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# Abundance of five sympatric stream dwelling mussels varies with physical habitat

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## Abstract

1. Freshwater mussel species regularly co-occur in streams forming assemblages, but the extent of shared versus unique instream habitat features that contribute to their distribution and abundance is poorly understood. In Massachusetts, a rare species, *Alasmidonta varicosa*, is often found with four other species: *Alasmidonta undulata*, *Strophitus undulatus*, *Margaritifera margaritifera*, and *Elliptio complanata*, yet variation in species composition within assemblages raises questions of potential species-specific habitat associations. Identifying species-level habitat information is critical at a spatial scale that malacologists can use to identify translocation or restoration areas.

2. This study investigated whether species abundance varied by mesohabitat type (riffle, run, dam pool, scour pool), instream habitat characteristics, and within-reach location (centre versus edge). From 2016 to 2019, freshwater mussel surveys were conducted in nine streams across Massachusetts and associated habitat information was collected.

3. Species abundances were similar across mesohabitat types. *Elliptio complanata* was the exception, whereby higher abundances occurred in runs and dammed pools than in riffles. Unique species relationships with habitat existed for *M. margaritifera* with macroalgae and emergent vegetation, and *A. varicosa* with heterogeneous substrate. Flow transitions, such as depositional areas that create heterogeneous substrates, may provide habitats for *A. varicosa*.

4. Most mussel species were distributed with higher abundance in the river centre than the edge; *E. complanata* was the only species with a higher abundance at the river edge. Locations with high abundance varied based on unique relationships with pebble heterogeneity (*A. varicosa*), depth (*A. undulata*), large wood (*A. undulata*), and canopy closure (*E. complanata*). Including physical characteristics in a holistic assessment of habitat that incorporates fish and landscape attributes may further an understanding of river reaches that best support translocated and propagated freshwater mussels.

## 1 | INTRODUCTION

River processes shape habitat features that contribute to the abundance and distribution of freshwater mussels (Order Unionida) (Atkinson et al., 2012; Vannote & Minshall, 1982). The limited mobility of mussels subjects them to human-driven disturbances to instream habitat, one of the leading causes contributing to their global decline (Downing et al., 2010; Gillis et al., 2017; Williams et al., 1993). Although hydrological alterations from urbanization and agriculture broadly affect mussel abundance and distribution and result in reduced mussel diversity and population loss (Watters, 1999), mussel distribution structured by habitat features within a river reach can be difficult to distinguish (Brim Box et al., 2002). The hierarchy of spatial constraints that influence mussel habitat within a catchment, river reach, and patch size often make it challenging to identify variables that predict mussel abundance and distribution (McRae et al., 2004; Strayer & Ralley, 1993; Vaughn & Taylor, 2000).

Effective freshwater mussel conservation requires an understanding of the river habitats of resident mussels and accurately identifying high-quality habitats for translocation (i.e., deliberate movement of organisms from one site for release in another; IUCN, 2013) during stream projects or reintroduction (i.e., aims to re-establish a viable population of the focal species within its indigenous range; IUCN, 2013) (Haag & Williams, 2014; Jourdan et al., 2018; McMurray & Roe, 2017). Applying nationally available data in large-scale spatial models to predict species distributions can help assess regional conservation challenges (Schartel et al., 2021). However, these models often lack the fine-scale field data necessary to understand the patchy distributions and abundances of mussels in rivers—the information needed to address local conservation challenges (i.e., within a 100-m river reach) (Zając et al., 2018). Modelling species abundance with local habitat correlates can help to form hypotheses concerning changes in abundance over time and define the effort needed to locate high-quality habitats supporting yet unknown populations. Furthermore, mussel relocations can result in high mortality if an unsuitable river reach is selected (Cope & Waller, 1995). Thus, local species-specific habitat criteria that include abundance may help identify relocation areas capable of supporting an augmentation of translocated species or new locations with the capacity to support the size of the translocated population (Barnes et al., 2022; Hamilton et al., 1997).

Lotic systems are a continuum of mesohabitat types (e.g., channel units: riffles, pools, runs), which can determine mussel abundance (Gagnon et al., 2006) and distribution (Howard & Cuffey, 2003; Smit & Kaeser, 2016). Furthermore, biological or physical processes measured within mesohabitats, such as shear stress, can predict mussel abundance and richness (Randklev et al., 2019). Thus, mesohabitats encompass microhabitat (e.g., substrate, depth) and reach scale (e.g., instream flow) measures, which may be useful for understanding local mussel abundance and distribution.

Mussel fauna in the north-eastern United States consists of patchily distributed dense mussel beds in which species have sympatric ranges (Haag, 2012), but differences among local species occurrences and abundances indicates the potential for species-specific habitat drivers. However, previous studies have demonstrated mixed results in their ability to distinguish species-specific habitat; occurrence or abundance have had either weak or nonsignificant relationships to habitat, and limited observations have precluded habitat classification for rare species (Brim Box et al., 2002; Holland-Bartels, 1990; Strayer, 1981; Strayer & Ralley, 1993).

The relationships of habitat to abundance for five mussel species: *Alasmidonta varicosa* (brook floater; Lamarck, 1819), *Alasmidonta undulata* (triangle floater; Say, 1817), *Strophitus undulatus* (creeper; Say, 1817), *Margaritifera margaritifera* (eastern pearlshell; Linnaeus, 1758), and *Elliptio complanata* (eastern elliptio; Lightfoot, 1786), which often co-occur to create relatively diverse assemblages for Massachusetts, have not been quantified, and existing information largely focuses on habitat correlations with species occurrence, with limited studies on abundance. For *A. varicosa*, a model weakly predicted occurrence with positive associations of moderate current speeds and a high proportion of medium sands (0.25–1 mm) in the Neversink River, New York (Strayer & Ralley, 1993). *Strophitus undulatus* is lotic and lentic adapted (Howells, 2014), occurring in wing dams of the upper Mississippi River (Miller, 1988) and most prevalent in runs within rivers (Hart, 1995). Despite their occurrence in lentic habitat, *S. undulatus* is intolerant of silt (Dean et al., 2002) and was shown to be negatively related to fine particles (<2 and 2 mm), bank angle, and lake plain clay in a Michigan river (McRae et al., 2004). Low abundances of *A. undulata* in previous studies preclude habitat interpretation (Pandolfo et al., 2017; Strayer & Fetterman, 1999). Habitat relationships for *M. margaritifera* are well studied in Europe where the species is endangered (Hastie et al., 2000, 2003; Morales et al., 2004; Young, 1991). In two European studies assessing substrate, *M. margaritifera* was negatively related to gravel/pebble, silt, and fine particles that could clog interstitial spaces (Geist & Auerswald, 2007; Hastie et al., 2003). In Scotland, *M. margaritifera* was negatively related to aquatic vegetation and positively related to types of riparian tree cover (Hastie et al., 2003). Excess aquatic vegetation can be more common in nutrient-rich environments (O'Hare et al., 2018) atypical of *M. margaritifera* habitat (Hastie et al., 2000). The abundance of *E. complanata* was not correlated

with any physical, chemical, or hydrological factors measured in a first order stream in Virginia (Balfour & Smock, 1995). The range of habitats that species occupy in different geographical regions suggests the need for understanding mussel–habitat associations in the north-eastern United States, where existing data on these species are sporadic and connected in inconsistent ways.

Despite the challenges of quantifying mussel habitat and predicting species abundance, it is vital to further species conservation. Predicting suitable habitat that supports a range in population sizes can inform effort needed to locate extant mussel populations and aid in selecting locations that may support high-abundance populations. This study aimed to predict abundance of five co-occurring species using biotic and abiotic variables collected across multiple catchments in Massachusetts. Specifically, the research questions were as follows: (i) Does abundance of each species differ among mesohabitats? (ii) Do habitat features predict the abundance of each species in river reaches? (iii) Does habitat affect the distribution in species abundance between the centre or edge of a river reach? Habitat and distribution of the common species *E. complanata* may be more difficult to predict, because of its generalist use of habitat, whereas species more limited in distribution (*A. varicosa*, *S. undulatus*, *A. undulata*, *M. margaritifera*) may have stronger associations with mesohabitat types and habitat features. Given the importance of stream-bed stability to mussels (Allen & Vaughn, 2010; Randklev et al., 2019), species may share preference in sediment metrics (e.g., median particle size), contributing to their co-occurrence, but differ in other habitat metrics, accounting for differences in their distributions.

## 2 | METHODS

### 2.1 | Study location

Mussels and habitats were sampled across four hydrological unit codes, which are hydrological delineations that define the extent of surface water that drains to a point (U.S. Geological Survey, 2019) for eight (HUC 8) subbasins in Massachusetts (Figure 1). Selected subbasins are mostly centrally located in the State and include the Farmington, Middle Connecticut, Chicopee, and Nashua. The river landscape in these subbasins was influenced by historical industrial and agricultural development that is common across Massachusetts. In the late 18th century and early 19th century, rivers in Massachusetts were intensely dammed to power machinery in mills (Graf, 1999; Stevenson, 2017) and 45%–65% of the New England region was cleared for agriculture (Foster et al., 1998). Remanent and intact dams formed during this period still influence the river landscape today, partly through impacts on sediment transport (Dow et al., 2020; Magilligan et al., 2021), temperature (Zaidel et al., 2021), and connectivity (Magilligan et al., 2016). This history of intense industrial and agricultural practices in Massachusetts is typical of New England and offers a critical backdrop for understanding present day mussel distributions.

### 2.2 | Site selection

Mussel surveys were focused in areas with extant populations of the rarest mussel (*A. varicosa*), and sites were identified within rivers
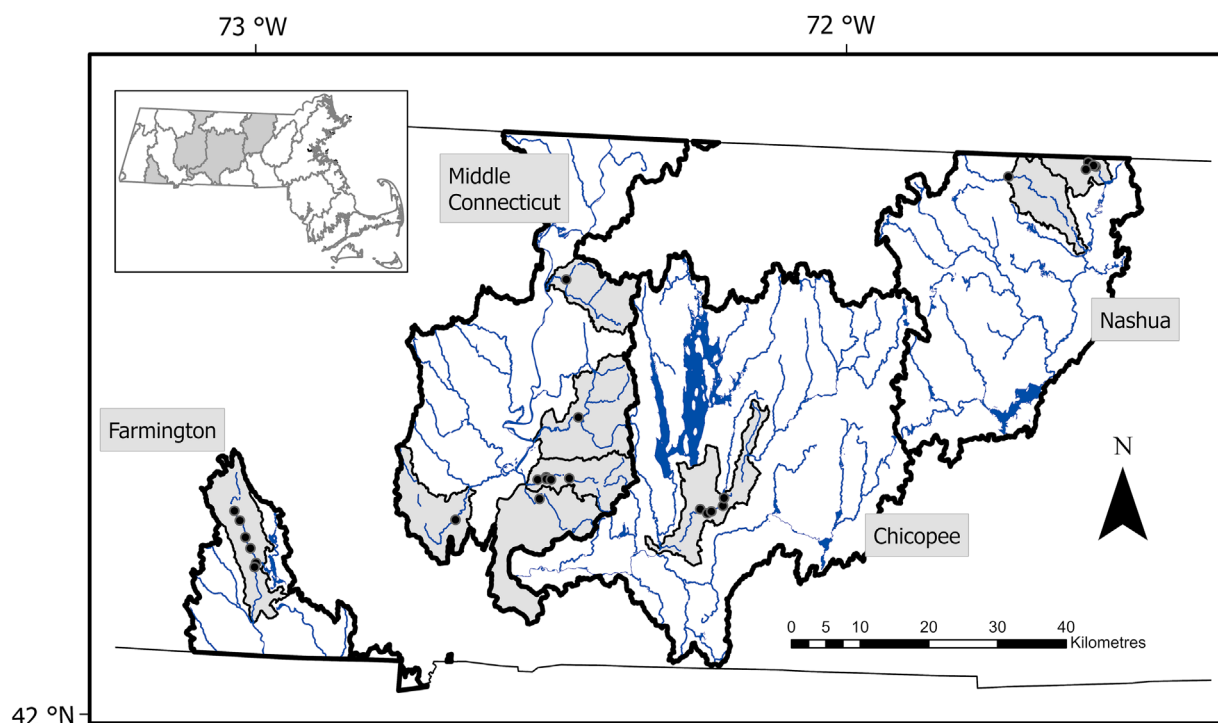


**FIGURE 1**   Study area of mussel sampling locations in 25 reaches (black dots) within four subbasins (HUC 8, upper left) and nine subcatchments (HUC 12, shaded grey) in Massachusetts.

based on occurrence records from reports (Nedeau, 2009a, 2009b) and the Massachusetts Natural Heritage and Endangered Species Program (NHESP) database. Before a formal survey, sites were first visited by two people who searched upstream and downstream of coordinates for up to 2 h. If target mussels (*A. varicosa*, *S. undulatus*, *A. undulata*, *M. margaritifera*) were found, the site was revisited for a formal survey with a larger field crew. Ultimately, 25 sites were sampled within the four HUC 8 subbasins and nine HUC 12 subcatchments (Figure 1).

## 2.3 | Mussel surveys

Surveys were nested within two spatial scales: reach and mesohabitat. At each site, a 100-m reach was selected that incorporated the range of mesohabitats representative of the larger river and observations of target species during site reconnaissance. Reaches were separated into different mesohabitat types: dammed pool, riffle, run, and scour pool (geological depression). If a mesohabitat was longer than 20 m, it was separated into more than one mesohabitat; this retained consistency in habitat assessments per mesohabitat within rivers.

Owing to the rarity of some target species, (*A. varicosa*, *S. undulatus*) semiquantitative timed surveys were conducted. Applying visual and tactile timed searches for mussels maximized efficiency in the search area compared with sampling quadrats, which can underestimate rare species detection (Smith, 2006). Three to seven surveyors spanned the width of the river and used masks and snorkels or clear-bottomed viewing buckets if stream depths prohibited snorkelling, to travel upstream within longitudinal transects (hereafter, 'lane') collecting mussels in a mesh bag (lane width ≤3 m) with a target search time of 1 min m$^{-2}$. Each mesohabitat was searched, and the timed search data were converted to abundance as catch per unit effort (CPUE) in mussels per min. All mussels (except *E. complanata*) were returned to the lane where they were found by placing the mussel into the sediment ($\sim$8 cm deep) so that the anterior was buried and the posterior was exposed to water. Due to the often high numbers of *E. complanata*, these were redistributed to the reach.

## 2.4 | Habitat surveys

To calculate the area of each mesohabitat surveyed, the wetted width was measured by extending a tape measure at a 90° angle to the flow to a point where the dry bank met the water and then multiplied by the length of the mesohabitat. Canopy closure was estimated in a single location in each mesohabitat in four ordinal directions near the centre of the mesohabitat using a spherical densiometer (Lemmon, 1957). Throughout the study, the same observer walked upstream and visually estimated the proportion of submerged vegetation, emergent vegetation, algae (=benthic macroalgae), and large wood (>10 cm in diameter) covering the mesohabitat. Within

each mesohabitat, 50 rocks were measured using the Wolman pebble count method for bed texture (Wolman, 1954). Surveyors walked upstream in a zig-zag pattern across each mesohabitat sampling pebbles randomly using a step-toe procedure in which a surveyor picks up the first pebble that touches their index finger next to their big toe and measures the intermediate axis (i.e., width) using a ruler (Wolman, 1954). Pebble counts in each mesohabitat were used to quantify pebble heterogeneity or the spread in particle sizes ($D_{84}/D_{16}$; 84th percentile/16th percentile) and median particle size ($D_{50}$), or the particle size that 50% of the samples are equal to or smaller than. Surveyors measured stream depth using a metre stick and walking each lane within each mesohabitat. Depth was measured every third step to obtain an average depth, and the maximum depth was recorded for each lane in each mesohabitat.

## 2.5 | Data analysis

Generalized linear mixed effect models (GLMMs) were used to address the three research questions. In all research questions, the count of each mussel species was modelled as catch per unit effort (CPUE) by including a logged offset (minutes) of search time in models (Zuur et al., 2009). Depending on the data error structure, GLMMs were fitted with Poisson, quasi-Poisson, or negative binomial errors and a log link function. Residual dispersion also contributed to the distribution (e.g., Poisson, quasi-Poisson, or negative binomial) used to model species. In all models, a random effect of river reach was included to account for spatial autocorrelation of multiple mesohabitats within one 100-m reach (Zuur et al., 2009). Zero inflation was assessed for inclusion in models by testing whether the expected number of zeros differed from the observed number using the DHARMa package (Hartig, 2021). All GLMMs were fitted in the glmmTMB package (Brooks et al., 2017) in R version 4.1.3 (R Core Team, 2022). For nonzero inflated models, the pseudo-$R^2$ values were fitted using Nakagawa's $R^2$ for mixed models (Nakagawa et al., 2017), and for zero-inflated models, the measure was fitted by computing the squared correlation between the model's actual and predicted response using the R package performance (Lüdecke et al., 2020). For each species, data from rivers was excluded where there were no species records of occurrence from the NHESP database; this eliminated false zeros owing to the species not occurring in the subcatchment (Blasco-Moreno et al., 2019). Model fit was inspected with residual Q–Q plots, a Kolmogorov–Smirnov test to assess deviation, and by simulating residuals to test dispersion and outliers in package DHARMa (Hartig, 2021).

The modelled mussel CPUE among mesohabitat types was compared to assess differences in abundance (Question 1). Pairwise contrasts were implemented using least-squares mean 95% confidence intervals in the lsmeans package in R (Length, 2016). For the reach scale analysis (Question 2), GLMMs were run using standardized habitat variables from mesohabitats as predictors of species abundance, and mesohabitat types were used as replicates. Predictor variables were assessed for correlation; maximum and

average depth were highly correlated (Pearson |r| > 0.7; Dormann et al., 2013); thus, maximum depth was randomly selected for use in global models across all species. Scatterplots between each habitat variable and mussel CPUE indicated potential nonlinear relationships; however, global models with habitat variables (*n* = 9) failed to converge when nonlinear terms were included (except for *M. margaritifera*). Therefore, global models were fitted including nonlinear terms (maximum depth for *A. varicosa* model, and pebble heterogeneity for *A. varicosa* and *A. undulata* models) using Least Absolute Shrinkage and Selection Operator (LASSO) (Fan & Li, 2012) in the R package glmmLASSO (Groll, 2015). The LASSO procedure was created to select the most important variables before modelling with GLMMs by applying a penalized log likelihood parameter lambda (λ). Penalizing log likelihood can cause instability in parameter estimates and is only used to select a number of variables for modelling with GLMMs. LASSO reduced the number of predictor variables from nine to five; if fewer than five variables were significant at the $\alpha = 0.05$ level in LASSO, then a higher penalization parameter was used until only five remained. All combinations of the five variables were compared using Akaike information criterion corrected for small sample size (AICc). The best models were considered to have the lowest AICc value and highest AICc weight (Burnham & Anderson, 2004). This two-step process allowed AICc model selection using a GLMM approach with more accurate parameter estimation than LASSO variable selection alone (Schelldorfer et al., 2014).

Habitat predictors influencing species distribution in abundance within rivers were assessed for Question 3. Abundance data collected within lanes was the modelled response and mesohabitats were replicates. Observer lanes abutting the bank edge were labelled as a categorical factor 'edge', whereas all other lanes were labelled as 'centre'. GLMMs were used to compare the river edge and centre capture rate. To account for differences in survey area between the river centre and the edge, survey effort was standardized in models using a logged offset in minutes. To assess which habitat variables explained differences in mussel CPUE between edge and centre lanes, an interaction was tested between edge and centre factors and habitat characteristics collected within each mesohabitat (canopy closure, emergent vegetation, submerged vegetation, large wood, macroalgae, D50, pebble heterogeneity) and within each lane (presence or absence of submerged vegetation, emergent vegetation, algae and large wood, mean and maximum depth). Predictor variables were checked for correlation; maximum and average depth were highly correlated (Pearson |r| > 0.7; Dormann et al., 2013); thus, for models containing a significant ($\alpha \leq 0.05$) depth term, model residuals were inspected to determine whether mean depth or maximum depth performed better (e.g., Q–Q plots, Kolmogorov–Smirnov test) to ultimately retain for use in a global model. Significant interactions ($\alpha \leq 0.05$) predicting mussel CPUE were included in a global model with their additive terms, and Akaike information criterion (AICc) corrected for small sample size (Burnham & Anderson, 2004) was applied to identify the model that fitted the data best.

## 3 | RESULTS

Mussel richness varied among the nine subcatchments with a maximum of eight species in the Fort River within one river reach and a minimum of one species in the Sawmill River (Table 1). Overall, nine species were identified: *A. varicosa*, *A. undulata*, *S. undulatus*, *M. margaritifera*, *E. complanata*, *Pyganodon cataracta* (eastern floater), *Lampsilis radiata* (eastern lampmussel), *Sagittunio nasutus* (eastern pondmussel), and *Alasmidonta heterodon* (dwarf wedgemussel). *Elliptio complanata* dominated mussel assemblages in all subcatchments except for the Squannacook River and the Sawmill River where *M. margaritifera* had the highest abundance or was the only species. When pooling mussel species, reach averages calculated from the total mussel abundance and density within mesohabitats ranged from 0.007 to 5.549 mussels per min and from 0.001 to 2.272 mussels per m², respectively (Table 1). The maximum CPUE within a reach (23.7 mussels per min) and within river location (edge of river: 50.0 mussels per min) was in the West Branch of the Farmington River below Hayden Pond dam. The Ware River had the highest CPUE within a mesohabitat (run: 9.97 mussels per min; Table S1). The total abundance and density estimate in each mesohabitat were correlated ($r = 0.74$).

### 3.1 | Mesohabitat type (Question 1)

Mesohabitat type was not a strong predictor of the abundance of each mussel species (Figure 2; Table S2). Trends showed higher *A. varicosa* and *A. undulata* abundances associated with dammed pools, runs, and scour pools, with lower abundances in riffles (all contrasts *P* > 0.05). *Strophitus undulatus* and *M. margaritifera* abundances depicted similar patterns with higher abundances in runs and dammed pools than in scour pools and riffles (all contrasts *P* > 0.05). *Elliptio complanata* had a higher abundance in runs than riffles ($P = 0.01$) and scour pools ($P = 0.05$).

### 3.2 | Habitat characteristics (Question 2)

Mussel species abundance was predicted by habitat variables within river reaches (Figures 3 and 4). LASSO variable selection for *A. varicosa* included canopy closure, D50, maximum depth, pebble heterogeneity, and algae. The top model consisted of four of the five variables, but there were multiple models (*n* = 10; Table S3) within two AICc units. Within the top model, *A. varicosa* had highest abundances at intermediate levels of pebble heterogeneity (unimodal, $\beta_{pebble(1)}$ $P = 0.032$, $\beta_{pebble(2)}$ $P = 0.090$) and maximum depth (unimodal, $\beta_{depth(1)}$ $P = 0.651$, $\beta_{depth(2)}$ $P = 0.026$) and a negative relationship with D50 ($P = 0.095$) and large wood ($P = 0.113$; Figure 3; Table 2). The top variables for *A. undulata* were emergent vegetation, submerged vegetation, canopy closure, D50, and maximum depth. Two models were within two AICc units of the top model containing only D50 (negative relationship; $P = 0.081$) and maximum depth (positive relationship; $P = 0.025$; Figure 4a,b;

**TABLE 1** River reaches surveyed for habitat. The mussel richness, number of mesohabitats (meso.), and area surveyed in each reach. Averages are calculated from the total mussel abundance or density within mesohabitats in the reach. ALVA = *Alasmidonta varicosa*, ALUN = *Alasmidonta undulata*, STUN = *Strophitus undulatus*, MAMA = *Margaritifera margaritifera*, ELCO = *Elliptio complanata*.

| Subbasin | Subcatchment | Reach | Meso. | Survey area (m²) | Richness | Average abundance (no. min⁻¹) | Average density (no. m⁻²) | ALVA | ALUN | STUN | MAMA | ELCO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chicopee | Ware River | WARE1 | 5 | 2426 | 5 | 1.296 | 0.273 | 0.0148 | 0.0019 | 0.0074 | 0.0019 | 1.2148 |
| | | WARE1.5 | 5 | 3166 | 5 | 1.762 | 0.305 | 0.0075 | 0.0149 | 0.0093 | 0.0056 | 1.7724 |
| | | WARE1.6 | 5 | 3380 | 5 | 2.540 | 1.193 | 0.0051 | 0.0103 | 0.0058 | 0.0039 | 2.5528 |
| | | WARE2 | 8 | 1840 | 3 | 0.896 | 0.326 | 0.0000 | 0.0081 | 0.0097 | 0.0000 | 1.0097 |
| | | WARE3 | 5 | 2660 | 4 | 5.549 | 0.911 | 0.0064 | 0.0468 | 0.0681 | 0.0000 | 4.8872 |
| Farmington | W.B. Farmington | FARM0 | 5 | 1495 | 1 | 0.007 | 0.001 | 0.0000 | 0.0000 | 0.0000 | 0.0071 | 0.0000 |
| | | FARM1 | 5 | 2026 | 2 | 0.025 | 0.006 | 0.0000 | 0.0000 | 0.0000 | 0.0155 | 0.0116 |
| | | FARM1.3 | 5 | 1566 | 3 | 0.176 | 0.054 | 0.0142 | 0.0000 | 0.0000 | 0.0244 | 0.1321 |
| | | FARM1.5 | 6 | 860.5 | 4 | 1.866 | 0.856 | 0.0519 | 0.0026 | 0.0052 | 0.0000 | 2.0831 |
| | | FARM1.7 | 7 | 663 | 2 | 0.985 | 0.566 | 0.0052 | 0.0000 | 0.0000 | 0.0000 | 1.2552 |
| | | FARM2 | 5 | 1640 | 3 | 5.338 | 1.247 | 0.0052 | 0.0155 | 0.0000 | 0.0000 | 23.7113 |
| Middle Connecticut | Bachelor Brook | BACH1 | 5 | 1084 | 2 | 0.902 | 0.289 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 1.1656 |
| | | BACH2 | 6 | 1227 | 3 | 3.396 | 1.439 | 0.0220 | 0.0000 | 0.0220 | 0.0000 | 3.0513 |
| | | BACH3 | 7 | 836 | 3 | 0.655 | 0.303 | 0.0000 | 0.0026 | 0.0079 | 0.0000 | 0.6587 |
| | | BACH4 | 5 | 799 | 3 | 3.844 | 1.852 | 0.0000 | 0.0029 | 0.0380 | 0.0000 | 4.4649 |
| | | BACH5 | 5 | 922 | 1 | 1.322 | 0.365 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 1.3276 |
| | Fort River | FORT2 | 6 | 1030 | 8 | 3.351 | 2.272 | 0.0000 | 0.0521 | 0.0063 | 0.4850 | 3.0111 |
| | Manhan River | MANH1 | 5 | 966 | 4 | 0.094 | 0.032 | 0.0000 | 0.0000 | 0.0038 | 0.0230 | 0.0728 |
| | Sawmill River | SAWM1 | 5 | 2010 | 1 | 0.101 | 0.019 | 0.0000 | 0.0000 | 0.0000 | 0.1224 | 0.0000 |
| | Stony Brook | STON2 | 7 | 653 | 3 | 0.811 | 0.399 | 0.0000 | 0.0000 | 0.0000 | 0.0032 | 0.7895 |
| Nashua | Nissitissit River | NISS0 | 7 | 1805 | 5 | 0.875 | 0.436 | 0.0049 | 0.0008 | 0.0008 | 0.0171 | 0.7072 |
| | | NISS1 | 5 | 1515 | 5 | 2.588 | 1.058 | 0.0065 | 0.0012 | 0.0018 | 0.2231 | 1.2964 |
| | | NISS2 | 7 | 3555 | 4 | 2.063 | 1.783 | 0.0410 | 0.0169 | 0.0000 | 0.0807 | 2.0434 |
| | Sucker Brook | SUCK3 | 8 | 510 | 6 | 1.483 | 1.250 | 0.0000 | 0.0237 | 0.0095 | 0.2725 | 1.2725 |
| | Squannacook River | SQUA1 | 6 | 1242 | 3 | 0.230 | 0.082 | 0.0000 | 0.0914 | 0.0026 | 0.2116 | 0.0000 |
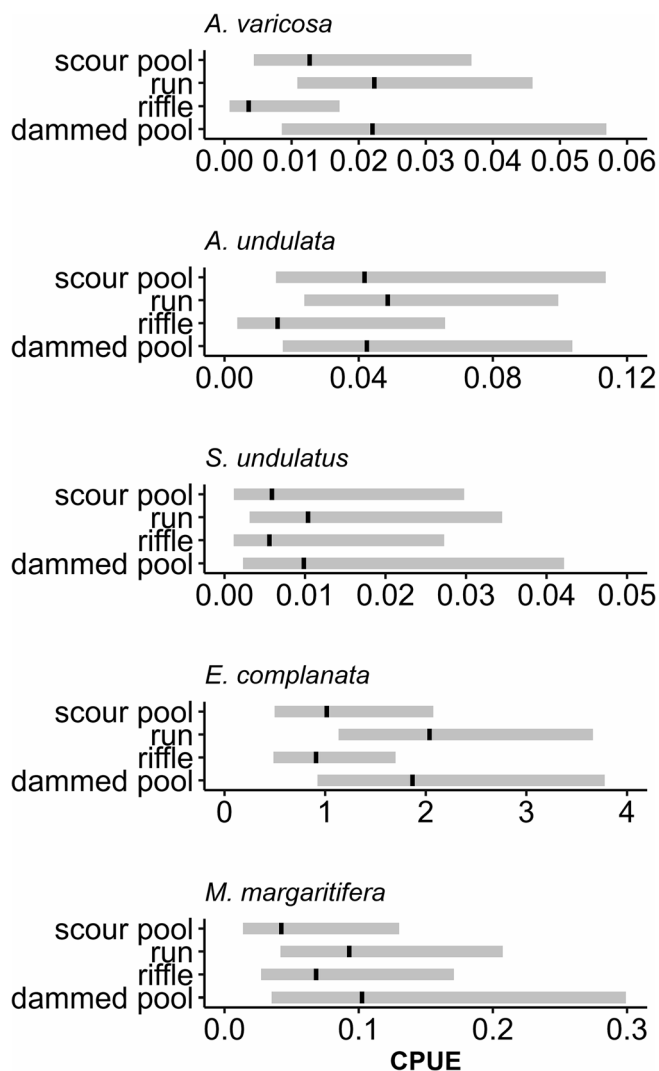
**FIGURE 2** Results from generalized linear mixed effects models on the response scale for each species comparing modelled abundance within mesohabitats. The species shown are *Alasmidonta varicosa*, *Alasmidonta undulata*, *Strophitus undulatus*, *Elliptio complanata*, and *Margaritifera margaritifera*. Variability across random effects is not shown. Black lines are model predictions and shaded grey areas are 95% confidence bands. CPUE = catch per unit effort in mussels per minute. The model details are in Table S2.

Table 2). Top habitat variables for *S. undulatus* were D50, large wood, algae, canopy closure, and submerged vegetation. Five models were within two AICc units, the top model predicted negative relationships between *S. undulatus* abundance and D50 ($P = 0.013$) and large wood ($P = 0.043$; Figure 4c,d; Table 2). The top five variables for *E. complanata* were large wood, emergent vegetation, submerged vegetation, maximum depth, and D50. There were five models within two AICc units, which consisted of different combinations of all variables except large wood, with the top model consisting of a negative relationship with D50 ($P < 0.001$; Figure 4e; Table 2). *Margaritifera margaritifera* was the only species where variable selection was not required prior to fitting the global model; this may have resulted in the large number of top models ($n = 17$) within two

AICc units (Table S3). Within the top model, *M. margaritifera* had a negative relationship both with algae ($P = 0.061$) and emergent vegetation ($P = 0.078$; Figure 4f,g; Table 2).

## 3.3 | Mussel distribution within river reaches (Question 3)

All mussel species except *E. complanata* were found more often in the centre of the river than the edge of the river (ratios > 1, P value < 0.05; Figure 5; Table S4). This contrast ratio was greatest for *A. varicosa* (ratio = 2.16) and relatively similar for *A. undulata* and *S. undulatus*, ratio = 1.66 and 1.67, respectively. *Margaritifera margaritifera* abundance was higher at the river centre than the edge, with a smaller contrast ratio between means than the other species (ratio = 1.29). *Elliptio complanata* abundance was higher at the river edge but with a relatively small contrast (ratio = 0.829).

Three species (*A. varicosa*, *A. undulata*, *E. complanata*) had habitat features that interacted with river centre versus edge to predict abundance (Figure 6; Table 3). Heterogeneous substrate in the river centre was positively related to *A. varicosa* abundance, compared with no relationship at the river edge (Figure 6a). There was a positive relationship between mean depth and *A. undulata* abundance in the centre of the river, whereas at the edge of the river, higher abundances were at intermediate depths (Figure 6b). The proportion of large wood covering the mesohabitat did not affect the abundance of *A. undulata* in the centre of the river, but an intermediate cover of large wood predicted high abundance at the edge of the river (Figure 6c). The abundance of *E. complanata* was highest at the river edge when canopy closure was approximately 25%, and the lowest abundance was in the river centre at intermediate levels of canopy closure (Figure 6d). Mean depth was an additive term with a nonlinear relationship to *E. complanata* abundance; thus, it was important for the species distribution across all lanes (Figure 6e).

## 4 | DISCUSSION

### 4.1 | Using mesohabitat type to predict mussel species abundance

There were no differences in species abundances among mesohabitat types for *A. varicosa*, *A. undulata*, *S. undulatus*, and *M. margaritifera*. The variability in habitat characteristics within mesohabitat units sampled across subcatchments may have partially obscured relationships in this study, suggesting that mesohabitat type may not be an important factor in predicting abundance across subcatchments. Other studies that associated mussels with mesohabitats were in a single catchment or river segment (Gangloff & Feminella, 2007; Hart, 1995; Howard & Cuffey, 2003). Trends indicated that all mussels had their lowest abundances in riffle habitats and shared the use of run and dammed pool habitats. The run and pool habitats may provide lower shear stress than riffles and thus provide suitable
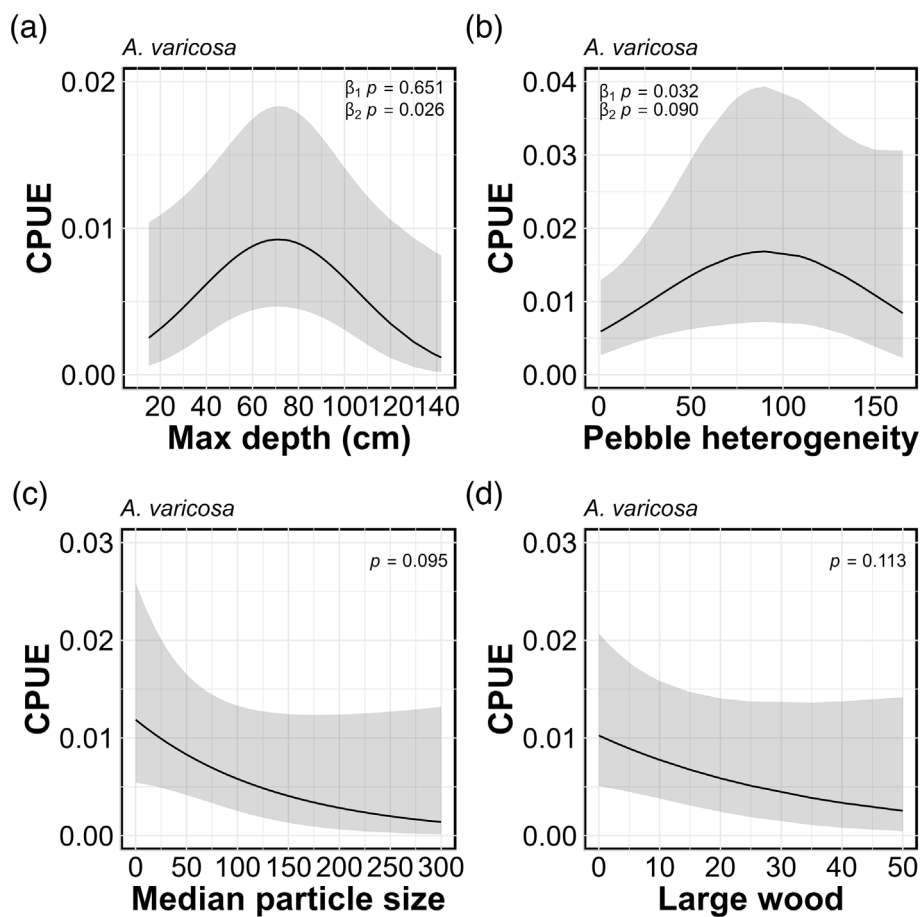
**FIGURE 3** Models of habitat features on the response scale predicting *Alasmidonta varicosa* abundance. Each fixed effect is conditioned on the mean of all additive variables for 1 min of search time and variability across random effects is not shown. Black lines are model predictions and shaded grey areas are 95% confidence bands. The model was developed with 125 *A. varicosa* individuals. CPUE = catch per unit effort in mussels per minute. The model details are in Table 2.

habitat for many mussel species (Davis et al., 2013; Gangloff & Feminella, 2007; Layzer & Madison, 1995; Morales et al., 2004; Strayer, 1999). Furthermore, pool habitat may serve as temporary refuge areas during droughts, providing areas where mussels avoid desiccation (Gough et al., 2012).

*Elliptio complanata* was the only species with statistical differences in abundance among mesohabitat types; they occurred in higher abundances in runs than in riffles and scour pools. Statistical differences may be the result of the larger sample size of *E. complanata* than the other species. However, any differences in abundance were surprising because the species is broadly categorized as a habitat generalist (Balfour & Smock, 1995; Clarke, 1980). It is likely that their habitat use differs regionally, considering that in the Flint River, Georgia, *E. complanata* was associated with sites with more pool habitat (Gagnon et al., 2006).

## 4.2 | Relationships between mussel abundance and habitat characteristics

Bed texture is an important aspect of physical habitat that may determine mussel abundance. The Wolman pebble count is typically biased towards larger sediment sizes; however, this study found an increase in mussel abundance associated with smaller sized particles

indicating that the data captured enough of the variability in sediment size. The mussels *A. varicosa*, *A. undulata*, *S. undulatus*, and *E. complanata* were recorded in higher abundances at particle sizes ≤2 mm (sand), a finding consistent with studies on *S. undulatus* in Michigan (McRae et al., 2004) and Minnesota (Hart, 1995). In New York, *A. varicosa* was associated with sands 0.25 to 1 mm, a substrate size category within this study's classification of sand (≤2 mm). Other studies have not identified habitat relationships with *E. complanata*, where their presence was not associated with any measures of substrate (e.g., porosity and heterogeneity) (Brim Box et al., 2002). In Massachusetts, this shared negative relationship with median particle size may indicate habitat where the four species co-occur.

Bed heterogeneity may also be important for freshwater mussel habitat. Maximum abundances of *A. varicosa* were recorded at intermediate values of bed heterogeneity. Bed heterogeneity represents substrate size variability and may result from several reach-scale characteristics including depositional flow areas, where particle size distributions change from coarse to fine (Bunte & Abt, 2001). This is congruent with observations in Massachusetts where *A. varicosa* are found in depositional river sections as opposed to steeper gradient reaches within the same river.

Depth is one of the most common variables thought to influence mussel abundance and distribution (Layzer & Madison, 1995; Strayer, 1993, 1999) and has been identified as important for several

**FIGURE 4** Models of habitat features (one per species) on the response scale predicting mussel abundance for four species. Black lines are model predictions and shaded grey areas are 95% confidence bands. Each fixed effect is conditioned on the mean of all additive variables for 1 min of search time and variability across random effects is not shown. CPUE = catch per unit effort in mussels per minute. The model was developed with (a, b) 155 *Alasmidonta undulata*, (c, d) 114 *Strophitus undulatus*, (e) 22,753 *Elliptio complanata*, and (f, g) 1,036 *Margaritifera margaritifera*. The model details are in Table 2.
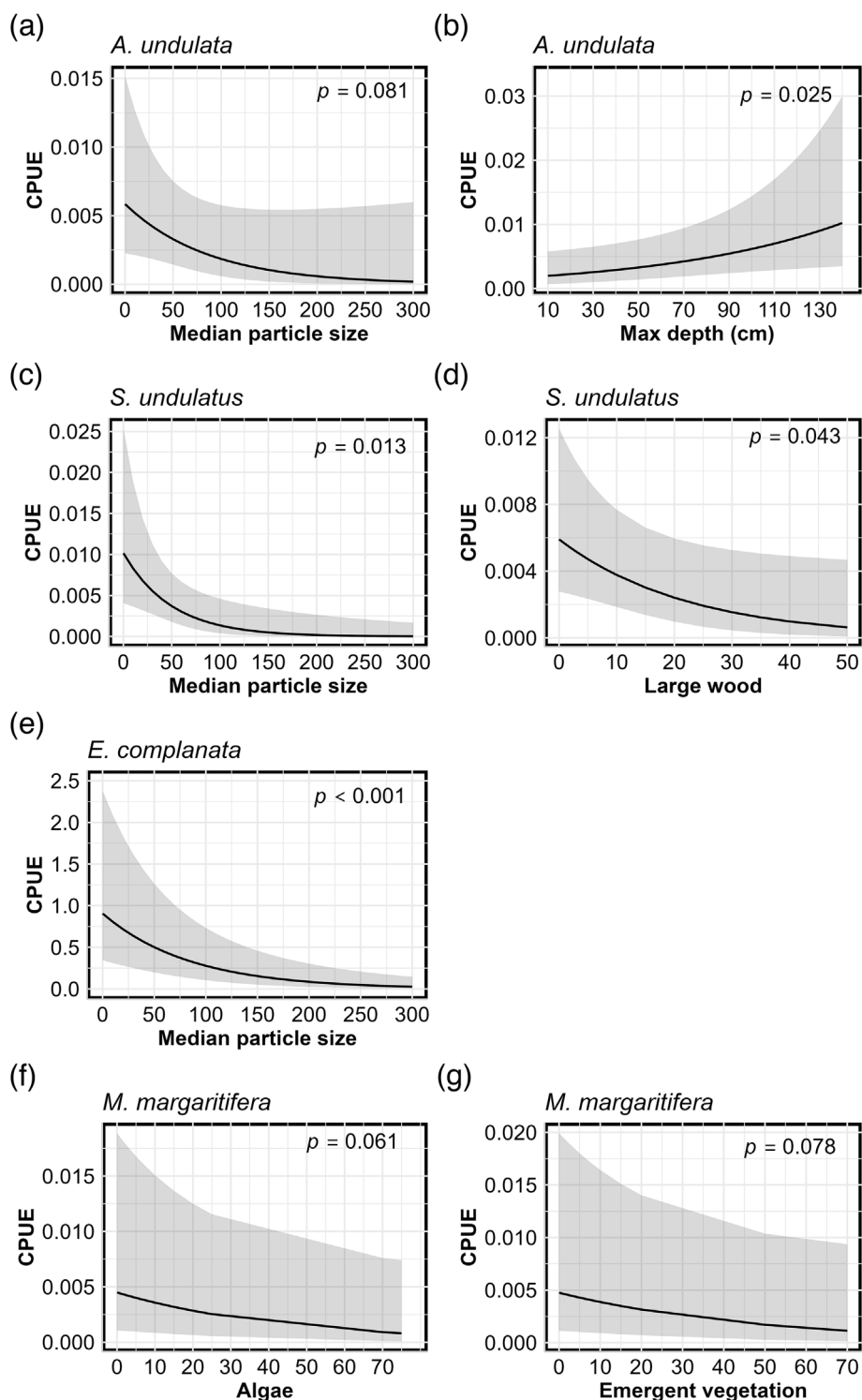


species (Geist & Auerswald, 2007; Pandolfo et al., 2016). In this study, both *Alasmidonta* species exhibited relationships to depth, but they differed in terms of absolute depth: *A. undulata* abundance was positively related to maximum depth whereas the abundance of *A. varicosa* was highest at an optimum depth of approximately 70 cm. *Alasmidonta varicosa* was also found at intermediate depths in the Neversink River in New York (Strayer & Ralley, 1993). The relationships of mussel species to depth is likely to be dependent on

the stream sizes surveyed. The depths in the wadeable streams surveyed in this study may allow *A. varicosa* persistence during drought conditions and associated secondary effects (e.g., low dissolved oxygen) (Haag & Warren, 2008).

The importance of physical characteristics for creating freshwater mussel habitat may depend on unique reach-level features. Across mussel species, there were weak relationships between mussel abundance and habitat characteristics, suggesting that models with

**TABLE 2** Habitat parameter estimates ($\beta$) predicting each species catch per unit effort (no. min$^{-1}$) from top models (based on AICc). For quadratic variables, two estimates (labelled 1 and 2) are included. Sigma ($\sigma$) is the variation in the reach-level random effect and variables are standardized. Pebble het. = pebble heterogeneity, D50 = median particle size, Emerg. veg. = emergent vegetation. In the pseudo-$R^2$, cond = conditional, and marg = marginal.

| Species (probability distribution) | Predictor | Estimate | Standard error | Pseudo-$R^2$ | $\sigma$ |
|---|---|---|---|---|---|
| *Alasmidonta varicosa* (zero-inflated Poisson) | | | | 0.746 | 1.057 |
| | Intercept | −5.146 | 0.340 | | |
| | Pebble het. (1) | 2.634 | 1.228 | | |
| | Pebble het. (2) | −2.489 | 1.469 | | |
| | D50 | −0.349 | 0.209 | | |
| | Large wood | −0.293 | 0.185 | | |
| | Max depth (1) | −0.923 | 2.037 | | |
| | Max depth (2) | −4.211 | 1.894 | | |
| *Alasmidonta undulata* (quasi-Poisson) | | | | 0.269$_{cond}$ 0.063$_{marg}$ | 1.782 |
| | Intercept | −5.639 | 0.416 | | |
| | D50 | −0.540 | 0.310 | | |
| | Max depth | 0.376 | 0.167 | | |
| *Strophitus undulatus* (negative binomial) | | | | 0.311$_{cond}$ 0.119$_{marg}$ | 1.545 |
| | Intercept | −5.699 | 0.370 | | |
| | D50 | −0.946 | 0.381 | | |
| | Large wood | −0.486 | 0.240 | | |
| *Elliptio complanata* (negative binomial) | | | | 0.810$_{cond}$ 0.047$_{marg}$ | 5.205 |
| | Intercept | −0.047 | 0.494 | | |
| | D50 | −0.012 | 0.003 | | |
| *Margaritifera margaritifera* (negative binomial) | | | | 0.611$_{cond}$ 0.009$_{marg}$ | 8.478 |
| | Intercept | −5.531 | 0.731 | | |
| | Algae | 0.261 | 0.139 | | |
| | Emerg. veg. | 0.201 | 0.114 | | |
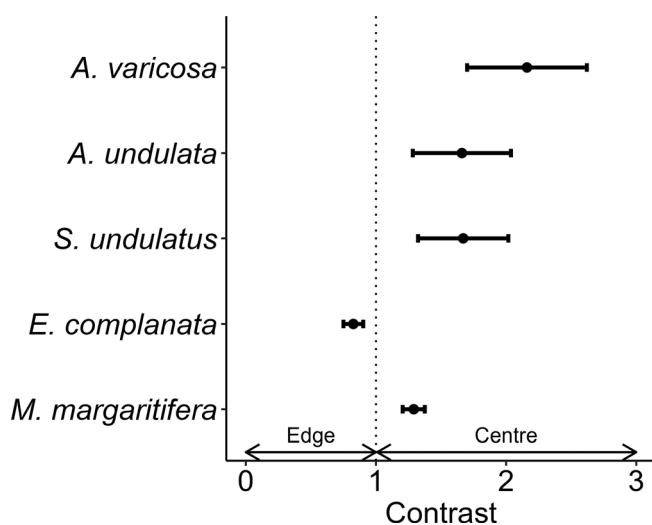


**FIGURE 5** Plot depicting each species contrast ratio (point) and standard error (bar) between river centre and edge from species-specific generalized linear mixed effects models. The species shown are *Alasmidonta varicosa*, *Alasmidonta undulata*, *Strophitus undulatus*, *Elliptio complanata*, and *Margaritifera margaritifera*. Contrasts are equivalent to a ratio where river centre is the numerator and river edge is the denominator. The model details are in Table S4.

habitat characteristics alone are not strong at predicting abundance; however, when reach-level characteristics (as a random effect) were included, models improved greatly. Thus, unknown factors that contributed to reach-scale variability improved the ability of models to predict habitat. Sampling for other factors within a reach that are important to mussel abundance such as fish hosts (Haag & Warren, 1998; Scully-Engelmeyer et al., 2023), food availability (Fogelman et al., 2022), and water quality (Gangloff et al., 2009) may improve predictions. More specifically, observations made during this study indicated reaches with relatively higher abundances of *A. varicosa* were directly affected by instream structures (intact or derelict run-of-river dams). A small run-of-river dam created habitat to support a robust mussel population directly downstream in Alabama (Singer & Gangloff, 2011) and in Michigan uncontrolled run-of-river dams supported higher mussel species richness compared with controlled dams and dam removal sites (Barnett & Woolnough, 2021). Suitable mussel habitat at run-of-river dams was partly attributed to heterogeneous substrate at sites in Michigan (Barnett & Woolnough, 2021), and heterogeneous substrate was an important habitat component in this study for *A. varicosa*. Despite the numerous relict structures in streams across New England, how these structures affect mussels is poorly understood.
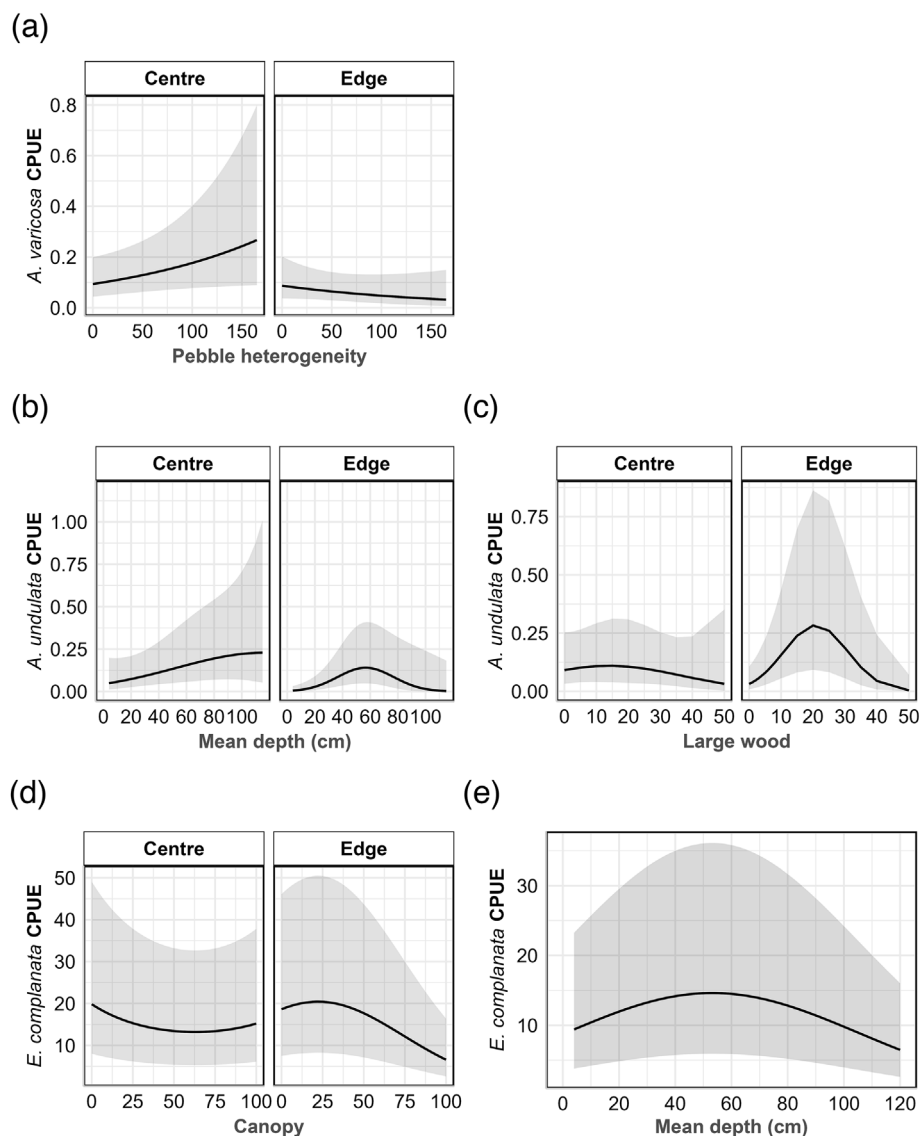
## 4.3 | Mussel distribution in the river centre and edge

*Elliptio complanata* responded differently to river centre versus edge characteristics than the other three species; they may be better adapted to lentic conditions at the river edge. This is consistent with another study that found higher abundances of *E. complanata* along banks rather than in the centre of channels (Brim Box et al., 2002). In short-term (30-day) laboratory studies, the species preferred muddy substrates to sand and gravel (Downing et al., 2000). Although mud or silt substrate were not quantified at the channel edge, observations made during this study indicated silt along banks where *E. complanata* were prevalent, which may further explain abundances in edge habitat.

Selected habitat characteristics influenced abundance between the river centre and the edge for *A. varicosa*, *A. undulata*, and *E. complanata*. Heterogeneous substrate may benefit *A. varicosa* in the river centre where larger pebble sizes buffer velocity at high flows,

and sand between cobbles allow burrowing (Hastie et al., 2001; Holland-Bartels, 1990; Troia & Ford, 2010; Vannote & Minshall, 1982). Edge habitat had higher abundances of *A. undulata* and *E. complanata* at intermediate depths, and for *A. undulata* intermediate levels of large wood. Adequate depth and large wood may provide habitat and cover for each species' host fishes (Scully-Engelmeyer et al., 2023). High abundances of *E. complanata* were prevalent at river edges when reaches had intermediate levels of canopy closure, suggesting that the species may benefit from forested areas with canopy openings. Canopy openings can increase light-promoting phytoplankton production (Hill & Knight, 1988), an important food source for mussels (Vaughn et al., 2008), and forested riparian areas increase bank stability and shade streams, reducing temperature fluctuations (Abernethy & Rutherfurd, 2000; Studinski et al., 2012). Phytoplankton abundance or composition from such habitats may support high abundances of *E. complanata* as mussel species can vary in their feeding preferences (Tran & Ackerman, 2019).

**TABLE 3** Parameter estimates ($\beta$) from the top models predicting distribution and habitat interactions for each species. For quadratic variables, two estimates (labelled 1 and 2) are included. C.E. = centre and edge, Peb. het. = pebble heterogeneity. Sigma ($\sigma$) is the variability in the reach-level random effect and variables are standardized. In the pseudo-$R^2$, cond = conditional, and marg = marginal. CPUE = catch per unit effort in mussels per minute.

| Response CPUE (probability distribution) | Predictor | Estimate | SE | P value | Pseudo-$R^2$ | $\sigma$ |
|---|---|---|---|---|---|---|
| *Alasmidonta varicosa* (negative binomial) | | | | | | |
| | Intercept | −4.47 | 0.36 | <0.001 | $0.260_{cond}$ | 1.44 |
| | Edge | 0.24 | 0.13 | 0.061 | $0.019_{marg}$ | |
| | Peb. het. | 0.01 | 0.13 | 0.964 | | |
| | C.E.*peb. het. | 0.24 | 0.11 | 0.030 | | |
| *Alasmidonta undulata* (zero-inflated Poisson) | | | | | | |
| | Intercept | −4.92 | 0.49 | <0.001 | 0.532 | 2.858 |
| | Edge | 0.42 | 0.15 | 0.005 | | |
| | Mean depth (1) | 10.99 | 4.27 | 0.010 | | |
| | Mean depth (2) | −12.05 | 4.56 | 0.008 | | |
| | Large wood (1) | 2.46 | 3.05 | 0.419 | | |
| | Large wood (2) | −10.20 | 3.30 | 0.002 | | |
| | C.E.*mean depth (1) | −1.12 | 3.51 | 0.751 | | |
| | C.E.*mean depth (2) | 9.83 | 4.44 | 0.027 | | |
| | C.E.* large wood (1) | −4.60 | 2.50 | 0.066 | | |
| | C.E.* large wood (2) | 6.96 | 2.84 | 0.014 | | |
| *Elliptio complanata* (zero-inflated Poisson) | | | | | 0.564 | 4.979 |
| | Intercept | 0.53 | 0.46 | 0.246 | | |
| | Edge | −0.02 | 0.01 | 0.002 | | |
| | Canopy (1) | −4.87 | 0.48 | <0.001 | | |
| | Canopy (2) | −0.92 | 0.37 | 0.012 | | |
| | Mean depth (1) | 1.07 | 0.28 | <0.001 | | |
| | Mean depth (2) | −3.31 | 0.18 | <0.001 | | |
| | C.E.*canopy (1) | 1.81 | 0.20 | <0.001 | | |
| | C.E.* canopy (2) | 3.16 | 0.19 | <0.001 | | |

## 4.4 | Conservation and management implications

Conserving mussels by identifying high-quality habitats is a priority for managers in the north-east United States when making rapid decisions about mussel translocations owing to construction projects and the accelerated rate of dam removals (Zarri et al., 2022). Although variables used in models do not represent underlying mechanisms related to mussel abundance, they are critical as they can be visually assessed in the field and applied to situations where complex hydrological models are not attainable or timely. In this study, models showed that mesohabitats may not be a valuable metric for identifying areas of highly suitable habitat across subcatchments. Instead, assessing substrate characteristics may provide more insight into high-quality physical habitat for species within river reaches. For example, in this study, substrate was a determinant of the abundance of *A. varicosa*. Thus, areas that create heterogeneous substrates, such as flow transition areas, may be important for identifying relocation or restoration sites. Furthermore, sediment characteristics can represent flow and turbulence (Lazzarin et al., 2023), both of which are components that structure mussel habitat but are relatively complex features to measure over longer timespans.

Freshwater mussels are patchy within aquatic habitats, and identifying habitat–mussel linkages remains challenging. Numerous factors can influence species patchiness within rivers, including host fish abundance and movement, water quality, and historical activities (Pandolfi et al., 2022; Strayer, 2008). Despite the complexity of freshwater mussel habitat, identifying species-specific habitat is particularly important given stream modifications that may affect species differentially (Sousa et al., 2021), including dam removal and flow alteration from agricultural practices and urbanization (Bellmore et al., 2017; Kondolf & Micheli, 1995). Furthermore, interest in population reintroduction requires identifying suitable catchments (Montesanto et al., 2023) and river reaches (Zając et al., 2018) that can support the focal species. Combining approaches in this study, mainly information on substrate, with larger-scale occupancy models that capture land use and flow over greater spatial scales, could improve predictions of high-quality habitat for population restoration.

Surveying for rare species can be time consuming and resource intensive. For example, in one river reach within this study, abundance in mussels per minute was lowest for *A. undulata* (0.0008 mussels per min), *S. undulatus* (0.0008 mussels per min), and *A. varicosa* (0.0049 mussels per min). This equates to approximately 20.8 h to detect a single *A. undulata* and *S. undulatus* and 3.4 h to detect a single *A. varicosa*. This search time highlights the effort required to locate extant low abundance populations within river reaches and emphasizes the importance of collecting habitat information for species that are not yet rare or declining. Assessing habitat before species declines could increase accuracy in habitat relationships with abundance (e.g., *E. complanata* mesohabitat model) and allows more cost-effective management actions to support populations (Sterrett et al., 2019).

Extreme flows from climate change can affect stream habitat and may result in devastating impacts to freshwater mussels. In the northeastern United States, projected hydrological adjustments from changing climate include increased precipitation, more extreme floods, and prolonged droughts (Demaria et al., 2016; Melillo et al., 2014). Extreme or prolonged droughts can dewater river reaches, and high flows can dislodge mussels or increase siltation contributing to mortality of all age classes (Hastie et al., 2001). Specifically, in the Connecticut and Nashua rivers, projected changes from 2021–2060 show increases in 25%–50% of stream flow compared with 1960–1999 (Siddique et al., 2020). In the Little River in south-eastern Oklahoma, hydraulic variables representing substrate stability during high flows inhibited mussel species abundance (Allen & Vaughn, 2010), and in a river in California, mussels lived almost exclusively in pools or habitats with low shear stress and low velocity (Howard & Cuffey, 2003). With projected hydrological extremes from climate change, the habitat for mussels in the northeast may be even more dependent on flow refuge areas (e.g., deep pools or areas with low shear stress). Identifying these habitats is crucial for the long-term conservation of mussels.

## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known conflict of interest.

## DATA AVAILABILITY STATEMENT

Data are available from Ayla Skorupa (askorupa@umass.edu) upon reasonable request.

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