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USE OF OCCUPANCY MODELING TO ASSESS THE STATUS AND HABITAT RELATIONSHIPS OF FRESHWATER MUSSELS IN THE LOWER FLINT RIVER, GEORGIA, USA

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ABSTRACT

The Flint River in southwestern Georgia is known for its historically diverse mussel fauna, but the current status of the fauna is poorly known. The rediscovery of two presumed extirpated and extinct species in 2006 and 2008 exemplifies the need for a large-scale survey of the river. We used an occupancy modeling approach to estimate the presence of mussel species at 39 locations along a 119 km reach of the lower Flint River between Lake Seminole and Albany Dam. Twenty species were collected and evidence of recent reproduction was documented for 8 species. *Elliptio crassidens*, *E. fumata/pullata*, and *E. nigella* were the most abundant species and accounted for 43%, 40%, and 8% of the total mussels collected, respectively. Among species, mean detection probabilities averaged 0.25 and ranged from 0.01 to 0.69, whereas occupancy averaged 0.56 and ranged from 0.03 to 1. We fitted models relating site-level and sample-level habitat characteristics and site location to detection and occupancy for nine species. Detection probabilities varied among species, substrate, searcher experience, and distance from Albany Dam. Estimated occupancy varied by species and substrate composition indicating different substrate use by different species. Our modeling approach indicated that our sampling design was efficient for detecting most species with the exception of rare species. The Lower Flint River continues to harbor a widely distributed and diverse assemblage of freshwater mussels. The occupancy modeling approach used in our study was a useful and efficient method to assess the status, distribution, and habitat use of freshwater mussels in the Flint River while also providing a measure of sampling efficiency. Similar model-based study designs may be effective in other streams, particularly when sampling resources are limited.

KEY WORDS Occupancy, Detection, Flint River, Freshwater Mussels, *Elliptoideus sloatianus*, *Elliptio nigella*

INTRODUCTION

The Apalachicola-Chattahoochee-Flint (ACF) River basin originates in the Blue Ridge and Piedmont physiographic provinces of Georgia and flows south into Florida before emptying into Apalachicola Bay in the eastern Gulf of Mexico. The basin is known for its unique and imperiled mussel fauna (family Unionidae), which historically included about 33 species (Brim Box & Williams, 2000). Mussel populations have declined or been extirpated from much of the basin due to impoundment, pollution, and sedimentation, and 15 species in the basin are now extirpated or imperiled. The Flint River basin supports some of the most important remnants of the ACF fauna including at least 27 species (Brim Box & Williams, 2000). However, most recent sampling efforts in the Flint River basin have focused on tributaries (e.g., Brim Box & Williams, 2000; Golladay et al., 2004; Gagnon et al., 2006; Shea et al., 2013), and the mainstem remains poorly sampled. Furthermore, most previous surveys focused on documenting species presence/

absence and distribution, which provides limited data for assessing temporal changes in populations. The recent rediscovery of the presumed extirpated *Amblema neislerii* and the presumed extinct *Elliptio nigella* in the Flint River suggests that the mainstem is an important conservation refuge in need of intensive survey and monitoring. Because of the large size of the river, sampling methods and analyses are needed that can maximize efficiency while also providing useful inferences about the status of the fauna.

Occupancy estimation is a model-based approach to estimate the probability of species presence in an area while accounting for the imperfect detection probabilities that are inherent in most sampling methods (MacKenzie et al., 2002). Detection probability, which may vary across species, time, and space (McKelvey & Pearson, 2001; MacKenzie et al., 2002), is the probability of detecting a species at a site and is conditional upon the species being present and collected when present. Presence/absence (hereafter referred to as detection/nondetection) data are used to jointly model species presence and detection in a hierarchical logistic regression model. Occupancy models are based on Capture-Mark-Recapture models and use replicate samples collected at a site to construct a binary capture history based on the detection (1) or non-detection (0) of target species. Replicate samples may be collected temporally through repeated visits to a site or spatially by taking replicate samples on a single occasion. The capture history is used to estimate the probability of detecting a target species in a single replicate sample when the species is present and available for capture. Occupancy is defined as the probability that a species is present at a site, but imperfect species detection can cause occupancy to be underestimated (MacKenzie et al., 2006, Wisniewski et al., 2013a). Occupancy models use detection probabilities to correct naïve occupancy (the proportion of sites observed occupied), which reduces bias due to imperfect sampling. Occupancy models can be scaled to large areas such as watersheds or species' ranges, and the influence of site-level or sample-level factors on detection and occupancy can be estimated, which provides insight into the factors influencing species distribution and abundance. Because freshwater mussels are often difficult to sample due to their burrowing habits and variable sampling conditions, occupancy modeling may provide more accurate depictions of species' status and a better understanding of the factors that affect them (McKelvey & Pearson, 2001; Tyre et al., 2003; Wisniewski et al., 2013a).

We used occupancy models to examine the status and distribution of freshwater mussels in the lower Flint River. First, we conducted detection/nondetection surveys throughout the study reach, and we modeled average detection and occupancy for all species found during our surveys. Second, we incorporated several site- and sample-specific habitat covariates in our models to examine the effects of these factors on occupancy and detection and how they varied among species. Specifically, we examined relationships between substrate composition, flow, and depth and mussel occurrence and detection. We also assessed how distance from a large hydropower dam was related to mussel occurrence because mussel species richness and abundance may increase with increasing distance from dams (Vaughn & Taylor, 1999). Lastly, we used estimated detection probabilities to assess the efficiency of our sampling design for detecting species

METHODS

Study area

We focused on a 119 km reach of the lower Flint River between Albany Dam in Albany, GA, downstream to the backwaters of Lake Seminole at river kilometer (rkm) 48, near Bainbridge, GA (Fig. 1). Albany Dam was constructed as a hydropower facility in 1919 and is currently operated by Georgia Power as a hydro-peaking facility but minimally increases river discharge during periods of operation (Couch et al., 1996). The study area is entirely within the Dougherty Plain physiographic district, which is underlain by karst, and the river receives substantial groundwater inputs from the Floridan aquifer via tributaries and in-channel springs. Substrates range from silt and sand to limestone boulders and bedrock. The river has a mean daily discharge of 113 m^3/s at the USGS gage station located in Newton, GA (Couch et al., 1996). Ichawaynochaway Creek is the only large tributary flowing into this reach of the river, entering the Flint River at approximately rkm 84. The river channel is deeply entrenched, often with vertical limestone bluffs. Woody debris is relatively abundant in the stream channel.

Mussel sampling

We sampled 39 sites in the study reach over 15 days between 23 May 2011 and 30 August 2011 (Fig. 1; Wisniewski et al., 2013a). Prior to sampling, a sequence of site characteristics was randomly selected according to two factors: (1) left ascending bank or right ascending bank and (2) dominant site macrohabitat (i.e., edgewater/stream margin, riffle, run, glide, and pool). We then travelled upstream on the river and sampled at the first location that met the characteristics of the first site on our sequence. After sampling this site, we moved upstream at least 2 km to the next specified site characteristic.

We randomly placed ten 10-m-long transect lines perpendicular to flow at each site. Searchers collected

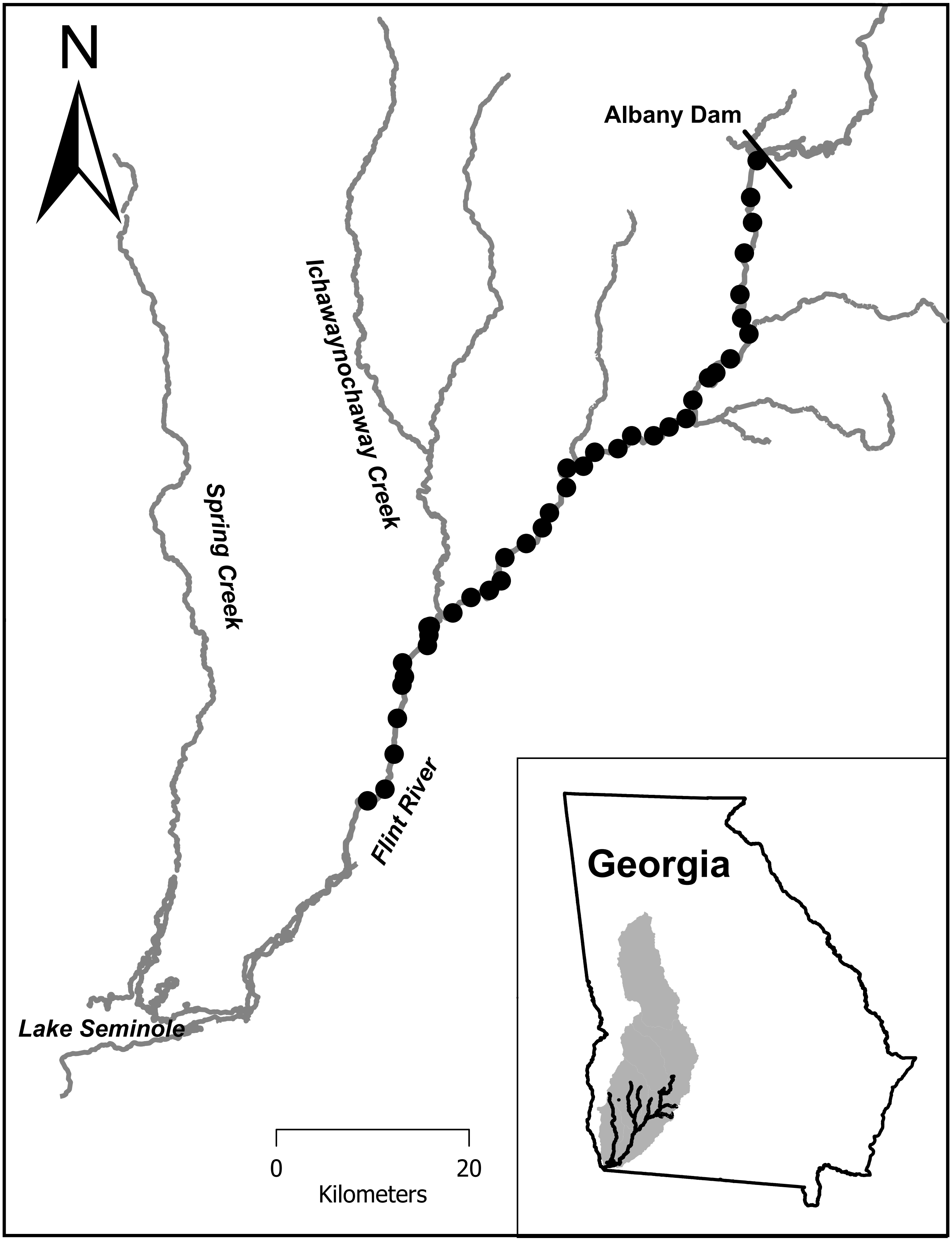


FIGURE 1

The lower Flint River, Georgia, with locations of the 39 sample sites.

all mussels within 0.5 m of each side of transects using tactile and visual survey methods with mask and snorkel in shallow water or surface-air-supply system in waters ≥1.5 m in depth. Crevices among and under coarse substrates were also searched using tactile searches. All mussels were identified to species, counted, and a maximum of 10 individuals per species per transect were measured along the longest axis parallel to the hinge-line. The smallest and largest individuals were measured when >10 individuals of a species were collected in a transect. We pooled *Elliptio fumata* and *Elliptio pullata* for all analyses due to the difficulty in separating these species reliably. After processing, all mussels were returned to the river. Sampling time per site ranged from 0.35 person-hours to 5.65 person-hours with a mean time per site of 1.40 person-hours. *Utterbackia peggyae* and *Villosa villosa* were collected only during resampling of a subset of sites used for an additional analysis included in a previously published study (Wisniewski et al., 2013a). These species are included here in overall estimates of species richness and cumulative detection (Tables 1 and 2), but they were not included in occupancy and detection models.

TABLE 1

Freshwater mussel species collected in the lower Flint River, Georgia. # of sites is the number of sites at which a species occurred; % of sites represents naïve occupancy.

Tribe	Species	Common Name	# of Sites	% of Sites	Total number	% of total
Amblemini						
	Amblema neislerii (Lea, 1858)	Fat Threeridge	1	3	5	<1
Lampsilini						
	Hamiota subangulata (Lea, 1840)	Shinyrayed Pocketbook	3	8	3	<1
	Lampsilis floridensis (Lea, 1852)	Florida Sandshell	28	72	85	1
	Lampsilis straminea (Conrad, 1834)	Southern Fatmucket	2	5	2	<1
	Toxolasma paulum (Lea, 1840)	Iridescent Lilliput	15	38	105	1
	Villosa lienosa (Conrad, 1834)	Little Spectaclecase	13	33	85	1
	Villosa vibex (Conrad, 1834)	Southern Rainbow	23	59	50	1
	Villosa villosa (Wright, 1898)	Downy Rainbow	1	3	1	<1
Pleurobemini						
	Elliptio arctata (Conrad, 1834)	Delicate Spike	9	23	70	1
	Elliptio crassidens (Lamarck, 1819)	Elephantear	28	72	3,139	44
	Elliptio fumata/pullata	*E. fumata/pullata*	34	87	2,817	39
	Elliptio nigella (Lea, 1852)	Winged Spike	15	38	539	8
	Elliptio purpurella (Lea, 1857)	Inflated Spike	1	3	2	<1
	Elliptoideus sloatianus (Lea, 1840)	Purple Bankclimber	17	44	98	1
Quadrulini						
	Megalonaias nervosa (Rafinesque, 1820)	Washboard	5	13	13	<1
	Quadrula infucata (Conrad, 1834)	Sculptured Pigtoe	21	54	143	2
	Uniomerus columbensis (Lea, 1857)	Apalachicola Pondhorn	3	8	3	<1
Anodontini						
	Alasmidonta triangulata (Lea, 1858)	Southern Elktoe	2	5	4	<1
	Utterbackia peggyae (Johnson, 1965)	Florida Floater	1	3	2	<1
TOTAL			39		7,166	

TABLE 2

Cumulative detection probabilities of freshwater mussel species collected in the lower Flint River, Georgia. Values indicate the probability of detecting a species when the given number of 10 m X 1 m transects are searched at a site under the condition that the species is present.

Tribe	Transects Searched									
Species	1	2	3	4	5	6	7	8	9	10
Amblemini										
Amblema neislerii	0.40	0.64	0.78	0.87	0.92	0.95	0.97	0.98	0.99	0.99
Lampsilini										
Hamiota subangulata	0.01	0.02	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.07
Lampsilis floridensis	0.21	0.38	0.52	0.62	0.70	0.77	0.82	0.86	0.89	0.91
Lampsilis straminea	0.01	0.01	0.02	0.02	0.03	0.03	0.04	0.04	0.05	0.05
Toxolasma paulum	0.30	0.51	0.65	0.76	0.83	0.88	0.92	0.94	0.96	0.97
Villosa lienosa	0.26	0.46	0.60	0.71	0.78	0.84	0.88	0.91	0.94	0.95
Villosa vibex	0.16	0.30	0.41	0.50	0.58	0.65	0.71	0.75	0.79	0.83
Villosa villosa	0.01	0.02	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.07
Pleurobemini										
Elliptio arctata	0.28	0.48	0.62	0.73	0.80	0.86	0.90	0.93	0.95	0.96
Elliptio crassidens	0.57	0.82	0.92	0.97	0.99	0.99	1.00	1.00	1.00	1.00
Elliptio fumata/pullata	0.69	0.90	0.97	0.99	1.00	1.00	1.00	1.00	1.00	1.00
Elliptio nigella	0.39	0.63	0.77	0.86	0.92	0.95	0.97	0.98	0.99	0.99
Elliptio purpurella	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.03
Elliptoideus sloatianus	0.28	0.49	0.63	0.74	0.81	0.86	0.90	0.93	0.95	0.96
Quadrulini										
Megalonaias nervosa	0.17	0.31	0.42	0.52	0.60	0.67	0.72	0.77	0.81	0.84
Quadrula infucata	0.34	0.57	0.72	0.81	0.88	0.92	0.95	0.97	0.98	0.98
Uniomerus columbensis	0.01	0.02	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.07
Anodontini										
Alasmidonta triangulata	0.17	0.31	0.42	0.52	0.60	0.67	0.72	0.77	0.81	0.84
Utterbackia peggyae	0.01	0.02	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.07

Covariate measurements

Searcher experience (years/searcher), substrate roughness, mean depth, mean velocity, and substrate composition were recorded or measured at each transect to model variability in detection probabilities related to these factors. Percent woody debris and substrate composition at the site level were measured as a composite from all transects at each site. Substrate composition categories were: clay (<0.06 mm and cohesive), silt (<0.06 mm), sand (0.06-2 mm), gravel (2-64 mm), cobble (64-256 mm), boulder (>256 mm), and bedrock (>256 mm, unbroken). Sites were visually characterized as swiftwater (riffles/runs/glides) or slackwater (pool/edgewater) because macrohabitat types defined when selecting sites are dependent on river stage. The distance from Albany Dam to each site was measured using the National Hydrography Database at a scale of 1:24,000 in ArcGIS 9.3 (ESRI, Redlands, CA). Site-level covariates were used to model variability in occupancy (Wisniewski et al., 2013a).

Data analysis

Single-season occupancy models were generated for all species (MacKenzie et al., 2006) to estimate mean occupancy and mean transect-level detection probabilities throughout the 119 km study area (Wisniewski et al., 2013a). We estimated occupancy and detection probabilities in relation to site- and transect-level characteristics only for species occurring at ≥10 sites to ensure sufficient power to estimate influences of covariates on parameters (Wisniewski et al., 2013a). We assessed the ability of our sampling design to detect a species at a site by calculating cumulative detection probability (p*):

$$p^* = 1-(1-p)^K$$

where p is the estimated detection for a single transect and K is the total number of transects (Bayley & Peterson, 2001; Hagler et al., 2011). Occupancy models were fit for each species in Program MARK (White & Burnham, 1999). We also developed an *a priori* set of 65 candidate models representing hypothesized relations between habitat variables and freshwater mussel occupancy and detection (see Wisniewski et al., 2013a; Table 1). To facilitate comparisons among models, we calculated Akaike weights, which range from zero to one with the best approximating candidate model having the highest weight (Burnham & Anderson, 2002). The most plausible models (confidence set) were those with Akaike weights that were at least 10% of that of the best-approximating model, which is similar to Royall's general rule-of-thumb of 1/8 or 12% for evaluating strength of evidence (Royall, 1997). To ease interpretation of parameter estimates, we calculated odds ratios (Hosmer & Lemeshow, 2000). The precision of each parameter estimate was evaluated by examining 95% confidence intervals. Parameter estimates with confidence intervals that contained zero were considered imprecise. Model structures and parameter estimates for *E. nigella*, *Elliptoideus sloatianus*, *Quadrula infucata* were previously reported (see Wisniewski et al., 2013a) and are not included in this study.

Single season occupancy models have four main assumptions in terms of our study: (1) the occupancy state of a site is closed during sampling, (2) sites are independent of one another, (3) probability of occupancy is equal across sites, and (4) detection probabilities are equal across all sites and transects given that a species is present (MacKenzie et al., 2006). Our sites were located a minimum of 2 km apart and sampling at a site was completed within 3 hours; therefore the occupancy state of freshwater mussels at a site is unlikely to change or influence occupancy states at other sites. Assumptions 3 and 4 likely are not met due to differences in physical habitat characteristics among sites, but the covariates (e.g., current, substrate) in our model structures account for these differences.

RESULTS

Twenty mussel species were collected across all 39 sites (Table 1), and observed site species richness ranged from 0-13 (mean = 6) but only one site yielded no mussels. A total of 7,166 individuals were collected, and two sites accounted for 48% of total individuals. The fauna was dominated by *Elliptio crassidens* and *E. fumata/pullata*, which together made up 83% of the total catch, and they were found at 72% and 87% of sites, respectively. Noteworthy was the collection of 539 individuals (8% of total catch) of *E. nigella*, which was previously considered extinct (see Discussion); all other species individually composed ≤2% of the fauna. Despite the relative rarity of most species, many were widely distributed in the river. In addition to *E. crassidens* and *E. fumata/pullata*, *Lampsilis floridensis*, *Q. infucata*, and *Villosa vibex* were found at >50% of sites, and four other species (including *E. nigella*) were found at >30% of sites.

For most species, results of occupancy and detection modeling closely reflected patterns of species distribution and assemblage composition based on naïve occupancy (Fig. 2). Cumulative detection probability based on 10 transects exceeded 0.80 for most species, indicating that our sampling design was adequate for detecting most species when present (Table 2). Cumulative detection probabilities were <0.07 for *Hamiota subangulata, Lampsilis straminea, Elliptio purpurella, Uniomerus columbensis, U. peggyae*, and *V. villosa*. Rankings of estimated detection probabilities at the transect level were roughly similar to rankings based on total catch, with the highest values for *E. fumata/pullata* and *E. crassidens* (Fig. 2, Table 1). Similar to cumulative detection, transect-level detection was low for *H. subangulata, L. straminea, E. purpurella*, and *U. columbensis* and reflected the rarity of these species in our samples. Estimated occupancy was nearly identical to naïve occupancy for all species except *H. subangulata*, *L. stra-*

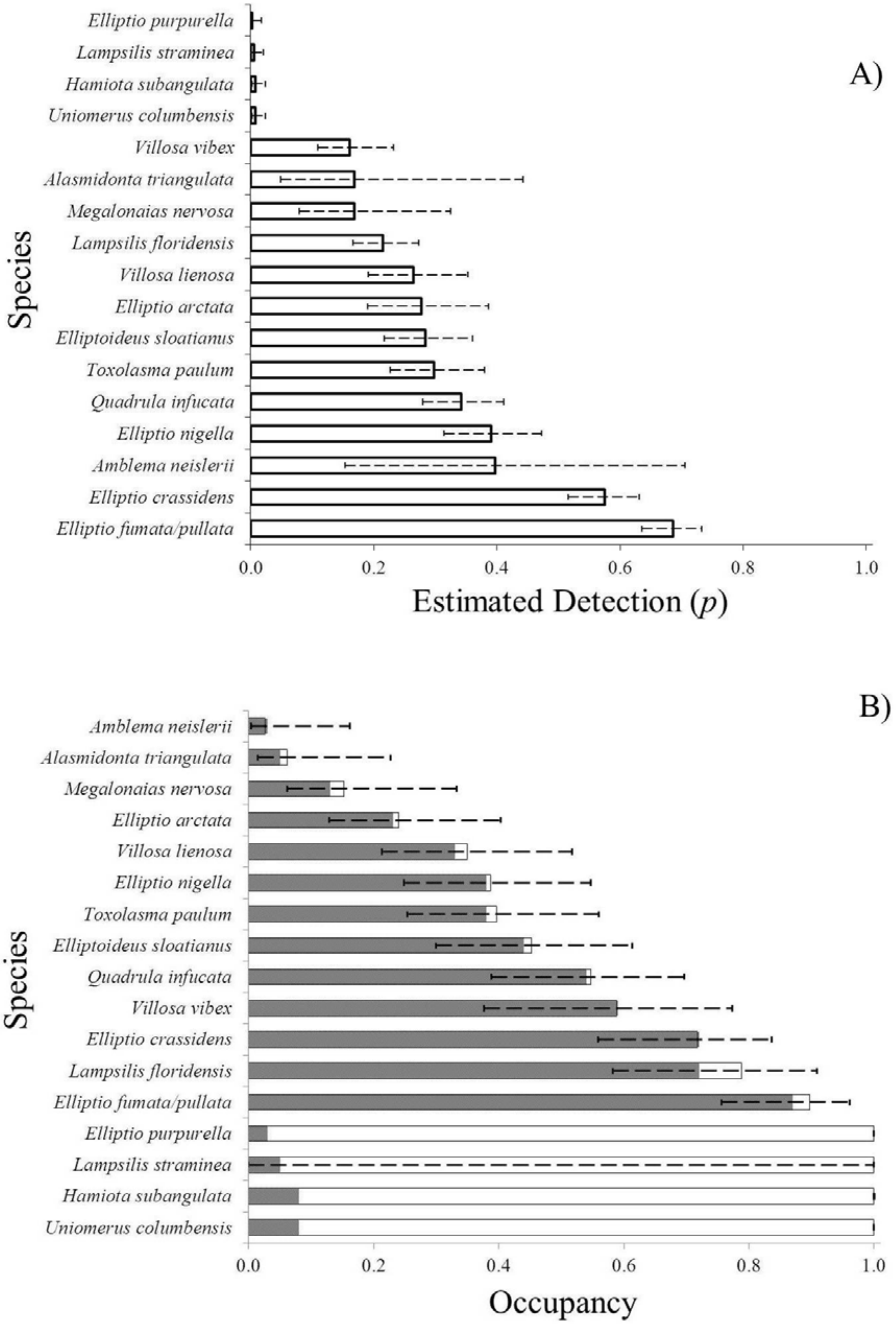


FIGURE 2

(A) Estimated detection probabilities and (B) occupancy for freshwater mussel species collected at 39 sites in the lower Flint River, Georgia. Error bars are 95% confidence intervals. In panel B, naïve occupancy is indicated by shading. Data from Wisniewski et al. (2013a).

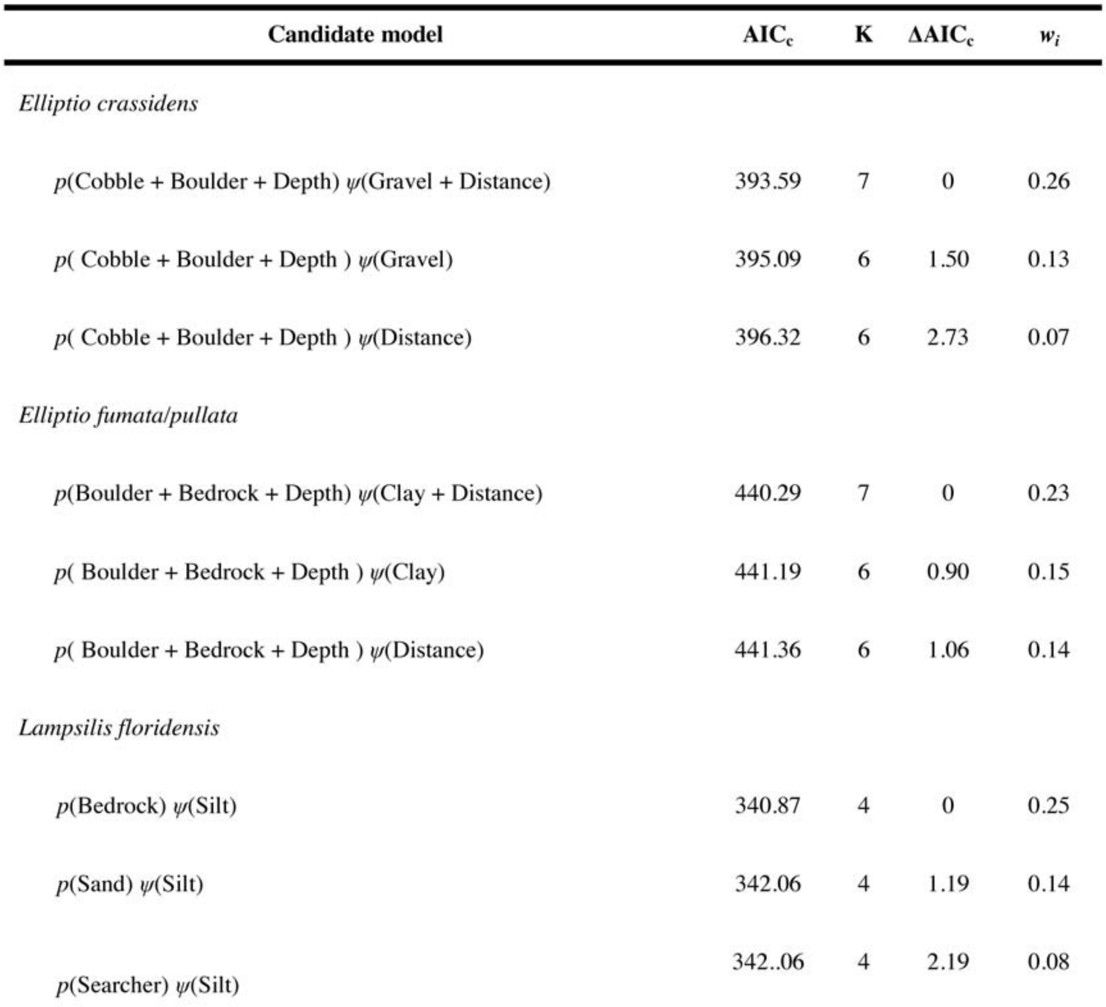
minea, E. purpurella, and *U. columbensis*. Estimated occupancy was 1.0 for all four of these species in contrast to their extreme rarity and limited distribution in our samples. However, 95% confidence intervals for these estimates were either unrealistically narrow (0.99-1.00 or 1.00-1.00) or extremely wide (0.00-1.00), suggesting that these estimates were biased by the low detection probability for these species.

Factors influencing species occupancy and detection

Thirteen models were included in the confidence set for *E. crassidens*. All models in the confidence set included detection varying by percent cobble and boulder substrates and water depth, and each of these covariates accounted for 94% of the model AIC_c weight. Occupancy modeled as a function of percent gravel and distance from Albany Dam accounted for 50% and 33% of the model AIC_c weight, respectively. The best approximating model had 2.11 times more support than the next best model and odds ratios indicated that detection of *E. crassidens* decreased by 2.18 times for every meter increase in depth (Tables 3 & 4). Detection greatly increased with increasing amount of cobble substrates. Estimated occupancy of *E. crassidens* increased by 1.02 times for every 1-km increase in distance from Albany Dam. Confidence intervals for detection varying by percent boulder substrate and occupancy varying by percent gravel substrate contained zero and we were unable to conclude if these effects were negative or positive.

TABLE 3

Akaike Information Criterion (AIC_c), number of parameters (K), ΔAIC_c, and AIC_c weights (w_i) for the three best approximating models estimating detection probability (p) and occupancy (ψ) for nine freshwater mussel species in the lower Flint River, Georgia. Distance corresponds to distance downstream from Albany Dam.



Candidate model	AIC_c	K	ΔAIC_c	w_i
Elliptio crassidens				
p(Cobble + Boulder + Depth) *ψ*(Gravel + Distance)	393.59	7	0	0.26
p(Cobble + Boulder + Depth) *ψ*(Gravel)	395.09	6	1.50	0.13
p(Cobble + Boulder + Depth) *ψ*(Distance)	396.32	6	2.73	0.07
Elliptio fumata/pullata				
p(Boulder + Bedrock + Depth) *ψ*(Clay + Distance)	440.29	7	0	0.23
p(Boulder + Bedrock + Depth) *ψ*(Clay)	441.19	6	0.90	0.15
p(Boulder + Bedrock + Depth) *ψ*(Distance)	441.36	6	1.06	0.14
Lampsilis floridensis				
p(Bedrock) *ψ*(Silt)	340.87	4	0	0.25
p(Sand) *ψ*(Silt)	342.06	4	1.19	0.14
p(Searcher) *ψ*(Silt)	342..06	4	2.19	0.08

TABLE 3
(cont.)

Toxolasma paulum				
p(Depth + Sand) *ψ*(Gravel + Boulder)	221.22	6	0	0.41
p(Depth + Sand) *ψ*(Gravel)	222.45	5	1.23	0.22
p(Depth + Sand) *ψ*(Boulder)	223.03	5	1.81	0.17
Villosa lienosa				
p(Clay + Bedrock) *ψ*(Boulder + Bedrock)	199.28	6	0	0.43
p(Clay + Bedrock) *ψ*(Boulder)	201.32	5	2.04	0.16
p(Clay + Bedrock) *ψ*(Boulder + Gravel)	202.58	6	3.30	0.08
Villosa vibex				
p(Searcher) *ψ*(Cobble)	226.42	4	0	0.82
p(Searcher) *ψ*(Woody debris + Cobble)	230.28	5	3.86	0.12
p(Searcher) *ψ*(Woody debris)	235.59	4	9.17	0.01

TABLE 4

Parameter estimates (standard errors), lower and upper 95% confidence limits, and scaled odds ratios for the best approximating models for occupancy (ψ), and detection (p) of six freshwater mussel species in the lower Flint River, Georgia.

Parameter	Estimate (SE)	Lower	Upper	Odds Ratio
Elliptio crassidens				
Detection (*p*)				
Intercept	0.506 (0.316)	-0.113	-1.126	
Cobble	4.556 (1.194)	2.216	6.896	95.19
Boulder	-6.675 (2.123)	-2.514	10.835	792.15
Depth	-0.781 (0.329)	-1.426	-0.136	2.18
Occupancy (*ψ*)				
Intercept	-1.294 (0.980)	-1.483	0.722	
Gravel	8.916 (4.728)	-0.351	18.184	> 1000
Distance	0.027 (0.013)	0.001	0.053	1.03
Elliptio fumata/pullata				
Detection (*p*)				
Intercept	1.767 (0.363)	1.056	2.478	
Depth	-0.884 (0.339)	-1.549	-0.220	2.42
Bedrock	-1.152 (0.366)	-1.869	-0.435	3.16
Boulder	6.781 (2.412)	-2.053	11.510	881.34
Occupancy (*ψ*)				
Intercept	-5.117 (2.512)	0.193	10.041	
Clay	2734.841 (0)	2734.841	2734.841	> 1000
Distance	-0.042 (0.029)	-0.099	0.014	1.04
Lampsilis floridensis				
Detection (*p*)				
Intercept	-1.130 (0.166)	-1.456	-0.805	
Bedrock	-1.111 (0.538)	-2.165	-0.057	3.04
Occupancy (*ψ*)				
Intercept	-0.008 (0.616)	-1.216	1.199	
Silt	1666.523 (0)	1666.523	1666.523	> 1000
Toxolasma paulum				
Detection (*p*)				
Intercept	-5.591 (1.021)	-7.593	-3.589	
Depth	3.049 (0.803)	1.476	4.622	21.10
Sand	3.270 (0.738)	1.823	4.717	26.31

TABLE 4
(cont.)

Occupancy (ψ)				
Intercept	-0.076 (0.555)	-1.163	1.012	
Boulder	68.301 (51.226)	-32.101	168.704	> 1000
Gravel	-9.020 (5.661)	-20.117	2.076	> 1000
Villosa lienosa				
Detection (p)				
Intercept	-0.905 (0.244)	-1.384	-0.427	
Bedrock	-0.872 (1.105)	-3.038	-1.293	2.39
Clay	-346.08 (0)	-346.084	-346.084	> 1000
Occupancy (ψ)				
Intercept	-0.440 (0.519)	-1.458	0.578	
Bedrock	-4.403 (2.474)	-9.251	0.446	81.68
Boulder	21.570 (11.423)	-0.819	43.959	> 1000
Villosa vibex				
Detection (p)				
Intercept	-2.869 (0.517)	-3.876	-1.862	
Searcher	0.156 (0.060)	0.038	-0.274	42.93
Occupancy (ψ)				
Intercept	-0.659 (0.551)	-1.739	0.4214	
Cobble	193.366 (239.382)	-275.820	662.550	> 1000

Thirteen models were included in the confidence set for the combined group of *E. fumata/pullata*. All models in the confidence set included detection varying by percent boulder, percent bedrock, and water depth, and these covariates each accounted for 99% of the model AIC_c weight. Occupancy modeled as a function of clay and distance from Albany Dam accounted for 48% and 47% of the model AIC_c weight, respectively. The best approximating model had 1.57 times more support than the next best model and indicated that detection decreased by 2.42 times for every 1-m increase in depth (Tables 3 & 4). Detection decreased by 3.16 times for every one percent increase in bedrock substrate. Detection also increased by 881.34 times for every one percent increase in boulder substrate but the confidence interval was imprecise and included zero. Occupancy of *E. fumata/pullata* was strongly and positively associated with clay substrate as this species was found at all sites having clay substrate. Confidence intervals for distance from Albany Dam contained zero and we were unable to conclude if occupancy of *E. fumata/pullata* was negatively or positively influenced.

Fourteen models were included in the confidence set for *L. floridensis*. Detection varying by percent bedrock, percent sand, and searcher experience, accounted for 36%, 14%, and 8% of the model AIC_c weight in the confidence set of models, respectively. All models in the confidence set included occupancy varying by percent silt at a site, which accounted for 92% of the model AIC_c weight (Table 3). The best approximating model had 1.81 times more support than the next best model and indicated that detection was 3.04 times less likely with each one percent increase bedrock substrate (Tables 3 & 4). Occupancy was strongly associated with the proportion of silt at a site as this species was rarely found in sites without silt (Table 4).

Six models were included in the confidence set for *Toxolasma paulum*. All models in the confidence set included occupancy varying by percent gravel substrate which accounted for 99% of the model AIC_c weight. Detection varying by percent sand substrate and percent bedrock substrate accounted for 94% and 5% of the model AIC$_c$ weight in the confidence set of models, respectively. Occupancy varying by percent gravel, percent boulder, and distance from Albany Dam accounted for 82%, 57%, and 16% of the model AIC$_c$ weight in the confidence set, respectively. The best approximating model had 1.85 times more support than the next best model and indicated that detection of *T. paulum* increased by 21.10 times for every 1-m increase in depth and increased by 26.30 times for every one percent increase in sand substrate (Tables 3 & 4). Confidence intervals for boulder and cobble substrate affecting occupancy of *T. paulum* contained zero and we were unable to conclude if this relationship was negative or positive.

Three models were included in the confidence set for *Villosa lienosa*. All models in the confidence set included occupancy varying by percent boulder and detection varying by percent clay and bedrock substrate, and these covariates accounted for 67% of the model AIC$_c$ weight. Occupancy varying by percent bedrock accounted for 43% of the AIC$_c$ model weight. The best approximating model had 2.77 times more support than the next best model (Table 3). Detection was strongly and negatively related to clay substrate as *V. lienosa* was rarely collected in this substrate (Table 4). Confidence intervals for bedrock and boulder substrate affecting occupancy and/or detection contained zero and we were unable to make inferences regarding these relationships.

Two models were included in the confidence set for *V. vibex*. Both models in the confidence set included occupancy varying by percent cobble substrate and detection varying by searcher experience, and these covariates each accounted for 94% of the model AIC$_c$ weight. The best approximating model had 6.88 times more support than the next best model and indicated that detection increased by 1.17 times for each year of searcher experience (Tables 3 & 4). Confidence intervals for percent cobble substrate included zero and we were unable to conclude if this relationship was negative or positive.

Population size structure

Populations of most species included individuals from a wide range of sizes (Table 5). Of the ten species for which we had robust estimates of size distribution (i.e., n > 30), all but *Elliptio arctata* had individuals ≤27 mm length, and for most, minimum size was <30% of maximum size indicating a wide range of sizes and ages in the population. For some species (e.g., *E. fumata/pullata, E. nigella, Q. infucata, T. paulum*), the smallest individuals we found were probably near the minimum size detectable by visual or tactile sampling (≤15 mm).

DISCUSSION

Status of lower Flint River mussels

High estimated occupancy of several species indicates that they are widely distributed throughout the lower Flint River, but low (≤0.30) detection probabilities suggest that about half of the fauna are not collected when they occur at a site. Species detection may vary in response to numerous factors including life-history characteristics, behavior, habitat complexity, environmental conditions, and sampling methodology (MacKenzie et al., 2002), but local abundance may also influence heterogeneity in detection (Bayley & Peterson, 2001; Royle & Nichols, 2003; Royle et al., 2005). Abundance-induced heterogeneity in detection is more influential when local populations are small and this effect decreases with increasing population size (MacKenzie et al., 2006). Hence, abundance-induced heterogeneity likely influenced estimated detection probabilities for *H. subangulata, L. straminea, E. purpurella*, and *U. columbensis*, which had exceptionally low detection. Consequently, the high estimated occupancies for these species are probably unrealistic because the models were unable to distinguish between true absence and nondetection (MacKenzie et al., 2002). We have no evidence to support that detection of these species was low because of behavioral or other ecological attributes, and our survey results indicate that these species are rare throughout the river. Estimated detection of other species exceeded 0.15 and provided relatively precise estimates of occupancy across the lower Flint River.

The Flint River continues to harbor a diverse and relatively abundant freshwater mussel assemblage. Additionally, evidence of recent reproduction (< about 25 mm shell length; Haag & Warren, 2007; Negishi & Kayaba, 2010) was apparent for most species with large sample sizes, and for several, the smallest individuals we found likely were 1-2 years old. These findings show the importance of the Flint River mainstem as a conservation refuge.

Most notably, *E. nigella* was considered a rare species even historically, and it was presumed extinct, with the last collection in 1958 (Brim Box & Williams, 2000; Williams et al., 2008). In our study, *E. nigella* was the third most abundant species (539 individuals) and our models predicted that it occupied nearly 40% of sites. Three individuals ≤25 mm were collected and several individuals were observed brooding embryos or glochidia. *Elliptio nigella* appears to be a large river species and it is most abundant in swift water in crevices among large boulders and cobble (Wisniewski et al., 2013a). The rarity and presumed extinction of this species may be due to the low amount of effort previously expended in the mainstem Flint River and the difficulty of sampling its spe-

TABLE 5

Population size structure of freshwater mussels collected in the lower Flint River, Georgia

Tribe		Length (mm)		
Species	Number Measured	Minimum	Mean	Maximum
Amblemini				
Amblema neislerii	5	48	54	64
Lampsilini				
Hamiota subangulata	3	30	57	58
Lampsilis floridensis	81	27	70	100
Lampsilis straminea	2	53	73	92
Toxolasma paulum	94	11	24	36
Villosa lienosa	55	24	43	55
Villosa vibex	37	14	58	75
Villosa villosa	1	48	48	48
Pleurobemini				
Elliptio arctata	58	45	61	85
Elliptio crassidens	595	17	71	111
Elliptio fumata/pullata	968	9	56	106
Elliptio nigella	130	15	53	106
Elliptio purpurella	2	56	57	58
Elliptoideus sloatianus	98	23	127	204
Quadrulini				
Megalonaias nervosa	13	98	121	140
Quadrula infucata	137	13	37	59
Uniomerus columbensis	3	56	59	61
Anodontini				
Alasmidonta triangulata	4	48	54	64
Utterbackia peggyae	1	30	30	30

cialized habitat. It is also possible that misidentifications may have contributed to its perceived rarity because the species has been synonymized by several previous authors (Frierson, 1927; Johnson, 1968; Brim Box & Williams, 2000) and the genus *Elliptio* provides particular identification challenges (e.g., Shea et al., 2011).

The rediscovery of *A. neislerii* in the Flint River in 2006 is important because it was previously known to survive only in the Apalachicola and Chipola rivers (Brim Box & Williams, 2000). High estimated detection of *A. neislerii* provided precise estimates of occupancy, which indicate that this species is rare and narrowly distributed in the Flint River. However, lengths of *A. neislerii* ranged from 41-70 mm suggesting the presence of several year classes and relatively recent reproduction; a previous age and growth study in the Apalachicola River found that a 42-mm *A. neislerii* was 3 years old (USFWS 2006). Although we were unable to evaluate habitat relationships of *A. neislerii*, we speculate that its rarity in the Flint River, both currently and historically, is a result of insufficient availability of suitable habitat. In the Apalachicola River, *A. neislerii* is found most frequently on gently sloping banks in stable, depositional habitats consisting of sandy silt (Brim Box & Williams, 2000), and the single site in the Flint River where we found the species strongly resembled these conditions. These habitats are exceptionally rare in the lower Flint River because much of the river is bordered by limestone bluffs. Furthermore, only 6 of 21 historical records of *A. neislerii* in the ACF are from the Flint River with 3 of these records specifically collected within our study reach (Brim Box & Williams, 2000); these observations suggest that the species has always been of restricted distribution in the river. Nevertheless, the presence of an additional, apparently viable population of this species lessens its extinction risk.

Other notable species include *Alasmidonta triangulata, E. sloatianus*, and *H. subangulata*. *Alasmidonta triangulata* was widely distributed historically in the ACF but has been found recently only at one site each in the Chattahoochee and Flint river systems (Brim Box & Williams, 2000). Although we collected only four live individuals at two sites and a recently dead individual at a third site, subsequent sampling in 2012 yielded 26 live individuals including several individuals ≤30 mm in length (J.M. Wisniewski, unpublished data). These records significantly increase the known distribution of *A. triangulata*, but our low occupancy estimates and the restriction of these populations to the extreme southern portion of Flint River near the backwaters of Lake Seminole suggest that total population size in the river is low. Although *E. sloatianus* composed only 1% of mussels collected in our study, it occurred at nearly 50% of our sites and its widespread distribution throughout the lower Flint River (see Brim Box & Williams, 2000) suggests that the overall population size is large and the Flint River population may be the largest remaining on Earth. We collected several apparent age classes including 23 mm and 39 mm individuals, which was unanticipated because access to the Flint River for the reported primary host fish, the migratory Gulf Sturgeon, has been blocked by Jim Woodruff Dam since 1957 (Fritts et al., 2012). This suggests that reported secondary hosts, the Blackbanded and Halloween darters, can facilitate recruitment to some extent in the absence of Gulf Sturgeon. *Hamiota subangulata* is rare in the mainstem Flint River and the largest remaining populations of this species are in tributaries (Brim Box & Williams, 2000; Peterson et al., 2011; Shea et al., 2013; Wisniewski et al., 2013b). However, the continued occurrence of this species in the mainstem, as well as other small stream species or stream size generalists, is vitally important because it shows that the river has the potential to serve as a migration corridor between tributary populations.

Factors associated with mussel detection or occupancy

Although many previous attempts to find quantifiable differences in habitat use among mussel species have been unsuccessful (e.g., Brim Box et al., 2002; Strayer & Ralley, 2003; reviewed in Haag, 2012), we found strong differences in habitat use among several species. The most marked and consistent differences among species were in the substrate types with which they were associated. *Elliptio crassidens* showed an affinity for coarse, cobble and boulder substrates, but *L. floridensis* and *T. paulus* were strongly associated with silt and sand, respectively. Similarly, *E. fumata/pullata* was strongly associated with clay, but *V. lienosa* was nearly absent from this substrate type; a similar dichotomy in use of clay was seen in the Flint River for *Q. infucata*, which was found predominantly in clay, and *E. sloatianus*, which avoided clay substrates (Wisniewski et al., 2013a). Parameter estimates for some of these associations (e.g., *E. fumata/pullata, V. lienosa*) were large with no variance, which indicates near perfect separation of species detection or occupancy based on these variables (Webb et al., 2004). These patterns suggest strong ecological differences among species that are expected to have important bearing on community assembly and vulnerability to human impacts.

Other model factors had only limited effects on mussel occupancy or detection. Distance from Albany Dam appeared in the best models for two species, but the magnitude of this effect was low for *E. crassidens* and imprecise for *E. fumata/pullata*. Similarly, searcher experience was an important factor only for *V. vibex*, and the effect of experience was modest. Although occupancy of *E. nigella* was strongly influenced by the presence of swiftwater habitat (Wisniewski et al., 2013a), we found little support for preference of swiftwater habitat among the six species in this study.

Application for freshwater mussel surveys and monitoring

Occupancy modeling was useful in our study because it allowed us to quantitatively estimate the status of mussels across a large study reach and assess habitat relationships with considerably less effort than required for other commonly employed sampling approaches. Our study was conducted during a period of record low flows in the lower Flint River Basin (USGS, 2012), and our detection probabilities may be higher than those estimated during higher flow years because conditions were conducive to sampling mussels. Nevertheless, an important benefit of occupancy modeling is that incorporation of detection probability provides an objective measure of sampling efficiency. Cumulative detection probabilities indicated that our sampling design was adequate to detect most species, with the exception of the rarest species. As in other mussel sampling approaches, consistent detection of very rare species requires an impractically large number of samples. In the context of occupancy modelling, sampling additional sites to increase precision of occupancy estimates would be a more efficient use of effort than increasing replication at a site in an attempt to increase detection.

Despite the routine use of occupancy modeling for other organisms (e.g., Bailey et al., in press), this method is used infrequently for freshwater mussels; rather, freshwater mussel studies often use presence/absence and species richness as response variables to examine factors affecting mussel populations (Spooner & Vaughn, 2009; Gangloff et al., 2011; Vaughn, 2012; Randklev et al., 2013). These approaches must assume that detection is a constant or random process rather than a systematic process related to population size, environmental variables, or search efficiency. However, heterogeneity in detection probabilities of freshwater mussels in response to various factors shows that this assumption is likely violated often (Meador, 2008; Shea et al., 2013; Wisniewski et al., 2013a). Consequently, species presence or richness frequently may be underestimated due to imperfect detection, and a failure to account for this bias can have serious effects on our understanding of mussel ecology (Wisniewski et al., 2013a).

We recommend the use of occupancy modeling for freshwater mussels for the following reasons: 1) it provides a level of confidence in sampling data, which accounts for false-absences that contribute bias into our understanding of factors affecting mussel occupancy; 2) it can be easily incorporated into many currently used freshwater mussel sampling designs with no or minimal modification to these designs; 3) sampling and analysis are practical to implement with limited resources; 4) analyses can be conducted with open-source software with extensive on-line documentation; and 5) similar models are available to estimate various demographic parameters of interest for freshwater mussel conservation (see Haag and Williams in press), including abundance (Royle, 2004; Nichols et al., 2007), species richness (Kéry & Royle, 2008), colonization/extinction (MacKenzie et al., 2003), recruitment and population growth (Pradel, 1996), and emigration (Kendall & Nichols, 1995). These analytical approaches can considerably advance our understanding of the processes affecting freshwater mussel populations, which ultimately will improve our ability to conserve these imperiled species.

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