

MONITORING CREATED SEASONAL POOLS FOR FUNCTIONAL SUCCESS: A SIX-YEAR CASE STUDY OF AMPHIBIAN RESPONSES, SEARS ISLAND, MAINE, USA

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Abstract: Assessing the success of created seasonal pools as mitigation for the loss of wooded wetlands is generally based on two or three years of monitoring. We monitored a wetland mitigation site in mid-coast Maine, USA, from 1999 to 2004 to track populations of wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) in three created seasonal pools. Our goal was to study breeding patterns for six years to assess if presence of breeding animals in the first three years corresponded with long-term reproductive success and to track changes in vegetation development and hydrology in the mitigated pools. Breeding effort (egg masses/female) and reproductive success (juveniles/egg mass) were assessed using full enclosure drift fence/pitfall trap arrays and egg mass counts. Breeding effort was similar in all three pools for both species. However, for wood frogs, reproductive success was inversely related to hydroperiod and highest in the single pool that successfully replicated the desired seasonal water regime. The other two pools developed permanent and semi-permanent hydroperiods, thereby supporting populations of green frogs (*Rana clamitans*). Green frog tadpoles within these pools preyed upon wood frog eggs and embryos, causing almost complete losses in the last four years of the study. While spotted salamander reproductive success was also reduced in the permanent pool, spotted salamanders were more successful at producing metamorphs in the presence of green frogs. Over the study period, common cattail (*Typha latifolia*) dominated the pools, and although wetland vegetation did develop, it was not typical of forested seasonal pools. Our work shows that the presence of breeding amphibians characteristic of seasonal pools in the first three years is not sufficient to determine reproductive success of target species in created pools. Hydrology and canopy cover are elements of critical concern if created pools are to support native amphibian communities associated with seasonal pools.

Key Words: *Ambystoma maculatum*, created wetlands, *Rana clamitans*, *Rana sylvatica*, seasonal wetlands, vegetation dynamics, vernal pools, wetland mitigation, wetland monitoring

INTRODUCTION

Compensatory wetland mitigation, including restoration and creation, is frequently used to achieve no net loss of wetlands. However, constructed wetlands frequently fail to replicate the hydrology (Galatowitsch and van der Valk 1996, National Research Council 2001) and vegetation (Reinartz and Warne 1993, Zedler and Callaway 1999) characteristic of the wetlands being replaced, often causing them to fail as habitat for wetland wildlife present before disturbance (Race and Fonseca

1996). The National Research Council (2001) report on compensating for wetland losses identified seasonal pools (also known as vernal pools) as one of the most difficult wetland types to create. The seasonal hydrology of these pools prevents the establishment of fish, bullfrogs (*Rana catesbeiana* Shaw), and other potential resident predators (Rowe and Dunson 1995, Snodgrass et al. 2000), providing optimal breeding habitat for amphibians with vulnerable egg and larval stages, including wood frogs (*Rana sylvatica* LeConte) and ambystomatid salamanders.

Created wetland monitoring efforts generally focus on vegetative cover as an indicator of success, while ignoring other important criteria, such as hydrology and use by wildlife (Mitsch and Wilson 1996, Breaux and Serefiddin 1999). Success of created seasonal wetlands is often based solely on presence of wetland vegetation and presence of amphibians (often not species-specific) and is often assessed during the first three years after mitigation (Lichko and Calhoun 2003). Amphibians are being used more often to assess ecosystem function, but long-term studies of amphibian responses to wetland restoration are few and limited to the southeastern USA (Pechmann et al. 2001, Petranka et al. 2003a,b). It is unclear what the metric for functional success of restored or created seasonal pools should be, what time frame should be evaluated, and if metrics and time-frames vary geographically (Pechmann et al. 2001, Lichko and Calhoun 2003, Petranka 2003a).

We monitored three created seasonal pools within a wetland restoration site on Sears Island, Maine, USA (44°27' N, 68° 53' W) from 1999 to 2004. The restoration was designed and carried out by an independent agent as directed by the Environmental Protection Agency (EPA). Our objectives were (1) to determine if the two EPA-stated measures of success, presence of breeding wood frogs and spotted salamanders, and colonization by wetland vegetation, were met within three years; and (2) to determine if the stated measures of success reflected longer-term reproductive success of the target amphibian species. To determine this, we documented breeding effort, reproductive success, and recruitment of wood frogs and spotted salamanders in each pool for three years beyond the required three-year monitoring period.

STUDY AREA

Sears Island, an uninhabited and relatively undeveloped island, is located in northern Penobscot Bay in mid-coast Maine. The 380-ha island is predominantly forested and has approximately 97 ha of freshwater wetlands, the majority of which are seasonally saturated/flooded mixed evergreen and deciduous forests (Normandeau Associates 1995). Preliminary site preparation for a cargo terminal in 1984 included clear-cutting and filling 4 ha of forested wetlands and a perennial stream and constructing three detention basins. The wetland filling was conducted without the permits required under the Clean Water Act and ensuing litigation resulted in termination of the project.

An amphibian survey conducted in 1992 detected breeding by wood frogs and spotted salamanders in roadside ditches, detention basins, and impounded areas within the construction site (Normandeau Associates 1995). It was assumed that these animals had been displaced by the destruction of the forested wetland and pool complex. No productive natural pools were located within 1 km of the study site.

Wetland restoration began in the fall of 1997. Fill material was excavated from the original forested wetland, exposing original wetland soil. Two pool basins within the original forested wetland were excavated (hereafter referred to as VP1 and VP2). In addition, one of the detention basins was converted into a third pool (VP3, Figure 1). The three pools (maximum area at spring high water = 350 m² for VP1, 600 m² for VP2, and 950 m² for VP3) were intended to replicate the functions of natural pools identified in the original forested wetland on topographic maps and aerial photographs. Conductivity, pH, dissolved oxygen, and temperature were similar among the pools in spring and summer (Vasconcelos 2003).

Approximately 200 small potholes (range = 0.3–110 m²) were excavated within the clearing around VP1 and VP2 to form a complex hummock-and-hollow microtopography to enhance seasonal saturation and flooding within the site. A mixture of annual rye (*Lolium multiflorum* Lam.) and Virginia rye (*Elymus virginicus* L.) was seeded in the matrix around the pools and potholes to stabilize soils immediately following construction, and a few small trees and shrubs were planted around each pool. Most of the site was left to revegetate naturally.

METHODS

Amphibian Monitoring

Amphibian activity in the three pools was monitored using 100% enclosure drift fence arrays from 1999 to 2004. Drift fences were constructed of black silt fence supported by wooden stakes, and were installed one to five meters out from the average high water mark of each pool. The fences were 60 cm high, with the lower edge buried 15 cm below the ground. Pitfall traps were constructed of 15-L (30 cm deep) plastic buckets buried flush with the ground and placed in pairs every 10 m along the fences. One member of each pair was placed along the fence interior and the other along the fence exterior (for a total of nine trap pairs at VP1, 10 at VP2, and 18 at VP3). We added up to two cm of water in each trap to prevent amphibian desiccation, rocks to provide cover for trapped amphibians, and



Figure 1. Locations of VP1, VP2, and VP3. Arrows represent water flow patterns.

sticks to facilitate the escape of small mammals (Gibbons and Semlitsch 1981, Perkins and Hunter 2002).

Traps were checked daily at 0700 hours from the onset of adult immigration (late March-early April) until the end of juvenile emergence (late September-early October). All amphibians captured were released approximately five meters from the trap of capture on the opposite side of the fence in the presumed direction of travel. All adult wood frogs and spotted salamanders were sexed (except in 1999), and the snout-to-vent length (SVL) of all juveniles was measured to the nearest 0.5 mm. No data on metamorphosing juveniles were collected in 2004.

The potential for undetected trespass was greatly reduced by frequent inspection and maintenance of the fences, the height of the fences, and by marking each individual adult and juvenile wood frog and spotted salamander upon exiting the pools as part of a separate study of amphibian movements and breeding pool fidelity (Vasconcelos and Calhoun 2004). Adult wood frogs and adult and juvenile spotted salamanders were never observed climbing out of traps or over the fences, even during rain events. Wood frog metamorphs climbed out of traps, but trespass over the fence was never observed and believed to be minimal.

Wood frog and spotted salamander egg masses were counted in the pools each year following the apparent peak of adult immigration for each species. Egg masses were identified to species, flagged, and re-counted several times to verify counts. From 1999 to 2002, egg masses were checked weekly and classified as developing, hatched, or dead (from drying or predation). When egg predation was observed, egg masses were checked daily to monitor predation rates. No spotted salamander egg mass count was obtained for VP2 in 2000 due to heavy siltation.

Pool Hydroperiod

A wooden stake was installed at the deepest point in each pool in 1999. Pool depth was measured at the stake using a meter stick (± 1 mm), biweekly in each year from 1999 to 2003. Pool area was estimated using field measurements of pool length, width, and perimeter at spring high water.

Vegetation Surveys

We completed vegetation surveys in the pools and potholes in May, July, and September 1999 to 2002. Plants growing within or overhanging the high water

mark of each pool were identified to species, and the percent cover of each species was estimated visually. The final percent cover estimates reported for each species for a given year were based on the peak cover achieved by each species (usually July). Aerial photographs (panchromatic, 1:2400) taken in early April and early September of both 1999 and 2002 were examined visually to determine the total vegetative cover of the pools.

Potholes

Potholes were monitored from 1999 to 2002. We randomly selected 50 potholes to monitor as representatives of the wetland habitat surrounding the pools. Vegetation and hydrology measurements were collected within each pothole in the same manner described for the pools. It was apparent in 1999 that some adult wood frogs and spotted salamanders were breeding in potholes, so egg mass counts were conducted in each pothole. All masses were checked weekly to monitor egg development, hatching, larval development, and mortality.

Data Analyses

We defined breeding effort as the total number of egg masses deposited in a pool divided by the number of females entering the pool through pitfall traps (egg masses/female). We defined reproductive success for each species as the number of juveniles emerging from a pool divided by the total number of egg masses deposited in the pool (juveniles/egg mass). We could not calculate pre-metamorphic survival directly because individual eggs were not counted. We therefore estimated pre-metamorphic survival in each pool by dividing our median values for juveniles/egg mass by published estimates of the number of eggs/mass for each species.

Since the data are counts, we used Poisson regression (Quinn and Keough 2002) to test for differences between the three pools and the six years in terms of amphibian adult breeding population size, the number of juveniles produced, breeding effort, and reproductive success. For each response variable, we fit a series of models to investigate whether any, some, or all interaction (year by pool) parameters were necessary to adequately explain the data. We worked to develop as parsimonious a model as possible, while maintaining a good fit, by removing non-significant parameters and combining parameters that were not significantly different from each other. All of the final fitted Poisson regression models required at least one interaction term ($p \leq 0.00$ in all cases). Herein, we present the

final goodness of fit statistic (a Chi-squared test of the residual deviance) and plots of the fitted response variables with confidence intervals by the combinations of year and pool.

One-way analysis of variance was used to test for differences in mean juvenile SVL across the three pools for both species, as these data were normally distributed. We then calculated Bonferroni adjusted pairwise comparisons to test which pools differed significantly. We used $\alpha = 0.05$ for all significance testing. All statistical analyses were conducted using SYSTAT version 11 software (SYSTAT Software Inc. 2004).

RESULTS

Pool Colonization

Adult wood frogs and spotted salamanders colonized the three pools during the spring following construction (< 10 egg masses per species per pool; A. Calhoun pers. obs. 1998), and bred in each year of the study. Green frogs (*Rana clamitans* Latreille) colonized the pools in 1999 and bred primarily in VP1 and VP2. Several American toad (*Bufo americanus* Holbrook) adults visited VP2 and VP3 each year from 1999 to 2001 but did not breed, and spring peeper (*Pseudacris crucifer* Wied-Neuwied) adults colonized VP3 in 2001 and bred successfully in 2001 to 2004.

Breeding Effort

For wood frogs, VP3 had the largest breeding population in five of six years (Figure 2, final fitted model $p = 0.1148$, $\chi^2 = 10.2$, $df = 6$). The sizes of the wood frog breeding populations in VP1 and VP2 were not significantly different from each other from 1999 to 2002, but from 2003 to 2004, the population in VP2 significantly exceeded that of VP1. For spotted salamanders, adult breeding population size was similar in all three pools for the first three years, but from 2002 to 2004 the population in VP1 increased and was significantly greater than the populations in VP2 and VP3 (Figure 2, final fitted model $p = 0.5801$, $\chi^2 = 7.55$, $df = 9$). Male wood frogs outnumbered females in each pool in all years, while spotted salamander sex ratios favored males in some years and females in others (Vasconcelos 2003).

Breeding effort was consistently high for both wood frogs (Figure 3, final fitted model $p = 0.362$, $\chi^2 = 8.77$, $df = 8$) and spotted salamanders (Figure 3, final fitted model $p = 0.362$, $\Pi^2 = 4.34$, $df = 4$). The number of egg masses/female did not

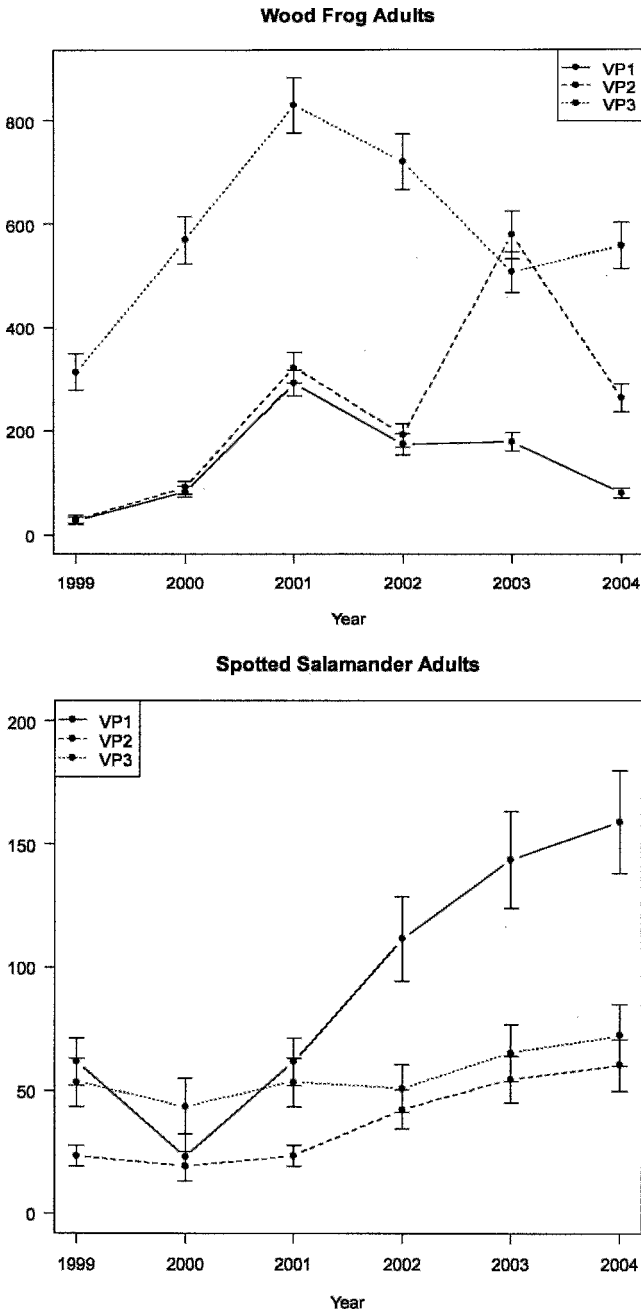


Figure 2. Final fitted model of number of breeding adult wood frogs and spotted salamanders entering VP1, VP2, and VP3, 1999–2004.

differ significantly between pools for wood frogs except in 2002 when egg predation in VP1 and particularly in VP2 prior to the beginning of egg mass counts led to reduced counts and estimates of breeding effort. For spotted salamanders, the number of egg masses/female did not differ significantly between pools except in 2000 and 2002 when breeding effort was significantly higher in VP1.

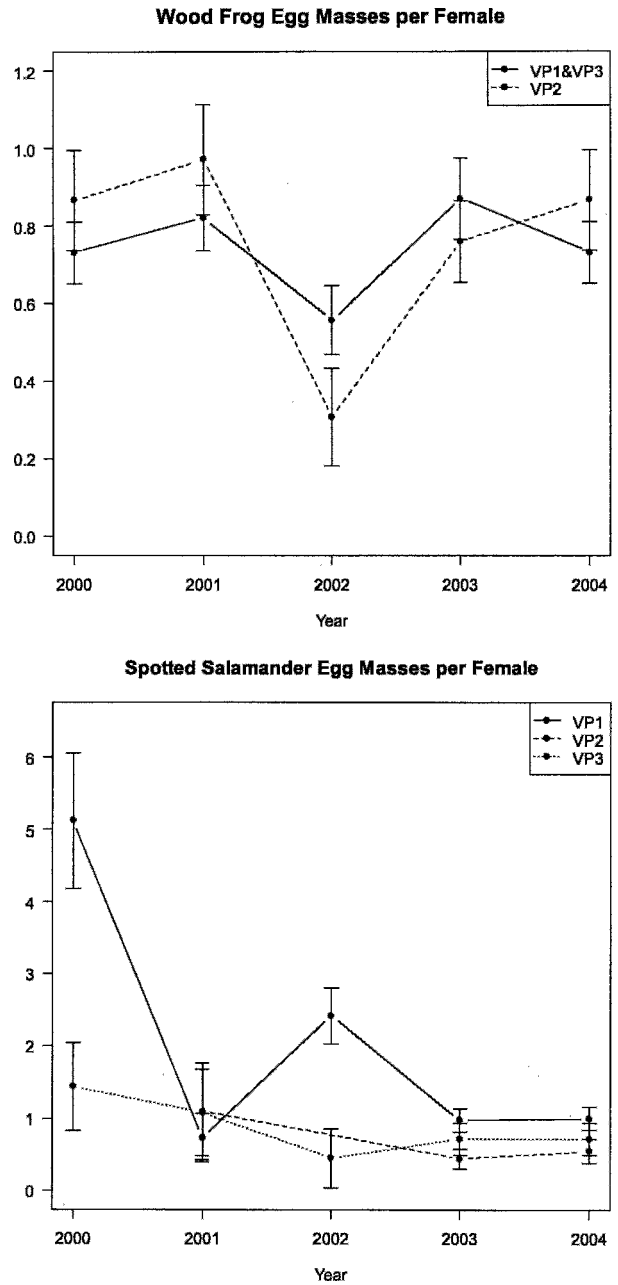


Figure 3. Final fitted model of breeding effort for wood frogs and spotted salamanders in VP1, VP2, and VP3, 2000–2004.

Reproductive Success

Over-wintering green frog tadpoles preyed heavily on wood frog egg masses in VP1 and VP2 from 2001 to 2004. Congregations of 20–50 green frog tadpoles were observed around wood frog egg masses consuming individual embryos. In 2001, green frog tadpoles consumed communal aggregations of 89 wood frog egg masses in VP1 and 95 wood frog egg masses in VP2 in seven days. Only five wood frog egg masses were deposited within the basin of VP1

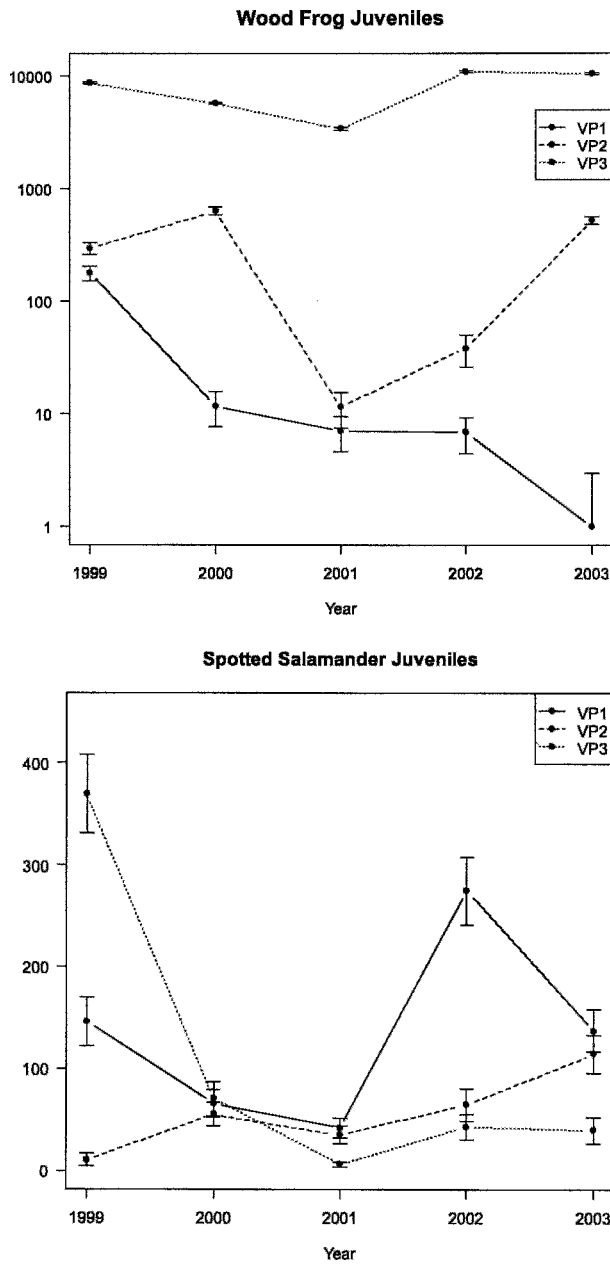


Figure 4. Final fitted model of number of juvenile wood frogs and spotted salamanders produced in VP1, VP2, and VP3, 1999–2003. Log scale used for y-axis for wood frog juveniles to clearly show differences.

during 2002, with the communal aggregation deposited in a nearly dry area on the edge of the pool; green frog tadpoles consumed the five masses in the pool in six days, and the communal aggregation dried and failed to develop. Egg mass counts in VP2 were conducted after initial predation had begun in 2002, and only 24 intact masses were found. Only one mass, protected in a shallow area of the pool, remained after six days. Green frog tadpoles and egg predation were rarely observed in VP3, and most

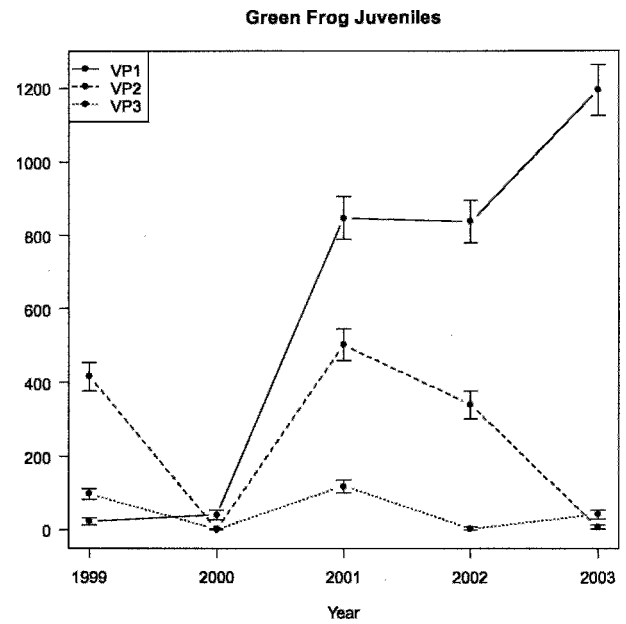


Figure 5. Final fitted model of number of juvenile green frogs produced in VP1, VP2, and VP3, 1999–2003.

wood frog masses developed and hatched. Green frog tadpoles did not prey upon spotted salamander egg masses in any pool.

VP3 produced a significantly greater number of wood frog juveniles than VP1 and VP2 each year (Figure 4, final fitted model $p = 0.832$, $\chi^2 = 0.871$, $df = 3$). VP2 had the second highest number of emerging wood frog juveniles in four of five years, experiencing alternating increases and decreases in juvenile output, while VP1 had the lowest number in four of five years and saw a steady decline from 1999 to 2003. The number of spotted salamander juveniles produced per year fluctuated over the course of the study (Figure 4, final fitted model $p = 0.5915$, $\chi^2 = 1.91$, $df = 3$). The number of green frog juveniles produced in VP1 increased steadily from 1999 to 2003 and was significantly higher than the number produced in VP2 and VP3 from 2000 to 2003 (Figure 5, final fitted model $p = 0.3368$, $\chi^2 = 3.38$, $df = 3$). VP2 experienced alternating increases and decreases in green frog juvenile production, while VP3 had little to no green frog juvenile output.

Wood frog reproductive success over the five years of available data was significantly greater in VP3 than in VP2 and VP1 and was generally lowest in VP1 (Figure 6, final fitted model $p = 0.776$, $\chi^2 = 0.534$, $df = 2$). The number of juvenile wood frogs/egg mass generally tended to decrease with increased numbers of green frog juveniles (Figure 7). For spotted salamanders, reproductive success fluctuated throughout the study, but was generally lowest in

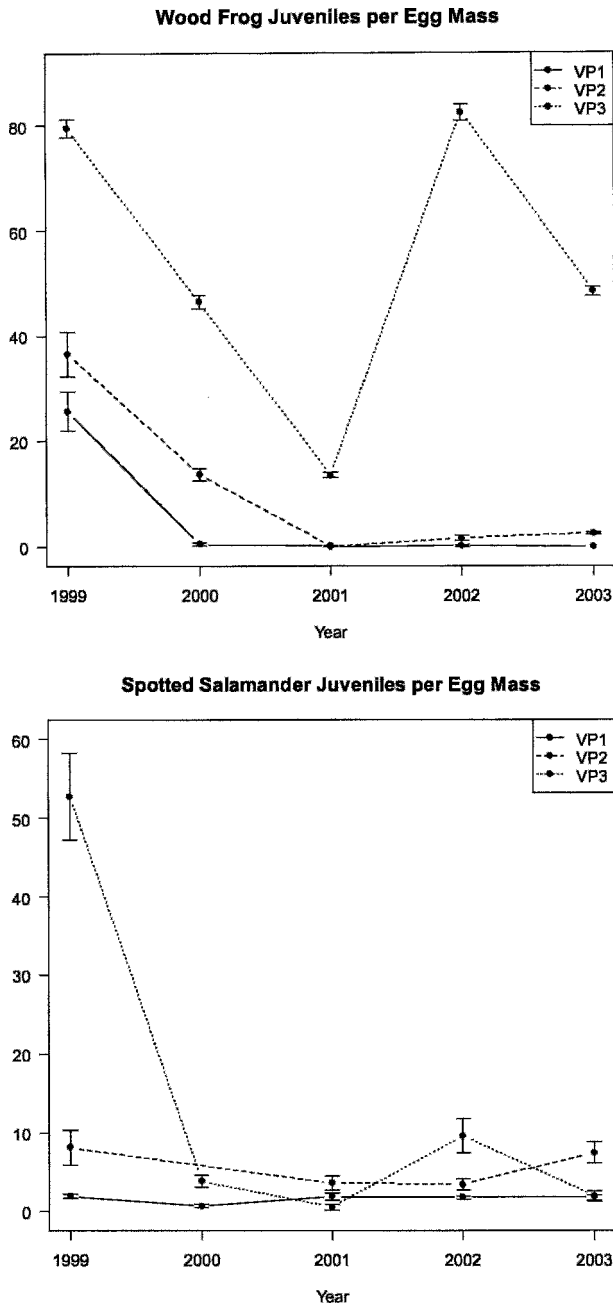


Figure 6. Final fitted model of reproductive success for wood frogs and spotted salamanders in VP1, VP2, and VP3, 1999–2003.

VP1 (Figure 6, final fitted model $p = 0.4735$, $\chi^2 = 2.51$, $df = 3$).

We used the median number of juveniles/egg mass for each species over the five years of available data, along with the highest published estimates of the number of eggs/mass for each species, to obtain the most conservative pre-metamorphic survival estimates for wood frogs and spotted salamanders in the three pools. Median reproductive success in this study was 0.2, 2.5, and 48.4 juveniles/egg mass for

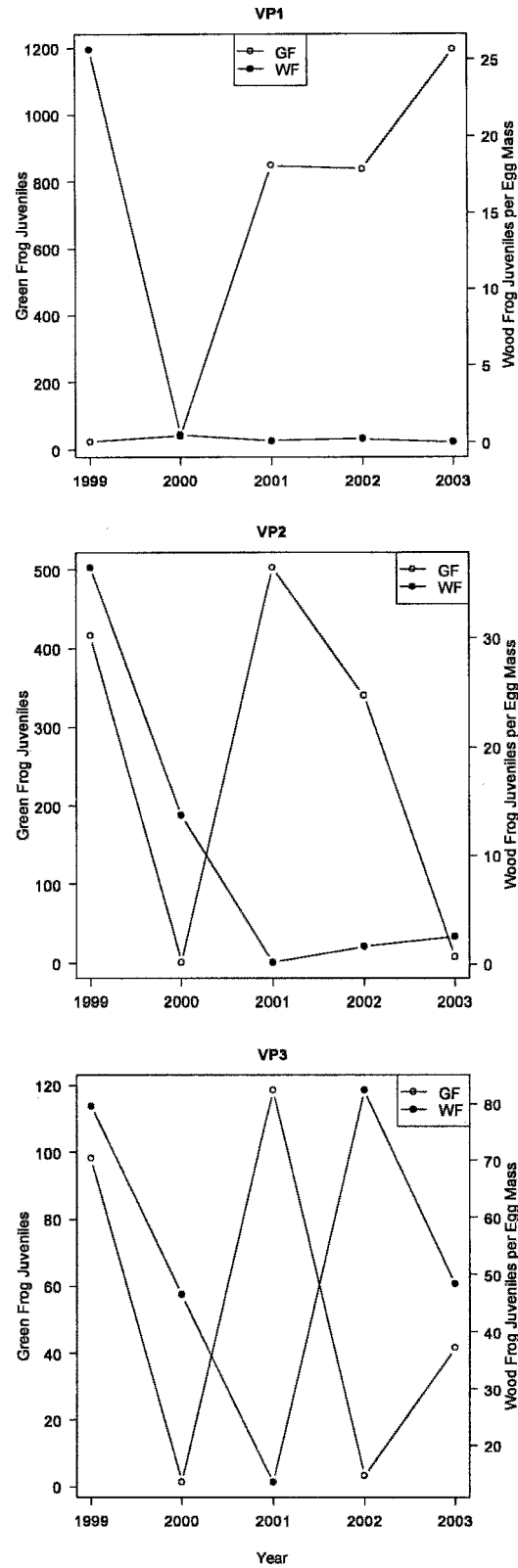


Figure 7. Number of green frog juveniles produced (GF) versus wood frog reproductive success (WF) in VP1, VP2, and VP3, 1999–2003.

wood frogs in VP1, VP2, and VP3, respectively, and 1.8, 5.4, and 4.2 juveniles/egg mass for spotted salamanders in VP1, VP2, and VP3, respectively. Published estimates of the number of eggs/mass range from 116-1006 eggs/mass for wood frogs (Herreid and Kinney 1966, Seigel 1983, Petranka and Kennedy 1999), and from 7-189 eggs/mass for spotted salamanders (Shoop 1974, Stenhouse 1987, Stangel 1988). Using 1006 eggs/mass for wood frogs and 189 eggs/mass for spotted salamanders, our wood frog premetamorphic survival estimates were 0.02% (VP1), 0.25% (VP2), and 4.81% (VP3), whereas our spotted salamander premetamorphic survival estimates were 0.95% (VP1), 2.86% (VP2), and 2.22% (VP3).

Mean juvenile SVL differed significantly between pools for wood frogs ($F = 4.334$, $df = 2$; $p = 0.041$). VP1 produced the largest wood frog juveniles (mean \pm SE = 16.1 ± 0.8 mm) followed by VP2 (14.4 ± 0.8 mm) and VP3 (13.3 ± 0.3 mm). Mean SVL differed significantly between VP1 and VP3 ($p = 0.04$) but not between VP1 and VP2 ($p = 0.324$) or VP2 and VP3 ($p = 0.698$). Juvenile spotted salamander SVL were similar in VP1 (mean \pm SE = 27.2 ± 0.9 mm), VP2 (27.1 ± 1.4 mm), and VP3 (26.8 ± 1.5 mm), and the differences were not significant ($p = 0.971$).

Pool Hydroperiod

VP3 had the greatest maximum spring depth (median = 65.8 cm) and surface area (950 m^2) but was the only pool to dry completely or into discrete shallow puddles by late August each year. VP1 had the lowest maximum spring depth (median = 56.5 cm) and smallest surface area (350 m^2) but remained flooded throughout the year. Two small streams fed VP1 and usually persisted through mid-summer, contributing to the permanent hydrology. Small streams also fed VP2 and VP3 following snowmelt, but these streams dried rapidly in late spring. VP1 was the only pool to develop an intermittent outlet stream that discharged into a large nearby pothole and then into a large detention basin across the road. For VP2, the maximum spring depth (median = 62.0 cm) and surface area (600 m^2) were intermediate between those of VP1 and VP3. VP2 dried substantially in most years, becoming highly reduced in area, but never completely dry.

Pool Vegetation

Vegetative cover and species richness increased in each pool from 1999 to 2002. VP1 had the lowest

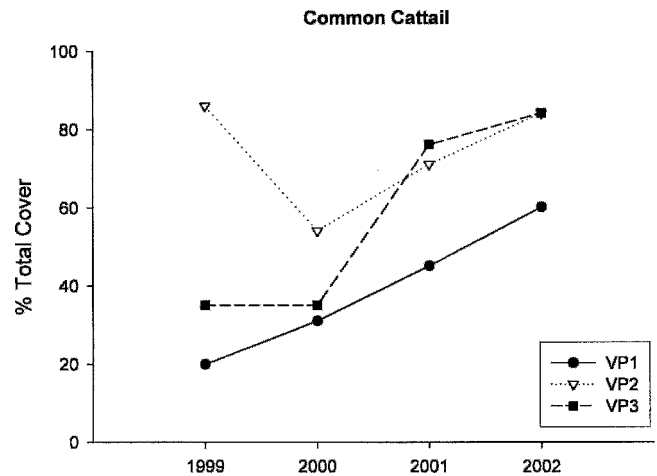


Figure 8. Percent of total vegetative cover represented by common cattail in VP1, VP2, and VP3, 1999–2002.

percent cover due to frequent feeding by muskrat (*Ondatra zibethicus* L.) and moose (*Alces alces* L.), which resulted in mostly open-water habitat. VP2 and VP3 were entirely vegetated by 2002. Despite annual increases in species richness, all three pools were dominated by common cattail (*Typha latifolia* L.) (Figure 8). Other plant species frequently were confined to pool margins and covered less than 1% of total pool area.

Potholes

Potholes varied greatly in area (range = $0.3\text{--}110 \text{ m}^2$, median = 4.9 m^2) and maximum spring depth (range = $3.3\text{--}37.0$ cm, median = 18.0 cm). Depending on the year, wood frog and spotted salamander breeding occurred in 10–14 (20–28%) and 3–12 (6–24%) of the 50 potholes monitored, respectively. The total number of egg masses deposited in potholes varied by year, ranging from 31 to 124 for wood frogs and 6 to 101 for spotted salamanders. Breeding occurred mostly in the deeper potholes for both wood frogs (median depth = 23.4 cm for potholes with breeding and 16.0 cm for potholes without breeding) and spotted salamanders (median depth = 22.5 cm for potholes with breeding and 16.8 cm for potholes without breeding). The majority of wood frog egg masses were deposited in a single pothole in 2001 (75 masses = 60.5% of total for the year) and 2002 (70 masses = 61.9% of total for the year). This pothole was the deepest, had the largest surface area of any pothole monitored, and was hydrologically connected to VP1 by an outlet stream from the pool. Water remained in this pothole into late August, potentially allowing enough time for larvae to metamorphose. The other potholes dried from mid-May through late-July.

Wood frog masses in these potholes usually hatched, but water levels often dropped before larvae could complete metamorphosis. Spotted salamander egg masses rarely hatched in potholes before dry-down.

Plant species richness increased in and around the potholes over the course of the study, but common cattail was by far the most abundant species, representing the dominant vegetation in 21 of 50 potholes (42%). Cattail generally dominated the deeper potholes, while native grasses, sedges, and rushes dominated shallower potholes. No shrubs were present in potholes in 1999, but by 2002, shrub species were found in 30 of 50 potholes (60%). However, shrubs were the dominant vegetation in only 7 of 50 potholes (14%).

DISCUSSION

Pool Colonization

Wood frogs and spotted salamanders recolonized the construction site during the first spring following restoration despite the change from a closed-canopy forest to an open clearing. Amphibian recolonization of restored wetlands is influenced by the proximity of source populations (Lehtinen and Galatowitsch 2001). Remnant breeding populations of wood frogs and spotted salamanders in detention basins and impounded areas within the construction site likely provided the colonists for these created pools.

Recent studies indicate that while amphibians can successfully colonize created and restored wetlands (Petranka et al. 2003a,b), the amphibian community structure of these wetlands often differs from that of the natural wetlands being replaced. These changes in community structure are frequently the result of amphibians with differing habitat preferences reacting to changes in vegetation structure (e.g., from forest to open habitat), or changes in hydrology from temporary to permanent water regimes (Dietsch et al. 1996, Mierzwa 2000, Pechmann et al. 2001). While the created pools on Sears Island were successful in attracting amphibians, the resulting community structure most likely differs from that of the original seasonal forest pools embedded in a forested wetland complex. The green frog has an over-wintering larval stage and tends to occur only in open-canopy ponds with permanent or intermediate hydroperiods (Skelly et al. 1999, Skelly et al. 2002). Failure to replicate the closed canopy and temporary hydrology of the natural wetland has allowed green frogs to establish successful breeding populations in VP1 and VP2. Although each pool continues to have breeding by the target species,

recruitment of wood frogs in VP1 and VP2 was poor or absent throughout the study.

Breeding Effort

Omitting the 2002 data when predation by green frogs prior to egg mass counts skewed the results, wood frog breeding effort ranged from approximately 0.7 to 0.9 egg masses/female (Figure 3). This indicates that roughly 70–90% of all females bred successfully in any given year, since each female wood frog produces one egg mass (Crouch and Paton 2000). Male-biased sex ratios are common in wood frogs (Berven 1990) and spotted salamanders (Whitford and Vinegar 1966, Sexton et al. 1986). Since male wood frogs were abundant, and trespass was never observed, the few females that did not produce egg masses were likely depredated. Evidence of depredation of adult wood frogs by raccoon (*Procyon lotor* L.), red fox (*Vulpes vulpes* L.), garter snake (*Thamnophis sirtalis* L.), and birds was observed, with depredated individuals found in and near traps, by the pool edge, or floating in the pool. No depredated adult salamanders were observed during the study. Spotted salamander breeding effort ranged from one to two egg mass per female in most years (Figure 3), which might suggest that nearly all female salamanders bred successfully, depositing at least one egg mass each. However, female spotted salamanders can produce from one to four masses of different sizes (Brodman 1995, Petranka 1998), making interpretations of our results difficult.

Reproductive Success

Successful colonization and breeding did not necessarily translate into reproductive success. The gradient in reproductive success and survival for wood frogs from lowest (VP1) to intermediate (VP2) to highest (VP3) corresponds to a gradient of hydroperiods from permanent (VP1) to semi-permanent (VP2) to temporary (VP3). The predation of egg masses by green frog tadpoles created the gradient in reproductive success observed for wood frogs, with the greatest predation pressure in VP1 and the least in VP3. For spotted salamanders, reproductive success and survival were also generally lower in VP1 than in the other two pools. However, direct predation on egg masses and larvae was not observed in the pools. In contrast to wood frogs, spotted salamander egg masses are encased in a relatively protective membrane that reduces egg predation by other amphibian larvae (Ward and Sexton 1981, Baldwin and Calhoun 2002). Tadpoles

can reduce the abundance of invertebrates in pools through predation (Petranka and Kennedy 1999) and competition for food resources (Wilbur 1972). Reduction of invertebrate prey abundance by green frog tadpoles may have caused the gradient in reproductive success for spotted salamanders, with the most intense competitive pressure in VP1 and the least in VP3.

Pre-metamorphic survival is generally low for pool-breeding amphibians due to loss of eggs and larvae to early pool dry-down (Shoop 1974), freezing (Harris 1980), and predation by invertebrates (Rowe et al. 1994). For wood frogs in seasonal pools, published estimates of pre-metamorphic survival range from 4.5% in a Maryland, USA, pond (Berven 1990) up to 63.5% in a nearly predator-free pond in New Jersey, USA (Seigel 1983). Herreid and Kinney (1966) reported an average of 3.7% survival for wood frogs in Alaskan ponds (hydroperiod not reported). Omitting the high survival found by Seigel, the estimated 4.81% survival for wood frogs in VP3 exceeds typical published levels, suggesting that VP3 provides excellent habitat for developing wood frog eggs and larvae.

For wood frogs in permanent ponds, Berven (1990) reported 0.95% survival in a Maryland pond containing predatory spotted turtles, painted turtles, and red-spotted newts, and Petranka and Kennedy (1999) reported that survival approximated 0% in natural and constructed ponds in North Carolina, USA, containing green frog tadpoles in high densities. Our estimates of 0.02% survival in VP1 and 0.25% survival in VP2 are between these two published estimates, suggesting that developing wood frogs in these two pools are under high levels of predation pressure.

Shoop (1974) reported pre-metamorphic survival rates for spotted salamanders of 1.0–12.6% in two temporary ponds in Massachusetts, USA, and Stangel (1988) reported survival rates of 0–3.1% in a temporary pond in Massachusetts. Our results of approximately 1–3% survival for spotted salamanders in the three pools are within the range observed by Stangel and on the low end of the range observed by Shoop. This suggests that spotted salamander survival is not reduced as greatly as wood frog survival in the presence of green frogs. However, spotted salamander larval survival can drop to 0% in the presence of fish (Ireland 1989), so there is a limit to the ability of spotted salamanders to coexist with opportunistic feeders and predators associated with permanent ponds.

The SVL data for juvenile wood frogs documented in this study may reflect a density-dependent function, with mean body size at metamorphosis

decreasing with increasing larval densities (Wilbur 1976). The largest wood frog juveniles emerged from VP1, which produced the fewest juveniles, and the smallest emerged from VP3 where the most juveniles were produced and larval densities were highest. The SVL data may also reflect a response to hydroperiod, with smaller size at metamorphosis required to survive the temporary hydroperiod of VP3 and larger size possible in VP1 due to the permanent hydroperiod (Wilbur and Collins 1973, Denver et al. 1998).

Wood frog populations are expected to decline in VP1 and VP2 in the face of continued egg predation. Wood frog populations may be sustained in VP1 and VP2 by subsidizing new colonists from potholes, detention basins, VP3, and other local breeding sites, with VP1 and VP2 potentially acting as population sinks. The data support this theory, as the extremely low wood frog juvenile output from VP1 and VP2 from 2001–2002 (Figure 4), for example, could not possibly produce the relatively large adult breeding populations observed in these pools in 2003 and 2004 (Figure 2). Spotted salamander populations may be stable given that pre-metamorphic survival was comparable to that reported for natural pools, juveniles were produced in large enough numbers to replace adults in most years, adult mortality is low for this species (Whitford and Vinegar 1966), and they may be more resistant to perturbations owing to selection for delayed reproduction and iteroparity (Petranka 2003b). The average number of breeding spotted salamander adults during the last two years of the study was greater than the average during the first four years, lending support to this supposition (Figure 2).

Implications for Seasonal Pool Creation and Monitoring

It is important to note that our monitoring results were conducted on created pools where historic pools were located and hence remnant populations of the target species were able to colonize pools the first spring of their construction.

In a number of recent studies, both wood frogs and spotted salamanders most commonly bred in seasonal pools with longer hydroperiods (16 to 18 weeks) (Skelly et al. 1999, Kolozsvary 2003, Baldwin in press); the number of breeding adult wood frogs in VP3 supports this finding, suggesting that it is preferable to create longer hydroperiod seasonal pools. The high levels of reproductive success for both species in VP3 support this theory. However, great care must be taken to avoid the

creation of permanent or semi-permanent hydroperiods as seen in VP1 and VP2.

The potholes have created a mosaic of small patches of water and wetland plants around the pools in an area that might otherwise be dry and inhospitable to amphibians. Adult and juvenile amphibians frequently entered potholes immediately after release from the pools and were often seen in and around potholes, suggesting that migrating amphibians used potholes as moist refugia in the open landscape. Yet, potholes were breeding sinks, as in most years, they dried before larvae could emerge. Although breeding occurred in only up to a quarter of potholes sampled, the number of egg masses deposited was substantial and would increase if all 200 potholes were surveyed. Since breeding occurred more often in deeper potholes, and these potholes were also generally dominated by cattail, we recommend that if potholes are to be used in wetland restoration projects, they should be kept shallow, at or below 16 cm in depth (the median depth of potholes without breeding). This should keep amphibian breeding to a minimum and allow a greater diversity of plants to grow, while maintaining the potential benefits to migration that potholes might afford. Combining potholes with more extensive tree and shrub plantings would better replicate wet forest conditions and provide more cover for amphibians.

The pool vegetation that has developed thus far is not characteristic of forested seasonal pools in the northeastern United States (Cutko 1997). Cattail is a typical species of marshes and ponds, and although it is hydrophytic vegetation, it should not be considered an indicator of success in this case. Cattail dominance and monocultures are common in newly created wetlands, especially when sites are not seeded with the desired vegetation following construction (Reinartz and Warne 1993, National Research Council 2001). Tree and shrub planting throughout the matrix of potholes and pools would have accelerated the process of canopy development and reduced cattail dominance of the site. This would benefit wood frogs and spotted salamanders, which occur most often in closed-canopy pools, and potentially would eliminate green frogs, which occur almost exclusively in open pools (Skelly et al. 1999).

This study exemplifies the need for long-term monitoring of created seasonal pools. Mitsch and Wilson (1996) stressed the need to monitor created wetlands for a minimum of 15 years, and possibly more for created forested wetlands, before determining success or failure. Three years of data on this site were not sufficient to assess pool success; it was not until the third year of the study that wood frog

recruitment bottomed out in VP1 and VP2, and the fourth year when it became clear that this was a trend that would be sustained while VP3 achieved peak wood frog juvenile production. In fact, six years of data for this and other open sites is not long enough to predict success. The pools may retain their current vegetative covers and hydroperiods in perpetuity. Conversely, the pools may develop closed canopies over time and achieve the desired temporary hydroperiods through the actions of evapotranspiration and the accumulation of dead plant material, excluding green frogs and allowing wood frogs to reproduce successfully. This study also makes it clear that the presence of breeding adults is often insufficient to assess the success of created seasonal pools as habitat for target amphibian species. Intensive monitoring, including measures of reproductive success and juvenile recruitment, is essential to properly assess the success of created seasonal pools as habitat for pool-breeding amphibians.

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