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## Hydrology and Aquatic Invertebrate Communities of Riverine Rock Pools: Effects of Seasonality and the Penobscot River

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HYDROLOGY AND AQUATIC INVERTEBRATE COMMUNITIES OF RIVERINE  
ROCK POOLS: EFFECTS OF SEASONALITY AND THE PENOBSCOT RIVER

by

Chase Gagne

A Thesis Submitted in Partial Fulfillment of the Requirements for a Degree with Honors

(Wildlife Ecology)

The Honors College

University of Maine

May 2017

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## **Abstract**

Small pools on rock outcrops are a common feature on the banks of Maine rivers, however the unique aquatic insects inhabiting these rock pools have been little studied. This is problematic, as climate change is altering seasonal river flooding and rainfall patterns that may control pool filling and drying. These changes may impact potentially unique species in these pools, or make them more susceptible to invasion by disease vectors such as mosquitos. This project surveyed the insect communities of 40 natural pools in a rocky outcrop on the Penobscot River near Milford. The pools were spread between four zones: two zones that were close to the river (A and B) and two zones that were out of the range of summer flooding (C and D). Both the physiochemical and biological aspects of pools were influenced by their distance to the river. The amount of both fine and coarse detritus was significantly greater in pools farther from the river than those pools near the river. Conductivity, pH, and the amount of time pools held water varied significantly across zones. Pools closer to the river had higher pH and were inundated longer than pools farther from the river. Conductivity showed different patterns, with pools of intermediate distance from the river having lower conductivity than those at either end of the gradient. Invertebrate communities reflected differences in environmental conditions among zones. Pools that were close to the river were dominated by river-dwelling taxa during the summer and pools that were farther from the river were dominated by mosquito and midge larvae. Pools became more similar in the fall as pools near the river lost some or all of their lotic specialist taxa found within them, with the second zone near the river losing all lotic-specialized taxa. Changes in river flow regimes

and rainfall patterns are likely to affect the hydrology of riverine rock pools and therefore will likely alter the structure of these unique insect communities

## **Dedication**

I dedicate this work to my parents, Jeff and Kami. Thank you for pushing me to be my best, encouraging me to follow my dreams, and for letting me use the China hutch to store my insect collections

## **Acknowledgements**

I'd like to acknowledge Hamish Greig for offering his guidance over the last year as I worked on this thesis and for allowing me to use his lab space and equipment to identify bugs (and many other insects) and collect various other data. I'd also like to acknowledge all those who helped me collect samples in the field and those who spent long hours picking the insects out of murky samples. Lastly, thank you to my committee members for providing their feedback and constant support throughout the creation of this thesis.

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## INTRODUCTION

Depressions 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 easily observed in Maine as they are ubiquitous along rivers that have mainly rocky banks. These rock pools are often filled with freshwater from rain or snowmelt, but can also be periodically filled through flooding events from nearby rivers. The amount of time that rock pools can hold water can vary widely depending on pool morphology and catchment, and the hydroperiod can range from less than one week to greater than ten weeks (Jocque et al. 2007a, Brendonck et al. 2016) .

Rock pools are often colonized by aquatic invertebrates, although the species comprising the potentially unique communities of these habitats have been seldom studied globally (Williams 2006) and are unstudied in Maine. Rock pools typically have a surface area less than one square meter, usually occur in exposed locations, and have highly variable hydroperiods. Pools are therefore likely only colonized by specialized taxa that possess unique traits to enable them to persist. A total of 480 species are currently known globally to occur in rock pools (Jocque et al. 2010b). However, this number does 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, Jocque et al. 2010a, Brendonck et al. 2016).

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 and Kolasa 2002,

Williams 2006, Calabrese et al. 2016). Pools that are less variable in pH, temperature, dissolved oxygen, and salinity are richer in diversity (Romanuk and Kolasa 2002). The size of the pool can also affect invertebrate communities. Larger pools typically contain more diverse communities (Oertli et al. 2002, Ripley and Simovich 2009) and some species only occupy the largest pools present in an area (Pajunen and Pajunen 2007). Nutrient enrichment, such as 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 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).

Hydroperiod also plays a major role in shaping invertebrate communities. 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, Brendonck et al. 2015, Egan and Ferrington 2015, Ptatscheck and Traunspurger 2015). Larger pools dry slower 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). Both pool size and hydroperiod are clearly important in shaping aquatic invertebrate communities, but separating their relative effects is difficult.

The hydrology and invertebrate communities of rock pools can be influenced based on their proximity to a larger body of water, such as a river, lake, or ocean. Pools farther away from a large body of water become more variable in terms of both water

chemistry and hydrology (Egan et al. 2014). Subsequently, the species composition of invertebrate communities changes as the distance of rock pools from larger bodies of water increases (Egan and Ferrington 2015). Pools that are close to a larger body of water have less of a chance of drying out because of splash and flooding, and therefore are able to support a more diverse invertebrate community (Therriault and Kolasa 2001, 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.

The invertebrate communities of rock pools may also be influenced by seasonal changes in water chemistry, resource availability, and temporal variation in the life histories of different species inhabiting the same pool. Inputs of detritus can vary between seasons, especially in temperate climates (Higgins and Merritt 1999, Bennion and Smith 2000). Ponds that contain high levels of detritus typically have a lower pH than those that contain less detritus, which influences the taxa that are able to persist in the pond (Higgins and Merritt 1999, Bennion and Smith 2000, Batzer et al. 2004). The effect of seasonality on resource availability and hydrology in rock pools remains understudied. Community structure can 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. Thus, the taxa that are present in the pool change over the course of a season (Jocque et al. 2007b, Vanschoenwinkel et al. 2010).

With climate change, flooding events are expected to become more frequent over time in the northeastern United States (Armstrong et al. 2012). This would cause more scouring of sediment and detritus, decreasing the ability for invertebrates to become established but potentially increasing deposition of river-dwelling taxa. Warmer temperatures and more variable rain patterns (Jacobson et al. 2009) may also cause an increase in the desiccation frequencies of rock pools that do not receive inputs of river water. This holds the potential to decrease the abundance of species that are not adapted to highly ephemeral habitats. With lowered diversity, invasive species may be able to invade rock pools more easily (Pfisterer et al. 2004) .

I surveyed habitat characteristics and invertebrate communities in 40 rock pools to address the following objectives: (1) determine how rock pools vary in hydrology and insect communities, (2) determine the effects of a nearby river system on insect community structure, and (3) to determine if insect communities and their relationship with rock pool habitat characteristics vary between summer and fall.

## **METHODS**

### **Study Area**

The study area was an exposed rock outcrop along the banks of the Penobscot River, about 1.2km downstream of the Milford dam. The outcrop, which forms rock benches of different elevations, was divided into four areas (A-D) based on distance from the river's edge, with A being the closest to the river's edge and D being the farthest

away from the river's edge (Figure 1). During spring flooding, most of zones A and B were covered by the river whereas zones C and D were elevated above the river's flood levels, as evidenced by a high-water mark of lichen and moss on the rocks that indicated long-term average flood height. Pools in zones C and D were also near the riparian edge, and their basins were often lined with moss and overhung by grasses and shrubs. Iron chains drilled into the rocks leftover from past logging operations were common around the outcrop. When the river was low, about 100 pools capable of holding water were present across the outcrop, with the majority being less than 1 m<sup>2</sup> in surface area.



**Figure 1.** The study site as seen from Zone D (i). Visible are zones A and B, zone C is out of the right side of the frame. Photos ii-v show representatives of Zones A-D, respectively.

## **Field Methods**

Forty rock pools were selected for the study. Pools were spread unevenly across the four areas of the outcrop, so we selected 16, 10, 7, and 7 pools for areas A, B, C, and D, respectively, based on their relative abundance. If there were many more pools in an area than what was planned for sampling, pools were selected to represent the range of pool sizes and shapes in the area. In the summer, pool sampling began on June 9 and was completed on June 30, so all pools were sampled within 21 days. In the fall, pool sampling began on September 21 and was completed on October 5 and thus all pools were sampled within 14 days.

During each sampling period, conductivity and pH were measured using a Hach HQ40d hand-held water chemistry meter. Aquatic insects and detritus were then sampled by stirring the pool water and sweeping the entire basin of each pool with a 500 $\mu$ m aquarium net through the water. If a pool was larger than 1m<sup>2</sup>, this sweeping procedure was performed within a 34 x 35 cm quadrat that was placed randomly in the pool. Samples were preserved in 70-80% ethanol. Each pool was photographed on the sampling date, and a water bottle placed adjacent to the pool provided a scale for the estimation of pool area using image analysis in Adobe Acrobat Pro. Pool maximum depth was measured on the sampling date and then on average every four days from July 5 until October 5. Pools were assumed to contain water until they were observed as dry and were assumed to stay dry until the next time they were observed with water.

## **Laboratory Methods**

All aquatic insects, excluding Chironomidae and Culicidae, were identified to genus using Peckarsky (1990). Culicid larvae were identified to species using Andreadis et al. (2005). Chironomids were not identified past the family level. Individuals were picked from the samples by hand and were identified under 10x – 63x magnification.

If samples contained a high abundance of one or more taxa, subsampling was done by placing the sample in a tray with a 1cm x 1cm grid. Individuals of one taxon were picked from randomly selected grid cells until 200 individuals were collected for identification. Abundance of the taxon in the full sample was then estimated by assuming the density was constant across grid cells and dividing by the proportion of grid cells sampled.

Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) were placed back into ethanol after all insects were removed. They were later sieved to separate FPOM from CPOM, dried at 60° C for 72 hours, and then weighed to determine dry mass.

### **Statistical Methods**

All data were analyzed using R version 1.0.136. Univariate analyses consisted of two-way ANOVAs to compare the relations between physical and biological response variables with zone (A-D) and season (summer and fall) and their interaction as categorical predictors. Conductivity, number of days the pools were filled, pH, CPOM, FPOM, and the abundance of lotic taxa were  $\text{Log}_e + 1$ -transformed prior to analysis to meet assumptions of normality. Lotic taxa were defined as those that are associated with

flowing water based on descriptions by (Merritt et al. 2008). Prior to analysis, taxa abundance, CPOM, and FPOM were scaled to units per square meter of pool surface area to enable comparisons among pools of different sizes and between pools sampled with quadrats vs. those in which the whole pool was sampled.

Redundancy analysis (RDA) was used to assess the role of environmental variables and season in determining the abundance and distribution of taxa across zones. The ordination was created on the species abundance matrix of all taxa found within all 40 pools. Species abundance data were  $\text{Log}_e +1$ -transformed prior to performing the ordination to meet the assumptions of normality. The matrix of environmental variables included pH, conductivity, CPOM, the number of days the pools were filled, the pool zone, and the season of sampling. FPOM was not included in the environmental matrix for the ordination because it was highly correlated with CPOM. A permutation ANOVA test (200 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”.

## RESULTS

### Environmental variables

The average number of days that rock pools contained water differed significantly by zone ( $P = 0.022$ ; Table 1), with pools in Zone C containing water for the least number of days ( $\bar{X} = 66.1 \pm 13.7$ ) and pools in Zone A containing water for the greatest number of days ( $\bar{X} = 85.8 \pm 3.3$ ; Figure 2).



Dry mass of CPOM, dry mass of FPOM, and pH all varied significantly by zone (Figure 3a, 3b, 3d; Table 1,  $P < 0.0001$ ). Zones C and D had greater of amounts of FPOM and CPOM, likely owing to the higher abundance of vegetation in and around the pools. pH was highest in Zone A and decreased across zones moving away from the river. Only pH differed significantly by season ( $P = 0.013$ ; Table1), owing to a general increase in pH from summer to fall in all zones (Figure 2d). There was some support for differences in conductivity across zones ( $P = 0.08$ ; Table1), with pools in Zones D and A having higher conductivity than intermediate zones, but variability was high within zones (Figure 3c).

### **Invertebrate diversity and abundance**

37 unique taxa representing 21 identified families and 7 orders were identified out of a total of 8015 individuals that were collected from all 40 rock pools over the sampling period. Only *Dasyhelea*, *Ochlerotatus atropalpus*, and *O. japonicus* were collected from pools in all four zones. The overall most abundant taxon was Chironomidae ( $n = 3308$ ), followed by *O. japonicus* ( $n = 2242$ ) and *Dasyhelea* ( $n = 1963$ ; Table 2). Together, these taxa alone comprised 93.7% of the total number of individuals collected during the sampling period.

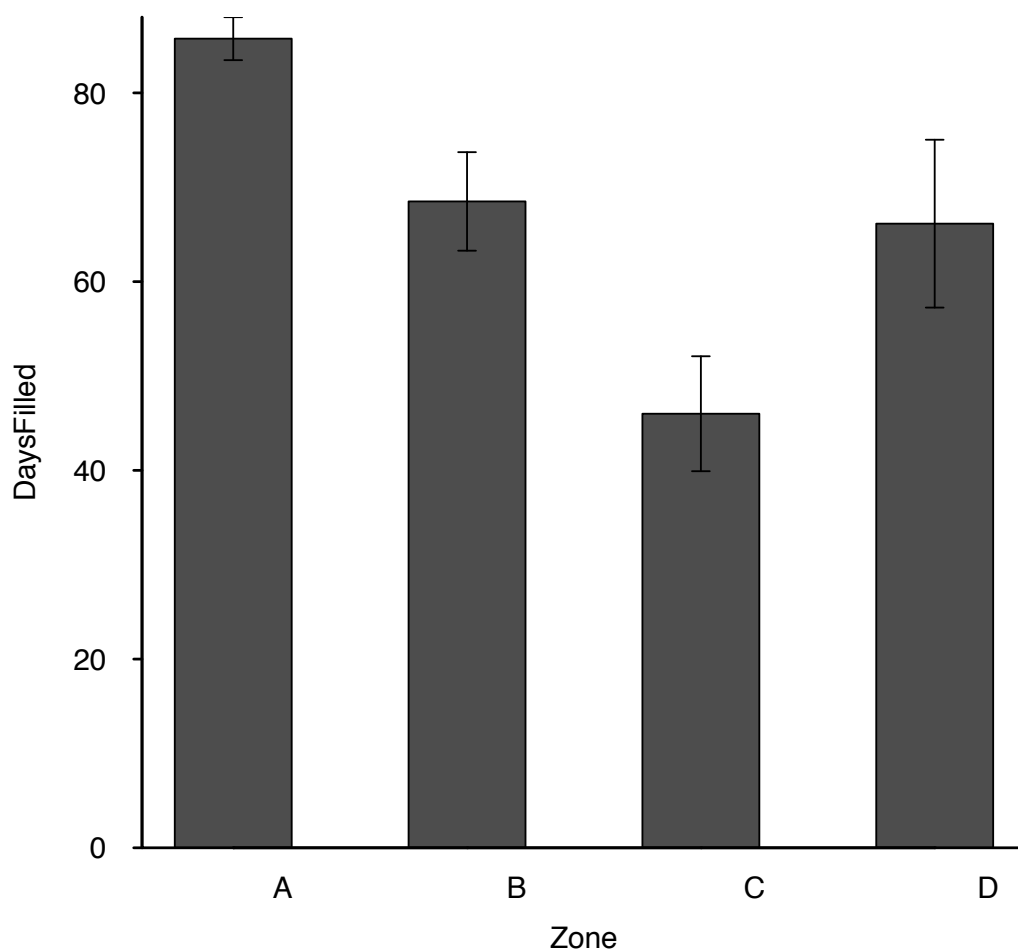
Taxa richness differed significantly by season ( $P = 0.018$ ) and by zone between seasons ( $P = 0.03$ ). Zone A exhibited the greatest absolute richness ( $n = 31$ ) and Zone C exhibited the lowest absolute richness ( $n = 6$ ; Table 2). Pools in Zone B exhibited the highest mean richness in the summer but the lowest mean richness in the fall (Figure 4a). Taxa abundance per  $m^2$  differed significantly only between zones ( $P = 0.01$ ), but the

abundance per m<sup>2</sup> of lotic taxa differed significantly between zones ( $P = 0.0005$ ), season ( $P < 0.0001$ ), and by zone between seasons ( $P = 0.001$ ; Table 1). Pools in Zone B also had the highest abundance per m<sup>2</sup> of lotic taxa in the summer, but lost all of these lotic taxa in the fall (Figure 4c). The abundance per m<sup>2</sup> of lotic taxa in Zone A decreased between summer and fall, but lotic taxa were still present at low abundances (Figure 4c).

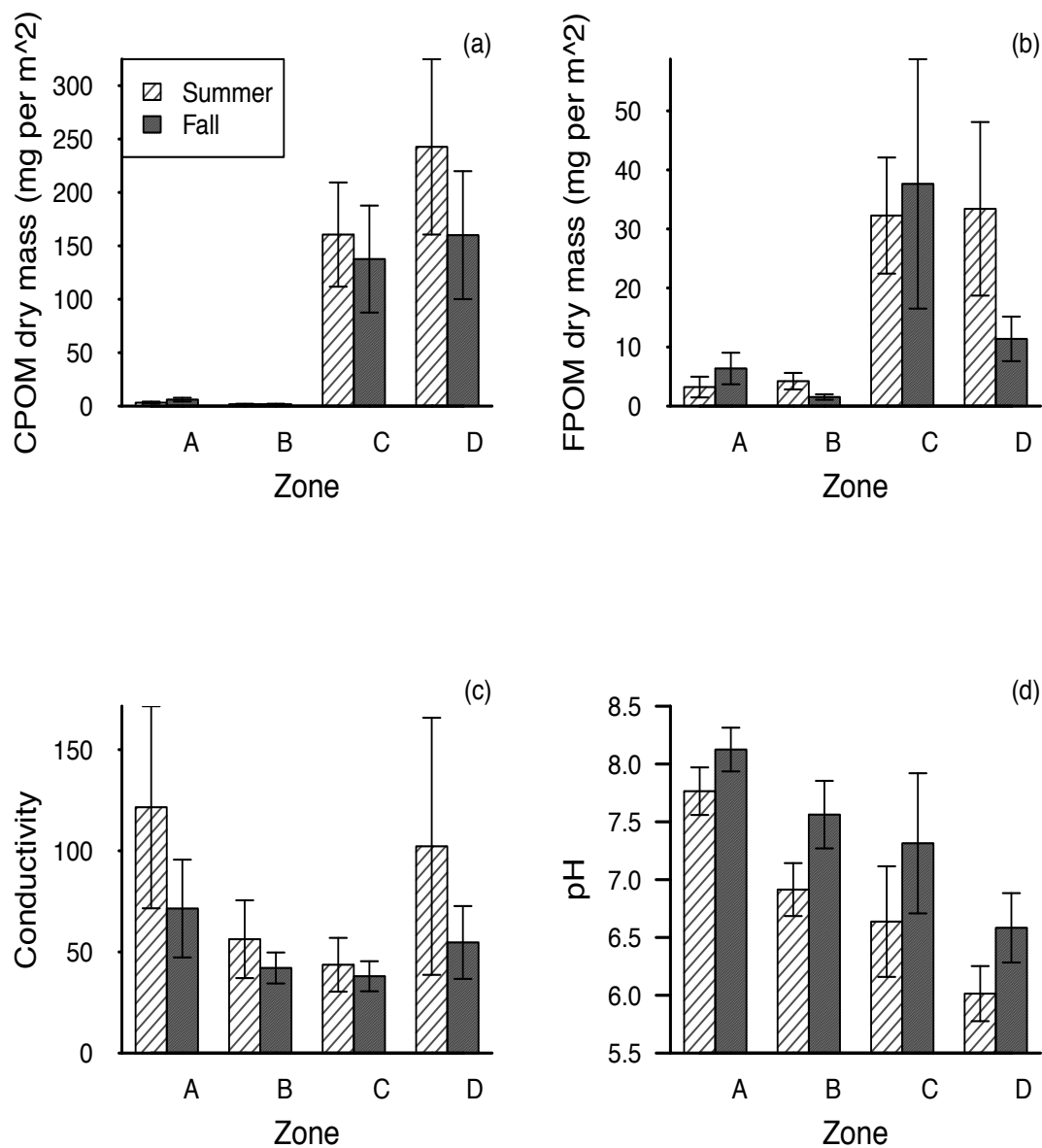
### **Invertebrate community structure**

The aquatic insect communities within the sampled rock pools differed significantly across zones ( $P = 0.001$ ), by season ( $P = 0.013$ ), and the influence of zone was altered by season ( $P = 0.011$ ). Pools in Zones A and B, which were closer to the river, contained a number of lotic taxa in the summer (e.g. *Eurylophella*, *Centroptilum*, and *Siphonurus*), and the predatory beetle *Laccophilus* was also common. In contrast, pools in Zones C and D were dominated by Dipterans (e.g. *Dasyhelea*, *Ochlerotatus* sp.) with only a few predatory taxa occupying a small number of the pools. These stark differences in communities resulted in wider separation between Zones A and B and Zones C and D (Figure 5a). In the fall however, pool communities became less distinct across all zones, as evidenced by the high degree of overlap between all four convex hull polygons that enclosed pools for each zone (Figure 5b). With the sharp decline of lotic taxa in Zones A and B, invertebrate communities in these pools shifted to become dominated by Chironomidae and *Ochlerotatus japonicus*. Similarly, pool invertebrate communities in Zones C and D exhibited a decline in *Dasyhelea* and had increases in abundance of both Chironomidae and *Ochlerotatus japonicus*.

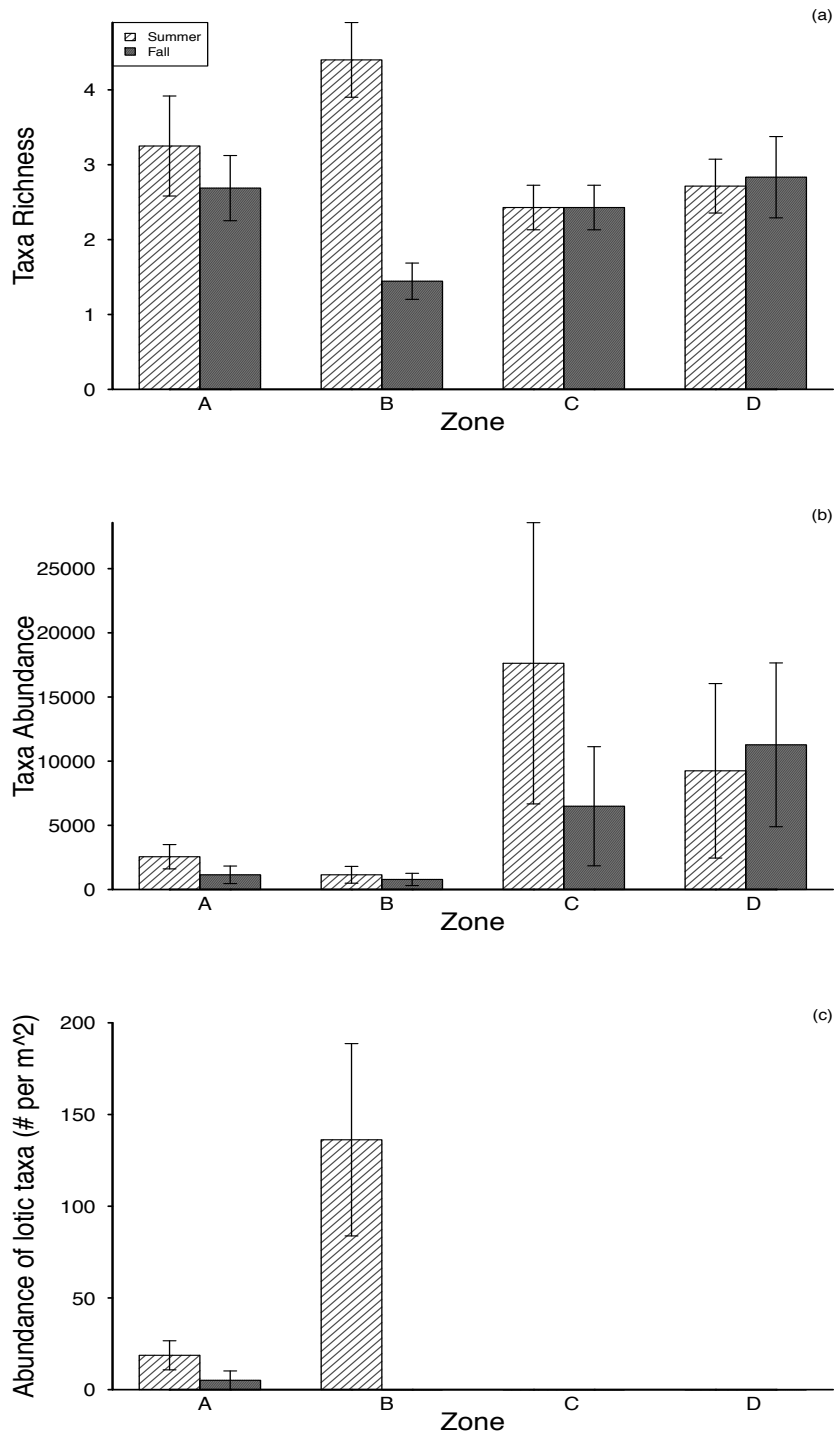
Invertebrate communities were also influenced significantly by pH ( $P = 0.005$ ) and the number of days the pools contained water ( $P = 0.003$ ). The amount of CPOM deposited in the pools did not have a significant effect on community structure ( $P = 0.317$ ; Table 1).



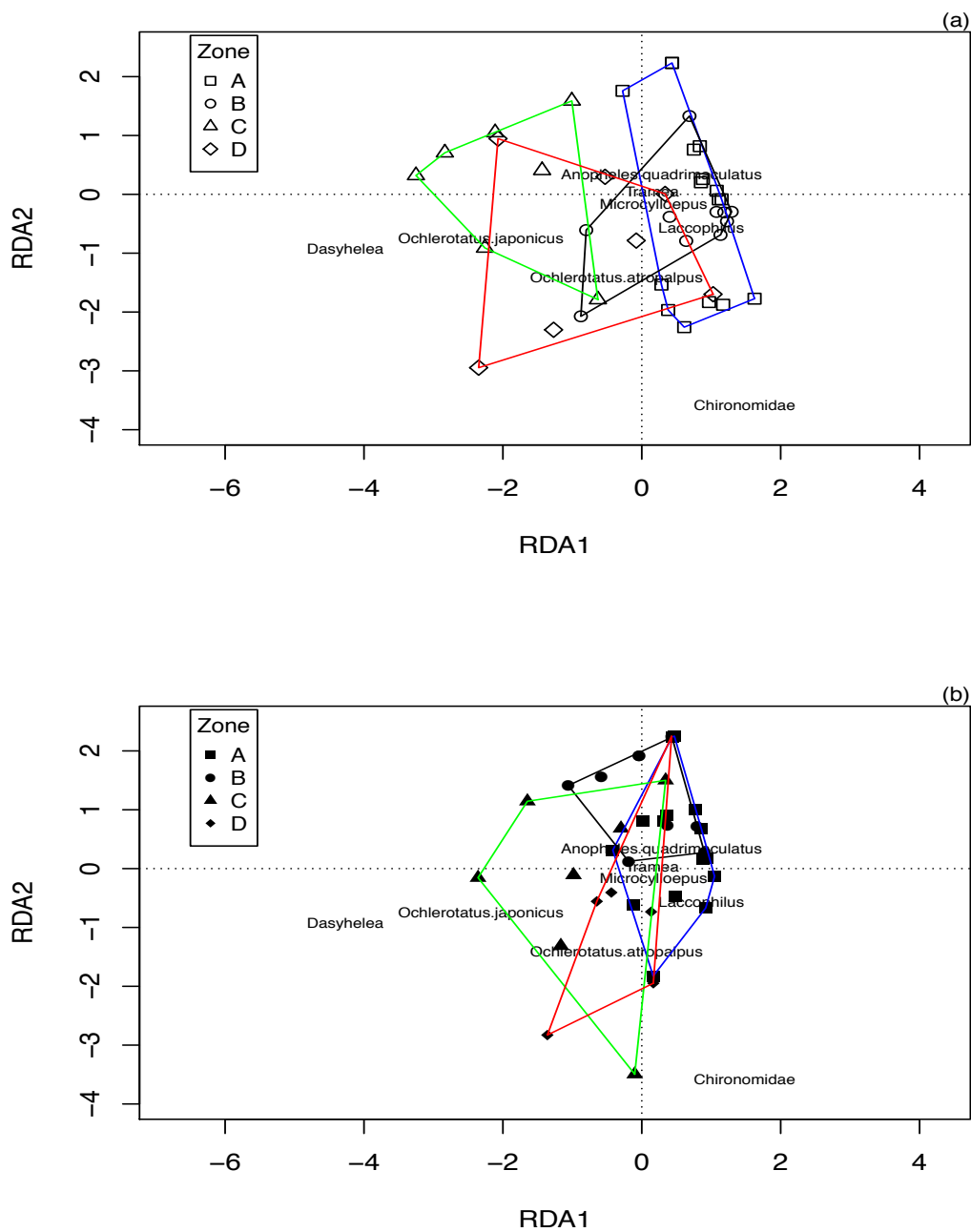
**Figure 2.** Average number of days that rock pools contained water from July 5 to October 5, 2016. Distance of each zone from the river's edge increased sequentially, such that Zone A was closest to the river's edge and Zone D was farthest from the river's edge.



**Figure 3.** Mean (+/1 SE) coarse particulate organic matter (CPOM) (a), fine particulate organic matter (FPOM) (b), Conductivity (c), and pH (d) measurements from 40 rock pools distributed among four zones (A-D) for both fall and summer. Zone distance from a river's edge increased sequentially, such that A was closest and D was farthest. Means are calculated with pools as replicates.



**Figure 4.** Mean ( $\pm 1$  SE) taxa richness (a), total taxa abundance per m<sup>2</sup> (b), and abundance of lotic taxa per m<sup>2</sup> (c) collected from 40 rock pools distributed among four zones (A-D) during fall and summer. Zone distance from the river's edge increased sequentially, such that Zone A was closest and D was farthest.



**Figure 5.** Ordination plots constructed from redundancy analyses (RDA) comparing taxa abundance and environmental variables during summer (a) and fall (b). Pools are plotted as points and taxa shown are the most important (dominant) in the community as identified by Simpson's diversity index. Convex hull polygons are drawn around the points of each zone to show the degree of overlap or separation between the pools of each zone. Blue = A, black = B, green = C, red = D.

**Table 1.** Two-way ANOVA results for the influence of Zone and Season on biotic and environmental response variables. Zone refers to four pool zones increasing in distance from a river's edge and period refers to the effect of summer and fall. P-values in bold indicate significant results for  $P \leq 0.05$ .

<b>Response</b>	<b>Factor</b>	<b>Df</b>	<b>F value</b>	<b>P value</b>
Richness	Zone	3	0.40	0.753
	Season	1	5.88	<b>0.018</b>
	Zone $\times$ Season	3	3.15	<b>0.030</b>
Abundance	Zone	3	4.11	<b>0.010</b>
	Season	1	0.78	0.380
	Zone $\times$ Season	3	0.88	0.456
Lotic Taxa	Zone	3	6.74	<b>0.0005</b>
	Season	1	21.24	<b>&lt;0.0001</b>
	Zone $\times$ Season	3	5.87	<b>0.001</b>
Conductivity	Zone	3	2.34	0.080
	Season	1	0.65	0.423
	Zone $\times$ Season	3	0.32	0.813
pH	Zone	3	12.37	<b>&lt;0.0001</b>
	Season	1	6.45	<b>0.013</b>
	Zone $\times$ Season	3	0.19	0.904
CPOM	Zone	3	74.05	<b>&lt;0.0001</b>
	Season	1	1.20	0.278
	Zone $\times$ Season	3	0.78	0.508
FPOM	Zone	3	18.29	<b>&lt;0.0001</b>
	Season	1	0.34	0.562
	Zone $\times$ Season	3	2.33	0.081
Days Filled	Zone	3	3.63	<b>0.022</b>
RDA	Zone	3	6.92	<b>0.001</b>
	Season	1	3.26	<b>0.013</b>
	CPOM	1	1.13	0.317
	pH	1	3.79	<b>0.005</b>
	Days Filled	1	4.54	<b>0.003</b>
	Zone $\times$ Season	3	1.91	<b>0.011</b>

**Table 2.** Summary of taxa identified from 40 rock pools along the Penobscot River in Milford, Maine. Shaded cells indicate that at least one individual was found in at least one pool in the specified zone (A-D) during at least one sampling occasion. Zones increased sequentially in distance from the river's edge, such that Zone A was closest and Zone D was farthest. Total taxa richness and abundance values are given in the bottom row. Blank cells in the Genus column indicate taxa that were not identified past the family level and count as a single taxon for the genera richness. Taxa for which the family could not be identified did not count towards either family or genus-level richness.

Order	Family	Genus	Abundance	A	B	C	D
Ephemeroptera	Baetidae	<i>Centroptilum</i>	33	■	■		
		<i>Cloeon</i>	8	■			
	Caenidae	<i>Caenis</i>	8	■			
	Ephemerellidae	<i>Eurylophella</i>	66	■	■		
	Heptageniidae	<i>Leucrocuta</i>	2	■	■		
		<i>Macdunnoa</i>	1		■		
		<i>Maccaffertium</i>	5	■			
	Leptophlebiidae	<i>Paraleptophlebia</i>	3	■			
Siphonuridae	<i>Siphonurus</i>	12	■	■			
Odonata	Corduliidae	<i>Cordulia</i>	16	■			■
		<i>Neurocordulia</i>	4	■			
	Libellulidae	<i>Sympetrum</i>	3	■			
		<i>Tramea</i>	7	■			
	Coenagrionidae	<i>Enallagma</i>	20	■			
Hemiptera	Corixidae	<i>Hesperocorixia</i>	4	■			
	Notonectidae	<i>Notonecta</i>	1	■			
Megaloptera	Sialidae	<i>Sialis</i>	1	■			
Coleoptera	Curculionidae		1	■			
	Dytiscidae	<i>Acilius</i>	9	■	■	■	■
		<i>Copelatus</i>	5	■	■		
		<i>Cymbiodyta</i>	1				■
		<i>Hydroporus</i>	2		■		■
		<i>Illybius</i>	2	■			
		<i>Laccophilus</i>	69	■	■		
	Elmidae	<i>Microcylleopus</i>	5	■	■		
		<i>Stenelmis</i>	7	■			
Hydrophilidae	<i>Berosus</i>	1	■				
Trichoptera	Calamoceratidae	<i>Heteroplectron</i>	1	■			
	Polycentropodidae	<i>Neureclipsis</i>	1	■			
	Unknown		4	■			
Diptera	Ceratopogonidae	<i>Dasyhelea</i>	1963	■	■	■	■
		<i>Leptoconops</i>	12			■	
		<i>Probezzia</i>	1		■		
	Chironomidae		3308	■	■	■	■
	Culicidae	<i>Anopheles quadrimaculatus</i>	12	■			
		<i>Culex territans</i>	54				■
		<i>Ochlerotatus atropalpus</i>	121	■	■	■	■
		<i>O. japonicus</i>	2242	■	■	■	■
<b>7</b>	<b>21</b>	<b>37</b>	<b>8015</b>	<b>31</b>	<b>17</b>	<b>6</b>	<b>9</b>



## DISCUSSION

My results indicate that natural rock pools vary both in their hydrology and in the structure of their invertebrate communities, and much of the variation appeared to also be reliant upon the distance of the rock pools to the nearby river system. Hydroperiod decreased as distance to the river increased, but only to a point as the average hydroperiod length increased again in the farthest pools. Effects of the riparian zone farther from the river were apparent as the dry mass of both CPOM and FPOM were significantly higher in Zones C and D than in Zones A and B and these inputs were likely a factor in the steady decrease in pH as distance to the river increased. Invertebrate communities varied between pools and were also dependent on the distance to the river. Lotic taxa were abundant in pools that were inundated by the river and were absent in pools that were not inundated by the river, clearly indicating that the river system has a role in shaping invertebrate communities of rock pools. However, seasonality had an effect on invertebrate communities as the lotic taxa declined in Zones A and B and *Dasyhelea* declined in Zones C and D between the summer and the fall, increasing community similarity between pools close to and far from the river. Below I consider the mechanisms underlying these responses and interpret their implications for rock pool communities in a changing climate.

### **Environmental variation among rock pools**

Hydroperiod varied substantially among pools and zones, and was a significant factor in determining the richness and composition of aquatic invertebrate communities; a finding which agrees with numerous studies (Bazzanti et al. 1996, Schneider and Frost

1996, Higgins and Merritt 1999, Spencer et al. 1999, Brooks 2000, Therriault and Kolasa 2001, Romanuk and Kolasa 2002, Batzer et al. 2004, Jocque et al. 2007, Waterkeyn et al. 2008, Vanschoenwinkel et al. 2009, Fontanarrosa et al. 2009, Brendonck et al. 2015, Brendonck et al. 2016). Rock pool morphology plays an important role in the length of a pool's hydroperiod, with deeper pools or those with smaller surface-area-to-water ratios holding water for longer stretches of time (Brendonck et al. 2016). The depths of the rock pools in our study had average max depths between 11 and 16cm with variation within zones. Thus, while it is unlikely that pool depth varied significantly by zone, it undoubtedly played a role in determining the lengths of hydroperiods of individual pools. Exposure of rock pools to evaporation, watershed properties that determine runoff collected during rain events, and proximity to river water during floods likely had a stronger influence on how long pools can hold water. Many of the pools in Zones A and B were located on slopes where rainfall runoff would be channeled into flow paths and enter pools, in addition to likely being flooded by the river during stronger rain events. Pools in Zones C and D were located on the top of the rock outcrop, and their smaller watersheds likely limited the amount of runoff they could collect during rainfall. These pools resided above presumed long-term flood levels, so they did not receive any river water when it flooded, even during stronger rain events. Additionally, Zone D had more bushes and grasses overhanging the pools than Zone C. This extra shade and humidity that the vegetation provided may have contributed to pools in Zone D remaining filled for longer durations than pools in Zone C. Several pools, especially those in Zone C, dried and filled multiple times throughout the study. On one sampling occasion, 20 out of the 40 pools included in the study were completely dry, but all of them refilled within two

weeks. Over the course of the study period, 23 of the 40 pools monitored dried out at least once. The rest of the pools, at least one in each zone, were able to hold water for the entirety of the study period. Thus, there was considerable variation in pool hydrology with respect to both inundation frequency and the duration the pools held water once filled.

The pH of the pools varied significantly by zone, and these patterns are consistent with differences in detritus inputs observed in pools; that is, pools in Zones C and D had consistently lower pH values and greater quantities of detritus than pools in Zones A and B. However, the rise in pH between the summer and fall was unexpected. The most likely explanation is that detritus accumulates in the fall and winter while the pool is dry and breakdown processes are slowed by lower temperatures. When the pools are inundated in the spring and early summer, organic acids, such as humic and fulvic acids, leach from the leaves and the concentrations of acids is higher, thus lowering pH (Higgins and Merritt 1999, Bennion and Smith 2000, Batzer et al. 2004). Over the summer and into the fall, repeated inputs by rain, river flooding, and runoff, as well as the breakdown of organic acids by bacteria, reduces the concentration of acids present in the pool, thus raising pH in the fall before the majority of fall abscission occurs. Primary production from benthic algae that has established by the fall could also cause a rise in pH due to the consumption of dissolved CO<sub>2</sub> (Allan and Castillo 2007). Differences in the biomass of detritus held in the pools is most likely due to differences in the amount of vegetation surrounding pools and the proximity to the river riparian zone. Zones C and D had much more vegetation overhanging the pools than Zones A and B and were also adjacent to large riparian trees. These differences, especially in the vegetation immediately adjacent

to the pools is likely linked to flood scour that occurs in pools closer to the river. In addition, flooding events from the river may have regularly scoured any detritus that happened to be deposited into the pools in Zones A and B.

Conductivity was higher in Zones A and D and lower in the intermediate zones. Though this variation between zones was not considered significant, conductivity was still likely influenced by the river. Pools in Zone A that were flooded often likely had conductivity resembling that of the Penobscot River, which is a major collector of road salt and additional urban runoff. Pools in Zone D likely had higher conductivity values due to more nutrient input from the surrounding vegetation, however this mechanism would need to be tested in the future to draw confident conclusions. The overall decrease in conductivity across all zones between the summer and fall is likely because nutrient concentrations were declining as they became incorporated into insect tissue and then removed through emergence (Jocque et al. 2010). Evaporation may have also been at a higher rate in the summer than in the fall, increasing the concentration of ions as water levels were lower at the time of water chemistry analysis.

### **Spatial and temporal variation in rock pool communities**

Aquatic invertebrate diversity in the rock pools was higher than expected, especially when it came to the diversity of lotic taxa that were found to be deposited in them. The presence of lotic taxa played a major role in community variability between zones, as did the variation in abundances of certain taxa between the summer and fall. Communities also varied between pools that exhibited different sets of environmental characteristics.

The differences in the abundance of individuals collected from each zone were primarily driven by the number of Dipterans present, namely *Dasyhelea*, *Ochlerotatus japonicus*, and Chironomidae. These taxa reached high abundances and dominated the invertebrate communities in Zones C and D, but were at much lower abundances in Zones A and B. This is potentially because there was a higher abundance of predatory taxa in Zones A and B than in Zones C and D. Lentic habitats with longer hydroperiods tend to support a higher abundance and diversity of large predators, because these taxa require additional time to complete their life cycles (Wellborn et al. 1996). The effect of predators is therefore likely to be much more significant than in pools with shorter hydroperiods (Schneider and Frost 1996, Spencer et al. 1999). In addition, many predators in longer-lived pools tend to select for more vulnerable prey species that generally dominate pools with shorter durations. This prey selection likely played a role in limiting abundances in pools with longer hydroperiods (Schneider and Frost 1996). The predatory beetle *Laccophilus* was present and numerous in only Zones A and B, and *Enallagma* damselflies were found only in Zone A. Both of these taxa are predators of larval Diptera and likely played a role in limiting their abundances in the pools in Zones A and B. *Dasyhelea* may have also been highly abundant in pools in Zones C and D because of the greater amounts of detritus present. *Dasyhelea* is known to be able to colonize rock pools and become established more easily when detritus is present and abundant (Romanuk and Kolasa 2005).

Environmental stressors, such as short hydroperiod or low pH, likely impacted the species richness of pools in Zones C and D and their differentiation from the riverside pools in community composition. Diptera are well adapted to living in highly ephemeral

habitats due to their generally short life cycles (Williams 1996) and the ability for some species of *Dasyhelea* to produce desiccation-resistant eggs that can persist in the basin sediment during dry periods (Brendonck et al. 2016). In contrast, Zones A and B were dominated by lotic taxa in the summer, likely a result of deposition from receding flood waters. However, the sharp decline in these taxa from the summer to the fall may be because lotic taxa are not well suited for the high environmental stress and variability of rock pool habitats. In addition to mortality of lotic taxa between summer and fall, many individuals may have emerged early to escape the stressful environment; a response potentially facilitated by the warmer water of the pools compared to the main-stem river (Drummond et al. 2015). The presence of several Plecopteran exuviae on the edges of many of the pools in Zones A and B provides support for these hypotheses. Moreover, although my sampling occurred soon after a flooding event, no live Plecoptera were found in the recently inundated pools and new exuviae were present on the pool sides. Exuviae from other taxa, such as Ephemeroptera and Megaloptera, were also frequently collected in the water column during sweeping. Taxa with the ability to crawl short distances over land, such as Megalopterans, may have spent a short time in the pools before dispersing to adjacent pools or back to the river. Differences in invertebrate communities between pools close to the river and pools farther from the river are therefore likely driven by interactions between flexible life histories and riverine dispersal of certain taxa, as well as environmental harshness.

The richness and abundance of invertebrates likely also changed between seasons because of the timing of life histories of different taxa. Temporal niche partitioning (i.e. when two functionally similar taxa employ different life history strategies so that they are

not competing for the same resources at the same time) is important to alleviate competition between species trying to exploit the same resources, especially in small container habitats (Jocque et al. 2007, Vanschoenwinkel et al. 2010). This is best reflected in the seasonal variation of *Dasyhelea* abundance, which decreased by over 97% between sampling periods, yet it was collected from only three fewer pools in the fall compared to the summer. In the near absence of *Dasyhelea* in the fall in Zones C and D, the abundance of both Chironomidae and *Ochelerotatus japonicus* mosquitos collected in Zones C and D increased by 29% and 33%, respectively. This suggests that some degree of temporal partitioning was evident in these pool communities.

The abundance of *O. japonicus* increased in all zones and nearly doubled overall between the summer and fall. One mechanism for this striking seasonal increase is that sampling may have occurred during the tail end of a peak larval development time in the fall but not in the summer. In southern New Hampshire, *O. japonicus* is known to have two main brood cycles, the first being from mid-April to mid-May and the second being from early August to mid-September (Burger and Davis 2008). Another potential mechanism is that, as an invasive species, *O. japonicus* may quickly colonize recently disturbed rock pools; my observations indicated that these pools dried and refilled several times between summer and fall. The loss of lotic taxa in Zones A and B also lowered the diversity within those pools, which could have further facilitated the establishment of a second brood of and invasive species such as *O. japonicus* (Parkes and Duggan 2012, Taylor and Duggan 2012). Since its first detection in Cumberland County in 2001, it has spread rapidly to inhabit seven of Maine's sixteen counties (Saunders et al. 2015) suggesting these seasonal colonization dynamics are critical to better understand.

*O. japonicus* was the dominant mosquito species across all rock pools likely because of its ability to outcompete native mosquito species, such as *Ochlerotatus atropalpus*. In a laboratory study, the short larval development time of *O. japonicus* meant that it outcompeted *O. atropalpus* for resources and in population establishment. As a result, populations of *O. atropalpus* declined due to reduced body size of individuals resulting in lower fecundity (Armistead et al. 2008). This same decrease in population size of *O. atropalpus* as a result of competition with *O. japonicus* has been documented in many of the areas in the northeastern United States where *O. japonicus* has become established (Andreadis and Wolfe 2010). Several other native mosquito species are also negatively impacted by the invasion of *O. japonicus*, some declining in abundance by over half since *O. japonicus* was first detected (Andreadis and Wolfe 2010). Our study indicated that rock pools are likely to be an important habitat in which to monitor the establishment and spread of *O. japonicus*, as well as track future population dynamics of native mosquito species in light of an ongoing biological invasion.

With future climate change, warmer and wetter summers (Jacobson et al. 2009) may cause pools that normally dry quickly to stay filled with water long enough to allow *O. japonicus* to complete development, but not long enough to allow *O. atropalpus* to complete its longer larval development. Inversely, longer hydroperiods may allow more species to colonize the pools, increasing the resistance of pool communities to invasion (Pfisterer et al. 2004). Increased disturbance frequency caused by an increasing frequency of river floods (Armstrong et al. 2012) may cause pools closer to the river to also become more susceptible to invasion (Hobbs and Huenneke 1992). Studying these



conflicting hypotheses and determining which is likely to occur in Maine is vital to the conservation of the unique invertebrate communities that reside in riverine rock pools.

## CONCLUSIONS

Rock pools along the banks of the Penobscot River in Maine contain diverse and unique aquatic invertebrate communities that vary in relation to distance from the river's edge as well as seasonally between summer and fall. The nearby river system appears to strongly influence the environmental characteristics of pools, which, in combination with the direct deposition of lotic taxa in them during river floods, shapes the composition of invertebrate communities in rock pools. These patterns vary seasonally, and by the fall, a decline in river taxa in the pools closest to the river shapes their community compositions to become more similar between pools close to and far away from the river. The processes structuring these rock pool communities is likely to be strongly influenced by the effects of climate change on precipitation, evaporation, and river flooding. Finally, my research revealed that the invasive mosquito *Ochlerotatus japonicus* is highly dominant in the local mosquito fauna and its potential to extirpate native species, such as *Ochlerotatus atropalpus*, may grow greater with future climate change. Riverine rock pools are deserving of further research as there is still much to learn about the dynamics and conservation of their unique invertebrate communities.

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After graduation, Chase plans to stay at the University of Maine and pursue a Master's degree in entomology, where he will continue his research on the invertebrate communities of riverine rock pools.