Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology

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Abstract: We tested the hypotheses that mussel species richness and density are related to landscape features of watersheds. Measures of species richness and mussel density were estimated at 118 sites in 36 watersheds in the state of Iowa, U.S.A., a landscape characterized by >90% agricultural development. Geographical Information Systems (GIS) and regression analyses examined seven land use categories and nine geological descriptors, determining that both mean density and species richness were best correlated with mean watershed slope and the prevalence of alluvial deposits. Our analyses imply that agricultural watersheds with high slopes impact mussel abundance and richness through siltation and destabilization of stream substrate. Because alluvial deposits improve groundwater flux to streams, results suggest that relatively stable stream flows in alluvial watersheds improve mussel persistence. A second set of 82 observations on 38 independent watersheds corroborates the analyses, although historical and local impacts cause correlations between new observations and predictions to be weak.

Résumé : Pour éprouver l'hypothèse selon laquelle la richesse en espèces et la densité des moules sont reliées aux caractéristiques du paysage du bassin versant, nous avons estimé la richesse en espèces et la densité des moules de 118 sites appartenant à 36 bassins versants en Iowa, un paysage utilisé à plus de 90 % pour l'agriculture. À l'aide de systèmes d'information géographique et d'analyses de régression, nous avons étudié sept catégories d'utilisation du territoire et neuf descripteurs géologiques et trouvé que la densité moyenne et la richesse en espèces sont en corrélation principalement avec la pente moyenne du bassin versant et l'importance des dépôts alluviaux. Nos analyses permettent de croire que les bassins versants agricoles à forte pente ont d'importantes répercussions sur l'abondance et la richesse des moules à cause de l'envasement et de la déstabilisation des cours d'eau. Parce que les dépôts alluviaux améliorent le flux des eaux souterraines vers les cours d'eau, nos résultats suggérent que les débits relativement stables dans les bassins versants alluviaux favorisent la persistance des moules. Une seconde série de 82 observations provenant de 38 autres bassins versants corroborent les résultats des analyses, mais à cause de facteurs historiques et des conditions locales, les corrélations entre ces nouvelles observations et nos prédictions sont faibles.

[Traduit par la Rédaction]

Introduction

Freshwater mussels are among the most imperiled animals worldwide (Master 1990). A variety of anthropogenic stressors, including habitat destruction and degradation, commercial exploitation, and water pollution, have been implicated in the disappearance of these animals (Pennak 1989; Bogan 1993; Williams and Neves 1995). Effective conservation and restoration of mussel populations depends upon an understanding of how they are impacted by landscape-driven alterations in water quality.

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The land–water interface can have important effects on the persistence of aquatic organisms (Karr and Schlosser 1978; Richards and Host 1994; Roth et al. 1996). Watershed characteristics are often closely related to biotic and abiotic characteristics of streams (Schlosser 1991; Rabeni and Jacobson 1993; Wang et al. 1997). For example, surficial geological features determine hydrologic patterns and channel morphology at the watershed scale and influence macroinvertebrate assemblages (Richards et al. 1996). In addition, landscape changes such as urbanization, logging, and the conversion of native land cover to agricultural crop production often lead to degraded habitat conditions.

Land use, topographic relief, and geologic history influence stream water quality. Land use activities that remove vegetative cover decrease infiltration rates and the moisture-holding capacity of soils (Brooks et al. 1997). Topographic relief of the landscape surrounding streams also influences water quality (Elliot and Ward 1995). For example, disturbed, high-relief watersheds have greatest overland flow, produce relatively large amounts of sediment in runoff water, and have high-gradient streams, all of which can destabilize substrates, rendering stream conditions unsuitable for freshwater mussels. Although low-relief watersheds have less runoff

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impact, low-gradient streams are prone to siltation. This is especially true in agricultural areas where sediment is often the major stream pollutant. Further, geologic features like surficial alluvial aquifers influence water recharge, and thus groundwater and surface water quality (Anderson 1998). The stable discharge of groundwater from alluvial aquifers in present-day stream valleys can prevent loss of the biota via desiccation of permanent rivers.

In spite of the potential importance of watershed characteristics, much of the study of mussel–habitat relationships has been performed on the scale of the local stream-reach (e.g., Strayer and Ralley 1993; Di Maio and Corkum 1995; Layzer and Madison 1995). Some studies have related mussel abundance and distribution to local stream attributes such as hydrologic variability (Di Maio and Corkum 1995) and substrate composition (Strayer and Ralley 1993), but local characteristics like sediment quality (e.g., granulometry) have explained little variation in stream mussel distributions (e.g., Strayer and Ralley 1993). Because larger-scale landscape features influence water quality, and thus, the development of aquatic communities (Richards and Host 1994; Richards et al. 1996; Roth et al. 1996), population persistence can be influenced by landscape features such as surface geology, soil, and riparian land use (Strayer 1983; Morris and Corkum 1996; Brim Box and Mossa 1999). Understanding relationships between watershed-scale landscape characteristics and mussel populations may therefore contribute to the protection of these threatened animals.

The objective of this study was to determine the relationship of watershed land use and geomorphic features to mussel species richness and population density in an intensely agricultural region that has been a historical center for mussel biodiversity. We sought to develop statistical models to characterize watershed characteristics conducive to high mussel species richness or density and to test these models on independent samples from different watersheds.

Materials and methods

Study design

The overall study plan was to use descriptive Geographic Information Systems (GIS) modeling to derive watershed attributes (e.g., land use, geology, and topographic relief) followed by regression analysis to determine relationships between landscape features and mussel density and mussel species richness. Specifically, we (*i*) used GIS descriptive modeling techniques to quantify selected landscape characteristics of watersheds surveyed in 1998 and 1999, (*ii*) used regression and correlation analysis to determine the significance of relationships between watershed characteristics and mussel species richness and population density data derived in a 1998 survey, (*iii*) used these models to identify potentially mussel-friendly watersheds to be sampled in the 1999 survey, and (*iv*) tested the strength of original predictive models using mussel density and species richness data collected in the independent 1999 field survey.

Study area

Our study sites were located in the Mississippi River basin, distributed over the state of Iowa (U.S.A.) (Fig. 1), which has been considered a historical center of mussel diversity in North America (Pennak 1989). The landscape features of this region are the result of recent and historical glacial and erosional processes. Geological landscape evolution left nine distinct geologic regions and widespread regional pockets of alluvial deposition (Prior 1991). Elevation ranges from a low (146 m above sea level) in the southeast corner to a high of 509 m in the northwest corner of the study area. Nearly 90% of the landscape is currently in agricultural production (Thompson 1992), so watersheds receive considerable agricultural impact.

Field survey

We surveyed mussel populations in 36 watersheds in 1998 and 38 watersheds in 1999 (see Fig. 1). Data on the occurrence of mussel species used in this analysis were collected in initial field surveys made during July–September 1998 at 118 sites and follow-up samples taken at 82 sites in July–September 1999. Sites sampled in 1998 were the inland stream sites that were previously sampled in 1984–1985 in an assessment of Iowa's "best" mussel habitat and thus represented much of the finest lotic habitat in the state at that time. Data collected in 1984–1985 and 1998 show substantial declines in species richness over this period (K.E. Arbuckle and J.A. Downing, unpublished data).

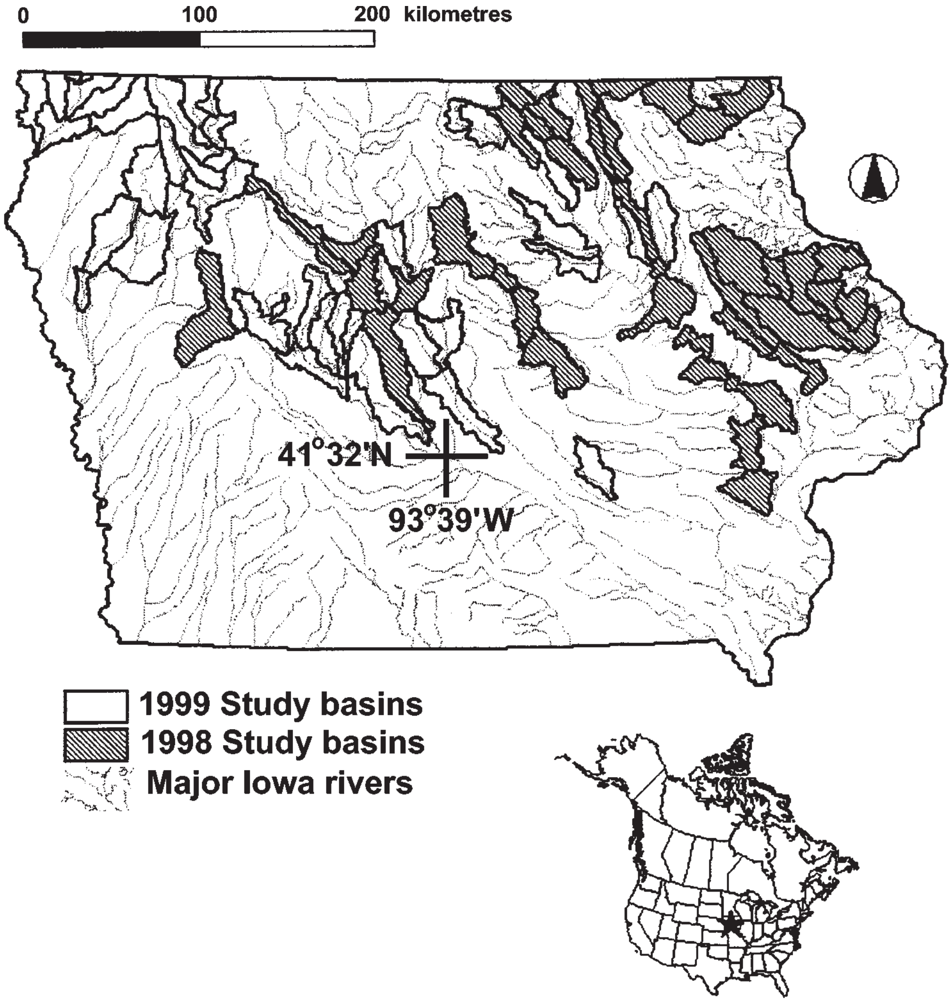
The criteria used to select sites sampled in 1998 included (*i*) streams (excluding Mississippi River sites) that had been previously surveyed as representative of the State's "best" mussel habitat (Frest 1987); but (*ii*) we only sampled streams where depth was suitable for use of visual and tactile survey methods while wading (i.e., <1.5 m depth). The criteria used in selecting streams for the 1999 survey included (*i*) interior stream reaches recommended (but not previously sampled) as representative of very good mussel habitat by Frest (1987); or (*ii*) areas identified by the 1998 predictive study (see below) as having the potential to support mussels. In 1999, only sites where stream depth was suitable for use of visual and tactile survey methods while wading were sampled.

At each of these sites, the survey segment was located at least 100 m from a road or bridge access area to minimize disturbance of these structures. All sites were systematically surveyed by three people searching while moving upstream along the stream segment. The length of stream surveyed varied by stream size. We surveyed 200 m in small streams (mean stream width (MSW) <10 m), 500 m in medium streams (MSW 10–25 m), and 1 km of stream in large systems (MSW >25 m). Medium and large streams were only surveyed during periods of low flow.

Mussel survey

Density was quantified using visual and tactile searches of 60 1-m^2 quadrats at each site. We used a restricted random sampling design (Hayek and Buzas 1997) to collect quadrat samples along the entire segment length and from a variety of water depths and habitat types. The stream area was divided into thirds across the channel and into 10 equally spaced segments along the length, and a random number table was used to assign the sample points to be covered by the quadrats sampled in each area. Twenty 1-m^2 quadrats

Fig. 1. Outlines of the 38 watersheds surveyed for freshwater mussels in 1998 (shaded) and 36 watersheds surveyed in 1999 (open), in the state of Iowa, U.S.A.



were inspected along the right bank, 20 along the left bank, and 20 in the mid-channel for a total of 60 quadrats at each site. Substrate within the quadrat was excavated to a depth of 20 cm and searched tactilely to locate mussels.

An extensive visual survey of the substrate in shallow water (<0.05 m) was performed simultaneously with the quadrat survey. In addition to the quadrat survey and visual inspections of the substrate outside the quadrats, we searched the stream banks and areas adjacent to the stream for shells. Shells were collected and returned to the laboratory for identification. Living mussels were identified, photographed, and returned to the stream.

A list of species and number of individuals observed inside and outside the quadrats was compiled for each site. Between 1 and 15 (average ca. 3) sampling sites were analyzed within each of 74 watersheds. Species identifications were confirmed in the laboratory using digital images of living animals and shell material obtained at each site. Mean mussel density ($\bar{D}_{98}$, $\bar{D}_{99}$) and mean species richness ($\bar{R}_{98}$, $\bar{R}_{99}$) estimates for each watershed were calculated as the arithmetic average of all densities or richness estimates from all sites within each of the watersheds. Although these data would be sufficient to calculate most indices of biotic diversity, we have chosen to analyze richness and density separately for clarity of interpretation and to avoid choosing among the aggregate indices of diversity.

GIS watershed analysis

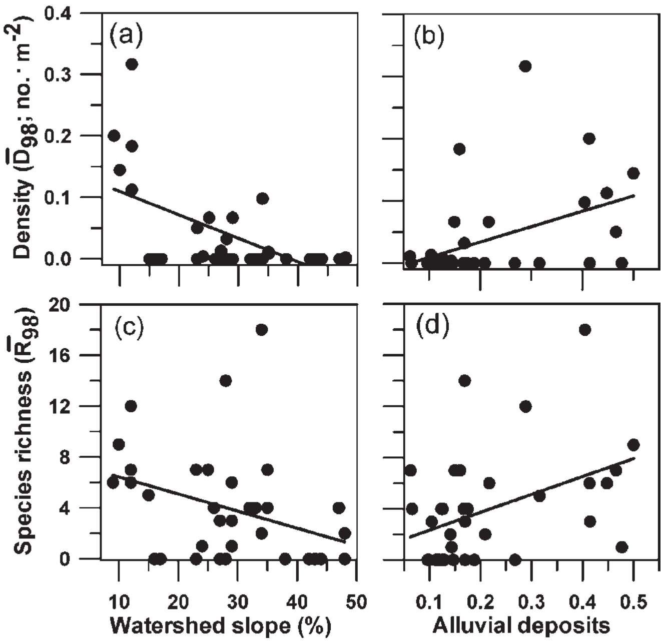
Watershed characteristics were assessed to relate population density and species richness to land use and geology. GIS analysis was used to prepare 17 watershed descriptions for each basin surveyed in 1998 and 1999. GIS data used in these analyses were obtained from the Iowa Department of Natural Resources (IDNR) Natural Resource GIS (NRGIS) library. Calculated variables derived from the GIS data included the fraction of land area composed of alluvial deposits, the average topographic relief (estimated as average percent slope), the incidence of eight important geologic formations (Cambrian, Cretaceous, Devonian, Jurassic, Mississippian, Ordovician, Pennsylvanian, Silurian; estimated as fractions of land area), and the incidence of seven land use types (urban, agricultural, range, forest, water, wetland, and barren land, estimated as fractions of land area). These landscape features were selected for this analysis because they each have the potential to influence water quality in ways that are relevant to mussel persistence. GIS software used to

Table 1. Results of the bivariate regression analyses of percent watershed alluvium and mussel density and species richness in watersheds analyzed in 1998 for 38 watersheds in the state of Iowa, U.S.A.

Dependent variable	Independent variable	r^2	T	P
Density ($\bar{D}_{98}$)	Slope	0.36	–4.41	0.000
Species richness ($\bar{R}_{98}$)	Slope	0.27	–3.43	0.002
Density ($\bar{D}_{98}$)	Alluvium	0.20	2.92	0.006
Species richness ($\bar{R}_{98}$)	Alluvium	0.12	2.10	0.043

Note: The T values and probabilities shown are for regression coefficients in eqs. 1–4. P indicates the probability that a T value of equal or greater magnitude would be obtained through chance alone.

Fig. 2. Bivariate relationships between mussels and watershed characteristics. Relationship between (*a*) average mussel density in watersheds and mean watershed slope, (*b*) average mussel density in watersheds and watershed alluvial deposits, (*c*) average mussel species richness in watersheds and mean watershed slope, and (*d*) average mussel species richness in watersheds and watershed alluvial deposits. Solid lines represent regression relationships (eqs. 1–4).



prepare the watershed descriptions were ArcView® extensions, X-Tools®, Spatial Analyst®, and Spatial Tools® (ESRI, Redlands, Calif.; http://www.esri.com).

Analytical methods

The statistical influences of watershed characteristics on watershed average mussel species richness ($\bar{R}_{98}$) and density ($\bar{D}_{98}$) were determined using regression analyses of the survey results from the 118 sites in 36 watersheds surveyed in 1998. We sought to determine statistically significant ($p <$ 0.05) bivariate relationships between $\bar{R}_{98}$ and $\bar{D}_{98}$ and a total of 17 candidate variables describing watershed landscapes (e.g., geology and land use characteristics, topography, and alluvium) using regression and correlation analysis. We then investigated potential multivariate relationships between $\bar{R}_{98}$ and $\bar{D}_{98}$ and those candidate variables found to be statistically significant in the bivariate analyses. This was accomplished using backward elimination multiple regression methods where independent variables were eliminated based on a retention criterion of $p < 0.05$ for partial significance of regression coefficients.

Independent model test

To test the efficacy of these regression models to predict mussel densities and species richness in independent data, the bivariate regression models were applied to an independent set of watershed $\bar{R}$ and $\bar{D}$ values collected at 82 sites in 38 watersheds during 1999. Models of $\bar{R}_{98}$ and $\bar{D}_{98}$ were used to predict mussel density ($\hat{D}_{99}$) and mussel species richness ($\hat{R}_{99}$) using 1999 watershed descriptors (e.g., landscape features and geology). To evaluate the effectiveness of individual models, correlation and graphical analyses were used to relate predicted values ($\hat{R}_{99}$, $\hat{D}_{99}$) to field measurements ($\bar{R}_{99}$, $\bar{D}_{99}$).

Results

Watershed-wide averages of mussel density within a stream reach were low (cf. Downing and Downing 1992), averaging only 0.04 (standard deviation, s = 0.07; n = 36) and 0.06 (s = 0.21; n = 38) animals·m^{-2} within the basins surveyed in 1998 and 1999, respectively. Watershed species richness averaged 2.05 for sites sampled in 1998 and 1.47 for those sampled in 1999. Thirty percent of the watersheds surveyed in 1998 and 37% of the watersheds surveyed in 1999 had no living mussels, even though these sites represent the best mussel habitat in this formerly mussel-rich region.

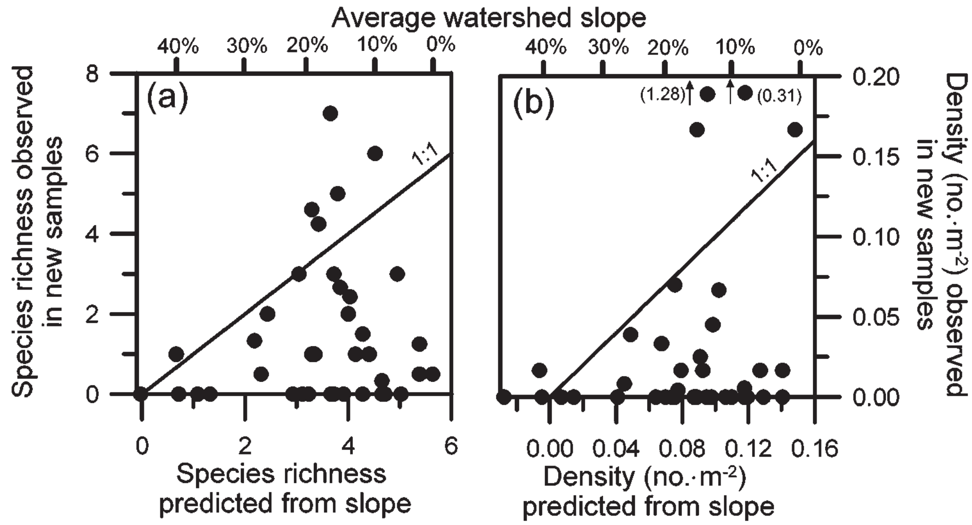
Bivariate regression analysis showed that topographic relief, as measured by mean percent slope, was significantly correlated with mussel density and mussel species richness (Table 1). The regression equations

$$(1) \qquad \bar{D}_{98} = 0.148 - 0.0038 S_{98}$$

$$(2) \qquad \bar{R}_{98} = 5.63 - 0.123 S_{98}$$

indicate that mussel density ($\bar{D}_{98}$) and species richness ($\bar{R}_{98}$) were negatively correlated with the average slope (S_{98}) of the watersheds. Both density and species richness decreased with increased watershed slope. Variation in mussel species richness and density with watershed slope was substantial; for example, mussel densities averaged about 0.18·m^{-2} in sites within watersheds with low slopes (<15%), but averaged <30% of this density at slopes >20% (Fig. 2*a*). Watershed species richness averaged around 8 species when slopes were <15% but less than 50% of this richness at slopes >20% (Fig. 2*c*).

Fig. 3. Correlations between predicted and observed (*a*) mussel species richness and (*b*) mussel density. Observations were based on an independent data set (data collected in 1999) using the slope models derived from data collected in 1998 (eqs. 1 and 2). Solid lines represent 1:1 correspondence of observations and predictions. Please note extremely high values that occurred off-scale of this graph (see arrows in panel *b*). Also shown on the upper abscissa are the watershed slopes corresponding to the predictions of mussel densities (eqs. 1–2).



Bivariate regression analysis also showed that alluvial deposits were significantly correlated with mussel density and mussel species richness (Table 1). The regression equations

(3) $\overline{D}_{98} = -0.016 + 0.0025A_{98}$

(4) $\overline{R}_{98} = 0.553 + 0.0716A_{98}$

indicate mussel density ($\overline{D}_{98}$) and species richness ($\overline{R}_{98}$) were positively correlated with average percent alluvial deposits (A_{98}) in the watershed. Variation in mussel density and species richness with alluvial deposits was substantial. For example, mean watershed mussel densities averaged around $0.1 \cdot m^{-2}$ in watersheds with >35% alluvium, whereas densities were generally <25% of this level in watersheds with <15% alluvium (Fig. 2*b*). Likewise, watersheds with >35% alluvium average around six species, whereas watersheds with <15% alluvium had about one third of this average richness (Fig. 2*d*).

Despite the large amount of data collected, we could find no multivariate relationships between $\overline{R}_{98}$ and $\overline{D}_{98}$ and the variables alluvial deposits and slope. Backward elimination multiple regression methods where independent variables were eliminated based on a retention criterion of $p < 0.05$ for partial significance of regression coefficients resulted in the removal of all candidate variables except mean watershed slope. There was only a very weak collinearity between these two watershed descriptors ($r = -0.5$), so both appear to have an effect.

Because regression models may be influenced by the specific structure of the data set used to construct them, or particular characteristics of the study sites, the general utility of the models can be checked by using them to predict independent sets of data. In this case, we used models based on observations made in 1998 to predict observations made on other sites sampled in 1999. Predictions of mussel density ($\hat{D}_{99}$) and mussel species richness ($\hat{R}_{99}$) were made by substituting the slope (S_{99}) and alluvial (A_{99}) descriptors prepared for the watersheds surveyed in 1999 into eqs. 1–4. To determine the strength of model(s) for predicting mussel density and mussel species richness in this independent set of data, comparisons were made between the predicted and actual values using the alluvial and slope models. Correlations between actual ($\overline{D}_{99}$) and predicted mussel density ($\hat{D}_{99}$), and actual ($\overline{R}_{99}$) and predicted species richness ($\hat{R}_{99}$) when using the slope (eqs. 1 and 2) and alluvial (eqs. 3 and 4) models, were quite weak (Spearman's $\rho = 0.11$–0.19; $p < 0.05$), but were characterized by positive triangular relationships rather than linear trends (e.g., Figs. 3*a*, 3*b*). Despite the absence of strong, linear, statistical relationships, the models yielded directionally correct predictions. For example, neither model predicted low species richness or low mussel density (Fig. 3) where field measurements were high. Rather, the models predicted high mussel species richness and mussel density in areas where actual observations of richness and density were often found to be low.

Discussion

The negative correlations of slope with mussel density and mussel species richness suggest a strong impact of erosional–depositional properties of watersheds. Topographic relief influences hydrologic regimes, and when used as a surrogate for stream gradient and erosional potential of agriculturally disturbed soils, is likely to relate to the biological and ecological limitations of mussel populations. Water is quickly removed from the landscape in areas of high relief, which can result in greatly increased soil erosion, flashy streams (Brooks et al. 1997), and high rates of substrate transport (Newbury 1984). Further, flashy streams and substrate transport can both interfere with mussels' ability to maintain a stable position on the stream bottom. Dislodged mussels, unable to preserve a suitable position for the removal of oxygen and food from the water, are unlikely to survive. Substrate stability generally has an important influence on freshwater mussel distributions (Stern 1983; Strayer and Ralley 1993; Di Maio and Corkum

1995). In disturbed landscapes such as Iowa, areas of high mean topographic relief are likely to present unfavorable mussel habitats and therefore have probably developed low mussel density and lower species richness over the course of impact.

Alluvial deposits may act to improve and (or) maintain conditions for mussels because they alter the quantity of groundwater in a watershed by increasing rates of freshwater transmission and storage (Anderson 1998). Agricultural development in Iowa and elsewhere has resulted in large-scale watershed alterations by draining wetlands and channelizing streams, both of which lead to increased inter- and intra-annual hydrologic variability. Stream flow during dry periods is typically maintained in this region by groundwater discharge from alluvial aquifers to streambeds (Prior 1991). Mussel populations in rivers with abundant alluvial deposits are probably less impacted by periods of extreme low flow than those in areas without this groundwater source. Aquatic species throughout Midwestern North America are adversely affected by extreme water fluctuations (Page et al. 1997), which are ameliorated by groundwater flux through alluvial deposits. Watersheds with the greatest deposits of alluvium are, therefore, relatively hydrologically stable, buffering the impacts of extreme environmental conditions on aquatic communities.

Few studies have used broad-scale field surveys to relate landscape features to mussel species richness or density. Although some have related landscape features such as surface geology (Strayer 1983) and land cover (Morris and Corkum 1996) to mussel species distribution, most have examined local effects (i.e., stream reach conditions), ignoring the broader aspects of watersheds that may influence mussels. Our analysis demonstrates the importance of incorporating terrestrial conditions at a watershed scale into studies investigating factors influencing mussel distribution and abundance.

It is rare that multiple data sets are collected from different broad-scale field surveys to develop and test predictive models of population abundance and biodiversity. Our analysis of watershed geomorphic features and mussel species richness and density indicate that slope and alluvium, reflecting patterns of siltation and habitat stability, are correlated with mussel persistence in this agricultural region. Although correlations between model predictions and new observations of species richness and density were weak, positive relationships and graphical patterns in the data indicate agreement in trends. Some of the variability and unpredictability hampering mussel conservation efforts may therefore result from failure to focus on the broader landscape factors influencing mussel distributions.

Our analyses suggest that watershed-scale GIS may be an important tool for evaluating aquatic resources. The predictive power of the independent variables was between 0.12 and 0.36, the lowest r^2 values in this study being consistent with those seen in other studies seeking relationships between mussel distributions and habitat characteristics (0.06–0.22; Strayer 1993; Strayer and Ralley 1993). Localized and historical effects of watershed impacts likely explain large residual variation in watershed-scale analyses. For example, the transitory and patchy nature of agricultural impacts (e.g., chemical spills, flooding, storm-driven erosion events) is impossible to account for and would contribute to low predictive power. This is especially clear if one considers that many of the zero values for current densities and species richness may have resulted from short-term mortality events unrelated to watershed characteristics. Watershed-mediated impacts on fish could also influence the viability of mussel species. This may be important for all but one of the species we studied, since most have obligate parasitic larval stages. Unfortunately, consistently collected fish abundance and richness data were too rare to be accounted for in this analysis.

Our analyses show that, on a large scale, mussel abundance and biodiversity in this agriculturally impacted region of the U.S. were related to landscape features linked to erosional and groundwater processes. On one hand, high slope, which might normally have a positive impact on mussels in unperturbed landscapes with stable land cover and intact riparian zones, can lead to great erosion and substrate instability in the altered geography of anthropogenic impacts. On the other hand, survival of mussels may be greatest where geological formations like alluvial deposits stabilize the variations associated with land clearing and altered drainage. Our analysis indicates that mussel conservation efforts are most critical in highly sloping landscapes with less permeable soils, where low groundwater flows might lead to unfavorable conditions. It also suggests that high rates of mussel disappearance in this region may be in part linked to large-scale watershed alterations. The persistence of mussel populations and the maintenance of aquatic biodiversity at specific sites are, therefore, dependent upon good management throughout the watershed.

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