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# AMPHIBIAN COLONIZATION AND USE OF PONDS CREATED FOR TRIAL MITIGATION OF WETLAND LOSS

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*Abstract:* Created ponds were built as an experiment in mitigating the loss of a wetland to construction. We monitored amphibian breeding population sizes and juvenile recruitment at these ''created ponds'' for 8.5 years and compared the populations to those observed at the original wetland, Sun Bay (≤ 600 m from the created ponds), and at an undisturbed reference wetland, Rainbow Bay. Some amphibians continued breeding migrations to Sun Bay even after it was filled with soil. Few of the anuran colonists of the created ponds had been previously captured at Sun Bay, but many of the salamander colonists had been collected. The created ponds became permanent, whereas Sun Bay and Rainbow Bay were temporary ponds. Juveniles of two salamander species and 10 species of frogs and toads metamorphosed and emigrated from the created ponds during the study. By the final years of the study, the community structure of adult and juvenile amphibians differed among the three created ponds, as well as between these ponds and the prior amphibian community at the filled wetland and the contemporaneous community at the reference wetland. Mean size at metamorphosis was smaller at the created ponds than at the reference site for two species of frogs, whereas the opposite was true for two salamanders. We conclude that the created ponds provided partial mitigation for the loss of the natural amphibian breeding habitat. Differences between the created ponds and the natural wetlands were likely related to differences in their hydrologic regimes, size, substrates, vegetation, and surrounding terrestrial habitats and to the limited availability of colonists of some species.

*Key Words:* wetland creation, mitigation, amphibians, migration

## INTRODUCTION

Creation or restoration of wetlands is frequently required in the United States as mitigation for filling legally protected wetlands (Salvesen 1994). Mitigation is usually expected to be ''in-kind'' with respect to wetland type, as well as ''on-site.'' However, post-construction monitoring of wetlands constructed from uplands is rare, so few data exist on the extent to which they serve as ecological equivalents of those they replaced (Kusler and Kentula 1990, Kentula et al. 1993). Monitoring, when conducted, is often qualitative and short-term, and it fails to consider faunal usage (Kusler and Kentula 1990, Kentula et al. 1993).

Constructed wetlands are typically planted with vegetation but not stocked with animals. A prevailing wisdom is that animals will colonize and use the site if vegetation and an appropriate hydrologic regime are provided and if the site is close to similar wetlands or has surface water connections (Brooks 1990, Broome 1990, Erwin 1990, Hammer 1992).

Large and diverse amphibian communities are often found in wetland habitats (Sharitz and Gibbons 1982, Moler and Franz 1988, Pechmann et al. 1989, Dodd 1992, Hammer 1992, Stebbins and Cohen 1995, Voris and Inger 1995). Concern has increased about declines and disappearances of amphibian populations worldwide, with habitat destruction and modification being a primary cause (Wake and Morowitz 1990, Stebbins and Cohen 1995, Alford and Richards 1999). Therefore, ascertaining the extent to which compensatory wetlands maintain comparable populations of amphibians is important.

A small South Carolina, USA wetland, Sun Bay, was filled in 1983 for a U.S. Department of Energy (DOE) construction project. Its amphibian populations were monitored prior to and during construction. Four created ponds were built on the periphery of the construction site three months before construction began. Amphibian colonization and population dynamics were studied at these ''created ponds'' for 8.5 years. Here, we report the results and compare data from the created ponds to population data from Sun Bay and a similar reference wetland, Rainbow Bay.

## Natural History of Wetland Amphibian Community

Most amphibians found at the study wetlands are terrestrial (often fossorial) species that migrate to ephemeral ponds for breeding. Breeding seasons vary among species and, collectively, span the entire year. Duration of the aquatic larval stage ranges from a few weeks (e. g., bufonid toads) to several months (e. g., ambystomatid salamanders). After metamorphosing, individuals typically disperse to surrounding terrestrial habitat. Terrestrial home ranges of pond-breeding amphibians are usually within a few hundred meters of their breeding pond (e.g., Jameson 1956, Kramer 1973, Williams 1973, Douglas and Monroe 1981, Semlitsch 1981, 1983b, Madison and Farrand 1998), although those of some bufonid toads can extend up to 3 km (Sinsch 1990, 1992, 1997). If a pond does not dry, larval *Ambystoma talpoideum* (Holbrook) and *Notophthalmus viridescens* (Rafinesque) can delay the onset or completion of metamorphosis and become paedomorphic, retaining gills and attaining sexual maturity while remaining in the pond (Semlitsch and Gibbons 1985, Harris 1987, Reilly 1987). Paedomorphs of both species may later metamorphose.

Many amphibian species are philopatric to the same breeding site every year (e.g., Twitty 1959, Oldham 1966, Whitford and Vinegar 1966, Oldham 1967, Gill 1978, Semlitsch 1981, Breden 1987, Semlitsch et al. 1988, Berven and Grudzien 1990, Reading et al. 1991, Scott 1994), often their natal pond (Breden 1987, Semlitsch et al. 1988, Berven and Grudzien 1990, Reading et al. 1991, Sinsch 1997, D. E. Gill *personal communication*). Many return to the same terrestrial home range (e.g., Haapanen 1970, Williams 1973, Breden 1987). However, philopatry is seldom absolute (Breden 1987, Reading et al. 1991). For example, 83% of adult *Bufo woodhousei fowleri* (Hinckley) bred in the same pond in consecutive years, while the other 17% relocated (Breden 1987). Adult *N. viridescens* are virtually 100% faithful to breeding ponds, but juveniles occasionally disperse to ponds many kilometers away (Gill 1978, *personal communication*). Marked adult *Rana pipiens* Schreber have been recaptured at wetlands up to 5.2 km from their natal pond (Dole 1971). Although adult philopatry to the natal pond is the rule for *Ambystoma talpoideum* (Semlitsch 1981, Semlitsch et al. 1988) and *A. opacum* (Gravenhorst) (Scott 1994), individuals of both species that were marked at Rainbow Bay at metamorphosis have been found breeding at a pond 1 km distant (personal observations). Philopatry can also vary with sex. Most male *Bufo calamita* Laur. are philopatric to their breeding pond, but female *B. calamita* are not (Sinsch 1992). Acoustic, magnetic, olfactory, and visual cues all play a role in orientation and homing in amphibians (Twitty 1961, Oldham 1967, Landreth and Ferguson 1967, Taylor and Adler 1973, Grubb 1975, Hershey and Forester 1979, Phillips 1986, McGregor and Teska 1989, Sinsch 1990, Rodda and Phillips 1992).

## Pond Creation, Pond Loss, and Amphibians

Amphibians commonly colonize ponds created intentionally or unintentionally by humans (Gill 1978, Fog 1988, Brooks 1990, Laan and Verboom 1990, Adam and Lacki 1993, Arntzen and Teunis 1993, Schlupp and Podloucky 1994, personal observations). Colonization rates can be affected by distance from other ponds, characteristics of the intervening terrestrial habitat, dispersal capacity and site fidelity of the species, and size of source populations (Laan and Verboom 1990).

Amphibians may return to former breeding sites even after wetlands are filled with soil (e. g., *Gastrophryne carolinensis* (Holbrook) (Anderson 1954), *B. bufo* (Heusser 1960, McMillan 1963), *A. talpoideum* (Shoop personal observation, cited in Shoop and Doty 1972), *A. laterale* Hallowell (Uzzell personal communication, cited in Shoop and Doty 1972), and unspecified frogs and toads (Frazer 1973)). Only Frazer (1973) reported the subsequent fate of these populations. He noted that a few frogs moved to an undrained part of the breeding canal, where they became established after being assisted over an embankment.

Schlupp and Podloucky (1994) successfully relocated *B. bufo* to a newly constructed breeding site by capturing them on their way to another pond, placing them in the new pond, and keeping them there with a fence throughout the breeding season. Within three years, most of the *Bufo* bred in the new pond of their own accord. Cook and Pinnock (1987), Cook (1989), and Matthews et al. (1991) established amphibian populations in newly built ponds by stocking eggs, larvae, or adults, mostly from nearby sites threatened by development.

In our study, new ponds were built a few months before the natural wetland and much of the surrounding terrestrial habitat were eliminated. It was clear that significant amphibian mortality would result from bulldozing and other construction activities, reducing the number of potential colonizers. A central question was whether surviving individuals would breed at the created ponds or return to the drained, filled, and altered area of Sun Bay.

We chose not to stock our ponds because amphibians and other fauna are not usually stocked in constructed wetlands. The philosophy of our study was to create ponds, let them fill with rainwater, and allow colonization and succession to take their course. We did not attempt to mitigate the loss of other functions of the filled wetland because, at the time of construction, the DOE was not required by law to mitigate. The area of the filled wetland was approximately 10,000 $m^2$; total area of the created ponds was 800 $m^2$. Consequently, our study should be viewed as an experimental ''pilot project,'' not as mitigation *per se.* Our research focused on how long it took for the new ponds to be colonized by amphibians, which species became established, and how these ''new'' amphibian communities compared to those from the filled wetland and a reference wetland.

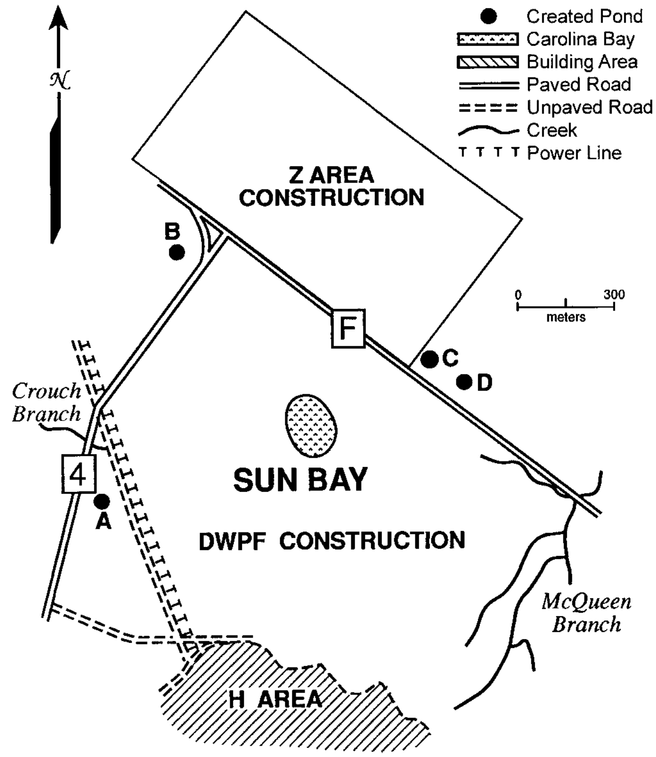


Figure 1. Location of the created ponds, Sun Bay, and the construction sites of the Defense Waste Processing Facility and Z-Area. ''H-area'' is an industrial site.

## SITE CONDITIONS AND THE CREATED PONDS

### Study Site

The study was conducted in Aiken County, South Carolina, USA on the DOE's 780-$km^2$ Savannah River Site (SRS). Sun Bay was a Carolina bay, one of thousands of elliptical depressions of unresolved geological origin common to the southeastern U.S. Atlantic Coastal Plain (Sharitz and Gibbons 1982, Ross 1987). Sun Bay usually filled in the winter and dried in the spring or summer, was approximately 1 ha in area, had a maximum depth of about 1 m, and had no surface connection to other bodies of water. Most Carolina bays are underlain by an impervious clay lens and usually receive no water input other than rain (Bryant and McCracken 1964, Sharitz and Gibbons 1982, Schalles and Shure 1989, Lide et al. 1995). Filling and drying dates varied widely from year to year, depending on temperature and rainfall (Semlitsch 1983a, 1987, Caldwell 1987, Pechmann et al. 1989). In 1978, before our study began, approximately 40% of the bay was cleared of vegetation and a ditch was dug that partially drained the bay for pre-construction seismic surveys. The ditch reduced water volume by about 75%, decreased depth (maximum was 0.35 m during our study), and caused the pond to dry earlier (Semlitsch 1983a, 1987, Caldwell 1987, Pechmann et al. 1989). Thus, our pre-construction studies of Sun Bay were not pre-disturbance. Consequently, we used data from a similar reference wetland (Rainbow Bay, located 4 km away; Semlitsch et al. 1996) for some site comparisons of juvenile amphibians because the ditching of Sun Bay greatly reduced the diversity and number of juveniles produced (see Semlitsch 1983a, 1987, Caldwell 1987, Pechmann et al. 1989).

In 1979, Sun Bay had a central herbaceous zone, a shrub zone (*Cephalanthus occidentalus* L.), and an outer forested zone (*Liquidambar styraciflua* L.). The composition and extent of these vegetation zones probably varied over time in response to variation in hydroperiod and other factors, as has been observed in Rainbow Bay (personal observations).

Terrestrial habitats within a 1-km radius of Sun Bay consisted primarily of managed pine plantations (*Pinus taeda* L. and *P. elliottii* Englem) on deep, well-drained sandy soils. Pine stands were 4–26 years old. Other nearby plant communities included *Pinus palustris* Miller stands and upland and bottomland hardwoods. Two of the created ponds, B and D (Figure 1), were located in *P. elliottii* plantations that also contained scattered *P. taeda.* Created Pond C was located in *P. palustris,* and Pond A was surrounded by mixed hardwoods and *P. taeda,* with a well-developed understory (Figure 1).

Individuals from Sun Bay were not the only potential source of colonists for the created ponds. An old farm pond lies 1.2 km east-southeast of the former bay, and four Carolina bays are each approximately 2 km away. Additional sources were roadside ditches and small, temporary puddles, habitats used extensively as breeding sites by species such as *Scaphiopus holbrookii* Harlan (eastern spadefoot toad), *G. carolinensis* (eastern narrow-mouthed toad), and *Hyla squirella* Bose (squirrel treefrog). Two small streams, McQueen Branch and Crouch Branch, are each located within 1 km of the site of Sun Bay (Figure 1), but these streams support stream-breeding species unlikely to colonize ponds.

## The Construction Project

Clearing and grading for DOE's Defense Waste Processing Facility and associated structures began in September 1983 and encompassed approximately 240 ha (Figure 1). Sun Bay was filled with soil in October 1983 while the bay was dry. Standing water collected in a low area on the NW side of the former wetland after rains in mid-November. The water remained until 21 December 1983, when a ditch was dug that permanently drained the site. The site of the former wetland became a parking lot for the facility. Construction impacts extended at least 300 m from Sun Bay in all directions and more than 500 m in most. Therefore, Sun Bay amphibians lost most of their terrestrial habitat, as well as their breeding site.

Five sedimentation ponds were built near the perimeter of the construction area. We did not monitor amphibian populations at these ponds, but they may have provided suitable breeding sites for some species.

## Design of Created Ponds

The four created ponds (A, B, C, and D) were sited 300–600 m from Sun Bay and from the buildings and parking lots being constructed. Ponds were lined with 20–25 cm of hard-packed clay so that they would collect and hold rainwater and potentially mimic the hydrodynamics of a Carolina bay. Each pond was circular, approximately 16 m in diameter (200 $m^2$ in area), and had a maximum depth of 1 m. Pond construction was completed on 20 June 1983. Rainfall was monitored daily with a rain gauge and water level weekly with a staff gauge. Plywood boards were placed around each pond following pond construction to provide shelter for amphibians until vegetation could redevelop.

Water retention of the created ponds was poor during the first year after they were built, in spite of high rainfall. To rectify this problem, fish-grade plastic (CPE) pond liners were installed on 19 November

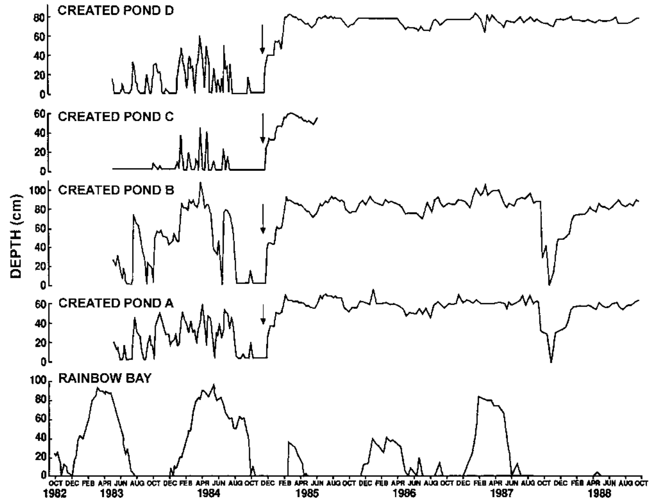


Figure 2. Water depth in the created ponds and a reference wetland, Rainbow Bay, October 1982–September 1988. Arrows indicate when plastic liners were installed in the created ponds.

1984. Terrestrial leaf litter was added to the ponds during February and March 1985 to supply cover, nutrients, and organic matter. After installation of the plastic liners, the created ponds became permanent ponds. Two ponds, A and B, were manipulated to simulate ''normal'' annual drying; each was pumped to one-third full depth from 28–29 September 1987. Both ponds were dried completely by pumping and hand bailing from 19 October 1987 to 22 October 1987, then allowed to refill with rain beginning 27 October 1987.

At DOE's request, Created Pond C was dismantled on 7 June 1985 to accommodate additional construction.

## The Created Pond Environment

The hydroperiods of the created ponds did not match that of the reference wetland, Rainbow Bay (Figure 2). Rainbow Bay usually filled in the winter and dried in the spring or summer, as had Sun Bay before construction. The created ponds dried too frequently at first, then not at all after pond liners were installed (Figure 2). Ponds A and B remained dry for less than a week after the water was pumped out of them in 1987 (Figure 2). This was a shorter dry period than experienced by Rainbow Bay during any year of the study.

Grasses (dominant *Digitaria sanguinalis* (L.)) and forbs initially colonized the bare soil that surrounded each new pond. Over time, pine seedlings (*Pinus taeda* at A, *P. elliottii* at B and D) became established adjacent to the ponds, and aquatic vegetation (*Scirpus* *cyperinus* (L.) and algae), insects, and zooplankton became established within each pond.

## METHODS

### Sampling Techniques

We monitored amphibian populations at Sun Bay (8 Feb. 1979–24 June 1982), the created ponds (21 June 1983–9 December 1991) and Rainbow Bay (21 September 1979–31 December 1994) using 40-L pitfall traps placed along terrestrial drift fences that encircled each pond (Gibbons and Semlitsch 1981, Dodd and Scott 1994). The capture efficiency of drift fences with pitfall traps differs among species and size classes (Gibbons and Semlitsch 1981, Dodd 1991, Corn 1994, Dodd and Scott 1994, personal observations), but efficiency should be comparable among these sites because we used the same drift fence design at each. Analyses of population changes over time make the assumption that there are no changes in the sampling efficiency of the drift fences, which is reasonable if the fences and traps are well-maintained.

Fences were of 50-cm-high aluminum flashing buried 10 cm in the ground, with traps on each side at 10-m intervals. Traps were checked daily, and animals released on the opposite side of the fence, the presumed direction of movement. Most amphibians captured were marked by toe-clipping. A combination of individual marks, year-pond cohort marks, and general group marks was used. Our sampling techniques provided a census of the numbers of adults that entered each pond to breed each year, as well as the numbers of newly-metamorphosed juveniles. The snout-vent length (SVL: tip of snout to posterior end of the vent) of most emigrating juveniles was measured ($\pm$ 0.5 mm). Adults that migrated to the ponds from September to December were counted as part of the following calendar year's breeding population because their larvae contributed to the following year's cohort of metamorphosing juveniles.

After construction activities began at Sun Bay, partial drift fences were employed intermittently beginning 13 December 1983. Small pitfall traps (4.5 L) were used to facilitate frequent installation and removal. These small traps were not as effective as the larger traps for capturing some species. The total length of fence differed among years, and the partial fences sampled only 50–100 m of the perimeter of the former wetland. Sampling differences cloud among-year comparisons of amphibian populations at Sun Bay during construction, as well as comparisons to the created ponds, but were unavoidable due to the construction activities. Monitoring of Sun Bay was discontinued after 16 September 1987 because captures had dwindled to near zero.

Before Sun Bay was completely drained, we used minnow traps (N=5) to sample the remaining patch of water from 12 to 21 December 1983. After the site was ditched, we sampled the drainage ditch with the minnow traps until 31 March 1984. Each created pond was sampled with three minnow traps from 10 January 1987 to 15 April 1987 in order to determine if paedomorphic salamanders were present. All minnow traps were checked daily, and all captured animals were released immediately. Adult amphibians and salamander larvae captured in minnow traps were marked by toe-clipping. Each created pond was surveyed qualitatively with dip nets and a seine on 17 April 1991 for the presence of adult *N. viridescens.*

### Statistical Analyses

We used the Mantel-Haenszel general association statistic (Kuritz et al. 1988, Stokes et al. 1995) to test for differences among years and locations in the community structure of adults entering ponds to breed and of newly metamorphosed juveniles emigrating from ponds. (Here ''community structure'' is the vector representing the number of individuals of each species.) The Mantel-Haenszel procedure is a contingency table analysis that tests for an association between two variables while adjusting for (stratifying by) a third variable or combination of variables. We analyzed data for salamanders and anurans separately and tested five null hypotheses. Two concerned the community structure of breeding adults: 1) the community did not differ among the created ponds during the last three years of the study, adjusting for year, and 2) the community at the created ponds (all pooled) for the last three years did not differ from that at Sun Bay prior to construction. Stratification by year was not employed in the latter analysis because the years compared differed between the two locations. Only data for the three years for which sampling took place throughout a species' entire breeding season at Sun Bay were used. These years differed among species (see Table 1). In the cases of *Rana utricularia* Harlan and *S. holbrookii*, which breed throughout the year, data for the first three years were used, although sampling commenced partway through the first year.

The other null hypotheses concerned the community structure of emigrating juveniles: 3) the community at the created ponds did not differ among years, adjusting for pond, 4) the community did not differ among the created ponds, adjusting for year, and 5) the community pooled across created ponds did not differ from that at Rainbow Bay (the reference wetland) during the same time period, adjusting for year. Analyses of

Table 1. Breeding population sizes (B) and juvenile recruitment (J) of amphibians at Sun Bay prior to its elimination.

| | 1979 | | 1980 | | 1981 | | 1982 | |
|---|---|---|---|---|---|---|---|---|
| | B | J | B | J | B | J | B | J |
| Salamanders | | | | | | | | |
| *Ambystoma opacum* | —[a] | 0 | 21 | 19 | 34 | 31 | 13 | 93 |
| *A. talpoideum* | 1000[b] | 0 | 6313 | 0 | 166 | 0 | 1983 | 0 |
| *A. tigrinum* | 45[b] | 1 | 21 | 0 | 3 | 0 | 26 | 0 |
| *Eurycea quadridigita* | —[a] | 0 | 5 | 0 | 1 | 0 | 2 | 0 |
| *Notophthalmus viridescens* | —[a] | 23 | 2276 | 0 | 638 | 0 | 323 | 0 |
| Frogs and Toads | | | | | | | | |
| *Acris gryllus* | 3 | 0 | 9 | 0 | 2 | 0 | 0[b] | 0 |
| *Bufo quercicus* Holbrook | 1 | 0 | 0 | 0 | 8 | 0 | 3[b] | 0 |
| *B. terrestris* | 305 | 617 | 817 | 0 | 114 | 0 | 185[b] | 0 |
| *Gastrophryne carolinensis* | 1201 | 0 | 123 | 0 | 480 | 0 | 78[b] | 0 |
| *Hyla chrysoscelis* | 7 | 0 | 2 | 0 | 0 | 0 | 0[b] | 0 |
| *H. femoralis* | 1 | 0 | 0 | 0 | 0 | 0 | 0[b] | 0 |
| *H. gratiosa* | 3 | 0 | 0 | 0 | 0 | 0 | 0[b] | 0 |
| *Pseudacris crucifer* | 324[b] | 50 | 495 | 166 | 288 | 75 | 57 | 377 |
| *P. nigrita* (Le Conte) | 0[b] | 0 | 14 | 0 | 4 | 0 | 0 | 0 |
| *P. ornata* | 122[b] | 31 | 303 | 19 | 118 | 55 | 117 | 423 |
| *Rana catesbeiana* | 0 | 0 | 2 | 0 | 0 | 0 | 0[b] | 0 |
| *R. clamitans* | 17 | 0 | 5 | 25 | 0 | 0 | 5[b] | 0 |
| *R. utricularia* | 94[b] | 0 | 83 | 0 | 32 | 0 | 4[b] | 0 |
| *Scaphiopus holbrookii* | 258[b] | 58 | 812 | 0 | 9 | 0 | 20[b] | 0 |

[a] Drift fence and pitfall traps not in place during breeding migration period.
[b] Drift fence and pitfall traps in place during only part of breeding migration period.

juveniles were restricted to the years following installation of plastic liners in the created ponds (i. e., 1985–1991). Pond C was excluded from these analyses because it was dismantled in 1985. Hypotheses 4 and 5 were tested separately for the periods 1985–1988 and 1989–1991. For each analysis, we deleted any species for which the expected value of any cell was $<5$, pooled over all strata. The exception was that *A. opacum* and *A. tigrinum* (Green) were combined rather than deleted for the test of hypothesis 2 because their combined expected value was $>5$, and this provided a more relevant test.

Analysis of variance was used to test for differences in mean SVL of juveniles between the created ponds (1985–1991, excluding Pond C) and Rainbow Bay (1979–1994, data from Caldwell 1987, Semlitsch 1987, Semlitsch et al. 1988 and unpublished). Data were log-transformed to meet the ANOVA assumption of homogeneity of variance. Each created pond and Rainbow Bay was used as a category in a one-way ANOVA in which years were treated as replicates. We used contrasts to test for differences between the created ponds as a group and Rainbow Bay, weighting each created pond by the number of cohorts produced at that pond. We analyzed data for individuals and used the pond-by-year interaction as the error term, rather than simply analyzing pond and year means. This allowed us to use information on the variance among individuals at a pond within a year (Wilbur 1987). Because the number of individuals differed among pond-year groups, it was necessary to include a portion of the individual mean square in the error term to obtain an appropriate expected error mean square. The Satterthwaite approximation was used to calculate degrees of freedom for these combined error terms (Milliken and Johnson 1992).

## RESULTS

### Filled Wetland

Four to five species of salamanders and 7–15 species of frogs and toads probably bred at Sun Bay prior to construction (Table 1). Breeding population sizes varied considerably during the pre-construction survey (1979–1982). Some species had no juvenile recruitment during this period, and for the others, recruitment was low and sporadic (Table 1). We observed that Sun Bay usually dried before many larvae could reach the minimum size for metamorphosis. *Ambystoma talpoideum* and *N. viridescens* were the most commonly captured salamanders before construction, and *Bufo terrestris* (Bonnaterre), *G. carolinensis*, *Pseudacris crucifer* (Weid.), *P. ornata* (Holbrook), and *S. holbrookii* were the most commonly captured frogs and toads.

Table 2. Number of adult amphibians captured during breeding migrations at Sun Bay after it was filled with soil.

| | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|
| Salamanders | | | | |
| *Ambystoma opacum* | 1[b] | 0[b] | 0[b] | 0 |
| *A. talpoideum* | 34[b] | 1[b] | 9 | 0 |
| *Notophthalmus viridescens* | 18[b] | 0[b] | 0[b] | 0 |
| Frogs and Toads | | | | |
| Bufo terrestris | 12[b] | 6 | 0 | 0 |
| *Gastrophryne carolinensis* | 3[b] | 4[b] | 0[b] | 0 |
| *Pseudacris crucifer* | 6[b] | 1[b] | 0 | 0 |
| *P. ornata* | 10[b] | 0[b] | 0 | 0 |
| *Rana clamitans* | 1[b] | 0[b] | 0 | 0 |
| *R. utricularia* | 13[b] | 0[b] | 1[b] | 1 |
| *Scaphiopus holbrookii* | 8[b] | 1[b] | 3[b] | 0 |

[a] Drift fence and pitfall traps not in place during breeding migration period.
[b] Drift fence and pitfall traps in place during only part of breeding migration period.

Some species continued breeding migrations to the site of Sun Bay for a period of time after it was filled with soil in 1983 (Table 2). By the 1987 breeding seasons, however, only one breeding adult was captured at Sun Bay, a female *R. utricularia.*

### Frogs and Toads

The anurans *B. terrestris, G. carolinensis, P. crucifer,* and *R. utricularia* colonized the created ponds within a year (Table 3). Breeding populations of these four species were present at the ponds during every year of the study, but population sizes fluctuated (Table 3). Smaller numbers of adults of 9 other species of anurans were captured during their breeding seasons in one or more years at the created ponds (Table 3). Sampling efficiency was low for adult *Acris, Rana, Hyla*, and *P. crucifer.* As an extreme example, no adult *H. gratiosa* Le Conte were ever captured in the created pond pitfall traps even though juveniles were produced at all three remaining ponds every year beginning in 1985 (Table 3, Figure 3). Species relative abundances changed through the years; by the last three years, ponds differed in their adult anuran communities ($\chi^2 = 115$, df = 8, $P < 0.001$). *Pseudacris crucifer* and *R. utricularia* were over-represented at Pond A and under-represented at Pond D relative to the total number of breeding adult anurans captured at these ponds, whereas *A. gryllus* was over-represented at Pond D and under-represented at Pond A (Table 3).

More individuals of all frog and toad species were caught at the created ponds than at the filled wetland each year that both locations were monitored, except 1984 for *P. ornata*, but sampling efficiency was greater at the created ponds (Tables 2 and 3). Only four *B. terrestris,* one *G. carolinensis,* and two of the *R. utricularia* captured at the created ponds had been marked at Sun Bay during pre-construction surveys. The community structure of adult anurans at the created ponds during their breeding season in the last three years of the study, pooled over ponds and years, was significantly different from that at Sun Bay prior to construction, pooled over years ($\chi^2 = 552$, df = 6, $P < 0.001$). There were more adult *B. terrestris, A. gryllus,* and *R. utricularia* and fewer *S. holbrookii* and *P. ornata* at the created ponds than were expected based on the numbers at Sun Bay.

No juveniles metamorphosed and emigrated from the created ponds in 1983. Only 7 juvenile *Hyla chrysoscelis* (Cope) and one juvenile *Hyla femoralis* Latreille were observed in 1984 (Figure 3). This low juvenile recruitment was due in part to the fact that the ponds dried frequently, killing the tadpoles that were present. Substantial production of frog and toad juveniles began in 1985 following installation of the pond liners. Juveniles of 10 species of frogs and toads emigrated from the created ponds during the study (Figure 3). The community structure of juvenile anurans varied significantly among years ($\chi^2 = 3120$, df = 24, $P < 0.001$) and among ponds (1985–1988: $\chi^2 = 1396$, df = 8, $P < 0.001$, 1989–1991: $\chi^2 = 1393$, df = 8, $P < 0.001$).

*Pseudacris crucifer* and *R. utricularia* produced the most anuran juveniles at the created ponds. The largest cohort of both species was produced in the first year with extended hydroperiods, 1985 (Figures 2 and 3). The next largest cohort of both species came in 1988, primarily from ponds A and B, which had been pumped dry in the autumn of 1987. Also, in other years, nearly all *R. utricularia* juveniles came from Ponds A and B, whereas Pond D produced the most *P. crucifer* juveniles overall. *Pseudacris crucifer* had been one of the three dominant species at Sun Bay in terms of juvenile recruitment during pre-construction studies, but no juvenile recruitment of *R. utricularia* was observed there from 1979 to 1982 (Table 1).

Relatively large numbers of juvenile *Acris gryllus, B. terrestris,* and *Hyla gratiosa* also metamorphosed and emigrated from the created ponds, especially Pond D (Figure 3). No juvenile recruitment of *A. gryllus* was observed at the ponds until 1987, the same year that adults were first captured. After 1987, a cohort of *Acris* was produced every year, the largest during the last year of the study. Most *B. terrestris* juveniles were produced in the latter part of the study, as was the only cohort of *Rana clamitans* Latreille. In contrast to the success of some species in later years, juvenile recruitment of *H. chrysoscelis* at the created ponds occurred primarily in the first part of the study (Figure 3). No juvenile recruitment of *A. gryllus, H. chrysos-*

Table 3. Number of adult amphibians captured entering the created ponds during breeding migrations (Pond C was dismantled 7 June 1985).

| | Pond | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
|---|---|---|---|---|---|---|---|---|---|---|
| Salamanders | | | | | | | | | | |
| *A. talpoideum* | A | —[a] | 0 | 0 | 8 | 5 | 1 | 1 | 2 | 1 |
| | B | —[a] | 0 | 1 | 9 | 11 | 9 | 29 | 63 | 40 |
| | C | —[a] | 6 | 2 | — | — | — | — | — | — |
| | D | —[a] | 3 | 0 | 45 | 35 | 23 | 51 | 138 | 124 |
| *A. tigrinum* | A,C,D | —[a] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | —[a] | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *E. quadridigitata* | A | —[a] | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B,C | —[a] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | D | —[a] | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *N. viridescens* | A | —[a] | 1 | 0 | 4 | 3 | 14 | 3 | 2 | 5 |
| | B | —[a] | 0 | 0 | 2 | 1 | 3 | 0 | 3 | 0 |
| | C | —[a] | 1 | 0 | — | — | — | — | — | — |
| | D | —[a] | 2 | 0 | 5 | 5 | 1 | 5 | 43 | 38 |
| Frogs and toads | | | | | | | | | | |
| *A. gryllus* | A | 0[b] | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| | B | 0[b] | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 |
| | C | 0[b] | 0 | 0[b] | — | — | — | — | — | — |
| | D | 0[b] | 0 | 0 | 0 | 4 | 0 | 6 | 15 | 22 |
| *B. quercicus* | A,C,D | 0[b] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 0[b] | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *B. terrestris* | A | 4[b] | 7 | 30 | 40 | 23 | 13 | 13 | 13 | 24 |
| | B | 2[b] | 7 | 56 | 71 | 14 | 14 | 13 | 7 | 34 |
| | C | 2[b] | 6 | 17[b] | — | — | — | — | — | — |
| | D | 1[b] | 3 | 37 | 34 | 11 | 26 | 26 | 36 | 34 |
| *G. carolinensis* | A | 11[b] | 24 | 33 | 29 | 18 | 13 | 12 | 11 | 17 |
| | B | 19[b] | 17 | 8 | 10 | 6 | 11 | 4 | 7 | 21 |
| | C | 8[b] | 4 | 8[b] | — | — | — | — | — | — |
| | D | 9[b] | 21 | 16 | 2 | 9 | 7 | 35 | 10 | 82 |
| *H. chrysoscelis* | A | 0[b] | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| | B | 0[b] | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| | C | 0[b] | 0 | 0[b] | — | — | — | — | — | — |
| | D | 0[b] | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| *H. femoralis* | A | 0[b] | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 10[b] | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | C | 0[b] | 0 | 0[b] | — | — | — | — | — | — |
| | D | 0[b] | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *P. crucifer* | A | —[a] | 2 | 3 | 25 | 3 | 22 | 29 | 19 | 0 |
| | B | —[a] | 13 | 7 | 115 | 2 | 8 | 7 | 5 | 1 |
| | C | —[a] | 4 | 15 | — | — | — | — | — | — |
| | D | —[a] | 1 | 10 | 34 | 5 | 0 | 6 | 10 | 6 |
| *P. nigrita* | A,C | —[a] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | —[a] | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| | D | —[a] | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| *P. ornata* | A | —[a] | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| | B | —[a] | 1 | 2 | 3 | 0 | 5 | 5 | 0 | 0 |
| | C | —[a] | 2 | 2 | — | — | — | — | — | — |
| | D | —[a] | 2 | 1 | 1 | 0 | 4 | 0 | 0 | 0 |
| *R. catesbeiana* | A | 0[b] | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 0 |
| | B | 0[b] | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | C | 0[b] | 0 | 0[b] | — | — | — | — | — | — |
| | D | 0[b] | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

Table 3. Continued.

| | Pond | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
|---|---|---|---|---|---|---|---|---|---|---|
| *R. clamitans* | A | 0[b] | 0 | 5 | 3 | 0 | 0 | 0 | 1 | 0 |
| | B | 0[b] | 4 | 4 | 4 | 0 | 1 | 0 | 0 | 0 |
| | C | 0[b] | 3 | 1[b] | — | — | — | — | — | — |
| | D | 0[b] | 2 | 0 | 1 | 0 | 0 | 2 | 0 | 1 |
| *R. utricularia* | A | 0[b] | 5 | 7 | 43 | 22 | 13 | 22 | 7 | 7 |
| | B | 0[b] | 15 | 6 | 42 | 3 | 4 | 6 | 4 | 3 |
| | C | 0[b] | 2 | 2[b] | — | — | — | — | — | — |
| | D | 0[b] | 1 | 2 | 16 | 0 | 1 | 0 | 0 | 1 |
| *S. holbrookii* | A | 0[b] | 1 | 0 | 0 | 5 | 2 | 1 | 0 | 0 |
| | B | 1[b] | 6 | 6 | 5 | 7 | 4 | 1 | 1 | 2 |
| | C | 2[b] | 13 | 1[b] | — | — | — | — | — | — |
| | D | 3[b] | 2 | 4 | 2 | 0 | 0 | 0 | 0 | 0 |

[a] Drift fence and pitfall traps not in place during breeding migration period.
[b] Drift fence and pitfall traps in place during only part of breeding migration period.

*celis*, or *H. gratiosa* was observed at Sun Bay from 1979 to 1982.

Only a few *Rana catesbeiana* Shaw and *Pseudacris ornata* juveniles and a single *H. femoralis* juvenile were produced at the created ponds (Figure 3). Most of the *P. ornata* came from Pond B in the year after it was pumped dry. *Pseudacris ornata* had been one of the dominant frogs at Sun Bay in terms of juvenile recruitment, but no *R. catesbeiana* or *H. femoralis* recruitment were observed there during pre-construction studies (Table 1). No juvenile *G. carolinensis* or *S. holbrookii* were produced at the created ponds, despite the fact that adults of these species were frequently captured there. *Scaphiopus holbrookii* was the only frog or toad that produced juveniles at Sun Bay during pre-construction studies but did not produce any at the created ponds.

The community structure of juvenile frogs and toads produced at the created ponds, pooled over ponds, was significantly different from that at the reference wetland during the same years (Figure 4; 1985–1988: $\chi^2 = 1948$, df = 6, $P < 0.001$, 1989–1991: $\chi^2 = 7554$, df = 9, $P < 0.001$). Cohorts of *G. carolinensis* and *S. holbrookii* were produced at Rainbow Bay but not at the created ponds during 1989–1991. More *P. ornata* juveniles metamorphosed at Rainbow Bay than at the created ponds throughout the study, whereas more *B. terrestris*, *A. gryllus*, and *H. gratiosa* metamorphosed at the created ponds (Figure 4). More juvenile *H. chrysoscelis* and *R. utricularia* were produced at the created ponds than at Rainbow Bay from 1985 to 1988, whereas juveniles of these two species were produced in approximately the expected proportions at each location from 1989 to 1991 (resulting in more from Rainbow Bay, where the total numbers of juvenile anurans was greater). Overall during the study, slightly more *H. chrysoscelis* were produced at the created ponds, whereas more *R. utricularia* were produced at Rainbow Bay (Figure 4).

Mean snout-vent length at metamorphosis of *P. crucifer* and *P. ornata* was significantly smaller at the created ponds than at Rainbow Bay (Tables 4 and 5). No significant difference in snout-vent length at metamorphosis between the created ponds and the reference wetland was detected for the other six anuran species that produced juveniles at both locations from 1985 to 1991 (Tables 4 and 5).

### Salamanders

More adult *A. talpoideum* and *N. viridescens* were caught at Sun Bay than at the created ponds in 1984, despite the less efficient sampling at Sun Bay (Tables 2 and 3). The few adult salamanders that entered the created ponds in 1984 left within several days. Few salamanders were captured at either location in 1985, a drought year. More adult *A. talpoideum* and *N. viridescens* were caught at the created ponds than at Sun Bay during 1986 and 1987, the last years the filled wetland was sampled (Tables 2 and 3). Numbers of immigrating adults remained high at the created ponds from 1987 to 1989 and increased again in 1990 (Table 3). Three of the 19 *N. viridescens* and 46 of the 99 *A. talpoideum* adults that entered the created ponds during the first 4 years of the study had been marked previously at Sun Bay.

The final community structure of adults at the created ponds, pooled over ponds during the last three years, was significantly different from that at Sun Bay prior to construction ($\chi^2 = 30$, df = 2, $P < 0.001$). *Ambystoma talpoideum* and *N. viridescens* were the most common adult salamanders at both Sun Bay (Table 1) and the created ponds (Table 3). There were more adult *A. talpoideum* and fewer *N. viridescens*

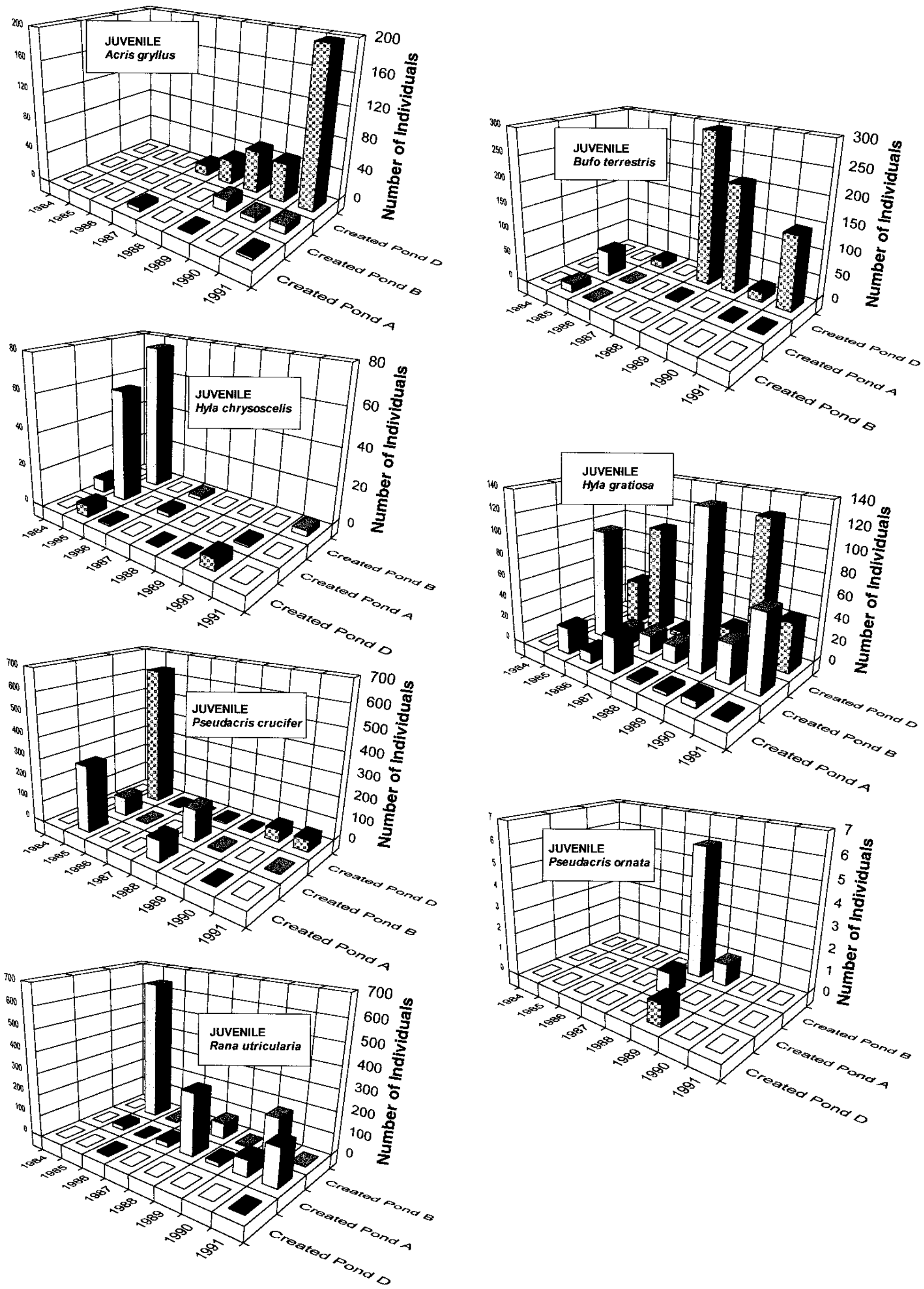


Figure 3. Total numbers of juvenile frogs and toads captured that metamorphosed and emigrated from the created ponds from 1984 to 1991. The order of the ponds on the axes differs among species to maximize the visibility of the bars, but the same bar pattern is consistently associated with each pond. In addition to those illustrated, the following juveniles were also captured: one *H. femoralis* at Pond A in 1984, nine *R. catesbeiana* at Pond B in 1987, six *R. catesbeiana* at Pond A in 1991, and 88 *R. clamitans* at Pond A in 1991.

captured at the created ponds from 1989 to 1991 than expected based on the numbers captured at Sun Bay from 1980 to 1982. Other species originally at Sun Bay (*A. opacum, A. tigrinum*, and *Eurycea quadridigitata* (Holbrook); Table 1) were rarely captured anywhere after construction began (Tables 2 and 3). The paucity of captures of these species contributed little to the significant difference in community structure between Sun Bay and the created ponds, however, as the expected number of captures of *A. opacum* and *A. tigrinum* combined was only 5.3 at the created ponds, and there were too few *Eurycea* to include in the anal-

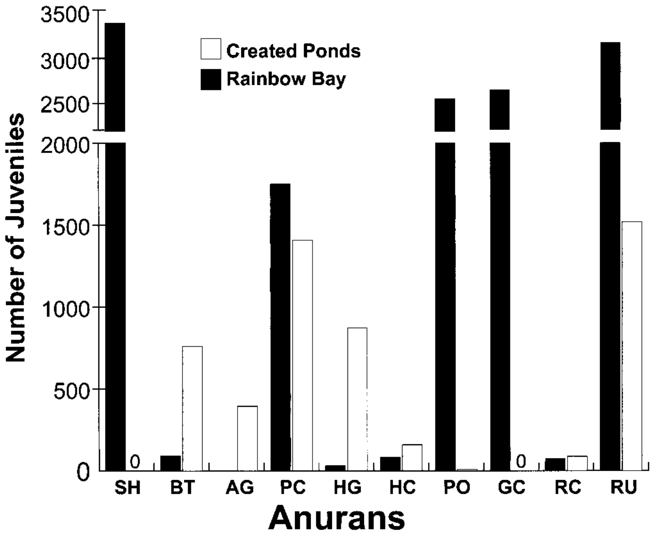


Figure 4. Total numbers of juvenile frogs and toads captured that metamorphosed and emigrated from Rainbow Bay (black bars; data from Semlitsch et al. 1996 and unpublished) and the three created ponds (shaded bars) from 1985 to 1991. SH = *Scaphiopus holbrooki,* BT = *Bufo terrestris,* AG = *Acris gryllus,* PC = *Pseudacris crucifer,* HG = *Hyla gratiosa,* HC = *H. chrysoscelis,* PO = *P. ornata,* GC = *Gastrophyrne carolinensis,* RC = *Rana catesbeiana,* RU = *R. utricularia.*

ysis. None of the *A. opacum, A. tigrinum,* or *E. quadridigitata* captured at the created ponds had been marked previously at Sun Bay.

Juvenile salamanders were not produced at the created ponds until 1986, the first year of notable colonization by adults (Figure 5). Only two species produced juveniles; hundreds of *A. talpoideum* and *N. viridescens* metamorphosed and emigrated from the created ponds from 1986 to 1991 (Figure 5). The relative numbers of juvenile *A. talpoideum* and *N. viridescens* produced at the created ponds from 1986–1991 varied significantly among years ($\chi^2$ = 294, df = 5, $P <$ 0.001) and among ponds (1985–1988: $\chi^2$ = 514, df = 2, $P < 0.001$, 1989–1991: $\chi^2$ = 1035, df = 2, $P <$ 0.001). Each of these species became established primarily at two of the three remaining created ponds (Figure 5). Only a total of ten *A. talpoideum* metamorphosed and emigrated from Pond A, and only two *N. viridescens* from Pond B. Pond D is the only one at which both species produced cohorts during the last four years of the study. There were analogous differences among the created ponds in the relative abundances of breeding adult salamanders captured during the last three years of the study ($\chi^2$ = 52, df = 2, $P$ $<$ 0.001; Table 3).

By the end of the study, most of the adult *A. talpoideum* migrating to the created ponds to breed had been born at them. Out of a sample of 228 *A. talpoideum* marked at metamorphosis that subsequently returned, 95% returned to their home created pond and 5% returned to a different created pond. All but one of the movements among ponds were between B and D.

The community structure of juvenile salamanders produced at the created ponds, pooled over ponds, was significantly different from that at Rainbow Bay during the same years (Figure 6; 1985–1988: $\chi^2$ = 1915, df = 4, $P < 0.001$, 1989–1991: $\chi^2$ = 563, df = 3, $P$ $<$ 0.001). Three species produced juveniles at Rainbow Bay but not at the created ponds: *A. opacum, A. tigrinum,* and *E. quadridigitata* (Figure 6). Small num-

Table 4. Snout-vent length (mm) at metamorphosis for juveniles at Rainbow Bay, 1979–1994 (data from Caldwell 1987, Semlitsch 1987, Semlitsch et al. 1988, and unpublished), and at the created ponds, 1985–1991, for species that produced juveniles at both locations, 1985–1991. Number of cohorts for which data were available, range of cohort means, and grand mean for each location. Juveniles from different created ponds were considered members of different cohorts. Data for *A. talpoideum* are for juveniles that emigrated from ponds 20 May–31 December (see text).

| | Rainbow Bay | | | Created Ponds | | |
|---|---|---|---|---|---|---|
| | *N* | Range | Mean | *N* | Range | Mean |
| Salamanders | | | | | | |
| *A. talpoideum* | 10 | 37.0–49.8 | 45.4 | 13 | 46.0–54.6 | 51.0 |
| *N. viridescens* | 7 | 18.3–25.5 | 21.7 | 13 | 23.3–29.0 | 26.4 |
| Frogs and toads | | | | | | |
| *A. gryllus* | 1 | | 15.8 | 11 | 14.7–18.5 | 16.6 |
| *B. terrestris* | 2 | 12.9–20.6 | 16.8 | 10 | 9.3–24.0 | 13.5 |
| *H. chrysoscelis* | 2 | 15.9–18.3 | 17.1 | 10 | 11.0–17.8 | 15.8 |
| *H. gratiosa* | 4 | 24.7–30.9 | 27.5 | 21 | 24.1–31.0 | 27.5 |
| *P. crucifer* | 11 | 13.0–17.0 | 14.4 | 15 | 10.5–15.5 | 12.9 |
| *P. ornata* | 12 | 19.6–25.7 | 22.2 | 1 | | 16.8 |
| *R. clamitans* | 7 | 28.2–36.0 | 32.6 | 1 | | 30.9 |
| *R. utricularia* | 10 | 25.8–40.9 | 34.8 | 15 | 26.4–41.7 | 33.3 |

Table 5. Analysis of variance of snout-vent length at metamorphosis (log-transformed) for juveniles at the created ponds and Rainbow Bay (Rainbow Bay data from Caldwell 1987, Semlitsch 1987, Semlitsch et al. 1988 and unpublished). Contrasts compare the created ponds as a group to Rainbow Bay, weighting each created ponds by the number of cohorts produced at that pond. The analysis for *A. talpoideum* was confined to juveniles that emigrated from ponds 20 May–31 Dec. (see text).

| Source | df | Type III MS | Test df | Test MS | *F* | *P* |
|---|---|---|---|---|---|---|
| Salamanders | | | | | | |
| *A. talpoideum* | | | | | | |
| Contrast Created vs Rainbow | 1 | 1.5564 | 19.4 | 0.3099 | 5.0217 | 0.0369 |
| Pond | 3 | 0.5653 | 19.4 | 0.3099 | 1.8238 | 0.1764 |
| Pond × Year | 19 | 4.2483 | | | | |
| Individual | 5586 | 0.0032 | | | | |
| *N. viridescens* | | | | | | |
| Contrast Created vs Rainbow | 1 | 2.0754 | 18.6 | 0.1239 | 16.7577 | 0.0006 |
| Pond | 3 | 1.5711 | 18.6 | 0.1239 | 12.6847 | 0.0001 |
| Pond × Year | 16 | 0.8916 | | | | |
| Individual | 1843 | 0.0104 | | | | |
| Frogs and toads | | | | | | |
| *A. gryllus* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.0050 | 29.0 | 0.0114 | 0.4392 | 0.5127 |
| Pond | 3 | 0.0078 | 29.0 | 0.0114 | 0.6903 | 0.5654 |
| Pond × Year | 8 | 0.0286 | | | | |
| Individual | 216 | 0.0069 | | | | |
| *B. terrestris* | | | | | | |
| Contrast Created vs Rainbow | 1 | 1.1929 | 9.0 | 0.6917 | 1.7247 | 0.2216 |
| Pond | 3 | 2.8316 | 9.0 | 0.6917 | 4.0938 | 0.0436 |
| Pond × Year | 8 | 1.3087 | | | | |
| Individual | 609 | 0.0773 | | | | |
| *H. chrysoscelis* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.058 | 8.2 | 0.0431 | 1.3463 | 0.2787 |
| Pond | 3 | 0.0301 | 8.2 | 0.0431 | 0.6995 | 0.5777 |
| Pond × Year | 8 | 0.0479 | | | | |
| Individual | 162 | 0.0041 | | | | |
| *H. gratiosa* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.0001 | 22.3 | 0.0631 | 0.0012 | 0.9727 |
| Pond | 3 | 0.0935 | 22.3 | 0.0631 | 1.4824 | 0.2464 |
| Pond × Year | 21 | 0.1419 | | | | |
| Individual | 963 | 0.0033 | | | | |
| *P. crucifer* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.3363 | 32.6 | 0.0244 | 13.7904 | 0.0008 |
| Pond | 3 | 0.1793 | 32.6 | 0.0244 | 7.3504 | 0.0007 |
| Pond × Year | 22 | 0.3523 | | | | |
| Individual | 1626 | 0.0046 | | | | |
| *P. ornata* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.1515 | 13.3 | 0.0313 | 4.8379 | 0.0461 |
| Pond | 1 | 0.1515 | 13.3 | 0.0313 | 4.8379 | 0.0461 |
| Pond × Year | 11 | 2.0607 | | | | |
| Individual | 2106 | 0.0029 | | | | |
| *R. clamitans* | | | | | | |
| Contrast Created vs Rainbow | 1 | 0.0315 | 6.2 | 0.1667 | 0.1887 | 0.6786 |
| Pond | 1 | 0.0315 | 6.2 | 0.1667 | 0.1887 | 0.6786 |
| Pond × Year | 6 | 0.3724 | | | | |
| Individual | 390 | 0.0058 | | | | |
| *R. utricularia* | | | | | | |
| Contrast Created vs. Rainbow | 1 | 0.0899 | 36.9 | 0.0910 | 0.9885 | 0.3266 |
| Pond | 3 | 0.1624 | 36.9 | 0.0910 | 1.7854 | 0.1669 |
| Pond × Year | 21 | 0.7147 | | | | |
| Individual | 2046 | 0.0248 | | | | |

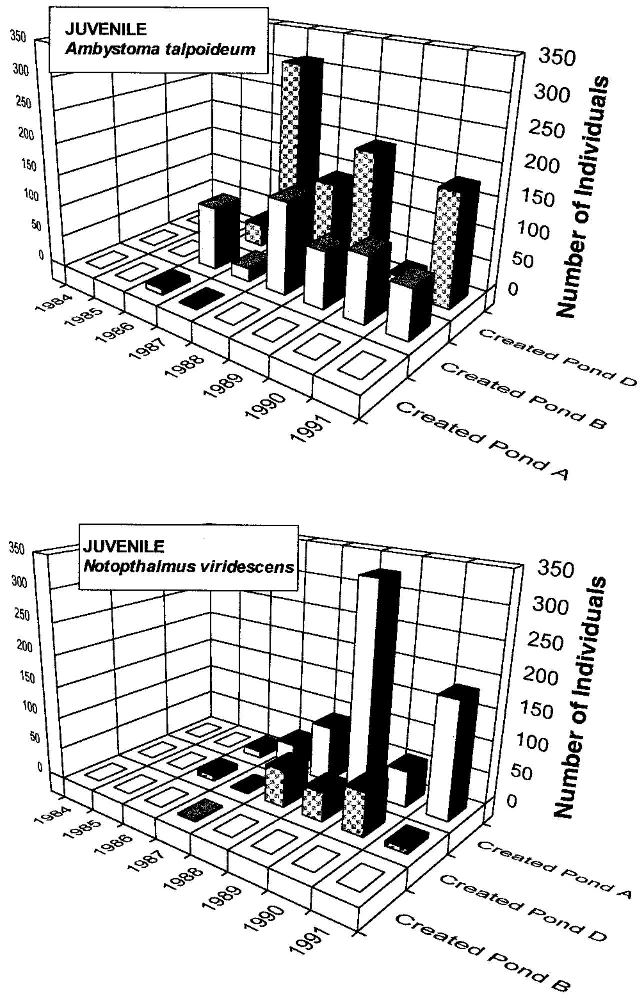


Figure 5. Total numbers of juvenile salamanders captured that metamorphosed and emigrated from the created ponds from 1984 to 1991. The order of the ponds on the axes differs for the two species to maximize the visibility of the bars, but the same bar pattern is consistently associated with each pond. Totals for *A. talpoideum* (except 1991) include individuals that emigrated from 1 January to 19 May of the next calendar year, which were juveniles that overwintered and paedomorphs that metamorphosed.

bers of juvenile *A. opacum, A. tigrinum,* and *N. viridescens* were produced at the hydrologically altered Sun Bay from 1979–1982 (Table 1). The mean size at metamorphosis of *A. talpoideum* and *N. viridescens* was ~5 mm larger at the created ponds than at Rainbow Bay (Tables 4 and 5).

Paedomorphic *A. talpoideum* and *N. viridescens* were captured in minnow traps at the created ponds during 1987 (Table 6). Some of these *A. talpoideum* metamorphosed and emigrated from the created ponds during March and April of that year, but none of the paedomorphic *N. viridescens* did so (Table 6). Some *N. viridescens* captured with nets in April 1991 were adults whose gills were reduced to small nubs, indicating that some paedomorphic individuals metamorphosed but remained in the ponds.

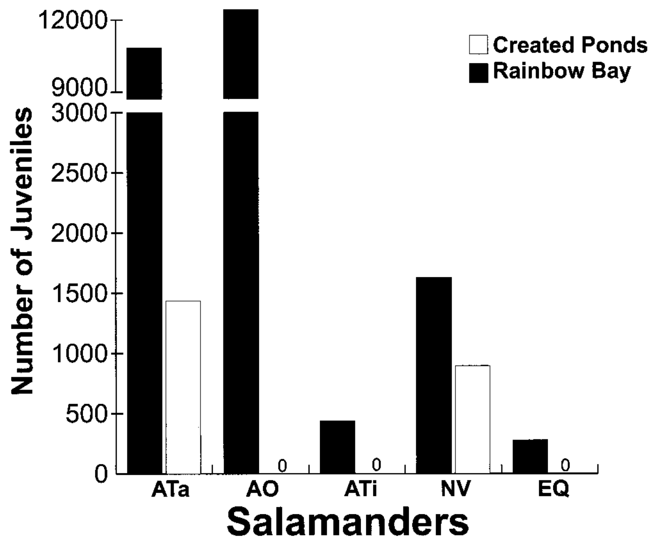


Figure 6. Total numbers of juvenile salamanders captured that metamorphosed and emigrated from Rainbow Bay (black bars; data from Semlitsch et al. 1996) and the three created ponds (shaded bars) from 1985 to 1991. Totals for *Ambystoma talpoideum* include paedomorphs that later metamorphosed. Ata = *A. talpoideum,* AO = *A. opacum,* Ati = *A. tigrinum,* NV = *Notophthalmus viridescens,* EQ = *Eurycea quadridigitata.*

*Ambystoma talpoideum* metamorphosed and emigrated from the created ponds throughout the year, although primarily in the spring and autumn and with a lull in mid-May. Sex and maturity could not be judged externally in most individuals that metamorphosed. A sample of 23 newly-metamorphosed individuals collected in March and April of 1987 and 1991 was dis-

Table 6. Number of gilled *N. viridescens* and *A. talpoideum* captured in aquatic funnel traps at the created ponds from 10 January to 15 April 1987 and number of these that metamorphosed and were recaptured emigrating from the ponds during March and April 1987. Female paedomorphs and overwintering larvae cannot always be differentiated without dissection, and were therefore pooled.

| Pond | Male Paedomorphs | Larvae/ Female Paedomorphs | Male Recaptures | Juvenile/ Female Recaptures |
|---|---|---|---|---|
| | | *N. viridescens* | | |
| A | 7 | 11 | 0 | 0 |
| B | 0 | 0 | 0 | 0 |
| D | 8 | 14 | 0 | 0 |
| | | *A. talpoideum* | | |
| A | 0 | 1 | 0 | 0 |
| B | 12 | 15 | 4 | 3 |
| D | 5 | 7 | 4 | 3 |

sected and found to consist of a mixture of juveniles and of former paedomorphs of both sexes. Thus, we classified emigrating metamorphs from 1 January to 19 May as a mix of overwintering juveniles and former paedomorphs, and these were added to the juveniles from the previous calendar year (Figure 5). Individuals that emigrated from the created ponds from 20 May–31 December were judged to be primarily young-of-the-year.

## DISCUSSION

A maxim of compensatory wetland mitigation is ''no-net-loss.'' To attain this goal, replacement wetlands should have both the structural and functional features of the destroyed wetlands (Zedler 1996). Created wetlands that differ significantly from the lost wetlands in critical characteristics such as hydrologic regimes or species composition are not valid substitutes. Ideally, replacement wetland ecosystems should be maintained in the long-term by self-sustaining natural processes and species interactions that are similar to those of the original wetland. Our study addressed the question of whether one wetland function (i. e., providing habitat for a selected group of animals) will be maintained by construction of ponds in the vicinity. Empirical evidence on all aspects of wetland ecosystems must ultimately be evaluated to determine whether wetland creation can fulfill the expectations of ''no-net-loss'' and elucidate principles for the design and location of created wetlands that accomplish this goal.

In our study, the created ponds provided some compensatory mitigation for the loss of Sun Bay. A number of amphibian species colonized the created ponds during the study, including marked individuals from Sun Bay. The created ponds afforded many of these species with suitable habitat for breeding and larval development. The community structure of reproductive adults that became established at the created ponds differed from that found at Sun Bay prior to construction, however. In addition, the community structure of juvenile amphibians produced at the ponds differed from that produced at the undisturbed reference wetland during the study period. These findings suggest that the created ponds did not strictly provide mitigation ''in kind.'' Community structure also varied significantly among the created ponds, providing further evidence that it is extremely difficult to duplicate any particular natural community (Kusler and Kentula 1990, Zedler 1996), as ''alternative stable states'' are commonly observed in ecological communities (Drake 1990).

### Comparison of Natural and Created Wetlands

Factors that may have contributed to the differences in amphibian communities between the created ponds and the natural wetlands include availability of colonists and differences in the amounts and types of aquatic and terrestrial habitat. The created ponds became permanent ponds, whereas Sun Bay and Rainbow Bay were both temporary ponds. Permanent ponds and temporary ponds support different amphibian communities, although some species may use both types of ponds (Heyer et al. 1975, Collins and Wilbur 1979, Wilbur 1980, Wilbur 1987, Werner and McPeek 1994, Skelly 1995, Smith and Van Buskirk 1995, Wellborn et al. 1996). The changes in community structure along a gradient of pond permanence are mediated by changes in the nature and intensity of predation and competition, the seasonal availability of the pond, and the length of time available to complete larval development. The relative success of species at different points along this gradient depends on trade-offs in morphological, physiological, and behavioral traits, as well as phenotypic plasticity in these traits (Heyer et al. 1975, Wilbur 1987, Werner and McPeek 1994, Skelly 1995, Smith and Van Buskirk 1995, Wellborn et al. 1996).

Among the species we studied, *S. holbrookii* (Bragg 1945, Richmond 1947, Pearson 1955), *P. ornata* (Caldwell 1987) and *G. carolinensis* (Pechmann et al. 1989, Semlitsch et al. 1996, personal observations; but see Brandt 1936, Anderson 1954) breed in newly-filled temporary ponds. *Ambystoma opacum* requires a dry pond bed or margin for oviposition, followed by inundation with water for the eggs to hatch (Noble and Brady 1933, Petranka 1990). Few adults and few or no juveniles of these species were captured at the created ponds compared to the numbers expected from abundances at Sun Bay and Rainbow Bay.

Conversely, temporary ponds such as Rainbow Bay and Sun Bay, which often dry in the spring or summer, are not available to species that breed in these seasons (e. g., *A. gryllus*, *B. terrestris*, and *H. gratiosa*). More adults and juveniles of these species were captured at the created ponds than expected based on their relative abundances at Sun Bay and Rainbow Bay. All three species produced more juveniles at Pond D, the only pond that was never pumped dry, than at any of the other created ponds.

Other species breed in both temporary and permanent ponds. These include *P. crucifer* (Collins and Wilbur 1979, Gibbons and Semlitsch 1991), *R. utricularia* (Caldwell 1986, Gibbons and Semlitsch 1991), *N. viridescens* (Hurlbert 1969, Gibbons and Semlitsch 1991), and *A. talpoideum* (Semlitsch 1988), although *A. talpoideum* and *R. utricularia* produce few juveniles in permanent ponds that contain fish. These four species were major components of the amphibian community at Rainbow Bay, Sun Bay, and the created ponds despite differences in hydroperiod, although most of the frogs were produced in created ponds that had dried the previous year.

The importance of replicating the hydrologic cycle of the target natural wetlands when constructing wetlands for mitigation is well known (Erwin 1990, Kusler and Kentula 1990, Willard and Hiller 1990, Zedler and Weller 1990). Unfortunately, hydrology is often given insufficient attention in wetland design and construction (Kentula et al. 1993). Wetlands are especially difficult to create where much of the soil is very porous, as at our sites. Replicating the hydrologic cycle of wetlands such as Carolina bays would require replicating the surface and subsurface sediments and geologic structure of the wetland as well as of its surrounding watershed. This is obviously not a trivial task. Another approach is to construct a wetland having control structures with which the water level could be adjusted as necessary. The problem with this strategy is that it requires active management *in perpetuity*. There is general agreement among scientists that no wetland can be replicated exactly (Kusler 1986, Kusler and Kentula 1990, Zedler and Weller 1990).

The created ponds also differed from Sun Bay and Rainbow Bay in other habitat characteristics that may affect amphibian community structure. The created ponds were smaller. Both colonization rates and species persistence can be influenced by habitat area (MacArthur and Wilson 1967, Holt 1993). We collected no data on vegetation at the created ponds but did observe that the diversity and abundance of aquatic macrophytes were much less than at the natural wetlands. The plastic liners, small size, and newness of the created ponds all may have limited their aquatic vegetation.

Differences in surrounding terrestrial habitats may also have contributed to the differences in amphibian communities, as most amphibians observed at these wetlands spend the majority of their lives on land (Wilbur 1980, Pechmann 1995). Forested habitats extended at least several hundred meters in all directions from the natural wetlands but only some directions from the created ponds, which were located near a construction zone where most trees had been replaced with lawns, old fields, buildings, and parking lots. The created ponds were also near paved roads, which migrating amphibians may avoid (Madison and Farrand 1998). These roads probably caused minimal direct mortality of amphibians because there was little traffic on them at night when most migration occurs (Semlitsch and Pechmann 1985, Pechmann and Semlitsch 1986).

Availability of colonists may also have had an influence. Only two salamander species became established at the created ponds, whereas adults of three additional species (*A. opacum, A. tigrinum,* and *E. quadridigitata*) were captured at Sun Bay and also produced juveniles at Rainbow Bay. The salamanders that failed to become established at the created ponds had substantially smaller breeding population sizes at Sun Bay than the two that did become established, *A. talpoideum* and *N. viridescens.* Our data suggest that *A. opacum, A. tigrinum,* and *E. quadridigitata* failed to become established at the created ponds in part because the source populations of these species were so small that an insufficient number of surviving individuals found and used the created ponds. If wetland creation is being undertaken primarily for the benefit of rare or endangered species, our results indicate that there is no guarantee that they would become established in the new habitat on their own. Consequently, in these situations, we recommend stocking the species of concern in the constructed wetland rather than relying on natural colonization (Erwin 1990).

## Temporal Variation

Breeding population sizes and juvenile recruitment varied substantially among years at the created ponds (this study) and at the undisturbed reference wetland, Rainbow Bay (Pechmann et al. 1991, Semlitsch et al. 1996). Extensive temporal fluctuations have also been observed in other amphibian populations and communities (e.g., Bannikov 1948, Bragg 1960, Berven and Grudzien 1990). The substantial variability in population sizes and community structure that can occur in natural as well as constructed wetlands presents a challenge for evaluating the success of wetlands constructed as mitigation (Zedler 1996). In our opinion, a minimum of several years of census data from both the constructed wetland and reference wetlands are necessary for meaningful comparisons of their amphibian faunas. Even the eight years of monitoring in this study may have been inadequate. Zedler (1993) suggested that constructed marshes should be monitored for at least 20 years, or until standards had been met for five consecutive, typical years. She based this conclusion on spatial and temporal variation and the ''lag effects of 'immature' ecosystems.'' Confer and Niering (1992) suggested monitoring constructed wetlands for a minimum of a decade or more, and D'Avanzo (1990) suggested 10–20 years. Although it is tempting to monitor easily-measured habitat variables such as hydroperiod as proxy indicators of the amphibian community, our results suggest that apparently suitable habitat is not always successfully colonized by all expected species.

### Variation Among Created Ponds

The created ponds were not exact replicates of each other. Although each pond was constructed in a similar manner, we artificially dried two of the three ponds in 1987. This cannot explain all of the differences among the ponds, however, as their amphibian communities differed before as well as after this manipulation. The created ponds also differed in the terrestrial habitats that surrounded them, which could contribute to differences in amphibian community structure as discussed above.

The created ponds also differed in their locations relative to Sun Bay and to other sources of colonists. Historical effects of initial colonization may have been responsible for some of the differences among the ponds (Gilpin 1987, Drake 1990). A few more *N. viridescens* than *A. talpoideum* bred in Pond A initially, while the reverse happened in Pond B. *Notophthalmus viridescens* was the only salamander breeding at Pond A at the end of the study, whereas *A. talpoideum* was the only salamander breeding at Pond B. Pond D had the largest initial number of colonists of both salamander species, and both became established there. In addition, Pond D developed a larger population of *A. gryllus* than the other ponds. An old farm pond located closest to created Pond D may have served as a source of colonists of *A. gryllus.*

### Site Fidelity and Wetland Filling

Many amphibians, including *A. talpoideum* and *N. viridescens,* are usually philopatric to their natal ponds (Semlitsch 1981, Semlitsch et al. 1988, D. E. Gill *personal communication*). Some individuals of these two species and others initially continued breeding migrations to Sun Bay even after it had been drained and filled with soil. This phenomenon has been noted previously at other filled breeding sites (Anderson 1954 for *G. carolinensis,* Heusser 1960, McMillan 1963. Shoop [personal observation, cited in Shoop and Doty 1972] for *A. talpoideum,* Uzzell [personal communication, cited in Shoop and Doty 1972] and Frazer 1973). Some amphibians previously marked at Sun Bay, primarily *A. talpoideum* and *N. viridescens,* responded to the elimination of Sun Bay and other disturbances from construction by eventually migrating to the created ponds rather than returning to Sun Bay. *Ambystoma talpoideum* populations philopatric to the individual created ponds have now been established from the Sun Bay populations.

### Individual Traits and Created Pond Quality

The average size at metamorphosis of *A. talpoideum* and *N. viridescens* was 5–6 mm larger at the created ponds than at Rainbow Bay, suggesting that the created ponds were good habitat. Size at metamorphosis can affect fitness-related traits in adults (Berven and Gill 1983, Smith 1987, Berven 1988, Semlitsch et al. 1988, Berven and Grudzien 1990, Pechmann 1994, Scott 1994). In contrast, mean size at metamorphosis of two chorus frog species was 2–5 mm smaller at the created ponds than at the reference wetland, suggesting that frogs produced at the created ponds might have lower fitness than those produced at Rainbow Bay. Small size at metamorphosis may result from larval crowding, low quantity or quality of food, reduced foraging in the presence of predators, and other ecological factors (Wilbur 1980, Alford 1999).

Paedomorphic *A. talpoideum* and *N. viridescens* were found at the created ponds. Paedomorphosis is thought to occur when growth rates are high and mortality risks low in the aquatic habitat relative to the terrestrial habitat (Wilbur and Collins 1973, Werner 1988). Thus, the expression of paedomorphosis can be interpreted as additional evidence that the created ponds provided favorable aquatic habitat for these two species (but see Whiteman 1994).

### Other Constructed Wetlands: Conclusion

Constructed wetlands have mixed success at duplicating the hydrologic conditions, soil, vegetation, and fauna of natural wetlands (D'Avanzo 1990, Confer and Niering 1992). Constructed intertidal marshes did not provide adequate habitat for the endangered light-footed clapper rail because cordgrass plants were shorter in these marshes than in the natural marshes (Zedler 1993). Nonetheless, some wetland creation projects have been judged to be successes. Pauley and Barron (1995) found that all the amphibian species that bred in a natural wetland were successfully breeding in a nearby, newly-created wetland within two years of its completion, as were two additional species. The old wetland was left intact in this case. Erwin et al. (1994) observed that vegetation, aquatic macroinvertebrates, and fish in a three-year-old constructed freshwater marsh were ''not unlike those found in nearby undisturbed wetlands.'' Macrophyte productivity, benthic infauna communities, organic carbon, and nutrient accumulation in 20–25 year-old constructed salt marshes were similar to those in natural marshes, although soil nutrient reservoirs were smaller (Craft et al. 1999). A goal of future studies should be to elucidate general conditions under which wetland creation is likely to be successful and, consequently, an acceptable policy option.

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