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"Island" Attributes and Benthic Macroinvertebrates of Seasonal Forest Pools

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Abstract - Seasonal forest pools (SFPs), also known as woodland vernal pools or simply vernal pools, are common throughout the forests of the northeastern United States. SFPs are inundated during all or part of the period between late fall of one year and late spring to mid-summer of the subsequent year. The pools dry every year or at sufficient frequency to preclude the establishment of fish populations, are preferred breeding habitat for a number of amphibian species, and support a rich, diverse, and abundant macroinvertebrate community. These pools exist as aquatic "islands" in a "sea" of forest, and occur over a range of sizes, degrees of isolation, and hydroperiod lengths. As islands, pool area and isolation should affect the composition of biotic communities. The hydroperiod of ephemeral wetlands has been considered a third "island" attribute and is also known to affect biotic composition. We surveyed aquatic, benthic macroinvertebrates (BMIs) for two years using leaf-packs in 24 SFPs, representing a broad range of surface areas, inter-pool distances (isolation), and hydroperiods. Nearly 35,000 specimens of 76 taxa were enumerated from 198 leaf-pack samples. Chironomidae and Oligochaeta were the most abundant and most common taxa. BMI richness and diversity were positively, but weakly, related to maximum pool surface area, but not to pool isolation. The same results were found for permanent resident and predator taxa. BMI richness and diversity were positively related with pool hydroperiod, as reported from numerous other studies of ephemeral aquatic habitats.

Introduction

The composition of the flora and fauna of islands is affected by island size and by the island's degree of isolation, with size affecting extinction rates and available habitat niches and isolation affecting immigration rates (MacArthur and Wilson 1967). As island size increases, extinction rates decrease and as an island is increasingly isolated, immigration rates decrease. The equilibrium species richness of an island can be modeled by the intersection of these two rates.

While island biogeographic theories were initially demonstrated using marine islands, the concepts have been applied to other isolated habitats including freshwater wetlands (Brose 2001, 2003; De Meester et al. 2005; Ebert and Balko 1987; March and Bass 1995; Ripley and Simovich 2009). Pool size has been shown to positively influence the richness of ephemeral pool snails (Lassen 1975), beetles (Nilsson 1984), chironomids (Driver 1977), and microcrustaceans (Mahoney et al. 1990); however, the effects have typically been

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weak or inconsistent (Holland and Jain 1981, Oertli et al. 2002). The effects of pool isolation are less well documented and, where assessed, have generally been found to be weak (Lopez et. al. 2002, Mahoney et al. 1990, Spencer et al. 2002). Where a significant isolation effect has been found, the results show that invertebrate communities in adjacent sites are more similar than those in distant pools (Briers and Biggs 2005).

The hydroperiod or duration or permanence of the wet phase of ephemeral wetlands has been considered a third island attribute of these systems (Ebert and Balko 1987, Kiflawi et al. 2003, Nilsson 1984, Ripley and Simovich 2009). The recurring dry phase of ephemeral waters precludes the occurrence of fish, and these systems are known for rich and diverse faunal communities, including both vertebrates (Mitchell et al. 2008, Semlitsch and Skelly 2008) and invertebrates (Colburn 2004, Colburn et al. 2008). Hydroperiod has been shown to be the dominant abiotic factor in structuring the invertebrate community of ephemeral wetlands (De Meester et al. 2005, Schneider and Frost 1996, Wellborn et al. 1996, Williams 1997), including seasonal forest pools (Batzer et al. 2004, 2005; Brooks 2000; Schneider 1999). Pool hydroperiod is also positively associated with richness of the breeding amphibian community (Babbitt 2005, Burne and Griffin 2005, Snodgrass et al. 2000).

Temporary pools occur commonly throughout the world (Ramsar 2002, Williams 2006). Temporary pools are typically small and shallow wetlands, characterized by alternating flooded and dry phases, and whose hydrology is largely autonomous (Ramsar 2002). Seasonal forest pools (SFPs; also "woodland vernal pools", Tiner et al. 2002; or simply "vernal pools", Calhoun and deMaynadier 2008, Colburn 2004), occur in every forest region of the United States, and are widely but not regularly distributed in forests of the glaciated northeastern United States and adjacent Canada (Brooks et al. 1998, Palik et al. 2003, Rheinhardt and Hollands 2008). SFPs are highly variable in most attributes, due to differences in climate, geology, hydrology, and other factors (Rheinhardt and Hollands 2008, Tiner et al. 2002). Many SFPs are technically autumnal pools, based on the timing and pattern of inundation (Brooks 2004, Brooks and Hayashi 2002, Higgins and Merritt 1999). The pools partially inundate in the fall with rains on saturated or frozen soil, fill to maximum capacity in the spring following snowmelt, and are generally dry by mid-summer. Most pools are hydrologically isolated and are expressions of direct precipitation and runoff from immediately adjacent uplands (Brooks 2004, Leibowitz and Brooks 2008), although interactions between pool water and local groundwater can also occur, especially in deeper, more porous soils (Palik et al. 2001, Sobczak et al. 2003). Pools can be classified as palustrine, unconsolidated bottom, emergent, or scrub-shrub, seasonally flooded wetlands (Cowardin et al. 1979) or as isolated depressions in the hydrogeomorphic classification system (Brinson 1993, Cole et al. 1997).

An inventory of SFPs on the Quabbin Reservoir watershed in central Massachusetts with information on individual pool size and degree of isolation (Brooks et al. 1998) provided an opportunity to test the theories of island biogeography and the composition of pool fauna. The objectives of this study were to determine if, after controlling for pool hydroperiod, pool surface area and/or inter-pool distance (i.e., isolation) of SFPs in northeastern US forests affect the composition of the benthic macroinvertebrate (BMI) community. We hypothesized that pool size and pool hydroperiod (i.e., permanence) were positively related to BMI richness and diversity and that inter-pool distance was negatively related to BMI richness and diversity. In addition to total community attributes, we also assessed island effects on invertebrate, predator taxa that have been shown especially sensitive to pool size (Pearman 1995, Spencer et al. 1999, Wilcox 2001) and passively dispersed taxa (e.g., microcrustaceans) that we felt would be particularly affected by pool isolation (Bagella et al. 2010).

Methods

Study area

The study pools were located on the Quabbin Reservoir watershed in central Massachusetts (72º21'W; 42º25'N). The publicly owned watershed is 23,473 ha of undeveloped forestland surrounding the 9713 ha Reservoir, which was created by damming the Swift River in 1938, and is managed by the Office of Watershed Management, Department of Conservation and Recreation (MA DCR 2007). Public ownership comprises approximately 64% of the entire Reservoir watershed. The watershed is composed of glacially sculpted valleys between gneiss domes. Soils are glacially derived and predominantly well drained. The forests are composed principally of *Quercus* spp. (oaks) or *Pinus strobus* L. (White Pine).

An aerial-photography-based inventory identified 430 SFPs on the Quabbin watershed (Brooks et al. 1998). Each identified pool was placed into one of 7 surface-area classes ranging from <0.025 ha to >0.4 ha. Numbers of pools declined rapidly with increasing pool area-class (Brooks et al. 1998). Of the 430 pools, 67% were less than 500 m^2 in surface area, and only 14% were 1000 m^2 or larger. Pool locations were later digitized, and the distance to the nearest-neighbor pool was calculated for each pool in the inventory. The spatial distribution of pools was significantly aggregated, with median distance between nearest-neighbor pools of 243 m and between-pool distances ranging between 19 m and 2.4 km. We have visited most of the pools located on the western (Pelham [PL] and New Salem [NS]) and the central (Prescott [PR]) management blocks of the property to verify the pool's occurrence and to describe general pool and catchment characteristics.

A sample of 24 SFPs was selected for the study. Three replicate SFPs were selected in 3 size classes (<300 m^2, 300–999 m^2, and ≥1000 m^2 maximum surface area) by 3 distance classes (<200 m, 200–999 m, and ≥1000 m to nearest neighbor SFP) (Table 1). Only 2 SFPs were identified in the intermediate size and distance class; no candidate SFPs occurred in the largest size-by-distance class. One additional SFP was selected for the largest size-by-nearest-distance class.

Pool and benthic macroinvertebrate sampling

Maximum SFP surface areas were calculated using data from bathymetric surveys (Brooks and Hayashi 2002). We calculated an index to SFP hydroperiod as the number of periodic visits to a SFP when surface water was present as a proportion of the number of all visits to the SFP (Brooks and Hayashi 2002, Snodgrass et al. 2000).

BMIs were sampled once annually in each SFP in 1998 and 1999 using leaf-pack substrates (Brooks 2000). We placed 5 leaf packs on each SFP bottom in late November–December, 1997 and 1998, following leaf fall. Typically, the SFPs were dry at the time of leaf-pack installation. We placed 1 pack at or near the center of the SFP basin and the remaining 4 packs mid-way between the center and the SFP edge at the cardinal directions. Each pack was composed of leaves collected in a 2.5-L plastic tub and enclosed in a 45-cm square of 15-mm mesh, black plastic garden netting. While litter composition has been shown to affect consumer communities (Rubbo and Kiesecker 2004, Rubbo et al. 2008), we collected leaves adjacent to each SFP basin so that they would represent the composition of leaf fall into the SFP. We tied the corners of each leaf pack closed with plastic flagging to form a loose "bag" and pinned each pack to the pool bottom with a wire-stake flag.

Leaf packs were left undisturbed for the late-fall, winter, and early spring duration of SFP flooding and removed from SFPs over a two-week period in April–May of the year following installation (1998, 1999). We removed the packs when the shortest-hydroperiod SFPs started to dry, removing packs from those first and subsequently from the less ephemeral SFPs. If SFPs were partially or totally dry, exposed packs were not collected. We removed leaf packs by placement in a dip net (mesh 0.8 *x* 0.9 mm) and raising the net vertically to avoid collecting water-column specimens. Leaf packs were then placed in a sealable plastic bag and transported to the laboratory. At the lab, we drained loose water from the packs and stored them in histological grade (90%) 2-Propanol (isopropyl alcohol). BMIs were sorted from each pack in both white and black enamel pans, and sorted specimens were enumerated and identified to family or genus using Merritt and Cummins (1984), Pennak (1989), Peckarsky et al. (1990), or Smith (1995). We assigned functional group and feeding-mechanism (e.g., predator) classifications to each taxon according to the trophic relations reported in Merritt and Cummins (1984). Life-history strategies were taken from Wiggins et al. (1980) and used to identify passively dispersed, overwintering taxa (Group 1). Taxonomy generally follows Peckarsky et al. (1990).

Data analysis

We calculated taxon diversity as $D' = (T-1) / \log_e N$, where T is the number of taxa and N is the abundance of individuals (Margalef 1968). Due to the unequal number of leaf-pack samples collected from each SFP, pool-level analyses were conducted using median macroinvertebrate sample statistics from each SFP. The direction of the relationships between macroinvertebrate richness and diversity and the pool island attributes were examined using Spearman correlation coefficients. The effects of maximum surface area and inter-pool distance on BMI richness and diversity were analyzed using analysis of covariance by ranks with arcsine-transformed SFP hydroperiod as the covariate. Significance for statistical analyses was determined by $P \leq 0.05$.

Results

Maximum (spring) surface area of the 24 SFPs ranged between 68 (PL394) and 2941 m^2 (PR246) (Table 1). The mean surface area was 743 m^2, but the median area was only 493 m^2, indicating the greater number of smaller-sized SFPs in the study. The distance from each study SFP to its nearest-neighbor pool ranged between 73 (PR243) and 1770 m (PL398), with a mean and median distance of 588 and 531 m, respectively. Hydroperiod indices ranged between 0.33 (PR489) and 1.0 (PL407, PR507), with a mean and median of 0.81. SFPs with indices of 1.0 had surface water at every visit during the study, but they have been observed dry at other times prior to and following the study.

Table 1. Maximum pool surface area, nearest-neighbor pool distance, area and distance class, hydroperiod index, and median sample taxa richness and diversity of benthic macroinvertebrates for 24 seasonal forest pools on the Quabbin Reservoir watershed, MA, 1998–1999.

						Median sample	
Pool	Area (m^2)	Area class	Distance (m)	Distance-class	Hydroperiod index	Richness	Diversity
PL401	146	1	119	1	0.46	5.0	0.664
NS445	284	1	110	1	0.95	10.0	2.191
NS446	229	1	110	1	0.85	8.0	1.683
PR508	129	1	474	2	0.67	7.0	1.379
NS472	243	1	966	2	0.80	6.0	1.179
PR489	283	1	715	2	0.33	6.0	0.933
PL394	68	1	1267	3	0.85	8.0	1.571
PR505	140	1	1092	3	0.56	4.0	0.414
PL398	152	1	1770	3	0.55	4.0	0.779
PR243	318	2	73	1	0.78	4.5	0.915
PR490	319	2	83	1	0.80	5.0	1.321
PR428	701	2	135	1	0.85	9.5	1.647
PR488	573	2	847	2	0.82	8.5	1.433
NS266	707	2	587	2	0.40	8.0	1.249
ON481	412	2	1051	3	0.82	14.0	2.429
NS448	580	2	1050	3	0.87	5.0	1.001
PL388	781	2	1398	3	0.95	8.0	1.469
PL407	1292	3	155	1	1.00	8.5	1.949
PL406	1482	3	155	1	0.97	7.0	1.461
PR507	1581	3	144	1	1.00	7.0	1.365
NS232	1602	3	137	1	0.82	7.0	1.279
PR241	1380	3	242	2	0.76	6.0	1.083
NS257	1489	3	802	2	0.87	11.0	2.358
PR246	2941	3	627	2	0.95	9.5	1.935

Over the two years of the study, 198 of 240 installed leaf packs were collected: 112 in 1998 and 86 in the drier 1999. The remaining 42 packs were either exposed or disturbed to the extent that they were unrecoverable. Nearly 35,000 (34,971) BMIs were sorted, identified, and enumerated. Of 76 taxa identified, nearly 60% were chironomids and another 15% were oligochaetes (Appendix I).

The median leaf-pack sample contained 100 individuals of 7 taxa (Table 2). Median sample richness was fairly consistent at 7 taxa across all surface area and inter-pool distance classes (Table 2). Total BMI richness and diversity were

Table 2. Number of samples, median number of taxa, and diversity of benthic macroinvertebrate taxa, by pool area and distance class of 24 seasonal forest pools on the Quabbin Reservoir watershed, 1998–1999.

	Distance class			All
Area/class	<200 m	200–999 m	≥1000 m	classes
<300 m^2				
Samples	23	25	19	67
Taxa	9	6	5	7
Diversity	1.741	1.169	0.973	1.202
300–999 m^2				
Samples	29	14	27	70
Ttaxa	6	8.5	8	7
Diversity	1.329	1.353	1.498	1.363
≥1000 m^2				
Samples	35	26	no samples	61
Taxa	7	9		8
Diversity	1.492	1.772		1.593
All classes				
Samples	87	65	46	198
Taxa	7	7	7	7
Diversity	1.460	1.333	1.280	1.385

Table 3. Spearman rank correlations among median richness and diversity of benthic macroinvertebrates and area, isolation, and hydroperiod of 24 seasonal forest pools on the Quabbin Reservoir watershed, MA, 1998–1999.

	Maximum surface area	Between-pool distance	Hydroperiod index
Total community			
Richness	0.387	0.001	0.543**
Diversity	0.344	-0.061	0.693**
Overwintering residents			
Richness	0.267	-0.152	0.258
Diversity	0.137	-0.124	0.041
Predators			
Richness	0.054	-0.049	0.487*
Diversity	0.243	-0.069	0.493*

*r_s significant for $P \leq 0.05$ ($r_s \geq 0.406$).
**r_s significant for $P \leq 0.01$ ($r_s \geq 0.521$).

moderately (i.e., non-significant) and positively correlated to SFP surface area, positively and significantly correlated with hydroperiod, and uncorrelated to inter-pool distance (Table 3). Similar correlation results were found for overwintering and predatory taxa.

No significant effects of island attributes of SFPs on total, overwintering, or predatory BMI richness and diversity were identified (Table 4). The best (i.e., largest r^2, smallest P) full model was of total BMI diversity ($r^2 = 0.539$, $P = 0.091$) with hydroperiod the only significant ($F = 10.6$, $P = 0.005$) variable. Most of the explanatory power of the models was achieved from the covariate, SFP hydroperiod (Table 4). Hydroperiod was most significant in explaining the richness and diversity in all taxa and of predator taxa (Table 4). The least significant results occurred between the richness and diversity of passively dispersed, overwintering resident taxa and pool "island" attributes (Table 4).

Discussion

Seasonal forest pools are geographically and hydrologically isolated wetlands that occur commonly throughout the temperate forests of the northeastern United States and adjacent Canada (Rheinhardt and Hollands 2008, Tiner et al. 2002). The pools are preferred breeding habitat for a number of amphibian species (e.g., *Lithobates sylvatica* Le Conte [Wood Frog] and *Ambystoma* spp. [mole salamanders]) and support an abundant, rich, and somewhat unique invertebrate fauna (Colburn 2004, Colburn et al. 2008, Semlitsch and Skelly 2008). Island biogeography theory proposes that if the pools function as islands, as their isolated condition suggests, the community attributes of pool biota should be affected by both the size and isolation of the pools (Holland and Jain 1981, March and Bass 1995, Ripley and Simovich 2009).

Table 4. Covariance statistics from analysis of relationships between seasonal forest pool benthic macroinvertebrate median richness and diversity and pool area, isolation, and hydroperiod of 24 seasonal forest pools on the Quabbin Reservoir watershed, MA, 1998–1999.

Invertebrate	Model		Area		Isolation		Hydroperiod	
taxa/statistics	Richness	Diversity	Richness	Diversity	Richness	Diversity	Richness	Diversity
All taxa								
r^2	0.475	0.539						
F	1.696	0.19	0.455	0.001	1.804	0.709	5.674	10.571
P	0.18	0.091	0.643	0.975	0.199	0.508	0.031	0.005
Overwintering taxa								
r^2	0.262	0.214						
F	0.667	0.511	0.736	0.061	0.638	0.016	0.542	0.021
P	0.713	0.83	0.496	0.941	0.542	0.901	0.473	0.886
Predator taxa								
r^2	0.363	0.433						
F	1.071	1.434	1.533	0.654	0.845	2.004	5.867	7.006
P	0.432	0.261	0.235	0.534	0.449	0.169	0.029	0.018

MacArthur and Wilson (1967) stated that there "is an orderly relation between the size of a sample area and the number of species found in that area", but that the relation is not a direct effect of area itself but rather an effect of the greater number of habitats occurring in larger areas. Studies investigating this hypothesis in temporary waters have had mixed results. The relationship between habitat area and species richness has been observed in aquatic invertebrates in small (<13 m^2) rockpools and in flatworm species in temporary pools in northern Israel (Eitam et al. 2004, Spencer et al. 1999). Neither study ascertained whether the relationships were the result of biotic factors (e.g., reduced extinction risk, habitat stability, or microhabitat diversity) or a sampling effect. In contrast, Bilton et al. (2001) found that size was not significantly related to invertebrate species richness in 16 ponds in Cornwall, UK. They postulated that the lack of an area effect might be due to a difference in scale, with the larger pools of the UK study (up to 2400 m^2) being above a size threshold where detection by dispersing invertebrates was more probable. They also suggested that any area effect might be marginal compared to the influence of permanence or hydroperiod.

Our findings parallel positive but weak correlations of biota with area that have been identified for vascular flora of California vernal pools (Holland and Jain 1981), plant and insect taxa of montane calcareous fens (Peintinger et al. 2003), vascular plants in temporary wetlands (Brose 2001), macrophytes in temporary pools (Bazzanti et al. 2003, Oertli et al. 2002), and breeding amphibians in vernal pools (Burne and Griffin 2005). The weak relationships we found between macroinvertebrate richness and SFP area may reflect both the small range in pool surface area and the limited extent of wetland plant cover in our study pools.

The small range in macroinvertebrate community diversity metrics over the 43-fold range in pool sizes in our study suggests that for SFPs, area alone may not be a reliable indicator of the within-pool habitat diversity (Tavernini et al. 2005). Classic studies of island biogeography encompass islands with sizes spanning several orders of magnitude (e.g., MacArthur and Wilson 1963). The range in size of vernal pools is limited. Our study encompassed the range of pool surface area of a representative sample of 34 pools on the Quabbin Reservoir watershed, MA (Brooks and Hayashi 2002). Larger pools are more likely to be permanent or to be physically or hydrologically connected to other aquatic systems (Colburn 2004). Smaller, more ephemeral (as versus seasonal, *sensu* Cowaradin et al. 1979) pools occur, but were not included in the pool inventory (Brooks et al. 1998) or this study.

Studies that documented relationships between pool size and macrophyte richness have also found weak positive associations between macrophyte richness and macroinvertebrate richness in temporary pools (Bazzanti et al. 2003, Oertli et al. 2002). In our study pools, wetlands vegetation was limited in distribution and composition. The most common benthic habitat in our pools, regardless of pool size, was non-vegetated substrate covered with leaf litter.

A second, less common sedge/rush-dominated habitat occurred infrequently in pools with greater solar exposure (i.e., pools ON481, NS257). Due to the small surface area of the study pools, to abundant overstory tree cover adjacent to the pools, and to their temporary inundation, submerged aquatic vegetation was absent, which is a common condition in SFPs (Higgins and Merritt 1999). When within-pool habitats are limited in number, regardless of pool size, area should have less or no effect on faunal composition (Della Bella et al. 2005, Oertli et al. 2002, Smith and Haukos 2002).

The dispersal of organisms among islands is affected both by the distance between source and recipient islands and by the dispersal capability of the organism (MacArthur and Wilson 1967). The effects of distance among temporary pools on faunal community composition have not been as well studied as have pool-size effects. Spencer et al. (2002) found no effect of inter-pool distance on invertebrate community similarity in a cluster of 25 rock pools and concluded that dispersal was not limited among the pools. The same conclusion was reached in studies of vascular plants (Brose 2001) and carabid beetles (Brose 2003) in temporary wetlands in an agricultural landscape. Our findings parallel those of these studies. The distance among SFPs is quite small compared to the distances among the islands of classic biogeographic studies. The median nearest-neighbor distance class for all pools on the Quabbin Reservoir watershed is only 200–299 m (Brooks et al. 1998), which is less than the median inter-pool distance for this study (531 m). These distances do not appear to constitute significant barriers to the dispersal of aquatic invertebrates, even for passively dispersed taxa.

The wide distribution of highly mobile Insecta among vernal pools was expected, although Angelibert and Giani (2003) found odonate species to be more philopatric than expected, which would limit dispersal. Insecta have developed strategies for adapting to the temporary existence of SFPs, typically through seasonal flight dispersal from permanent water bodies for annual colonization of pools (Wiggins et al. 1980). The occurrence, regardless of pool isolation, of passively dispersed, overwintering taxa in SFPs was unexpected. However, King et al. (1996) found no association between the geographic proximity of California vernal pools and the similarity of their crustacean assemblages, and Mura and Brecciaroli (2003) reported the wide distribution of 25 species of microcrustaceans among 12 temporary pools in a Mediterranean plain forest of coastal Italy, which they ascribe to dispersal by vertebrates. The passive dispersal of smaller aquatic organisms by vertebrates and wind has been documented (Bilton et al. 2001, Brendonck and Riddoch 1999, Maguire 1963), but may not occur frequently (Jenkins and Underwood 1998). Distance from source habitats has been shown experimentally to affect dispersal, with the number of taxa declining with distance beyond 58.5 m (64 yards) from the source pond (Maguire 1963). The passive dispersal of invertebrate taxa can occur relatively quickly. Maguire (1963) reported that colonization of experimental water bodies by additional taxa ceased by about 6 weeks; however, Jenkins (1995) reported the continued colonization of experimental pools by rotifers and microcrustaceans up to one year into the study. Based on these dispersal statistics, even passively dispersed taxa should have been able to colonize the most remote pool of this study over the near 60 years that these pools have existed in their present protected, forested watershed environment.

Positioned at the top of SFP food webs, predatory taxa were expected to be most sensitive to pool size (Nilsson 1984, Pearman 1995, Spencer et al. 1999, Wilcox 2001). Our results support this hypothesis, but again, only weakly. Nilsson and Söderström (1988) suggested that pool size creates a threshold for the entry of predatory species based on prey density and minimum population size. Increasing pool area increases the threshold and allows for additional predatory species of increasing size. Another potential reason for increased predator species richness in larger pools would be that larger pools are better buffered against fluctuations in physiochemical conditions and are more likely to have increased microhabitat diversity (Spencer et al. 1999). Additionally, larger pools typically have longer hydroperiods, and longer hydroperiods typically support richer aquatic communities due to reduced stress associated with avoiding desiccation (Colburn 2004, Wiggins et al. 1980, Williams 1983). This last hypothesis appears to hold the strongest explanatory power in relation to our data, as hydroperiod was the strongest variable in our analyses of predatory taxa. The dominant influence of hydroperiod on predator community composition was not unexpected (Bilton et al. 2001, Spencer et al. 1999). The degree of pool isolation had little effect on predator community composition, given that most members are highly mobile, annual migrants (Wiggins et al. 1980).

The hydroperiod of temporary aquatic habitats has been suggested to function as a third, temporal dimension of island biogeographic effects (Bilton et al. 2001, Ebert and Balko 1987). Permanence, rather than pond area, was strongly related to overall species richness and the proportion of predators found in ponds in southwest England (Bilton et al. 2001). Hydroperiod, or habitat duration, was a dominant influence on invertebrate community composition of temporary woodland ponds of the midwestern US (Higgins and Merritt 1999, Schneider 1999, Schneider and Frost 1996). The invertebrate community of short duration (i.e., days) pools was dominated by overwintering taxa, composed predominantly of grazers or filterers; longer-duration (i.e., months) pools allowed for colonization by predators. Duration acts by mediating the relative importance of life histories and biotic interactions, particularly predation, in determining the distribution and abundance of taxa. As vernal pool hydroperiod approaches permanency, biotic richness and diversity should approach that of permanent ponds (Driver 1977).

The hydroperiod of short-duration ponds studied by Schneider (1999) and Schneider and Frost (1996) was much less (i.e., <10 days; temporarily flooded) than the seasonally flooded hydroperiod of the SFPs in this study. Nevertheless, even with a much smaller range in hydroperiod among study pools, the relationship between hydroperiod and BMI community diversity was significant. Total community richness and diversity increased significantly with increasing hydroperiod. The effect was also observed in predatory taxa, but not in overwintering taxa. Predatory taxa are most often spring or summer migrants, and larval forms should occur more often in pools with longer hydroperiod pools. Overwintering taxa are drought resistant and are expected to occur in all but the most temporary pools (Brock et al. 2003, Wiggins et al. 1980).

The effects of hydroperiod would likely have been enhanced if invertebrates had been sampled over the full annual hydrologic cycle of the pools. There is a successional pattern in aquatic invertebrate taxa occurrence in temporary wetlands (Brooks 2000, Williams 1983). Early spring inhabitants are dominated by overwintering, grazing- and filter-feeding taxa; later arrivals are dominated by migrant, predatory taxa (Higgins and Merritt 1999). In this study, all invertebrate samples were taken at one point in time. If samples had been taken later in the year (e.g., mid-summer) in longer hydroperiod pools, it is likely that the influence of hydroperiod on taxa richness and diversity would have been stronger, but comparisons could not have been made to shorter-hydroperiod pools.

From this study, we draw several conclusions about seasonal forest pools in the context of island biogeography theory, and two methodological observations about studying these systems. First, we assessed the effects of pool size and isolation predicted by island biogeography theory, plus the effects of pool hydroperiod, on benthic macroinvertebrate communities of SFPs. Our study confirmed the expected results of increased richness and diversity in larger pools, but we did not observe the expected effects of pool isolation. The distance among our study pools, even for those most removed, appears to be less than the maximum dispersal distance of even passively dispersed taxa. As demonstrated in many studies, pool hydroperiod affected the richness and diversity of BMIs. The strength of the significant relationships between faunal diversity and pool attributes was minimal, with all relationships collectively accounting for less than half the variation in faunal diversity. These results suggest that the BMI community of SFPs is relatively uniform (Stein et al. 2003), at least over the spectrum of pool attributes included in this study. This study supports the findings of others that hydroperiod is a dominant influence in temporary aquatic systems, but that many biotic and abiotic factors, as well as chance, structure the BMI community of SFPs. Additionally, since hydroperiod and pool surface area are related, it is difficult to separate the individual effects in field studies.

The findings of this study would likely be strengthened by methodological improvements. We sampled all SFPs with the same number of leaf packs, regardless of surface area. The result was that larger pools were sampled with less effort (i.e., fewer samples per unit area). A potential consequence would be the under-representation of the true taxa richness of larger pools. This problem is somewhat ameliorated by the simplicity of the benthic habitats within the SFPs. Predatory taxa were most likely under-represented in benthic, leaf-pack samples as they are more active in the water column (Hanson et al. 2000). A second sampling issue was the length of time over which the samples were collected each year. Even in these short-duration systems, a succession of macroinvertebrate species can occur with time (Williams 1983). However, in an earlier study (Brooks 2000), within-year variation in diversity was more a function of abundance than occurrence, and samples in that study were taken over the course of two months, rather than just two weeks as in this study.

Finally, the classification of specimens to family or genus is likely to have negatively impacted the estimation of taxa richness and diversity and may have hindered our ability to detect more differences among pool area and distance treatments. A more detailed classification, especially of family-level identifications, would have resulted in increased community diversity (King and Richardson 2002). Chironomids and oligochaetes from organic sediments have long been used in the classification and bioassessment of lakes (Brinkhurst 1974, Langdon et al. 2006), and chironomid diversity in fresh waters is often exceptionally high (Ferrington 2008). However, classification below family would have been difficult and time consuming, especially for Chironomidae, which accounted for a majority of the specimens. It is an open question whether a more detailed classification would have affected the results of the study.

Overall, our study suggests that island biogeography theory has limited application to SFPs, at least within the forested watershed in which our study pools are found. Further investigations focused on quantifying hydroperiod differences, incorporating more extensive sampling over time, and carrying out more detailed systematic analyses of the fauna, are likely to contribute to better understanding of the factors influencing community richness and diversity in SFPs.

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Appendix I. Number of benthic macroinvertebrates in seasonal forest pool samples by taxa and year, Quabbin Reservoir watershed, MA, 1998–1999.

Phylum	Class	Order	Family	Genus species	1998	1999
Nematoda						13
Platyhelminthes					12	
	Turbellaria				1	307
Annelida						
	Oligochaeta				2013	2747
	Hirudinea					
		Arhynchobdellida				
			Erpobdellidae			
				Erpobdella sp.	2	8
		Rhynchobdellida				
			Glossiphoniidae			7
				Batracobdella (*Placobdella*) *picta* (Verrill)	5	
Mollusca						
	Gastropoda					2
		Basommatophora/Mesogastropoda				
			Lymnaeidae		1	1
				Fossaria parva (I. Lea)	5	19
				Pseudosuccinea columella (Say)	1	
			Physidae			
				Physa sp.	2	17
	Pelecypoda (Bivalvia)					
		Veneroida/Sphaeracea				
			Sphaeriidae			186
				Musculium securis (Prime)	215	
				Pisidium casertanum (Poli)	56	
Arthropoda						
	Hydrachnida				132	141
	Crustacea				24	
		Anostraca				
			Chirocephalidae			
				Eubranchipus vernalis (Verrill)	23	16
				Eubranchipus sp.		3
		Cladocera			208	105
		Copepoda			115	16
		Ostracoda			1110	628
	Insecta				6	
		Collembola				2
			Entomobryidae		57	607
			Hypogastruridae		13	
			Isotomidae		653	
			Poduridae		340	
			Sminthuridae		5	2

Phylum	Class	Order	Family	Genus species	1998	1999
		Odonata				2
			Libellulidae		8	83
				Sympetrum sp.		1
				Pachydiplax longipennis (Burmeister)		2
				Nanothemis bella (Uhler)		1
			Coenagrionidae			1
				Lestes sp.	15	16
		Plecoptera			11	
			Leuctridae		1	1
		Hemiptera			1	
			Corixidae		1	
			Gerridae			
				Gerris sp.	2	3
			Hydrometridae			
				Hydrometra sp.	3	
		Trichoptera				
			Polycentropodidae			
				Polycentropus sp.	167	4
				Cernotina sp.		166
			Limnephilidae			2
				Limnephilus sp.	83	188
			Phryganeidae			
				Banksiola sp.	3	2
				Ptilostomis sp.	17	13
		Coleoptera				
			Dytiscidae			2
				Acilius sp.	9	8
				Agabus sp.	25	27
				Dytiscus sp.	4	
				Hydrocolus sp.	5	
				Hydroporus sp.	14	47
				Hygrotus sp.		1
				Ilybius sp.	4	
				Neoporus sp.		2
			Gyrinidae			9
				Gyrinus sp.	10	2
			Haliplidae		2	8
				Haliplus sp.	3	3
			Noteridae		1	
			Hydraenidae			
				Hydraena sp.		21
			Hydrophilidae		1	5
				Anacaena sp.	2	
				Enochrus sp.		2
				Helocumbus sp.	1	14
				Hydrochus sp.		2
				Helophorus sp.	3	
				Tropisternus sp.		9

Phylum	Class	Order	Family	Genus species	1998	1999
			Scirtidae			26
				Cyphon sp.	22	253
		Megaloptera				
			Corydalidae			
				Chauliodes sp.	10	17
		Diptera			50	4
			Ephydridae			4
			Dolichopodidae			3
			Empididae			1
			Stratiomyidae		18	6
			Tabanidae		6	1
				Tabanus sp.		1
			Ceratopogonidae		197	403
			Chaoboridae			30
				Chaoborus sp.	2	
				Mochlonyx sp.	553	378
			Chironomidae		13,294	5518
			Culicidae			1
				Psorophora sp.		11
				Aedes sp.	488	336
			Dixidae			2
				Dixella sp.		6
			Tipulidae		4	3
				Phalarocera sp.	2	