). Total potential habitat for each flow was then calculated as the sum of suitable pixels. This procedure is similar to the traditional weightable useable area (WUA) used in standard Instream Flow Incremental Methodology studies. However, for sedentary taxa, WUA estimates are likely to be exaggerated because of mobility issues. Therefore, we calculated the amount of persistent habitat available to *A. heterodon*. For this analysis, we identified and summed only pixels that under all flows were deemed suitable. A 'baseline' estimate of persistent habitat was quantified as the sum of pixels that were deemed suitable over all modelled flows >40 $m^3 s^{-1}$ (average flow) except 4078 $m^3 s^{-1}$, because this was a hypothetical extreme flood. We then quantified the amount of persistent habitat 'lost' at lower flows by adding in suitable pixels at lower flows in a sequential order. Geospatial analyses were performed using ArcGIS (ESRI, Redlands, CA, U.S.A) with automated Python scripts (version 2.5.1, http://www.python.org), and data analyses were conducted in R (R Development Core Team, 2011).

Finally, because *A. heterodon* is presumably sensitive to large bed movement events, we examined how mussel beds related spatially to bed stability. For one reach (DEL3), we had comparable bed topography surveys from an earlier topographic survey (2005) that used similar equipment and personnel (Bovee *et al.*, 2007). For this site, we calculated the change in bed height over the 5-year period. We further divided the mussel bed into a 'persistent' population, defined by finding mussels during each survey, and a 'marginal' population, defined as populations where individuals were found sporadically or that were lost following large flow events in 2005/6.

Results

Hydrological conditions

A visual representation of River2D modelling results showed high variability in hydrological variables across each reach (Figure S2). These maps also enabled a visualisation of areas that became disconnected at lows flow (Figure S3), which aided in identifying a threshold flow that may be affecting mussels.

At the individual mussel locations, five of the six modelled hydrological variables showed rapid increases with increasing flow up to ~40 $m^3 s^{-1}$, after which they increased more slowly, levelled off or decreased (Fig. 2). Reynolds number continued to increase with flow for two sites. Depth at mussel locations in DEL3 increased from an average of 0.24 m at 4 $m^3 s^{-1}$ to 5.99 m at 4078 $m^3 s^{-1}$; in DEL1, it increased from 0.23 to 8.28 m and in DEL2 from 0.66 to 8.29 m (Fig. 2a; Table S2). Mussel site-average velocity in DEL3 increased from 0.08 m s^{-1} at 4 $m^3 s^{-1}$ to 2.81 m s^{-1} at 4078 $m^3 s^{-1}$; in DEL1, it increased from 0.003 m s^{-1} to 1.67 m s^{-1} at 2500 $m^3 s^{-1}$; and in DEL2 from 0.02 m s^{-1} at 4 $m^3 s^{-1}$ to 3.18 m s^{-1} at 4078 $m^3 s^{-1}$ (Fig. 2b; Table S2). Shear velocity at mussel sites was lowest at the lowest flows (e.g. in DEL3 at 4 $m^3 s^{-1}$ = 0.03 m s^{-1}) and highest at high flows (e.g. 0.18 m s^{-1} in DEL3 at 4078 $m^3 s^{-1}$: Fig. 2c; Table S2). Froude number at mussel sites was lowest in DEL1 at 4 $m^3 s^{-1}$ (0.002) and highest in DEL3 at 4078 $m^3 s^{-1}$ (0.37; Fig. 2d), and Reynolds number was lowest in DEL1 at 4 $m^3 s^{-1}$ (1376) and highest in DEL2 at 4078 $m^3 s^{-1}$ (2.62×10^7; Fig. 2f). Average shear stress at mussel sites for two sites (DEL3 and DEL2) showed a sporadic relationship with discharge, often increasing then decreasing (Table S2), but in general, the highest shear stress values were modelled at high flow events (Fig. 2e).

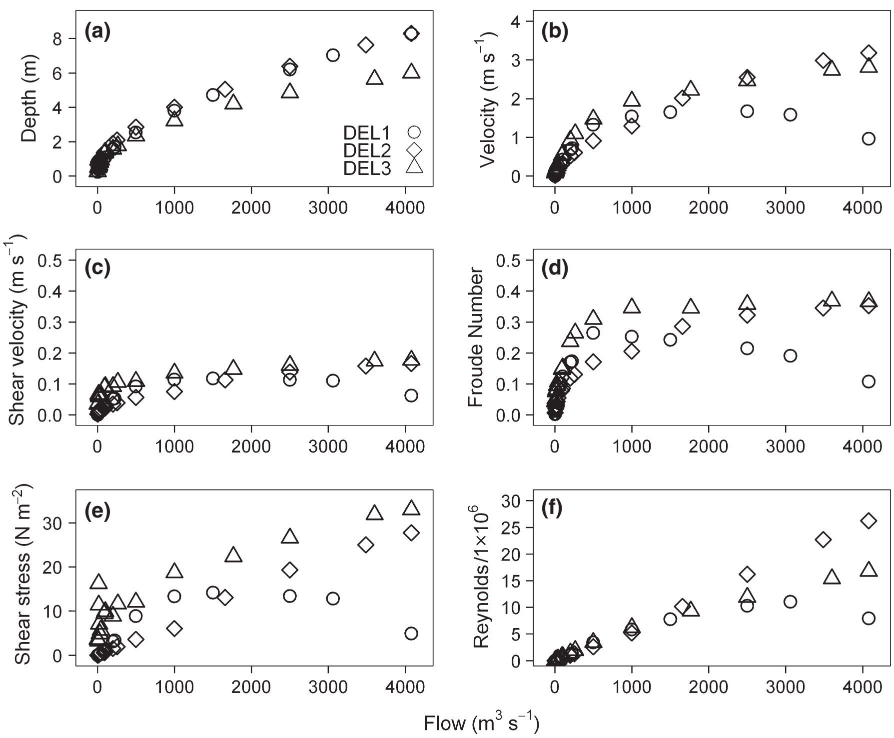

Fig. 2 Mean values of the six habitat variables measured for each flow at the individual mussel locations for each reach. (a) depth, (b) velocity, (c) shear velocity, (d) Froude number, (e) shear stress and (f) Reynolds number.

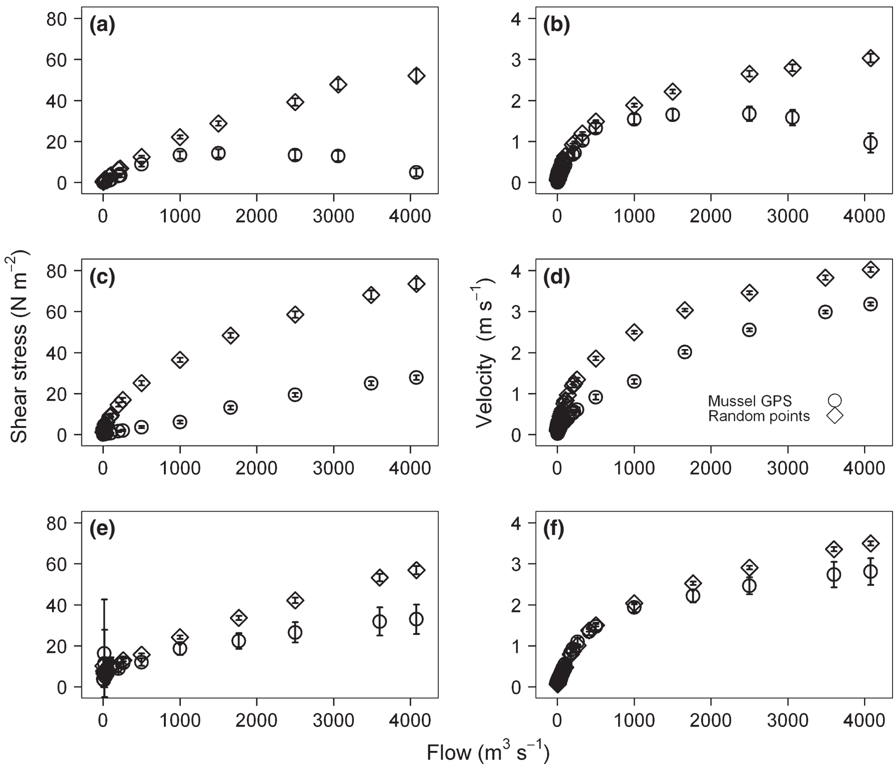

Fig. 3 Mean (±95% CL) shear stress (left column) and average velocity (right column) by flow for each reach (DEL2, DEL2 and DEL3) for mussel locations (open circle) and 1000 random points in reach (open diamond). (a) DEL1 shear stress, (b) DEL1 velocity, (c) DEL2 shear stress, (d) DEL2 velocity, (e) DEL3 shear stress and (f) DEL3 velocity. Values for other hydrological variables are listed in Table S2.

In DEL1, all hydrological variables at the mussel sites, except depth, reached a maximum at intermediate flows and then decreased (Fig. 2). Values quantified at the mussel bed scale were almost identical to those quantified at the mussel site scale (Figure S4).

Hydrological variables at individual mussel locations differed from average reach conditions (Fig. 3; Table S2). In DEL1 and DEL2, individual mussels were located in areas that had lower velocity, shear velocity, shear stress, Froude number, Reynolds number and depth than random conditions in their associated reach (Fig. 3; Table S2). In DEL3, these variables differed only at higher flows. Shear stress was lower at mussel locations than average reach conditions at all three sites at flows >1000 m^3 s^{-1} (Fig. 3a,c,e).

The maximum velocity over a mussel was 3.3 m s^{-1}, maximum shear velocity was 0.22 m s^{-1}, maximum Froude number was 0.44, and maximum shear stress was 47.3 N m^{-2}. These values were used as upper thresholds in the habitat suitability calculation. We also used a lower threshold velocity of 0.02 m s^{-1}, and for depth, we used a lower threshold of 0.06 m (Layzer & Madison, 1995; Galbraith *et al.*, 2010), which we assumed sufficient to reduce the potential for dewatering effects on *A. heterodon*. Thus, a pixel was deemed to be suitable if it had values of these five hydrological variables below and/or above these thresholds (Reynolds number was not used because a threshold was not identified).

Habitat exposure

In DEL1, the percentage of the mussel bed exposed decreased rapidly from 8.7% at 4 m^3 s^{-1} to <1% at 25 m^3 s^{-1} and breaks in slope occurred at 9.0 and 23.1 m^3 s^{-1} (Fig. 4a). The extended bed in DEL1 had more exposed bed at most of the lower flows than the mussel bed extent; at 4 m^3 s^{-1}, 21.8% was exposed and 1.5% remained exposed at 100 m^3 s^{-1}, breaks in slopes were identified at 10.6, 23.5 and 97.5 m^3 s^{-1}. In DEL2, the amount of exposed bed decreased at a slower rate than in either DEL1 or DEL3, decreasing from 6.5% at 4 m^3 s^{-1} to <1% at 70 m^3 s^{-1}; breaks in the slope occurred at 24.1 and 80.7 m^3 s^{-1} (Fig. 4b). The extended bed in DEL2 had a similar degree of exposure to these values, decreasing from 5.9% exposure at 4 m^3 s^{-1} to <1% at 135 m^3 s^{-1}; breaks in slope occurred at 35 and 153.3 m^3 s^{-1} (Fig. 4b). Per cent exposure of the mussel bed rapidly decreased with flow in DEL3, decreasing from 14.6% at 4 m^3 s^{-1} to

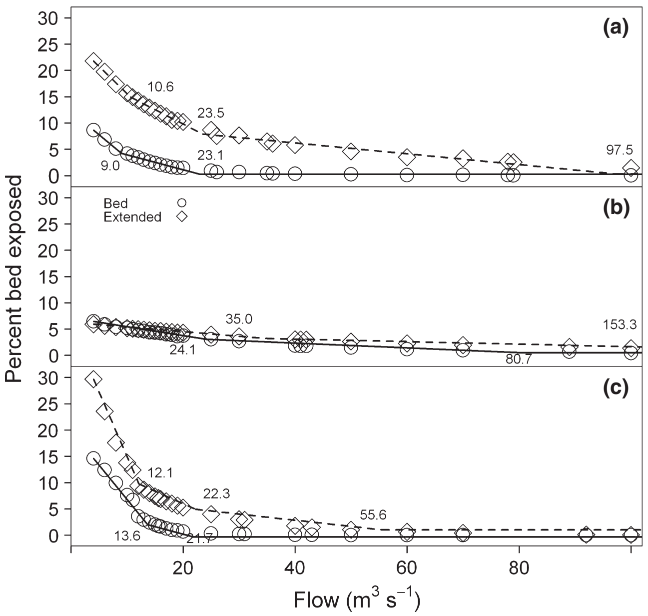

Fig. 4 Per cent of mussel bed exposed by flow in each reach (open circles mussel bed defined as convex hull, open diamond mussel bed was extended to river banks). Numbers indicate the flow where a break in slope was identified by the piecewise regression. Reaches: (a) DEL1, (b) DEL2, (c) DEL3.

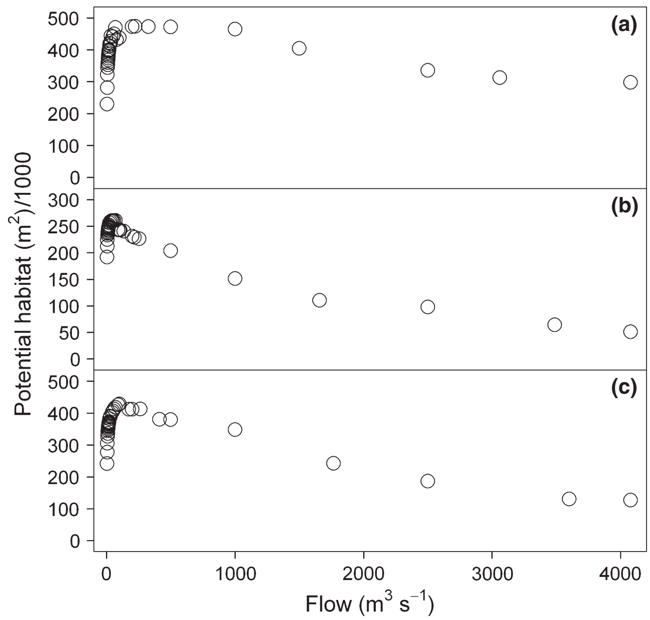

Fig. 5 Potential habitat available by flow for the entire reach, (a) DEL1, (b) DEL2 and (c) DEL3.

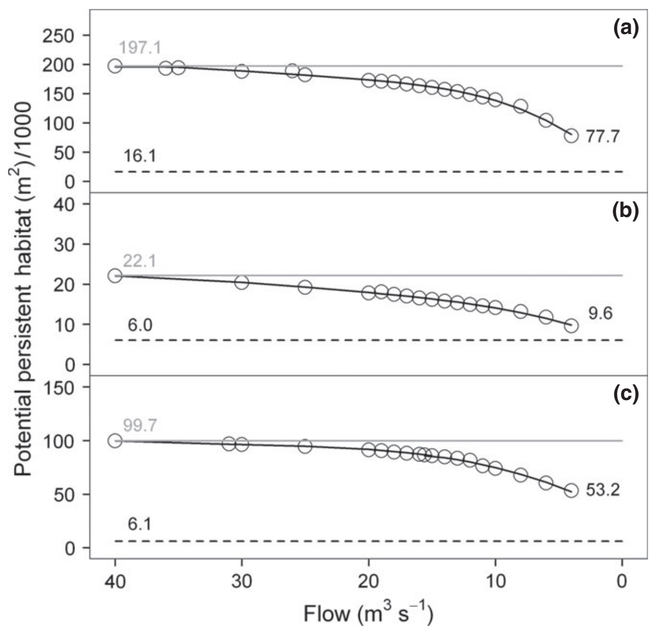

Fig. 6 Potential persistent habitat available at low flows for the entire reach, (a) DEL1, (b) DEL2 and (c) DEL3. Grey lines and numbers indicate the potential flow at 40 $m^3 s^{-1}$ (taken to be non-low flow available habitat); black dashed lines and associated numbers indicate the amount of habitat in the mussel bed (convex hull). Numbers on right side indicate available habitat within the reach at the lowest modelled flow (4 $m^3 s^{-1}$). Circle = potential modelled habitat, lines = 4th order polynomial fit to potential modelled habitat. For DEL1: $y = -0.2481x^4 + 26.738x^3 - 1085.2x^2 + 21\,115x + 11\,201$, $R^2 = 0.995$; For DEL2: $y = -0.0132x^4 + 1.3905x^3 - 56.908x^2 + 1313.7x + 5386.3$, $R^2 = 0.997$; For DEL3: $y = -0.0185x^4 + 3.7641x^3 - 242.18x^2 + 6602.8x + 29\,483$, $R^2 = 0.996$.

<1% at 19 $m^3 s^{-1}$; breaks in slopes were identified at 13.6 and 21.7 $m^3 s^{-1}$ (Fig. 4c). The amount of exposed bed was highest with the extended bed in DEL3 (29.7% at 4 $m^3 s^{-1}$); however, this percentage rapidly decreased and was <1% at 60 $m^3 s^{-1}$; breaks in slopes occurred at 12.1, 22.3, and 55.6 $m^3 s^{-1}$ (Fig. 4c).

Potentially suitable, persistent habitat and bed stability

For all three sites, potential habitat rapidly increased with flow reaching a maximum (DEL1 at 70 $m^3 s^{-1}$ and 470 436 m^2, DEL2 at 70 $m^3 s^{-1}$ and 261 045 m^2, and DEL3 at 100 $m^3 s^{-1}$ and 428 294 m^2; Table S3) and then decreased with higher flows (Fig. 5). Potential persistent habitat decreased from baseline (40 $m^3 s^{-1}$) values with decreasing flow (Fig. 6). In DEL1, 197 077 m^2 of habitat was available at 40 $m^3 s^{-1}$ and slowly decreased with decreasing flow reaching a low of 77 730 m^2 at 4 $m^3 s^{-1}$ (Fig. 6a; Table S3). The identified mussel bed occupied an area of 16 100 m^2 in DEL1. DEL2 had a baseline level of persistent habitat of 22 099 m^2, at 4 $m^3 s^{-1}$, this value was reduced to 9587 m^2 (Fig. 6b). The mussel bed in DEL2 occupied 6000 m^2. DEL3 had 99 660 m^2 of persistent habitat, which was reduced to 53 225 m^2 at 4 $m^3 s^{-1}$ (Fig. 6c; Table S3). The mussel bed in DEL3 occupied 6100 m^2. Persistent habitat within the identified beds

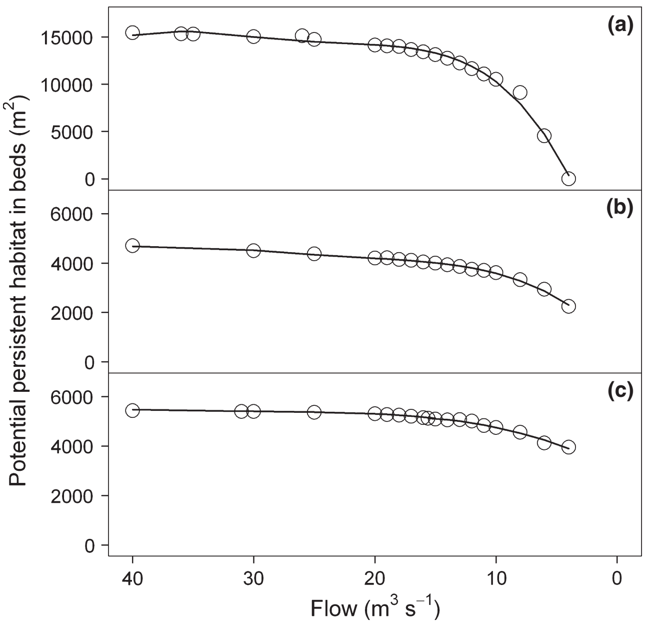

Fig. 7 Potential persistent habitat available at low flows for each mussel bed, (a) DEL1, (b) DEL2, (c) DEL3. Circle = potential modelled habitat, lines = 4th order polynomial fit to potential modelled habitat. For DEL1: $y = -0.0569x^4 + 6.0947x^3 - 238.81x^2 + 4141.2x - 12\,772$, $R^2 = 0.992$; For DEL2: $y = -0.0081x^4 + 0.8306x^3 - 31.008x^2 + 531x + 626.88$, $R^2 = 0.997$; For DEL3: $y = -0.0015x^4 + 0.2211x^3 - 11.77x^2 + 275.82x + 2972.4$, $R^2 = 0.989$.

decreased in DEL1 from 15 444 m^2 (or 95.7% of identified bed) at 40 m^3 s^{-1} to 0 m^2 at 4 m^3 s^{-1} (Fig. 7a) because the right branch of the river disconnected and velocity over the mussel bed was modelled below our 0.02 m s^{-1} threshold. Persistent habitat in the DEL2 bed decreased from 4705 m^2 (78.4% of identified bed) at 40 m^3 s^{-1} to 2246 m^2 (37.4% of bed) at 4 m^3 s^{-1} (Fig. 7b) and persistent habitat in DEL3 deceased from 5434 m^2 (89.7% of identified bed) to 3964 m^2 (65.4% of bed; Fig. 7c). A spatial map shows that the identified persistent habitat contained the mussel beds, although these often extended to other areas (Fig. 8). Persistent habitat in DEL2 was most closely aligned with the identified bed, only showing additional potential persistent habitat downstream and immediately upstream of the bed (Fig. 8b). The other two sites showed ample potential additional persistent habitat, mostly near the mussel beds (Figs 4 & 8a,c; Figure S5).

Bed change in marginal beds in DEL3 covered a larger area than in the persistent bed (Fig. 9). Most (77.3%) of the persistent mussel bed did not change (i.e. between −0.1 and 0.1 m change), 20.4% scoured (>−0.1 m change) and 2.3% experienced deposition (>0.1 m change). Only 39.5% of the marginal mussel bed experienced no change (53.0% experiencing scouring and 7.5% deposition).

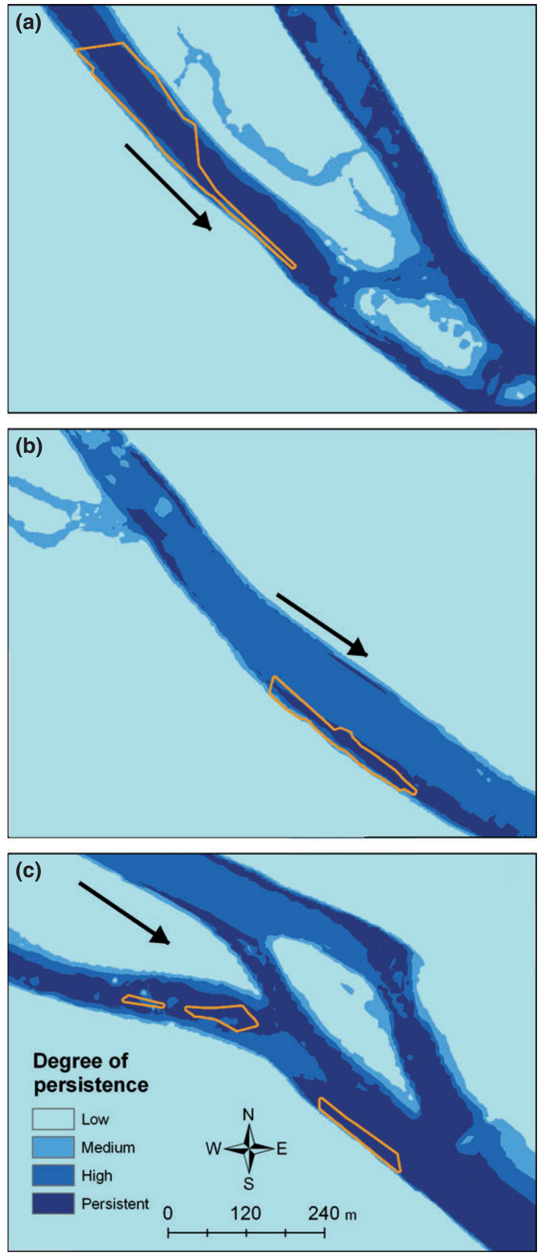

Fig. 8 Potential persistent habitat at mussel beds (orange polygons) at 12 m^3 s^{-1} for each site: (a) DEL1, (b) DEL2, (c) DEL3. Arrows indicate direction of flow.

Discussion

In regulated systems, such as the Delaware River, mussel populations are constrained by hydrological stresses at both high and low flows. Mussel beds are often reported to occur in refuge areas, where shear stress, velocity and bed movement at high flows remain minimal (Strayer, 1999; Howard & Cuffey, 2003; Gangloff & Feminella, 2007; Allen & Vaughn, 2010). Our results support this paradigm, as *A. heterodon* beds identified were located in areas

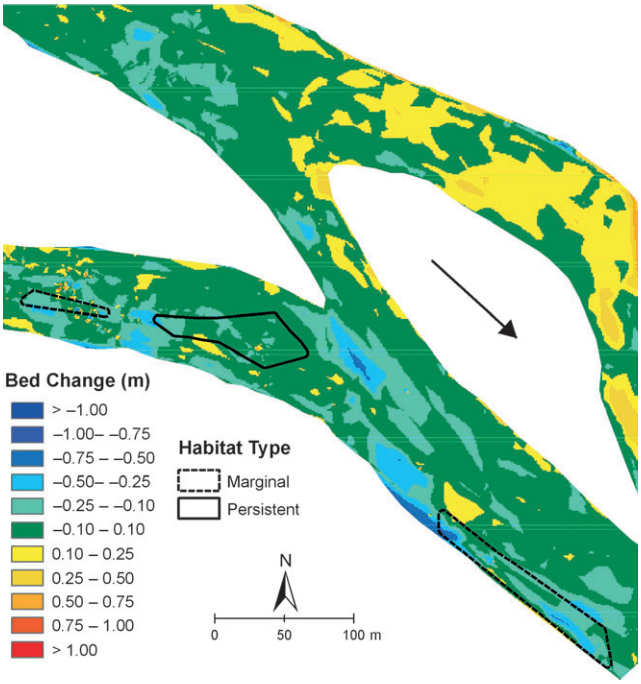

Fig. 9 Bed height change at DEL3 between 2005 and 2010. Negative values infer scouring, positive values deposition. Arrow indicate direction of flow.

with lower shear stress and velocity and that had stable beds over a 5-year period. However, low flow events may also stress mussels by reducing velocity and depth, increasing temperature, lowering dissolved oxygen and increasing exposure to the air (Haag & Warren, 2008; Galbraith *et al*., 2010). Our results support this as, at low modelled flows (i.e. 12 m^3 s^{-1}), portions of the mussel bed became unsuitable. In fact in one site, DEL3, the branch of the river containing the mussel bed became disconnected at ~12 m^3 s^{-1}. To conserve *A. heterodon* and other mussel species more effectively, we suggest a measure of persistent suitable habitat that combines the limiting factors of high flow (e.g. shear stress) and low flow (low velocity and restricted depth) will prove more useful than examining each factor independently.

Few previous studies have addressed *A. heterodon* habitat preferences. Strayer & Ralley (1993) suggest *A. heterodon* prefer areas with patches of sandy substratum and moderate water velocity (~6 to 16 cm s^{-1}). The results of Michaelson & Neves (1995) also suggest a preference for finer substratum, but they found no preference for velocity when tested at 8.9 and 3.7 cm s^{-1}. Michaelson (1993) reports that the most suitable velocities for *A. heterodon* in Aquia Creek, Virginia ranged from 2 to 10 cm s^{-1}, and the most suitable depths from 21.5 to 36.5 cm. Our results contain these values, but because simple hydraulic variables like velocity and depth vary with flow, *A. heterodon* in our study occupied areas where depths ranged from 0.0 to 7.9 m and velocities ranged from <0.001 to 3.3 m s^{-1}. Variability in simple hydraulic variables is probably one reason for their inability to quantify effectively habitat suitability for mussels (Strayer & Ralley, 1993; Layzer & Madison, 1995). However, simple variables like depth help identify possible low flows issues, such as bed exposure or side channel disconnection. At one site, DEL3, the established mussel beds occurred on the right-side channel, which potentially becomes disconnected from the main channel at low flow. Our analysis indicates this disconnection occurs at between 12 and 13 m^3 s^{-1}, a flow similar to that reported previously (Cole, Townsend & Eshleman, 2008).

Unlike the simple hydraulic variables, complex hydraulic variables such as Froude number, shear velocity, Reynolds number and shear stress (particularly when estimated during high flow events) have shown promise in identifying the factors governing mussel populations (Layzer & Madison, 1995; Howard & Cuffey, 2003; Gangloff & Feminella, 2007; Allen & Vaughn, 2010). Our models identified *A. heterodon* mussel beds in areas that had lower shear stress, shear velocity and Froude number than average reach conditions and support the hydrological refuge hypothesis (Strayer, 1999). Our results also show that for two of the study reaches (DEL1 and DEL2), these complex hydraulic variables were different from average conditions even at low flows. These differences at low flow are likely to be because of spatial correlation (i.e. a refuge site at high flow is a refuge site at low flows), although further study is required to confirm this. Interestingly, in DEL1, complex variables (and velocity) reached their maximum values at intermediate flows (Fig. 2). One possible reason for this is the presence of an island downstream of the mussel beds (Fig. 8a), which may have served to buffer the area upstream during the higher flows, in effect creating a refuge area. A more detailed hydrological study is needed to confirm this.

For our purposes, we sought to combine the limiting factors structuring *A. heterodon* populations at high and low flows into one measure of persistent habitat. The amount of persistent habitat was much less than the amount of potential habitat estimated at each flow (Figs 5 & 6), which is probably due to the dependence of the persistent habitat on other flows (i.e. if a patch was not suitable at 50 m^3 s^{-1}, it was not suitable at 40 m^3 s^{-1}, regardless of the flow-specific habitat suitability). This finding highlights the potential overestimation of suitable habitat with the traditional WUA approach for sedentary taxa. Moreover, model estimates of persistent habitat were higher than those for the identified mussel beds, which could be driven by several factors, including issues with mussel surveys, inappropriate thresholds and omission of important driving factors such as temperature, host fish and juvenile dispersal. However, persistent habitat always decreased with flow, and for one site (DEL2), predicted areal coverage at low flows was close to that covered by the mussel bed identified. This, together with the high spatial overlap of mussel beds and predicted persistent habitat (Fig. 8), illustrates that our estimates of persistent habitat were able to identify areas of high probability of mussel presence.

Model estimates may be improved by addressing the factors mentioned above. Regarding missed individuals during surveys, the degree of misses are dependent on surveyor training/experience and environmental conditions. It is likely that environmental conditions played a much larger role than surveyors because: (i) all surveyors were experienced, and (ii) some reaches were difficult to survey because of dense aquatic vegetation (W. Lellis, pers. observ.). Given that *A. heterodon* is an endangered species, its abundance was extremely low and the probability of missed individuals high. However, we established our bed boundaries based on 10 years of sampling in which *A. heterodon* were routinely located, which minimised errors in bed delineation.

Inappropriate thresholds might also be responsible for the higher model estimates of persistent habitat, as organisms often do not exhibit such abrupt responses to environmental variables. Layzer & Madison (1995) cautioned against using their lower depth threshold of 6 cm and velocity threshold of 2 cm s^{-1}. Of these two, the depth criterion may be more subject to criticism, because our modelled results and the previous work of others (Michaelson & Neves, 1995) indicate that *A. heterodon* may prefer water deeper than 6 cm. However, laboratory studies are finding that *A. heterodon* generally does not move in response to dewatering (H. Galbraith, USGS, unpubl. data). Further experimentation is needed to confirm how *A. heterodon* responds to hydrological stressors at both high and low flows. Mussels have the ability to move or bury to escape inhospitable conditions (Balfour & Smock, 1995; Amyot & Downing, 1997). Incorporation of these abilities into habitat suitability criteria for *A. heterodon* may improve our estimates of persistent habitat. Many mussels may also occur near their upper thermal tolerances (Pandolfo *et al*., 2010), so developing a response curve to temperature will probably improve models. Temperature preferences for *A. heterodon* are not known; however, preliminary laboratory studies suggest they are highly sensitive to temperature (H. Galbraith, USGS, unpubl. data). Incorporation of habitat suitability for juvenile life stages and the main fish hosts (e.g. tessellated darter) would probably identify additional areas unsuitable for *A. heterodon*. These additional attributes have proved fruitful in simulation modelling of mussel communities (Morales *et al*., 2006; Daraio *et al*., 2010), and host fish dispersal is a strong correlate of mussel diversity (Haag & Warren, 1998; Schwalb *et al*., 2011); however, such analyses are beyond the scope of this study.

Bed stability is likely to be a main factor determining the persistence of mussel populations. Normally, bed stability is inferred from modelled bankfull shear stress and critical shear stress estimates (Gangloff & Feminella, 2007; Allen & Vaughn, 2010). We were fortunate to have bed topography maps from two periods (2005, 2010) that included several large flood events for one site. Our spatial analysis on bed change indicated that the stable sub-mussel bed occurred in an area that had little bed change. However, marginal beds were located in areas that experienced some degree of scouring or deposition. In fact, in one of the marginal beds that experienced a high degree of scouring, *A. heterodon* were not found following the large storm events of 2005/2006.

Persistent habitat synthesises the effects of variable stressors and flows into a single manageable value. We chose to estimate baseline persistent habitat as available habitat over all modelled flows ≥40 $m^3 s^{-1}$, as this was the median flow at the Callicoon gauge, and we wished to focus on the effects of low flows. By definition, persistent habitat needs to be quantified over a range of flows, but this range is flexible and contingent on research goals. For example, we could have estimated baseline persistent habitat over the 30–60 $m^3 s^{-1}$ range and then estimated the effects of high and low flows on this baseline amount. However, on the Delaware River, low flows are the main threat that can be addressed by management decisions. We also considered a patch as suitable only if all thresholds were satisfied over all flows. This assumption can be relaxed, and a more continuous measure of persistence can be calculated. However, more research is needed on the habitat requirements of mussels (e.g. can mussels persist if one of the habitat parameters is not met?) before such an approach is undertaken. Finally, models such as those described here can be integrated into a more holistic decision support system (Bovee *et al*., 2007) that would incorporate other taxonomic groups (fish, insects) to provide managers with a more complete analyses of management options and instream processes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Hydrograph of average daily flows from the U.S. Geological stream gauge at Callicoon (USGS Gauge No. 01427510), NY, U.S.A.

Figure S2. Example River2D model output for depth, Froude number, shear velocity and average velocity.

Figure S3. Spatial representation of depth results of the River2D hydrodynamic model for DEL3 site at 8, 10, 11 and 12 $m^3 s^{-1}$.

Figure S4. Mean values of the six habitat variables measured for each flow at the mussel bed scale for each reach.

Figure S5. Potential persistent habitat at the reach scale at 12 $m^3 s^{-1}$ for each site.

Table S1. Discharge values at which the River2D hydrodynamic models were run.

Table S2. Mean and upper and lower 95% confidence intervals of modelled habitat parameters for each flow for mussel GPS sites and the 1000 random points.

Table S3. Potential suitable and potential persistent habitat (m^2) for the three reaches at each modelled flow.

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