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This is to certify that the thesis prepared by Chtaura Romayne Jackson entitled
**FACTORS INFLUENCING MACROINVERTEBRATE DIVERSITY AND
COMMUNITY COMPOSITION IN RIVERINE FRESHWATER ROCK POOLS**
has been approved by her committee as satisfactory completion of the thesis
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FACTORS INFLUENCING MACROINVERTEBRATE DIVERSITY AND COMMUNITY
COMPOSITION IN RIVERINE FRESHWATER ROCK POOLS

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
at Virginia Commonwealth University.

by

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Abstract

FACTORS INFLUENCING MACROINVERTEBRATE DIVERSITY AND COMMUNITY COMPOSITION IN RIVERINE FRESHWATER ROCK POOLS

By Chtaura Romayne Jackson, Masters of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
at Virginia Commonwealth University.

Virginia Commonwealth University, 2010

Major Director: Dr. James Vonesh,
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I examined a system of 378-riverine rock pools situated along the James River in Richmond, Virginia, to uncover the factors influencing their macroinvertebrate diversity and community composition. I characterized (total = 60) the physical characteristics, water quality, hydrology, and community assemblages in July 2009 for a subset of pools. I examined whether selected environmental factors (pH, nearest neighbor distance, depth, surface area and inundation height) were related to macroinvertebrate diversity and community composition. Species richness and total abundance of all taxa increased with pool pH and surface area. Ordination indicates that nearest neighbor distance (NND) and pH varied significantly among pools. My findings indicate that macroinvertebrate diversity in this rock pool system were mainly related to

the surface area, pH and NND.

CHAPTER 1 Introduction

Identifying the factors important in shaping patterns of species among habitats is a central goal of community ecology (Death and Winterbourn 1995, Jocque' et al. 2007a). Across many systems, species diversity can be regulated by local biotic factors (such as competition, predation and disease), local abiotic factors (such as pH, disturbance, temperature, light, and soil composition) and regional factors (such as dispersal of individuals between habitats; Menge and Sutherland 1987, Hillebrand and Blenckner 2002, Silberbush et al. 2005). Local factors have been shown to regulate species diversity mainly by setting constraints on colonization success and the replacement of taxa over time (Jocque' et al. 2007b). In contrast, regional factors regulate species diversity by regulating which taxa and in what quantity may arrive in a community (Jocque' et al. 2007b).

Freshwater rock pools provide an excellent system for empirically testing questions related to diversity and community composition. Rock pools form when depressions in rocky substrate along old riverbeds are filled by rain and/or river water (Jocque' et al. 2010). The aquatic communities in freshwater rock pools naturally assemble through terrestrial or riverine colonization as the river level drops. These habitats have many advantages for studying factors driving diversity, because they are often locally numerous, vary in both frequency and degree of factors known to alter diversity such as disturbance, and are easy to manipulate due to their small size (Jocque' et al. 2007, Vanschoenwinkel et al. 2007).

Temporary rock pools can present an obvious challenge to any aquatic organisms that reside in them. Because rock pools are temporary they typically pass through three distinct phases: filling, aquatic and drying. Each phase may contain different fauna and flora groups (Therriault and Kolsa 2001). During these phases rock pools may experience extreme fluctuation in temperature and a wide variations in pH values from 4.0 to 11.0 (Wellborn et al. 1996, Jocque' et al. 2010). Species diversity and community composition in rock pools can be highly dependent on rock pool hydroperiod (Wellborn et al. 1996, Kiflawi et al. 2003). Rock pools that have relatively long hydroperiods tend to have higher species diversity, due to reduced local extinction, increased effects of predation, and longer time for colonists to accrue (Kiflawi et al. 2003, Joque' et al. 2007). Rock pools that have shorter hydroperiods may be less diverse, since only organisms that have rapid growth/development, or desiccation-resistant stages in their life cycles can establish in such pools (Wellborn et al. 1996, Williams 2006).

Habitat size has been shown to influence species composition. Habitats that are larger in area and are nearer to source populations tend to have higher immigration and often offer a wider range of macrohabitats/niches and decreased local extinction, which result in higher species diversity (Simberloff 1976, Kiflawi et al. 2003). In contrast, habitats that have smaller area and are more isolated are known to have lower species diversity, due to a lower rate of immigration and higher rate of local extinction (Simberloff 1976, Kiflawi et al. 2003).

Disturbance has been identified to play an important role in shaping patterns of diversity across a wide range of systems. Disturbance can be defined as any relatively discrete event in time or space that removes and opens up space or resources that can be used by the same or different species (Townsend et al. 1997). For a system to have the greatest diversity, these systems must contain the following three components; first, some form of disturbance must

occur; second, competition must be operating within the community and third, disturbance must result in a resetting of the system (Shea et al. 2004). In addition, variation in the temporal patterns of disturbance has been shown to greatly influence invertebrate community composition (Jocque' et al. 2007).

The purpose of the study was to characterize a system of riverine rock pools along the James River in Richmond, Virginia and describe factors correlated with species richness, diversity, total abundance and community composition. In particular, I examined the relationship between pH, depth, surface area, inundation height, and nearest neighbor distance.

CHAPTER 2 Methods

Study Area

The rock pool system examined in this study is located on the south side of Belle Isle along the James River in Richmond, Virginia (37°31'44.98"N, 77°27'9.14"W). The Virginia Electrical Company dammed the river in 1940 and rerouted the flow from the south of Belle Isle and as a result this altered the hydrology such that pools became exposed more frequent (c.f. Richmond Times Dispatch, www.discoverrichmond.com).

Mapping Rock Pools

Areas of exposed granite on the south side of Belle Island were systematically searched January 23 -31, 2009 and 378-rock pools were discovered and geo-referenced. Pools were geo-referenced using a Leica GX1230 unit that accurately assessed the location of each of the 378-rock pools to within 3cm. The data were projected onto Virginia State Plane NAD 83, vertical NAVD88 (with post-processing accurate to ~ 6mm). A high-resolution photograph of the study area (3 bands, 6 inch pixels) taken from an airplane in 1998 by the City of Richmond (datum: North American 1983, spatial reference: Lambert Conformal Conic) was then used to create a spatially referenced map of the rock pools (ArcGIS 9.3, Richmond, Virginia; Fig 1). I used the map to calculate nearest neighbor distance (NND) for focal pools by hand. In the field, I also collected basic morphometric data on each individual pool (pool length, width, and depth), which I used to calculate approximate surface area (m^2) of each pool.

Estimating the Frequency and Time of Pool Inundation

In this system, a major form of natural disturbance occurs when the river inundates these rock pools. However, due to variation in the topography of this system, pools can vary in the frequency and duration of the disturbance. To determine the height at which the river inundates each rock pool, I conducted regular observations of each of the rock pools in this system from April 4-20, 2009, and associated each incidence of inundation with the concurrent river heights in the main stem of the James River. I detected pool inundation heights using binoculars at 3 points to visually identify which pools were currently underwater. River gage height data was provided through the U.S. Geological Service on the James River near Richmond, Virginia (http://ida.water.usgs.gov/ida/available_records.cfm?sn=02037500). The river height for when each pool became inundated was estimated by fitting a logistic regression, this was done for each pool (i.e. river height when pools were and were not inundated), and using the inflection point of the regression as the estimate the height of inundation. To understand patterns of past disturbance for each pool I used historical river gage data over the last 18-years (Fig. 3) and river level data from spring and summer 2009, which were then used to estimate how long pools formed prior to biodiversity sampling.

Sampling Pool Biodiversity and Habitat Characteristics

Between July 17 and 31, 2009, I quantified the environmental characteristics and macroinvertebrate community in a subset of the rock pools. I focused on pools that fell between 25-90 cm length x 20-30 cm depth (n=105). These were pools that could be effectively sampled using similar macroinvertebrate sampling approaches. From the pools that fell within this range,

I randomly selected 60 pools. For each of these pools I characterized presence and absence of aquatic vegetation and estimated percent terrestrial plant cover using a densitometer. I sampled four water quality parameters temperature (°C) and dissolved oxygen (DO, mg/L) were both measured using a YSI 85 Dissolved Oxygen Meter, hydrogen ion concentrations (pH) was measured using a YSI 60 pH meter, and a relative estimate of chlorophyll a (*in situ*) was measured using a Aquafluor Handheld Fluorometer. I then sampled macroinvertebrate communities in the field by conducting 3 sweeps along the contours of each rock pool using an 8-inch standard mesh aquatic dip net with a mesh size of 1.6 mm and then preserved all samples in 70% ethanol. Macroinvertebrates collected in the field were then identified to the lowest possible taxonomic level and assigned to morpho-taxa in the lab between August – December 2009. All aquatic invertebrates were identified using Peckarsky et al. (1990) and Merritt and Cummins (1995).

Explaining Patterns of Abundance and Diversity

I examined the relationship between the response variables species richness, diversity, total abundance and six most common individual species, with abiotic pool characteristics using multiple regressions. I focused on a subset of environmental characteristics (depth, NND, surface area, pH, dissolved oxygen, and temperature of individual pools), previous literature on rock pool systems suggested their importance (Jocque' et al. 2007a). Species diversity within this rock pool system was calculated using the Shannon-Wiener diversity indices, which looks at not only the number of species in the community, but also the relative abundance of each species.

Multiple regression assumes that the data are independent and normally distributed. I used a scatter plot matrix to uncover which response variables had non-linear relationships with

which predictor variable. I performed Shapiro-Wilks test to assess normality and log transformed variables to improve fit when indicated. I adopted a model-fitting approach to multiple regression based on the principle of parsimony, which is that the best model is the simplest model that explains the data well, in which redundant parameters have been removed. I achieved this by fitting the maximal model and then simplifying it through the following steps; I removed non-informative interaction terms, quadratic terms, and explanatory variables via stepwise forward/backward selection. This study area consisted of 55 rock pools; this allowed me to have between 15-18 parameters without over-paramizing of my model. Based on this information I chose to focus on the following six explanatory variables and their quadratic terms, pH, NND, depth, flood, surface area, and abundance. I thus decided to examine only additive effects, which I assumed to be independent effects. My initial multiple regression models included main effects of all 6 variables and polynomial terms, but with no interactions terms, given that I was not originally interested in interactions. Using the forward/backward stepwise selection approach, I was able to narrow down my initial regression model to the best fitting model based on AIC (Akaike's Information Criterion). This forward/backward stepwise model addresses the issue of multicollinearity, which occurs in a multiple regression model when two or more explanatory variables are highly correlated to one another. The forward/backward stepwise selection approach addresses this issue by adding in or taking out predictor variables to see whether it will add anymore to the model, in turn only leaving in the explanatory variables that add the most to the model.

To describe major axes of variation in habitat quality among pools and macroinvertebrate distribution along these gradients I used Non-metric multidimensional scaling (NMDS) analyses on the 55 rock pools. NMDS is an ordination technique, which uses the rank distances between

sites to explore similarities and dissimilarities in data (Beals 2006). I chose to use this type of ordination for a number of reasons: because NMDS can use data that have many zero values and also since it is based on rank similarities along environmental gradients, rather than quantitative ranks (Oksanen 2009). I used the MetaNMDS application in the “vegan” package in R, which repeats the initial model multiple time, then selects the best model, which is the model that best represents the rank order of distances best in the matrix with minimal stress (Oksanen 2009). All statistical analyses were performed using the statistical program R (version 2.6.1, Murdoch 2010).

CHAPTER 3 Results

System Characteristics

The 378-rock pools ranged from 15.2 to 510.3 cm length to 6.4 to 149 cm depth. Nearest neighbor distance ranged from 0.73 to 14.7 m and averaged (mean \pm SD here and throughout) 2.71 ± 2.71 . Pools ranged in surface area from 0.02 to 1.2 m² and averaged 0.33 ± 0.24 m². Rock pool depth ranged from 10.2 to 99.0 cm and averaged 32.5 ± 17.89 . PH measurements ranged from 7.2 to 9.2 and averaged 8.3 ± 0.61 . Dissolved oxygen concentrations ranged from 0.33 to 2.47 mg/L and 0.81 ± 0.48 mg/L. Temperature varied from 26.2 to 37 °C and averaged 32.0 ± 2.73 °C. Five of the rock pools were excluded from the survey, because these pools had dried up during the course of my field collection time.

Pools were inundated at an estimated river height of 2.3 m (1.6 m - 3.2 m, Fig.1). Based on the data from the USGS instantaneous data site, river levels over the last 18 years seemed to be the highest during the month of March with a gage height averaging greater than 1.8 meters and the lowest during the months of July and August (Fig 3). Based on the data from the spring and summer 2009, rock pools with estimated inundation heights of < 2.44 m were last inundated during the rain event on June 28, 2009. Pools with estimated inundation heights > 3.20 m would have been last inundated on June 8, 2009.

In total, 19 morpho-species were collected from the 55 rock pools (July 17-31, 2009, Table 2). Across all pools, rock pool fauna were numerically dominated by snails, of which 3 taxa were recorded, the most abundant being Physidae. The most abundant invertebrates in this

rock pool system were Physidae snail sp. A, Planorbidae snail sp. A, Diptera *chironomide* sp. A, *Aedes altropalpus*., *Culex* mosquito sp. A, Hydrophilidae beetle sp. A, Coenagrionidae damselfly sp. A, and Libellulidae dragonfly sp. A. The total macroinvertebrate species per pool ranged from 1 to 7 species.

The best fitting model for explaining species richness included depth, pH, log abundance, log area, and log (area + curvature) (Table 3; $F_{5,49} = 11.6$, $P < 0.001$, $R^2 = 0.5$). Increasing depth and pH were negatively associated with taxa richness, while log abundance had a positive effect and log area had a unimodel (hump-shape) relationship.

The best fitting model for explaining species diversity included depth, NND, inundation height, pH and log area (Table 3; $F_{5,49} = 1.9$, p-value: 0.12 , $R^2 = 0.2$). Increasing depth, inundation height and pH were negatively associated with species diversity, while increasing NND and log area both had a positive effect. Results from the Shannon-Wiener diversity index revealed that pools ranged in index value from 0.90 to 1.79. These results indicated that the majority of rock pools had low species richness and evenness.

The best fitting model for explaining total abundance of all taxa included the terms log area, inundation height, pH, and log NND, (Table 3; $F_{6,48} = 5.2$, $P < 0.001$, $R^2 = 0.4$). This model indicated that inundation height, pH, and log NND were negatively associated with taxa abundance, while log area had a positive effect.

Regression analyses run on abundance of the six most common taxa appeared to be explained by the following explanatory variables temperature, pH, NND, and surface area (Table 4). The Physidae model revealed that pH and temperature were the most important abiotic factors in determining Physidae abundance. The *Aedes altropalpus* model revealed that both NND and temperature are appeared to explain *Aedes altropalpus* abundance. The Hydrophilidae

and Planorbidae results both showed that log area was the only abiotic factor that appeared to explain abundance. For *Culex*, pH was the most important factor in this model. For Libellulidae both log area and pH were important abiotic factors in determining dragonfly abundance.

Community variation

The stepwise selection in the NMDS analysis of the community composition isolated nearest neighbor distance ($P = 0.001$) and pH ($P = 0.029$) as underlying environmental factors, varying with community composition in this system (Fig.4). The NMDS1 axis scaled negatively with pH, log area, NND and depth, but positively with flood (Table 5). These results showed that as you increase along the NMDS1 axis pools tended to have lower pH values, smaller surface areas, shallower and be located closer to one another. In addition, these pools also tended to get inundated at higher flood heights. Comparatively, the NMDS2 axis also scaled negatively with NND, but positively with pH, logs area, depth and flood. This shows that as you increase along the NMDS2 axis pools tended to have higher pH values, larger surface areas, be isolated from other pools and tended to be deeper. The stress value for this model was 0.096, which is relatively large meaning that when interrupting this diagram do so carefully. This stress value could have been made better by possibly adding more axes to the model.

CHAPTER 4 Discussion

The purpose of this study was to examine environmental factors influencing macroinvertebrate diversity and community composition in a system of riverine rock pools. The surface area of the pools, as well as the depth and pH were the most important local factors associated with species richness and abundance in this rock pool system. Individual taxa composition in this rock pool system was associated with spatial arrangement, surface area, and temperature. Nearest neighbor distance and pH appeared to explain much of the variation along the environmental gradient in the NMDS analyses. Surprisingly, time since last inundation and height of inundation did not significantly explain any variation in either pool or community characteristics.

Macroinvertebrate communities within this rock pool system were dominated by: snails, flies, beetles, one species of coenagrionid damselfly, and one species of libellulidae dragonfly. Macroinvertebrates varied substantially among pools, only *Physa* were found in nearly every rock pool. Herbivores, which included collectors-gatherers, some scrapers (2), detritivores (1), and filter feeders (2) comprised primarily of snails and fly larvae (Culidae and Chironomidae), were the predominant functional feeding groups in this system.

Hydrologic disturbances in riverine rock pool communities have been identified to play an important role in shaping patterns of diversity, by means of bringing in and removing organisms, opening up space and resources, and resetting water quality parameters (Townsend et al 1997). The intermediate disturbance hypothesis predicts that the highest level of diversity will

occur at the intermediate level of disturbance (Shea et al. 2004). If disturbances occur too often, then species that have slower colonization rates will not be able to survive in the system or if disturbances occur not often enough, then competitive exclusion will occur, which in both cases will result in low biodiversity within the system (Shea et al. 2004). Surprisingly, I found that inundation in the form of river flooding did not appear to be a significant predictor of species richness, diversity or total abundance in this rock pool system. Inundation might not have been a significant predictor because pools were only sampled once and the time in which these pools were sampled had very little disturbance (Fig 3).

Surface area was revealed to be an important predictor of both species richness and abundance even though I only examined a small subset of size variation present in this system. Simberloff (1976) examined the effects of island size on biotic richness, specifically the effects of area on species richness. Larger islands contained more habitat than smaller islands, thus leading to more species. My survey revealed similar results, that in general, rock pools that had larger surface areas were characterized by higher species richness, while rock pools with smaller surface areas were characterized by lower richness. The influences of rock pool surface area on macroinvertebrate assemblages may generally have been a consequence of higher immigration, wider range of habitat niches, and decreased local extinction (Simberloff 1976, Kiflawi et al. 2003).

Spatial patterns such as isolation and connectivity of aquatic habitat patches can be important in determining the composition of local communities (MacArthur and Wilson 1967, Vanschoenwinkel et al. 2007). Rock pool communities that are located closer to one another may be similar, because they might be linked by active dispersal (Spencer et al. 2002). I found that certain species like snails, tadpoles, leeches, and one species of coenagrionid damselfly were

associated with pools that were closer to other pools, which could be linked to the ability of these species to actively disperse from one to another. Certain species such as flies and *Aedes* mosquitoes were mainly associated with pools that were more isolated from one another, which could be due to the absence of predators in these pools.

Species diversity and the total abundance of individual taxa appeared to be structured primarily by local environmental variables, such as surface area, temperature, and pH, as well as regional factors, such as connectivity and isolation, with variation among the different taxa. Surface area and spatial arrangement may be a common cause for variation in pH, because pools with larger surface area and that are located closer to one another may contain higher numbers of aquatic organisms, which will tend lower pH values (Bell 1971). There was a significant effect of both local and regional (spatial) factors on community composition. A similar conclusion was drawn by Kiflawi (2003) who stated that local and regional processes were both important in macro-invertebrate composition in temporary pools, but acknowledges that it may be difficult to generalize which process had a greater influence on structuring aquatic communities.

Variation in local abiotic factors such as pH, dissolved oxygen, and temperature in aquatic habitats can restrict biodiversity. Variation in pH affects food quality, primary production, grazing, leaf litter decomposition, and imposes physiological constraints on aquatic life (Petrin et al. 2007). However, biotic processes can also affect pH. Likewise, the availability of oxygen in aquatic systems can affect the overall distribution of aquatic species (Connolly, Crossland and Pearson 2004), while changes in dissolved oxygen concentration can vary within a system due to respiration of aquatic organisms, photosynthesis by plants, atmospheric losses and gain, and the presence of anthropogenic substances in the system (Connolly et al. 2004).

Temperature is also a very important environmental variable, having direct and indirect effects

on species distribution as well as dissolved oxygen concentrations (Boulton 2010). In my study, increasing pH had a negative affect on both species richness and species diversity. PH could have been influenced by a number of factors like pool permanence, which is the amount of time these pools hold water, which could lead to increased amounts of aquatic macrophytes in these pools. The presence of macrophytes has been shown to have important effects on pH in aquatic systems, because high rates of photosynthesis can deplete dissolved inorganic carbon, which in turn can increase pH values (Turner and Chrislock 2010).

Studies have shown that interspecific interactions, such as competition and predation are important biotic processes that can influence community structure in aquatic systems (Ransom and Jaeger 2006). Competition in these systems can limit taxa richness, by reducing the availability of resources and refuge area, however, competition can also increase species richness by bring in more immigrants and allowing more species to find empty niches and resources (Hixon and Jones 2005, Cadotte et al. 2006). Predation has been considered to be an important biotic factor structuring aquatic communities (Romero and Srivastava 2010, Jocque' et al. 2010). Studies have shown that abundance of predatory species can be very low or even completely absent in temporary aquatic systems and that development constraints were probably the key factor that restricted some of the larger predatory species from living in this temporary rock pool system (Wellborn et al. 1996). The low count of predators in this system may have allowed for higher species richness. Previous reports illustrate that predation by both amphibians and various invertebrates can potentially affect prey dynamics, in turn regulating rock pool communities. Predation can have a positive effect on species richness, by reducing competitive exclusion, freeing resources, opening up a wide range of microhabitats' (Cadotte et al. 2006). In addition, colonists that exhibit habitat selection, example avoidance of predators can also reduce

immigration into those pools (Resetarits and Binckley 2009). My study illustrates that predators such as coenagrionid damselfly, fish, libellulidae dragonfly and Corixidae, as well as prey species such as Chironomides and *Aedes atropalpus* all tend to prefer pools that have high pH and are isolated from other pools, while species such as Physidae, Planorbidae and Glossiphoniidae tended to prefer pools that had higher pH and also pools that were located closer to one another (Fig 4).

In conclusion, macroinvertebrate abundance and diversity in this rock pool system in July seemed to be mainly influenced by surface area, pH, depth and NND. This study was conducted during the summer months (Fig 3). If conducted at a different time of the year, other factors might have played a larger role in affecting diversity and community composition. This study will not only help to contribute to the scientific community, but the attainment of a better understanding of how biodiversity is shaped within these aquatic communities. In addition, this study will also help the James River Park System to more efficiently manage these natural resources and also help increase public awareness of these unique microcosms.

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Table 1: Physical and chemical characteristics of the 55 rock pools at Belle Isle, James River, Virginia. Averages (Avg), standard deviations (SD), maximum and minimum values (max. and min.) nearest neighbor distance (NND) are presented.

	Avg	SD	Max	Min
Depth (cm)	32.50	17.89	99.06	10.16
NND (m)	2.71	2.71	14.73	0.73
Surface Area (m ²)	0.33	0.24	1.24	0.02
pH	8.30	0.61	9.15	7.18
Dissolved Oxygen (mg/L)	0.81	0.48	2.47	0.33
Temperature (°C)	32.03	2.73	37	26.2

Table 2: Collected taxa in the 55 rock pools at Belle Isle.

Type	Abbreviations	Family	Genus/species	Number of Individuals
Invertebrates:				
Isopods	BRANC	Branchipodidae	<i>Branchipus</i> sp. A	26
Snails	PHY	Physidae	<i>Physa</i> sp. A	1120
	PLAN	Planorbidae		139
	PLEU	Pleuroceridae		23
Leeches	GLOSS	Glossiphoniidae	<i>Glossiphonia complanata</i>	98
Insects:				
Mosquitoes	AEDES	Culicidae	<i>Aedes atropalpus</i>	332
		Culicidae	<i>Anopheles</i> sp. A	1
	CULEX	Culicidae	<i>Culex</i> sp. A	345
Midges	CHIRONO	Chironomidae		204
Mayflies	EPHE	Ephemeraidae		1
Beetles	DYTISC	Dytiscidae		95
	HYDRO.B	Hydrophilidae		182
		Staphylinidae		1
Water boatmen	CORI	Corixidae		34
Caddisflies		Hydropsychidae		1
Damselflies	ZYGO.C	Coenagrionidae		152
Dragonflies	ANIS.LI	Libellulidae		180
		Corduliidae		73
Vertebrates:				
Fish	FISH	Catostomidae	<i>Carpiodes cyprinus</i>	4
Frogs	TADP			46

Table 3: Stepwise multiple regression results for relationship between species richness, abundance and diversity, with rock pool characteristics. Standard Error (SE), t-value (t), and Pr(>|t|) (P) area presented.

Predictor	Coefficient	SE	t	P
Richness				
Depth	-0.007	0.002	-2.42	0.02
Log area	5.24	2.15	2.44	0.02
pH	-0.12	0.08	-1.59	0.12
Log abun	0.23	0.04	5.62	<0.001
Log area^2	-10.92	6.66	-1.64	0.11
Abundance				
Log area	3.29	2.23	1.47	0.15
Inundation height	-0.69	0.29	-2.38	0.02
pH	-0.76	0.25	-3.07	0.003
Log NND	-2.86	1.06	-2.68	0.01
Log NND^2	-4.86	1.27	3.82	<0.001
Depth^2	<0.001	<0.001	-1.91	0.06
Diversity				
Depth	-0.007	0.003	-2.26	0.03
NND	0.01	0.02	0.62	0.54
Inundation height	-0.0007	0.11	-0.007	0.99
pH	-0.03	0.09	-0.37	0.71
Log Area	0.22	0.08	2.73	0.01

Table 4: Standard multiple regression models based on AIC of the six most common invertebrate taxa on abiotic factors. Only significant taxa and abiotic factors were included.

Taxa	Abiotic	Pr(> t)	R squared	Coefficient	SE
<i>Physa</i>	-pH	0.01	0.14	-16.47	6.09
	+Temperature	0.06		2.63	1.38
<i>Aedes</i>	+NND	<0.001	0.51	5.79	0.79
	-Temperature	0.13		-1.06	0.69
Hydrophilidae	+Log area	0.07	0.06	3.62	1.92
Planorbidae	+Log area	0.11	0.04	1.69	1.03
<i>Culex</i>	-pH	0.17	0.03	-11.90	8.44
Libellulidae	+Log area	0.05	0.17	2.25	1.13
	+pH	0.04		2.99	1.39

Table 5: Summary of the NMDS results based on the coefficient loadings of each environmental predictor variable for both axis NMDS1 and axis NMDS2. R squared value R^2 , P-value ($Pr(>r)$)

	NMDS1	NMDS2	R^2	$Pr(>r)$
Flood	0.47	-0.87	0.05	0.25
pH	-0.43	0.89	0.11	0.05
Log area	-0.68	0.72	0.05	0.28
NND	-0.56	-0.82	0.13	0.09
Depth	-0.63	0.77	0.04	0.33

Rock Pools South of Belle Isle

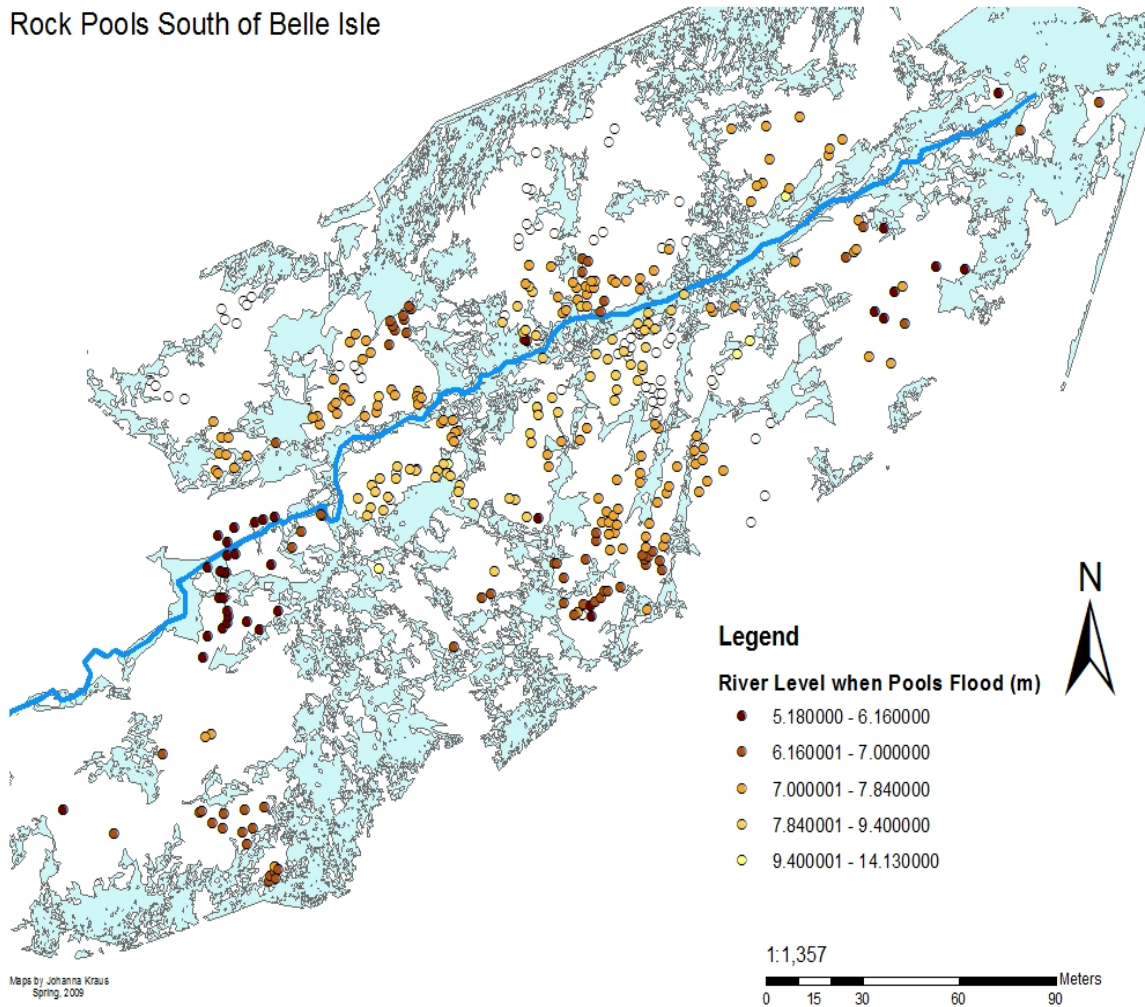


Figure 1: A spatially reference map of the rock pools in the study area (ArcGIS 9.3, Richmond, Virginia). Estimated river gage heights for each of the 378-rock pools are represented by dots that are color coordinated which indicates at what river height that pool became inundated. Red dots represent pools that become inundated at very low flood levels and yellow dots represent pools that get inundated at very high flood levels. The blue line running through the center of the map is the main water channel. The white areas are the exposed river bedrock.

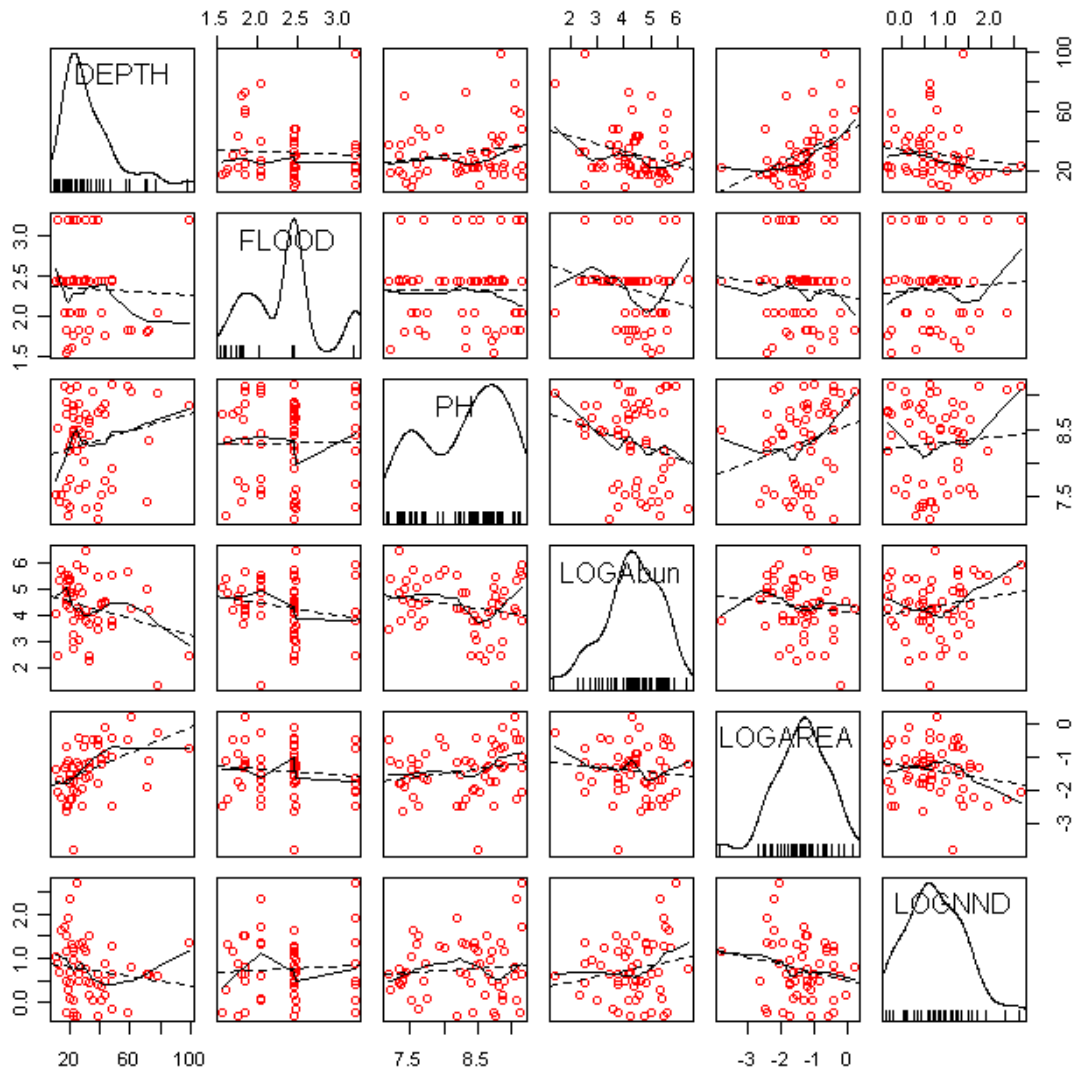


Figure 2: Scatter plot matrix of the predictor variables (depth, flood, pH, log abundance, log area, and log nearest neighbor distance). Each column contains an X-axis and each row contains a Y-axis. The dotted line represents the best fit line for each chart in order to better study the correlation between the two variables.

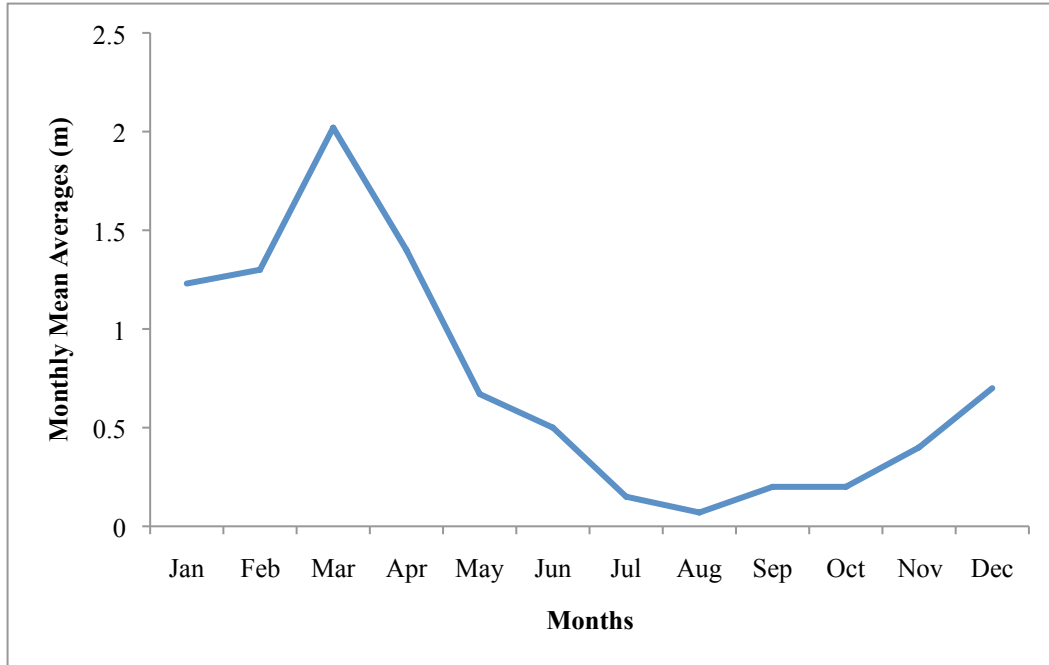


Figure 3: River level data from 1990 to 2007 summarized from the National Weather Service-Advance Hydrological Prediction Service Instantaneous Data Base. This graph represents the average flood heights (m) for each month over an 18-year period.

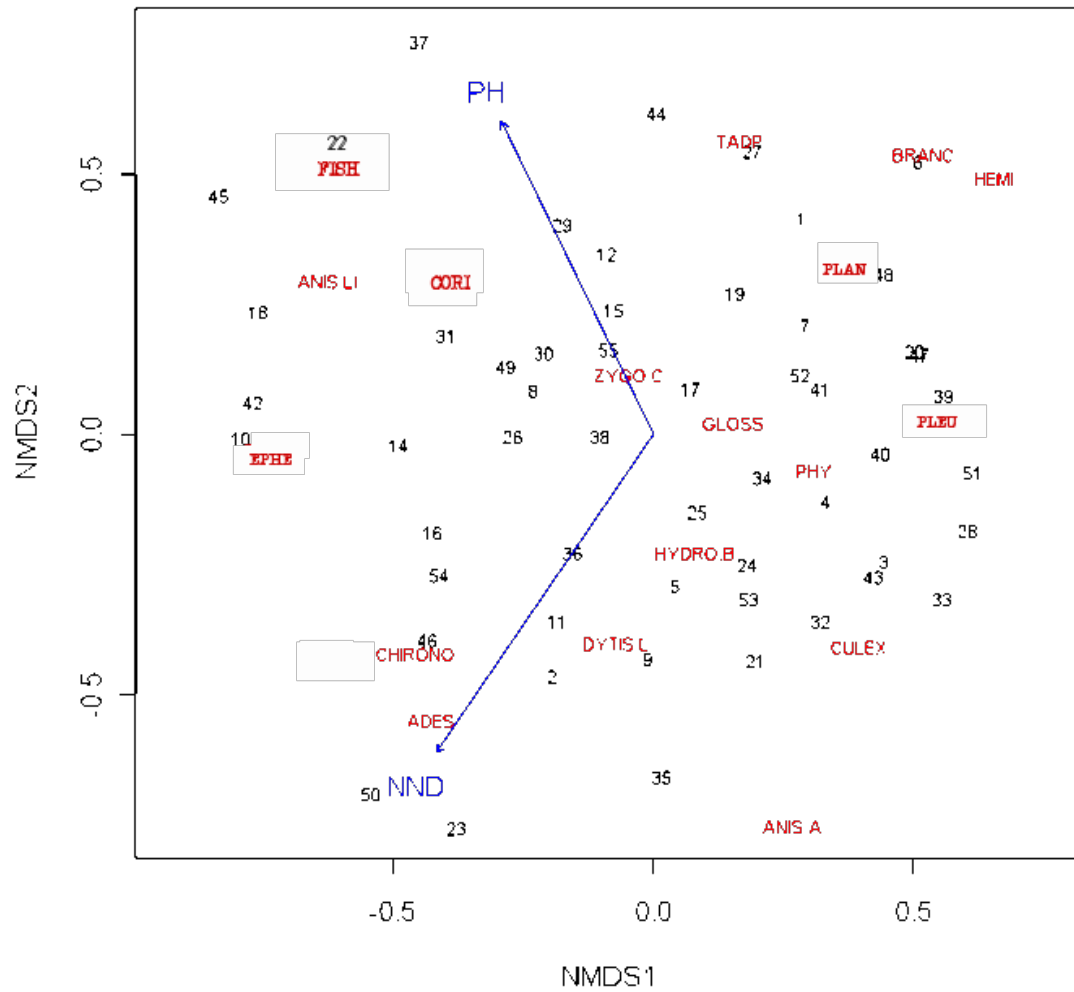


Figure 4: Ordination graph for a two-dimensional Non-metric multidimensional scaling of environmental predictor variables with weighted species abundance overlaid on top. Each number identifies a single rock pool. The names represent the weighted abundance of that species (species names provided in Table 2). Ph and NND are the predictor variables that were selected to explain much of the variation in this model. The direction in which the arrows are pointing means that the predictor variable is increasing in that direction. The coefficient loadings for both axis NMDS1 and axis NMDS2 are located in (Table 5).

VITA

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