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MICROHABITAT SUITABILITY AND NICHE BREADTH OF COMMON AND IMPERILED ATLANTIC SLOPE FRESHWATER MUSSELS

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ABSTRACT

    Knowledge of the habitat suitability of freshwater mussels (family Unionidae) is necessary for effective decision making in conservation and management. We empirically measured microhabitat use for 10 unionid mussel species, including the U.S. federally endangered *Alasmidonta heterodon*, at 20 sites in the Tar River basin, North Carolina, USA. We also quantified habitat availability at each site, and calculated habitat suitability for each mussel species. The majority of available habitat across all sites consisted of shallow, slow-moving water with penetrable silt or sand substrate. Among species, mean water depth of occupied habitats ranged 0.23 – 0.54 m, mean bottom velocity ranged 0.001 – 0.055 m/s, average mean-column velocity ranged 0 – 0.055 m/s, and mean substrate penetrability ranged 0.11 – 11.67 on an index scale. The most commonly measured dominant substrate materials were silt, sand, very coarse sand, pea gravel, and coarse gravel. The most common cover types were coarse woody debris and fine woody debris. These findings revealed a relationship between the niche breadth and conservation status of four species. Federally endangered *A. heterodon* consistently showed a narrower suite of suitable microhabitats than the common mussel *Elliptio complanata*. The range of suitable habitat characteristics for *Fusconaia masoni* and *Villosa constricta*, listed as North Carolina (USA) state endangered and special concern, respectively, was typically narrower than those of *E. complanata* and wider than those of *A. heterodon*. These habitat suitability criteria and relationships will be useful to guide identification of suitable sites for habitat protection, mussel relocation, or site restoration.

KEY WORDS - Unionid, habitat use, habitat availability, suitability, conservation, microhabitat

INTRODUCTION

Freshwater ecosystems are losing biodiversity at a higher rate than terrestrial or marine systems (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). Among North American freshwater species, 39% of fishes, 48% of crayfishes, and 74% of gastropods are considered to be extinct or imperiled (Taylor et al. 2007; Jelks et al. 2008; Johnson et al. 2013). Among the most imperiled aquatic taxonomic groups in North America are freshwater mussels (order Unionida); of the 297 species of freshwater mussel in North America, 72% are at risk, including the 37 species that are already presumed extinct (Williams et al. 1993; Lydeard et al. 2004, Master et al. 2000).

These widespread declines in freshwater fauna have been broadly attributed to habitat degradation, contaminants, stream fragmentation, flow alteration, and the presence of nonindigenous species (Neves et al. 1997; Richter et al. 1997; Strayer et al. 2004; Dudgeon et al. 2006; Cope et al. 2008; Jelks et al. 2008). Among these and many other possible causes, habitat degradation or destruction is ranked the most detrimental threat to about 50% of the imperiled species in the United States (Richter et al. 1997). For freshwater mussels in the eastern United States, some of the greatest contributors to mussel decline

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are habitat degradation due to increased sediment load from agricultural land use, mining impacts, and urbanization (Richter et al. 1997; Diamond et al. 2002; Gillies et al. 2003). The role of habitat preservation in the conservation of animals is clear, and a lack of information regarding the habitat requirements of freshwater species impedes conservation (Abell 2002). Freshwater mussels may represent an extreme case for the importance of elucidating habitat requirements because many imperiled mussels may require human intervention to persist. It is critical to identify optimal and suitable habitat characteristics to assist in habitat protection, management, and restoration, as well as mussel relocation site selection.

The majority of published habitat studies conducted with freshwater mussels have developed habitat models to predict mussel distribution and abundance (e.g., Brim Box et al. 2002; McRae et al. 2004; Gangloff and Feminella 2007; Allen and Vaughn 2010). These modeling efforts have met with mixed success (Layzer and Madison 1995; Johnson and Brown 2000), but there is currently general agreement that microhabitat characteristics alone are not effective predictors of mussel distribution (e.g., Strayer and Ralley 1993; Haag and Warren 1998; Brim Box et al. 2002). Freshwater mussel habitat preferences also have been examined in controlled laboratory studies (Michaelson and Neves 1995; Downing et al. 2000). However, research on habitat suitability indices for freshwater mussels is lacking (but see Layzer and Madison 1995).

Habitat suitability indices have been widely developed for fishes and other aquatic organisms (e.g., Hamilton and Nelson 1984; Raleigh et al. 1986; Simon and Cooper 2014). A primary application of habitat suitability indices is to conduct instream flow modeling (Bovee 1986; Annear et al. 2004). Such models apply site-specific stream flow and habitat suitability data for a species to project how the availability of suitable habitat may change with fluctuations in stream flow, which is especially applicable to regulated river systems. Habitat suitability indices provide the biological input for instream flow models, and describe the relative importance, or suitability, of different microhabitats based on measures of habitat use in proportion to availability of that habitat. The application of habitat suitability indices for aquatic species extends beyond flow modeling. They are also relevant for use in varied applications, such as targeted field surveys (Midway et al. 2010), animal relocations or reintroductions (Fisk et al. 2014), site restoration (Quinn and Kwak 2000; Hewitt et al. 2009; Fisk et al. 2015; Yao et al. 2015), conservation planning (Spooner et al. 2011), or more complex species distribution or niche modeling efforts (Elith and Leathwick 2009).

In this study, we investigated the habitat suitability of common and imperiled mussel species in a lotic ecosystem of the eastern United States. We measured microhabitat use and habitat availability to determine habitat suitability for a suite of microhabitat parameters for 10 species of freshwater mussels. These suitability results can be used to infer relative selectivity of freshwater mussels for a variety of microhabitats and target suitable ranges of habitat parameters for conservation and management (Johnson 1980).

METHODS

Field Surveys

We selected twenty sites within the upper Tar River basin, North Carolina, USA, from three subbasins with similar drainage areas: the Upper Tar, Swift Creek, and Fishing Creek subbasins (Figure 1). Sites were selected to reflect a range of environmental conditions (e.g., land use, stream size, etc.) and for accessibility via bridge crossings. We targeted sites with known occurrences of rare species, particularly *Alasmidonta heterodon*, based on documented occurrences and the past mussel survey data and experience of the North Carolina Wildlife Resources Commission (NCWRC) personnel. We conducted freshwater mussel snorkel surveys in the summer of 2010. Mussel surveys began at the start location of prior surveys by the NCWRC and where habitat appeared amenable for mussels (e.g., away from bridge pools). Mussel surveys continued for 6 person-hours, and the length of the survey reach depended on the number of survey personnel and size of the stream, but ranged from about 100 m to 500 m. We conducted surveys of mussel microhabitat use concurrent with freshwater mussel surveys. We flagged precise mussel locations, and we measured microhabitat characteristics at these precise locations. For the most common species, *Elliptio complanata*, up to 20 individuals were flagged per site and their data recorded. For all other species, microhabitat characteristics were measured for all mussels detected during a survey.

We recorded measurements of six microhabitat parameters for each mussel location for base-flow conditions, including water depth (m), bottom water velocity (m/s), mean-column water velocity (m/s), substrate penetrability (index), dominant substrate type, and closest cover type. Depth and velocity measurements were included as an indication of conditions at base flow, and these measurements are always included in standard habitat suitability criteria in support of the IFIM methodology (Bovee 1986). Substrate penetrability was included as a quantitative measure of the compaction of the substrate. It is indicative of the degree of embeddedness or sedimentation at a site, and is an important consideration for burrowing organisms. Dominant substrate type is a categorical indicator of substrate composition. Closest cover type was included as an indicator of potential flow refugia for mussels. In addition, some species are anecdotally associated with certain cover types (e.g., *Alasmidonta heterodon* is associated with root structures; personal communication T. R. Black, N.C. Wildlife Resources Commission), and we wanted to investigate such associations. All of these parameters are useful in describing species' basic habitat requirements or niche, with some focus on factors attributing to mussel decline (i.e., substrate penetrability as a measure of sedimentation).

We measured depth and water velocity using a top-set wading rod and a Marsh-McBirney Model 2000 digital flow meter, with bottom velocity measured at the stream bed and mean velocity measured at 60% of depth (Bain and Stevenson
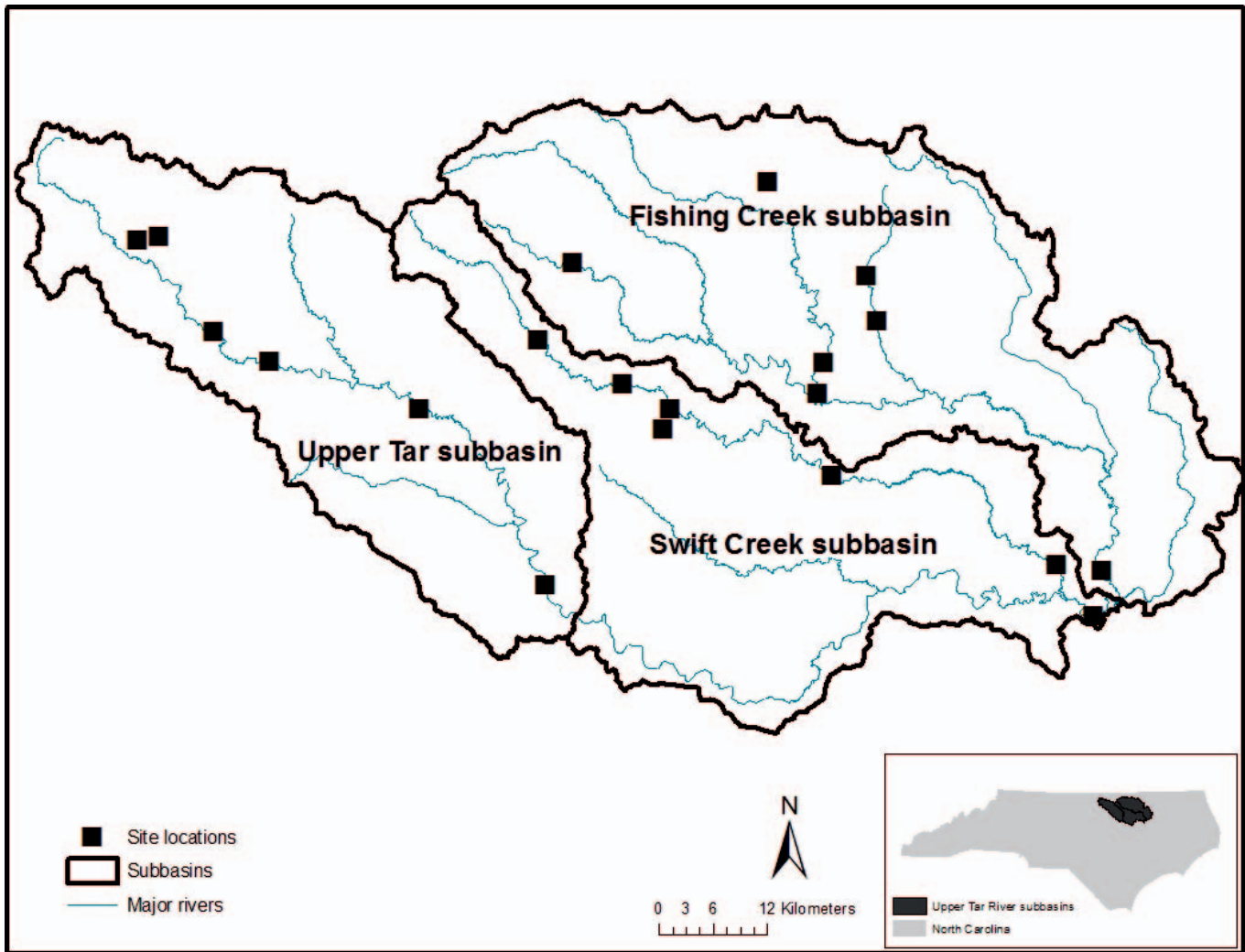
Figure 1. Locations of 20 mussel and habitat survey sites in the Tar River basin, North Carolina, USA.

1999). Dominant substrate type (Table 1) was assessed visually based on a modified Wentworth particle size scale (Bovee and Milhous 1978). We measured substrate penetrability using the index scale of a Lang Penetrometer (Johnson and Brown 2000). Force-pound conversions for the index measurements were provided by the manufacturer for comparison (Table 1). The closest cover type was the nearest material, upstream or downstream, that could slow water velocity or provide shelter for a mussel (Table 1). Where appropriate, the Wentworth particle size scale was used to determine the type of cover (e.g., boulders). Woody debris was considered fine with a diameter of <10 cm, and coarse with a diameter >10 cm. Vegetation was considered cover if the plant was rooted and stable. Trash was considered cover if it was large enough to be stable during moderate flows, e.g., tires, furniture. We measured mussel survey reach lengths using a digital rangefinder, and we recorded GPS coordinates to ensure habitat availability surveys would be conducted at locations corresponding to mussel micrhabitat use surveys.

We assessed microhabitat availability by conducting instream habitat surveys at each site under base-flow conditions. At each site, we determined a mean stream width and then, starting with the placement of the first cross-sectional transect within the mussel survey reach based on a location determined by a random number generator, 10 transects were spaced every two mean-stream-widths apart to determine the end of the survey reach (Simonson et al. 1994). At a minimum of 10 equally-spaced points within each transect, we measured six microhabitat parameters to characterize microhabitat availability. These were the same parameters measured in the mussel microhabitat use assessment.

Habitat Suitability Analysis

Mussel species with at least five individuals sampled at one site were considered for further analysis. Nine species met this criterion, including *E. complanata*, *E. icterina, E. congaraea*, *E. roanokensis*, *E. fisheriana*, *Alasmidonta heterodon*, *Villosa*

Table 1. Classification and abbreviations of substrate, cover type, and substrate penetrability for habitat use and availability analyses.

Covariate	Value	Abbreviation/Index
Substrate	mm	
Silt-clay	<0.062	Silt
Sand	0.062-1	Sand
Very coarse sand	1-2	VCS
Pea gravel	2-4	PG
Fine gravel	4-8	FG
Medium gravel	8-16	MG
Coarse gravel	16-32	CG
Very coarse gravel	32-64	VCG
Small cobble	64-130	SC
Large cobble	130-250	LC
Small boulder	250-500	SB
Medium boulder	500-1,000	MB
Large boulder	1,000-2,000	LB
Very large boulder	2,000-4,000	VLB
Mammoth boulder/bedrock	>4,000	Bedrk
Cover Type		
Coarse woody debris		CWD
Fine woody debris		FWD
Vegetation		Veg
Roots		Roots
Undercut bank		Bank
Small boulder		SB
Medium boulder		MB
Very large boulder		VLB
Mammoth boulder/bedrock		Bedrk
Tire, trash, misc.		Other
Substrate Penetrability	Force pounds	
(highest penetrability,	3.57	1
lowest compaction)	4.64	2
	5.72	3
	6.79	4
	7.86	5
	8.94	6
	10.01	7
	11.09	8
	12.16	9
	13.24	10
	14.31	11
	15.39	12
	16.46	13
	17.54	14
	18.61	15
	19.68	16
	20.76	17
	21.83	18
(lowest penetrability,	22.91	19
most compaction)	23.98	20

constricta, *Fusconaia masoni*, and an undescribed *Lampsilis* species. Data were limited for an endemic federally endangered species, *E. steinstansana*. Though this species did not meet the analysis criteria, because the species is so rare and information on the species is so scarce, we have included an anecdotal analysis of the habitat suitability for the three individuals sampled.

We calculated and graphed microhabitat suitability values as distributions for each of the 10 investigated species using the microhabitat use and availability data. For each habitat parameter, we calculated suitability by dividing microhabitat use at a site by availability at that site over a range of values for each parameter (Bovee 1986). Availability data for only the individual sites where each mussel species was found were used in suitability calculations. Each habitat parameter's entire range of values was normalized to a maximum of 1.0 to provide a scale where 1.0 indicates the most optimal, or suitable habitat, and 0 indicates the least suitable. When a mussel species was encountered at more than one site, data from multiple sites were combined by weighting suitability for each site by the number of individuals at that site, and then summing the weighted suitability values and again normalizing to a maximum of 1.0. In cases where proportional use for a particular interval or category of a parameter was greater than its availability, we set suitability to 1.0 because the suitability scale is proportional and reaches its maximum at 1.0 (i.e., optimal range of the parameter).

We further analyzed data for *A. heterodon*, *F. masoni*, *V. constricta*, and *E. complanata*, because sufficient sample sizes were attained and these species represent a range of conservation statuses (i.e., endangered to common). We graphed the habitat suitability of the six parameters for these four species together to compare the range of suitability according to species and conservation status. Data for these species were analyzed using a bootstrap, two-sample Kolmogorov-Smirnov test (R statistical software; Sekhon 2011) to test for significant differences between habitat use and habitat availability distributions (i.e., non-random use of habitat by a mussel species) and pairwise comparisons of cumulative habitat suitability between species for each parameter, except closest cover type. Closest cover type was a categorical variable, and thus, a likelihood ratio chi-square test was used to test for differences between use and availability and habitat suitability between species (JMP statistical software, SAS, Cary, North Carolina).

RESULTS

Microhabitat Use and Availability

The most ubiquitous species, *E. complanata,* was represented by 357 individuals from 20 sites (Table 2), whereas the rarest species, *E. steinstansana*, was represented by three individuals from two sites. Among species, mean depth of occupied habitats ranged 0.23 – 0.54 m, mean bottom velocity

Table 2. Count (N), mean, range, and standard deviation (SD) of habitat availability for 20 sites and microhabitat use measurements for 10 species of freshwater mussels of depth (m), bottom and mean-column velocity (m/s), substrate penetrability, dominant substrate, and cover type.

| Species	N indiv	N sites	Depth (m) Mean (Range)	Depth (m) SD	Bottom Velocity (m/s) Mean (Range)	Bottom Velocity SD	Mean Velocity (m/s) Mean (Range)	Mean Velocity SD	Substrate Penetrability (Index) Mean (Range)	Substrate Penetrability SD	Dominant Substrate (Type) Mode	Dominant Substrate Types	Closest Cover (Type) Mode	Closest Cover Types
Alasmidonta heterodon	19	2	0.26 (0.08 - 0.55)	0.12	0.003 (0.00 - 0.02)	0.01	0.004 (0.00 - 0.02)	0.01	0.11 (0 - 1.5)	0.36	VCS, PG	6	CWD	4
Elliptio complanata	357	20	0.38 (0.02 - 1.36)	0.24	0.019 (0.00 - 0.31)	0.05	0.047 (0.00 - 0.64)	0.08	3.42 (0 - 20)	4.93	Silt	14	CWD	9
Elliptio congaraea	22	3	0.53 (0.24 - 0.80)	0.17	0.055 (0.00 - 0.43)	0.10	0.074 (0.00 - 0.56)	0.13	6.98 (0 - 18.5)	5.94	Sand	9	CWD	5
Elliptio fisheriana	11	2	0.30 (0.10 - 0.53)	0.15	0.017 (0.00 - 0.04)	0.01	0.033 (0.00 - 0.06)	0.02	8.36 (0 - 20)	7.50	Sand	6	CWD	5
Elliptio icterina	62	7	0.43 (0.06 - 1.02)	0.24	0.016 (0.00 - 0.31)	0.05	0.051 (0.00 - 0.52)	0.08	5.60 (0 - 20)	5.84	Sand	11	CWD	7
Elliptio roanokensis	13	2	0.52 (0.14 - 1.19)	0.33	0.050 (0.00 - 0.18)	0.06	0.151 (0.00 - 0.32)	0.10	3.42 (0 - 16)	4.65	Sand, CG	5	CWD	3
Elliptio steinstansana	3	2	0.47 (0.13 - 0.65)	0.29	0.013 (0.00 - 0.04)	0.02	0.023 (0.00 - 0.07)	0.04	11.67 (7 - 14.5)	4.07	Sand	2	CWD	2
Fusconaia masoni	14	2	0.54 (0.41 - 0.69)	0.08	0.036 (0.00 - 0.14)	0.06	0.080 (0.00 - 0.30)	0.11	9.29 (0 - 14.5)	4.08	Sand	5	CWD	4
Lampsilis sp.	5	1	0.23 (0.07 - 0.40)	0.13	0.000 (0.00 - 0.00)	<0.01	0.004 (0.00 - 0.01)	0.01	NA	NA	NA	5	CWD	3
Villosa constricta	24	2	0.48 (0.05 - 0.86)	0.25	0.001 (0.00 - 0.02)	<0.01	0.010 (0.00 - 0.05)	0.02	6.98 (0 - 13)	4.92	Sand	8	FWD	4
Habitat availability	2,398	20	0.35 (0.00 - 2.70)	0.34	0.013 (−0.05 - 0.65)	0.07	0.037 (−0.05 - 0.89)	0.10	4.19 (0 - 20)	6.26	Silt	15	CWD	10
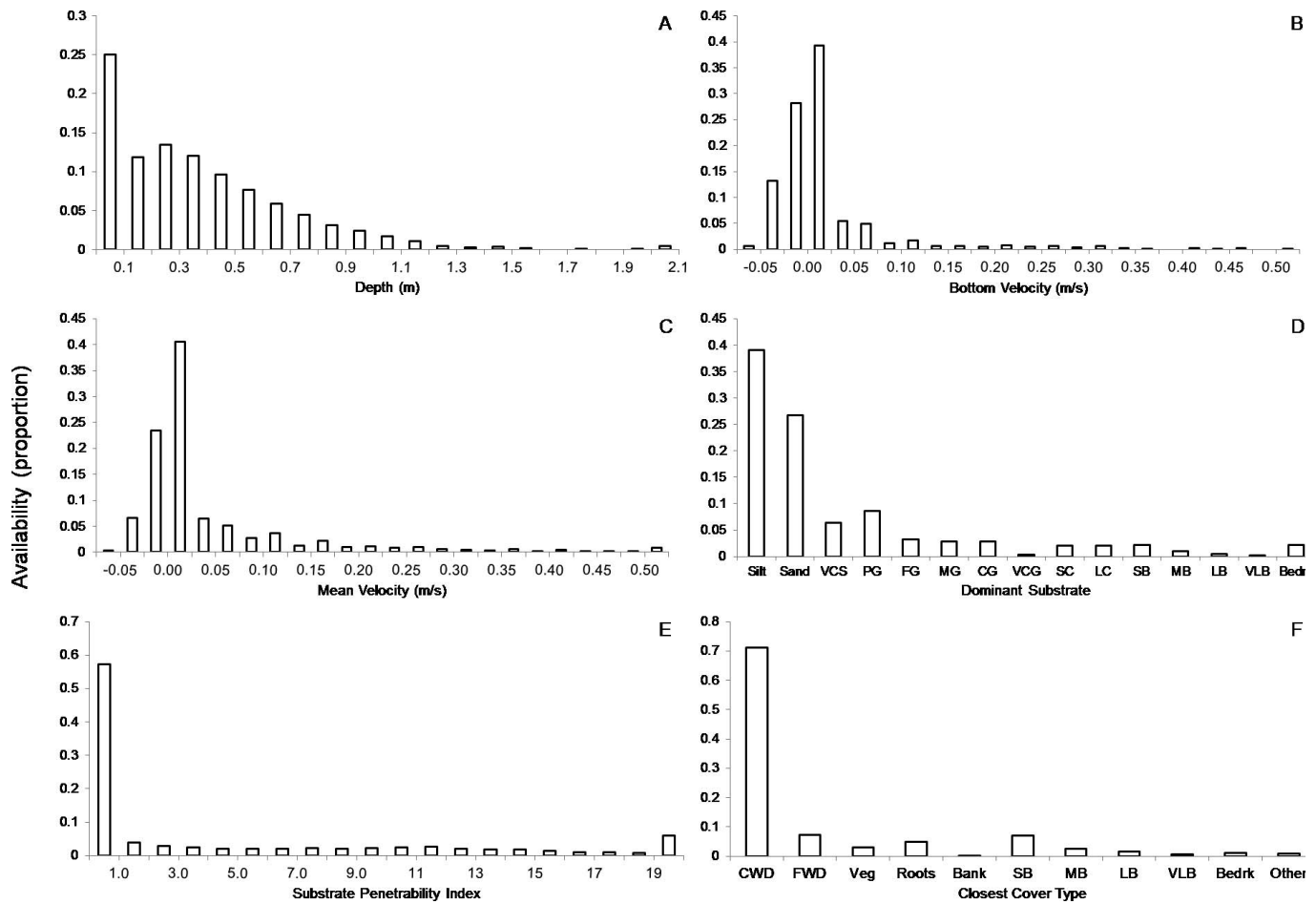
Figure 2. Availability of six microhabitat parameters from 20 sites in the Tar River basin, North Carolina, USA.

ranged 0.001 – 0.055 m/s, average mean-column velocity ranged 0 – 0.055 m/s, and mean substrate penetrability ranged 0.11 – 11.67 on an index scale. The most commonly measured dominant substrate materials were silt, sand, very coarse sand, pea gravel, and coarse gravel. The most common cover types were coarse woody debris and fine woody debris.

We surveyed habitat availability at a mean of 120 (range 80 – 161) points within each of 20 sites (Table 2, Figure 2). The majority of available habitat across all sites consisted of shallow, slow-moving water with penetrable silt or sand substrate. The most abundant cover type was coarse woody debris.

Habitat Suitability Distributions

Habitat suitability distributions for depth, bottom velocity, mean velocity, substrate penetrability, dominant substrate, and closest cover type varied among species (Figures A1 – A10), reflecting differences among habitat niches occupied, but influenced by the range in sample sizes (i.e., suitability distributions of species with the greatest numbers of habitat

use measurements, *E. complanata* and *E. icterina*, more closely resembled a continuous distribution).

Differences among species microhabitat suitability were evident (Table 3). For example, *A. heterodon* tended to occupy shallow, slow-flowing sites with penetrable silt, coarse sand, and gravel. Tree roots and vegetation provided suitable cover, in addition to woody debris. *V. constricta* also utilized shallow slow-flowing locations, but moderately penetrable gravels and cobble were the most suitable substrates. Boulders and woody debris provided the most suitable cover. Suitable habitat for *F. masoni* was similar to that of *V. constricta*, but slightly deeper and faster flowing water was more suitable. The undescribed *Lampsilis* species was most suited to habitats like those preferentially occupied by *V. constricta*.

The most common species, *E. complanata*, was at least marginally suited to almost all available habitat. The most suitable habitats for this species were shallow, slow-flowing sites with penetrable substrates. *E. icterina* had similar suitability, but moderately penetrable coarse sand was its most suitable substrate. *E. congaraea* occurred in slightly deeper water with slow velocity, though it tolerated even the swiftest flows (> 0.50 m/s). Many substrates were suitable for *E. congaraea*, but silt was not. *E. fisheriana* was suited to

Table 3. Most suitable conditions (habitat suitability ≥ 0.5) of depth, bottom and mean-column velocity, substrate penetrability, dominant substrate, and cover type for 10 species of freshwater mussels. Habitat conditions with optimal suitability (habitat suitability = 1.0) are shown in bold.

Species	Depth (m)	Bottom Velocity (m/s)	Mean Velocity (m/s)	Substrate Penetrability (Index)	Dominant Substrate (Type)	Closest Cover (Type)
Alasmidonta heterodon	**0.30–0.39** 0.10–0.29	**0–0.024**	**0–0.024**	**0–0.9** 1.0–1.9	**VCS** Silt, PG, FG, MG	**FWD** Veg
Elliptio complanata	**0.30–0.39** 0.10–0.69	**0–0.024**	**0–0.024**, 0.025–0.074, 0.100–0.124	**0–0.9** 1.0–3.9, 5.0–6.9, 8.0–10.9	**VCG** Silt, Sand, VCS, PG, FG, MG, CG, SC, LC	**FWD** Bank
Elliptio congaraea	**0.60–0.69** 0.40–0.49	**0–0.024**	**0–0.024** 0.200–0.224	**3.0–3.9, 8.0–8.9** 5.0–5.9, 9.0–9.9, 13.0–13.9	**VCS, VCG** Sand, CG, LC	**SB** FWD, MB
Elliptio fisheriana	**0.50–0.59** 0.30–0.39	**0.025–0.049**	**0.025–0.049** 0.050–0.074	**9.0–9.9** 12.0–12.9	**SC** Sand, CG, VCG, MB, Bedrk	**FWD** MB, Bedrk
Elliptio icterina	**0.50–0.59** 0.10–0.29, 0.60–0.69	**0–0.024**	**0–0.024** 0.050–0.074, 0.100–0.124	**8.0–8.9** 10.0–11.9, 13.0–13.9	**VCS** VCG	**FWD**
Elliptio roanokensis	**0.20–0.29**, 0.70–0.89	**0.050–0.074** 0–0.124, 0.175–0.199	**0.225–0.249** 0.100–0.124, 0.300–0.324	**6.0–7.9** 1.0–2.9, 16.0–16.9	**CG**	**FWD** SB, Other
Elliptio steinstansana	**0.60–0.69**	**0.025–0.049**	**0.050–0.074**	**7.0–7.9** 13.0–14.9	**VCS**	**SB** CWD
Fusconaia masoni	**0.40–0.49** 0.50–0.69	**0–0.024**	**0–0.024**, 0.100–0.124, 0.175–0.224, 0.250–0.274, 0.300–0.324	**7.0–7.9** 6.0–8.9, 14.0–14.9	**PG** FG, LC	**SB** FWD, MB
Lampsilis sp.	**0.40–0.49**	**0–0.024**	**0–0.024**	NA	**SC** VCG, LC	**FWD** SB
Villosa constricta	**0.60–0.69** 0.10–0.19, 0.50–0.59	**0–0.024**	**0–0.024**	**7.0–7.9** 4.0–4.9, 6.0–6.9, 10.0–11.9, 13.0–13.9	**VCG** FG, MG, SC	**SB** FWD

Table 4. Results from two-sample Kolmogorov-Smirnov tests (D-statistic and p-value) and likelihood ratio chi square test (χ^2-statistic and p-value) of the difference between microhabitat use and microhabitat availability distributions. Statistically significant results ($p < 0.05$, in bold font) indicate non-random use of habitat.

Species	Depth (m)		Bottom Velocity (m/s)		Mean Velocity (m/s)		Substrate Penetrability		Dominant Substrate		Closest Cover	
	D	p	D	p	D	p	D	p	D	p	$\chi2$	p
Alasmidonta heterodon	0.579	**0.001**	0.833	**<0.001**	0.667	**0.018**	0.850	**<0.001**	0.364	0.328	107.6	**<0.001**
Elliptio complanata	0.478	**<0.001**	0.541	**<0.001**	0.480	**<0.001**	0.498	**<0.001**	0.230	**<0.001**	1,182.0	**<0.001**
Fusconaia masoni	0.750	**<0.001**	0.571	**0.010**	0.353	0.124	0.703	**<0.001**	0.708	**<0.001**	328.2	**<0.001**
Villosa constricta	0.524	**0.004**	0.800	**0.002**	0.444	0.256	0.588	**<0.001**	0.300	0.229	161.8	**<0.001**

shallow, slow-flowing habitats with moderately penetrable substrates. *E. roanokensis* was suited to coarse gravel habitats with deeper and swifter water than the other species. The federally endangered *E. steinstansana* was anecdotally associated with moderately penetrable coarse sand and slow velocity with woody debris and boulders as cover.

Non-random Habitat Selectivity

We tested habitat use of *E. complanata*, *A. heterodon*, *F. masoni*, and *V. constricta* against habitat availability to detect randomness in habitat selectivity among species (Table 4). Depth, bottom velocity, substrate penetrability, and closest cover type were non-randomly selected among all four species. *E. complanata* exhibited non-random habitat use for all six measured microhabitat parameters. Mean-column velocity use was also non-random for *A. heterodon*, and *F. masoni* exhibited non-random use of dominant substrate.

Habitat Suitability Among Conservation Statuses

Habitat suitability for four species with different conservation statuses, *E. complanata*, *A. heterodon*, *F. masoni*, and *V. constricta*, was plotted together for relative species comparisons (Figure 3). Most suitable depths for *A. heterodon*, *F. masoni*, and *E. complanata* ranged 0.3 – 0.5 m, whereas slightly deeper waters of 0.6 – 0.7 m were most suitable for *V. constricta*. All four species were suited to velocities up to 0.025 m/s, which were also the most widely available. A range of substrates could be considered at least moderately suitable for all species, but the species differed in substrate penetrability suitability. *A. heterodon* was suited to the most penetrable substrates, although those were the only substrates available at the sites where it occurred. *E. complanata* was also most suited to highly penetrable substrates, whereas *V. constricta* and *F. masoni* found mid- to high-range compaction most suitable. Woody debris was suitable cover for all four species. *V. constricta* and *F. masoni* also utilized boulders, and *A. heterodon* was associated with vegetation, roots, and undercut banks. Federally endangered *A. heterodon* consistently showed a narrower suite of suitable microhabitats than the common mussel *E. complanata*. The range of suitable

habitat characteristics for *F. masoni* and *V. constricta*, listed as North Carolina (USA) state endangered and special concern, respectively, was typically narrower than those of *E. complanata* and wider than those of *A. heterodon*.

Statistical analysis confirmed that differences in habitat suitability among mussels of different conservation statuses were significant (Table 5). Among 36 between-species comparisons of 6 habitat suitability variables, 22 (61%) detected significantly different distributions. Habitat suitability of *E. complanata* differed significantly from that of federally endangered *A. heterodon* and NC state endangered *F. masoni* for all six parameters measured. Habitat suitability of *E. complanata* significantly differed from that of NC state special concern *V. constricta* for four of six parameters: bottom and mean velocity, substrate penetrability, and closest cover type. There were no significant differences detected among any of the uncommon species (*A. heterodon*, *F. masoni*, and *V. constricta*) for depth, bottom velocity, or dominant substrate. *A. heterodon* and *F. masoni* exhibited significantly different habitat suitability distributions for mean velocity. All species differed significantly from one another in suitability of closest cover type and substrate penetrability, with the exception of *F. masoni* and *V. constricta* for substrate penetrability.

DISCUSSION

Relationship Between Freshwater Mussels and Microhabitat

Our results indicated that freshwater mussels generally occupied microhabitat non-randomly and that mussel conservation status may correspond to niche breadth. Although freshwater mussels are broadly described as habitat generalists (Tevesz and McCall 1979), results of this study demonstrated that some characteristics are more suitable than others when habitat use is adjusted for availability. Habitat requirements are thought to be one of the primary controls on animal distribution and abundance (Haag and Warren 1998). However, defining this relationship for freshwater mussels has been complicated. The value of traditional microhabitat parameters, such as depth and substrate type, is greatly surpassed by complex hydraulic variables, which influence
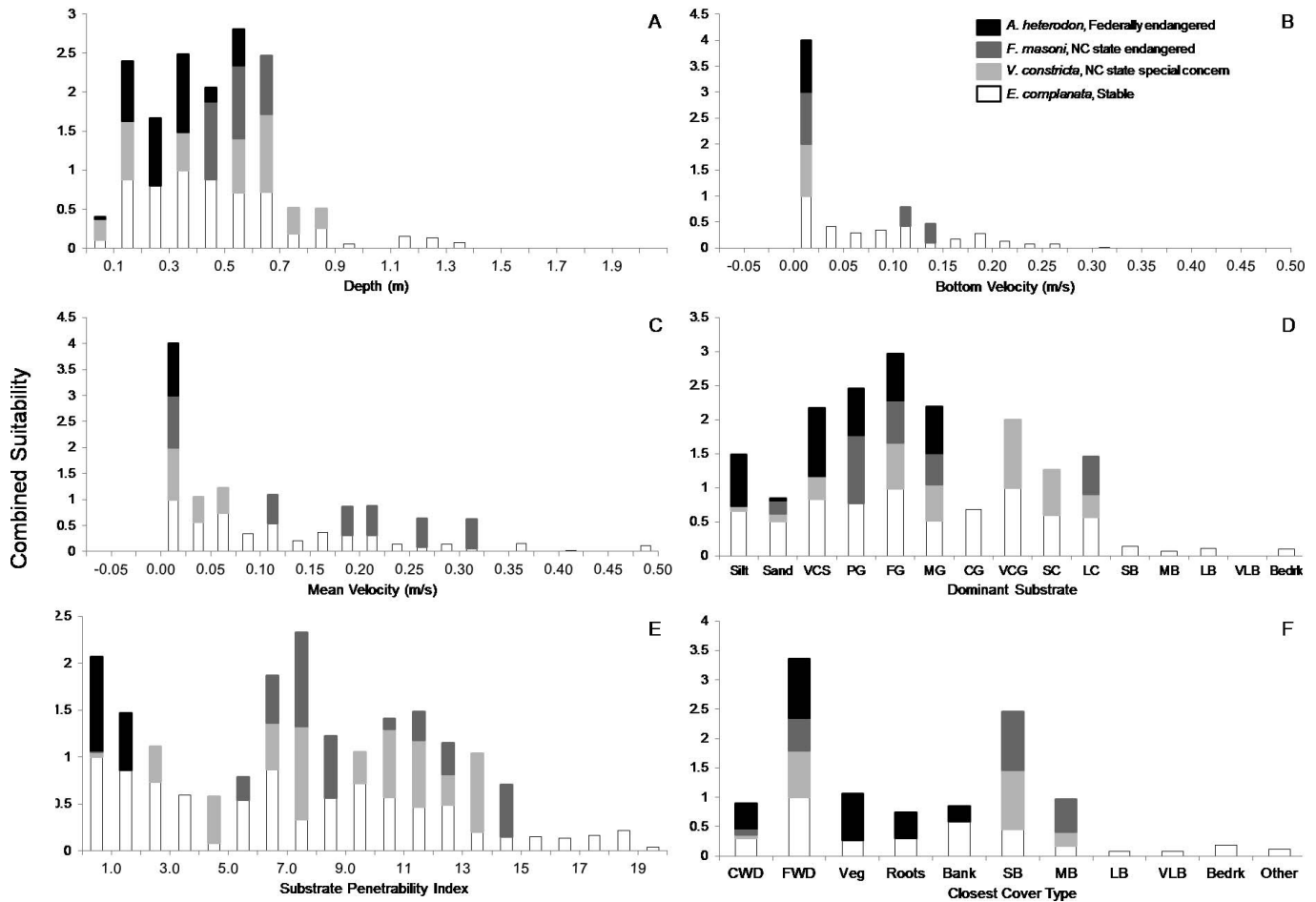
Figure 3. Habitat suitability distributions for four freshwater mussel species with different conservation status: federally endangered *Alasmidonta heterodon*, North Carolina (USA) state endangered *Fusconaia masoni*, North Carolina state special concern *Villosa constricta*, and stable *Elliptio complanata*. Combined suitability is for relative comparison only.

substrate stability, in the ability to predict the distribution and abundance of freshwater mussels (Layzer and Madison 1995; Zigler et al. 2008; Allen and Vaughn 2010). Despite the general lack of broad predictive value, multiple investigators have found correlative relationships between some microhabitat parameters and freshwater mussel occurrence and abundance (Salmon and Green 1983; Strayer and Ralley 1993; Johnson and Brown 2000). These mixed conclusions suggest that microhabitat may not directly control mussel occurrence *per se*, but it is a factor influencing the distribution of freshwater mussels (Strayer and Ralley 1993; Layzer and Madison 1995; Haag and Warren 1998; Downing et al. 2000; Strayer 2008). Habitat is almost certainly a limiting factor in mussel distributions, but the relationship is complex and involves dynamics at multiple interacting spatial and temporal scales (e.g., McRae et al. 2004, Pandolfo 2014).

Further complicating these relationships is the fact that some parameters are indicative of conditions at multiple scales. In this study, all parameters were measured at a microhabitat scale, and habitat use measurements in particular were taken at precise mussel locations. However, these data can also provide information on habitat conditions at the macrohabitat scale, or even at the reach scale. For instance, measures of substrate penetrability can reflect bank erosion in a reach or overall land use in a watershed.

Substrate composition and flow are among the most often measured habitat characteristics in mussel habitat studies, and they are also the parameters most often found to correlate with freshwater mussel occurrence (Salmon and Green 1983; Holland-Bartels 1990; Strayer and Ralley 1993; Johnson and Brown 2000), though there is not always a strong relationship (Neves and Widlak 1987; Strayer et al. 1994; Layzer and Madison 1995; Haag and Warren 1998). The microhabitat parameters that we examined in this study were aligned with these two characteristics: water depth, velocity, dominant substrate, substrate penetrability, and cover type. Depth, velocity, and substrate penetrability were selected non-randomly by all four species tested (*E. complanata*, *A. heterodon*, *V. constricta*, and *F. masoni*). This further supports the notion that freshwater mussels are responding to habitat gradients and findings of previous studies that demonstrate the importance of flow and substrate stability for freshwater

Table 5. Results from two-sample Kolmogorov-Smirnov tests and likelihood ratio chi-square tests (*p*-value) of the difference between cumulative habitat suitability distributions for four mussel species with different conservation statuses. Statistically significant comparisons ($p < 0.05$, in bold font) indicate non-random differences in habitat suitability between species.

	Parameter					
	Depth			Dominant substrate		
Species	*E. com*	*F. mas*	*V. con*	*E. com*	*F. mas*	*V. con*
Alasmidonta heterodon	**0.0426**	0.5420	0.6981	**0.0072**	0.3325	0.4013
Elliptio complanata		**0.0043**	0.2015		**0.0057**	0.1570
Fusconaia masoni			0.3252			0.6636
Villosa constricta						
	Bottom Velocity			Substrate Penetrability		
	E. com	*F. mas*	*V. con*	*E. com*	*F. mas*	*V. con*
Alasmidonta heterodon	**0.0011**	0.4913	1.0000	**<0.0001**	**0.0325**	**0.0114**
Elliptio complanata		**0.0155**	**0.0009**		**0.0005**	**0.0084**
Fusconaia masoni			0.4968			0.5567
Villosa constricta						
	Mean Velocity			Closest Cover		
	E. com	*F. mas*	*V. con*	*E. com*	*F. mas*	*V. con*
Alasmidonta heterodon	**<0.0001**	**0.0662**	0.4918	**<0.0001**	**<0.0001**	**<0.0001**
Elliptio complanata		**0.0060**	**0.0002**		**<0.0001**	**<0.0001**
Fusconaia masoni			0.1115			**0.0003**
Villosa constricta						

mussel habitat (e.g., Layzer and Madison 1995, Allen and Vaughn 2010).

In those studies that observed a correlation among mussels and microhabitat, mussel abundance, recruitment, and density were most often positively associated with slow to moderate flows and moderately coarse substrates with few fines (e.g., Salmon and Green 1983; Holland-Bartels 1990; McRae et al. 2004; Geist and Auerswald 2007). Measures of substrate compaction with a penetrometer have been applied in a limited number of studies (Johnson and Brown 2000; Geist and Auerswald 2007), and those studies have shown that this microhabitat measure is relevant to mussel ecology. Sediment compaction was positively related to mussel abundance, but negatively affected recruitment (Johnson and Brown 2000; Geist and Auerswald 2007).

The common mussel, *E. complanata*, exhibited non-random selectivity of all habitat parameters tested. However, suitability values for dominant substrate indicated a broad substrate suitability ranging in size from silt to large cobble. Other studies of *E. complanata* have found a similar broad tolerance of substrate types. In the coastal plain of the Apalachicola, Chattahoochee, and Flint River basins in Alabama, Georgia, and Florida, USA, the presence of *E. complanata* and *E. icterina* was not correlated with substrate composition (Brim Box et al. 2002). A study of *E. complanata*

in Virginia, USA, found no habitat characteristics that explained the mussels' clumped distribution (Balfour and Smock 1995). In a laboratory study, *E. complanata* most commonly occurred in muddy substrates, which differed from the sand and gravel that were most commonly occupied in their lake environment (Downing et al. 2000). In the Hudson River, New York, USA, low percentages of fine sand were significantly correlated with the abundance of unionids, including *E. complanata* (Strayer et al. 1994), and in the Neversink River, New York, USA, high percentages of medium sand were correlated with the occurrence of *E. complanata* and other species (Strayer and Ralley 1993). These cumulative results concur to describe the wide niche breadth of *E. complanata* that is reflected in its ubiquitous distribution throughout eastern North America (Johnson 1970).

We found that the federally endangered *A. heterodon* was most suited to slow flowing, shallow locations with fine to medium-fine substrate. These results generally agree with habitat suitability criteria from the Delaware River suggesting moderately deep, slow-flowing water, and laboratory studies that confirm a preference for slow to moderate velocity (Michaelson and Neves 1995; Parasiewicz et al. 2012). Field and laboratory studies also suggest fine sand substrates are most suitable for *A. heterodon* (Strayer and Ralley 1993;

Michaelson and Neves 1995). Empirically, the other federally endangered species in the Tar River basin, *E. steinstansana*, often occurs in fast-flowing, well-oxygenated water and relatively silt-free substrate composed of gravel or coarse sand (USFWS 1992). The very limited data on *E. steinstansana* from this study suggest a slow velocity with moderately compacted sand or coarse sand substrate.

The importance of microhabitat influence on mussel distribution may depend on the species (Huehner 1987; Brim Box et al. 2002). Minor microhabitat differentiation among species has been shown in some species (Salmon and Green 1983; Holland-Bartels 1990). In the Mississippi River, USA, mussels occurred in a broad range of sediment types that indicated a general lack of species differences; the endangered *L. higginsii* was present in habitats similar to those as the most common species, *A. plicata* (Holland-Bartels 1990). Subtle differences in habitat dynamics among mussel species have been found, however, and they could be broadly grouped into those with affinities for fine to medium-fine sands and those with coarser sand affinities (Holland-Bartels 1990). These slight microhabitat differences among species may explain niche partitioning that allows the coexistence of numerous mussel species within a single bed (Salmon and Green 1983). However, habitat is certainly not the only factor that determines mussel distribution; species traits, distribution of host fishes, and availability of resources are all important factors as well (Haag and Warren 1998, Strayer 2008, Schwalb et al. 2013).

Species Differences in Habitat Suitability Distributions

We found evidence of both subtle and distinct species differences in habitat suitability distributions among the 10 species examined. There was evidence of some species occupying habitat non-randomly for specific parameters, whereas other species occupied habitat randomly for the same parameter. For instance, *A. heterodon* and *E. complanata* appeared to select mean velocity non-randomly whereas this was not true for *F. masoni* and *V. constricta*. There was also evidence of differences among species related to their conservations status. Significant differences between habitat suitability distributions for the common species, *E complanata*, and the rarer species, *A. heterodon*, *F. masoni*, and *V. constricta*, suggest that, for these species, conservation status serves as a proxy for niche breadth and degree of habitat specialization. Conservation status was positively related to the range of suitable habitats for a species, which suggests, as would be expected, that the rarest mussels have narrower microhabitat niches than ubiquitous species. Results also show that the most ubiquitous species, *E. complanata*, was the only one that demonstrated non-random habitat use for all habitat parameters. It is relevant, however, that the sample size for this species was much larger than that of the other species, and statistical significance may have been more likely due to greater statistical power.

Utility of Habitat Suitability Distributions

Habitat suitability index models are a useful method for identifying environmental factors that may limit species occurrence, but these relationships are not necessarily causal and should be considered primarily as a premise for further investigation and management planning (Morrison et al. 1998). Absolute statements regarding the suitability of habitats are not recommended, but relative comparisons of suitability distributions can be informative (Johnson 1980). Any habitat suitability study is constrained by the researcher's options and choice of available habitat, and suitable conditions that were not measured or present in the defined study area may exist. However, given a region with similar habitat characteristics (e.g., coastal plain systems), results of this study represent a valid relative comparison of the suitability of a variety of habitat components (Johnson 1980).

Another consideration in the applicability of habitat suitability studies is that the use of habitat by an animal does not necessarily imply active selection, rather than an unmotivated presence (Johnson 1980; Beyer et al. 2010). In addition, substrate use by freshwater mussels is probably more complex than can be measured via simple microhabitat use (Layzer and Madison 1995). Mussels may require combinations of fine substrate materials for burrowing, and also coarser substrates to function as cover and velocity breaks (Layzer and Madison 1995). It is also possible that the apparently random habitat use measured by some parameters (mean velocity, substrate, and cover) for three species in this study was influenced by low sample size. In some cases, the lack of correlation between substrate and freshwater mussel distribution or abundance may be due to an inadequate sampling effort (Brim Box and Mossa 1999). In this study, *E. complanata* had the largest sample size, and non-random habitat use was detected for all six measured habitat variables. The species with fewer microhabitat use measurements exhibited both random and non-random use of habitat according to the particular parameter. This may be due to the lack of statistical power or adequate representation of suitability distributions in these samples, or it may be due to an actual ecological difference among species.

The complications arising from the limited number of rare mussels encountered during habitat use surveys is a common problem when working with rare species (Brim Box et al. 2002). Our results indicate that rarer mussel species may have a narrower and significantly different habitat suitability distribution than the most common species. However, this association is not unequivocal because of the confounded issue of limited sample size inherent in the study of rare species. The ability to detect and measure microhabitat use for representative numbers of rare species was limited, even with the intensive sampling effort in this study. The typical level of effort applied in timed search mussel assemblage surveys in streams is 1.5 person-hours per site (Metcalfe-Smith et al. 2000), yet we expended 6.0 person-hours of effort at each sampling site in this study, suggesting that the low sample sizes for some species reflect

actual low site densities, rather than low detection probability. This was particularly the case with the federally endangered *E. steinstansana*, of which only three individuals were found. This highlights the difficulty of studying the rarest species; it is often very difficult to collect information on the species in greatest need of conservation and in which we are most concerned. Future research that aims to characterize the microhabitat of rare species would be enhanced by using sampling designs and methods, such as adaptive sampling, that will allow these species to be sampled more frequently (Brim Box et al. 2002, Strayer and Smith 2003).

Habitat Suitability Distributions in Mussel Conservation

Quantitative methods of habitat assessment, such as habitat suitability indices, are more valuable and ecologically relevant than anecdotal descriptions of habitat (Bovee 1986). The habitat suitability method adopted in this study empirically measured habitat use and availability independently for each site, thus allowing the relative selectivity for habitats to be quantified (Bovee 1986). Microhabitat characteristics that are associated with mussel occurrence can be simply and quickly assessed in the field, making habitat suitability a useful tool in practical applications, if not in predictive modeling exercises. This knowledge can be useful in targeting field surveys for rare species (Midway et al. 2010), identification of relocation sites for imperiled species (Fisk et al. 2014), or for the planning of conservation measures, including site restoration (Quinn and Kwak 2000; Fisk et al. 2015). Microhabitat is one in a scale and suite of variables to be considered, it may not limit or predict distribution on its own, but neither is it inconsequential. It appears that no one scale and approach of habitat assessment may adequately describe the ecological relationships between freshwater mussel populations and their dynamic environment.

Habitat degradation is among the most prominent threats facing freshwater mussels, and the habitat requirements of mussels must be understood to develop the best spatial scale and specific conservation practices to protect them from future decline. The assessment of microhabitat can be useful in quantifying suitable and optimal habitat to guide conservation strategies and management plans for endangered mussel species (Johnson and Brown 2000). Microhabitat preferences are already being used to relocate the endangered *Margaritifera hembeli* to suitable sites when their beds are threatened by channel alterations (Johnson and Brown 2000). Habitat suitability criteria such as those we developed for 10 species in this study can similarly be used to target habitat protection, mussel relocations, reintroductions, or site restoration within acceptable macrohabitats.

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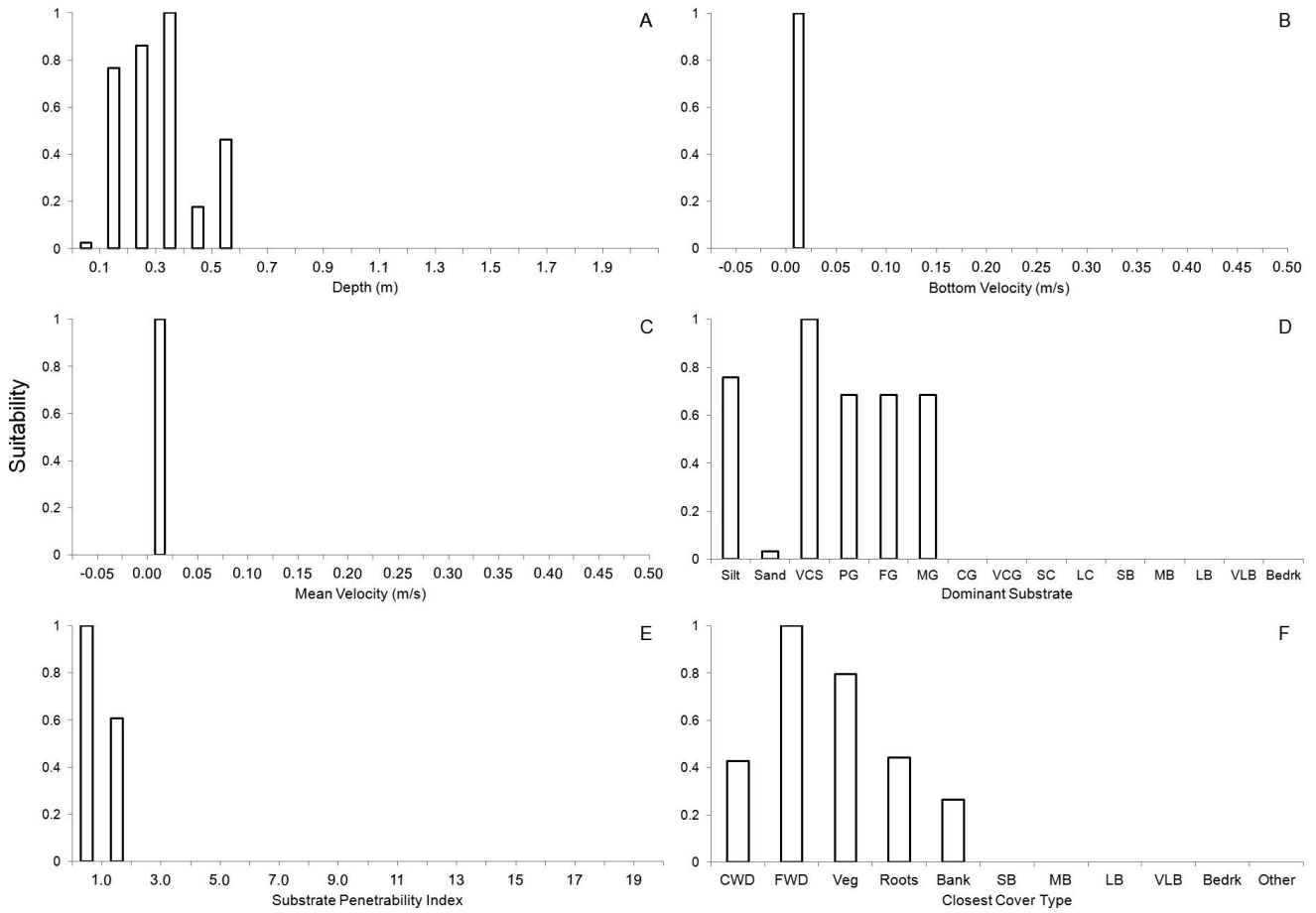
Appendices

Figure A1. Microhabitat suitability distributions for *Alasmidonta heterodon*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
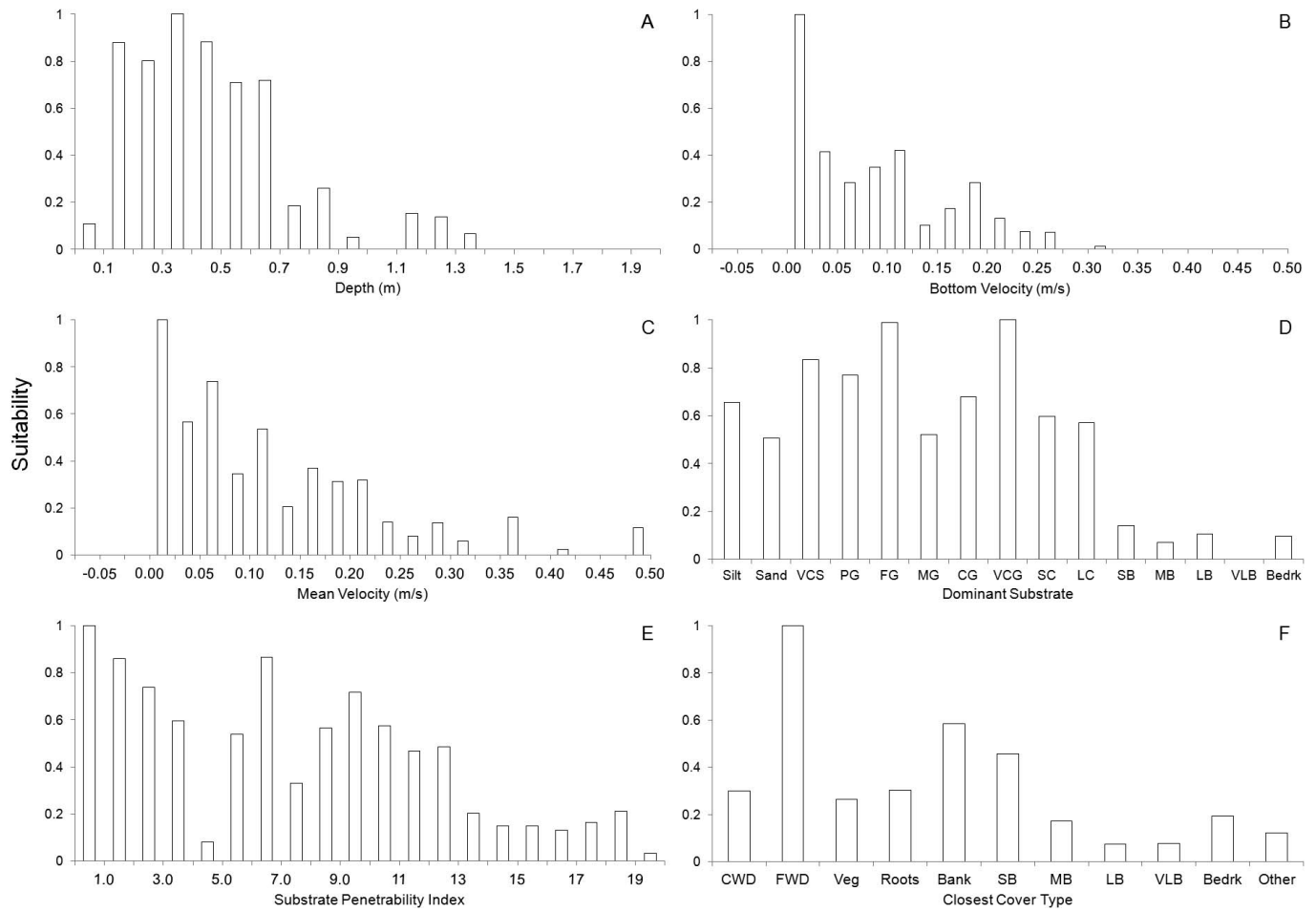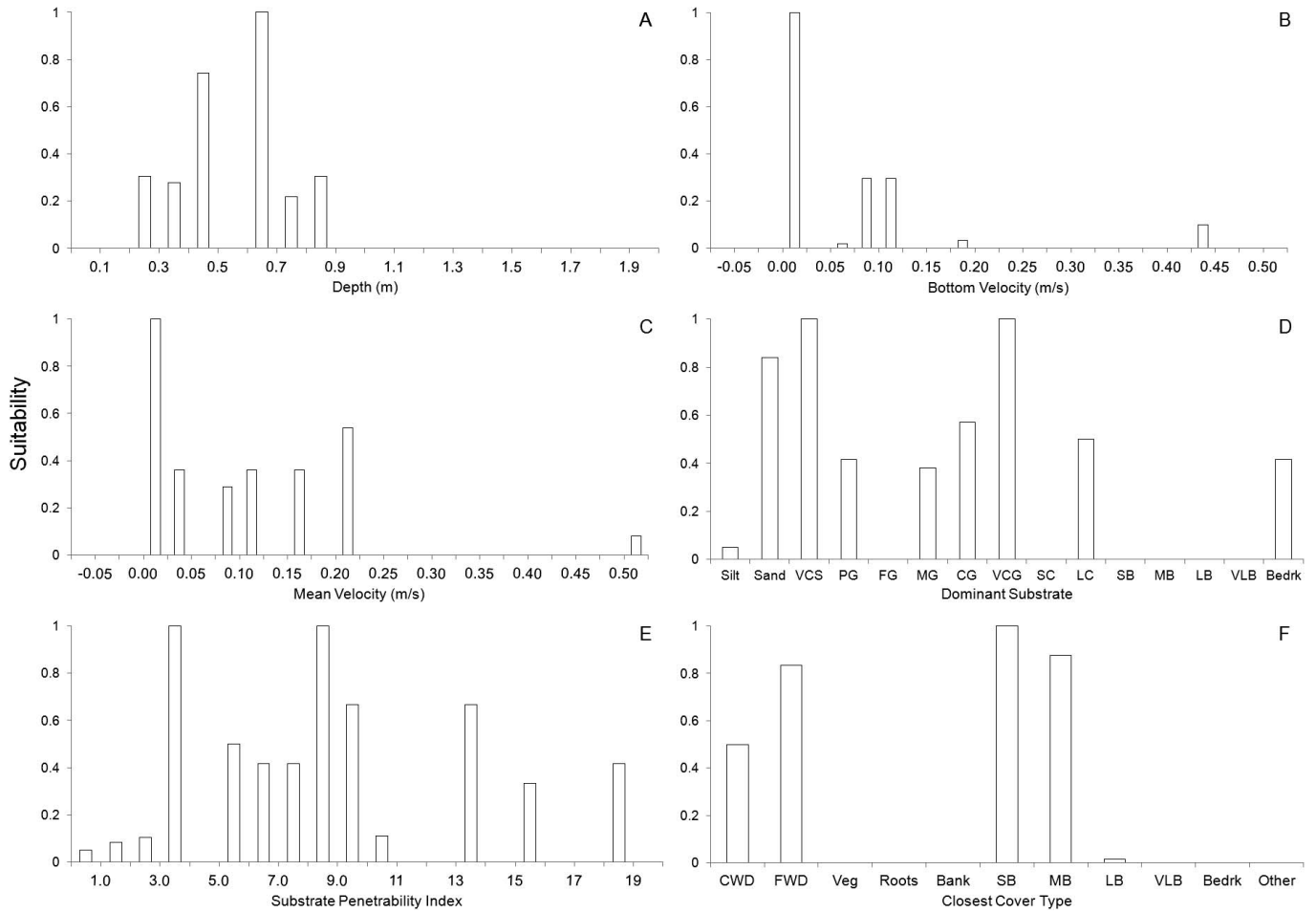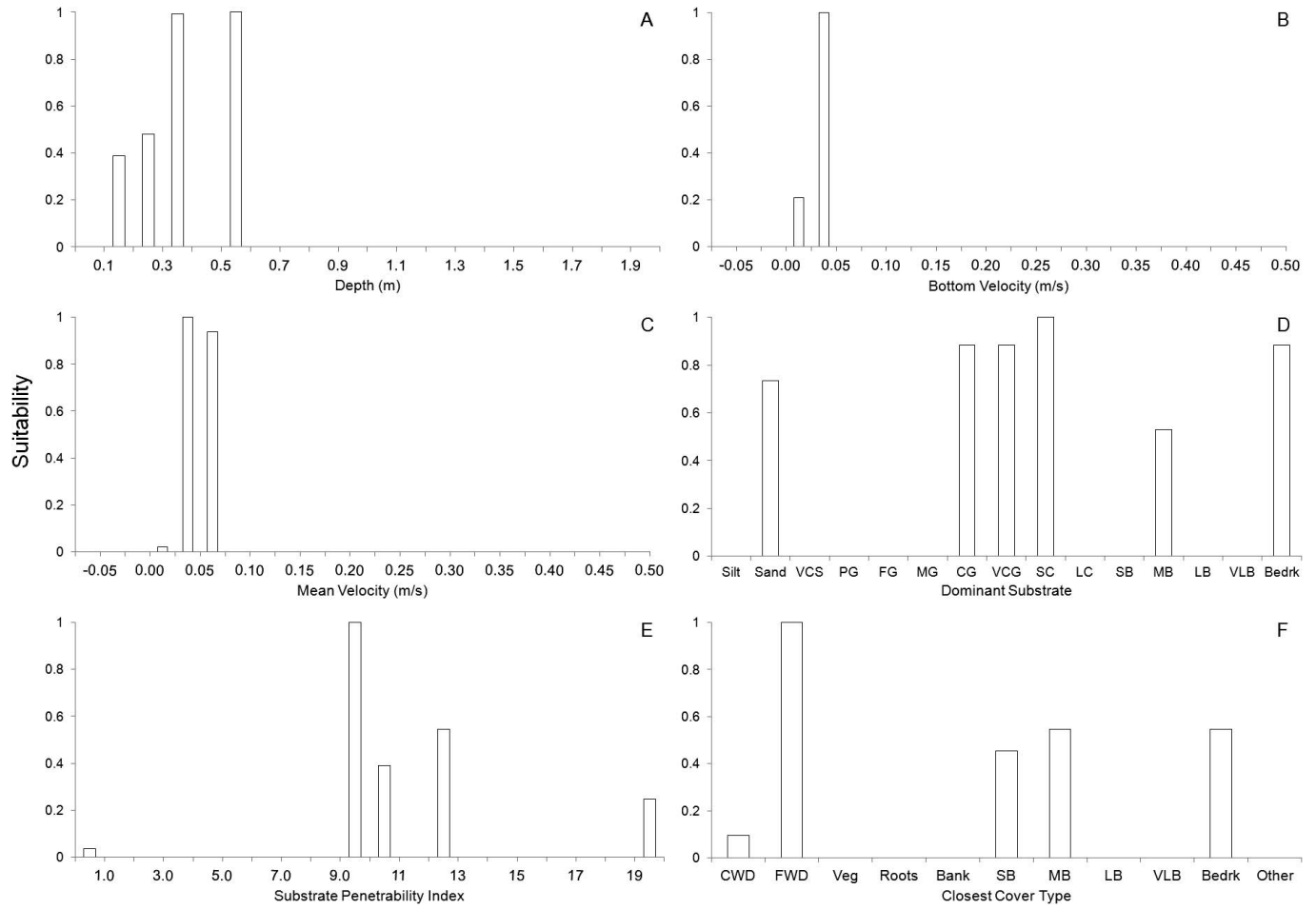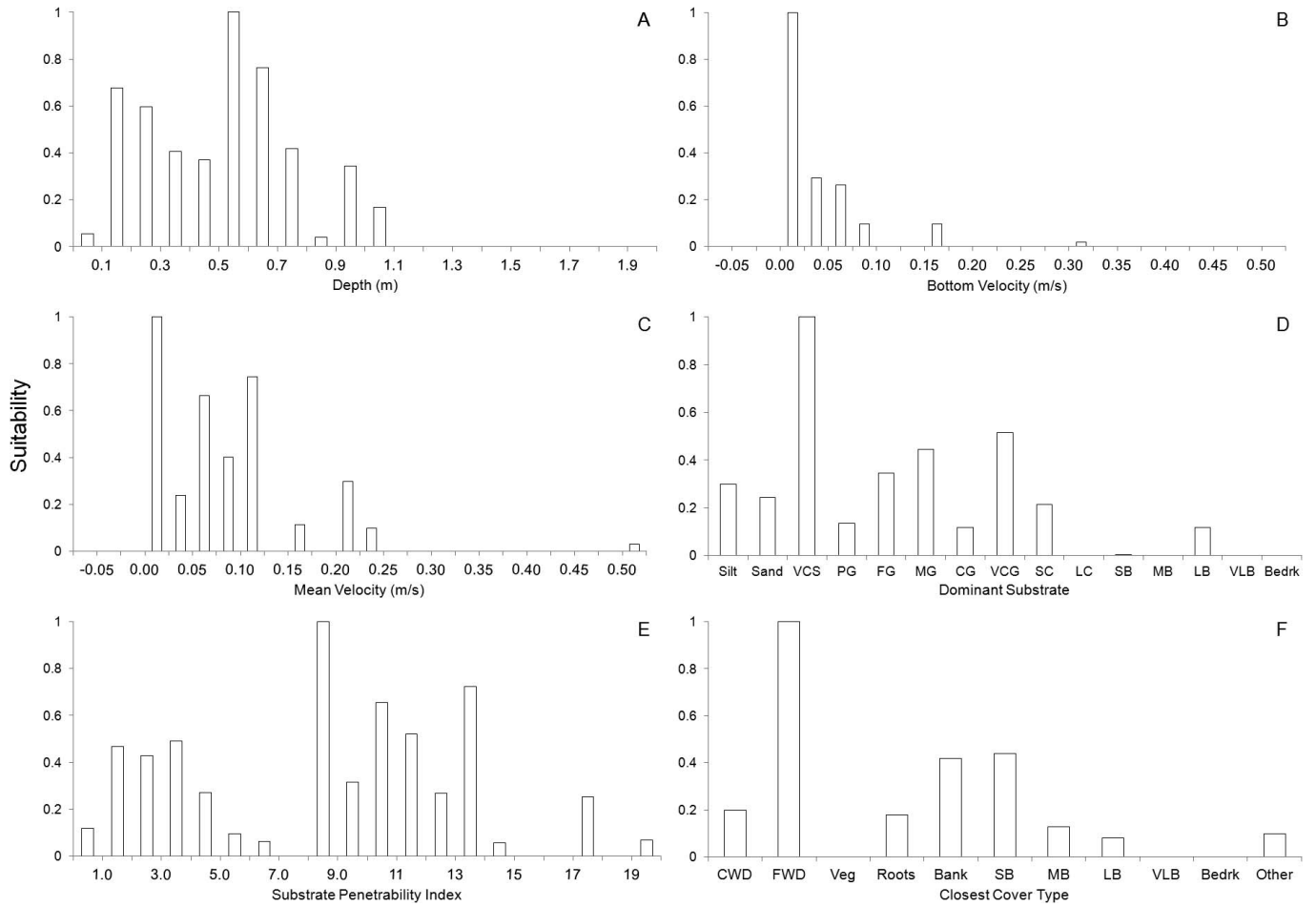
Figure A2. Microhabitat suitability distributions for *Elliptio complanata*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).

Figure A3. Microhabitat suitability distributions for *Elliptio congaraea*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
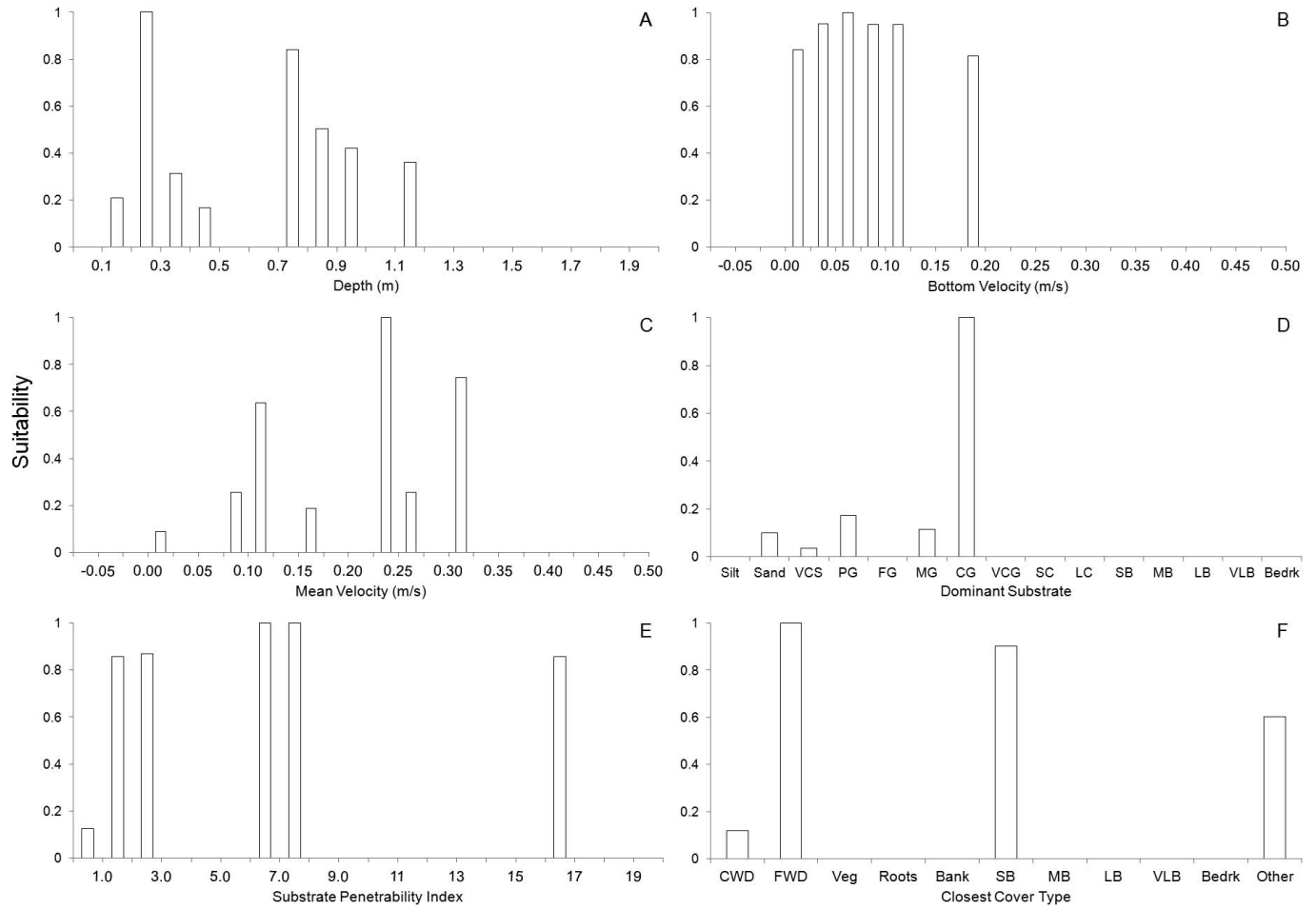
Figure A4. Microhabitat suitability distributions for *Elliptio fisheriana*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
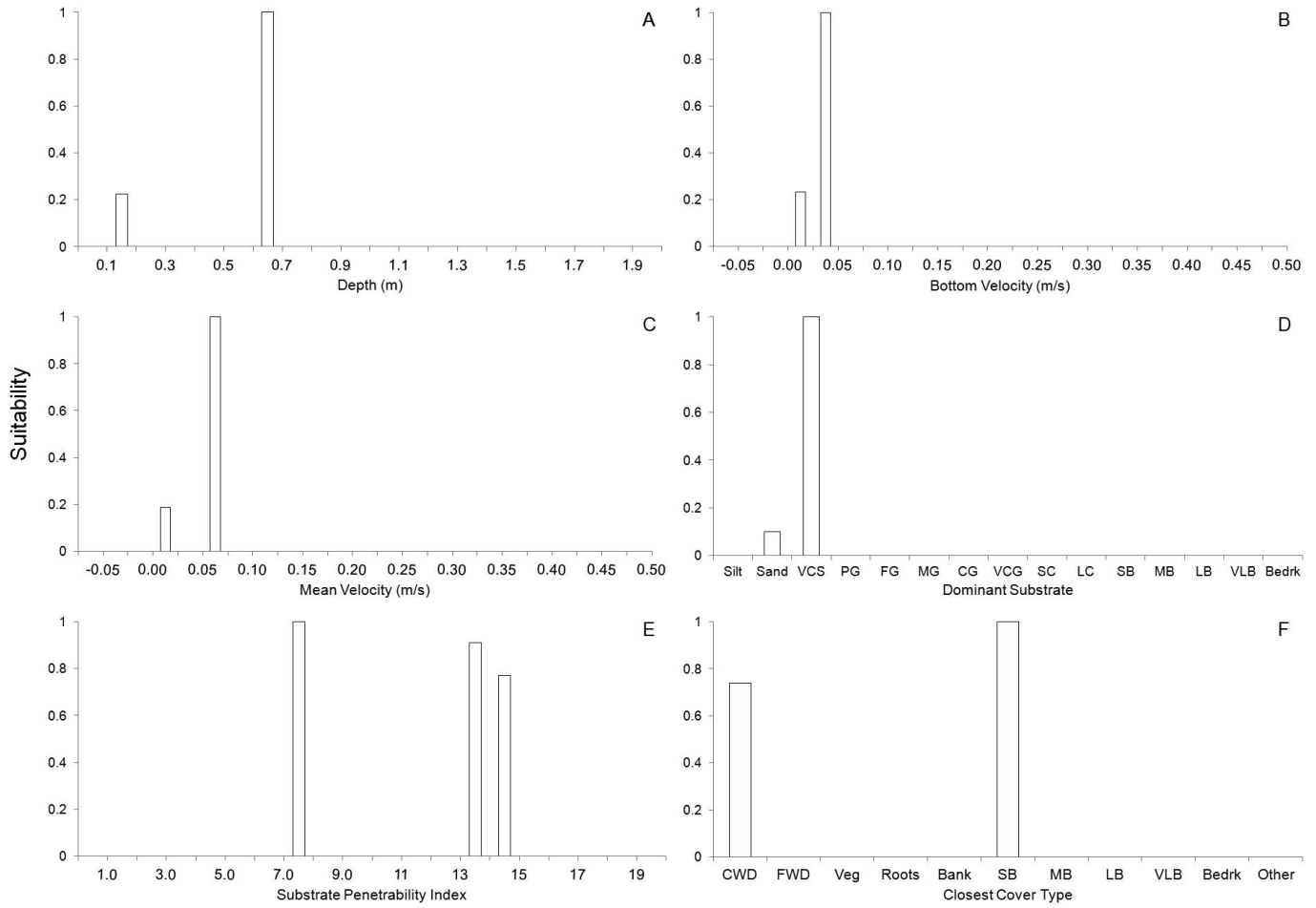
Figure A5. Microhabitat suitability distributions for *Elliptio icterina*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).

Figure A6. Microhabitat suitability distributions for *Elliptio roanokensis*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).

Figure A7. Microhabitat suitability distributions for *Elliptio steinstansana*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
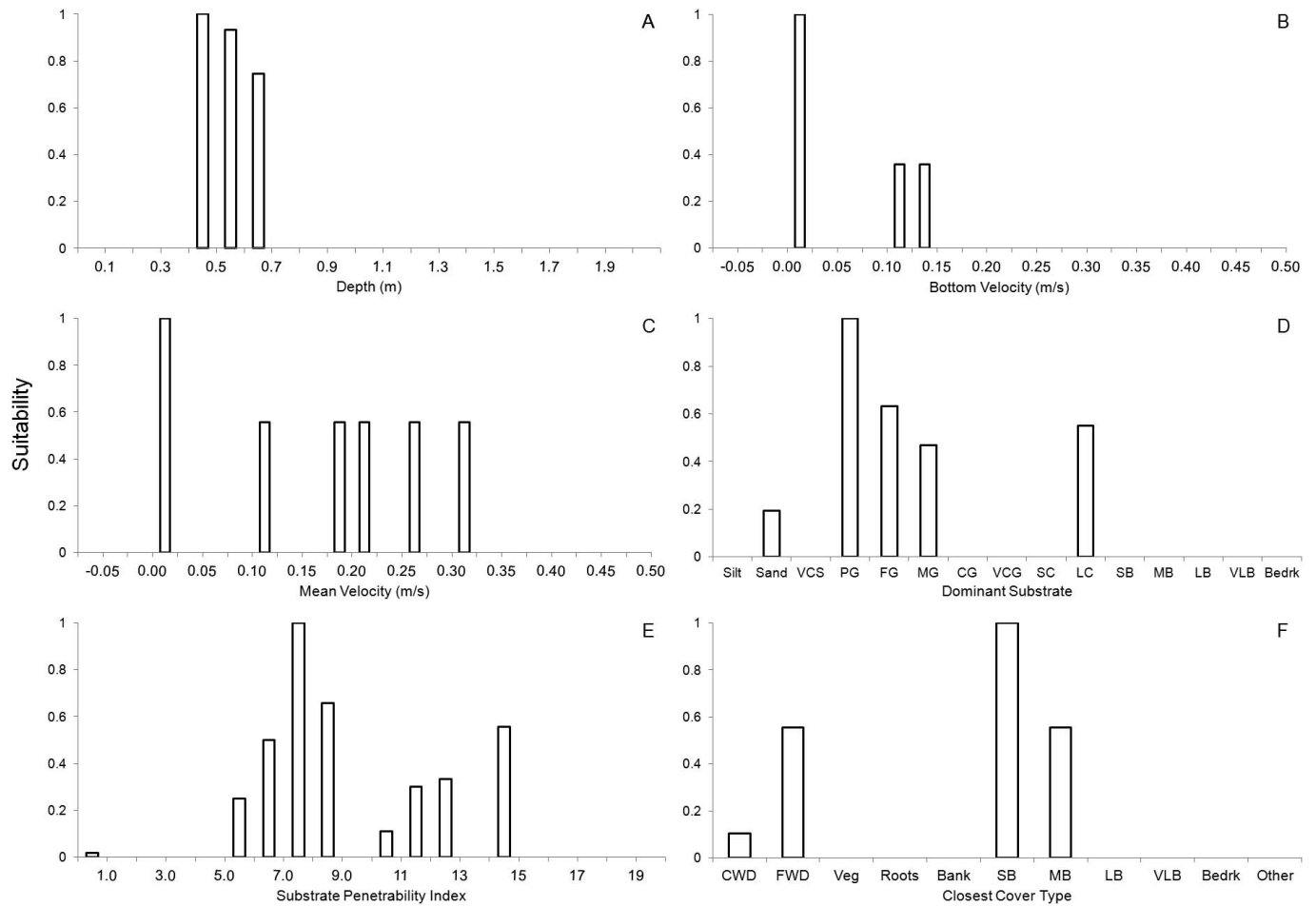
Figure A8. Microhabitat suitability distributions for *Fusconaia masoni*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
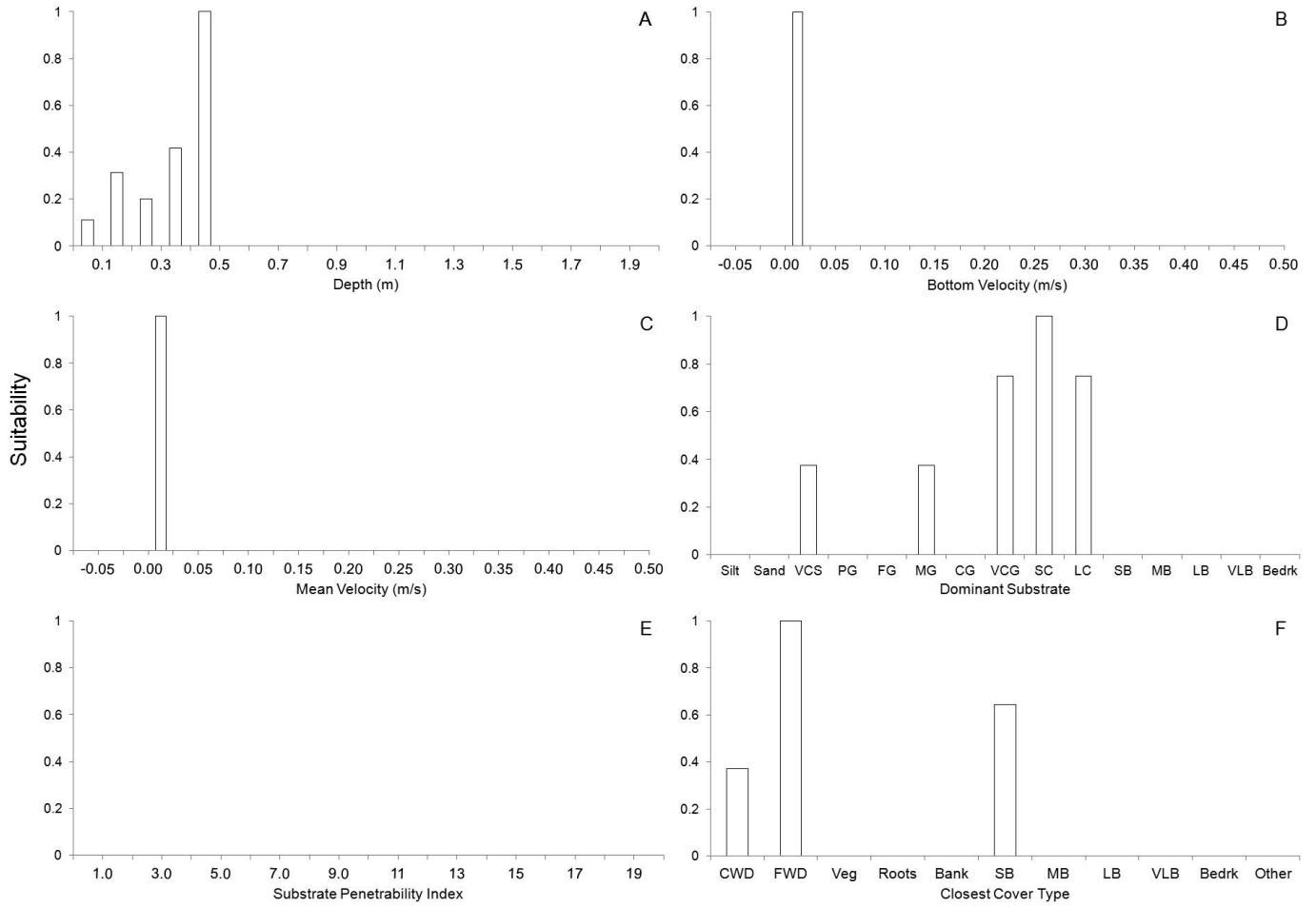
Figure A9. Microhabitat suitability distributions for an undescribed *Lampsilis*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).
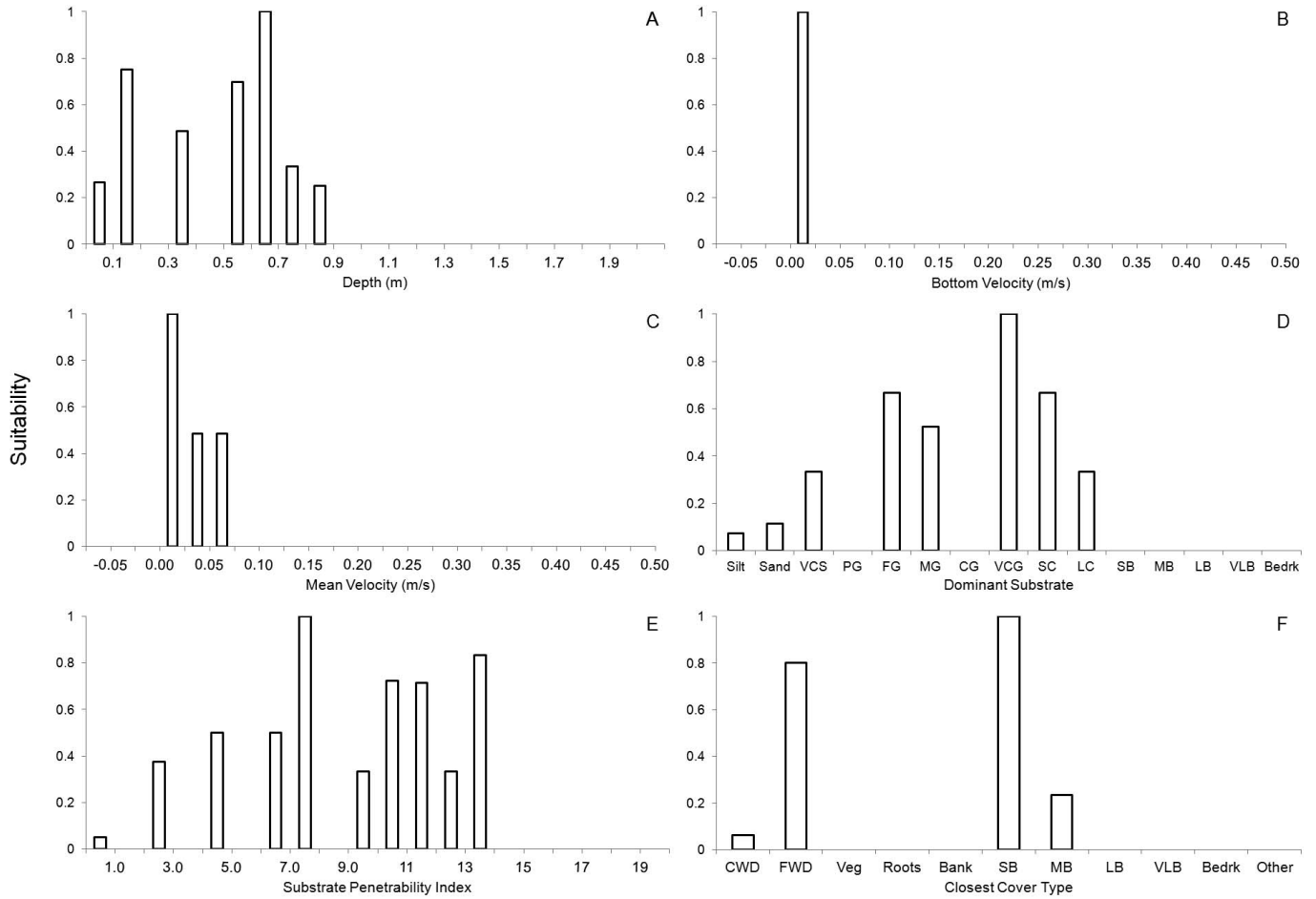
Figure A10. Microhabitat suitability distributions for *Villosa constricta*. Suitability for depth (A), bottom velocity (B), mean velocity (C), dominant substrate (D), substrate penetrability index (E), and cover type (F) are graphed from 0 (least suitable) to 1 (most suitable).