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ANNUAL AND SEASONAL VARIATION AND THE EFFECTS OF HYDROPERIOD ON BENTHIC MACROINVERTEBRATES OF SEASONAL FOREST (''VERNAL'') PONDS IN CENTRAL MASSACHUSETTS, USA

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Abstract: Seasonal forest ponds (SFPs) are isolated, ephemeral lentic habitats in upland forest ecosystems. These ponds occur commonly throughout temperate forests. Faunal communities of these ponds are dominated by invertebrates. Composition of these communities varies temporally both between years and also seasonally within a single hydrologic year, composition is most affected by pond permanence or hydroperiod. Benthic macroinvertebrates (BMIs) were sampled up to three times a year in five SFPs between 1994 and 1996. The ponds were of short, intermediate, and long hydroperiod. Hydroperiod also varied among years, based on precipitation patterns. During the study, 64,000 specimens of 57 taxa were collected. No pattern was identified in the variation of BMI abundance among years and pond hydroperiod; abundance increased with successive surveys within years. Taxon richness and diversity varied significantly with pond hydroperiod, increasing with increasing hydroperiod. Diversity measures increased over the three years of the study but without obvious pattern across the successive surveys within years. Insects dominated the samples, but large numbers of other Arthropoda and Oligochaeta were also collected. Chironomidae were dominant in most ponds, years, and surveys; chironomid dominance was significantly greater in shorter hydroperiod ponds. Seasonal forest ponds function as aquatic islands in a ''sea'' of terrestrial forest. The effect of hydroperiod on the composition of the benthic macroinvertebrate community is analogous to that of size on marine island fauna, longer hydroperiod ponds generally have richer invertebrate communities just as larger marine islands typically have richer faunas. However, the effect is confounded by the close relationship between pond hydroperiod and pond size/volume.

Key Words: benthic macroinvertebrates, seasonal forest ponds, hydroperiod, temporal variation, island biogeography

INTRODUCTION

Ephemeral natural water bodies experience a recurrent dry phase of varying duration and are found in most ecosystems throughout the world (Williams 1987). Temporary or seasonal forest ponds (SFPs) are common aquatic habitats in the forests of eastern North America (e.g., Cook 1983, Brooks et al. 1998 [Massachusetts], Mahoney et al. 1990 [South Carolina], Blem and Blem 1991 [Virginia], Sadinski and Dunson 1992 [Pennsylvania], Scott and Twombly 1994 [Kentucky, Tennessee], Hecnar and M'Closkey 1996 [Ontario], Skelly 1996 [Michigan], Folkerts 1997 [Gulf Coast]) and elsewhere in temperate forests (e.g., Jeffries 1991 [Scotland], Collinson et al. 1995 [Britain], Bazzanti et al. 1996 [Italy]).

The water regime of SFPs varies from intermittently to semipermanently flooded. In eastern North American, ephemeral ponds are typically recharged by fall precipitation (autumnal) or spring snowmelt and precipitation (vernal) followed by drying in the summer months (Wiggins et al. 1980). The aquatic phase or hydroperiod of ponds varies from days and weeks (temporarily flooded) to months (seasonally flooded) to most of a hydrologic year (semipermanently flooded) (Cowardin et al. 1979).

Hydroperiod is the most influential hydrologic parameter in temporary waters, affecting many ecological functions. Pond hydroperiod has been shown to affect vertebrate and invertebrate species richness and community composition (Wiggins et al. 1980, Spencer et al. 1999), invertebrate abundance, biomass, and production (Leeper and Taylor 1998a), predator size, diversity, and abundance (Schneider and Frost 1996, Skelly 1996), and invertebrate and amphibian reproductive success (Pechmann et al. 1989, Rowe and Dunson 1995, Semlitsch et al. 1996, Leeper and Taylor 1998b).

Faunal communities of ephemeral ponds are distinct, with many taxa having developed adaptations to enable survival of the dry phase (Kenk 1949, Wiggins

et al. 1980, Williams 1987). The macroinvertebrate communities are dominated by microcrustaceans, mites, and three insect groups: true bugs, beetles, and midges or gnats (Williams 1987). These taxa have special characteristics of either their physiology or life cycle that allow successful colonization and survival in temporary waters (Wiggins et al. 1980).

The study assessed seasonal and annual variation in relative abundance of dominant benthic macroinvertebrate (BMI) taxa and in indices of community composition of seasonal forest ponds in southern New England oak woodlands and investigated effects of pond hydroperiod on attributes of BMI composition and relative abundance of dominant taxa. I theorized that pond hydroperiod affects the composition of the BMI community in the same manner that island size affects attributes of island fauna community. I assumed that as hydroperiod lengthened, the richness and diversity of BMI taxa would increase, as it does for island faunal with increasing island size. My use of substrate sampling restricted the study to benthic fauna.

STUDY AREA

I conducted my study between 1994–96 in five seasonal forest ponds on the Prescott Peninsula of the Quabbin Reservation in central Massachusetts, USA (72° 21' W; 42° 25' N). Four ponds were located in two pairs and the fifth pond was solitary. The northern pond pair was approximately 9.4 km north-northwest of the southern pair; the fifth pond was located midway between the pairs. Topography and vegetation of the pond basins and catchments were surveyed in 1993 on plots located on a 5-m grid in the pond basin and a 20-m grid in the pond catchment. As part of a subsequent study, maximum spring water depths were measured on a 5 x 1 m grid in a single northern and southern pond to estimate pond volume.

The northern pair of ponds, identified as ponds 1710 and 1711, were 204 m apart. The maximum dimensions of pond 1710 were 33 x 21 m. The long dimension of the pond was oriented at 014°. It had a maximum depth of 54 cm and an average depth of 27.2 cm (C.V. = 40.8%). When full, the pond surface area is 605 m^2 and volume is 157 m^3. The pond basin was heavily vegetated with highbush blueberry (*Vaccinium corymbosum* L.), buttonbush (*Cephalanthus occidentalis* L.), and sedges (*Carex* sp.). Pond 1711 was 44 x 30 m and oriented at 006°. Its maximum depth was 101 cm, with an average depth of 40.2 cm (C.V. = 61.7%). The basin was heavily vegetated with highbush blueberry and buttonbush. The catchment vegetation of the northern pond pair was dominated by large eastern white pine (*Pinus strobus* L.), with co-dominant red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), and northern red oak (*Q. rubra* L.). The understory was a mixture of ferns, graminoids, forbs, and deciduous shrubs. Blueberry and witch hazel (*Hamamelis virginiana* L.) were common shrub species.

The southern pair of ponds, numbered 503 and 504, were located 168 m apart. The maximum dimensions of pond 503 were 28 x 12 m, the long axis oriented at 029°. The maximum depth of the pond was 52 cm, with an average depth of 26.6 cm (C.V. = 66.2%). The maximum spring surface area was 251 m^2 and volume was 55 m^3. The pond basin was sparsely vegetated with highbush blueberry. Pond 504 was roughly 18 x 14 m, oriented at 160°, with a maximum depth of 54 cm and an average depth of 17.8 cm (C.V. = 70.2%). The north end of the pond basin was sparsely vegetated with sedges, and the south end was more heavily vegetated with highbush blueberry. The overstory vegetation in the southern pond catchments was dominated by northern red oak, with white oak and red maple co-dominating. The understory was dominated by lowbush blueberry (*Vaccinium angustifolium* Ait.). Fern cover was extensive in the pond 503 catchment.

The maximum pond dimensions of the centrally-located single pond (1001), were 47 x 15 m, and the long dimension of the pond was oriented at 040°. The basin of this pond was not surveyed because the pond retained water throughout the study and had a deep muck substrate. The maximum depth of the pond was approximately 1 m and typically varied by ± 10 cm throughout the year. The pond basin was mostly unvegetated. The catchment forest was composed principally of white pine, northern red oak, and red maple.

METHODS

Pond water levels were monitored weekly from ice melt to freeze-over during the study. Water levels were measured at a single steam gauge located in the deepest point in the pond. Pond hydroperiods were calculated as the number of days a pond held water in a hydrologic year (1 Oct− 30 Sep). Pond hydroperiods could not be calculated for the first year of the study, hydrologic year 1993–94, because the fall 1993 refilling dates were not recorded.

Benthic macroinvertebrates were sampled using leaf packs as artificial substrates (Gessner and Dobson 1993, Dobson 1994). This method under-samples or entirely fails to sample invertebrate taxa of the water surface or water column. I tried and rejected dip-net and core sampling due to the difficulties in taking standardized samples in structurally complex habitats. Leaf packs were constructed of approximately 2.5 L of

Table 1. Date of artificial substrate macroinvertebrate samples by year, survey, and seasonal forest pond, Quabbin Reservation, Massachusetts, 1994–1996. Five samples were removed from each pond at every occasion except for the 29 June 96 survey of pond 503 when only 3 samples were inundated.

		Seasonal Forest Pond				
Year	Survey	503	504	1001	1710	1711
1994	1	27 Apr	27 Apr	No	4 May	4 May
	2	24 May	24 May	samples	26 May	26 May
	3	Dry	Dry	taken	21 Jun	21 Jun
1995	1	14 Apr	Dry	14 Apr	14 Apr	14 Apr
	2	16 May	Dry	16 May	16 May	16 May
	3	12 Jun	Dry	12 Jun	12 Jun	12 Jun
1996	1	7 May	7 May	7 May	7 May	7 May
	2	2 Jun	Dry	2 Jun	2 Jun	2 Jun
	3	29 Jun	Dry	29 Jun	29 Jun	29 Jun

leaves enclosed in a ''bag'' made of a 45-cm square of 15-mm-mesh black plastic garden netting. The leaves were collected from each pond catchment adjacent to the pond basin so as to be representative of the leaf fall in each pond. Biases between the size or composition of invertebrates of leaf pack samples and pond basin litter are unknown but assumed to be trivial.

Between 1993–95, five sets of three leaf pack samples were deployed annually on the bottom (at the center and cardinal directions) of each pond basin. The leaf packs were installed each autumn following leaf fall and generally prior to autumnal flooding of the ponds. Leaf packs were closed with plastic flagging and then tied to stake-wire flag. One leaf pack from the set of three at each location was removed at each of three sampling dates the following spring, if the location was inundated (Table 1). Leaf packs were removed using a dip-net (mesh 0.8 x 0.9 mm) to minimize loss of specimens. The leaf pack was then placed in a sealable plastic bag and transferred to the laboratory.

Leaf pack samples were stored in histological grade (90%) 2-Propanol (isopropyl alcohol) for processing. Macroinvertebrates from each leaf pack were sorted in both white and black enamel pans. Sorted specimens were stored in isopropol alcohol. Specimens were identified using Merritt and Cummins (1984), Pennak (1989), Peckarsky et al. (1990), or Smith (1995) and enumerated to family or occasionally genus. Taxonomy generally follows Peckarsky et al. (1990). Taxon diversity was calculated for each pond-survey as $D' = (T-1)/\log_e N$, where T = the number of taxa per sample and N = the number of individuals in the sample (Margalef 1968).

Differences in abundance (number of specimens per sample), taxon richness (number of taxa per sample), and taxon diversity by hydroperiod class (see Results) were analyzed using the Friedman's test (Zar 1996: 267–270), a nonparametric, randomized, block repeated-measures analysis of variance. Nonparametric procedures were used because of concerns about normality and homoscedasticity of richness and diversity data. Since the longest hydroperiod pond (1001) was not sampled in 1994, only 1995–96 invertebrate data were used in statistical testing, resulting in 3 (hydroperiod classes) and 6 (surveys) degrees of freedom. Where significant treatment differences were found, pairwise comparisons were made using calculations similar to the Tukey procedure (Zar 1996:271–272). Statistics were hand-calculated following the formulae in Zar.

RESULTS

Pond Hydrology

The northern pair of ponds had intermediate hydroperiods among all ponds, generally exceeding 300 days (Table 2). These ponds typically held water at the start of the hydrologic year (1 Oct) and continued to hold water well into the summer months of the following year. If a pond held water throughout the year, it was greatly reduced in depth and volume late in the hydrologic year. Over the last two years of the study, pond 1710 had an average hydroperiod of 307 days and pond 1711 of 330 days. The southern pair of ponds had the shortest hydroperiods, typically less than 250 days (Table 2). These ponds typically refilled by mid- to late fall dates and were generally dry by June. Between 1994 and 1996, pond 503 had an average annual hydroperiod of 252 days and pond 504 an average 168 days. In 1995, pond 504 was dry before any macroinvertebrate samples could be taken. The single central pond was the most permanent of the ponds with a hydroperiod of 365 days. While this pond never dried completely over the duration of the study, by the end of the 1994–95 hydrologic year, it was reduced to two small ''puddles.''

The ponds can be ordered along a hydroperiod gradient, with pond $504 < 503 < 1710 < 1711 < 1001$. Based on average pond hydroperiods over the study, the ponds were assigned to three hydroperiod classes: short (ponds 503, 504), intermediate (ponds 1710, 1711), and long (pond 1001). Based on the date of drying or on calculations, the hydroperiods for most ponds in hydrologic year 1994–95 were shorter than those for hydrologic year 1993–94 or 1995–96 (Table 2).

Benthic Macroinvertebrates

Over the study, 64,383 benthic macroinvertebrates were collected, identified, and enumerated. An addi-

Table 2. Dates of hydrologic events and the number of days in the hydroperiods of seasonal forest ponds by hydrologic year (1 Oct–31 Sep) and seasonal forest pond, Quabbin Reservation, Massachusetts, 1993–1996.

Hydrologic Year	Event	Seasonal Forest Pond				
		503	504	1001	1710	1711
1993–94	Rehydrate	No data				
	Dry	21 Jun 94	7 Jun 94	30 Sep 94[1]	30 Sep 94[1]	30 Sep 94[1]
	# Days			Unable to calculate		
1994–95	Rehydrate	22 Nov 94	6 Dec 94	1 Oct 94	1 Oct 94	1 Oct 94
	Dry	27 Jun 95	4 Apr 95	30 Sep 95[1]	11 Jul 95	1 Aug 95
	# Days	217	119	365	284	305
1995–96	Rehydrate	31 Oct 95	31 Oct 95	1 Oct 95	10 Oct 95	10 Oct 95
	Dry	13 Aug 96	4 Jun 96	30 Sep 96[1]	3 Sep 96	30 Sep 96[1]
	# Days	287	217	365	329	355

[1] Ponds not dry at the end of the hydrologic year.

tional 300 invertebrate specimens were unidentifiable. Total BMI abundance was generally higher in 1995 and roughly equivalent in 1994 and 1996 (Tables 3 and 4). BMI abundance increased between successive surveys within years (Tables 3 and 4). Total BMI abundance was greater in ponds of intermediate hydroperiod (Table 4), but the differences in abundance among hydroperiod classes were not significant ($X^2_r = 4$, $p = 0.2$).

A total of 57 taxa were identified. Macroinvertebrate richness and diversity increased with pond permanence (Table 3). The number of BMI taxa differed significantly among hydroperiod classes ($X^2_r = 9.3$, $0.01 > p > 0.005$). Significant differences in richness were

Table 3. Total number (N) of benthic macroinvertebrates (BMI), cumulative number of taxa (T), and taxon diversity (D') by seasonal forest pond, year, and survey, Quabbin Reservation, Massachusetts, 1994–1996.

Year	Survey	BMI Attribute	Seasonal Forest Pond				
			504	503	1710	1711	1001
1994	1	N	1180	1605	1855	392	
		T	13	13	22	19	No
		D'	1.7	1.63	2.79	3.01	samples
	2	N	3904	1946	1515	1224	taken
		T	16	12	21	19	
		D'	1.87	1.45	2.73	2.53	
	3	N			3621	933	
		T	Dry	Dry	17	18	
		D'			1.95	2.49	
1995	1	N		2300	1611	614	1082
		T	Dry	12	16	10	27
		D'		1.42	2.03	1.4	3.72
	2	N		1977	4694	1221	952
		T	Dry	12	18	15	25
		D'		1.45	2.01	1.97	3.5
	3	N		2310	8332	1414	2080
		T	Dry	14	22	21	32
		D'		1.68	2.33	2.76	4.06
1996	1	N	117	692	1742	1285	482
		T	9	14	19	19	25
		D'	1.68	1.99	2.41	2.51	3.88
	2	N		2529	2318	1095	797
		T	Dry	22	15	19	28
		D'		2.68	1.81	2.57	4.04
	3	N		1835	2344	563	2610
		T	Dry	21	18	19	26
		D'		2.66	2.19	2.84	3.18

Table 4. Average abundance (number per artificial substrate [#/AS]) of common seasonal forest pond benthic macroinvertebrates, average diversity (D′), cumulative taxon richness, and significant treatment and pairwise differences[1] by hydroperiod classes, Quabbin Reservation, MA, 1994–1996.

	Hydroperiod Class[2]			Year			Survey		
BMI Metric	Short	Intermediate	Long	1994	1995	1996	1	2	3
Abundance (#/AS)									
Total	282[ns]	409	267	347	477	282	230	390	543
Chironomidae	332[a]	177[ab]	89[b]	178	297	156	112	246	296
Oligochaeta	11[a]	128[b]	93[ab]	37	103	105	38	74	160
Culicidae	9[ns]	2	<1	9	3	1	9	1	1
Cyperididae	<1[a]	28[b]	1[a]	20	16	9	23	9	11
Eremaeidae	5[ns]	33	<1	63	1	1	14	15	28
Daphnia	<1[a]	12[b]	4[ab]	11	9	2	2	9	11
Gastropoda	—	<1	9	—	4	<1	1	1	3
Pelecypoda	—	—	8	—	1	3	<1	1	3
Amphipoda	<1	—	32	—	15	1	9	5	2
Hirudinea	—	<1	12	—	4	1	1	2	3
Copepoda	2	5	3	<1	8	1	5	4	1
Hydrachna	2	2	<1	3	1	2	3	2	1
Richness									
Total	39	44	43	36	40	48	50	52	49
$\bar{x}$/AS	8.1[a]	11.3[ab]	16.7[b]	10.9	12.1	10.6	10.6	11.2	12.1
Diversity									
Total	3.84	4.1	4.67	3.59	3.8	4.79	5.1	5.07	4.72
$\bar{x}$/AS	1.27[a]	1.83[a]	2.96[b]	1.80	1.93	1.82	1.87	1.81	1.88

[1] Values with common superscripts within each individual treatment were not significantly different at $p \leq 0.05$; the superscript *ns* indicates no significant treatment effect.
[2] Short hydroperiod ponds are ponds 503 and 504; intermediate are 1710 and 1711; long is 1001.

evident between the longest and shortest hydroperiod ponds ($q = 4.3$, $0.01 > p > 0.005$) but not for any other pairwise comparison (Table 4). Taxon richness across all samples in a year increased with successive years; average richness among samples was highest in 1995 and similar in 1994 and 1996 (Table 4). Taxon richness across all samples in a survey increased from the first to second surveys in a year and then declined in the third survey; average richness among samples increased between successive surveys (Table 4). Taxon richness is probably most affected by the number of samples. Average richness among samples should be a better reflection of environmental influences.

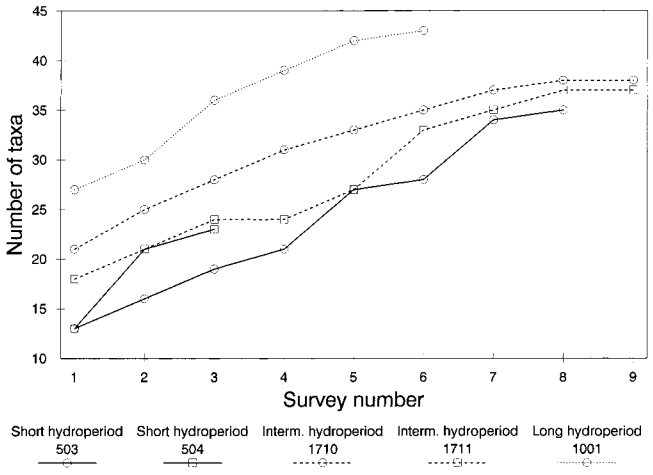

Figure 1. Cumulative number of seasonal forest pond macroinvertebrate taxa by successive survey and pond, Quabbin Reservation, Massachusetts, 1994–1996.

Taxon richness of individual pond surveys ranged between nine (recorded in the first survey in 1996 in pond 504) and 32 (from the third survey of pond 1001 in 1995) (Table 3). Taxon richness increased with successive surveys in each hydroperiod class and reached a maximum of 35 taxa after eight surveys for short hydroperiod ponds, 38 taxa after nine surveys for intermediate hydroperiod ponds, and 43 taxa after six surveys for the longest hydroperiod pond (Figure 1). At each successive survey, cumulative taxon richness was greater in ponds with longer hydroperiod. Taxon richness would generally plateau at less than 35 taxa for the shortest hydroperiod ponds, less than 40 for intermediate hydroperiod ponds, and 45 taxa for the longest hydroperiod ponds (Figure 1). Taxon diversity (*D'*) differed among hydroperiod classes ($X^2_r = 10.3$, $0.002 > p > 0.001$). Diversity increased with hydroperiod length (Table 4). This difference was most evident between the longest pond and shortest hydroperiod ponds ($q = 4.5$, $0.005 > p > 0.001$).

Insects (Arthropoda: Insecta) dominated all ponds and all surveys, with large numbers of other Arthropoda (Eremaeidae, Daphnidae, Cyperididae) and Oligochaeta (Annelida) also encountered. Chironomidae (Insecta: Diptera) were dominant in most ponds and over most years and surveys. Chironomid abundance differed by hydroperiod ($X^2_r = 7$, $p = 0.05$). They were most abundant in short hydroperiod ponds and decreased in abundance with increasing hydroperiod length (Table 4). These differences were most obvious between shortest and longest hydroperiod ponds ($q = 3.67$, $0.05 > p > 0.02$). Chironomid abundance was high in 1995 and roughly equivalent in 1994 and 1996. Average chironomid abundance more than doubled between the first and second survey and increased marginally between the second and third survey.

Oligochaeta were the only other taxa common across all ponds, years, and surveys (Table 4). Oligochate abundance differed by pond hydroperiod classes, with the greatest abundance occurring in intermediate duration ponds ($X^2_r = 9.3$, $0.01 > p > 0.005$). The difference was greatest between intermediate and short hydroperiod ponds ($q = 4.1$, $0.025 > p > 0.01$) but also evident between long and short hydroperiod ponds ($q = 3.3$, $0.1 > p > 0.05$). Oligochate abundance was low the first year of the study and increased 3-fold during the last two years; abundance doubled between successive surveys each year (Table 4).

Culicidae were most abundant in the most ephemeral ponds, but the differences among hydroperiod classes were not great (Table 4). Cyperididae abundance differed by hydroperiod class ($X^2_r = 9$, $p = 0.01$). The taxon was most abundant in intermediate hydroperiod ponds, and the difference was obvious for comparisons with both short ($q = 3.5$, $0.05 > p$ 0.025) and long hydroperiod ponds ($q = 3.9$, $0.025 > p$ 0.01). Eremaeidae and *Daphnia* were other abundant taxa in the ponds of intermediate hydroperiod (Table 4). Mollusa (Gastropoda and Pelecypoda), Amphipoda, and Hirudinea were most abundant in, and often unique to the long hydroperiod pond.

The general pattern was toward increasing BMI abundance with successive surveys. This resulted from the dominant Chironomidae, which increased over two-fold between the first survey in late April-early May and the second in mid- to late May-early June (Table 4). A lesser increase in chironomids was evident between the second and third surveys. Oligochates were less common but showed a similar pattern of increase in relative abundance between sequential surveys. Major taxa whose abundance differed from this overall pattern were Cyperididae, Amphipoda, Copepoda, and *Hydrachna*; these generally declined with subsequent surveys (Table 4). Culicidae nearly disappeared after the first survey.

DISCUSSION

Benthic macroinvertebrates of seasonal forest ponds have a major role in detritus processing and are a critical food resource for higher order taxa (Wilbur 1972, Taylor et al. 1988). They are abundant, readily surveyed, and taxonomically rich (Kenk 1949, Wiggins et al. 1980). BMI communities are characterized by complex trophic relations (Merritt and Cummins 1984) and by varied physiological and life-history strategies for tolerating or avoiding the environmental stresses of these highly dynamic habitats (Wiggins et al. 1980). These attributes justify the use of BMIs to study ecosystem- and landscape-scale effects on pond fauna.

Benthic macroinvertebrate abundance in seasonal forest ponds I studied fluctuated both annually and monthly within years (Tables 3 and 4). On the year-to-year time scale, the most important event affecting abundance seemed to be the unusually short pond hydroperiods of 1995 (Table 2). The presumed effect was reduced BMI abundance in both short and long hydroperiod ponds early the following year (Table 3). The abbreviated hydroperiod of hydrologic year 1994–95 could have resulted in a short-term shift in BMI community composition to taxa more tolerant of the lengthened dry phase and a loss of taxa unable to tolerate desiccation (Wiggins et al. 1980). That was not seen in this study; abundance was down in early 1996, but composition was relatively stable. The composition of the benthic invertebrate taxa of these ponds represents an accommodation to a temporally variable environment.

A major component of the BMI community of the ponds in this study is composed of life history Group 1 of Wiggins et al. (1980), passively dispersed overwintering residents. These are non-insects, and in the ponds of this study, include principally oligochaetes and crustaceans. The year-to-year abundance of these taxa should be less affected by hydroperiod length, as they are best adapted to highly ephemeral ponds (Wiggins et al. 1980). Kenk (1949) suggested that the annual variation in pond fauna is greater than that of any other aquatic habitat. While abundance certainly varied annually, composition was stable. It appears that the effects of abbreviated pond hydroperiods on the BMI community are restricted to the year of occurrence.

Masters (1968), Williams (1987, 1996), and Bazzanti et al. (1996) described a seasonal succession of invertebrate taxa in temporary fresh waters. Williams (1996) additionally reported seasonal increases in richness and relative abundance. Within-year variation in the BMI community of my study was more a function of changes in abundance than occurrence. Total abundance and the abundance of principal taxa increased across successive surveys (Table 4). Ten taxa showed

clear patterns of increased abundance with successive surveys, and seven taxa declined in abundance with time. Of the decreasing taxa, two of the most abundant were crustaceans, taxa adapted to highly ephemeral ponds (Wiggins et al. 1980). Two other abundant taxa that declined with time were dipterans, both with brief aquatic life phases (Merritt and Cummins 1984). Greater numbers of taxa decreasing in abundance would have been expected if the study had been continued through the end of each pond's wet phase, allowing animals with longer life histories to reproduce and die or metamorphose to their adult phase and emigrate.

The ponds in this study are of fall (autumnal) origin, so the invertebrate communities had several months to develop prior to the first sampling in mid-April to early May. Stronger patterns of taxon succession would likely have been observed had BMIs been sampled across the full hydroperiod of the ponds, from fall rehydration through late spring to summer drying (Kenk 1949).

Ephemeral ponds in upland environments are thought to share characteristics of traditional islands, where there is a relationship between island area and the number of species (MacArthur and Wilson 1967). Area itself in these environments is not the controlling effect, area is positively related to habitat diversity. The richness of the biotic community of ephemeral ponds is influenced by pond size (Lassen 1975 [snails], Nilsson 1984 [beetles], Ebert and Balko 1987 [vascular plants], Mahoney et al. 1990 [microcrustaceans], March and Bass 1995 [invertebrate community]).

Ebert and Balko (1987) and Mahoney et al. (1990) added another dimension that is unique to ephemeral lentic habitats: hydroperiod, the time period when a pond holds water. Size and hydroperiod are not independent, as size (surface area or especially volume) is a major determinant of hydroperiod. Hydroperiod also varies among ponds based on their hydrology and whether their hydrologic systems are dominated by surface or ground water (Gay 1998). Finally, pond hydroperiods vary temporally with individual precipitation events and seasonal patterns in precipitation. As pond size increases or as ponds trend towards permanence, the number of habitats within the pond can increase as a function of space and/or hydroperiod (Lassen 1975). With increasing hydroperiod, concentric biotic zones can be created, with the more ephemeral peripheral zones differing from central zones with more permanent water. Faunal communities can increase in richness with increased hydroperiod based solely on life history (overwintering and reproductive) strategies (Wiggins et al. 1980).

The results from this study conform to the expectation that richness and diversity of the benthic macroinvertebrate community of seasonal forest ponds increase with increasing hydroperiod (Table 3 and 4). The pattern was especially noticeable in the Group 1 taxa of Wiggins et al. (1980) or fully aquatic taxa (Lassen 1975). Mollusca and Hirudinea taxa were found almost exclusively in pond 1001, the long hydroperiod pond (Table 4). For Crustacea taxa and numbers, including both micro- and macrocrustacean taxa (Peckarsky et al. 1990), 6 specimens of 2 taxa were taken from pond 504, the most ephemeral pond in the study. Two additional taxa and a total of 97 crustacean specimens were taken in pond 503, which was slightly less ephemeral. Over a thousand specimens of Crustacea of 5 to 6 taxa were taken in each of the less ephemeral 1710, 1711, and 1001 ponds.

The pattern of sensitivity of BMI richness to hydroperiod was not as strong as expected. The range in size and hydroperiod among the small sample of 5 ponds of this study was smaller than that of comparable studies. All of the ponds of this study, with the exception of the semi-permanent 1001, were of autumnal (fall) origin and their hydroperiods were of similar duration, compared to what would be expected from ponds of vernal (spring) origin. Despite their shorter hydroperiods, ponds 503 and 504 were nevertheless autumnal ponds, and therefore, their BMI community would likely be more similar to ponds 1710 and 1711, autumnal ponds with longer hydroperiods, and more distinct from strictly vernal ponds, representatives of which were not included in this study (Wiggins et al. 1980).

The increase in the number of habitats with increasing pond size has resulted in increased richness of aquatic beetles (Nilsson 1984) and freshwater snails (Lassen 1975). The relationship between pond size (or hydroperiod) and the number of habitats within ponds was seen to a small degree in this study. Short hydroperiod ponds were more open, with a few scattered shrubs and with a litter benthos. Intermediate hydroperiod ponds were mostly shrub habitat, with small areas of emergent graminoids, very little open water, and a mixed litter and muck benthos. The long hydroperiod pond was open, with a small area of emergent graminoids with a muck benthos. The small numbers of artificial substrate samples (5) in each pond were not stratified to subsample different habitats within each pond. The differences in BMI composition among ponds could be an effect of hydroperiod, habitat, or both. This would be a difficult issue to assess, as the two attributes are closely related.

MANAGEMENT CONSIDERATIONS

There is relatively little literature on the effects of forest management activities on seasonal forest ponds,

and the papers that has been published focus mostly on ponds as amphibian breeding habitat (deMaynadier and Hunter 1995, 1999). Preliminary management guidelines for the protection of SFPs have been developed and issued as Best Management Practices (BMPs) (Kittredge 1996, Calhoun 2000). Common features of BMPs for ponds are the full protection of the pond basin and the recognition and protection of concentric buffer zones surrounding ponds. The innermost zones, adjacent to the pond, receive the greatest protection, with the permanent retention of forest cover and the exclusion of heavy equipment. Guidelines for more remote zones limit the construction of landings and heavily used skid roads to minimize disturbance to the forest floor. A more conservative approach considers the upland forest adjacent to forest ponds to constitute a critical life zone for pond-breeding fauna (Semlitsch 1998). Buffer zones would then encircle this pond-upland complex to reduce possible edge effects in the upland component.

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