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WEATHER-RELATED EFFECTS ON WOODLAND VERNAL POOL HYDROLOGY AND HYDROPERIOD

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Abstract: Woodland vernal pools occur commonly throughout northeastern North America. These pools provide preferred breeding habitat for mole salamanders (*Ambystoma* spp.) and wood frogs (*Rana sylvatica*) and support an abundant and diverse macroinvertebrate fauna. Vernal pool hydrology, and especially hydroperiod or duration of the wet phase, affects the composition and productivity of pool fauna. The hydrology of ephemeral wetlands is dominated by local weather conditions. In this paper, I report a ten-year record of the relationships between precipitation and evapotranspiration and water-level change and hydroperiod in four typical southern New England vernal pools. Long-term average precipitation is evenly distributed throughout the year in the Northeast; potential evapotranspiration peaks in the summer months and exceeds precipitation from mid-June through mid-September. This period of water deficit causes the period of maximum vernal pool drying. Vernal pool hydroperiods were shorter and pools dried earlier in those years with larger cumulative water deficits, especially when early spring ground-water resources were below long-term means and late winter snowpack was reduced or absent. Weekly water-level change in vernal pools was significantly related to precipitation and potential evapotranspiration, with precipitation having 2–5 times greater effect than evapotranspiration. Under climate-change predictions of more episodic precipitation and increased evapotranspiration, vernal pools would dry earlier in the year and remain dry longer. These changes would adversely affect the successful reproduction of pool-breeding amphibians and isolate the remaining productive pools.

Key Words: hydrology, hydroperiod, potential evapotranspiration, precipitation, vernal pools, woodland vernal pools

INTRODUCTION

Woodland vernal pools (Tiner et al. 2002) occur commonly throughout the eastern temperate forests of North America (Brooks et al. 1998, Burne 2001, Palik et al. 2001). In the northeastern United States, the hydrologic cycle of most vernal pools is that of seasonal water bodies of autumnal origin. The vernacular term "vernal" is used to facilitate communications. The pools fill at least partially in the fall, are filled to capacity with spring rains on snow pack, and then dry by early to mid-summer. Vernal pools support a rich and diverse invertebrate community that is adapted to the annual drying of the pools (Kenk 1949, Wiggins et al. 1980, Brooks 2000). The composition and diversity of the faunal community of ephemeral wetlands are strongly affected by the duration of the wet phase or hydroperiod of the wetland (Wiggins et al. 1980, Semlitsch et al. 1996, Schneider 1999). As hydroperiod increases, invertebrate richness generally increases, but the relationship is complex, as biotic factors, especially predation, also increase in importance with increasing hydroperiod, affecting community organization (Schneider 1999).

Vernal pools are considered preferred breeding habitat for mole salamanders (*Ambystoma* spp.) and wood frogs (*Rana sylvatica* Le Conte) (DeGraaf and Yamasaki 2001). Wood frogs and most mole salamander species migrate to vernal pools in early spring (*circa* April 1 depending on latitude) to mate and lay eggs. The period of time between egg laying and development to metamorphosis and emergence from pools ranges between 8 and 19 weeks for wood frogs and 13 to 24 weeks for spotted salamanders (*A. maculatum* Shaw) (DeGraaf and Yamasaki 2001). Therefore, the continuation of the hydroperiod of vernal pools through egg laying and metamorphosis (e.g., April through July) is critical to the annual production and fitness of pool-breeding amphibians. Annual faunal production is affected by inter-annual variation in hydroperiod, with both the richness and abundance of

amphibian metamorphs increasing with hydroperiod (Semlitsch et al. 1996). Additionally, amphibian metamorphosis occurs later in longer hydroperiod pools, and metamorphs are larger, with implications for fitness and survival (Semlitsch et al. 1988).

While not fully understood, the long-term hydrology and hydroperiod of small, isolated, ephemeral wetlands are influenced by the physical properties of the site, the size of the wetland, the connection of the wetland to local and regional ground-water resources, and to long-term climatic conditions (Larson 1995, Lent et al. 1997, Kirkman et al. 1999, Hayashi and Rosenberry 2001, Winter et al. 2001, Brooks and Hayashi 2002). Annual variation in pool hydroperiod is presumed to reflect the variation in weather, especially precipitation (Winter et al. 2001). In studies in South Carolina (Lide et al. 1995, Kennamer 2001), Minnesota (Palik et al. 2001), Maine (Joyal et al. 2001), and Florida (Mansell et al. 2000), the hydrology of temporary ponds was controlled by precipitation and evapotranspiration. These relationships between precipitation and evapotranspiration and the hydrology of ephemeral wetlands found in other regions should be applicable to woodland vernal pools in the northeastern United States.

Long-term precipitation in the northeastern United States is evenly distributed throughout the year, with small peaks in late fall and late spring (Figure 1A). Little to no evapotranspiration occurs during the colder months when the vegetation is senescent and/or the pools are ice-covered; evapotranspiration peaks in mid-summer and exceeds precipitation during the months of June, July, and August. The general pattern and timing of vernal pool filling and drying parallels these long-term patterns of precipitation and evapotranspiration (Figure 1A). The annual water regime of vernal pools follows an October-to-September water year. Pools are typically dry at the beginning of the water year and begin to refill with fall rains, as evapotranspiration demands decrease and after soil-water content and ground water have been recharged and/or after the ground freezes. Pools fill to their maximum size with spring snowmelt and rains. As temperatures warm and as the adjacent forest reaches full foliage, increasing evapotranspiration results in pools drying in the absence of regular and substantial precipitation. Smaller (i.e., lesser depth, surface area, and/or volume) pools dry more quickly than larger pools (Brooks and Hayashi 2002).

Multi-year observations of water level-change in four woodland vernal pools were analyzed using a simple climate-water balance equation (Lide et al. 1995):

$$\Delta SW = PPT - PET \pm GW$$

where:

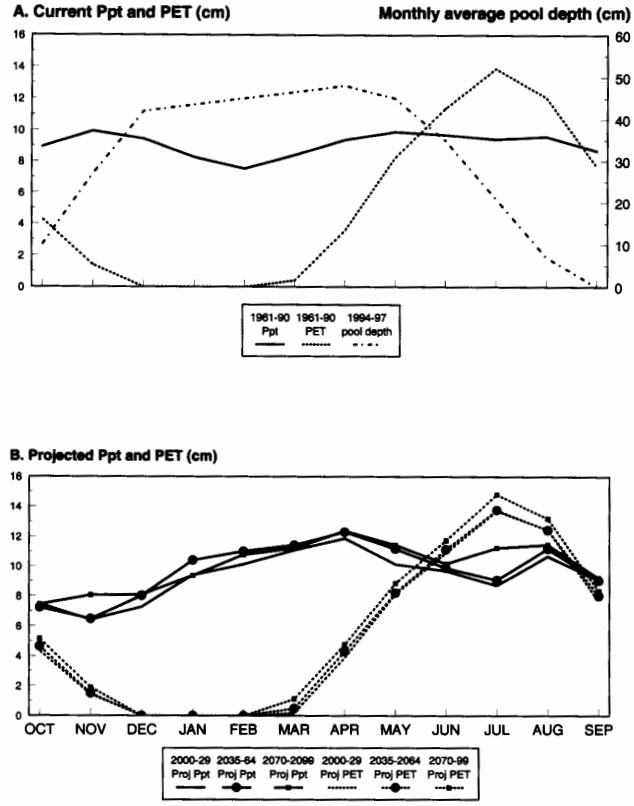

Figure 1. Current (A) and projected (B) thirty-year average monthly precipitation (Ppt) and potential evapotranspiration (PET), and (A) monthly average depth of pool 1710 (1994–97), by month, Quabbin Reservation, Massachusetts.

ΔSW = weekly change in pool surface water depth (cm)
PPT = weekly precipitation (cm)
PET = weekly potential evapotranspiration (cm)
GW = ground-water contribution

Surface flow to and from woodland vernal pools is minimal or non-existent; surface flow may occur in some pools for very brief times during spring snowmelt or extreme precipitation events. Ground-water exchange was not considered in this study, except indirectly through transpiration demand from basin and adjacent catchment vegetation.

The long-term goal of this work is to model vernal pool hydrology, to be able to predict the potential effects of timber harvesting in pool catchments and of climate change on vernal pool hydrology (e.g., Poiani and Johnson 1993a, Poiani et al. 1996, Sun et al. 1998a, 1998b, Mansell et al. 2000). In this paper, I report on the relationships between precipitation and potential evapotranspiration and water-level change in four vernal pools in central Massachusetts, USA. I then discuss how these relationships relate to annual variation in pool hydroperiod and explore possible im-

pacts of projected climate change on the hydrology of these small, isolated, but important systems.

STUDY SITES AND METHODS

Four woodland vernal pools were selected in the early 1990s for the study of pool fauna (Brooks 2000, Brooks and Doyle 2001, Milam and Melvin 2001) and vernal pool hydrology (Gay 1998). All pools are located on the Prescott Peninsula of the Quabbin Reservation in central Massachusetts (72° 21′ W; 42° 25′ N). The pools are located in two pairs, and the pairs are located approximately 15 km apart in a north-south direction. Pools at the northern location (identified as 1710, 1711) occur on glacial till underlain by gabbro, while those at the southern location (numbered 503, 504) are on till over gneiss bedrock (Gay 1998). A preliminary study of the hydrology of the pools determined that water input to all pools was principally from precipitation, with a greater influence of ground water at the northern pools (Gay 1998). When full, the maximum depth of the pools is about 0.5 m, except for pool 1711, which has a small deeper hole with a maximum depth of 1.15 m. All pools are less than 1000 m^2 in surface area when at maximum capacity; pools 503 and 504 are smaller than pools 1710 and 1711. The overstory vegetation of the catchments of the northern pools is dominated by white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), and oaks (*Quercus* spp.), that of the southern pools by red maple and oaks.

Pool water levels have been monitored on a regular basis since 1992. Water levels were monitored weekly during the spring and early summer of 1992 and 1993 and during the ice-free periods for the years 1994 through 2002. Water levels were recorded from a staff gauge located in the deepest point of each pool.

Weekly precipitation (Ppt) amounts were collected at NADP (National Atmospheric Deposition Program) site MA08 using a Belfort rain gage; the site is centrally located between the pool locations. Monthly potential evapotranspiration (PET) was calculated using the Thornthwaite equations (Dunne and Leopold 1978):

$$\mathrm{PET} = 1.6\ [10T/I]^a$$

where:

PET = potential evapotranspiration in cm/mo

T = mean monthly air temperature (°C)

$I = \text{annual heat index} = \sum [T/5]^{1.5}$

$a = 0.49 + 0.0179I - 0.0000771I^2 + 0.000000675I^3$

PET was first estimated using mean monthly temperatures provided by the Metropolitan District Commission (MDC), collected at their administrative headquarters approximately 12 km south and at the same elevation as the study sites. Weekly PET values were calculated using the coefficients I and a from monthly PET calculations and average weekly temperatures from the MDC. Estimates were then adjusted for day length at 42° N latitude. This process allocates monthly-calculated PET to 52 weekly values. The average absolute difference between annual totals of monthly- and weekly-calculated PET was 1.03 cm. There was no significant difference between the two sums (i.e., monthly, weekly) of annual PET (paired-t = 0.564, n = 9, p = 0.586). Average monthly and weekly temperatures were calculated as the means of daily average temperatures, collected and reported by the Metropolitan District Commission at a weather station located approximately 9.5 km south of the southern pool location. The MDC also provided late winter snowpack data, in cm snow-water equivalent, collected at six stations around the Quabbin Reservation.

Thirty-year (1961–90) average monthly precipitation and PET were estimated for the Quabbin Reservation using published weather station statistics from Amherst, Barre Falls, East Brimfield, and Tully Lake, Massachusetts (Climatological Data: New England, National Climatic Data Center, Asheville, NC). Station precipitation amounts and temperatures were spatially averaged, weighted by the inverse of the distance of the station from the Quabbin Reservation. To explore the potential effects of climate change on vernal pool hydrology, average monthly Ppt and PET were estimated for the 30-year periods 2000–2029, 2035–2064, and 2070–2099. Monthly precipitation and minimum and maximum temperatures for 30-year intervals were estimated using both the Canadian and Hadley General Circulation Models (Stephen Hale, Complex Systems Research Center, University of New Hampshire, Durham). The results from both models were then averaged, and the temperature data were used to estimate PET using the Thorthwaite equations.

Relationships between precipitation and potential evapotranspiration and pool water-level change were explored using correlation coefficients and multiple linear regression. The regression models were of the form:

$$\text{Pool water-level change} = b_0 + b_1(\mathrm{Ppt}) + b_2(\mathrm{PET}) + \varepsilon$$

where ε is the error term and includes the groundwater component of the Lide et al. (1995) water-balance equation and is the change in surface-water storage that is unexplained by either Ppt or PET. This model is a simplification of the climate-water budget equation of Lide et al. (1995), with the effects of

Table 1. Total precipitation (Ppt) and potential evapotranspiration (PET) by water year (1 October–30 September) and for 1 April–30 September, Quabbin Reservation, Massachusetts, water years 1992–2001 and 30-year averages for 1961–1990, 2000–2029, 2035–2064, and 2070–2099.

Water year(s)	Full water year		1 April–30 September	
	Ppt	PET	Ppt	PET
	cm			
1992	101.2	62.5	47.8	57.5
1993	145.3	63.2	70.3	57.4
1994	98.1	67.1	46.0	57.6
1995	172.2	62.3	87.2	55.7
1996	125.8	60.4	52.8	53.8
1997	117.3	66.8	56.7	60.4
1998	124.6	66.6	63.1	58.9
1999	135.0	63.4	81.8	54.5
2000	108.5	65.5	54.0	60.4
2001	92.2	67.5	56.4	58.6
Mean	122.0	64.5	61.6	57.5
1961–1990	109.0	63.1	56.6	57.0
2000–2029	111.9	62.7	62.3	56.8
2035–2064	117.2	64.5	66.2	57.9
2070–2099	120.8	69.9	65.3	61.7

ground-water exchange included in the intercept and error terms. The relative strengths of these relations for each pool were examined using standard partial regression coefficients from multiple linear regression analysis (Zar 1974:261–262, Damon and Harvey 1987: 236). Standard partial regression coefficients are unitless, calculated when all variables are expressed in standard measure, and eliminate the effect of differences in measurement scale among the independent variables (Sokal and Rohlf 1995:614). This relationship was analyzed for both the full water-year (1 October–30 September) and for the second-half of the water year (1 April–30 September), the critical period when the amphibian eggs and larvae are developing. The pool regression models were compared, using the test recommended by Zar (1974:273), to see if there could be common pool models.

RESULTS

Estimated thirty-year (1961–1990) average annual precipitation (Ppt) for the Quabbin Reservation was 109 cm, and average annual potential evapotranspiration (PET) was 63.1 cm; over the past decade (1992–2002), the averages were 122 and 64.5 cm, respectively (Table 1). Long-term average monthly precipitation ranged between a low of 7.7 cm (February) and a maximum of 10.2 cm (November), while monthly potential evapotranspiration was zero between December and February and peaked at 13 cm in July (Figure 1A). Over the water years 1992 to 2001, annual precipitation exceeded potential evapotranspiration by an average of 575 mm (Table 1). In the driest year (2001–2002), annual Ppt was only 1.4 times PET, while for the wet year (1995–1996), annual Ppt was 2.7 times PET.

Fall and winter precipitation typically result in the recharge of soil- and ground-water resources, so that spring snowmelt and overland flow generally fill vernal pools to capacity (Figure 1A). In some years, 1995, 1999, and 2002 for example, late winter snowpack and spring ground-water levels were below normal (Table 2). During those years, snow-pack levels were the lowest of the nine-year record, and regional ground-water levels were about 30 cm below the long-term mean and generally below the lower quartile, indicating drought conditions. Dry early spring conditions frequently foreshadow early pool drying.

Negative water balances or water deficits (i.e., Ppt < PET) typically occurred between the months of June and August. Between April and September, average Ppt was only 41 mm greater than average PET for the ten years of the study. In six years, total PET exceeded total Ppt for the six months (Table 1). During the second half of the water year, the cumulative weekly water balance (i.e., Ppt—PET) was generally positive until early July (week 40, Figure 2). In extremely dry years (e.g., 1999), the water balance was negative early in the period (week 36), while in wet years (e.g., 2000), the balance remained positive through the end of the water year. These periods of excessive moisture or drought strongly affected vernal pool hydroperiods. The vernal pools dried almost every year, but they typically dried earlier in dry years (e.g., 1995, 1999) and later or not at all in wet years (Table 3). Pool 504 was the most ephemeral, drying earliest, followed respectively by pools 503, 1710, and 1711. In two of the ten years, pool 1710 never dried; 1711 held surface water through three of nine years. In the dry year 1999, as water deficits accrued, the pools dried rapidly (Figure 3A). Pool 504 was dry by the second week of April (week 28), briefly held water during two weeks in May following heavy precipitation, and then dried for the year. Pool 503 dried in early June (week 36), followed by 1710 in mid-June (week 38) and 1711 in mid-July (week 42). The water balance remained positive throughout the second half of the following year, 2000 (Figure 3B). The pools retained surface water much later into 2000, with pools 1710 and 1711 holding surface water through September 30.

Water-level changes in vernal pools were strongly correlated with weather attributes (Table 4). Weekly water-level change in all pools was positively correlated with Ppt in the current week but was not correlated with the preceding week's Ppt, except in pool

Table 2. Multi-year mean, lower quartile (Q25), annual April ground-water levels, and average deviation from the multi-year mean for U.S. Geological Survey wells adjacent to the Quabbin Reservation by well and year and late winter MDC snowpack (cm snow-water equivalent) by calendar year, 1993–2002.

Year	April ground-water level: U.S. Geological Survey well[1]						Deviation	MDC Snowpack (cm)
	Hardwick 1	Hardwick 31	Orange 63	Pelham 24	Petersham 16	Ware 43		
	(meters below ground level)							
Mean	3.73	3.26	1.97	0.96	3.45	2.53		
Q25	4.21	3.33	2.20	1.12	4.07	2.77		
1993	3.34	3.14	1.96	0.71	2.20	2.10	+0.41	4.34
1994	3.07	3.07	1.62	0.85	2.48	2.29	+0.42	6.91
1995	4.44	3.4	2.15	1.09	4.16	2.79	−0.35	2.29
1996	3.0	3.12	1.47	0.84	2.67	2.31	+0.41	5.54
1997	3.23	3.23	1.74	0.89	3.27	1.55	+0.33	3.33
1998	3.83	3.24	1.95	0.87	3.87	2.37	−0.04	2.69
1999	4.24	3.26	2.18	1.15	4.11	2.75	−0.30	0.0[2]
2000	2.8	3.09	1.71	0.84	3.09	1.89	+0.41	4.83
2001	3.34	3.02	1.57	0.95	2.06	2.29	+0.44	16.0
2002	4.58	3.35	2.27	1.25	3.94	2.74	−0.37	0.0

[1] Data at http://ma.water.usgs.gov/water_g.htm.
[2] No snow pack.

1711. Conversely, pool water-level change was negatively correlated with PET, although the relationships were only significant for pools 1710 and 1711 ($p \leq 0.05$; Table 4). The weekly water balance includes the net effect of both weather attributes and was more strongly correlated with water-level change in the vernal pools than either individual attribute. The same patterns of relationships occurred for the period between 1 April and 30 September, as occurred for the full water year; however, PET was significant only for pool 1711 for this subset of weeks (Table 4).

Ppt and PET were good descriptors of the weekly change in pool water levels, explaining between 40–70% of the variability in water-level change (Table 5). The intercept values for all models were negative, indicating a loss of pool water additional to that from PET, likely to ground water. As anticipated, the coefficients for Ppt were all positive, and those for PET were consistently negative. Individual pool regressions differed significantly among pools for the full water year and for the April–September period, implying individual pool responses to Ppt and PET and precluding the development of a single, common model. Paired-pool comparisons revealed that the difference among pool models for the full water year were due to differences between pool 1710 and the other three pools.

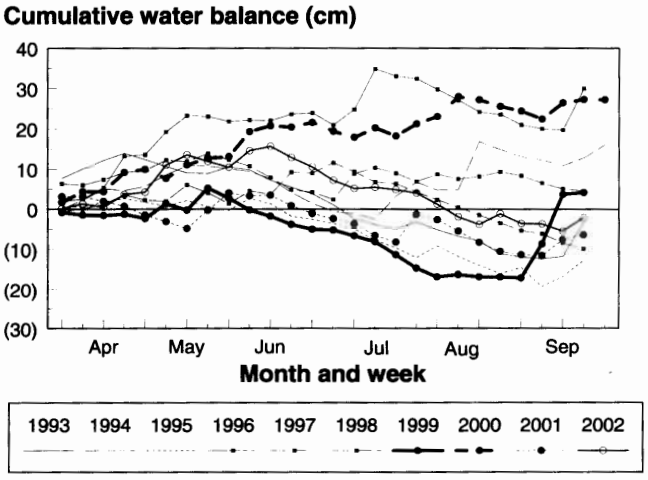

Figure 2. Cumulative difference in weekly precipitation and potential evapotranspiration (water balance), Quabbin Reservation, 1 April–30 September, 1993 through 2002.

Table 3. Latest date that a vernal pool held surface water, by pool and year, Quabbin Reservation, calendar year 1993–2002.

Year	Vernal pool			
	503	504	1710	1711
1993	Jun 15	May 11	Jun 23	n/a[1]
1994	Jun 14	May 31	Not dry[2]	Not dry
1995	Jun 20	Apr 25	Jul 3	Jul 25
1996	Aug 6	May 28	Aug 28	Not dry
1997	Jun 10	May 27	Jul 15	Jul 29
1998	Jul 14	May 20	Aug 4	Aug 25
1999	Jun 1	Apr 6	Jun 15	Jul 13
2000	Jul 3	Jun 27	Not dry	Not dry
2001	Jun 26	May 1	Aug 21	Sep 4
2002	Jul 9	Jun 4	Jul 16	Aug 13

[1] Pool not monitored through end of water year.
[2] Pool held surface water through the end of the water year.

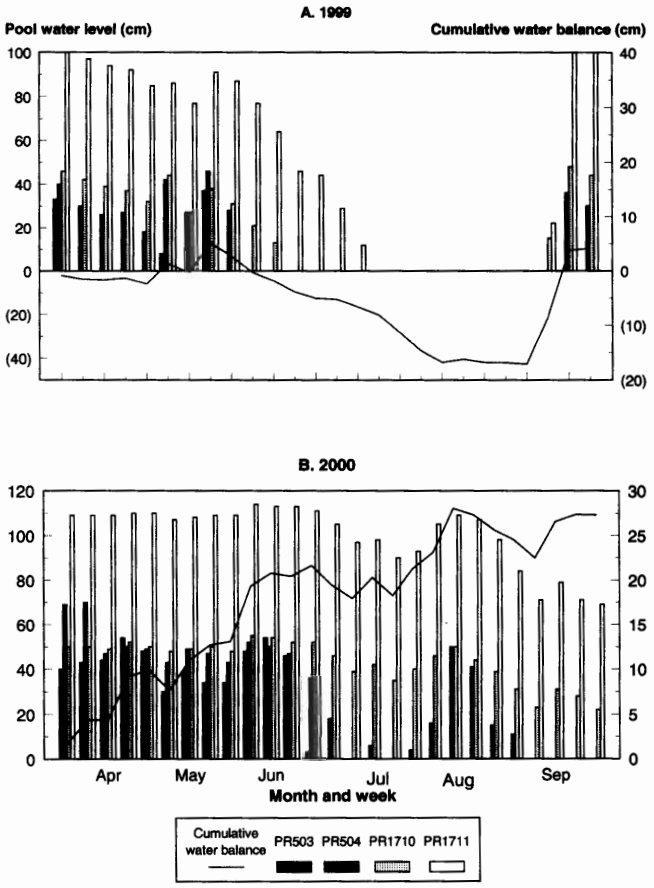

Figure 3. Cumulative difference in weekly precipitation and potential evapotranspiration (water balance) and water depths for four vernal pools, Quabbin Reservation, 1 April–30 September, 1999 (top) and 2000 (bottom).

Paired-pool comparisons for the April–September period showed that all four individual pool models were unique (i.e., significantly different). The absolute values of the standard partial regression coefficients for Ppt were two to six times those for PET (Table 5), showing the greater importance of Ppt in explaining pool water-level change.

Precipitation is projected to increase over the 21st century, with 30-year, full water-year averages exceeding the 1961–1990 period but less than the recent ten-year average (Table 1). Precipitation between 1 April–30 September is also projected to increase, with future long-term averages exceeding the 1960–1990 period and also the more recent 1992–2002 average. Due to increased projected temperatures, projected potential evapotranspiration exceeds the 1960–1990 and 1992–2002 periods for both the full water year and the 1 April–30 September period but only after 2050. Projected increases in PET would result in water deficits occurring earlier in the year, lasting later in the year, and of greater magnitude (Figure 1B).

DISCUSSION

The hydroperiod of ephemeral wetlands is the most important abiotic factor affecting faunal composition and productivity (Semlitsch et al. 1996, Schneider 1999). The long-term hydroperiod of small, isolated, ephemeral wetlands, such as woodland vernal pools, is affected by site, morphological, and climatic factors (Hayashi and Rosenberry 2001, Winter et al. 2001, Brooks and Hayashi 2002). Annual variation in hydro-

Table 4. Pearson correlation coefficients between weekly water-level change in four vernal pools and weekly weather attributes for the full water year and for the 1 April–30 September period, Quabbin Reservation, 1992–2002.

Weather attribute	Vernal pools			
	503	504	1710	1711
	Full water year			
Precipitation (Ppt)	0.714**[a]	0.576**	0.779**	0.691**
1-week-lag Ppt	−0.042	−0.101	0.045	0.203*
Pot. Evapotranspiration (PET)	−0.210	−0.195	−0.230*	−0.311**
1-week-lag PET	−0.220	−0.100	−0.242*	−0.314**
Water balance (Ppt-PET)	0.771**	0.642**	0.828**	0.765**
1-week-lag water balance	0.045	−0.075	0.141	0.320**
	1 April–30 September			
Precipitation (Ppt)	0.772**	0.613**	0.828**	0.725**
1-week-lag Ppt	−0.040	−0.075	0.043	0.234*
Pot. Evapotranspiration (PET)	−0.096	−0.177	−0.089	−0.230*
1-week-lag PET	−0.136	−0.071	−0.117	−0.252*
Water balance (Ppt-PET)	0.795**	0.656**	0.832**	0.766**
1-week-lag water balance	−0.002	−0.062	0.078	0.305**

[a] * indicates Bonferroni-corrected $p \leq 0.05$; ** $p \leq 0.001$.

Table 5. Results of the multiple regression analysis of weekly water-level change in four vernal pools and concurrent weekly precipitation (Ppt) and potential evapotranspiration (PET) for the full water year and for the 1 April–30 September period, Quabbin Reservation, water years 1992–2000. Standard partial regression coefficients are reported in parenthesis.

				Partial and standard partial regression coefficients					
Pool	N[a]	Adj. R^2	F	Intercept	p	Ppt	p	PET	p
				Full water year					
503	152	0.589	109.3	−5.233 (na)	<0.001	3.657 (0.745)	<0.001	−3.741 (−0.274)	<0.001
504	74	0.398	25.1	−6.747 (na)	0.014	3.460 (0.616)	<0.001	−4.288 (−0.257)	0.006
1710	229	0.685	248.4	−3.553 (na)	<0.001	2.138 (0.797)	<0.001	−1.773 (−0.251)	<0.001
1711	233	0.583	163.5	−3.466 (na)	0.002	3.063 (0.7)	<0.001	−3.512 (−0.313)	<0.001
				1 April–30 September					
503	120	0.627	101.1	−6.962 (na)	<0.001	3.811 (0.796)	<0.001	−3.221 (−0.196)	0.001
504	57	0.414	20.8	−5.459 (na)	0.159	3.466 (0.639)	<0.001	−4.96 (−0.246)	0.020
1710	173	0.702	203.5	−5.162 (na)	<0.001	2.182 (0.837)	<0.001	−1.206 (−0.143)	0.001
1711	178	0.582	124.0	−4.122 (na)	0.009	2.908 (0.731)	<0.001	−3.141 (−0.245)	<0.001

[a] Includes only those weeks when a pool held surface water throughout the week.

period is thought to be an expression of year-to-year changes in weather patterns, especially precipitation (Winter et al. 2001). This study assessed the influence of precipitation and evapotranspiration on weekly water-level change and on annual hydroperiod in four vernal pools over a 10-year period.

Vernal pools in the northeastern United States typically have an annual hydrologic cycle that coincides with annual patterns in precipitation (Ppt) and potential evapotranspiration (PET) (Figure 1A). In this study, the rate of weekly water-level change in vernal pools and the timing of pool drying were clearly affected by Ppt and PET. Precipitation was positively correlated with weekly water-level change in all four pools, over both the full water year and the April–September period (Table 4). The relationship between PET and pool water-level change, while less strong, was consistently negative, reflecting the loss of pool water from direct surface evaporation and transpiration by pool and adjacent upland vegetation.

The relationships between weekly water-level change in vernal pools and weather effects were highly significant in all pools, and weather effects explained greater than 50% of the variability in water-level change in three of the four pools (Table 5). The significant difference among the individual pool models implies that each pool responds uniquely to Ppt and PET. This suggests that a common vernal pool—weather model would be less precise than individual pool models. It also means, if there are no common responses among pools, that the investigation of vernal pool—weather relations and vernal pool hydrology will be more difficult.

Based on a comparison of standard regression coefficients, Ppt had a much greater effect on pool water-level change than did PET. The greater importance of Ppt is likely due to Ppt inputs occurring over a longer portion of the year than do the more seasonal PET-driven losses. Additionally, there is likely some highly ephemeral surface runoff of Ppt from adjacent uplands or exposed pool basins that concentrates and enhances Ppt effects on pool-water levels. Solving the regression equations, when setting the pool water-level change to zero, showed that rainfall of 1 to 2 cm per week, additional to that needed to replace PET losses, would be required to maintain constant pool levels during the critical spring-summer period of larval amphibian development and metamorphosis. Increasing PET during this period would require additional, regular rainfall to maintain pool water levels or reduce the rate of water-level decrease.

The large unaccounted loss of water in the regression models, represented by the negative intercept term (Table 5), could be attributed to early spring overflow from the pools, infiltration to root-zone soil moisture, an underestimate of actual evapotranspiration-associated water loss (AET) (Lide et al. 1995), and/or an inaccurate estimate of precipitation. Water overflow from the vernal pools was negligible, occurring briefly, if at all, immediately following snowmelt. Shallow ground-water-exchange rates at the pools are unknown, but a preliminary study suggested that the northern pools were more influenced by ground water than were the southern pools (Gay 1998). As the pools occur on impervious soil horizons or bedrock (Gay 1998), pool water is assumed to flow laterally to adjacent uplands, mostly to replace water lost to transpiration by forest vegetation (Hayashi et al. 1998, van der Kamp and Hayashi 1998). Pool-specific estimates of precipitation were likely inaccurate. Weekly precipitation inputs to all pools were derived from a single, centrally located site. Spatial variation in precipitation

would result in inaccurate estimates of precipitation at the individual pool locations.

While estimated PET values in this study were similar to other estimates of PET for the northeast using the water-balance method (e.g., 50–60 cm/yr, Church et al. 1995), the estimates were likely different than AET from the vernal pool sites. While appropriate for regional-scale characterizations of PET, the Thornthwaite methods under-performs at site scales by failing to account for the influences of increasing water and sediment temperatures as a wetland dries (Poiani and Johnson 1993a) and for the structural complexity of wetland vegetation (Lott and Hunt 2001). However, in regions where there is rarely a moisture deficit, Thornthwaite PET closely approximated AET (Yin and Brook 1992) and has been shown to provide adequate estimates of evapotranspiration in temperate, humid climates (Hammer and Kalec 1986). The climate of the study area matches these conditions, where the 30-year average Ppt is 1.8 times PET and Ppt < PET only in June, July, and August. A more rigorous assessment of evapotranspiration effects on vernal pool hydrology would use energy-based calculations and account for differences in forest composition and structure at each pool.

The climate of the northeast is projected to warm and become wetter over the next century (New England Regional Assessment Group 2001). Both annual and seasonal minimum temperatures are predicted to increase at a greater rate than maximum temperatures. Predicted changes are large relative to the historical record. Precipitation is also projected to increase but at a lesser rate and with greater uncertainty. The projected increases in temperatures would result in an increase in annual PET from the 30-year (1961–1990) average PET by 2050 (Table 1). Under this scenario, the balance between Ppt and PET would become negative (i.e., Ppt < PET) approximately three weeks earlier by 2100 (Figure 1B). Water deficits would be of greater magnitude during the summer months and would also extend later into the year, delaying pool reinundation. Evapotranspiration is a component of the hydrologic cycle that is difficult to model, but it is the most sensitive to climate change and variability (Hobbins et al. 2001). The linkage of climate change forecasts and hydrologic models should be a useful and productive method to examine the effects of projected climate change on water resources and wetlands (Kletti and Stefan 1997, Mortsch 1998), recognizing that improvements in both sets of models need to be made (Leavesley 1994).

Any increase in PET would increase the rate of water loss from vernal pools. An increase in PET and the rate of pool water loss over the critical spring/early summer period would lead to decreased hydroperiod lengths and the more frequent loss of the annual reproductive effort of pool-breeding amphibians (Donnelly and Crump 1998). Precipitation is projected to increase concurrently with temperature but not at a similar rate (New England Regional Assessment Group 2001). Additionally, precipitation patterns are expected to become more variable or episodic, with a greater number of drought periods followed by downpours and fewer low-intensity rain events (Karl et al. 1995, Moore et al. 1997). This more episodic pattern of precipitation would cause pools to dry during the intervening drought periods, to be refilled later by downpours, but after larval amphibians have died. Additionally, due to the limited maximum volume of most pools (< 500 m^3, Brooks and Hayashi 2001), pools are unable to capture and store additional input from low-frequency, high-intensity precipitation events, and the excess water is lost to ephemeral overflow. Additional focus on projecting changes in precipitation patterns (i.e., pattern of precipitation events and length of inter-event periods) will be critical to the assessment of climate change effects on isolated wetlands.

Poiani and Johnson (1991) and Larson (1995) reported a similar pattern of effects of climate and climate change on the number and distribution of isolated wetland basins in the northern prairie region of North America. The percentage of basins holding surface water was inversely related to increasing temperature and directly related to increasing precipitation. Increasing temperatures would increase evapotranspiration and potentially extend the growing season of wetland vegetation, which would increase cumulative annual evapotranspiration. A simulation of the effects of climate change on the hydrology of a single semi-permanent wetland by Poiani and Johnson (1991, 1993b) projected drier hydrologic conditions in the wetland due to higher temperatures and increased evapotranspiration, despite increased precipitation. Water levels were predicted to be lower and pool drying was expected to occur more frequently.

Pool-breeding amphibians are naturally adapted to the irregular hydroperiod of vernal pools. Amphibian recruitment is often episodic; reproduction fails partially or fully in most years but is compensated by large cohorts in the few favorable years (Marsh 2001). Wood frogs and spotted salamanders require between 52 and 135 days and 92 and 164 days, respectively, for the eggs to hatch and for the larvae to metamorphose to terrestrial juveniles (DeGraaf and Yamasaki 2001). Assuming spring migration to the pools and egg laying about April 1 in average years, wood frogs require surface water until about July 3 (i.e., 94 days) and spotted salamanders until August 6 (128 days). Based on the latest date that the pools of this study held water (Table 3), the hydroperiod of pool 503 was

long enough for wood frog metamorphosis for four years out of ten and only one year out of ten for spotted salamanders. The hydroperiod of pool 504 was never sufficient for successful amphibian reproduction. The hydroperiod of pool 1710 was adequate seven out of ten years for wood frogs and four out of ten for spotted salamanders; in pool 1711, hydroperiod in all years was sufficient for wood frog reproduction and in six out of nine for spotted salamanders. Any shortening of pool hydroperiods due to climate change would further reduce the occurrence of productive years. Delayed reinundation of pools in the fall due to extended water deficits would disrupt the breeding of marbled salamanders (*A. opacum* Gravenhorst). The females of the species constructs nests in the autumn in dry pool basins and broods her eggs until inundation (Jackson et al. 1989). If inundation is delayed, the eggs are increasingly likely to be abandoned and lost to predation or exposure. If vernal pool hydrology and hydroperiods become increasingly irregular as projected, due to an increased episodic pattern of Ppt and increased PET under climate change, amphibian reproductive capabilities may be taxed beyond their capacity to adapt, especially in smaller, more ephemeral pools.

Root and Schneider (2002) suggest that animals most likely to be affected earliest by climatic change are those whose populations are fairly small and are limited to isolated habitat islands. Climate-change effects have been predicted for montane mammals, as their habitats would be displaced upward and reduced in area with increasing warming (McDonald and Brown 1992). Climate-change effects are also predicted for depressional wetlands with small catchments (McCarthy et al. 2001). Vernal pools are depressional wetlands with small catchments and are isolated by definition, occurring as aquatic islands in a sea of forest. Individual pools provide breeding habitat for a small number of amphibians, organized with animals of nearby pools as metapopulations (Sjogren 1991). If smaller, more ephemeral pools were excluded as potential breeding habitat due to reduced hydroperiods, the average "between pool distances" of the remaining pools would increase. Based on among-pool distances from the survey of Quabbin Reservation pools (Brooks et al. 1998), eliminating pools smaller than 0.025 ha would increase the average distance between nearest-neighbor pools from 293 to 701 m. Eliminating pools less than 0.2 ha would increase average between-pool distances to 2431 m. Increased between-pool distances would affect the abilities of juvenile amphibians to disperse to new pools (Gibbs 1993, Semlitsch and Bodie 1998). This would affect the recolonization of pools where breeding populations may have gone extinct and the maintenance of genetic diversity of populations in the remaining breeding pools.

CONCLUSIONS

Precipitation was shown to have a greater effect on water-level change in woodland vernal pools than evapotranspiration. The relationships between pool hydrology and precipitation and evapotranspiration differ among pools, suggesting that it will be difficult to develop a single hydrologic model applicable for all vernal pools. On average, it takes more than 2 cm of rain per week to maintain pool water levels during the growing season. Projected temperature increases over the next century, due to global climate change, will increase evapotranspiration losses from pools, resulting in shortened hydroperiods and increased frequency of reproductive failures by pool-breeding amphibians. While precipitation is also projected to increase, it is likely that rainfall will be more variable, characterized by less frequent, heavy intensity events, separated by longer dry periods. While total precipitation may increase, this pattern of rainfall will cause isolated pools to dry during the drought periods, to be reinundated later, but resulting in the death of amphibian eggs or larvae. The loss of smaller, more ephemeral pools would result in the increased isolation of the remaining pools and their amphibian metapopulations.

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LITERATURE CITED

Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts. Wetlands 20:707–715.

Brooks, R. T. and K. L. Doyle. 2001. Shrew species richness and abundance in relation to vernal pond habitat in southern New England. Northeastern Naturalist 8:137–148.

Brooks, R. T. and M. Hayashi. 2002. Depth-area-volume and hydroperiod relationships of ephemeral ("vernal") forest pools in southern New England. Wetlands 22:247–255.

Brooks, R. T., J. Stone, and P. Lyons. 1998. An inventory of seasonal forest ponds on the Quabbin Reservoir watershed, Massachusetts. Northeastern Naturalist 5:219–230.

Burne, M. R. 2001. Massachusetts Aerial Photo Survey of Potential Vernal Pools. Massachusetts Division of Fisheries and Wildlife, Westborough, MA, USA.

Church, M. R., G. D. Bishop, and D. L. Cassell. 1995. Maps of regional evapotranspiration and runoff/precipitation ratios in the northeast United States. Journal of Hydrology 168:283–298.

Damon, R. A., Jr. and W. R. Harvey. 1987. Experimental design, ANOVA, and regression. Harper and Row, Publishers, New York, NY, USA.

DeGraaf, R. M. and M. Yamasaki. 2001. New England Wildlife: Habitat, Natural History, and Distribution. University of Press of New England, Hanover, NH, USA.

Donnelly, M. A. and M. L. Crump. 1998. Potential effects of climate change on two neotropical amphibian assemblages. Climatic Change 39:541–561.

Dunne, T. and L. B. Leopold. 1978. Water in Environmental Planning. W. H. Freeman and Company, New York, NY, USA.

Gay, D. E. 1998. A comparison of the hydrology and aqueous geochemistry of temporary ponds on the Prescott Peninsula of the Quabbin Reservoir watershed in central Massachusetts. M.S. Thesis. Department of Geosciences, University of Massachusetts, Amherst, MA, USA.

Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13: 25–31.

Hammer, D. E. and R. H. Kadlec. 1986. A model for wetland surface water dynamics. Water Resources Research 22:1951–1958.

Hayashi, M. and D. Rosenberry. 2001. Effects of groundwater exchange on the hydrology and ecology of surface waters. Journal of Groundwater Hydrology 43:327–341.

Hayashi, M., G. van der Kamp, and D. L. Rudolph. 1998. Water and solute transfer between a prairie wetland and adjacent uplands, 1. water balance. Journal of Hydrology 207:42–55.

Hobbins, M. T., J. A. Ramirez, and T. C. Brown. 2001. Trends in regional evapotranspiration across the United States under the complementary relationship hypothesis. p. 106–121. *In* J. A. Ramirez (ed.) Proceedings of the 21st Annual AGU Hydrology Days. Colorado State University, Ft. Collins, CO, USA.

Jackson, M. E., D. E. Scott, and R. A. Estes. 1989. Determinants of nest success in the marbled salamander (*Ambystoma opacum*). Canadian Journal of Zoology 67:2277–2281.

Joyal, L. A., M. McCollough, and M. L. Hunter, Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15: 1755–1762.

Karl, T. R., R. W. Knight, D. R. Easterling, and R. G. Quayle. 1995. Trends in U. S. climate during the twentieth century. Consequences 1:3–12.

Kenk, R. 1949. The Animal Life of Temporary and Permanent Ponds in Southern Michigan. University of Michigan, Museum of Zoology, Ann Arbor, MI, USA. Misc. Publ. No. 71.

Kennamer, R. A. 2001. Relating climatological patterns to wetland conditions and wood duck production in the Southeastern Atlantic Coastal Plain. Wildlife Society Bulletin 29:1193–1205.

Kirkman, L. P., S. W. Golladay, L. Laclaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society 18: 553–562.

Kletti, L. L. and H. G. Stefan. 1997. Correlations of climate and streamflow in three Minnesota streams. Climatic Change 37:575–600.

Larson, D. L. 1995. Effects of climate on numbers of northern prairie wetlands. Climatic Change 30:169–180.

Leavesley, G. H. 1994. Modeling the effects of climate change on water resources—a review. Climatic Change 28:159–177.

Lent, R. M., P. K. Weiskel, F. P. Lyford, and D. S. Armstrong. 1997. Hydrologic indices for nontidal wetlands. Wetlands 17:19–30.

Lide, R. F., V. G. Meentemeyer, J. E. Pinder, III, and L. M. Beatty. 1995. Hydrology of a Carolina bay located on the upper coastal plain of western South Carolina. Wetlands 15:47–57.

Lott, R. B. and R. J. Hunt. 2001. Estimating evapotranspiration in natural and constructed wetlands. Wetlands 21:614–628.

Mansell, R. S., S. A. Bloom, and G. Sun. 2000. A model for wetland hydrology: description and validation. Soil Science 1656:384–397.

Marsh, D. M. 2001. Fluctuations in amphibian populations: a meta-analysis. Biological Conservation 101:327–335.

McCarthy, J. J., O. E. Osvaldo, N. A. Leary, D. J. Dokken, and K. S. White. 2001. Climate change 2001: impacts, adaptation, and vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, UK.

McDonald, K. A. and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409–415.

Milam, J. C. and S. M. Melvin. 2001. Density, habitat use, movements, and conservation of spotted turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35:418–427.

Moore, M. V., M. L. Pace, J. R. Mather, P. S. Murdoch, R. W. Howarth, C. L. Folt, C. Y. Chen, H. F. Hemond, P. A. Flebbe, and C. T. Driscoll. 1997. Potential effects of climate change on freshwater ecosystems of the New England/Mid-Atlantic region. Hydrological Processes 11:925–947.

Mortsch, L. D. 1998. Assessing the impact of climate change on the Great Lakes shoreline wetlands. Climatic Change 40:391–416.

New England Regional Assessment Group. 2001. Preparing for a changing climate: the potential consequences of climate variability and change. New England regional overview. U. S. Global Change Research Program, University of New Hampshire, Durham, NH, USA.

Palik, B., D. P. Batzer, R. Buech, D. Nichols, K. Cease, L. Egeland, and D. E. Streblow. 2001. Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. Wetlands 21:532–542.

Poiani, K. A. and W. C. Johnson. 1991. Global warming and prairie wetlands. BioScience 41:611–618.

Poiani, K. A. and W. C. Johnson. 1993a. A spatial simulation model of hydrology and vegetation dynamics in semi-permanent prairie wetlands. Ecological Applications 3:279–293.

Poiani, K. A. and W. C. Johnson. 1993b. Potential effects of climate change on a semi-permanent prairie wetland. Climatic Change 24: 213–232.

Poiani, K. A., W. C. Johnson, G. A. Swanson, and T. C. Winter. 1996. Climate change and northern prairie wetlands: simulations of long-term dynamics. Limnology and Oceanography 41:871–881.

Root, T. L. and S. H. Schneider. 2002. Climate change: overview and implications for wildlife. p. 1–56. *In* S. H. Schneider and T. L. Root (eds.) Wildlife Responses to Climate Change: North American Case Studies. Island Press, Washington, DC, USA.

Schneider, D. W. 1999. Snowmelt ponds in Wisconsin: influence of hydroperiod on invertebrate community structure. p. 299–318. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger (eds.) Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, Inc., New York, NY, USA.

Semlitsch, R. D. and J. R. Bodie. 1998. Are small, isolated wetlands expendable. Conservation Biology 12:1129–1133.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184–192.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structural dynamics of an amphibian community. p. 217–248. *In* M. L. Cody and J. A. Smallwood (eds.) Long-term Studies of Vertebrate Communities. Academic Press, Inc., San Diego, CA, USA.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnean Society 42:135–147.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry: the Principles and Practice of Statistics in Biological Research, 3rd Edition. W. H. Freeman and Company, New York, NY, USA.

Sun, G., H. Riekerk, and N. B. Comerford. 1998a. Modeling the

forest hydrology of wetland-upland ecosystems in Florida. Journal of the American Water Resources Association 34:827–841.

Sun, G., H. Riekerk, and N. B. Comerford. 1998b. Modeling the hydrologic impacts of forest harvesting on Florida flatwoods. Journal of the American Water Resources Association 34:843–854.

Tiner, R. W., H. C. Bergquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically isolated wetlands: a preliminary assessment of their characteristics and status in selected areas of the United States. U.S. Department of the Interior, Fish and Wildlife Service. Northeast Region, Hadley, MA, USA. (http://wetlands.fws.gov/Pubs_reports/isolated/report.htm).

van der Kamp, G. and M. Hayashi. 1998. The groundwater recharge function of small wetlands I the semi-arid northern prairies. Great Plains Research 8:39–56.

Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie, Supplement 58:7–206.

Winter, T. C., D. O. Rosenberry, D. C. Buso, and D. A. Merk. 2001. Water source to four U.S. wetlands: implications for wetland management. Wetlands 21:462–473.

Yin, Z. and G. A. Brook. 1992. Evapotranspiration in the Okefenokee Swamp watershed: a comparison of temperature-based and water balance methods. Journal of Hydrology 131:293–312.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ, USA.

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