Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A.

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SUMMARY

1. Studies of North American streams have shown that hydraulic parameters and stream geomorphology can explain unionid mussel abundance at both the reach and catchment scale. However, few studies have examined applicability of hydrogeomorphic variables across broader spatial scales, such as across whole catchments, or have elucidated conditions under which spates can affect mussel populations in streams.

2. We quantified freshwater mussel abundance and species richness and their physical habitat at 24 sites in eight streams in southern Appalachian catchments in 2000 and 2001. In addition, we modelled site-specific hydraulic parameters during summer baseflow and bankfull stages to estimate high- and low-discharge conditions, respectively.

3. Mussel abundance was related to stream geomorphology, whereas richness was related to stream size. Baseflow habitat parameters explained only minor variation in abundance or richness, and both measures were highly correlated with mean current velocity or stream size. Bankfull shear stress composed a relatively low proportion of overall mussel habitat variability, but it accounted for significant variation in abundance and richness.

4. Mussel abundance was highly variable at sites subject to low-shear stress during spates, whereas abundance always was low at sites subject to high-shear stress. These data suggest that habitat conditions during floods, rather than those at summer baseflow, limit the abundance of mussels in Appalachian streams. These data also suggest that mussel abundance and assemblage structure may be sensitive to any changes in channel geomorphology and hydraulic conditions that might result from land use in the catchment.

Keywords: Alabama, floods, habitat, shear stress, stream geomorphology, Unionidae

Introduction

Freshwater mussels (Bivalvia: Unionoida) are among the world's most endangered organisms. Some estimates indicated that approximately 70% of the approximately 300 North American taxa are endangered, threatened, or locally at risk (Williams *et al.*,

1993; Strayer *et al.*, 2004). Impoundments, exotic species and degraded water quality have all played a role in mussel declines (Lydeard *et al.*, 2004). However, mussel populations also have declined in unimpounded catchments where national or local legislation has restricted large-scale habitat modifications. Regrettably, few broadly applicable explanations for mussel declines in free-flowing streams have been proposed, which has hampered the ability of regulatory agencies to slow declines or rehabilitate populations (Strayer *et al.*, 2004).

The degree to which physical habitat affects freshwater mussel populations has long perplexed

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biologists. Early workers noted a strong association between some taxa and specific microhabitats (van der Schalie, 1938), whereas recent empirical studies have found few linkages between stream physical habitat characteristics and mussel abundance (Strayer & Ralley, 1993; Strayer, 1993; Layzer & Madison, 1995; Haag & Warren, 1998). This disparity may be because physical properties of streams are highly influenced by stream size (catchment area) and thus may not adequately characterise variability in local habitat conditions on a scale that is relevant to mussels. In this context, Newbury (1984) and Statzner, Gore & Resh (1988) hypothesised that conventionally measured 'simple' physical variables, such as current velocity, depth, and substratum size, are ineffective in explaining patterns of benthic invertebrate abundance in streams because they do not adequately describe the complex three-dimensional influence of flow on biota. Instead, use of 'complex' hydraulic characteristics (e.g. Froude and Reynolds numbers, shear stress and shear velocity) has been advocated to more effectively model interactions between the nature of stream flow processes and benthic organisms (Statzner *et al.*, 1988; Hardison & Layzer, 2001).

The results of several recent studies suggest that nearbed hydraulic parameters, such as bed stability, can explain mussel aggregations at the individual stream reach (i.e. 0.1–1.0 km, Strayer, 1999; Johnson & Brown, 2000; Hardison & Layzer, 2001) and larger stream segment (sensu Bisson & Montgomery, 1996) spatial scales. Strayer (1999) and Johnson & Brown (2000) both reported that mussel aggregations occurred primarily within 'hydraulic refugia' (i.e. areas of the stream bed that remain stable during spates or are protected from the direct force of scouring flows). Comparatively few studies, however, have examined the applicability of hydraulic parameters over broader scales, such as within whole catchments. Additionally, most published studies have only described physical habitat conditions experienced during relatively benign baseflow conditions.

Recently, Howard & Cuffey (2003) modelled high-flow events across much of a high-gradient California coastal river catchment and found that mussel aggregations occurred in reaches experiencing relatively low-energy flows during spates. We know of no other published studies that have empirically modelled freshwater mussel responses to high-flow events across entire river catchments. Catchment-scale stud-ies can be used alongside smaller, local-scale efforts to provide a more comprehensive means of assessing the relative importance of local versus large-scale environmental influences on mussels. Stream physical characteristics are often dramatically affected by gradations in geology and climate across river catchments. In this sense, associations between mussels and physical habitat parameters measured across several tributary sub-catchments can provide a more spatially relevant estimate of the importance of local habitat models and thus help guide effective management of imperiled populations and their habitats.

We examined associations between freshwater mussel abundance and species richness and stream hydraulic parameters at across eight Appalachian catchments in the south-eastern U.S.A. Many of these catchments have experienced dramatic declines in mussel species richness (and presumably abundance) from historical conditions (Gangloff & Feminella, in press). Mussel populations in many study streams are restricted to highly localised sub-catchment reaches but the habitat factors contributing to their persistence in these reaches are poorly understood. Conservation and recovery of these often highly endangered populations will require an understanding of how habitat conditions contribute to mussel persistence. Specifically, we (i) examined the degree to which directly and indirectly measured physical habitat attributes predicted mussel abundance and richness, and (ii) modelled site-specific nearbed shear stress and bed stability, at both baseflow and bankfull (spate) conditions, to assess the importance of scouring flows and potential for streambed movement on mussel distribution and abundance.

Methods

Study area

We quantified mussel and habitat variables in 24 sites in eight subcatchments of the Coosa River (Fig. 1), which drains 26 589 km² in Alabama, Georgia and Tennessee (Hurd, 1974). Historically, this catchment supported approximately 50 species of unionid mussels, with richness being highest in the main stem and in the larger tributaries including Conasauga and Chattooga rivers and Choccolocco Creek (Hurd, 1974; Gangloff & Feminella, in press). Similar to many large Appalachian rivers, the Coosa has long been known
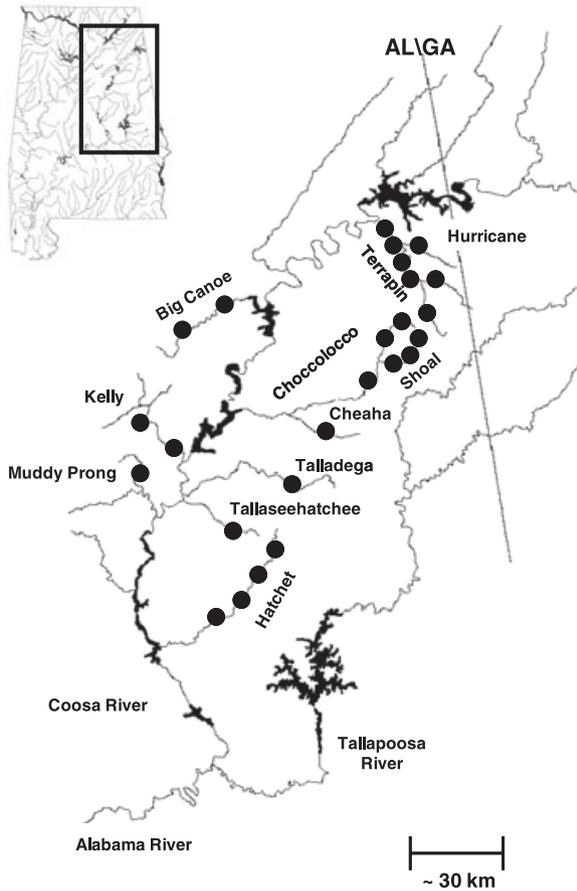
Fig. 1 Map showing locations of study sub-catchments and sites (closed circles) in the Coosa River Catchment of Alabama, U.S.A.

for its broad, shallow shoals, which provided stable, well-oxygenated, and heterogeneous habitats favoured by many mussel species (van der Schalie, 1938).

Impoundments, channelisation, agriculture and urban development are widespread in the Coosa Catchment; collectively, these land uses can radically alter stream channel geomorphology (Morris & Corkum, 1996; Pringle, Freeman & Freeman, 2000; Groffman *et al.*, 2003; Poole & Downing, 2004). Widespread impoundments have reduced the extent of unregulated reaches in the main stem Coosa River (Hurd, 1974). Diverse (approximately 20 species) mussel assemblages presently are restricted to two free-flowing reaches of the main stem (Gangloff & Feminella, in press). Whereas diverse assemblages (>20 species) also persist in several tributary sub-catchments, other subcatchments have lost all or most of their mussel assemblages (Gangloff & Feminella, in press).

We selected study streams based on prior documentation of mussel presence during qualitative surveys. We quantified mussels and their habitats at 24 sites in eight Coosa tributary sub-catchments (Fig. 1). Streams ranged from third to sixth order, and occur in three physiographic provinces, including the Ashland Plateau (Hatchet Creek), Cahaba Ridge and Valley (Big Canoe and Kelly creeks, Muddy Prong), and the Coosa Valley (Cheaha, Choccolocco, Hurricane, Shoal, Talladega, Tallaseehatchee and Terrapin creeks; Hurd, 1974; Gangloff & Feminella, in press).

Mussel sampling

We sampled mussels in three 50-m reaches per site from May to October in 2000 and 2001. We detected mussels visually using timed searches with mask and snorkel or using an AquaScope II[TM] (Lawrence Enterprises, Seal Harbor, ME, U.S.A.); we also used tactile detection of mussels in small gravel, sand, or silt substrata to detect buried mussels. Additionally, larger cobbles were dislodged and the substratum beneath them examined for species that aggregate in these microhabitats (e.g. *Elliptio arca*, *E. arctata*). We expressed mussel abundance as catch per unit effort (CPUE). We chose to use timed searches rather than quadrat excavation because preliminary quantitative sampling in many sites revealed low unionid densities (<0.1 mussels m^{-2}) (M.M. Gangloff, unpublished data). Although timed searches may result in less precise estimates of unionid abundance, they typically provide more accurate estimates of species richness than more conventional quantitative sampling (Strayer, Claypool & Sprague, 1997; Vaughn, Taylor & Eberhard, 1997; Strayer & Smith, 2003).

We conducted all sampling during summer base-flow conditions, a time when clear, low water facilitated detection of mussels. We sampled from a downstream to upstream direction, with a single observer (M.M.G.) searching each 50-m reach for approximately 1 h. We field-identified all unionids to species and returned animals to the stream whenever possible; in some instances, live mussels were retained as voucher specimens. Otherwise, shells were retained as vouchers and deposited into the Auburn University Museum Invertebrate Collection.

Habitat and hydraulic measurements

We used link magnitude (the number of first-order tributaries upstream of the sampling reach), as an index of catchment size (Haag & Warren, 1998; Gordon *et al.*, 2004). We quantified mean water depth, bottom and mid-depth current velocity (Flow-Mate^{TM} model 2000; Marsh-McBirney Inc., Frederick, MD, U.S.A.), and nearbed shear stress (T, the downward force exerted by flow on the stream; Newbury, 1984) along six evenly spaced cross-stream transects per reach, at intervals, corresponding to 0.1, 0.3, 0.5, 0.7 and 0.9× channel width ($n = 30$ measurements per reach). We measured channel gradient using a clinometer and stadia rod at the left and right banks and in mid-channel at 10-m intervals ($n = 15$ measurements per reach). We also measured bankfull depth and width at these points (Gore, 1996), with a single observer (M.M.G.) making all bankfull depth measurements ($n = 6$ measurements per reach). We used flood debris or direct observation of high water events to verify bankfull depth estimates. Last, we quantified bed substratum size by measuring the maximum diameter of 20 randomly selected particles along each transect ($n = 120$ particles per reach).

We quantified T using two different methods at each site. First, we estimated point-specific (localised) shear stress using Fliesswasserstammtisch (FST) hemispheres (T_{FST}). FST hemispheres have a fixed surface area but are of different densities (Statzner & Müller, 1989). We placed individual hemispheres on a smooth, level platform on the stream bottom, and recorded the downstream movement of the largest sphere; the sphere density (1–14) directly corresponds to nearbed shear stress at that point (Statzner & Mller, 1989). We made T_{FST} measurements at 30 evenly spaced intervals per reach. Secondly, we empirically derived T ($T_{empirical}$) for each site using site morphometry parameters. We obtained $T_{empirical}$ estimates by multiplying the depth (or bankfull depth, for bankfull $T_{empirical}$) of each channel by the mean slope and the gravitational constant (Gordon *et al.*, 2004). We assumed that hydraulic radius (R) was equal to mean water depth, a condition characteristic of broad, shallow channels with width-to-depth ratios ≥20 : 1 (Gordon *et al.*, 2004), and typical of many Appalachian streams.

We also used mean depth and current velocity measures to calculate Reynolds (R_e) and Froude numbers (F_r). Hardison & Layzer (2001) found that both R_e

and F_r were useful local-scale predictors of mussel abundance. R_e is a dimensionless quantity that describes the ratio of internal to external turbulent forces or the degree of laminar (linear) flow (Vogel, 1981; Statzner *et al.*, 1988). In contrast, F_r describes the ratio of inertial to gravitational forces in flow, and has important implications for the size and shape of hydraulic refugia associated with obstacles (e.g. boulders or woody debris) in the channel and local substratum composition (Gordon *et al.*, 2004). At low F_r, disturbance waves (i.e. energy) are transmitted both upstream and downstream (i.e. subcritical flow), whereas at high F_r disturbances are only transmitted downstream (i.e. super-critical flow; Gordon *et al.*, 2004).

Substratum particle size and its variation (roughness) may be both a component of, and be affected by, T, such that highly variable substrata may increase bed roughness and decrease T (Newbury, 1984; Gordon *et al.*, 2004). We did not account for substratum roughness in $T_{empirical}$ estimates; instead, we estimated the susceptibility of substratum particles to be displaced downstream using an index of streambed disturbance (D_I; Cobb & Flannagan, 1990), by dividing $T_{empirical}$ both at baseflow and at bankfull by the median particle size. Low and high index values corresponded to high and low bed stability, respectively (Cobb & Flannagan, 1990).

Hypotheses and statistical analyses

We described relationships between mussel CPUE and stream physical habitat variables using a combination of correlation and multiple regression analyses. First, we tested all variables for normality using Kolmogorov–Smirnov tests, and transformed all non-normal variables using $\log_{10}(x_i + 1)$ prior to analysis (Sokal & Rohlf, 1995). Secondly, we used principal components analysis (PCA) to reduce the number of physical habitat variables in multiple regression models and minimise procedure-wise error rates (Sokal & Rohlf, 1995). We then used PCA scores as derived, orthogonal variables in subsequent correlative and multiple regression analyses describing variation in mussel abundance across sites.

We examined associations between habitat PCA scores, mussel CPUE and species richness (as the number live animals of different species collected at each site) using Pearson correlations. We analysed 2000 and 2001 data separately because a different suite

of sites was visited during each year. We hypothesised that $T_{empirical}$ would better predict mussel abundance and richness than T_{FST} because empirically derived values integrate and represent physical forces impinging on mussels at the reach ($T_{empirical}$) rather than the microhabitat (T_{FST}) scale. We used stepwise multiple regressions to examine the degree to which habitat PCA scores predicted mussel abundance and richness, to test the hypotheses that (i) sites with higher mussel abundance and richness had low T (as indicated either by $T_{empirical}$ or T_{FST}) and (ii) that bankfull $T_{empirical}$ was a better predictor of abundance and richness than baseflow $T_{empirical}$. We also predicted that (i) abundance and richness would be highest in sites experiencing a low potential bedload movement (PBM) as indicated by D_I and (ii) bankfull PBM would explain mussel abundance and richness better than baseflow PBM. All statistical analyses were conducted using SPSS (Version 11.01, SPSS Inc., Chicago, IL, U.S.A.) and we set alpha levels at $P = 0.05$.

Results

The first four principal components accounted for approximately 89% of the variation in physical habitat parameters among the study sites (Table 1).

Table 1 Principal components with eigenvalues >1.5 explaining approximately >10% of the instream variation among the 24 study sites surveyed for mussels in 2000 and 2001 in the Coosa River Catchment. Maximum factor loadings for each variable and the total proportion of habitat variability among sites explained by each component are given.

Variable	PC_1	PC_2	PC_3	PC_4
Link magnitude	0.869			
Gradient			0.877	
Width	0.918			
T_{FST}		0.853		
Depth	0.813			
Velocity		0.843		
Bankfull depth	0.599			
Bankfull width	0.956			
F_r		0.880		
R_e		0.783		
Baseflow $T_{empirical}$			0.791	
Bankfull $T_{empirical}$			0.983	
Median particle size				−0.908
D_I				0.958
Bankfull disturbance index				0.877
% of total variation	27.4	23.9	19.2	18.5

T, shear stress; F_r, Froude number; R_e, Reynolds number. FST, Fliesswasserstammtisch; D_I, disturbance index

PC_1 accounted for 27% of the variability, with variables showing high positive loadings being related to factors associated with stream size (link magnitude, mean channel width, depth and bankfull depth; Table 1). PC_2 explained 24% of the variation, with factors describing flow conditions showing high loadings (T_{FST}, current velocity, Fr and Re; Table 1). PC_3 explained an additional 19% of the variation, with factors largely describing shear stress conditions, with channel gradient, baseflow $T_{empirical}$, and bankfull $T_{empirical}$ all showing positive loadings. Finally, PC_4 (19%) consisted mostly of factors describing substratum size and mobility, including median particle size (negative loading) and baseflow and bankfull D_I (positive loadings, Table 1).

Pearson correlations revealed few significant relationships between habitat PCA scores and mussel abundance and richness. However, there was a negative relationship between PC_3 (shear stress, channel gradient) and abundance in 2001 ($r = -0.752$, $P = 0.003$, $n = 13$), but not richness ($r = -0.479$, $P = 0.098$, $n = 13$). In addition, there were few significant relationships between simple physical habitat variables and abundance or richness in either year; most variables were related to stream size (as link magnitude, 67% of significant correlations) rather than mussel response variables (33%, Table 2).

Backward stepwise multiple regression revealed that PC_3 (shear stress, channel gradient) was the best predictor of mussel abundance, explaining approximately 57% of the variation in abundance in 2001 (ANOVA, $F_{1,12} = 14.28$, $P = 0.003$). Addition of other PCs did not significantly increase model predictive power. Multiple regression indicated that PC_3 was the best predictor of mussel abundance, so we also examined the separate relationships between abundance and factors loading high on PC_3 (gradient, bankfull $T_{empirical}$, baseflow $T_{empirical}$) using Pearson correlations. Univariate analysis revealed a significant relationship between abundance and bankfull $T_{empirical}$ only in 2001 (Fig. 2). Further, correlations revealed negative relationships between abundance and gradient ($r = -0.615$, $P = 0.025$ $n = 13$, Table 2) and bankfull $T_{empirical}$ ($r = -0.697$, $P = 0.008$, $n = 13$, Fig. 2) in 2001. Correlations also revealed a significant negative relationship between richness and gradient ($r = -0.661$, $P = 0.014$, $n = 13$, Table 2).

Curve-fitting procedures determined that the relationship we observed in 2001 between mussel abun-

Table 2 Significant Pearson correlations between physical habitat parameters and site link magnitude, mussel catch per unit effort (CPUE), and species richness at study sites in 2000 and 2001

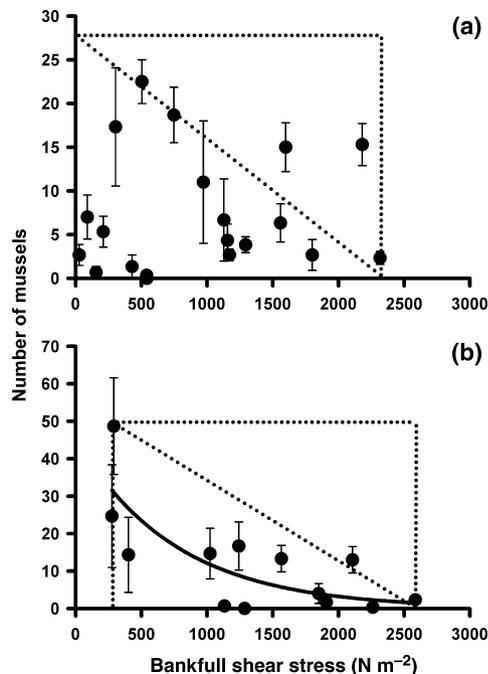| Habitat parameter	2000 Link magnitude ($n = 20$)	2001 CPUE ($n = 13$)	2001 Richness ($n = 13$)	2001 Link magnitude ($n = 13$)
Stream depth	$r = 0.720, P < 0.001$			$r = 0.785, P = 0.001$
Mid-depth velocity	$r = 0.599, P = 0.005$			
T_{FST}	$r = 0.510, P = 0.022$		$r = -0.615, P = 0.025$	
Channel gradient		$r = -0.615, P = 0.025$	$r = -0.661, P = 0.014$	
Channel width	$r = 0.897, P < 0.001$			$r = 0.871, P < 0.001$
Bankfull $T_{empirical}$		$r = -0.697, P = 0.008$		
R_e	$r = 0.729, P < 0.001$			
F_r	$r = 0.527, P = 0.017$			

Fig. 2 Mean (±standard error) number of mussels per 50 m reach and bankfull shear stress estimated using site mean channel gradient and bankfull depth in 2000 (a: $r^2 = 0.005$, $P = 0.757$, $n = 20$) and 2001 (b: $r^2 = 0.60$, $P = 0.0012$, $n = 13$). Dashed vertical lines represent boundaries of independent variable and horizontal line represents upper boundary of dependent variable. Diagonal represents cut point for random (50 : 50) distribution.

dance and bankfull $T_{empirical}$ was best explained by a logarithmic model ($r^2 = 0.6$, $F_{1,11} = 17.97$, $P = 0.0012$; Fig. 2). Therefore, we conducted *post-hoc* χ^2 analyses to determine if mussel abundance data were randomly distributed with respect to bankfull $T_{empirical}$. We drew horizontal and vertical lines connecting the maximum x and y values and then constructed a diagonal line connecting the maximum x and y values

(Fig. 2). All points falling above the diagonal line were given a score of 1 whereas those below the diagonal were given a score of −1. If data on the scatter plot were random, the number of points above and below the diagonal should approximate a 50:50 distribution. *Post-hoc* χ^2 analysis revealed that in both 2000 ($\chi^2 = 5.0$, $P = 0.025$, d.f. = 1) and 2001 ($\chi^2 = 3.8$, $P = 0.052$, d.f. = 1) the distribution of mussel data points was significantly non-random, with high variation in abundance observed at low bankfull $T_{empirical}$ and progressively lower abundance at higher levels of this measure (Fig. 2).

Discussion

Role of shear stress on mussel assemblages

Our data suggest that shear stress during high-flow periods is a critical factor affecting mussel distributions in southern Appalachian streams, as sites experiencing higher shear stresses during bankfull floods had fewer mussels than sites with lower bankfull shear stresses. Moreover, multiple regression revealed that bankfull $T_{empirical}$, both as a single variable and combined with other correlated physical variables as PC_3, was the most important environmental factor affecting abundance. Mussel species richness was negatively related to measured T_{FST} and stream channel gradient, and both shear stress and gradient decreased with increasing link magnitude, suggesting richness was largely a function of stream size (Strayer, 1983, 1993; Haag & Warren, 1998). Surprisingly, T_{FST} was not related to abundance, possibly because shear stress measurements were affected by local substratum conditions. Irregular stream beds, such as in our study, may yield highly

variable estimates of T_{FST} (Frutiger & Schib, 1993). Further, our results suggest that T_{FST} appears to increase with current velocity and stream size (Tables 1 and 2), suggesting that T_{FST} may be most useful at estimating within-reach (<50 m) variation in shear stress.

The abundance patterns we observed are similar to those observed for *Margaritifera falcata* in the Eel River, California, where Howard & Cuffey (2003) found that mussels were more aggregated in reaches with lower flow velocities and boundary shear stress during floods than in reaches with higher levels of these measures. However, our data show that shear stress is important across much broader spatial scales (i.e. across multiple streams within a large catchment). This suggests that stream channel attributes that contribute substantially to bankfull $T_{empirical}$ values (notably gradient and bankfull depth) are useful predictors of mussel habitat suitability and provide a basis for habitat-based management of endangered mussel populations in the Coosa and other Appalachian streams.

Our data revealed a high degree of variability in mussel abundance at low-shear stress sites. The resulting wedge-shape pattern is referred to by Brown (1995) as a 'constraint envelope'. In constraint envelopes, an ecological parameter (bankfull $T_{empirical}$ in our study) limits the abundance of a population at high levels but not at lower levels. Populations experiencing a low level of some constraining factor may be regulated by other, unmeasured factors. Constrained patterns in our data are likely result from other environmental factors that limit mussel populations at low shear stress habitats, such as variation in host fish abundance, interannual variation in climate and associated flow regimes, and spatial variation in the influence of physicochemical stressors such as sedimentation associated with landscape disturbance on mussel populations (Haag & Warren, 1998; Brim-Box, Dorazio & Liddell, 2002; Diamond, Bressler & Serveiss, 2002; Gillies et al., 2003; Golladay et al., 2004). In contrast, hydraulic disturbance in high shear stress habitats appeared regular enough, perhaps even in dry years, to consistently limit mussel abundances.

Shear stress (as PC_3) explained only 16% of the overall variation in instream habitat conditions, yet this factor was the best predictor of mussel assemblages in terms of both abundance and richness. This result suggests that relatively minor variation in physical habitat conditions, especially spatial variation in channel gradient and bankfull depth, in Appalachian streams may have dramatic effects on mussel assemblages. Surprisingly, much of the remaining variation in habitat conditions was related to stream size and current velocity, yet PC_1, a component largely describing stream size, and PC_2, a component largely reflecting nearbed flow conditions, were not useful predictors of abundance or richness. We surmise this pattern occurs because nearly all lotic habitat parameters vary predictably along longitudinal gradients. Channel width, bankfull width, current velocity, and channel depth all increase with stream size (Hynes, 1970; Table 2). Thus, simple physical habitat parameters likely have limited utility to explain variation in freshwater mussel abundance, especially at small (i.e. microhabitat) scales.

Bankfull vs. baseflow shear stress

Studies examining the relationships between mussel assemblages and physical habitat parameters at baseflow conditions have often found equivocal results (Strayer, 1993; Strayer & Ralley, 1993; Haag & Warren, 1998). However, studies that have focused on habitat conditions during spates have found that mussel assemblage structure (Di Maio & Corkum, 1995) or aggregation patterns (Strayer, 1999; Johnson & Brown, 2000; Howard & Cuffey, 2003) are limited by conditions experienced during high-flow periods. Of these, only Howard & Cuffey (2003) quantified force exerted by the stream at along its bed during spates. In their study, mussel abundance showed the same nonrandom relationship with boundary shear stress that we observed, which they speculated was the result of mussels aggregating in deep, low-gradient reaches that served as refugia from scouring flows (Howard & Cuffey, 2003).

Bankfull floods occur regularly (approximately yearly) in many Appalachian streams, and such events can have strong effects on mussel populations in other streams (Vannote & Minshall, 1982; Tucker, 1996; Hastie et al., 2001). *In situ* measurement of bankfull shear stress conducted during low-flow periods provides a useful method to estimate hydraulic forces experienced by benthic organisms when direct measurements of T are impossible.

Newbury (1984) and Cobb, Galloway & Flannagan (1992) both noted that tractive force is approximately equal to the diameter of a rounded particle displaced under friction-free conditions. Thus, a flow exerting a shear stress of 50 N m^{-2} is capable of displacing a 50-cm diameter particle under laboratory conditions. Obviously, a combination of factors including substratum irregularity and entrainment limit substratum movement in natural systems, but this example illustrates the amount of energy available for substratum (and mussel) displacement in fluvial systems.

Year-to-year variation in mussel abundance

We only observed significant linear relationships between shear stress and mussel abundance during 2001 (vs. 2000), yet χ^2 analyses revealed that in both years the shear stress–abundance relationship was statistically significant, and, thus, biologically meaningful. In 2000, high mussel variability at low-shear stress sites decreased linear and curvilinear model fit, whereas in both years, high variability in mussel abundance occurred at low-shear stress sites (Fig. 2). During 1999 and 2000, drought reduced flows in many south-eastern streams (Golladay *et al.*, 2004). In our study, higher flows in 2001 (vs. 2000) may have reduced accumulated fine sediments and increased mussel detection effectiveness at low shear stress sites. Alternatively, displacement of mussels from hydraulically unstable habitats may have decreased mussel abundance in high shear stress sites from 2000 to 2001 and contributed to between-year differences in observed patterns.

Anthropogenic modification of stream hydraulic properties

Human activities, primarily agriculture and urbanisation, likely have played an important role in shaping the present geomorphology of many Appalachian streams (Glenn, 1911; Gillies *et al.*, 2003; Poole & Downing, 2004). Removal of native vegetation and conversion to row crops and urban landscapes may diminish soil water retention, increase overland and instream flow, ultimately causing increased bed erosion and channel degradation (Glenn, 1911; Lyons & Beschta, 1983; Potter, 1991; Groffman *et al.*, 2003). As stream channels become increasingly incised their cross-sectional areas increase, which in turn increases the bankfull channel capacity and, ultimately, nearbed shear stress during storm events (Newbury, 1984; Groffman *et al.*, 2003).

It is important that future studies address the role of upstream and local land use on changes in stream geomorphology and associated shear stress in other Appalachian catchments. Other studies have noted that mussel assemblages varied among streams differing in forested versus agricultural riparian land use (Morris & Corkum, 1996) and flood responsiveness (Di Maio & Corkum, 1995). Many southern Appalachian streams have experienced dramatic declines in mussel species richness over the past 100 years (Parmalee & Bogan, 1998; Brim-Box & Williams, 2000; Gangloff & Feminella, in press). The recent rapid growth of human populations in this region has been linked to dramatic shifts in the composition of stream insect and fish assemblages (Sutherland, Meyer & Gardiner, 2002; Roy *et al.*, 2003; Walters *et al.*, 2003; Helms, Feminella & Pan, 2005), although the precise effects of urbanisation on mussel assemblages remain poorly understood.

We hypothesise that changes in mussel assemblages in many southern Appalachian streams may be explained by modification of stream channel geomorphology resulting from changing land use. Mussel declines in other North American streams have been linked with changes in land use or stream geomorphology (Arbuckle & Downing, 2002; Poole & Downing, 2004). Unfortunately, many southern U.S. states still provide minimal or no legal protection to streams or riparian zones. Conservation of remaining Appalachian mussel populations will require that state or federal agencies take steps to implement riparian safeguards within critical stream catchments designed to limit destabilisation of stream channels. Current (voluntary) restrictions on development in and removal of riparian zones are clearly insufficient to minimise impacts to endangered freshwater mussel populations.

Acknowledgments

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