RESPONSE OF AMPHIBIANS TO RESTORATION OF A SOUTHERN APPALACHIAN WETLAND: A LONG-TERM ANALYSIS OF COMMUNITY DYNAMICS

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Abstract: Although amphibians are increasingly being used to assess ecosystem function of compensatory wetlands, there are almost no long-term studies of responses to ecological restoration. Consequently, much uncertainty exists about the appropriate timeframes and best criteria for evaluating responses to wetland restoration. We studied aspects of pond colonization and long-term community dynamics in ponds created at a mitigation site in western North Carolina. We examined whether landscape variables influenced the initial colonization of 22 constructed ponds and conducted a long-term study of changes in species richness and community composition in ten constructed and ten reference ponds over seven breeding seasons. During the first year of pond filling, species richness and the number of egg masses of the wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*) were positively correlated with pond size, depth, and hydroperiod but independent of distance to the nearest forest, paved road, or source pond. The ten constructed ponds in the long-term study first filled in 1996 and were larger, deeper, warmer, more oxygen-rich, and of longer seasonal hydroperiod than reference ponds. Seven species bred in the constructed ponds during the first year of filling, and species richness reached equilibrium within two years of initial pond filling. Most species colonized constructed ponds rapidly, but frequency of use by eastern newts (*Notophthalmus virides-cens*) increased slowly over five years. Constructed ponds supported significantly more species than reference ponds, and the annual turnover rate of breeding populations was approximately 25% for both pond types. Our data suggest that post-restoration monitoring for 2–3 years may be sufficient to characterize species and communities that will utilize ponds for the first decade or so after pond creation.

Key Words: amphibians, pond colonization, community dynamics, North Carolina, mitigation banks

INTRODUCTION

Although seasonal ponds are primary breeding sites for many amphibians in the eastern United States, they have received little legal protection because of their small size (surface area generally < 5 ha) and a lack of understanding of their ecological significance (Gibbs 1993, Semlitsch and Bodie 1998, Snodgrass et al. 2000a, b). Restoration ecologists are increasingly incorporating seasonal ponds as elements of wetland restoration and are using amphibians to assess success. Amphibians are useful indicators of restoration success because they are important faunal elements of seasonal ponds and are sensitive to altered hydrology (Pechmann et al. 1989, Semlitsch et al. 1996, Semlitsch

2000, Paton and Crouch 2002). The hydroperiod affects the likelihood of larvae achieving metamorphosis and influences the distribution and abundance of predators that feed on amphibian eggs and larvae (Heyer et al. 1975, Schneider and Frost 1996, Wellborn et al. 1996). Predation, competition, and behavioral constraints associated with maximizing foraging efficiency and predator avoidance prevent most amphibian species from occupying the entire hydrologic gradient (Kats et al. 1988, Wellborn et al. 1996, Skelly 1997). Consequently, both individual species and amphibian assemblages vary predictably along the gradient from highly seasonal to permanent ponds (e.g., Skelly et al. 1999, Snodgrass et al. 2000a, b).

A primary goal of restoration ecology is to improve

the structural and functional elements of ecosystems to levels that will sustain viable populations of community members. Although amphibians are increasingly being used to assess mitigation for loss of small freshwater wetlands, much remains to be learned about the best criteria for measuring responses to mitigation or the appropriate timeframes for estimating long-term success. Criteria for measuring success might include population change, population persistence, or pond colonization and the development of species-rich assemblages.

The best evidence of restoration success is a long-term increase in adult populations. However, population responses of pond-breeding amphibians are difficult to assess within short timeframes because of dynamic reproductive patterns (Gill 1978, Berven 1995, Semlitsch et al. 1996, Semlitsch 2000, Pechmann et al. 2001), long population lags between the time of metamorphosis and first reproduction, and sensitivity to stochastic events that mask underlying population trends (Semlitsch et al. 1996, Thomas 1997, Gibbs et al. 1998, Babbitt and Tanner 2000, Marsh 2001). In addition, adult populations are influenced by landscape characteristics near breeding sites (Richter 1997, Semlitsch 2000, Marsh and Trenham 2001).

The alternative success criterion of demonstrating that created ponds support breeding populations of resident amphibians is less desirable. Of particular concern is the lack of a direct link between the presence of a breeding population and adult population size (Pechmann et al. 2001, Petranka et al. 2003). For example, created ponds could attract breeding adults from adjoining ponds but act as population sinks due to high premetamorphic mortality. Even when metamorphs are produced, recruitment into the terrestrial population may be at or below replacement levels, and adult populations may fail to increase with time.

Despite these limitations, researchers have mostly assessed mitigation success using data on amphibian communities that assemble within a few years of pond construction (e.g., Mierzwa 2000, Pollet and Bendell-Young 2000, Lehtinen and Galatowitsch 2001, Stevens et al. 2002). A current limitation of this approach is that few data are available on long-term community dynamics and patterns of colonization (e.g., Semlitsch et al. 1996, Skelly et al. 1999, Pechmann et al. 2001) that would provide a basis for establishing appropriate timeframes for assessing restoration success. Local pond communities that develop in created ponds should increase in diversity as colonization proceeds, then reach equilibrium as communities become saturated or population turnover rates stabilize. Since reference ponds presumably are at or near equilibrium, the minimum period for monitoring species richness in constructed ponds should equal or exceed the time required for developing communities to reach equilibrium. If this requires many years, then short-term comparisons of reference and constructed ponds may be biased and underestimate the ecological value of created wetlands.

We conducted a study from 1995 to 2002 to examine the responses of amphibians to restoration of a degraded wetland in the southern Appalachian Mountains, USA. This was part of a holistic effort to assess wetland function using data on hydrology, soils, stream function, vegetation, and vertebrates (Moorhead et al. 2001). We constructed an array of ponds on site to enhance breeding habitats for amphibians. We gathered data to assess wetland function and to enhance the design and monitoring of future restoration sites. Our primary objectives were to (1) compare physiochemical characteristics of created ponds relative to reference ponds, (2) examine landscape attributes that influence initial pond colonization, (3) document colonization rates of created ponds, (4) document long-term changes in species richness and community composition of created ponds relative to reference ponds, and (5) document population responses of two focal species to wetland creation. This paper focuses on objectives (1)-(4). The demographic responses to pond creation are presented in Petranka et al. (2003).

METHODS

Site Description and History

The Tulula Wetlands Mitigation Bank is a 95-ha wetland restoration site located 4.8 km west of Topton in Graham County, North Carolina, USA (35°17′N, 83°41′W; elevation range 784–800 msl; Figure 1). The site is within the floodplain of Tulula Creek and is surrounded by the Nantahala National Forest that provides extensive forested habitat for adult amphibians. The site originally contained scattered depressional fens (Moorhead and Rossell 1998) but was degraded in the mid-late 1980s by a failed attempt to build a golf course on site. During this period, Tulula Creek was channelized, drainage ditches were dug, and spoil was spread over the floodplain to create fairways. About 40% of the forest was removed, and cattle later grazed the site. The site was purchased in 1994 and enhanced from 1996 to 2002 by restoring the original stream channel, filling drainage ditches, creating ponds for aquatic organisms, removing fill from underlying wetland soils, and planting native trees (Moorhead et al. 2001).

We located 155 ponds at Tulula in 1995, including 11 golf course ponds and 144 smaller ponds (median surface area = 12.1 m^2) that were mostly non-natural
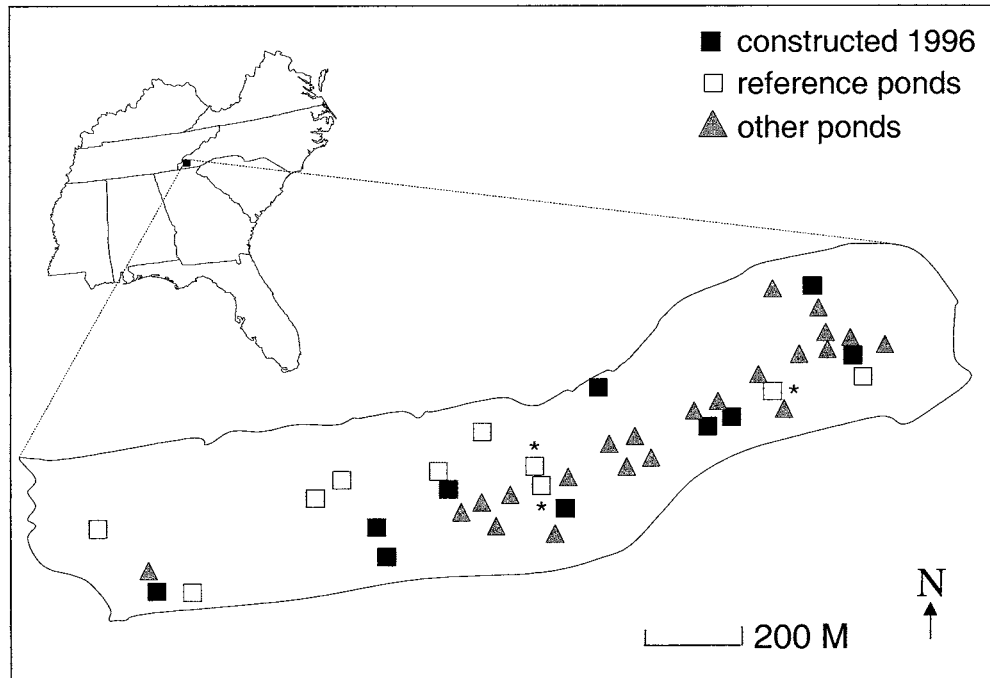
Figure 1.   Location of the study site and ponds. Reference ponds with asterisks were eliminated in fall 2001 during stream reconstruction. 'Other ponds' are primary breeding sites other than the ten reference ponds and ten constructed ponds that were created in 1996.

habitats such as puddles and test wells for pond sites. No more than 15 ponds were considered to be natural ponds, and many were degraded from timber removal or siltation.

Creation of Ponds and Selection of Reference Ponds

To compensate for the loss of natural breeding sites, seven seasonal and three permanent fish-free ponds were created between October 1995 and January 1996. Ponds were constructed in areas with no canopy closure. The mean surface area and maximum depth at full capacity were 480 ± 68 m² and 64 ± 5 cm (± 1 SE here and throughout), and the distance between adjacent constructed ponds averaged 190 m (range = 70–513 m). Within one year of filling, the constructed ponds developed complex assemblages of invertebrates and amphibians and a dense growth of macrophytes along their margins and bottoms. Although some shrubs and saplings have established along the margins, the ponds have remained as open, sunny habitats (forest canopy cover <10%) since 1996.

Small ponds previously existed where four ponds were constructed (surface area <20 m² compared with 655 m² after enlargement). These were used as breeding sites by small numbers of wood frogs (*Rana sylvatica* Le Conte), spotted salamanders (*Ambystoma maculatum* (Shaw)), and spring peepers (*Pseudacris crucifer* Wied-Neuwied) in 1994 and 1995, but most

functioned as population sinks due to mass mortality of larvae from premature seasonal drying. At the remaining sites, established small pools were <80 m from constructed pond sites and supported source populations for colonization. Second growth forest that provided adult habitat occurred within 33 m of all constructed ponds (mean distance = 13 m). Although construction during the restoration phase caused significant site disturbance in the immediate vicinity of Tulula Creek, disturbance to the study ponds, adjoining forest, and interconnecting habitats was minimal, with the exception of three reference ponds that were eliminated in 2001 (see below).

We were unable to locate suitable reference ponds off site because of the rarity of vernal ponds and other seasonal depressions in the southern Appalachians. In addition, undisturbed ponds with mature forest canopies are poor reference habitats because amphibian assemblages differ markedly between shaded ponds beneath mature forest canopies compared with ponds where the overstory is poorly developed (Skelly et al. 1999). Because several decades may be required for forest canopy development at our site, constructed ponds would not be expected to develop similar communities as fully shaded ponds in mature forest within the timeframe of the study. As a practical alternative, we selected the ten largest and most natural ponds that remained on site as reference ponds. These were smaller and shallower than the constructed ponds and varied

from being sunny to partially shaded by tag alder (*Alnus serrulata* (Aiton) Willdenow) or mixed pine-hardwoods. Estimated mean canopy cover ranged from 0 to 100% and averaged 60%. Five ponds lacked emergent macrophytes and had bottoms covered with leaf litter. The remaining ponds were less shaded and had emergent vegetation and less leaf litter. Six ponds were natural, while the remainder were semi-natural (e.g., stream channel cut-offs or vegetated seasonal depressions >10–yr old). Seminatural ponds were similar in surface area ($t_8 = -0.37$; $P = 0.72$) and depth ($t_8 = -0.62$; $P = 0.28$) to the natural ponds, and all 10 reference ponds were used as breeding sites by *R. sylvatica* and *A. maculatum* during the two years prior to pond construction.

We monitored reference ponds from 1996 to 2002, but three were unavoidably destroyed in fall 2001 in conjunction with the reconstruction of Tulula Creek. A moderate drought that occurred from 1998 to 2002 caused several reference ponds either not to fill or to dry after holding water for < one month (Moorhead 2001, Moorhead et al. 2001). These were excluded from analyses, so yearly sample sizes varied from 5–10 reference ponds.

We compared the ten created and ten reference ponds in order to assess whether created ponds improved breeding habitat for amphibians. Because most ponds on site were small and prone to premature seasonal drying, our short-term goal was to create larger habitats with longer seasonal hydroperiods that would support a greater diversity of amphibians (Wellborn et al. 1996). Our long-term goal was to increase annual juvenile output and the size of breeding populations on site (Petranka et al. 2003).

Additional ponds were created after 1996 as part of restoration efforts and were used to study first-year colonization (see below). Most fish-filled golf course ponds were partially filled in 1999 to create shallower sites. Some were successfully converted into seasonal ponds that lacked fish. Sections of the restored stream channel were blocked with check dams in fall 1999 to allow revegetation of channel banks prior to initiating stream flow. Small pools formed in the deepest sections of these channel segments and were used as breeding sites in 2000 and 2001. In February 2002, the site contained 39 primary breeding sites (Figure 1).

Comparisons of Physiochemical Characteristics

We compared pH, temperature, conductivity, and oxygen saturation of constructed and reference ponds from 1996 to 2001. Water samples were taken at 1–6 week intervals during the day (900–1700 hrs) between February and September. All ponds were sampled on each visit. Water temperature was measured, and three subsamples of water were taken from each pond at approximately equidistant points along the center of the long axis and approximately 5–10 cm below the water surface. Subsamples were pooled, and readings were taken from the pooled sample. Samples were placed in a cooler with ice during warm weather, and dissolved oxygen was measured in the field < 3 h after samples were collected using Corning Check-mate© meters. Conductivity and pH were measured using Corning Check-mate© and Corning 430© bench meters, respectively. To avoid pseudoreplication, we computed yearly means for all parameters and used these values in statistical comparisons of reference and constructed ponds.

Comparisons of Species Assemblages

All ponds that were constructed in autumn–winter 1995 filled with water before amphibians began breeding in February 1996. We monitored constructed and reference ponds annually from 1996 to 2002 to determine changes in species richness, community composition, and annual pond use. Species that overwintered in ponds were not included on species lists unless eggs or hatchlings were found co-occurring with overwintering larvae. We visited ponds every 1–3 weeks between January and August and searched for amplexed adults, eggs, or larvae. We collected larvae by dipnetting ponds (typically for 10–30 min per visit depending on pond size and microhabitat complexity) or when sampling with open-bottom samplers to estimate survival of *R. sylvatica* and *A. maculatum* larvae as part of a separate study (Petranka et al. 2003). Larvae of seasonal pond breeders reach high densities (often exceeding 5–10 larvae/m^2), and most species on individual pond lists were collected after taking only a few open-bottom samples or sweeps of dip-nets. Given the extensive seasonal sampling that was conducted, it is unlikely that any species in ponds went undetected.

We assembled a species list for every pond and calculated annual occupancy as the percentage of ponds used by each species. We measured community similarity between years using the Coefficient of Community (Pielou 1974):

$$CC = (200a)/(b + c)$$

where: *a* is the number of species shared in common and *b* and *c* are the total number of species in each community. CC ranges from 0 (no species shared) to 100 (all species are found in both communities).

Correlations between Pond Colonization and Landscape Features

We examined relationships between landscape attributes and species richness using data from the first

year of pond use. Data for subsequent years were not used because colonization events could not be distinguished unambiguously from return breeding events. We selected the six constructed ponds that did not have small breeding sites *in situ* immediately prior to pond construction in 1996, along with 16 ponds that were constructed or modified in 1999. The latter included golf course ponds that were partially filled to create shallower sites without fish, water-filled sections of the revegetating stream channel, and several pools formed during stream restoration. The golf course ponds were not used by vernal pond breeders prior to partial filling and fish elimination; thus, they were treated as newly created fish-free depressions.

We also censused the number of egg masses of *R. sylvatica* and *A. maculatum* that were deposited during the breeding season. We selected these species because they used a high percentage of ponds and lay large egg masses that can be censused accurately to assess relative breeding population size (e.g., Crouch and Paton 2000).

To obtain an estimate of annual breeding effort, we censused egg masses every 1–3 weeks by systematically wading through all areas of a pond and scoring masses. We censused seasonally until no new masses were found and used the cumulative number of egg masses laid as a relative index of the number of pond colonists. We examined whether the number of egg masses was correlated with pond size, maximum pond depth, relative pond hydroperiod, distance to the nearest source pond, size of the breeding population in the nearest source pond, distance to nearest forest cover, average distance from forest cover, distance to the nearest paved highway, and distance to Tulula Creek. The latter contained steep banks that may have been a dispersal barrier to migrating adults. We also examined whether species richness was correlated with pond size, depth, and hydroperiod; and distance to the nearest pond, forest, paved road, and Tulula Creek.

We used GIS data layers of streams, roads, ponds, and forest cover that were prepared from aerial photographs to estimate distance (± 1 m) to landscape features using ARC/INFO and ArcView. Pond perimeters were mapped using GPS readings with corrections to approximately 1-m accuracy, and surface area and maximum depth of ponds were estimated using meter sticks or meter tapes when ponds were at full capacity. Distance between ponds was estimated from the closest pond edge of nearest neighbors using ARC/INFO and ArcView. We estimated both the distance to the nearest forest cover and the mean distance to forest cover from the closest pond edge to nearest forest edge. The latter was determined by averaging distance to forest in each of the four cardinal directions. We estimated the size of the nearest conspecific breeding

population of *R. sylvatica* and *A. maculatum* using the number of egg masses that were deposited the year before pond filling. We did not consider small breeding sites such as flooded tire ruts to be source ponds since they rarely supported more than a few breeding adults. Instead, we restricted the analysis to the primary breeding sites in Figure 1. Because we were unable to determine hydroperiod precisely, we ranked ponds into categories that ranged from highly ephemeral (1) to permanent (5). Approximate drying times were category 1: early to late spring; category 2: late spring to mid-summer; category 3: mid-summer to early autumn; category 4: early autumn to winter (semi-permanent); and category 5: no seasonal drying (permanent).

Statistical Analyses

We analyzed data using Statistical Analysis System, Proprietary Software Release 8.2 (SAS Institute, Cary, North Carolina, USA). Because data from the same pond may not be statistically independent across years, we used repeated measures ANOVA to compare overall species richness, community similarity, and physiochemical characteristics of ponds. We used *t*-tests for comparisons within years. Data for richness were transformed ($\log_{10}N$) to increase homogeneity of variances, and analyses of community similarity indices were performed on ranked data (Proc Rank of SAS) because assumptions of normality were violated and could not be corrected through data transformations. Reference ponds that did not fill or that dried within one month of filling were excluded from analyses of richness and community similarity.

We used backward stepwise linear regression to examine relationships between number of egg masses and landscape attributes. A preliminary correlation analysis indicated that pond size, maximum depth, and hydroperiod were positively correlated (size versus depth: $r = 0.72$; $P < 0.0001$; size versus hydroperiod: $r = 0.61$; $P = 0.0008$; depth versus hydroperiod: $r = 0.75$; $P < 0.0001$). This reflects the fact that small, shallow ponds tended to dry earlier in the year than larger, deeper ponds. Because of the strong colinearity of these variables, we elected to use only pond size in the regression analyses. Egg mass number was transformed to $\log_{10} (N + 1)$ to minimize violations of the assumption of homogeneity of variances in Y values and regressed on landscape variables. Because we were conducting a fine-scale analysis with variation in parameters that is far less than that seen at larger spatial scales, we used a Type I error rate of 0.20 as a minimum value to be retained in the stepwise analysis.

Table 1. Summary of physiochemical characteristics of reference and constructed ponds. Values are means + 1 SE. Test statistics are for either *t*-tests or for repeated measures ANOVA.

Parameter	Reference Ponds	Constructed Ponds	Test Statistic	P
Surface area (m²)	82.5 + 21	480 + 69	$T_{18} = -5.54$	0.0003
Maximum depth (cm)	37 + 4.5	64 + 4.6	$T_{18} = 4.14$	0.0001
Conductivity (μS/cm)	42.5 + 3.8	37.3 + 2.8	$F_{1, 16} = 0.37$	0.55
pH	5.57 + 0.07	5.65 + 0.05	$F_{1, 16} = 0.27$	0.61
Temperature (C)	14.9 + 0.4	17.6 + 0.4	$F_{1, 16} = 14.75$	0.001
Oxygen saturation (%)	61.9 + 2.7	81.4 + 1.9	$F_{1, 16} = 14.40$	0.002

RESULTS

Abiotic Characteristics of Ponds

Constructed ponds were approximately six times larger and twice as deep on average as reference ponds (Table 1). Constructed ponds were also less prone to premature drying. For example, all constructed ponds held water for a sufficient duration to allow *A. maculatum* to initiate metamorphosis during the summer months, with the exception of 2001 when 20% of ponds dried prior to metamorphosis. In contrast, from 20 to 100% of reference ponds either did not fill or dried before *A. maculatum* initiated metamorphosis, depending on the severity of annual drought.

Means for pH and conductivity did not differ significantly for any year (Figure 2) or for the 6–yr interval (Table 1). However, constructed ponds were significantly warmer in four of six years and had significantly greater oxygen saturation levels in all but one year (Figure 2, Table 1). Year effects were significant

($P < 0.0001$) for all variables except conductivity ($F_{5, 80} = 1.78$; $P = 0.13$) but no year-by-pond type interaction term was significant (range of *P* values = 0.06–0.66).

General Pond Use by Amphibians

Resident amphibians rapidly occupied constructed ponds that first filled in 1996 (Figure 3; upper panel). Seven species bred in the constructed ponds within one year of construction, and ten species used constructed ponds through 2002 (Table 2). Reference ponds were also used by ten species of amphibians, but only the Blue Ridge two-lined salamander (*Eurycea wilderae*) was unique to reference ponds (breeding in one of ten reference ponds). This species typically breeds in streams, and adults may have used the pond because it receives seepage flow from the pond bank. The red salamander (*Pseudotriton ruber*) and three-lined salamander (*E. guttolineata)* also occurred in several

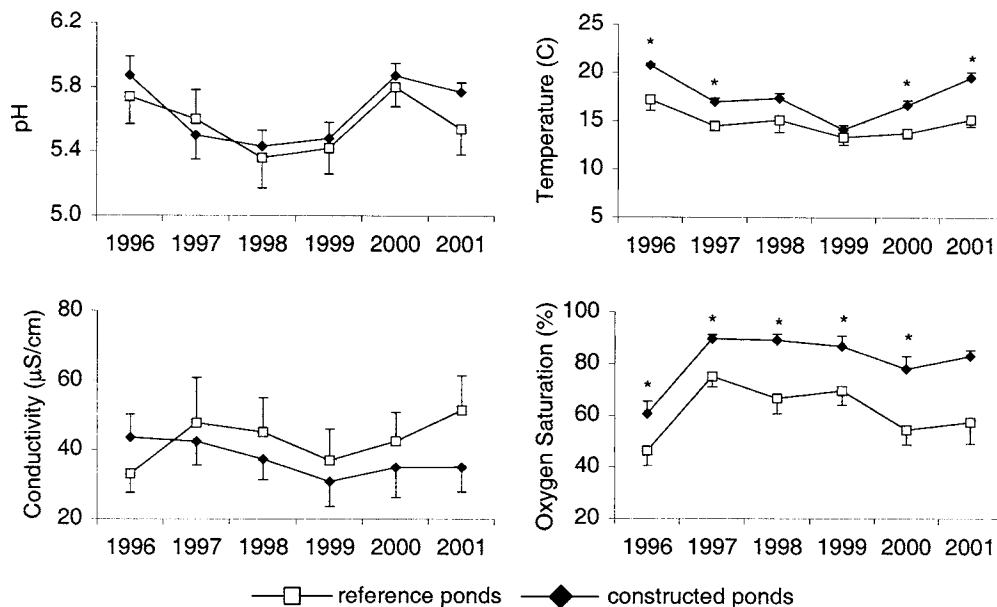Figure 2. Comparisons of physiochemical characteristics of constructed and reference ponds from 1996 to 2001. Symbols and bars are means +1 SE and asterisks indicate means that differed significantly within years.
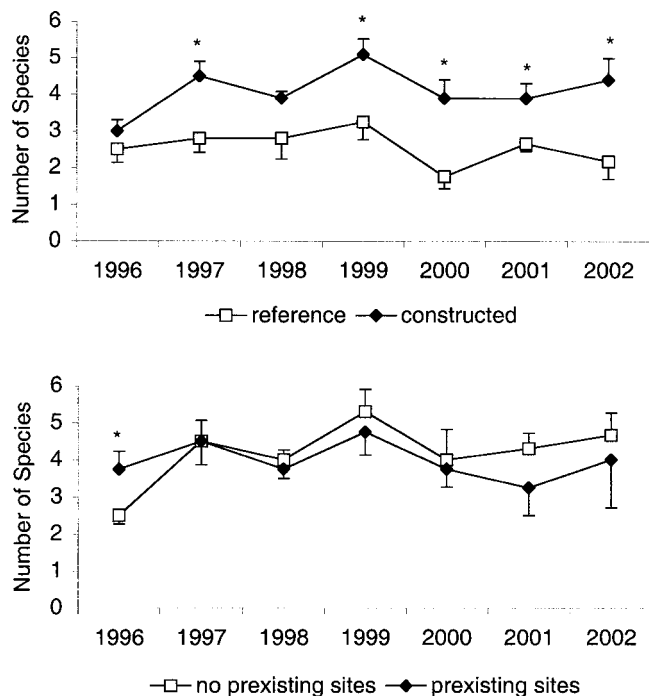
Figure 3. Changes in average species richness from 1996 to 2002. Upper panel shows means +1 SE for constructed and reference ponds; lower panel contrasts constructed ponds where small breeding sites either were or were not present *in situ* prior to pond construction. Asterisks indicate means that differ significantly within years.

ponds that received seepage flow from pond banks. The only species unique to constructed ponds was the American bullfrog (*Rana catesbeiana*), which prefers permanent or semipermanent habitats.

Constructed ponds contained significantly more breeding species than reference ponds from 1996 to 2002 (respective means = 4.10 ± 0.25 versus 2.56 ± 0.18 species: $F_{1, 12} = 6.53$; $P = 0.03$). The year effect

was significant ($F_{6, 72} = 3.13$, $P = 0.009$), but the year-by-pond type interaction was not ($F_{6, 72} = 1.40$, $P = 0.23$). For individual years, the mean number of species per pond was significantly greater in constructed ponds for five of seven years (Figure 3; upper panel). Mean species richness differed significantly among years for constructed ponds ($F_{6, 63} = 2.41$, $P = 0.04$) but not for reference ponds ($F_{6, 51} = 0.95$, $P = 0.47$), and pairwise comparison with Tukey's Studentized Range Test indicate that richness only differed significantly in 1996 (initial year of filling) versus all other years. The mean number of species using ponds of either type did not increase annually from 1996 to 2002 (regression analysis: $F_{1, 5} = 0.80$, $P = 0.41$ for reference ponds; $F_{1, 5} = 0.71$, $P = 0.44$ for constructed ponds). These results indicate that constructed ponds reached equilibrium during the second breeding season after pond construction.

Ponds constructed where pre-existing ponds occurred *in situ* did not have significantly greater richness than other constructed ponds from 1996 to 2002 ($F_{1, 8} = 0.24$, $P = 0.64$), and differences in richness were only significant during the initial year of filling (Figure 3; lower panel).

Annual Variation in Occupancy and Community Similarity

Pond occupancy from 1996 to 2002 differed significantly between reference and constructed ponds for many species (Table 2, Figure 4). Occupancy did not differ significantly for the American toad (*B. americanus*), *E. wilderae*, *E. guttolineata*, and *P. ruber* that used both pond types at low frequencies (<20%), or for *A. maculatum* that used both pond types at high frequencies (>92%). The remaining pond-breeding

Table 2. Mean annual occupancy rates (percent of ponds used) for amphibians that bred in 10 constructed and 10 reference ponds from 1996 to 2002. Probability values are for Wilcoxon Two-sample tests with *t*-approximations, using the percentage of years that a species occupied each pond.

| Common Name	Scientific Name	Mean Occupancy (%)		P
		Constructed	Reference	
Spotted salamander	*Ambystoma maculatum* (Shaw)	98.6	92.7	0.25
Three-lined salamander	*Eurycea guttolineata* (Holbrook)	2.9	12.0	0.68
Blue Ridge two-lined salamander	*Eurycea wilderae* (Dunn)	0.0	13.6	0.38
Red salamander	*Pseudotriton ruber* Sonnini	1.4	15.7	0.29
Eastern newt	*Notophthalmus viridescens* (Rafinesque)	47.1	19.0	0.009
American toad	*Bufo americanus* Holbrook	5.7	8.6	0.38
American bullfrog	*Rana catesbeiana* Shaw	32.9	0.0	0.007
Green frog	*Rana clamitans* Latreille	34.3	13.9	0.006
Wood frog	*Rana sylvatica* Le Conte	98.6	78.0	0.05
Gray treefrog	*Hyla chrysoscelis* Cope	47.1	7.6	0.004
Spring peeper	*Pseudacris crucifer* (Wied-Neuwied)	47.1	16.9	0.01
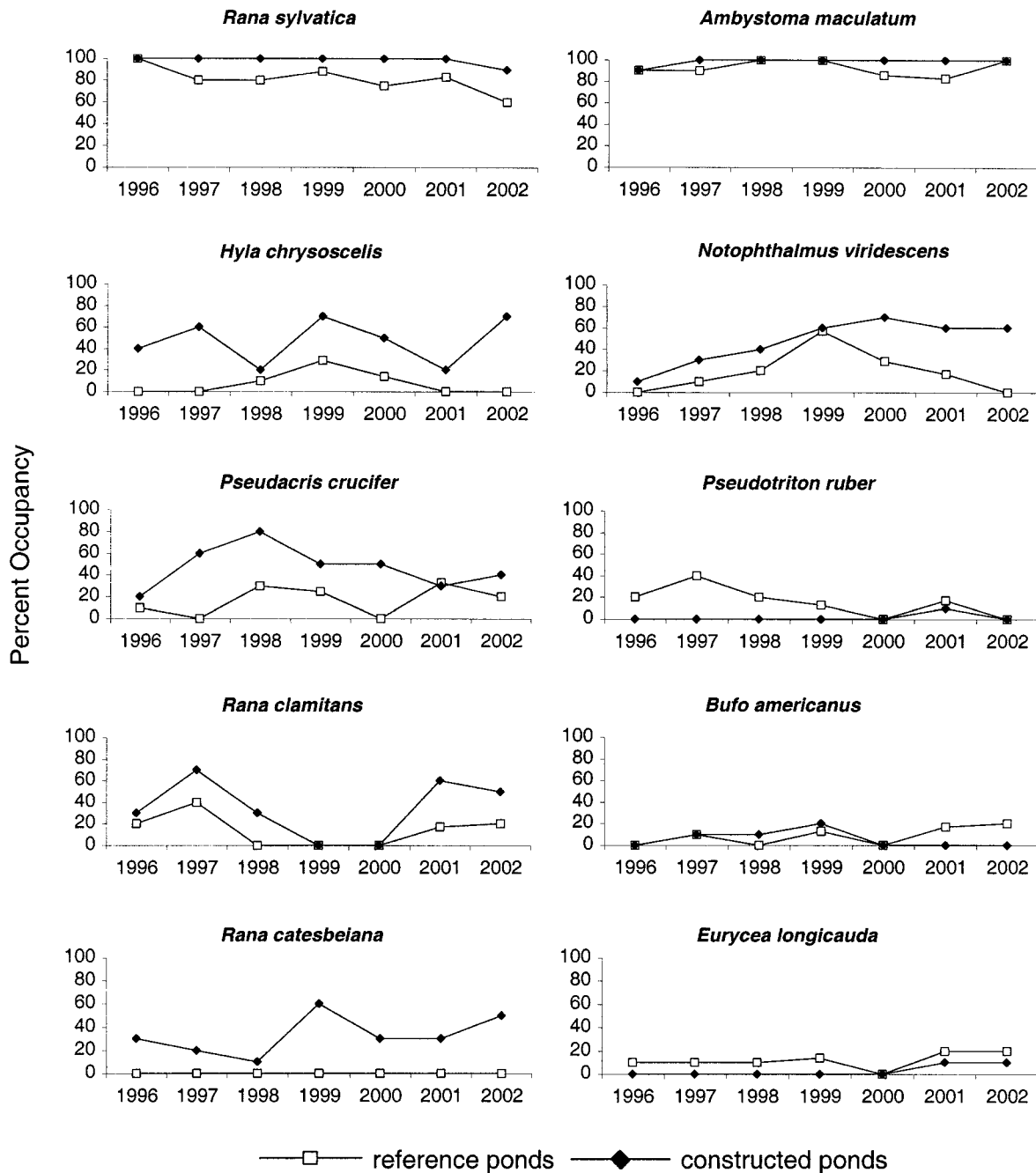
Figure 4. Percentage of constructed and reference ponds used annually by resident amphibians from 1996 to 2002. Constructed ponds first filled in 1996.

species used constructed ponds at a greater frequency than reference ponds (Figure 4).

Species often differed in temporal patterns of pond use. Occupancy of constructed ponds by the eastern newt (*Notophthalmus viridescens*) increased slowly during the first five breeding seasons, suggesting a longer lag in pond colonization relative to other species. Frequency of pond use by *B. americanus* and *P. crucifer* peaked during the first 2–3 breeding seasons after pond filling, while use by *R. clamitans* was erratic

across years. The most conspicuous pattern for reference ponds was a decrease in use by *P. ruber*, *H. chrysoscelis*, *R. clamitans*, and *N. viridescens* during the 1998 to 2002 drought. These species either breed late in the year, have long larval periods, or adults live in semipermanent or permanent habitats. *Rana catesbeiana* was mostly restricted to permanent ponds and was not strongly affected by drought.

We examined changes in community similarity between consecutive years, as well as long-term changes
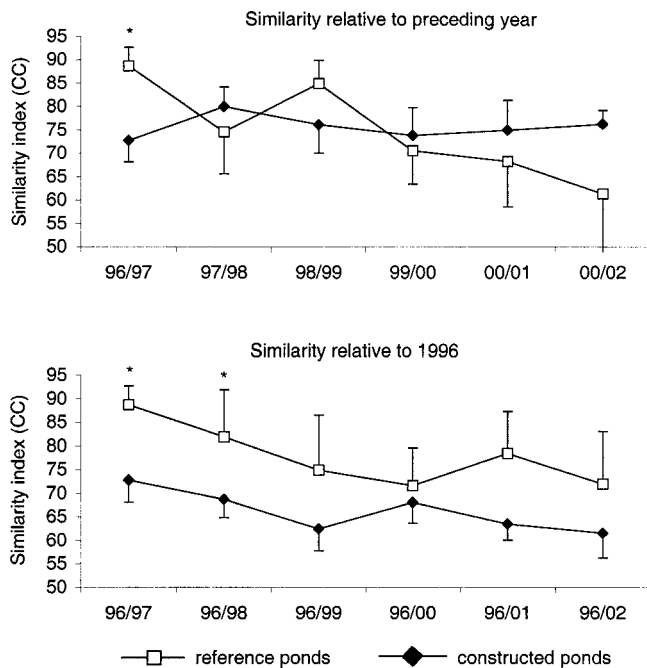
Figure 5. Changes in community similarity in reference and constructed ponds based on the coefficient of community (CC). Values may range from 0 (no species shared) to 100 (communities identical in composition). Symbols and bars are means +1 SE and asterisks indicate means that differ significantly. Upper panel indicates similarity to the preceding year; lower panel is similarity relative to communities that were present in 1996.

relative to 1996 when constructed ponds were first colonized. Average community similarity (CC) between consecutive years did not change directionally across years for constructed ponds (regression analysis: $F_{1, 4}$ = 0.001, P = 0.97, r^2 = 0.003) and averaged 74.8 ± 4.2. The mean for reference ponds was similar (75.7 ± 1.0), but yearly means decreased across years ($F_{1, 4}$ = 13.22, P = 0.02; r^2 = 0.77; Figure 5; upper panel). Repeated measures ANOVA indicate no overall significant effect for pond type ($F_{1, 12}$ = 0.05, P = 0.83), year ($F_{5, 60}$ = 1.87, P = 0.11), or the interaction term ($F_{5, 60}$ = 2.26, P = 0.06).

Average community similarity relative to 1996 assemblages was consistently greater in reference ponds compared with constructed ponds (grand means for similarity indices = 78 versus 66; Figure 5; lower panel), but not significant overall ($F_{1, 12}$ = 4.51, P = 0.055). Comparisons within years were significant in two of seven cases. The year ($F_{5, 60}$ = 0.59, P = 0.70) and year-by-pond type interaction ($F_{5, 60}$ = 2.02, P = 0.09) were not significant. Despite the absence of a significant overall year effect, similarity indices for both reference and constructed ponds showed a moderate tendency to decrease from 1997 to 2002 (regression analysis: $F_{1, 4}$= 6.62, P = 0.06; r^2 = 0.62 for

reference ponds; $F_{1, 4}$ = 7.47, P = 0.052; r^2 = 0.65 for constructed ponds).

Correlations between Landscape Attributes and First Year Colonization

Correlations with landscape variables were examined at a very fine scale. Respective means and ranges for landscape variables were (1) distance to the nearest source pond (52 m, 13–133 m); (2) distance to the nearest forest cover (18 m, 0–66 m); (3) the average distance from forest cover (65 m, 0–112 m); (4) distance to the nearest paved highway (142 m, 45–294 m); and distance to Tulula Creek (44 m, 5–156 m). The number of egg masses of *R. sylvatica* was positively correlated with pond size (P = 0.001; r^2 = 0.40; Figure 6) and the associated variables of depth and hydroperiod. Distance from Tulula Creek was also positively correlated with the number of masses laid and was the only other variable that met the 0.20 criterion for remaining in the backwards elimination model (P = 0.12). Inclusion of this variable resulted in only minor improvement of the overall model (r^2 = 0.47 with both variables entered). A similar pattern occurred for *A. maculatum* (size of pond: P = 0.01; r^2 = 0.28; Tulula Creek; P = 0.07; combined r^2 = 0.40). Pond size was the only variable that remained in the model for species richness (P = 0.0002; r^2 = 0.39; Figure 6).

DISCUSSION

Compensatory mitigation for wetland loss was established in the United States to help achieve a national goal of no-net-loss of wetlands (Marsh et al. 1996). The effectiveness of this policy has come under scrutiny because of significant failure rates of projects and the difficulty of assessing long-term success within the 3–5 year post-restoration window that is set by most regulatory agencies (Mitsch and Wilson 1996, Zedler 1996, Whigham 1999, Brown and Veneman 2001, National Resource Council 2001). Researchers primarily have assessed restoration success using hydrology and vegetation, with the assumption that faunal elements will become established at levels that are sufficient to maintain viable populations if these components are successfully restored. As a result, researchers have devoted little attention to monitoring vertebrates and other long-lived species for a sufficient duration to judge long-term responses to mitigation (Pechmann et al. 2001, Petranka et al. 2003).

Amphibians are increasingly being used to assess the function of seasonal wetlands. However, suitable timeframes for assessing both demographic and community responses are poorly resolved because almost
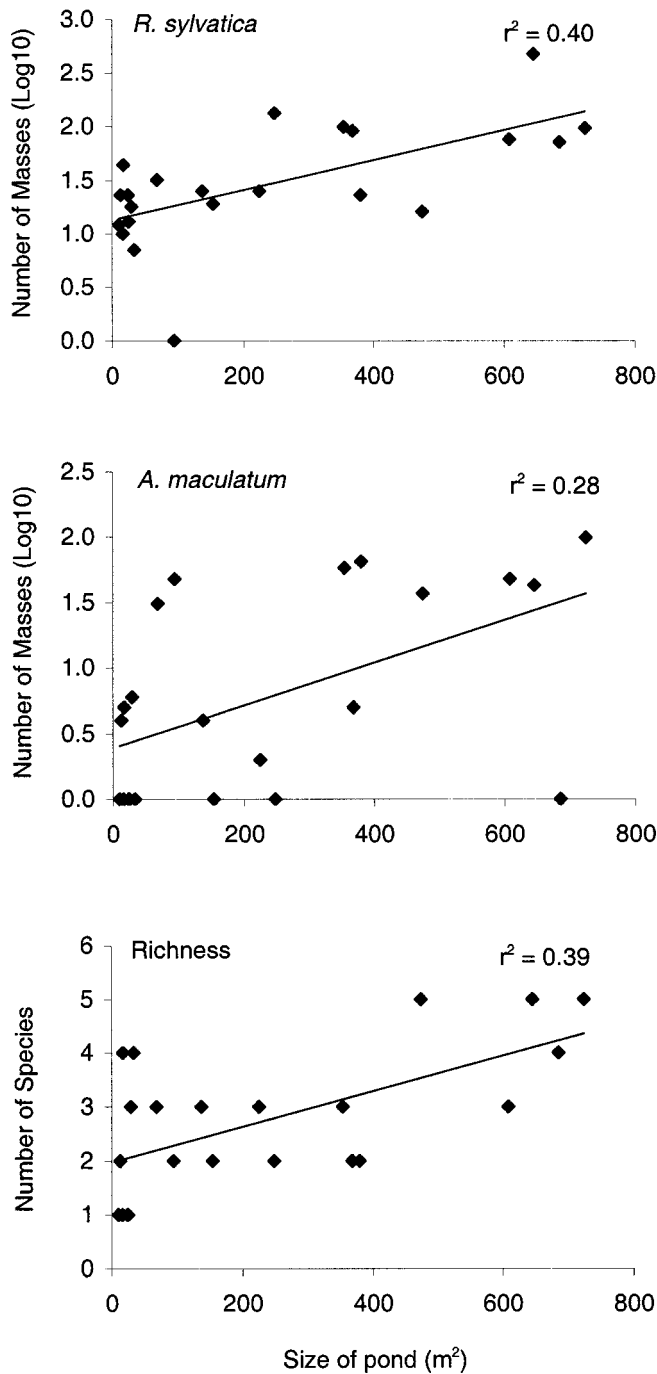
Figure 6. Relationships between pond size and the number of egg masses of *R. sylvatica* (upper), the number of egg masses of *A. maculatum* (middle), and the total amphibian species using ponds one year after pond construction.

all studies have been of short duration (i.e., 1–2 yr). In addition to generating data for assessing wetland function on site, this work provides insights into the long-term dynamics of amphibian communities that develop following pond creation that are of general use in determining timeframes for monitoring amphibian community responses.

We observed rapid colonization of constructed ponds during the first year of filling, which is consistent with observations at other mitigation sites (e.g., Marcus and Smith 1993, Lehtinen and Galatowitsch 2001, Pechmann et al. 2001, Stevens et al. 2002). The presence of pre-existing breeding sites where ponds were constructed had little influence on species richness except during the first year of filling. Stronger effects would be expected if most first-time breeders returned to their natal ponds or repeat breeders showed strong site fidelity between years. Instead, egg mass censuses show that *R. sylvatica* and *A. maculatum* greatly reduced use of smaller breeding sites that existed prior to pond construction in favor of larger and deeper ponds (Petranka et al. 2003). These observations suggest that site philopatry is weak at very fine scales and amphibians rapidly exploit newly created ponds with reduced levels of competitors and predators.

Attributes other than pond size, depth, and hydroperiod did not strongly influence colonization rates or species richness, although studies have identified other factors that influence local diversity. For example, amphibian species richness in local wetlands tends to be negatively correlated with road density and the degree of urbanization, deforestation, and wetland isolation (Lehtinen et al. 1999, Snodgrass et al. 1999, Findlay et al. 2001). With respect to pond attributes, richness of seasonal ponds is negatively correlated with degree of pond shading (Skelly et al. 1999) and often positively correlated with size and hydroperiod (Findlay and Houlahan 1997, Kolozsvary and Swihart. 1999, Snodgrass et al. 1999, 2000a, b).

We examined relationships between landscape features and pond use at a smaller spatial scale than has been used in other studies, which may explain some of the contradictory patterns. For example, degree of isolation did not influence species richness or the number of egg masses deposited in ponds, a pattern that might be expected given that the mean distance to source ponds was only 52 m (range = 13–133 m). Because emergent vegetation was poorly established when most species bred during the first year of pond filling, differences in vegetation cover or structure did not appear to be a proximate factor influencing site selection. Studies of landscape features that affect pond use by amphibians have rarely been conducted at very fine scales, even though the information is useful when considering how created ponds should be arrayed spatially at a restoration site. Additional fine-scale studies are needed to delineate which landscape attributes influence pond colonization and community development within restoration sites.

Species richness reached equilibrium levels within 1–2 yr of initial pond filling and remained relatively

stable thereafter. This brief lag is presumably why similarity indices were consistently lower for constructed ponds relative to reference ponds when compared to communities that existed in 1996. Data on frequency of pond use suggest that *N. viridescens* required as long as 4–5 breeding seasons to colonize constructed ponds fully, but other species required only 1–2 yr.

Frequency of pond use by *B. americanus* and *P. crucifer* reached a peak 2–3 yr after pond-filling, perhaps in response to the accumulation of predators in ponds. *Rana sylvatica* larvae are efficient egg predators of *B. americanus* and other amphibians (Petranka et al. 1994, 1998, Petranka and Kennedy 1999). Adult *B. americanus* actively avoid ovipositing in ponds with high densities of *R. sylvatica* tadpoles (Petranka et al. 1994) and appeared to exploit ponds during the first few years after pond filling when densities of *R. sylvatica* larvae were relatively low (Petranka et al. 2003). We are uncertain whether the decrease in pond use by *P. crucifer* after 1998 reflects similar avoidance behavior.

The composition of breeding assemblages changed annually by about 25% in constructed and reference ponds. Similarly high rates of community turnover have been documented by others at a wide range of temporal scales (e.g., Semlitsch et al. 1996, Hecnar and M'Closkey 1996, Skelly et al. 1999, Pechmann et al. 2001, Marsh and Trenham 2001). These data provide evidence of local extinction and population rescue events. However, lack of site fidelity and behavioral shifts to alternative breeding sites may have contributed significantly to the disappearance of breeding populations from local ponds (Marsh and Trenham 2001).

In addition to species such as *B. americanus* that actively avoid ponds with high densities of *R. sylvatica* larvae, species appeared to shift habitats in response to altered hydroperiod associated with drought. Annual turnover rates increased for reference ponds between 1996 and 2002, particularly from 1998 to 2002 when drought accelerated seasonal drying and reduced the suitability of these breeding sites for certain species such as *N. viridescens*, *P. ruber*, and *H. chrysoscelis*. A similar pattern did not occur in constructed ponds that had longer hydroperiods and were less vulnerable to the effects of drought.

The fact that overall community composition did not change markedly relative to communities that existed in 1996 reflects the fact that patterns of temporal use did not vary strongly among species. Nonetheless, similarity indices for both constructed and reference ponds showed a weak tendency to decrease across years relative to communities that existed in 1996. Although similar in magnitude and direction, the trends were more strongly linked to drought and altered hy-

droperiod in reference ponds and colonization lags in constructed ponds.

We are using several physical and biotic parameters to assess restoration success at the Tulula Wetlands. These include pond hydroperiod and physiochemical characteristics, pond colonization and use by resident amphibians, and population trends of two focal species, *R. sylvatica* and *A. maculatum* (Petranka et al. 2003). Because reference ponds generally were of lower quality than undisturbed natural wetlands, our goal in 1996 was to create ponds with more favorable hydroperiods that would provide suitable breeding habitats for a greater diversity of species. We considered ponds that were constructed in 1996 to be of higher quality than reference ponds because they were less vulnerable to premature drying and were warmer and more oxygen-rich. They also supported more community members and produced more metamorphs (Petranka et al. 2003).

Our long-term data on hydroperiod and species richness of breeding assemblages indicate that the first two goals have been met. In contrast, *R. sylvatica* and *A. maculatum* populations increased during the first 4–5 yr after pond construction but have since decreased to levels that are slightly below those in 1995 immediately prior to pond construction (Petranka et al. 2003). The decrease in latter years was associated with two stochastic events, a moderate drought from 1998 to 2000 and outbreaks of iridoviral infections that caused catastrophic larval mortality in most pond populations. Although we have tracked population responses for seven breeding seasons, we are still uncertain whether we have achieved the long-term goal of increasing breeding populations above pre-restoration levels.

Emerging data will hopefully clarify trade-offs among criteria used to assess amphibian response to wetland restoration. For example, our data suggest that post-restoration monitoring for 2–3 years may be sufficient to characterize species and communities that will use ponds for the first decade or so after pond creation. Thus, short-term monitoring of pond use is attractive in that it has strong predictive value with respect to longer-term use. Unfortunately, pond use *per se* could be a poor indicator of whether ecosystem function is fully restored because of the potential disconnect between pond use and adult population size.

Population responses provide a direct measure of whether site improvements are sufficient to sustain viable populations of community members. However, a decade or more may be required to sort out true population trends from non-trend variation due to stochastic events such as drought and disease outbreaks (Thomas 1997, Gibbs et al. 1998, Marsh 2001). At our site, rapid colonization and the widespread use of constructed ponds by *R. sylvatica* and *A. maculatum* has

not resulted in long-term increases in the size of breeding populations, presumably because of stochastic events. However, it is likely that the size of breeding populations will increase if drought and *Ranavirus* outbreaks diminish in future years.

Researchers who have examined the response of amphibians to compensatory mitigation have rarely tracked both pond use and population responses, or conducted studies for more than 2–3 years. Longer-term studies that couple pond use and demographic responses (e.g., Pechmann et al. 2001) are clearly needed to delineate success criteria more effectively. Long-term studies may not be panaceas for resolving assessment issues, but they do provide insights that will help delineate appropriate timeframes for measuring long-term success. We encourage researchers to incorporate both elements into amphibian monitoring programs and encourage funding agencies to support long-term studies that will help resolve assessment issues.

ACKNOWLEDGMENTS

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