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Spatial and Temporal Variation in the Aquatic Invertebrate Community Structure of Rock Pools Along the Penobscot River, Maine

Chase R. Gagne
University of Maine, chase.gagne@maine.edu

SPATIAL AND TEMPORAL VARIATION IN THE AQUATIC INVERTEBRATE COMMUNITY STRUCTURE OF ROCK POOLS ALONG THE PENOBSCOT RIVER, MAINE

By

Chase R. Gagne

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Advisory Committee:

Hamish S. Greig, Associate Professor of Stream Ecology, Advisor

Allison Gardner, Assistant Professor of Arthropod Vector Biology

Francis A. Drummond, Professor Emeritus of Insect Ecology and Insect Pest Management

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Thesis Advisor: Dr. Hamish S. Greig

An Abstract of the Thesis Presented
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Pools of water that form in the fissures and depressions of rock outcrops, known as rock pools, are fairly common aquatic habitats that can easily be found along the rocky banks of many of Maine's major rivers. In general, rock pools and the aquatic invertebrates inhabiting them have received little research attention and, though ubiquitous, have never been studied in Maine. My research addressed this knowledge gap by surveying 40 rock pools at four sites along the Penobscot River in Maine. The rock pools themselves had highly variable environmental characteristics and differed across sites and over time, especially in hydroperiod. They contained surprisingly abundant and diverse communities, totaling 71 invertebrate taxa across 16 orders. The non-biting midge *Dicrotendipes* and the biting midge *Dasyhelea* were the most abundant genera. Community composition differed significantly between sites in June, largely associated with differences in pool size, hydroperiod, influence of the adjacent river, and food resources. However, over the course of the summer, communities across sites became more similar to each other, likely due to the combination of phenologically-driven life histories for some taxa and the loss of stress-intolerant taxa.

I also conducted an experiment in which I artificially extended rock pool hydroperiods to determine the independent effect of hydroperiod on invertebrate community structure. I hypothesized that pools with longer hydroperiods would contain more diverse and abundant invertebrate communities and that pools with longer hydroperiods would contain more long-lived taxa, such as Odonata and Coleoptera. To test this hypothesis, I prevented ten rock pools from desiccating by adding deionized water to them and left ten rock pools to naturally dry. Hydroperiod was not a significant driver of overall invertebrate abundance or richness and was only important in determining the individual abundance of one of five taxa collected in the experiment. Pool volume, location on the rock outcrop, and water chemistry (pH and conductivity) were the significant factors determining community structure. This suggests that the effect of hydroperiod observed in my survey and in other rock pool surveys may be confounded by pool size and by environmental variables mediated by hydroperiod.

DEDICATION

       I dedicate this thesis to my parents. Thank you for supporting me and bearing with me all the times I called you to vent, talk about a cool bug I found, and vent about how the cool bug got away. You've always inspired me to be better in everything I do and thank you for supporting my decision to go for my Master's.

ACKNOWLEDGEMENTS

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CHAPTER ONE:

HYDROLOGY AND AQUATIC INVERTEBRATE COMMUNITIES OF RIVERINE

ROCK POOLS ALONG THE PENOBSCOT RIVER, MAINE

1.1 Introduction

Depressions or cracks in rocky outcrops that fill with water, known as rock pools, are a common sight in areas with large amounts of exposed rock. They are widely distributed both geographically and ecologically, having been studied in semi-arid areas of Botswana (Brendonck et al. 2002), on mountains in Zimbabwe (Anusa et al. 2012), in ocean-influenced coastal areas in Jamaica (Therriault and Kolasa 2001) and Finland (Häggqvist and Lindholm 2015), Australia (Timms 2014, 2018; Brendonck et al. 2015; Calabrese et al. 2016), in Nova Scotia (Romanuk et al. 2010), and in Michigan (Smith 1983; Egan and Ferrington 2015) and Utah (Baron et al. 1998; Jocqué et al. 2007a) in the United States. In Maine, they are commonly observed along rivers that have mainly rocky banks with bedrock outcrops. These rock pools are often filled with freshwater from rain or snowmelt but can also be periodically filled through flooding events from adjacent rivers. Rock pools typically have a surface area less than one square meter, usually occur in exposed locations, and have highly variable durations of inundation (Jocque et al. 2010). They are often colonized by aquatic invertebrates, typically by specialized taxa that possess unique traits to enable them to persist in these time-constrained environments (Williams 1996). Rock pool communities and the potentially unique invertebrates comprising them are understudied globally (Jocque et al. 2010) and have never been studied in Maine. A total of 480 species are currently known globally to occur in rock pools (Jocque et al. 2010). Over 200 of these species are from Australia (Pinder et al. 2000), which is among the most well-documented regions in terms of research on rock pool communities. However, these numbers do not include

taxa found in pools that are within reach of, and may have been influenced by, an adjacent river or lake. In fact, rock pools that are influenced by flooding rivers are often not included in studies or in reviews of the rock pool literature (Jocque et al. 2010; Brendonck et al. 2016) and their ecology and fauna are poorly understood.

As small container ecosystems, the environmental characteristics of rock pools can vary widely even within close proximity, and these habitat properties affect the aquatic invertebrate communities inhabiting the pools (Romanuk & Kolasa 2002; Calabrese et al. 2016). Pools that are less variable in pH, temperature, dissolved oxygen, and salinity are richer in taxa diversity (Romanuk & Kolasa 2002). The size of the pool can also affect invertebrate communities. Deeper pools and pools with greater surface areas typically contain more diverse communities (Oertli et al. 2002; Ripley and Simovich 2009), and some species, such as *Daphnia longispina* and *D. magna*, prefer to occupy the largest pools present in an area (Pajunen and Pajunen 2007). Resource availability, such as through inputs of detritus from nearby vegetation, can also influence invertebrate communities. For example, detritus inputs determine the establishment success of native ceratopogonid midges (Romanuk and Kolasa 2005) and increase establishment success rates of invasive ostracods (Beisner et al. 2006). However, studies examining the effects of resource availability on rock pool invertebrate diversity are lacking (Brendonck et al. 2016) and we do not yet know how resources interact with other physiochemical drivers of invertebrate communities.

The amount of time that rock pools can hold water, known as the hydroperiod, can vary widely depending on pool morphology and catchment, ranging from less than one week to greater than ten weeks (Jocque et al. 2010; Brendonck et al. 2016). Hydroperiod often plays a major role in shaping aquatic invertebrate communities in rock pools and other small lentic

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habitats. For example, pools that dry out more often over a season or are inundated for a shorter duration of time once filled, typically have lower species richness and abundance (Therriault and Kolasa 2001; Romanuk and Kolasa 2002; Altermatt et al. 2009; Vanschoenwinkel et al. 2009, 2010; Romanuk et al. 2010; Brendonck et al. 2015; Egan and Ferrington 2015; Ptatscheck and Traunspurger 2015; Calabrese et al. 2016). Conversely, colonization during longer hydroperiods allows for succession of pool communities and subsequent species-sorting dynamics that filter potential colonists based on their life history traits and the environmental properties of the pools (Jocqué et al. 2007b; Vanschoenwinkel et al. 2010). The effects of pool volume are often entangled with hydroperiod since larger pools tend to dry more slowly than smaller pools and are able to support more diverse invertebrate communities (Calabrese et al. 2016). Similarly, rock pools that are deeper often have longer hydroperiods and higher invertebrate diversity (Vanschoenwinkel et al. 2009). Clearly, hydrology appears to be an overarching environmental driver of invertebrate communities in rock pool systems.

The hydrology and invertebrate communities of rock pools may be influenced based on their proximity to a larger body of water, such as a river, lake, or ocean, but there has been little research on this aspect. Pools farther away from a large body of water become more variable in terms of both water chemistry and hydrology (Jocqué et al. 2007a; Egan et al. 2014). Subsequently, species compositions of invertebrate communities change as the distance of rock pools from larger bodies of water increases (Egan and Ferrington 2015). Pools that are close to larger bodies of water have less of a chance of drying out because of splash, flooding, or drainage, and therefore are able to support a more diverse invertebrate community (Therriault and Kolasa 2001; Jocqué et al. 2007a; Egan and Ferrington 2015). However, rock pools near rivers may be more species poor than rock pools near lakes or intertidal zones because the fast-

flowing water of the river scours out the sediment at the bottom of the pool, which is often important for the establishment of invertebrate egg banks (Brendonck et al. 2016). Conversely, pools farther away from the edge of a river may possess more sediment and detritus because of a lack of frequent scouring and because of being closer to riparian zones, assisting in the establishment of invertebrate egg banks. This however is an area that has received little study and is in need of further research.

Finally, invertebrate communities of rock pools may also be influenced by seasonal changes in water chemistry, resource availability, and temporal variation in life histories of different species inhabiting the same pool. For example, inputs of detritus can vary between seasons, especially in temperate climates (Bennion and Smith 2000; Higgins 2000). Ponds that contain high levels of detritus typically have a lower pH than those that contain less detritus, which influences taxa that are able to persist in the pond (Bennion and Smith 2000; Higgins 2000; Batzer et al. 2004). Community structure can also change between seasons in rock pools due to temporal differences in invertebrate life histories. For example, certain taxa may be present in the pool early in the season but emerge from the pool later in the season to be replaced by late-colonizing or late-hatching taxa (Brendonck et al. 2015). However, the effect of seasonality on resource availability, hydrology, and their interactions with invertebrate communities in rock pools still remain understudied.

I addressed these research gaps by surveying habitat characteristics and invertebrate communities in 40 rock pools across four sites to meet the following objectives: (1) determine how rock pool hydrology varies across space and time, (2) determine how aquatic invertebrate communities vary spatially and temporally and which abiotic and biotic factors may be important

drivers of variation, and (3) determine whether a nearby river system has an effect on pool hydrology and invertebrate community composition.

1.2 Methods

1.2.1 Study Area

Four exposed rock outcrops were selected as sites along the Penobscot River between Old Town and Eddington, Penobscot County, Maine. Sites were designated a number based on location along the river, with Site 1 being the furthest upstream and Site 4 being the furthest downstream. Site 1 was the least likely to be flooded by the river during the summer (based on vertical distance from the river in June), whereas Sites 3, 4, and parts of Site 2 were prone to regular flooding events. All sampled areas except for an elevated bench of Site 2 were flooded by the river during peak spring runoff in April. Site 3 was the only site that was located directly underneath riparian trees, whereas the other three sites were well-removed (>15m) from the riparian zone (Fig. 1.1).

(a)   (b)   (c)
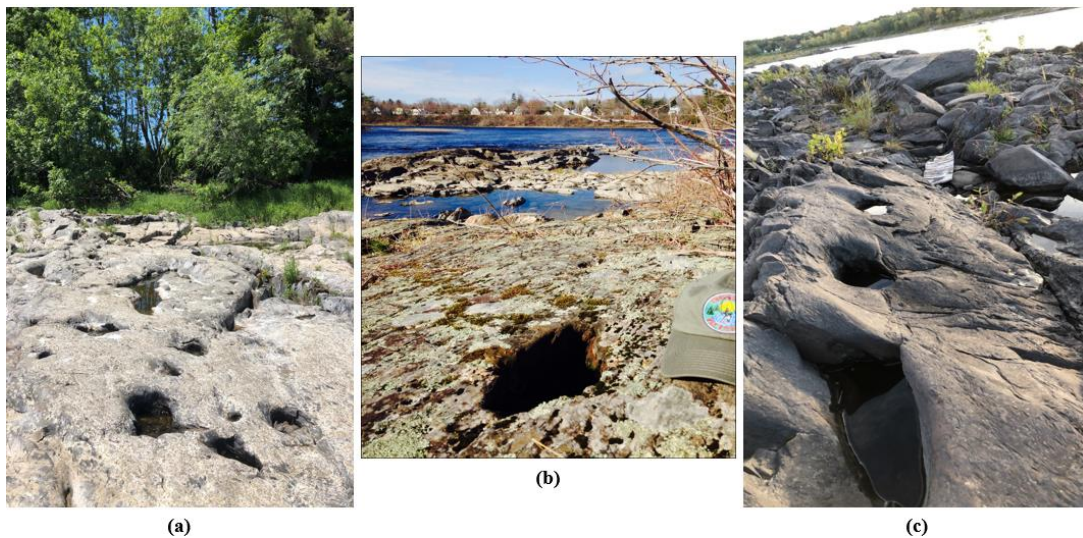
Figure 1.1 Examples of rock outcrops and pools sampled. Site 3 (a), Site 2 from the pool closest to the riparian zone (b), and Site 4 (c) along the Penobscot River near Milford, Maine.

Ten rock pools between 10cm and 1 m in diameter were sampled at each site between June 20 and September 26, 2018. Pools were chosen in a stratified manner at each site to account for different microhabitats in different areas of the outcrops. For example, if a portion of the rock outcrop was shaded by riparian trees then pools were selected from both the shaded portion and sunlit portion. Pool elevation with respect to the adjacent river varied within sites, such that during an increase in river height one or several pools were likely to be flooded with river water. Pool volumes ranged from 0.72 liters to 28.05 liters, with a median of 4.07 liters.

1.2.2 Field Methods

The aquatic invertebrate communities were sampled in each pool in late June, early August, and mid-September. Invertebrates were collected with a fine-mesh (250µm) aquarium net by sweeping through the pool for three minutes after the substrate had been disturbed. Samples were immediately transferred to 70% ethyl alcohol and stored for later sorting and identification. Both coarse and fine particle organic matter (CPOM and FPOM, respectively) were collected simultaneously with the aquatic invertebrate samples using a 250µm aquarium net. CPOM was defined as any detritus greater than one millimeter and FPOM was defined as any detritus between 250 micrometers and one millimeter.

Pool volume was estimated using the mean depth, based on three randomly taken depth measurements, and surface area. Given the uneven shape of most pool basins, pool volumes were most likely overestimated. Surface area was calculated by measuring pools in scaled photos with Adobe Acrobat Pro. Water chemistry parameters (conductivity and pH) and pool depth were measured every five days. Conductivity and pH were measured using a Hach HQ40d multi-probe. Water samples were collected for chloride and chlorophyll-a analyses in June, August, and September.

1.2.3 Laboratory Methods

All invertebrates, with the exception of mosquitos, zooplankton, bivalves, and gastropods, were identified to genus using Peckarsky et al. (1990) and Merritt et al. (2008). Zooplankton, bivalves, and gastropods were identified only to family. Mosquitos were identified to species using Andreadis et al. (2005). Chironomids were subsampled by first randomly selecting twelve individuals from each sample to mount, then visually scanning the remaining sample and picking out unique individuals that were missed. Chironomid larvae were slide-mounted in CMC-10 following methods outlined by Epler (2001).

CPOM and FPOM detritus fractions were dried for one week at 50 degrees Celsius and then ashed for two hours at 500 degrees Celsius to determine ash-free dry mass (AFDM). Chloride analyses were conducted using Method 4500Cl from Standard Methods for the Examination of Water and Wastewater by Eastern Analytical, Inc. in Concord, New Hampshire. Raw fluorescence of chlorophyll-a pigments was measured with 24 hours of sample collection using a Trilogy Laboratory Fluorometer (Turner Designs, Inc.) equipped with an in-vivo chlorophyll-a module.

1.2.4 Statistical Methods

Data were analyzed using R version 3.5.1. Univariate analyses consisted of two-way ANOVAs to compare the relations between physical and biological response variables with site (1-4), month (June, August, September), as well as their interactions included as fixed categorical predictors. The responses of taxa richness and abundance to environmental variables were analyzed using linear models with average depth, hydroperiod, pool volume, chloride concentration, conductivity, pH, algal biomass, CPOM, and FPOM included as fixed, continuous

variables. Prior to analysis, invertebrate abundances were adjusted to individuals per liter and environmental variables were standardized and scaled using the R-package "dplyr". Lotic taxa were defined as those that are associated with flowing water based on descriptions by Merritt et al. (2008).

Redundancy analysis (RDA) was used to assess the role of environmental variables, site, and season in determining the abundance and distribution of taxa across sites. This ordination was created on the species abundance matrix of all taxa found within all 40 pools. Species abundance data were Log_e +1-transformed prior to performing the ordination to meet the assumptions of normality. The matrix of environmental variables included pH, conductivity, CPOM, FPOM, average depth, raw algal fluorescence, chloride, pool volume, hydroperiod, site, and month. All continuous predictors were scaled prior to analysis. A permutation ANOVA test (500 permutations) on the RDA was used to determine which variables were most important in characterizing the invertebrate communities of rock pools. RDA analysis, plots, and the permutation ANOVA were performed using the R-package "vegan".

1.3 Results

1.3.1 Pool Environmental Conditions

Hydroperiod varied significantly between sites, months, and within sites between months (Fig. 1.2, Table 1.1). Collectively throughout the sample period, pools in Site 4 spent an average of 16 days without containing water out of a total 92 days (17.4%). Conversely, pools in Site 3 averaged 0.2 days without containing water out of a total 96 days (0.002%).
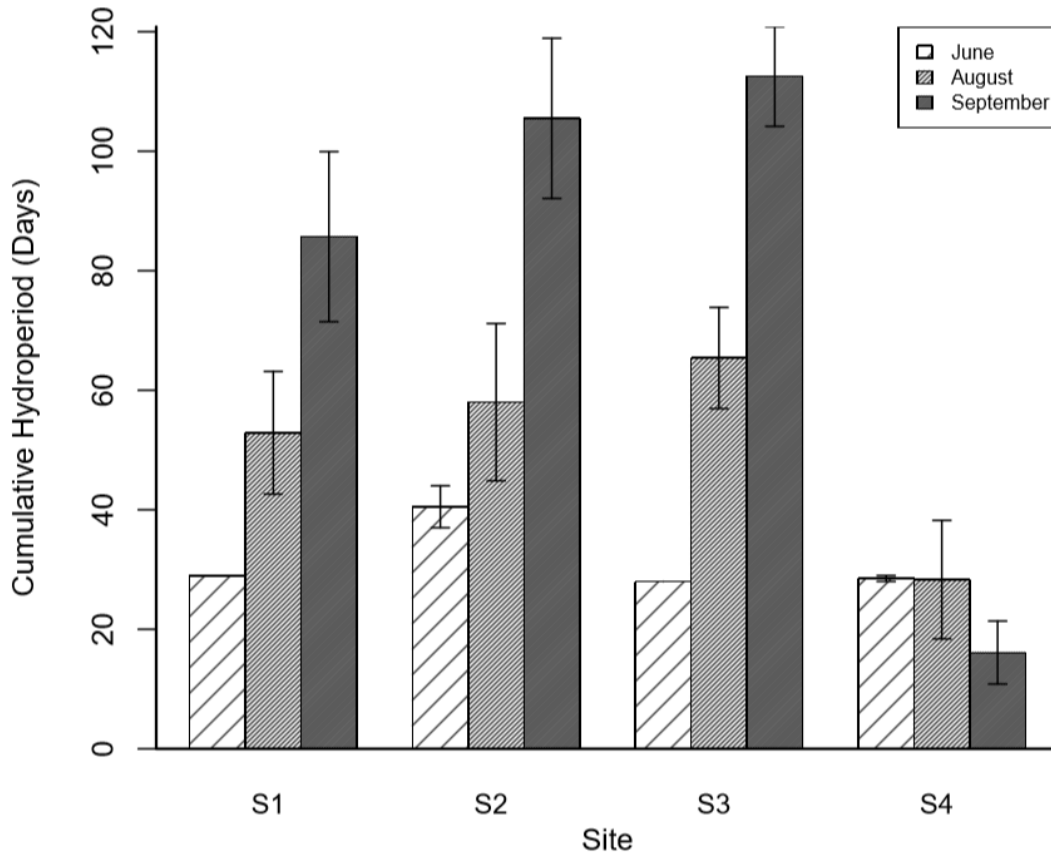
Figure 1.2 Cumulative hydroperiods measured in riverine rock pools at four sites along the Penobscot River, Maine. Hydroperiod measurements for each pool began the first full day that the pool was exposed above the river after May 1. Error bars are +1 SE of the mean.

Table 1.1 Linear regression results of biotic and abiotic variables. Data collected from 40 riverine rock pools at four sites along the Penobscot River, Maine. Significant predictor variables (P<0.05) are shown in bold.

Response	Factor	Df	F value	P value
Richness	Site	1	<0.01	0.931
	Month	**2**	**10.02**	**<0.001**
	Site × Month	2	0.63	0.534
	Average Depth	**1**	**4.11**	**0.045**
	Hydroperiod	1	1.13	0.291
	Pool Volume	**1**	**10.26**	**0.002**
	Chloride	1	<0.01	0.956
	Conductivity	1	0.36	0.551
	CPOM	1	0.01	0.920
	FPOM	1	0.17	0.684
	pH	1	0.02	0.880
	Algal Biomass	1	<0.01	0.993
Abundance	Site	1	0.01	0.941
	Month	**2**	**5.32**	**0.006**
	Site × Month	2	1.51	0.226
	Average Depth	**1**	**11.13**	**0.001**
	Hydroperiod	1	3.36	0.069
	Pool Volume	**1**	**28.19**	**<0.001**
	Chloride	**1**	**5.06**	**0.026**
	Conductivity	**1**	**6.60**	**0.012**
	CPOM	**1**	**9.70**	**0.002**
	FPOM	**1**	**24.98**	**<0.001**
	pH	1	1.30	0.257
	Algal Biomass	1	2.91	0.091
Lotic Taxa Abundance	Site	1	2.82	0.096
	Month	**2**	**3.82**	**0.025**
	Site × Month	2	2.67	0.074
	Chloride	1	0.40	0.527
	Conductivity	1	1.10	0.297
	CPOM	1	0.08	0.775
	FPOM	1	0.12	0.729
	pH	1	**8.04**	0.005
	Algal Biomass	1	0.06	0.809
	Pool Depth	1	0.15	0.699
	Pool Volume	1	0.37	0.546
	Hydroperiod	1	0.88	0.351
RDA permANOVA	**Site**	**1**	**1.63**	**0.164**
	Month	**2**	**6.50**	**0.001**

Table 1.1 Continued

Response	Factor	Df	F value	P value
RDA permANOVA	**Site × Month**	**2**	**2.36**	**0.017**
(Cont.)	Chloride	1	0.75	0.531
	Conductivity	1	0.95	0.416
	CPOM	**1**	**6.10**	**0.002**
	FPOM	**1**	**4.66**	**0.003**
	pH	**1**	**5.42**	**0.001**
	Algal Biomass	1	0.35	0.891
	Pool Depth	**1**	**13.18**	**0.001**
	Pool Volume	**1**	**5.98**	**0.001**
	Hydroperiod	**1**	**5.80**	**0.002**
Conductivity	Site	1	1.40	0.239
	Month	2	0.70	0.501
	Site × Month	**2**	**5.05**	**0.008**
Chloride	Site	1	0.55	0.461
	Month	**2**	**8.45**	**<0.001**
	Site × Month	2	<0.01	0.997
CPOM	Site	1	2.93	0.090
	Month	2	0.07	0.935
	Site × Month	2	0.04	0.965
FPOM	Site	1	2.28	0.134
	Month	2	1.54	0.219
	Site × Month	2	0.14	0.872
Algal Biomass	**Site**	**1**	**11.68**	**<0.001**
	Month	**2**	**8.60**	**<0.001**
	Site × Month	**2**	**13.31**	**<0.001**
Hydroperiod	**Site**	**1**	**11.72**	**<0.001**
	Month	**2**	**20.98**	**<0.001**
	Site × Month	**2**	**4.14**	**0.018**
pH	Site	1	2.28	0.134
	Month	**2**	**5.20**	**0.007**
	Site × Month	2	0.73	0.484

The ashed mass of CPOM did not vary between months or within sites between months (Table 1.1). There was some support for a difference in CPOM between sites (site effect: p=0.09), however there was a large amount of variation within sites (Fig. 1.3a). Algal biomass measured as water column chlorophyll -a varied significantly across sites, month, and between months within sites (Fig. 1.3c, Table 1.1). Pools in Site 1 experienced algal blooms during August and contained substantially greater algal biomass than pools at other sites during the same sampling period (Fig. 1.3c). A small bloom of filamentous algae occurred in pools at Site 2 in August, however not to the level observed in pools at Site 1.
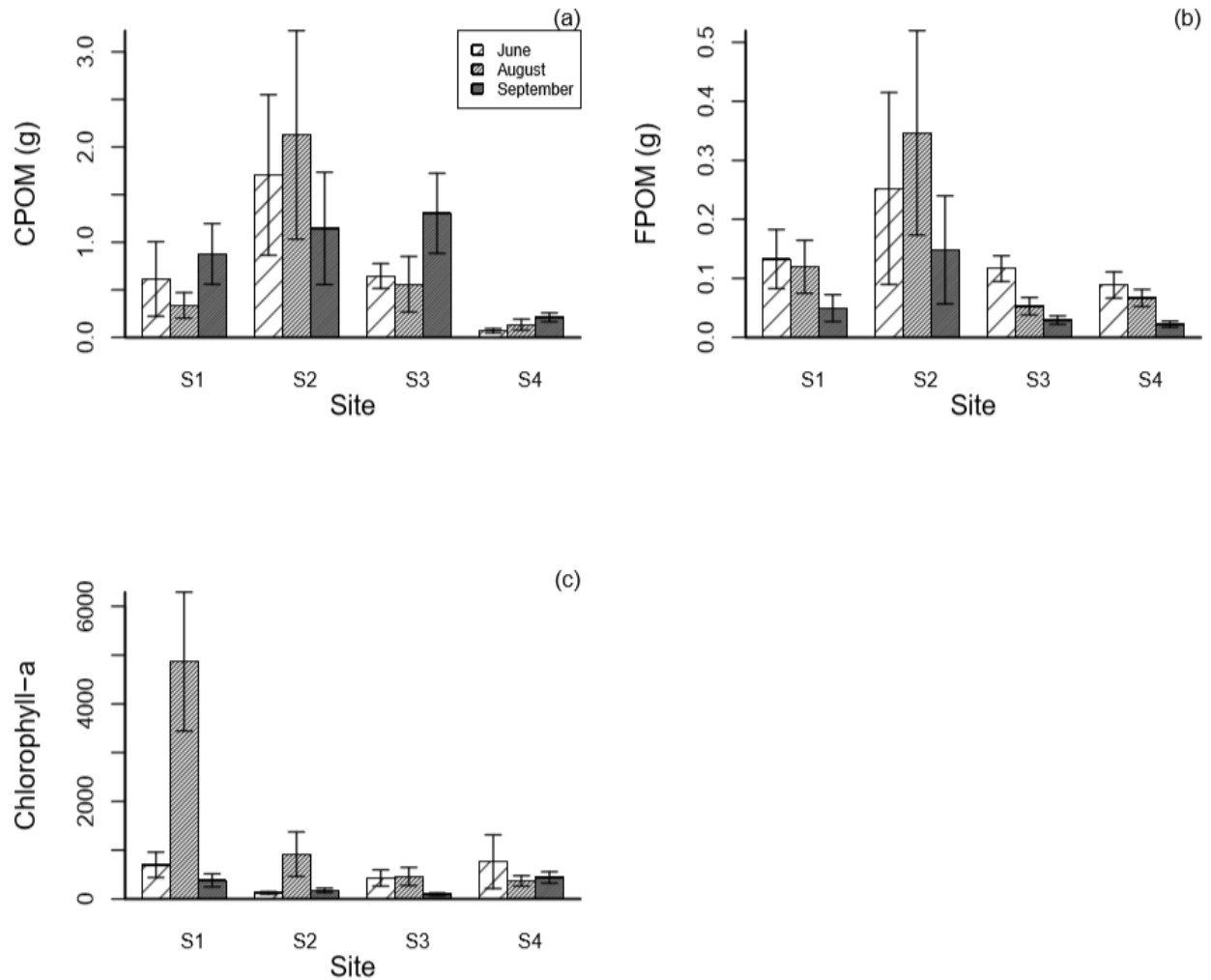
Figure 1.3 Mean ash-free dry mass of Coarse Particle Organic Matter (a), Fine Particle Organic Matter (b), and water column chlorophyll-a (c). Data collected from40 riverine rock pools at four sites along the Penobscot River, Maine. Error bars are +1 SE of the mean.

Average pH typically ranged from 8-9, and varied significantly over time (Table 1.1), largely due to especially high pH during June in Site 3 (Fig. 1.4a). Chloride varied significantly by month, with most sites exhibiting low average chloride concentrations in June and September. Only Site 3 had high chloride concentrations in June but all sites had high chloride

concentrations in August (Fig. 1.4c). Conductivity varied significantly between months within

sites (Table 1.1). Pools at Site 4 had especially high conductivity measurements in the low water-

level month of August (Fig. 1.4b), whereas the conductivity of pools in Site 3 declined from June

to September.
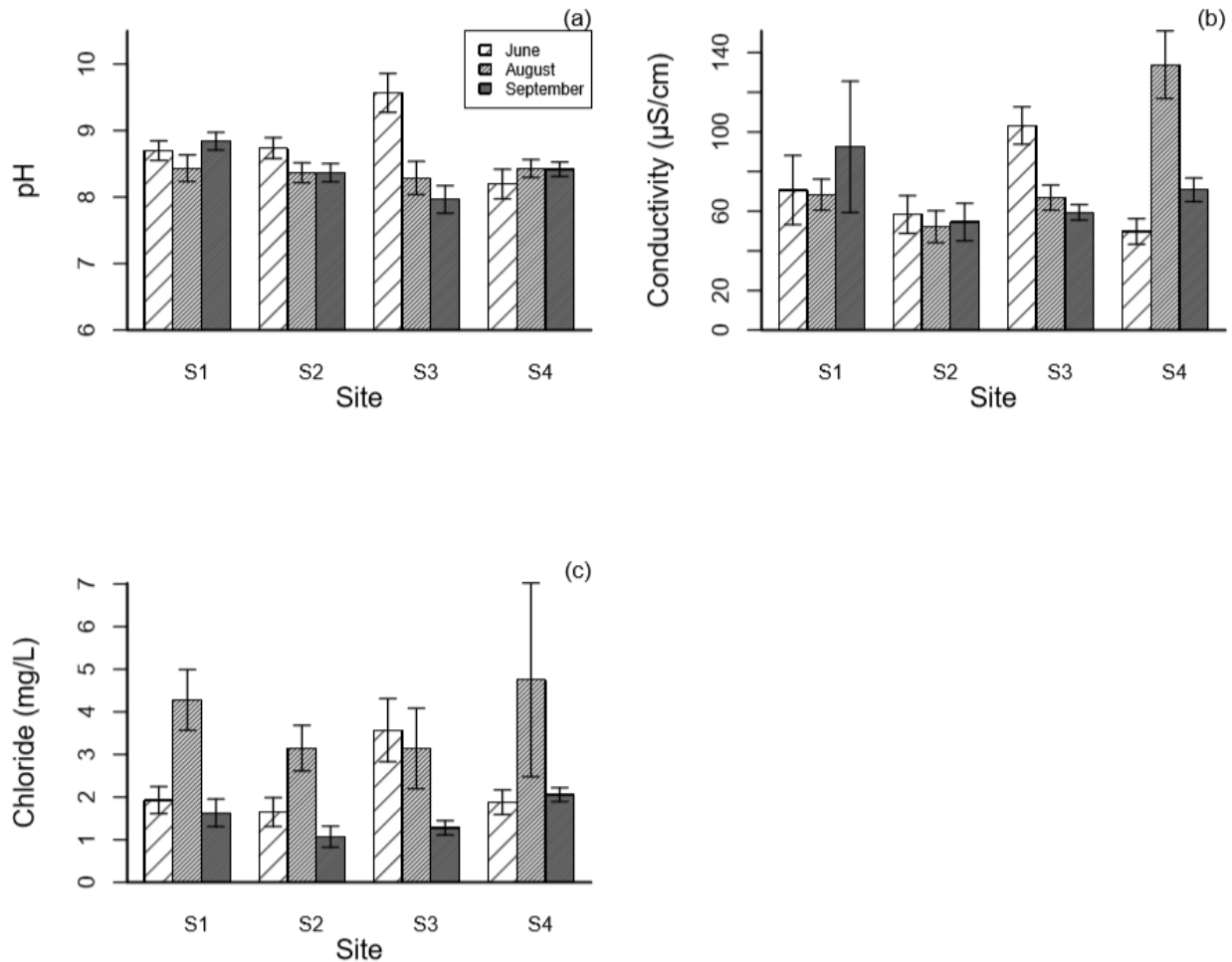
Figure 1.4 Average pH (a), conductivity (b), and chloride (c). Data collected from 40
riverine rock pools at four sites along the Penobscot River, Maine. Error bars are +1 SE of
the mean.

1.3.2 Invertebrate Richness and Abundance

Rock pools along the Penobscot River contained a high abundance of individuals and higher richness than what I anticipated. 30,478 individuals were collected and 71 unique taxa were identified during the course of this study. These taxa spanned 61 insect genera representing 30 families in eight orders (Table 1.2). The most abundant taxa were *Dicrotendipes* (n=9,247) and *Dasyhelea* (n=8,802) midges. *Chironomus* (n=3,380) midges and two mosquito species, *Aedes atropalpus* (n=3,998) and *Ae*. *japonicus* (n=1,891), were also abundant (Table 1.2). Ten taxa were found at all four sites, of which only *Cloeon dipterum*, a baetid mayfly, and *Stenelmis*, a riffle beetle, were not Diptera. Chironomidae exhibited considerable diversity with 18 genera present, representing three subfamilies: Chironominae, Orthocladiinae, and Tanypodinae.

Of the 61 insect genera found during the study, 26 were considered to be primarily lotic-dwelling taxa. *Stenelmis* (n=165), *Laccophilus* (n=91), and *Cloeon* (n=89) were the most notable genera within this group. Both *Stenelmis* and *Laccophilus* were collected from the pools as larvae and adults. The abundance of lotic taxa varied significantly over time (Table 1.1) and were more abundant during June than in other months. Nevertheless, lotic taxa were present at all sites in all months except for during September at Site 4 (Fig. 1.5).

Insect abundance was positively associated with conductivity and the ADFM of CPOM and FPOM (Table 1.1). There were no significant differences in abundance over time or between sites. However, there was considerable variability in invertebrate abundance within sites, especially during August at Site 1 and June at Site 2 (Fig. 1.6a). Richness varied significantly over time but did not differ between sites. Hydroperiod also did not have a significant effect on abundance (Table 1.1), however abundance was higher in larger, deeper pools, even after correcting for pool volume in density estimates. Richness at all sites was the lowest in September

(Fig. 1.6b). Interestingly, while richness greater in larger, deeper pools (Table 1.1), it was not significantly associated with any other environmental variable.

Several genera of predaceous insects were collected during the study. The most abundant taxa were *Libellula* and *Pantala* (Libellulidae), *Laccophilus*, and *Berosus* (Hydrophilidae) (Table 1.1). The abundance of *Libellula*, *Pantala*, and the other three odonate genera (*Boyeria*, *Enallagma*, and *Cordulia*) was positively associated with hydroperiod (linear regression: F=7.07, p=0.009) and pool volume (linear regression: F=6.30, p=0.013). The abundance of coleopteran predators was not associated with hydroperiod (linear regression: F=1.03, p=0.313) or pool volume (linear regression: F=0.11, p=0.737) (Table 1.1).

Table 1.2 List of all taxa collected from 40 rock pools across four sites along the Penobscot River, Maine. Taxa denoted with an asterisk (*) are those that have not previously been reported in literature as inhabiting rock pools.

Order	Family	Genus	Abundance	1	2	3	4
Ephemeroptera	Baetidae	Acerpenna*	1			▪	
		Baetis	5			▪	
		Cloeon dipterum	89	▪	▪	▪	▪
	Ephemerellidae	Eurylophella*	7			▪	
	Heptageniidae	Leucrocuta	1		▪		
		Maccaffertium*	1			▪	
	Leptophlebiidae	Habrophlebiodes*	4		▪	▪	
	Siphlonuridae	Siphlonurus*	25			▪	
Odonata	Aeshnidae	Boyeria*	1			▪	
	Coenagrionidae	Enallagma	1			▪	
	Corduliidae	Cordulia*	6	▪	▪		
	Libellulidae	Libellula	29	▪	▪		
		Pantala	98	▪			
Hemiptera	Gerridae	Trepobates*	1			▪	
	Hydrometridae	Hydrometra*	2				▪
Megaloptera	Corydalidae	Nigronia*	1			▪	
Coleoptera	Dytiscidae	Agabus	5		▪	▪	
		Laccophilus	91	▪		▪	
		Liodessus	3			▪	
	Elmidae	Ancyronyx*	2	▪	▪		
		Microcylloepus*	2			▪	
		Promoresia*	1		▪		
		Stenelmis*	165	▪	▪	▪	▪
	Hydrophilidae	Berosus	64	▪	▪	▪	
		Enochrus	10	▪			▪
		Hydrophilus	1			▪	
	Psephenidae	Psephenus*	4			▪	
Trichoptera	Brachycentridae	Micrasema*	5				▪
	Helicopsychidae	Helicopsyche*	2	▪			
	Hydropsychidae	Cheumatopsyche*	1		▪		
	Lepidostomatidae	Lepidostoma	2		▪	▪	
	Leptoceridae	Mystacides*	1			▪	
	Limnephilidae	Pycnopsyche*	2				▪
	Odontoceridae	Marilia*	2			▪	
	Philopotamidae	Chimarra*	1		▪		
	Phryganeidae	Ptilostomis*	1		▪		
	Psychomyiidae	Lype*	1			▪	
Lepidoptera	Crambidae	Parapoynx*	5	▪		▪	

Table 1.2 Continued

Order	Family	Genus/Taxon	Count				
Diptera	Ceratopogonidae	*Dasyhelea*	8,802	■	■	■	■
		*Leptoconops**	163	■	■	□	■
	Chironomidae	*Ablabesmyia*	30	■	■	□	□
		Chironomus	3,380	■	■	■	■
		Corynoneura	9	□	■	□	■
		Cricotopus	114	□	■	■	□
		Dicrotendipes	9,247	■	■	■	■
		Labrundinia	36	□	■	□	□
		Microtendipes	99	■	□	□	□
		*Nilotanypus**	7	□	□	■	■
		Paratanytarsus	12	■	□	□	□
		Phaenopsectra	35	□	□	□	■
		Polypedilum	536	■	■	■	■
		Procladius	104	■	■	■	■
		Psectrocladius	404	□	■	□	■
		*Pseudochironomus**	4	□	□	■	□
		Rheotanytarsus	4	□	□	■	□
		*Smittia**	1	■	□	□	□
		Tanytarsus	108	■	■	■	■
		*Tribelos**	68	□	□	■	□
	Culicidae	*Aedes atropalpus*	3,998	■	■	■	■
		Aedes japonicus	1,891	■	■	■	■
		*Anopheles quadrimaculatus**	72	□	■	■	□
Amphipoda	Crangonyctidae	*Crangonyx**	109	□	■	□	□
Isopoda	Asellidae	*Lirceus**	1	□	□	□	□
Basommatophora	Lymnaeidae*		34	□	■	□	□
	Physidae		38	□	□	■	■
	Valvatidae*		1	□	■	□	□
Unionida	Unionidae*		9	■	■	□	□
Venerida	Sphaeriidae*		4	□	■	■	□
Cladocera			500	□	■	□	□
Nematoda			22	□	□	□	■
Decapoda	Cambaridae	*Orconectes**	1	■	□	□	□
16	**38**	**64**	**30,486**				
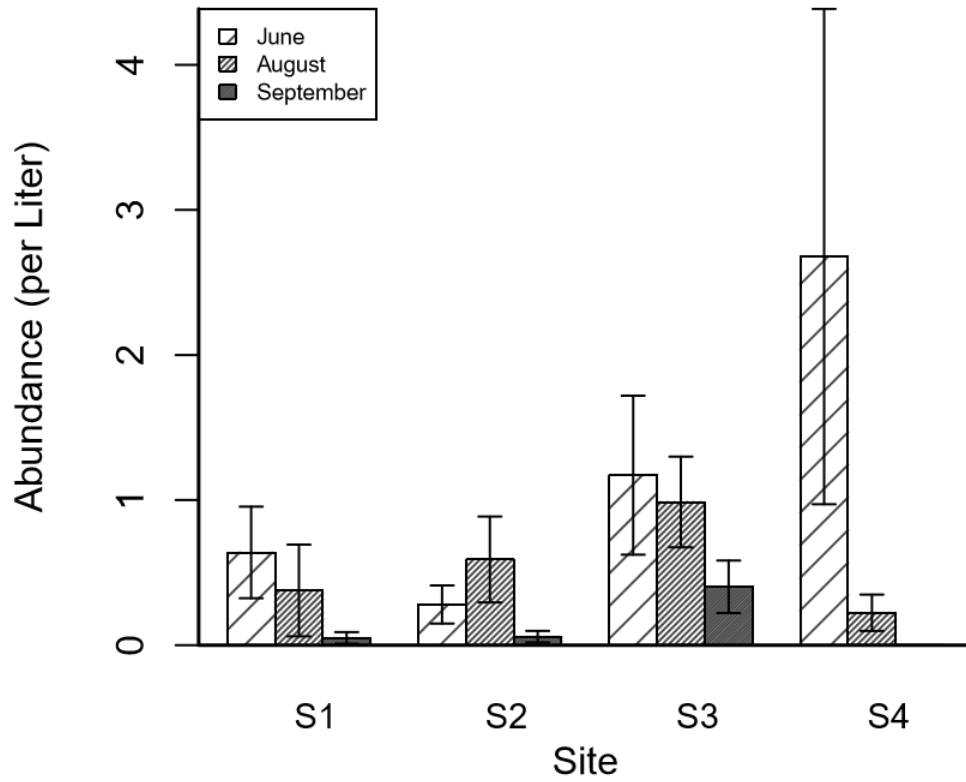
Figure 1.5 Average abundance per liter of lotic invertebrates from 40 riverine rock pools at four sites along the Penobscot River, Maine. Lotic taxa determined by descriptions in Merritt et al. (2008) collected Error bars are +1 SE of the mean.
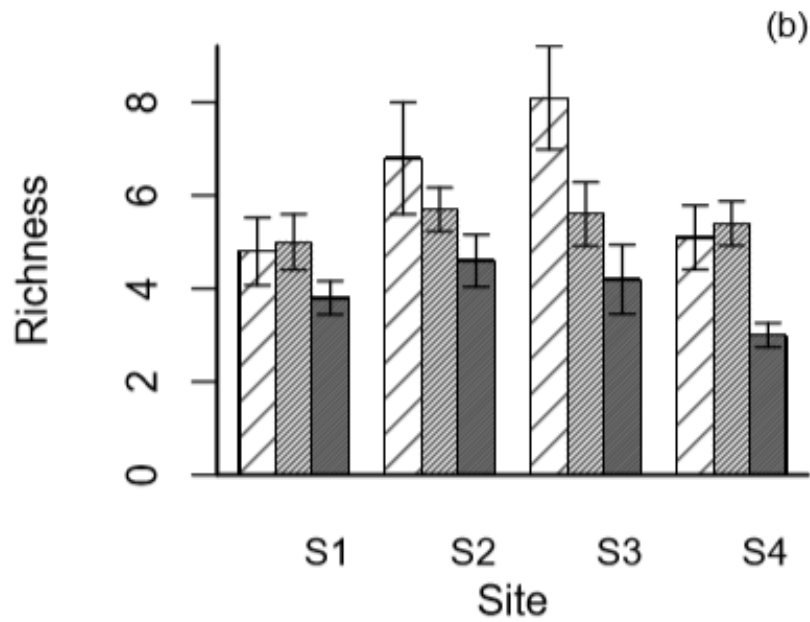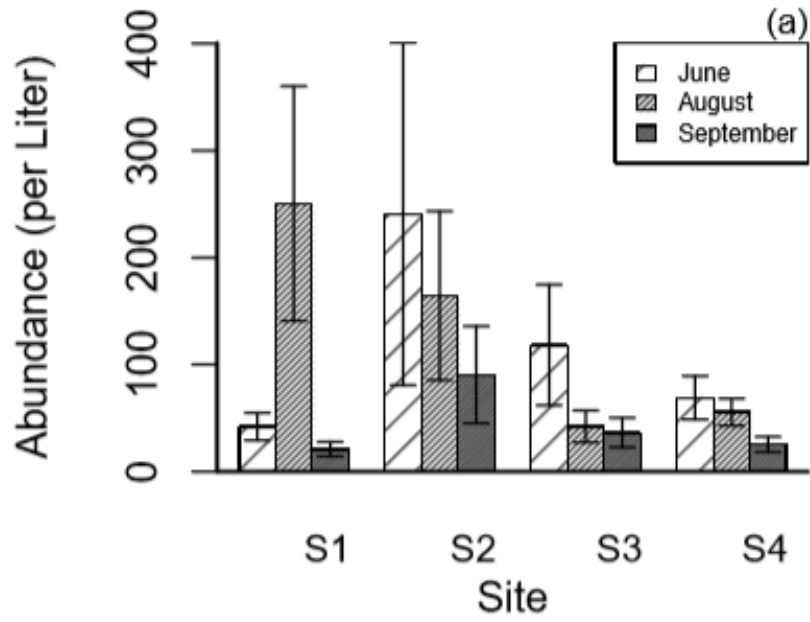
Figure 1.6 Mean invertebrate abundance per liter (a) and mean taxa richness (b) of aquatic invertebrate communities collected from riverine rock pools along the Penobscot River, Maine. Error bars are +1 SE of the mean.

1.3.3 Invertebrate Community Analysis

The aquatic invertebrate community composition varied significantly between months and this variation differed over time between sites (Site x Month interaction, Table 1.1). Sites supported unique communities in early summer, but differences between communities across the four sites decreased over time such that communities became fairly homogenous by September (Fig. 1.6). Pool depth, volume, and hydroperiod were all significant factors in determining community structure, as were pH, CPOM, and FPOM (Table 1.1).
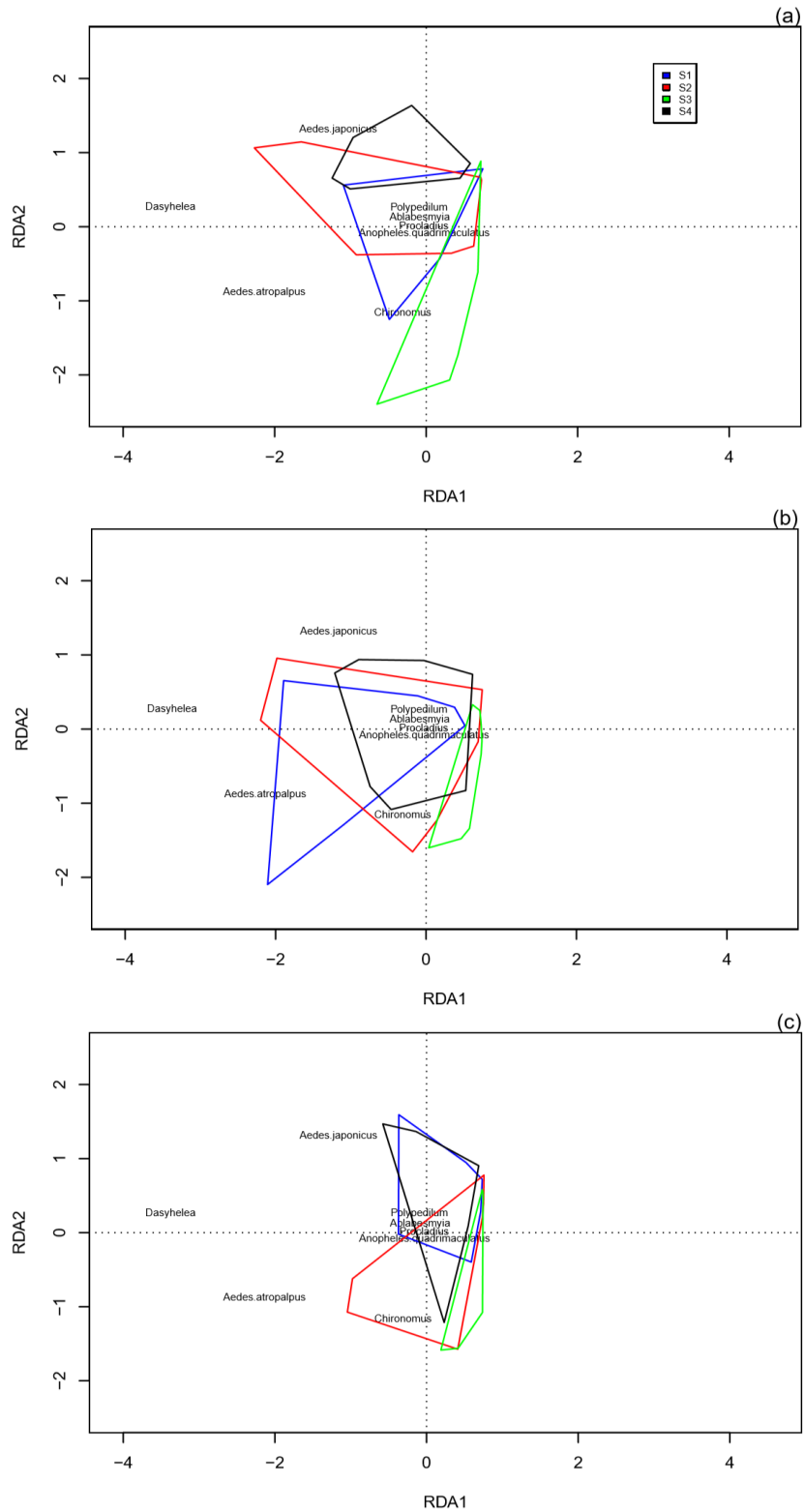
Figure 1.7 Redundancy analysis ordinations based on a log-abundance matrix of aquatic invertebrates collected from riverine rock pools in June (a), August (b), and September (c) along the Penobscot River, Maine. Polygons enclose all 10 pools sampled within each of the four sites in a given season.

1.4 Discussion

1.4.1 Invertebrate Communities Across Space and Time

71 unique taxa were identified during this study, which is a similar number to other studies on rock pool communities (Baron et al. 1998; Fontanarrosa et al. 2009; Timms 2014; Brendonck et al. 2016). Out of these 71 taxa, 38 have never been reported in the rock pool literature (Table 1.2). By abundance, these communities were dominated by Diptera, which is a similar finding to other studies on rock pool communities (Pinder et al. 2000; Fontanarrosa et al. 2009). Diptera made up 95.5% of all individuals collected during the study, of which all were Chironomidae, Ceratopogonidae, or Culicidae. These taxa all either have cutaneous gas exchange (Chironomidae and Ceratopogonidae) or use a siphon (Culicidae) (Barrera 1988), which enable them to be exceptionally well-suited for the low availability of dissolved oxygen in rock pool environments. Furthermore, midges and mosquitos generally have short life histories which offsets mortality risk from drying, and are also often tolerant to other environmental stressors, such as fluctuations in temperature and desiccation in at least one life history stage (Brendonck et al. 2016). Chironomid midges in particular have the potential to be exceptionally diverse in rock pool habitats (Egan and Ferrington 2015). However, the diversity of Chironomidae in rock pools and many other aquatic habitats is often not fully explored because of taxonomic difficulty (Pinder 1983). Describing the chironomid fauna in any freshwater study below the subfamily-level is important in understanding the invertebrate community as a whole because Chironomidae is often the most abundant and diverse taxon in freshwater environments (Oliver and Roussel 1983). In this study alone, I was able to document 18 different genera of Chironomidae and even greater diversity may have been uncovered if larvae had been reared out to adulthood.

One mechanism potentially explaining why communities at different sites became more similar over time is that repeated environmental stressors, such as fluctuations in temperature, resource availability, or desiccation, excluded taxa that are less tolerant to environmental stress, resulting in more homogenous communities (as in Chase 2007). Similarly, in pools that experienced frequent disturbances, such as desiccation, it is likely that only rapid colonizing taxa became established in the pools and late successional taxa or those with longer life histories were excluded (Vanschoenwinkel et al. 2017). In coastal rock pools in Jamaica, temporary pools had less variable community structures than permanent pools because temporary pools were generally dominated by taxa capable of rapid dispersal into and colonization of disturbed pools (Therriault and Kolasa 2001). Strong environmental filtering of invertebrate communities is likely to be commonplace among rock pools and other small container habitats.

The composition of the aquatic invertebrate communities differed across sites, but these communities became more similar over time. Much of this may have been driven by a decline in the abundance of *Dasyhelea* between August and September in all four sites. While the phenology and life history of most *Dasyhelea* species are not well-documented, some populations have been shown to be tolerant to environmental stress in tree-holes (Petermann et al. 2016), which are fairly similar abiotically to rock pools. Therefore, it's more likely that *Dasyhelea* abundances are more driven by phenology than by fluctuations in the environment within seasons. Populations of *Dasyhelea* in German tree-holes was dependent on seasonality, with individuals present only during the winter and spring (Gossner 2018). In Pennsylvania, *Dasyhelea* were only abundant during June and July (Barrera 1988). While the occurrence of *Dasyhelea* was observed during different times of year between these two studies, it suggests that the life histories of species within *Dasyhelea* are seasonal.

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Predatory taxa were present in many of the pools in this study. Several genera of predaceous Chironomidae (*Ablabesmyia*, *Labrundinia*, *Nilotanypus*, and *Procladius*) were collected at relatively low abundances compared to other chironomid genera, with only *Procladius* being present at all four sites (Table 1). Large-bodied predators, such as *Berosus*, *Laccophilus*, *Pantala*, and *Libellula* were collected in moderate numbers. Interestingly, none of these large-bodied taxa were present in pools at Site 4 throughout the study, and the only large predator that was collected at that site was the hydrophilid beetle *Enochrus*. Four individuals were collected in June and one individual was collected in August. The limited distribution of most predatory taxa between sites may be due to environmental constraints such as short hydroperiods, since pools in Site 4 averaged significantly lower hydroperiods than pools at the other three sites (Fig. 1). In particular, Odonata collected during this study were strongly associated with larger pools and pools with long hydroperiods (Table 2). As with other predatory taxa, dragonflies and damselflies typically have longer life histories and may only be found in pools that rarely or never dry out (Williams 1996; Anusa et al. 2012). Moreover, larger pools support more prey biomass that might attract and retain large-bodied predators (Spencer et al. 1999). Regardless of the mechanism, my results suggest that pools may vary substantially in trophic structure, which has wider implications for community and ecosystem processes.

1.4.2 Lotic Taxa as Components of Riverine Rock Pools

Several taxa found in this study were those that primarily inhabit lotic environments. Many of these taxa have never been reported from rock pools, which can be expected given that riverine rock pools are generally overlooked in reviews of rock pool diversity (Jocque et al. 2010; Brendonck et al. 2016). While lotic taxa might be expected to colonize pools adjacent to the river during high flows, several lotic taxa were found later in the season inhabiting rock pools

that were well above the river's high-water mark. Notably, 66 early-instar *Cloeon dipterum* nymphs were collected in August from a pool at Site 2 that was likely never flooded by the river, even during significant spring flows. Similarly, adult and occasionally larval *Stenelmis* were found in pools that were near the river's edge but had not been inundated by the river for several weeks prior. These cases suggest that river-dwelling taxa might enter rock pools through dispersal or oviposition and that they can survive in rock pools for at least a short time, providing the pools do not dry out.

Interestingly, *Nilotanypus* and *Rheotanytarsus* were the only chironomids collected during this study that are known to inhabit exclusively lotic environments (Merritt et al. 2008). *Rheotanytarsus* was only collected in one pool in Site 3 in June, so larvae likely entered the pool from the river during high spring flows. *Nilotanypus* on the other hand was found in two pools in August, of which one pool was never flooded by the river between the June sample and the August sample and one pool was flooded once. The presence of *Nilotanypus* in a pool that was not flooded in the weeks prior to sampling suggests that *Nilotanypus* adults flying over and around the river may potentially oviposit in nearby riverine rock pools. Another possibility is that eggs were deposited in the vicinity of the pool while spring flows were in progress and the larvae subsequently hatched during the summer and were detectable after the June sampling occurred. However, definitive conclusions about pool colonization pathways by lotic taxa cannot be drawn from the data collected during this study. As colonization of riverine rock pools by lotic taxa is undoubtedly important in determining invertebrate community structure, more research attention is needed to shed light on colonization pathways and processes.

1.4.3 Pool Hydrology and Environmental Conditions

The pools included in this study exhibited high variability in hydroperiod, especially between sites. This was a significant factor in determining invertebrate composition within and among pools, which a finding that is consistent with numerous studies (Bazzanti et al. 1997; Batzer et al. 2004; Fontanarrosa et al. 2009; Vanschoenwinkel et al. 2009, 2010, 2017; Brendonck et al. 2015, 2016; Calabrese et al. 2016). Morphological characteristics of rock pools, such as pool area and maximum depth, can be directly correlated with pool hydroperiod and subsequently affect overall pool hydroregime (Vanschoenwinkel et al. 2009). For example, deeper pools or those with smaller surface-area-to-volume ratios will hold water for longer stretches of time than shallow pools or pools with larger surface areas (Brendonck et al. 2016). Pool maximum depths in my study ranged from 11.4cm to 29.8cm with an average of 17.7cm. Pools in Sites 1 and 4 had the shortest average hydroperiods and the lowest mean depths whereas those in Sites 2 and 3 had longer hydroperiods and were deeper on average. This suggests that pool depth may have had a role in determining pool hydroperiod during this study. The morphology of the rock outcrops at each site may have also been an important factor. At sites 2 and 3, most pools occurred in sloped areas of the outcrops and it is likely that during rain events, the sloped surface of the rock outcrop allowed water to be channeled into flow paths leading directly into the pools. In contrast, pools in flat areas of an outcrop, such as those in Site 4, did not receive water from runoff and therefore were not substantially filled during rain events (C. Gagne, *pers. obs.*). The ability to delineate catchments for each rock pool studied on an outcrop would be useful for describing and understanding pool hydrology at a more detailed level.

Another factor influencing differences in hydroperiod is the amount of shade that pools received from riparian vegetation. Riparian trees adjacent to Site 3 provided shade such that

pools were only exposed to direct sunlight for a short period of time, likely limiting the amount of water evaporation from the pools. In contrast, pools at Site 4 were well-removed from any vegetation and were not situated underneath rock benches or ledges, so every pool was exposed to direct sunlight and high rates of evaporation for the entire day.

Several other environmental variables linked to food resources varied among sites and over time. All sites except for Site 2 experienced increases in the amount of coarse detritus present in September, which is consistent with leaf litter accumulation from fall abscission from deciduous riparian trees. Pools at Site 2 were flooded by the river less often than pools at Site 3, however many of the flood-prone pools at Site 2 were well-removed from the riparian zone. Leaves seldom entered these pools, unlike the pools at Site 3 that were situated directly under riparian trees, so infrequent flooding events at Site 2 were likely enough to keep pools devoid of leaf litter. While several pools at other sites were also well-removed from the riparian zone, the increase in leaves falling from nearby trees likely increased the chances that leaves got blown into the pools, and infrequent or nonexistent flooding events allowed these leaves to accumulate. Undoubtedly, coarse detritus is likely to be an important resource component for riverine rock pool invertebrates, and in this study I observed significant relationships between CPOM and invertebrate abundance and community structure. An opposite temporal trend occurred with fine detritus, in which detritus mass decreased in all sites between August and September and, except for Site 2, decreased from June to August. However, much like CPOM, there was much variation within sites. Much of this variance can likely be attributed to the physical position of rock pools on each individual rock outcrop. This is especially evident at Site 2 where some pools were situated directly under shrubs and near patches of moss, whereas other pools were in areas devoid of any vegetation. The amount of FPOM present in the pools at Site 2 was highly

variable, but steadily decreased over time in the other three sites (Fig. 1.2b). The decrease in

Sites 1, 3, and 4 was likely due to consumption over the course of the season by invertebrates

inhabiting the pools, along with low detritus input rates due to pools being removed from low-

lying vegetation and areas where sediment accumulates. High variation in Site 2 likely stems

from some pools being situated under or near low-lying vegetation, or in depressions on the rock

outcrop where sediment can accumulate.

Interestingly, all sites exhibited high chloride concentrations in August and only the pools

at Site 3 had high chloride in June. The reason for high chloride concentrations in the rock pools

during August is quite unclear. While rivers affected by road salt have been shown to have peaks

in chloride concentrations during the summer months (Kelly et al. 2019), pools in Site 1

experienced substantial increases in chloride but were never flooded by the river between the

June and August sampling dates. After further analysis, chloride was found to be negatively

correlated with both hydroperiod length and average depth. Thus, chloride concentrations within

the rock pools included in this study are likely determined by the amount of water present in the

pools rather than the frequency of inundations by the Penobscot River.

1.5 Conclusion

Riverine rock pools along the Penobscot River hosted surprisingly diverse and unique

aquatic invertebrate communities. These communities were comprised of both lentic and lotic-

dwelling taxa, suggesting that invertebrates from the adjacent river colonize and utilize rock

pools intentionally or become trapped when river levels drop during the summer. Invertebrate

communities varied substantially between sites, but a combination of phenologically-driven life

histories and highly variable environmental conditions within the pools likely caused

communities to become more similar throughout the sampling period. Several of the taxa

collected during this survey have never before been reported in rock pool literature, highlighting the paucity of research on the diversity and community structure in riverine rock pools. Finally, while resource availability, pool size, and hydroperiod were all identified as factors influencing invertebrate abundance and community composition, the intercorrelated nature of these variables suggests that experimental work is needed to fully understand the mechanisms of environmental controls of rock pool communities.

CHAPTER TWO:

IS HYDROPERIOD A KEY DRIVER OF INVERTEBRATE COMMUNITY

STRUCTURE IN RIVERINE ROCK POOLS? AN EXPERIMENTAL APPROACH

2.1 Introduction

The amount of time that a body of water is inundated, known as the hydroperiod, is often cited as one of the most important driving factors of invertebrate community composition in small temporary water bodies, including rock pools (Bazzanti et al. 1997; Batzer et al. 2004; Altermatt et al. 2009; Fontanarrosa et al. 2009; Ripley and Simovich 2009; Vanschoenwinkel et al. 2009, 2010, 2017; Brendonck et al. 2016; Calabrese et al. 2016). Pools with short hydroperiods desiccate more frequently and for longer durations, limiting the range of taxa that can live in them to only those that have rapid life histories and/or desiccation-resistant phases. Taxa that fit these characteristics include several dipterans, such as midges and mosquitos, and small rapidly-reproducing crustaceans, such as branchiopods, cladocerans, and ostracods (Williams 1996; Brendonck et al. 2016). Conversely, pools with long hydroperiods are inundated for periods of time sufficient to support taxa with longer life histories, such as Coleoptera, Trichoptera, Hemiptera, and Odonata. In particular, Coleoptera and Hemiptera are capable of active dispersal as adults. Adults of these taxa may be present in pools regardless of hydroperiod length because they are able to easily disperse to refuges if the pool desiccates (Wissinger 1997). However, juvenile stages of these and other long-lived taxa are only present in the latter stages of community succession as adults selectively oviposit in deeper, less ephemeral pools (Jocqué et al. 2007b; Vanschoenwinkel et al. 2010). Thus, the presence of juvenile stages of Coleoptera, Odonata, and Hemiptera may be used as indicators of long-lived, relatively stable rock pool environments.

Temporary aquatic habitats, including rock pools, that have longer hydroperiods tend to have higher species diversity than those with shorter hydroperiods (Bazzanti et al. 1997; Spencer et al. 1999; Batzer et al. 2004; Fontanarrosa et al. 2009; Vanschoenwinkel et al. 2009, 2010, 2017; Brendonck et al. 2015, 2016; Calabrese et al. 2016). Short hydroperiods can truncate community succession and limit the invertebrates inhabiting the pools to only those that can tolerate desiccation. Conversely, long hydroperiods allow more generalist taxa that are less tolerant of desiccation to colonize pools, which leads to more complex and diverse invertebrate communities (Jocqué et al. 2007b; Vanschoenwinkel et al. 2010). Along with these changes in the invertebrate community comes the addition of predators. Most predatory taxa colonize pools later during community succession, so longer hydroperiods allow for more time and opportunities for predators to enter communities (Bilton et al. 2001). Furthermore, the addition of predators adds trophic complexity to long-lived pools and allows for biotic interactions to become the dominant drivers of community structure (Jocqué et al. 2007a). In some cases, predators can greatly reduce the abundance of species within a community that are vulnerable to predation (Brendonck et al. 2002). It is likely that in rock pools with long hydroperiods, colonizing predators play important roles in determining community structure by reducing or excluding populations of prey species.

Habitat size, usually in the form of pool area or depth, can also be an important predictor of taxa richness in freshwater habitats. Larger temporary pools may be able to host a wider range of taxa due to more available microhabitats and more stable environmental conditions (Wissinger et al. 1999). Indeed, positive species-area relationships have been detected in several studies of rock pool communities (Spencer et al. 1999; Kiflawi et al. 2003; Vanschoenwinkel et al. 2009; Anusa et al. 2012). As generally small habitats with limited dispersal of taxa between them, rock

pool communities can be modeled reasonably well using island biogeography theory; a key

mechanism of which is the positive relationship between habitat size and colonization rate

(MacArthur and Wilson 1967). Kiflawi et al. (2003) found that an island-biogeographical model

explained 62% of the variation of species richness in 47 temporary pools based on pool size and

hydroperiod. The presence of certain taxa may also be particularly sensitive to habitat size,

especially larger predators such as beetles (Nilsson 1984) and odonates (Oertli et al. 2002). Thus,

rock pool size is likely an important environmental variable structuring invertebrate communities

in rock pools.

While both hydroperiod and habitat size are generally accepted as being important drivers

of community composition in freshwater habitats, these two variables are often tightly correlated

(Wissinger 1999). Larger pools tend to have longer hydroperiods, and very few studies have

attempted to directly separate and isolate the effects of these different environmental drivers.

Vanschoenwinkel et al. (2009) used a hydrological model based on field observations to

reconstruct the hydroregime (the frequency of both desiccation and water-input events) of rock

pools in South Africa and determine the effects of hydroregime on aquatic invertebrate

communities. There were both unique and shared effects of hydroregime and habitat size on rock

pool communities, however isolating these variables mechanistically was difficult because

hydroperiod was strongly correlated with pool area and weakly correlated with depth. Studies

isolating hydroperiod from habitat size variables through experimental manipulation of

hydroperiod are lacking, especially in a field setting. The present study addressed this gap in

knowledge by experimentally manipulating the hydroperiod of natural rock pools varying in size

to determine its effect on rock pool invertebrate communities. I hypothesized that rock pools

with manipulated long hydroperiods will have greater taxa richness and total abundance, as well

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as greater abundances of large predatory taxa (Coleoptera, Hemiptera, Odonata), than pools with short natural hydroperiods.

2.2 Methods

2.2.1 Study Area

I selected 20 rock pools for this experiment from one outcrop along the Penobscot River near Milford, Maine. The outcrop was stratified such that ten pools were situated at a low elevation on the outcrop and were therefore at risk of flooding during high river flows, while ten pools were at a higher elevation out of the range of summer flood stage. Pool volumes ranged from 0.25L to 2.31L and were not significantly different between outcrop sections (p=0.661). Within each of the lower and higher sections of the outcrop, five of the ten pools were randomly assigned to either natural hydroperiods or water additions that artificially extended hydroperiod. The entire rock outcrop was devoid of vegetation except for sparse grasses and lichens around pool edges.

2.2.2 Field Methods

The experimental manipulations of hydroperiod began on 27 June and ran until 27 September 2018. The treatment pools were prevented from desiccating by adding water every other day whereas pools in the control group were allowed to dry out and refill naturally. Rainwater was collected and used to keep treatment pools filled for the first month of the experiment, however infrequent rain events forced a switch to using deionized water for the final two months. When control pools were inundated, some water was removed with a small cup and poured back into the pool to control for the mechanical disturbance caused by adding water to the treatment pools.

Aquatic invertebrates were sampled and removed from all pools prior to beginning the experiment to standardize pool communities. Doing so allowed the focus of the experiment to be on the colonization and establishment of pool communities from late June onward. Invertebrates were collected at the conclusion of the experiment in September by sweeping a fine-mesh (250µm) aquarium net through the pool for three minutes after the substrate had been disturbed. Samples were immediately transferred to 70% ethyl alcohol and stored for later sorting and identification. Both coarse and fine particle organic matter (CPOM and FPOM, respectively) were collected simultaneously with the June and September sweep samples using a 250µm aquarium net. CPOM was defined as any detritus greater than one millimeter and FPOM was defined as any detritus between 250 micrometers and one millimeter.

Pool volume was estimated by using the mean depth and surface area of each pool. Surface area was calculated by measuring pools in scaled photos with Adobe Acrobat Pro. Pool depth from the deepest point was measured every other day prior to the addition of water. Conductivity and pH were measured every two days using a Hach HQ40d multi-probe.

2.2.3 Laboratory Methods

All invertebrates, excepting mosquitos and chironomid midges, were identified to genus using Peckarsky et al. (1990) and Merritt et al. (2008). Mosquitos were identified to species using Andreadis et al. (2005) and chironomid midges were not identified past the family level. CPOM and FPOM detritus fractions were dried for one week at 50 degrees Celsius and then ashed for two hours at 500 degrees Celsius to determine ash-free dry mass (AFDM).

2.2.4 Statistical Methods

Data were analyzed using R version 3.5.1. Differences in environmental variables across pools were assessed with ANOVAs with treatment (hydroperiod manipulation), outcrop section, and pool volume as fixed, categorical predictors. Invertebrate abundances were adjusted to the number of individuals per liter based on calculations of pool volume.

Model selection based on backwards stepwise model fitting using the R-function "step" was conducted to determine the variables most important in determining richness, overall invertebrate abundance, and abundances of individual taxa. The stepwise procedure for model selection ended when removal of variables did not significantly reduce model AIC scores. Subsequent linear models were run on the best-fitting model for each biological factor to calculate model R^2 and the significance of each predictor.

2.3 Results

The experimental treatment significantly increased rock pool hydroperiod by an average of 29 days compared to the control pools (Table 2.1, Fig. 2.1). Conductivity was significantly higher in pools with artificially extended hydroperiods (Table 2.1), but no other environmental variables differed between hydroperiod treatments. Resource availability, measured as CPOM and FPOM mass, was significantly greater (p=0.005 and p=0.049, respectively) in pools in the high section than those in the low section of the rock outcrop (Table 2.1). In addition, FPOM was more abundant in larger pools. Average pH was also significantly higher in pools in the high section (p<0.001) (Table 2.1). Although data on chlorophyll-a concentrations were not collected in this experiment, sporadic algal blooms were observed in pools in the high section during the experiment and none were recorded in pools in the low section (Gagne, *pers. obs.*).

Table 2.1 Univariate ANOVA results for environmental variables measured during an experimental manipulation of hydroperiod of rock pools (n=20) along the Penobscot River, Maine.

|	Treatment			Section			Pool Volume		
	df	F	P	df	F	P	df	F	P
Hydroperiod	1	**18.03**	**<0.001**	1	1.36	0.247	**1**	**7.58**	**0.007**
Conductivity	1	**4.95**	**0.028**	1	1.75	0.188	1	1.96	0.164
pH	1	2.95	0.088	1	**89.70**	**<0.001**	1	**6.01**	**0.016**
CPOM	1	0.57	0.459	1	**10.29**	**0.005**	1	0.74	0.400
FPOM	1	0.40	0.536	1	**4.47**	**0.049**	1	**4.69**	**0.044**
Average Depth	1	0.01	0.928	1	**11.14**	**0.001**	1	**90.47**	**<0.001**
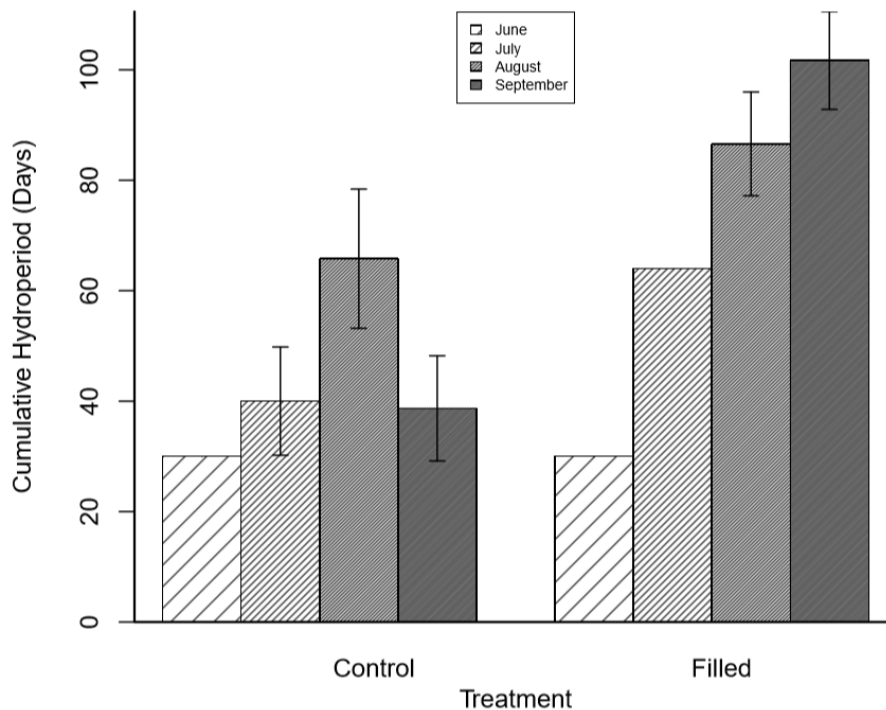
Figure 2.1 Average cumulative hydroperiod during a hydroperiod manipulation experiment in riverine rock pools by the Penobscot River, Maine. Hydroperiod was artificially lengthened in "Filled" pools. Error bars are ±1 SE of the mean.

Only five taxa were collected from the rock pools at the conclusion of the manipulation, and of these, the dragonfly *Pantala* was the only long-lived (univoltine) taxon present in the pools (Table 2.2). The other four taxa present were multivoltine dipterans that are common in riverine rock pools (Chapter 1). Despite the vast difference in hydroperiod lengths between treatment and control pools, hydroperiod treatment was not selected in the best model as one of the important variables for determining invertebrate richness or abundance. Interestingly, the only variable significantly associated with invertebrate richness was average pH ($p<0.001$) (Table 2.3), with higher pH pools supporting more taxa. FPOM and pool volume were also included in the best model predicting invertebrate richness, however these variables themselves did not explain significant variation in richness (Table 2.3). Invertebrate abundance was best explained by a model including conductivity, section of the outcrop, and pool volume (Table 2.3). Pools in the high section of the outcrop contained greater invertebrate abundance than pools in the low section ($p=0.001$), and abundance increased with pool size ($p=0.035$) (Table 2.3). There was also a strong positive correlation between average conductivity and abundance ($p<0.001$) (Table 2.3).

Table 2.2 Aquatic invertebrate taxa collected at the conclusion of experimental manipulation of hydroperiod in rock pools along the Penobscot River, Maine. Abbreviations: LC=Low Control, LT=Low Treatment, HC=High Control, HT=High Treatment. Five rock pools were used in each category.

Order	Family	Genus	LC	LT	HC	HT
Odonata	Libellulidae	*Pantala*	0	0	1	13
Diptera	Ceratopogonidae	*Dasyhelea*	0	0	22	4
	Chironomidae	-	18	54	120	208
	Culicidae	*Aedes atropalpus*	15	1	37	16
		Aedes japonicus	14	7	93	61
2	4	4	47	62	273	302

Table 2.3 Model selection results of relationships between environmental predictors and biological responses in an experiment manipulating hydroperiod of rock pools (n=20) along the Penobscot River, Maine. Important environmental variables for each response were determined through AIC-based backwards stepwise model selection of a full model including treatment and outcrop section as fixed categorical variables and pH, conductivity, pool volume, and FPOM and CPOM biomass as continuous predictors. Only variables included in the best model are shown.

Response	Effect	df	F	P	AIC	r^2
Richness	**Average pH**	1	**19.53**	**<0.001**	**1.07**	**0.574**
	FPOM	1	2.02	0.175		
	Pool Volume	1	0.01	0.934		
Abundance	**Conductivity**	1	**21.58**	**<0.001**	**174.97**	**0.725**
	Section	1	**15.27**	**0.001**		
	Pool Volume	1	**5.28**	**0.035**		
Pantala	**Pool Volume**	1	**32.65**	**<0.001**	**-19.92**	**0.764**
	FPOM	1	**22.39**	**<0.001**		
Aedes atropalpus	Pool Volume	1	4.23	0.056	**96.26**	**0.277**
	Average pH	1	2.29	0.149		
Aedes japonicus	**Conductivity**	1	**14.74**	**0.002**	**134.97**	**0.648**
	Section	1	**8.59**	**0.010**		
	Pool Volume	1	**6.09**	**0.025**		
Chironomidae	**Conductivity**	1	**15.66**	**0.001**	**158.86**	**0.739**
	Section	1	**14.75**	**0.002**		
	Treatment	1	**7.89**	**0.013**		
	Pool Volume	1	4.15	0.060		
Dasyhelea	Average pH	1	2.55	0.130	**83.74**	**0.251**
	FPOM	1	2.14	0.163		
	Pool Volume	1	0.68	0.421		

The responses of individual taxa mirrored these patterns. The individual abundances of *Aedes japonicus* and Chironomidae, in particular, were significantly associated with conductivity (p=0.002 and p=0.001, respectively) (Table 2.3). Resource variables (FPOM and CPOM) were important factors determining the abundance of *Pantala*, *Aedes atropalpus*, and *Dasyhelea*. Pool

volume was included in the best models for *Pantala* and *Aedes japonicus*, but interestingly, Chironomidae was the only taxon significantly affected by the experimental hydroperiod treatment: Chironomidae abundance was higher in manipulated pools than in control pools (Table 2.3). Together these results suggest that hydroperiod has weak to no effects on rock pool insects compared to pool size, resource availability, and water chemistry.

2.4 Discussion

Overall, pool volume and the section of the outcrop in which a pool was located were much more important factors in determining community structure was than hydroperiod length. This finding is contradictory to most other studies on rock pools and other small temporary freshwaters, which generally agree that hydroperiod is one of the most important factors for determining invertebrate community structure (Jocqué et al. 2007a; Vanschoenwinkel et al. 2009, 2010; Brendonck et al. 2015, 2016). For example, Batzer et al. (2004) found in their study of 66 temporary woodland ponds that hydroperiod was a significant driver of species richness, largely through influencing the presence and abundance of rare taxa. However, common species collected during the study were found at high abundances regardless of hydroperiod length, so overall invertebrate abundance was not affected significantly by hydroperiod. It's likely that a similar pattern was observed in my experiment. *Pantala* was the only invertebrate collected that was not one of the taxa that were found to make up the vast majority of riverine rock pool invertebrates in my study system (Chapter 1). The four Dipteran taxa that dominated communities in the experimental pools are likely much more tolerant of shortened pool hydroperiod than *Pantala* is, so a manipulation of hydroperiod would only have a small effect on abundance, if any. In addition, these dipterans are mostly multivoltine with short life histories or overlapping generations (Menzie 1980; Giberson et al. 2001; Burger and Davis 2008), increasing

the likelihood of multiple colonization events during the wet phases of the control pools. If more rare taxa were collected, detecting a difference if it existed in taxa richness and overall community composition in pools with extended hydroperiods would be much more likely.

A likely explanation for the low diversity of rare taxa and the robustness of communities to changes in hydroperiod is the time of year in which the communities were sampled. Late in September, it's possible that the only taxa persisting in rock pools are those that are tolerant of environmental instability. Other studies of environmental characteristics of rock pools show that they can be quite variable, even over the course of a single day (Jocque et al. 2010). In particular, temperature in small rock pools is often similar to ambient air temperature, so large differences in maxima and minima during a single day are common (Brendonck et al. 2000). High variability in temperature, pH, and other water chemistry parameters place a high level of stress on rock pool invertebrates, and these effects compound as temperatures rise during the summer. This variability can act as an ecological filter, eliminating less tolerant taxa and driving communities to become more similar by allowing only a subset of the regional fauna to inhabit rock pools over time (Chase 2007; Vanschoenwinkel et al. 2007). Therefore, it's likely that high variability in environmental factors reduced community richness over the course of the season until only taxa tolerant of environmental stress were present in the pools in September.

The only invertebrate taxon that was associated with the experimental treatment was Chironomidae. While chironomids are known to be among the most common rock pool inhabitants due to their rapid life histories and tolerance to desiccation (Jocque et al. 2010; Brendonck et al. 2016), they were found at significantly greater abundances in pools with extended hydroperiods than in pools with short hydroperiods. In pools with long hydroperiods, multiple different instars were observed in the same sample and adults were seen emerging at

multiple times throughout the season (Gagne, *pers. obs.*), indicating that there may have been

several generations present simultaneously which increased total abundance. Furthermore, active

dispersing insects have more opportunities to colonize long-lived pools and successfully become

established (Bilton et al. 2001; Vanschoenwinkel et al. 2010). Thus, it's possible that midge

abundances were greater in manipulated pools because opportunities for colonization were

greater then in shorter hydroperiod pools. Alternatively, resource availability may have been

higher in manipulated pools because longer inundations enabled algal and microbial biomass to

accumulate more than in pools that dried out frequently. Drying events can cause a considerable

decline in bacterial biomass and additionally reduces colonization and breakdown of leaf litter

(Arroita et al. 2018). Thus, chironomids may have had more food resources available to them in

pools that did not desiccate.

Habitat size, which includes surface area and volume, has been determined by several

studies to be an important factor driving community structure in rock pools (Ranta 1982; Spencer

et al. 1999; Kiflawi et al. 2003; Vanschoenwinkel et al. 2009; Anusa et al. 2012). Proposed

mechanisms are consistent with those of species-area relationships, namely a diversity of feeding

and spatial habitat niches that promote complex and diverse communities (Anusa et al. 2012). In

my experiment, pool volume was not found to explain significant variation in invertebrate

richness. This is an interesting finding given that species-area relationships are fairly well-

documented in rock pools (Ranta 1982; March and Bass 1995; Kiflawi et al. 2003; Anusa et al.

2012). Conversely, pool volume was an important factor in determining the abundances of all

five individual taxa and was significantly associated with abundance for *Aedes japonicus* and

Pantala. In a study using constructed ponds of different sizes ranging from $0.3m^2$ to $1.2m^2$,

Mitchell and Lasswell (2018) found that *Pantala flavescens* populated the ponds in increasing

abundance as pond size increased. Interestingly, *P. flavescens* nymphs were not found in any of the 0.3m^2 ponds. This suggests that *P. flavescens* selects for larger ponds when choosing where to oviposit. In my experiment, *Pantala* may have been selecting for larger pools in a similar fashion and generally avoiding smaller pools. Regardless of the mechanism of pool size, my results suggest that the strong and consistent effects of hydroperiod detected in surveys (including Chapter 1) may in fact be due to covarying effects of larger pool size.

Overall, taxa richness was most strongly associated with average pH. There was also a significant difference in average pH between outcrop section, with pools further from the river (and closer to riparian vegetation) exhibiting greater pH values than the low section. It's likely that this difference in pH is due to differing rates of primary production between the high and low outcrop sections. Algal blooms were occasionally observed in pools in the high section, but none were recorded from pools in the low section. Additional food resources in the form of algae and FPOM in pools in the high section likely allowed the four dipteran taxa to inhabit the same pool without experiencing strong competition from resource limitation. Positive productivity-species-richness relationships similar to this have been found in several freshwater invertebrate communities (Cusens et al. 2012). *Pantala* may also have been found in these pools because algae and settled layers detritus provide structural components to the rock pool basin and may allow for higher predation success. Thus, pools with higher pH may have had more food and structural resources available and were able to support more diverse invertebrate communities.

2.5 Conclusion

This study was the first to directly manipulate rock pool hydroperiod and attempt to isolate the effects of hydroperiod from tightly correlated variables such as pool size. I hypothesized that rock pools with artificially extended hydroperiods would contain greater invertebrate taxa richness and contain higher abundances of long-lived taxa than rock pools with natural, short hydroperiods. This hypothesis was not supported because taxa richness and individual abundance of all taxa except for Chironomidae were not strongly associated with the experimental treatment. Outcrop section, pool volume, and chemical variables, including average pH and conductivity, were more important than hydroperiod in determining community structure in riverine rock pools. This result is surprising because hydroperiod is often found to have the greatest effect on rock pool communities in most surveys of rock pool invertebrates. My findings suggest that the observed effect of hydroperiod on rock pool communities in other studies may be confounded by pool size and by indirect effects of other environmental variables mediated by hydroperiod.

CHAPTER THREE

SYNTHESIS

The results from Chapter 1 indicate that riverine rock pools in Maine contain surprisingly diverse communities of aquatic invertebrates. These communities are highly variable over the course of the season and environmental drivers likely coupled with seasonally abundant taxa are responsible for this variability. Resource variables (CPOM and FPOM), pH, and hydrological variables (volume, depth, and hydroperiod) were the most important factors for determining invertebrate community structure. However, separating the effect of hydroperiod on community assemblage from the effect of pool volume is difficult and likely not possible in a community survey. Experiments involving the manipulation of hydroperiod have not been done in a field setting, so it is unclear whether hydroperiod itself drives community structure in rock pools or if it is another tightly covarying variable, such as pool size.

The results from Chapter 2 suggest that hydroperiod is not a significant factor in determining invertebrate community structure. Instead, environmental variables such as pH and resource availability as well as pool size and location were more important factors for community assemblage. These results give interesting insight into the mechanisms driving community structure in rock pools and may inform future studies on which factors are important when studying species distributions on rock outcrops.

This thesis highlights the uniqueness of rock pools as container habitats. They are often removed from vegetative cover and subsequently are exposed to sunlight and have limited input of detrital resources, making them environmentally variable and unpredictable habitats for the invertebrates colonizing them (Jocque et al. 2010). The aquatic invertebrates inhabiting rock

pools are therefore highly specialized and adapted to deal with the stressful environment (Brendonck et al. 2016). While research quantifying the contribution of rock pool communities to the regional fauna has not been undertaken, it's likely that rock pools support a significant portion of the local populations of container-dwelling mosquitos and midges. Due to the specialized nature of these taxa (Brendonck et al. 2016), it's unlikely that large populations inhabit other aquatic habitats in the area such as ponds or rivers. The destruction of rock outcrops and the rock pools situated on them therefore has potentially serious implications for the conservation of invertebrate diversity (Porembski et al. 2016). Specific to riverine rock pools, the creation of dams may cause water levels to rise and cover entire rock outcrops, rendering the rock pools on the outcrop functionally destroyed. This was the case for many rock outcrops along the Penobscot River, as inspection of aerial photographs indicate that the rock pool outcrops sampled in this thesis have only recently become exposed again after the removal of several dams. Though the aquatic invertebrates inhabiting rock pools have been little studied, they are undoubtedly diverse and highly specialized to these unique habitats. Rock pools are often overlooked, but their conservation is vital to the survival of their specialist taxa.

Continued work on rock pool communities is desperately needed. Very few surveys of rock pool invertebrates have been conducted and the breadth of their diversity is still poorly known (Jocque et al. 2010). This thesis helped shed light on the diversity of invertebrates in rock pools along the Penobscot River, however it is unknown if similar patterns of diversity will be observed in other parts of Maine and the northeastern United States. Other mechanisms important for determining community structure, such as active and passive dispersal and resource limitation, are still fairly unexplored in rock pools relative to other larger aquatic environments like vernal pools and ponds. These two thesis chapters aimed to set a baseline of

knowledge on riverine rock pools in Maine and did so successfully. The future directions of rock

pool research building upon this baseline are all but boundless, but I believe that a mix of

community surveys and manipulative experiments will likely best serve to continue

understanding invertebrate diversity in rock pools and the mechanisms responsible for

influencing it.

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BIOGRAPHY OF THE AUTHOR

Chase Gagne was born in Concord, New Hampshire in March, 1995. He was raised in Goffstown, New Hampshire and spent large parts of his childhood catching spiders in plastic bottles and attempting to rear entire webs of eastern tent caterpillars in (poorly) sealed hamster cages. After graduating from Goffstown High School, he attended the University of Maine for his undergraduate career and pursued a Bachelor's degree in Wildlife Ecology. During the program's May term field course, he conducted a small study with Karla Boyd on the effects of forest succession on ground-dwelling invertebrate communities. Doing this project inspired him to seriously pursue entomology as both a hobby and a lifestyle. Over the last two years of his undergraduate career, Chase worked several jobs throughout the entomology department including working with pests such as browntail moth, European fire ant, and winter moth. He completed an undergraduate Honors thesis in May 2017 on riverine rock pools and ended up with more questions about those little container habitats than he started with. As a result, he continued on with the same study system at the University of Maine and attempted to further understand riverine rock pools He is a candidate for the Master of Science degree in Entomology from the University of Maine in December 2019.