

Species traits and catchment-scale habitat factors influence the occurrence of freshwater mussel populations and assemblages

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SUMMARY

1. Conservation of freshwater unionid mussels presents unique challenges due to their distinctive life cycle, cryptic occurrence and imperilled status. Relevant ecological information is urgently needed to guide their management and conservation.

2. We adopted a modelling approach, which is a novel application to freshwater mussels to enhance inference on rare species, by borrowing data among species in a hierarchical framework to conduct the most comprehensive occurrence analysis for freshwater mussels to date. We incorporated imperfect detection to more accurately examine effects of biotic and abiotic factors at multiple scales on the occurrence of 14 mussel species and the entire assemblage of the Tar River Basin of North Carolina, U.S.A.

3. The single assemblage estimate of detection probability for all species was 0.42 (95% CI, 0.36–0.47) with no species- or site-specific detection effects identified. We empirically observed 15 mussel species in the basin but estimated total species richness at 21 (95% CI, 16–24) when accounting for imperfect detection.

4. Mean occurrence probability among species ranged from 0.04 (95% CI, 0.01–0.16) for *Alasmidonta undulata*, an undescribed *Lampsilis* sp., and *Strophitus undulatus* to 0.67 (95% CI, 0.42–0.86) for *Elliptio icterina*. Median occurrence probability among sites was <0.30 for all species with the exception of *E. icterina*. Site occurrence probability generally related to mussel conservation status, with reduced occurrence for endangered and threatened species.

5. Catchment-scale abiotic variables (stream power, agricultural land use) and species traits (brood time, host specificity, tribe) influenced the occurrence of mussel assemblages more than reach- or microhabitat-scale features.

6. Our findings reflect the complexity of mussel ecology and indicate that habitat restoration alone may not be adequate for mussel conservation. Catchment-scale management can benefit an entire assemblage, but species-specific strategies may be necessary for successful conservation. The hierarchical multispecies modelling approach revealed findings that could not be elucidated by other means, and the approach may be applied more broadly to other river basins and regions. Accurate measures of assemblage dynamics, such as occurrence and species richness, are required to create management plans for effective conservation.

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Introduction

Unionid mussels are an important component of many freshwater ecosystems. They process organic matter (Howard & Cuffey, 2006), contribute to nutrient cycling (Vaughn, Gido & Spooner, 2004; Spooner & Vaughn, 2006), filter large quantities of water (Strayer *et al.*, 1994), influence assemblages of macroinvertebrates (Vaughn & Spooner, 2006) and act as ecosystem engineers (Gutierrez *et al.*, 2003). Their vast ecological contribution is at risk, as freshwater mussels are among the most threatened taxa globally (Williams *et al.*, 1993; Master *et al.*, 2000; Lydeard *et al.*, 2004). Freshwater mussels are particularly susceptible to environmental stressors, in part because of their reliance upon a host fish to complete their life cycle. The larval life stage (glochidia) is an obligate parasite that requires encystment on a host fish to transform into the juvenile life stage (e.g. Kat, 1984). Habitat alteration or destruction has been identified as a leading cause of mussel decline (Downing, Van Meter & Woolnough, 2010), and many studies have attempted to clarify the influence of habitat on the distribution of freshwater mussels at multiple spatial, temporal and organisational scales (e.g. McRae, Allan & Burch, 2004; Steuer, Newton & Zigler, 2008). However, mussel distribution has also been connected to biotic factors such as species traits and the distribution and habitat affinity of host fish (Haag & Warren, 1998; Pandolfo, Kwak & Cope, 2012; Schwab *et al.*, 2013).

Imperfect detection is a critical component of any description of mussel distribution because animals are rarely perfectly detected (i.e. detection probability is <1 ; MacKenzie *et al.*, 2002). Although mussels are often difficult to detect due to their tendency to burrow and form patchy distributions (Strayer & Smith, 2003), only very recently have predictive models of freshwater mussel occurrence that formally incorporated imperfect detection been developed (Shea *et al.*, 2013; Wisniewski *et al.*, 2013). Assessing detection probability for freshwater mussels is inherently difficult because many species are imperilled and rare, and methods for estimating detection are data intensive and require large sample sizes. Some techniques for addressing this dilemma include borrowing information from related species or sites and determining occurrence probability or species richness rather than abundance (MacKenzie *et al.*, 2005). A recently developed community-modelling approach

utilises both of these approaches and allows for the inclusion of rare species while producing estimates of occurrence and species richness (Kery & Royle, 2009; Zipkin, DeWan & Royle, 2009).

Not only does freshwater mussel conservation depend on accurate measures of mussel occurrence, distribution and species richness, but also management decisions rely on an accurate understanding of factors that influence these measures. We adopted a community occurrence modelling approach in a Bayesian framework, which has heretofore not been applied to freshwater mussel populations or assemblages, to determine site-specific and basin-wide mussel species richness, and to investigate the effects of mussel species traits, host fish and stream habitat on the detection and occurrence of freshwater mussels in the Tar River Basin of North Carolina. This research was designed at the river basin spatial scale, and thus, our scientific inference extends only to the catchment level; however, the approach was developed and applied with the intention of demonstrating its novel utility to be applied more broadly in understanding freshwater mussel ecology and conservation.

Methods

Freshwater mussel and fish surveys

We conducted freshwater mussel surveys at 20 sites throughout the Tar River Basin of North Carolina, including three subbasins with similar drainage areas: the upper Tar River, Swift Creek and Fishing Creek (Fig. 1). The sites represented a longitudinal gradient spanning a range of environmental conditions (e.g. catchment area and land cover) within the river basin. Snorkelling and tactile searches for freshwater mussels were conducted in collaboration with the North Carolina Wildlife Resources Commission during the summer of 2010. A minimum of six person-hours of effort was expended at each 200- to 500-m stream reach. Each site was visited once, and surveys were conducted by three independent observers at each site to provide replicates to estimate detection probability for occurrence modelling (MacKenzie & Royle, 2005). Independent observers identified and counted mussels during concurrent timed search periods in their own site-representative transects. This procedure was analogous to a qualitative timed search commonly utilised by mussel biologists,

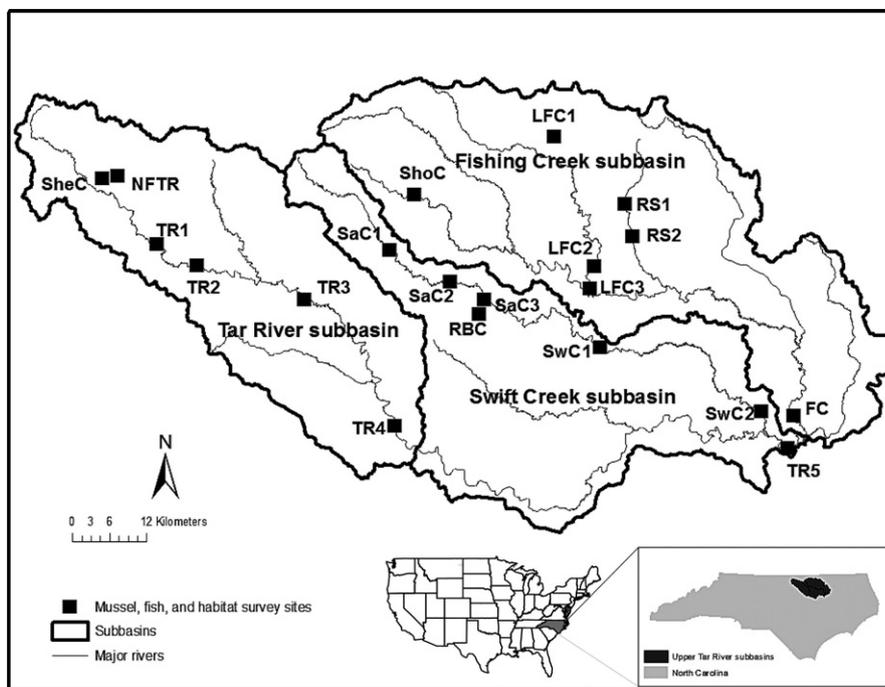


Fig. 1 Location of 20 study sites within the upper Tar River Basin, North Carolina.

but the collection of data by independent observers allowed for the generation of quantitative estimates of mussel detection and occurrence (MacKenzie & Royle, 2005). When an uncommon species was encountered, mussels were bagged by observers for shell measurement and identification to species. Only mussels that were confidently identified to species were included in occurrence analyses.

We also conducted electrofishing surveys at each site in 2010 and used the resulting data to estimate fish species richness and calculate an Index of Biotic Integrity score. Each electrofishing survey consisted of two pulsed-DC backpack electrofishers and two dipnetters sampling 200 m upstream along the stream banks followed by a return pass down the centre of the stream (NCDENR, 2006).

Habitat covariates

We measured microhabitat characteristics at precise mussel capture locations within mussel survey reaches. Microhabitat use measurements were recorded for all encountered individuals of non-abundant species, and for up to 20 individuals of the ubiquitous *E. complanata*, at each site. Microhabitat measurements included water depth, bottom and mean-column water velocity, embeddedness, roughness, distance to nearest cover and nearest cover type. Dominant and subdominant substrate types were classified using a modified Wentworth particle size

scale (Bovee & Milhous, 1978), and substrate heterogeneity was calculated by determining the number of different dominant and subdominant substrate types at a site. Substrate compaction was measured using a Lang penetrometer (Johnson & Brown, 2000), such that low resistance was associated with the least compacted/most penetrable substrates (e.g. silt and sand). All other parameters were measured using established methods for stream habitat assessment (Bain & Stevenson, 1999).

At the reach scale, 10 transects were delineated every two mean-stream widths apart (Simonson, Lyons & Kanehl, 1994). Stream shading was determined by measuring riparian open canopy with a densiometer at both banks and in the centre of each transect (Platts *et al.*, 1987), and bank angle was measured on both banks in each transect. A cross-sectional area survey was conducted once per site using the tape-down method to determine the bankfull width, bankfull cross-sectional area, bankfull mean and maximum depth, and width-to-depth ratio (Harrelson, Rawlins & Potyondy, 1994). A pebble count was conducted at the location of the cross-sectional area survey to determine median particle size (D50) as well as D16 and D84 (16th and 84th percentile of particle size, respectively; Potyondy & Hardy, 1994). Continuous hourly temperatures were measured in the water column 10 cm above the sediment/water interface and in the substrate at 5 and 15 cm below the interface at each site by deploying two replicate monitoring units that utilised iBCod 22L data loggers from

Alpha Mach, Inc. (Mont-St-Hilaire, Quebec; Pandolfo, 2014) in July and August 2010.

Catchment boundaries for each sampling location were delineated in ArcGIS (Environmental Systems Research Institute, version 9.31; Redlands, CA) from GPS coordinates taken at each site. Catchment area and the proportions of different categories of catchment land use, riparian land use (15- and 30-m buffers), ecoregion and geologic rock type were calculated via ArcGIS using existing data files (NCGS, 2007; USEPA, 2010; USGS, 2011). Stream power was calculated using discharge and slope measurements for each catchment based on the mean annual flow from 2010.

Covariate selection

Data on a total of 144 continuous covariates for habitat and fish were collected. We reduced the list to 35 representative covariates after careful review of previous mussel distribution studies (e.g. Hardison & Layzer, 2001; McRae *et al.*, 2004; Strayer, 2008). Correlation analysis was used to determine the final list of covariates for our analysis ($r < 0.60$), with the criterion that at least one variable from each habitat scale (microhabitat, reach, and catchment scale) was retained and either species richness or Index of Biotic Integrity score was included as a fish covariate. The selected covariates were then stratified into occurrence covariates (i.e. variables expected to influence mussel occurrence) and detection covariates (i.e. variables expected to influence mussel detection). The resulting eight occurrence covariates were substrate compaction, substrate heterogeneity, bankfull maximum depth, 2010 substrate degree days, geologic rock type, catchment agricultural land use, stream power and fish species richness (Table 1). The three detection covariates were dominant substrate type, D84 and water depth. All occurrence and detection covariates were included in models as site-specific values based on measurements taken at each individual site (see Table 1 for details and Table S1 in Supporting Information for complete list of models).

The effects of different mussel species traits on occurrence were tested in separate models. We chose to explore species traits separate from the other covariates to utilise greater statistical power to estimate potential effects. We included each species' tribe as an indicator of taxonomic classification (Graf & Cummings, 2007). Host specificity refers to the number of host fish species that a mussel species is known to successfully parasitise, with specialists successfully transforming to the juvenile life stage on only one or a few species, whereas a generalist may have

upwards of 20 host species (Strayer, 2008). Brood time is the length of time that a female mussel retains larval glochidia in the marsupia before release. Bradytictic or long-term brooders brood glochidia over the winter months and generally release in early spring. Tachytictic or short-term brooders brood and release glochidia within a season (i.e. late spring and summer) (Barnhart, Haag & Roston, 2008). Reproductive strategy, for our purposes, is the presence or absence of specialised adaptations, such as mantle lures, that serve to attract host fish (Bauer & Wachtler, 2000; Barnhart *et al.*, 2008). Each species' tribe, host specificity (generalist or specialist), brood time (tachytictic or bradytictic) and reproductive strategy (attractor or non-attractor) were tested in the absence of other covariates (Table 1). Pairwise chi-square likelihood ratio comparisons indicated that tribe, host specificity and brood time were correlated parameters ($P < 0.05$), but reproductive strategy was not correlated to the other species traits. Because of the varying biological basis for the three correlated parameters, we included all three as candidate parameters in our models, while recognising that an effect of any of these parameters may indicate influence by any of the three.

Modelling framework

Hierarchical multispecies models 'borrow' information across all species in an assemblage, which leads to more precise species-level inferences (Dorazio & Royle, 2005). In these models, each species influences the parameter estimates of all other species in the assemblage. As a result, individual species-level estimates are a combination of species-specific data and the mean estimate of those parameters for the entire assemblage (or group of species). The extent to which estimates are pooled together, rather than estimated separately (i.e. pooling or 'shrinkage'), is dependent on the quality and quantity of available data (e.g. number and locations of species detections; Gelman & Hill, 2007). A major benefit of shrinkage is the ability to estimate parameters for species that are rarely detected and would otherwise not be estimable or would be too imprecise for meaningful inference (Kery & Royle, 2008).

We followed procedures of Dorazio *et al.* (2006) to model the mussel assemblage and estimate species richness. Site-specific occurrence for species $i = 1, 2, \dots, n, \dots, N$ at site j , denoted z_{ij} , is a latent random variable where $z_{ij} = 1$ if species i occurs in site j and zero otherwise. We specified the occurrence model as $z_{ij} \sim \text{Bern}(\Psi_{ij})$, where Ψ_{ij} is the probability that species i is present at site j . True occurrence is only partially observed through the

Table 1 Descriptions, model abbreviations, mean, standard deviation and range of covariates used in candidate models for the occurrence and detection probabilities of the freshwater mussel assemblage in the Tar River Basin of North Carolina. Category values are given for categorical variables (0 represents baseline condition).

Scale and covariate	Abbreviations	Description	Mean	SD	Min	Max
Detection						
D84	d84	Particle size which is larger than 84% of other particles (mm)	18.7	26.4	0.5	90
Dominant substrate	domsed	Modal substrate type based on index of Modified Wentworth Scale	2.1	2.4	1	11
Water depth	depth	Median water depth (m)	0.31	0.16	0.10	0.64
Occurrence						
Microhabitat scale						
Substrate compaction	penet	Median penetrability of substrate (psi)	21.0	30.4	0.0	86.9
Substrate heterogeneity	sedtypes	Total number of dominant and subdominant substrate types	8.9	2.96	4	14
Reach scale						
Bankfull max depth	bmax	Depth (m) to bottom of channel from bankfull maximum height	2.23	1.04	0.77	5.00
Degree days	degdays	Cumulative degrees per day from hourly substrate temperatures	2033	134	1793	2312
Catchment scale						
Geologic rock type	geob	Proportion of catchment classified as biotite gneiss	0.12	0.14	0.00	0.46
Land use, agriculture	wsag	Proportion of catchment classified as agriculture	0.23	0.05	0.13	0.31
Stream power	spow	Discharge*slope (Watts/m), based on mean annual 2010 flow	0.06	0.04	0.00	0.12
Fish species richness	fish	Number of fish species sampled during electrofishing surveys	18.3	4.85	10	28
Species traits						
Brood time	brood	Bradytictic (0) or tachytictic (1)	Categorical			
Host specificity	host	Host generalist (0) or host specialist (1)	Categorical			
Reproductive strategy	strategy	Host attractor (0) or non-attractor (1)	Categorical			
Tribe	tribe	Anodontini (0), Pleurobemini (1), Lampsilini (1) pairwise comparisons	Categorical			

detection/non-detection data, where x_{ijk} (recorded as a one if a species is observed and zero otherwise) for species i at site j for observer k is $x_{ijk} \sim \text{Bern}(p_{ijk} * z_{ij})$. The parameter p_{ijk} is the detection probability of species i at site j for the k th observer. If species i is present ($z_{ij} = 1$) at site j , then the probability of detecting that species is p_{ijk} ; otherwise if $z_{ij} = 0$, then $x_{ijk} = 0$, and we ensure that detection is a fixed zero when a species is not present.

We incorporated covariate effects into the occurrence and detection models linearly on the logit-probability scale. We modelled occurrence as a function of eight site-level covariates (Table 1) on the logit scale as follows:

$$\begin{aligned} \text{logit}(\psi_{ij}) = & \mu_i + \alpha 1_i \text{spow}_j + \alpha 2_i \text{wsag}_j + \alpha 3_i \text{geob}_j \\ & + \alpha 4_i \text{bmax}_j + \alpha 5_i \text{degdays}_j + \alpha 6_i \text{sedtypes}_j \\ & + \alpha 7_i \text{penet}_j + \alpha 8_i \text{fish}_j \end{aligned}$$

We similarly modelled the detection probability for species i as a function of three covariates (Table 1): $\text{logit}(p_{ijk}) = v_i + \beta 1_i \text{d84}_{jk} + \beta 2_i \text{domsed}_{jk} + \beta 3_i \text{depth}_{jk}$. All covariates were centred and normalised (mean = 0, variance = 1), such that the inverse-logit of μ_i , for example, is the occurrence probability for species i in sites with 'average' site conditions.

An additional hierarchical component was added to the model, wherein we assumed that the species-level parameters were random effects governed by assemblage hyperparameters (i.e. parameters of the prior distribution). All model coefficients were assumed to come from a normal distribution (e.g. $\alpha 1_i \sim N(\mu_{\alpha 1}, \sigma_{\alpha 1})$) where the mean of the distribution represents the community response to that particular covariate and the standard deviation is the variation among species within the particular group. We used a parameterisation of the

unconditional likelihood and data augmentation to estimate species richness N (Dorazio *et al.*, 2006).

Model selection

Preliminary model runs indicated that *E. complanata* could not be included in model estimations because of the lack of any absence data (i.e. *E. complanata* was always present; $\Psi = 1$); therefore, data from the remaining 14 species were modelled. We fit 36 models that varied in complexity with the goal of understanding which covariates influenced mussel occurrence and detection (Table S1). We explored all possible combinations of having species-specific random effects and constant effects for the intercept and covariates influencing occurrence and detection. We used the deviance information criterion (DIC; Spiegelhalter *et al.*, 2002) to select the most parsimonious model. The most parsimonious model was used to estimate detection probabilities, a mean occurrence probability for each species, site and species-specific occurrence probabilities, projected occurrence probabilities over a range of covariate values, basin-wide species richness and site-level species richness.

We explored species-level trait effects (host, tribe, brood, strategy) by setting up four separate models with occurrence as a function of each species-level effect and a constant intercept, e.g. $\text{logit}(\Psi_{ij}) = \mu + \alpha 1\text{host}_i$. We modelled detection as a constant intercept across all species.

Model evaluation

We fit each of the models separately following a Bayesian approach in WinBUGS (Spiegelhalter *et al.*, 2003) through R statistical software (R2WinBUGS; Sturtz, Ligges & Gelman, 2005) by running three parallel chains, each of length >77 000 with burn-in of at least 25 000 and thinning by 25. We used vague priors for all hyperparameters in all models. Convergence was confirmed through trace plots, correlation and the Gelman-Rubin statistic (Gelman & Rubin, 1992).

For all analyses, covariate effects were evaluated using the posterior distribution of each covariate parameter estimate. When the 95% credible interval of a parameter estimate did not include 0, a strong effect of the covariate was evident. If the interval included 0, but the bulk of the parameter's distribution was either positive or negative, a less precise but supported effect of the covariate was evident. For covariates deemed to have an effect on occurrence or detection, we calculated odds ratios (ORs) for ease of interpretation. The OR of a covariate represented the associated change in odds

given a change of one standard deviation in the covariate.

Results

A total of 16 491 mussels representing 15 species were collected at the 20 study sites in the Tar River Basin (Table 2). *Elliptio complanata* accounted for most individuals and was the only species found at all 20 sites. Two species listed as federally endangered under the United States Endangered Species Act of 1973, *Alasmidonta heterodon* and *E. steinstansana*, were encountered during surveys.

Two models emerged as the most plausible fits for our data, with a very small ΔDIC (0.3) between them (i.e. equivalently plausible models; Table S1). Both models had an occurrence intercept that randomly varied among species and a constant detection intercept that did not vary among species. The model with the lowest DIC value (260.5) did not include covariates for either occurrence or detection, whereas the other most plausible model (DIC = 260.8) included effects of occurrence covariates that were constant among species. Because there was virtually no difference between DIC values for these models, the second model was chosen as the basis of further analysis because our main objective was to examine effects of abiotic and biotic covariates on mussel occurrence.

Our model indicated that there was a strong negative effect of catchment-scale agricultural land use on mussel occurrence, and evidence of a positive, but imprecise,

Table 2 Number of sites where a species was detected, naive occurrence (Ψ , number of sites detected/total number of sites), total count and proportion of total catch for 15 freshwater mussel species sampled in surveys at 20 sites in the Tar River Basin, North Carolina.

Species	Number of sites detected	Naive Ψ	Total count of individuals	Proportion of total catch
<i>Alasmidonta heterodon</i>	3	0.15	20	0.001
<i>A. undulata</i>	1	0.05	1	<0.001
<i>Elliptio complanata</i>	20	1.00	14 057	0.852
<i>E. congaraea</i>	7	0.35	453	0.027
<i>E. fisheriana</i>	3	0.15	23	0.001
<i>E. icterina</i>	14	0.70	1788	0.108
<i>E. lanceolata</i>	2	0.10	2	<0.001
<i>E. roanokensis</i>	3	0.15	69	0.004
<i>E. steinstansana</i>	2	0.10	3	<0.001
<i>Fusconaia masoni</i>	7	0.35	25	0.002
<i>Lampsilis cariosa</i>	3	0.15	5	<0.001
<i>Lampsilis</i> sp.	1	0.05	6	<0.001
<i>Strophitus undulatus</i>	1	0.05	1	<0.001
<i>Utterbackia imbecillis</i>	1	0.05	4	<0.001
<i>Villosa constricta</i>	5	0.25	34	0.002

effect of stream power on mussel occurrence (Table 3). Species occurrences over a range of catchment agricultural land use values were predicted for two representative species, *E. roanokensis* and *V. constricta* (Fig. S1). Odds ratios indicated that predicted mussel occurrence would be 2.33 times lower with every increase of 5.0% in catchment agricultural land use (OR = 0.43, 95% CI = 0.19–0.85). The predicted relationship between stream power and mussel occurrence was also explored using *E. congaraea* and *A. heterodon* as representative species (Fig. S1). Odds ratios indicated that with every predicted 0.04 W/m increase in stream power, mussel occurrence probability would be 1.68 times higher (OR = 1.68, 95% CI = 0.93–3.15). Geologic rock type, bankfull maximum depth, substrate degree days, substrate heterogeneity, substrate compaction and fish species richness were not identified as influences on occurrence of freshwater mussels at our study sites (Table 3).

A separate analysis to investigate the influence of four mussel species life-history traits indicated that brood time and host specificity strongly influenced mussel species occurrence, but reproductive strategy did not (Table 3; Fig. 2). Tribe exhibited a strong influence between Lampsilini and Anodontini tribes, and a less precise influence between Pleurobemini and Anodontini. The mean estimated occurrence probability for a host generalist (0.08, SD = 0.03) was less than that of a host specialist (0.24, SD = 0.11), and bradytictic (long-term) brooders had a mean estimated occurrence probability

of 0.11 (SD = 0.03) compared with 0.28 (SD = 0.13) for tachytictic (short-term) brooders. Of the three unionid tribes represented in our study, Anodontini had the lowest mean occurrence probability (0.08, SD = 0.03), followed by Pleurobemini (0.15, SD = 0.09) and Lampsilini (0.28, SD = 0.13). The occurrence probabilities between host attractors and non-attractors did not differ.

A mean detection probability of 0.42 (SD = 0.03) was estimated for all mussel species (Tables 4 & 5). The occurrence probability predicted for each mussel species in an average habitat ranged from 0.04 (SD = 0.03–0.04) for *A. undulata*, *Lampsilis* sp. and *S. undulatus* to 0.67 (SD = 0.12) for *E. icterina* (Tables 4 & 5). The median occurrence probability for each species predicted with site-specific covariate information at 20 sites was generally low, <0.30 (Fig. 3). *Elliptio icterina* was the exception to this trend, with a median occurrence probability of 0.62 (SD = 0.17). When compared, site occurrence probabilities for *E. icterina*, North Carolina state endangered *F. masoni*, and federally endangered *A. heterodon* and *E. steinstansana* in the Tar River Basin indicate distinct patterns that relate to conservation status (Fig. 4). Federally endangered *E. steinstansana* and *A. heterodon* had the lowest site occurrence probabilities of the four species, with the majority of sites having an occurrence probability of ≤ 0.20 . North Carolina endangered species *F. masoni* was predicted to have occurrence probabilities ≤ 0.20 at 20% of sites, whereas the stable species *E. icterina* was predicted to occur at all sites with a probability > 0.20 .

A total of 15 freshwater mussel species were sampled during surveys in the Tar River Basin, whereas the estimated mean species richness for the basin was 21 with a 95% credible interval of 16–24 species. This suggests it is likely that we failed to detect at least one species in our surveys. Predicted estimates of mussel species richness at each site were similar to the observed species richness for all 20 sites (Fig. 5). In all cases, the observed value occurred within the 95% credible interval for the site prediction.

Discussion

Imperfect detection

We incorporated imperfect detection while examining the effects of various factors on occurrence of a mussel assemblage using a simple and novel framework which can be of value when sampling resources are limited. We used multiple independent observers to collect the repeat survey data that are required to estimate species

Table 3 Mean effect, standard deviation (SD) and 95% credible interval (CI) of habitat and species trait occurrence covariates from the most plausible occurrence and detection models; see Model 2, Table S1 for model details. See Table 1 for baseline conditions of species traits.

Scale and covariate	Mean effect (SD)	95% CI	
Microhabitat scale			
Substrate compaction	-0.19 (0.29)	-0.77	0.34
Substrate heterogeneity	0.28 (0.29)	-0.26	0.86
Reach scale			
Bankfull max depth	-0.09 (0.36)	-0.80	0.59
Degree days	-0.02 (0.31)	-0.64	0.62
Catchment scale			
Geologic rock type	0.08 (0.27)	-0.46	0.58
Land use, agriculture	-0.85 (0.38)	-1.65	-0.17
Stream power	0.52 (0.31)	-0.07	1.15
Fish species richness	0.36 (0.30)	-0.23	0.97
Species traits			
Brood time	1.13 (0.34)	0.50	1.80
Host specificity	1.30 (0.44)	0.50	2.20
Reproductive strategy	0.35 (0.32)	-0.24	0.99
Tribe			
Lampsilini – Anodontini	1.48 (0.46)	0.64	2.44
Pleurobemini – Anodontini	0.67 (0.55)	-0.45	1.77

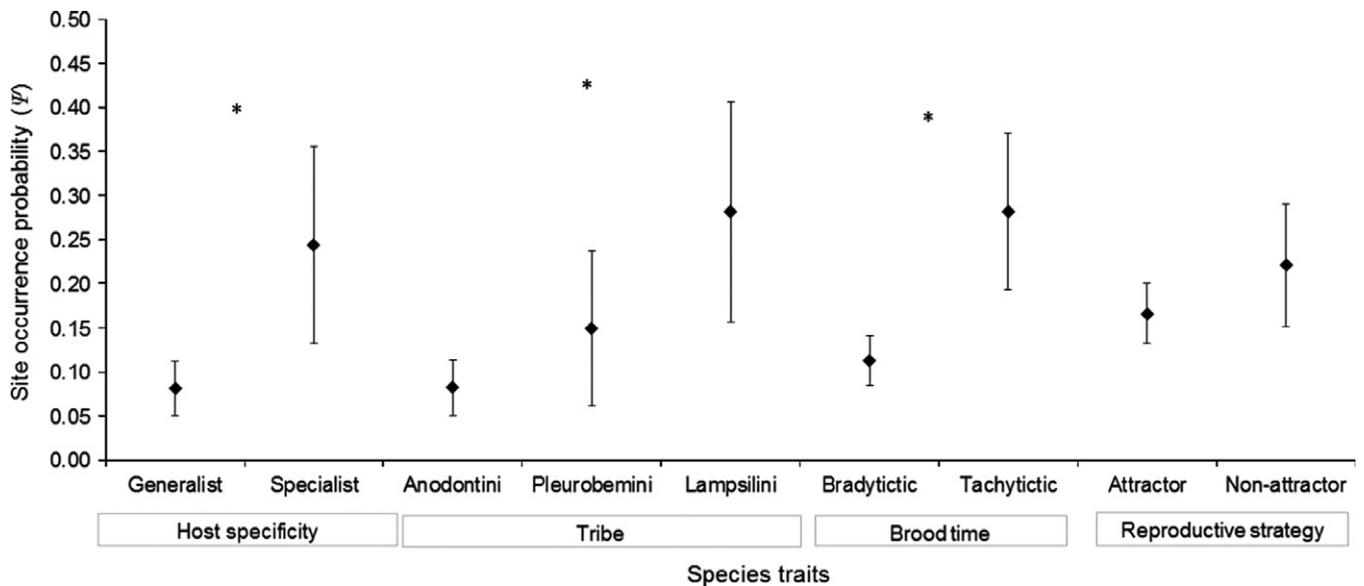


Fig. 2 Estimated mean occurrence probability (\pm standard deviation) for four freshwater mussel species traits, host specialisation, tribe, brood time and reproductive strategy. An asterisk indicates that the 95% credible interval for the mean effect of the species trait did not include 0.

Table 4 Parameter estimates, with standard deviation (SD) and 95% credible intervals (CI) from the most plausible occurrence (Ψ) and detection (p) models; see Model 2, Table S1 for model details.

Parameter	Estimate (SD)	95% CI	
Detection (p) intercept, grand mean	-0.21 (0.99)	-2.28	1.83
Occurrence (Ψ) intercept, grand mean	-2.20 (0.48)	-3.22	-1.32
Occurrence intercept, by species			
<i>Alasmidonta heterodon</i>	-2.05 (0.63)	-3.37	-0.91
<i>A. undulata</i>	-3.07 (0.87)	-5.04	-1.64
<i>Elliptio congaraea</i>	-0.89 (0.50)	-1.89	0.07
<i>E. fisheriana</i>	-2.10 (0.63)	-3.41	-0.96
<i>E. icterina</i>	0.71 (0.55)	-0.33	1.80
<i>E. lanceolata</i>	-2.47 (0.71)	-3.90	-1.12
<i>E. roanokensis</i>	-2.06 (0.65)	-3.35	-0.86
<i>E. steinstansana</i>	-2.51 (0.73)	-4.02	-1.24
<i>Fusconaia masoni</i>	-0.89 (0.51)	-1.86	0.08
<i>Lampsilis cariosa</i>	-2.11 (0.67)	-3.49	-0.93
<i>Lampsilis</i> sp.	-3.06 (0.87)	-4.91	-1.59
<i>Strophitus undulatus</i>	-3.06 (0.82)	-4.86	-1.55
<i>Utterbackia imbecillis</i>	-3.05 (0.87)	-5.03	-1.63
<i>Villosa constricta</i>	-1.43 (0.56)	-2.54	-0.39

detection probabilities (MacKenzie & Royle, 2005). The use of multiple observers during a single-site visit allows for statistically sound data collection while optimising resources, such as time, cost and availability of trained personnel.

The single assemblage estimate of detection probability for the freshwater mussels in our study was well below 1.0 (i.e. the assumption that every species is

always detected); mussel recapture or detection probability in other studies was also generally low (i.e. <0.30; Vilella, Smith & Lemarie, 2004; Meador, Peterson & Wisniewski, 2011; Wisniewski *et al.*, 2013), but ranged up to 0.69 for some species (Wisniewski *et al.*, 2013). Our detection probability estimate of 0.42 may reflect our intensive sampling effort at each site, but may be biased high because of the data structure we applied. Our findings did not support a species or habitat effect on detection probability, although others have found a relationship with species, burrowing behaviour, habitat and survey characteristics (Smith, Vilella & Lemarie, 2001; Strayer & Smith, 2003; Vilella *et al.*, 2004; Huang, Cao & Cummings, 2011; Meador *et al.*, 2011; Shea *et al.*, 2013; Wisniewski *et al.*, 2013).

Analysis of rare species

Because methods of determining detection probability are relatively data intensive, the investigation of rare species is often troublesome (MacKenzie *et al.*, 2005). Rare mussel species are often overlooked in surveys, with less than half of rare species found in a typical 1.5 person-hours survey (Metcalf-Smith *et al.*, 2000). We designed our mussel surveys to detect rare species by investing a greater effort (minimum of six person-hours) than is applied in typical mussel surveys (Metcalf-Smith *et al.*, 2000). Our intensive surveys accomplished the goal, with the observed species richness for each site occurring within the 95% credible interval of the

Table 5 Mean occurrence (ψ) and detection (p) probabilities for 14 species of freshwater mussels, with standard deviation (SD) and 95% credible intervals (CI); see Model 2, Table S1 for model details.

Species	p (SD)	95% CI	ψ (SD)	95% CI
<i>Alasmidonta heterodon</i>	0.42 (0.03)	0.36–0.47	0.11 (0.06)	0.03–0.29
<i>A. undulata</i>	0.42 (0.03)	0.36–0.47	0.04 (0.04)	0.01–0.16
<i>Elliptio congaraea</i>	0.42 (0.03)	0.36–0.47	0.29 (0.10)	0.13–0.52
<i>E. fisheriana</i>	0.42 (0.03)	0.36–0.47	0.11 (0.06)	0.03–0.28
<i>E. icterina</i>	0.42 (0.03)	0.36–0.47	0.67 (0.12)	0.42–0.86
<i>E. lanceolata</i>	0.42 (0.03)	0.36–0.47	0.08 (0.05)	0.02–0.25
<i>E. roanokensis</i>	0.42 (0.03)	0.36–0.47	0.11 (0.07)	0.03–0.30
<i>E. steinstansana</i>	0.42 (0.03)	0.36–0.47	0.08 (0.05)	0.02–0.23
<i>Fusconaia masoni</i>	0.42 (0.03)	0.36–0.47	0.29 (0.11)	0.13–0.52
<i>Lampsilis cariosa</i>	0.42 (0.03)	0.36–0.47	0.11 (0.06)	0.03–0.28
<i>Lampsilis</i> sp.	0.42 (0.03)	0.36–0.47	0.04 (0.04)	0.01–0.17
<i>Strophitus undulatus</i>	0.42 (0.03)	0.36–0.47	0.04 (0.03)	0.01–0.17
<i>Utterbackia imbecillis</i>	0.42 (0.03)	0.36–0.47	0.05 (0.04)	0.01–0.16
<i>Villosa constricta</i>	0.42 (0.03)	0.36–0.47	0.19 (0.09)	0.07–0.40

estimated species richness which accounted for imperfect detection. With the hierarchical community-modeling approach we adopted, we were able to generate estimates of occurrence for even the rarest species in the Tar River Basin, including *A. heterodon*, *E. steinstansana* and *F. masoni*.

Abiotic and biotic influences

Our primary goal was to investigate the effects of a range of multiscale covariates on mussel occurrence. Measurements of microhabitat characteristics have shown mixed success in predicting mussel distributions (e.g. Salmon & Green, 1983; Strayer & Ralley, 1993),

whereas reach and catchment-scale variables such as hydraulics and geomorphology have proven to be more reliable (e.g. McRae *et al.*, 2004; Gangloff & Feminella, 2007; Newton, Woolnough & Strayer, 2008). We found that two catchment-scale covariates, stream power and agricultural land use, influenced mussel occurrence.

Our results supported a positive link between mussel occurrence and stream power. Conversely, a majority of studies have found a negative association between mussel distribution and related hydraulic variables, including Layzer & Madison's (1995) finding that stream power is negatively related to mussel density. However, we measured very low stream power at some of our sites (0.0 W/m), and a positive relationship between flow and mussel occurrence may exist below a certain threshold (Layzer & Madison, 1995; Steuer *et al.*, 2008). These results should be interpreted with caution, however, because the positive relationship we found between stream power and occurrence was imprecise, and one of the best supported models in our candidate set did not include covariates such as stream power.

The negative relationship between mussel occurrence and agricultural land use is well-established (e.g. Poole & Downing, 2004; Cao *et al.*, 2013; Daniel & Brown, 2013), with impacts such as hydrologic instability (Gangloff & Feminella, 2007), sedimentation (Arbuckle & Downing, 2002), nutrient runoff (Richter *et al.*, 1997) and pesticides (Fleming, Augspurger & Alderman, 1995) identified as stressors to freshwater mussels. In the Tar River Basin, nutrient runoff may be of particular importance as the entire basin is classified as nutrient sensitive waters and requires a comprehensive nutrient management strategy (NCDENR, 2010).

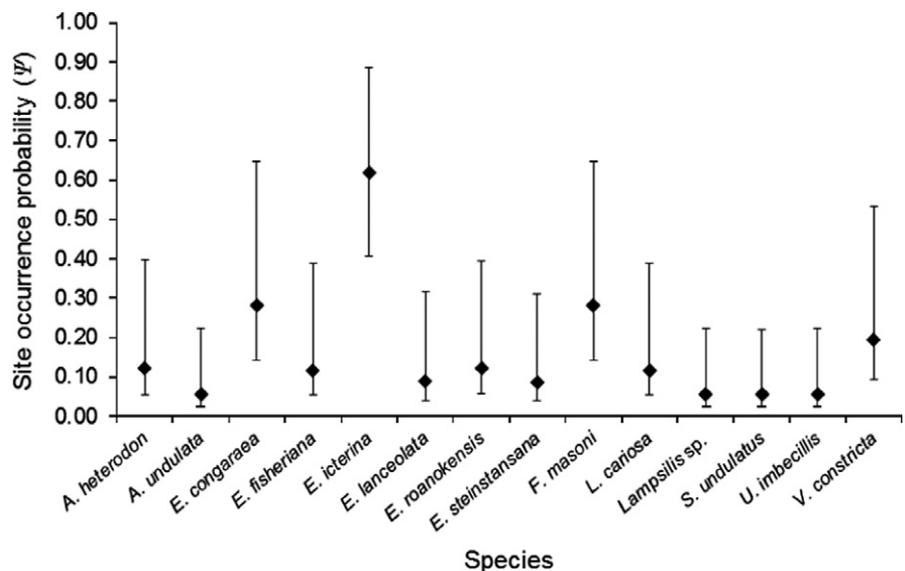


Fig. 3 Median estimated occurrence probability of 14 species of freshwater mussels from 20 study sites in the Tar River Basin, North Carolina. Error bars represent range of occurrence probabilities among sites for each species; see Model 2, Table S1 for model details.

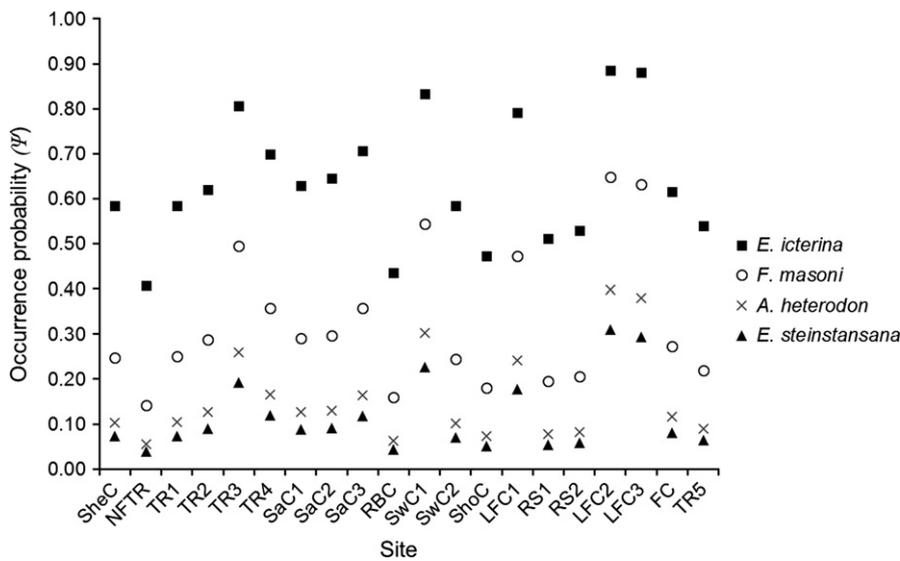


Fig. 4 Estimated occurrence probabilities at 20 sites in the Tar River Basin, North Carolina, for four mussel species of varied conservation concern: stable *Elliptio icterina*, NC state endangered *Fusconaia masoni*, and federally endangered *Alasmidonta heterodon* and *E. steinstansana*; see Model 2, Table S1 for model details.

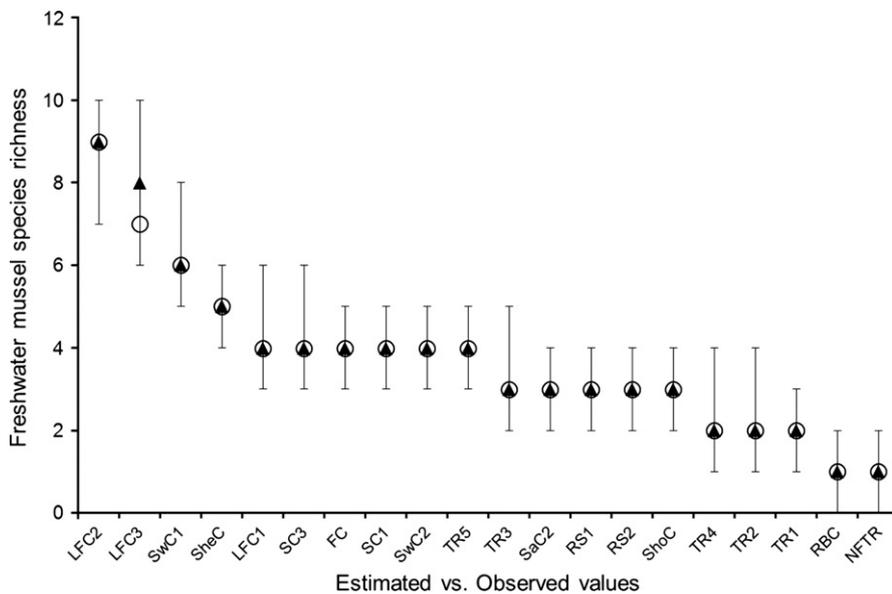


Fig. 5 Estimated (black triangles) and observed (open circles) mussel species richness at 20 sites in the Tar River Basin, North Carolina. Error bars are 95% credible intervals of estimate.

The mussel species traits that were found to influence mussel occurrence in this study are correlated and broadly relate to mussel reproductive strategy. Thus, the interpretation of the influence of these three parameters on mussel occurrence suggests that any one, or all, of the three parameters may influence mussel occurrence in the Tar River Basin. Our results suggest that host generalists have a lower occurrence probability than host specialists, possibly because host specialists often have adaptation strategies which lead to a higher reproductive success rate (Kat, 1984; Barnhart *et al.*, 2008). We did not detect an effect of attraction strategy on mussel occurrence; however, this distinction often falls along genetic boundaries (Barnhart *et al.*, 2008). Most Unionidae (such as the Anodontini) broadcast glochidia without specialised attraction strategies (Barnhart *et al.*,

2008), whereas members of the Amblemini subfamily, such as Pleurobemini and Lampsilini, tend to use host attraction mechanisms to enhance reproductive success (Graf & Cummings, 2007; Barnhart *et al.*, 2008). Therefore, it is reasonable to speculate that the apparent influence of tribe on mussel occurrence probability may relate to reproductive strategy, and specifically to host attraction strategy, although these parameters were not significantly correlated in this study.

The influence of brood time on occurrence is also related to overall reproductive strategy. Long-term brooders were expected to have a lower occurrence probability than short-term brooders, which may be attributed to the longer period for some stressors, such as chemical contaminants or thermal extremes, to interfere with the reproductive process in long-term

brooders. Alternatively, these findings may be related to detection, as mussels are more likely to be epibenthic during periods of reproductive activity, resulting in long-term brooders being less available for detection during the typical summer field season (Amyot & Downing, 1998; Schwalb & Pusch, 2007; Eads & Levine, 2013).

Although we did not detect an effect of fish species richness on mussel occurrence, several studies have found that variability or abundance of fish relates to the distribution of mussels (Haag & Warren, 1998; Vaughn & Taylor, 2000; Cao *et al.*, 2013; Schwalb *et al.*, 2013). We are not the only investigators to find little or no support of a link between fish community metrics and mussel distribution (Poole & Downing, 2004; Daniel & Brown, 2013), but our community-modelling approach averaged effects across species, so if a few species exhibited a positive relationship with fish richness, but others did not, the overall effect may be negligible or undetected.

Conservation and management implications

Our results indicate that environmental factors influence mussel species at a catchment-level scale and that factors such as land use and water flow may affect all species with a similar magnitude. On a broad scale, any management actions taken to protect natural flow regimes or restrict detrimental land use applications will likely be protective of an entire mussel assemblage. However, our results also indicated that mussel occurrence was influenced by species traits, specifically those related to reproductive strategy. This suggests that habitat restoration and management alone may not be sufficient for the conservation of all species. Species-specific management may be necessary as not all mussel species in an assemblage will thrive under the same conditions. When restoring or augmenting mussel populations, it would be beneficial to be cognizant of reproductive strategies and recognise that some species may need more monitoring and direct intervention.

Another valuable conservation tool is an accurate measure of species richness. As an indicator of biodiversity, species richness can provide information on the integrity of ecosystem processes (e.g. Chapin *et al.*, 2000; Purvis & Hector, 2000; Schwartz *et al.*, 2000). Conversely, biased measures of species richness will in turn bias estimates of species turnover, local extinction and colonisation (MacKenzie *et al.*, 2005; Kery & Royle, 2009), which could lead to false assumptions and inefficient conservation planning. Therefore, accurate estimates of mussel populations, including occurrence and species richness,

are necessary for developing successful conservation and management strategies, and our findings demonstrate an important advance in improving accuracy of such estimates in a modelling approach that may be applied more broadly to other river basins and regions towards effective conservation.

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Supporting Information

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

Figure S1. Estimated responses in the occurrence probability of freshwater mussels over a range of agricultural land use and stream power values in a catchment.

Table S1. Candidate models for the occurrence (ψ) and detection (p) probabilities of a freshwater mussel assemblage, with deviance information criterion (DIC) rankings and DIC difference in successive candidate models (Δ DIC).

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