Kirkwood-Cohansey Project

The Potential Impact of Simulated Groundwater Withdrawals on the Oviposition, Larval Development, and Metamorphosis of Pond-breeding Frogs

State of New Jersey Pinelands Commission

Cover: A calling male Pine Barrens tree frog (*Hyla andersonii*). Photograph taken by John F. Bunnell.

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The Pinelands Commission

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Abstract

Wetland hydroperiod is a key factor for the reproductive success of pond-breeding amphibians. Groundwater withdrawals may cause intermittent ponds to dry prematurely, potentially affecting amphibian development. In three intermittent ponds, we monitored hydrology and tracked oviposition, larval development, and metamorphosis for three frog species that represented a range of breeding phenologies. The three species were the southern leopard frog (*Lithobates sphenocephalus*), spring peeper (*Pseudacris crucifer*), and Pine Barrens treefrog (*Hyla andersonii*). We simulated groundwater withdrawals by subtracting from 5 to 50 cm (in 5-cm increments) from the measured water-depth values at the ponds over a short-term (two-year) period and a long-term (ten-year) period to estimate the potential impact of hydroperiod alterations on frog development. Short-term simulations indicated that 5-cm and 10-cm water-depth reductions would have resulted in little or no impact to hydroperiod or larval development and metamorphosis of any of the species. Noticeable impacts were estimated to occur for reductions ≥15 cm. Long-term simulations showed that impacts to the appearance of the first pre-metamorphs and metamorphs would have occurred at reductions ≥10 cm and impacts to initial egg deposition would have occurred at reductions ≥20 cm. For all simulations, successively greater reductions would have caused increasing impacts that varied by species and pond, with the 50-cm reductions shortening hydroperiods enough to practically eliminate the possibility of larval development and metamorphosis for all three species. Compared to the spring peeper and southern leopard frog, the estimated impacts of the simulations on the various life stages were the greatest for the Pine Barrens treefrog.

Introduction

Wetland hydroperiod, defined here as the length of time when standing water is present, is a key factor that directly shapes the community composition and reproductive success of pond-breeding amphibians. The timing and duration of wetland flooding must coincide with amphibian-breeding biology for successful oviposition, hatching, larval development, and metamorphosis to occur (Paton and Crouch 2002). Long-term studies in natural ponds (Pechmann et al. 1989; Semlitsch et al. 1996) and experimental manipulations in artificial ponds (Rowe and Dunson 1995, Ryan 2007, Ryan and Winne 2001) have shown that early pond drying can result in fewer amphibian species metamorphosing, reduced metamorphic success for individual species, or complete larval mortality.

Shallow depression wetlands are a common feature throughout the New Jersey Pinelands, which is a 379,827-ha coastal plain region located in the southern portion of the state (Figure 1). Often embedded in a forested matrix, these coastal plain wetlands typically support open-water with herbaceous and shrub communities and sometimes dry one or two times per year (Zampella and Laidig 2003). Although salamanders and fish are largely absent, up to nine species of anurans may utilize these intermittent wetlands as breeding ponds (Bunnell and Zampella 1999, Zampella and Bunnell 2000).

Seasonal water-depth fluctuations in Pinelands ponds reflect those for pitch pine forest water tables, suggesting that pond-water levels mirror regional groundwater patterns (Zampella et al. 2001a, Zampella and Laidig 2003). Groundwater-level changes due to human-induced hydrologic alterations, such as water withdrawals to serve development and agriculture, may cause intermittent ponds to dry prematurely, potentially affecting the larval development and metamorphosis of pond-breeding anurans. Both the tight connection between groundwater and pond-water levels (Lide et al. 1995, McHorney and Neill 2007) and reductions in pond-water levels from nearby groundwater pumping (McHorney and Neill 2007) have been shown for coastal plain ponds in other regions.

The goal of our study was to assess the potential effects of groundwater withdrawals on the larval development and metamorphosis of pond-breeding anurans. We monitored hydrology and tracked oviposition, larval development, and metamorphosis for three frog species in three intermittent Pinelands ponds. We applied simulated water-depth reductions to the measured hydroperiods of the three ponds over a short-term (two-year) period and a long-term (ten-year) period to estimate the potential impact of hydroperiod alterations on the oviposition, larval development, and metamorphosis of each species and to determine the relative vulnerability of each species to hydrologic stress. This study was part of the Kirkwood-Cohansey Project (Pinelands Commission 2003), a larger research effort designed to evaluate

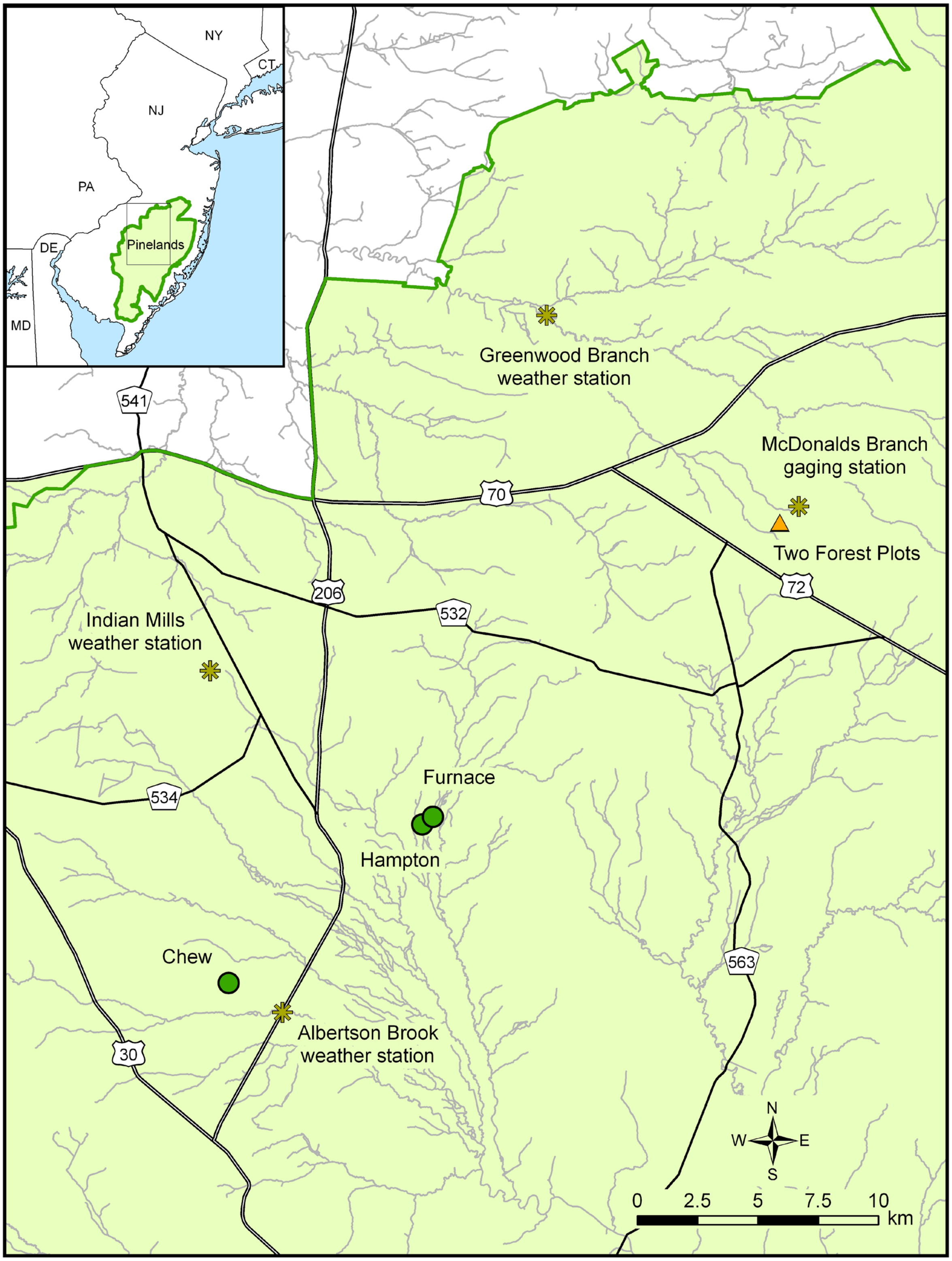

Figure 1. Location of three intermittent ponds (dots), three weather stations and one stream-gaging station (stars), and two forest plots (triangle) in the New Jersey Pinelands.

the potential effects of groundwater withdrawals on aquatic and wetland communities associated with the Kirkwood-Cohansey aquifer, the primary water-table aquifer in the Pinelands (Rhodehamel 1979a, 1979b, Zapecza 1989).

Methods

Study Ponds

We chose three excavated ponds (Chew, Hampton, and Furnace) for the study (Figure 2). All three ponds are associated with the Kirkwood-Cohansey aquifer system and are located on state land in the northwestern portion of the Mullica River watershed (Figure 1). The three ponds were part of earlier studies of anuran composition (Bunnell and Zampella 1999) and functional equivalency (Zampella and Laidig 2003) of ten natural and four excavated ponds.

We selected Chew, Hampton, and Furnace from the group of 14 ponds because these three ponds supported similar anuran assemblages and displayed hydrologic regimes comparable to natural Pinelands ponds, but lacked the thick shrub border, dense *Sphagnum*, and extremely dark water (Bunnell and Zampella 1999, Zampella and Laidig 2003) that makes sampling anuran larvae difficult in natural ponds of the region. Based on bathymetric maps and monthly water-depth measurements for April - September 1996, April - October 1997, and March - October 1998, mean pond depth was 63 cm for Chew, 51 cm for Hampton, and 65 cm for Furnace (Laidig et al. 2001, Zampella and Laidig 2003). Chew was the largest of the three ponds (2,148 m^2) and was embedded in a pine-scrub oak upland matrix, whereas Hampton (420 m^2) and Furnace (153 m^2) were smaller and were located in dry to wet pitch pine lowlands (Laidig et al. 2001, Zampella and Laidig 2003). Chew was located about 10 km from Hampton (Figure 1). Furnace and Hampton were 515 m apart. All three ponds were acidic (median pH of Hampton = 4.69, Furnace = 4.49, and Chew = 4.39, Bunnell and Zampella 1999).

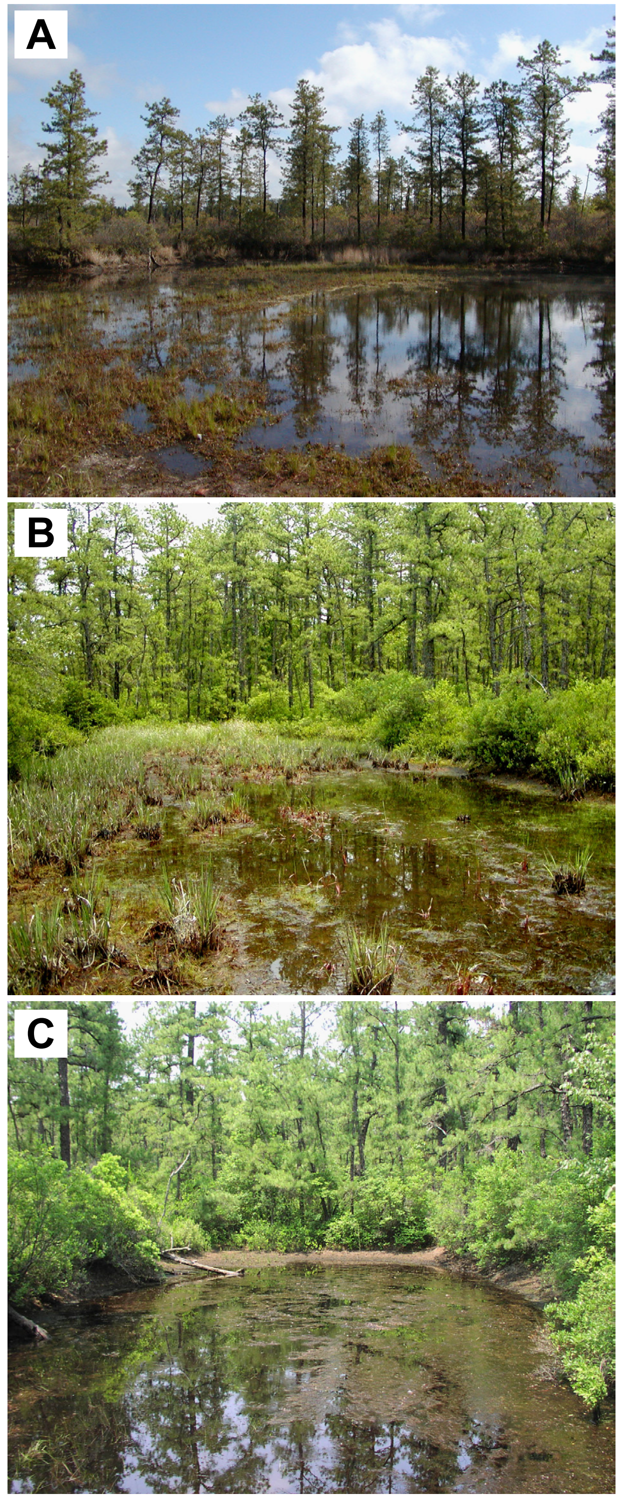

Figure 2. Three intermittent Pinelands ponds selected for monitoring frog development. Chew (A), Hampton (B), and Furnace (C).

Anuran Sampling

We sampled breeding adult anurans at the three ponds from 1996 to 2006 by completing monthly nighttime-vocalization surveys from March through June (N = 4) of each year. All anurans calling in a five-minute period were identified. Vocalization surveys were used to document which species were attempting to breed at the ponds each year (Figure 3A).

In addition to vocalization surveys, we sampled anuran eggs, larvae, and metamorphs in the three ponds in 2005 and 2006. We sampled larvae using 1-m sweeps with a 38 × 38-cm dip net (4.8-mm mesh size). During each sampling event, we completed 30 dip-net sweeps in Hampton and Furnace and, because of its larger size, 70 dip-net sweeps in Chew. Although we reduced the number of dip-net sweeps per visit when a drop in water depth decreased the volume of water in the pond, the mean (± 1 SD) number of sweeps per visit for the 2005 and 2006 seasons was 30 ± 0.0 for Hampton, 29 ± 4 for Furnace, and 63 ± 17 for Chew. In 2005, sampling frequency was biweekly (every other week) from April 14 to May 31 and weekly from June 1 to August 31 (N = 17). In 2006, sampling frequency was weekly from March 31 to October 13, 2006 (N = 28). Larvae in advanced stages of metamorphosis that were encountered near the edge of water were also captured. The presence of anuran eggs of each species was recorded during larval-sampling events.

Anuran larvae were identified to species using Altig (1970) and staged according to Gosner (1960). We refer to developmental stages 25 - 38 as larvae, stages 39 - 41 as pre-metamorphs, and stages 42 - 46 as metamorphs (Figure 3B - D). A 10x hand lens was used to examine limb development to determine larval stage in the field. All larvae were returned to the pond. Taxonomic nomenclature follows Crother (2008).

Focal Species

Nine anuran species have been heard calling from Chew, Hampton, and Furnace (Table 1). We focused on three species, the spring peeper (*Pseudacris crucifer*), Pine Barrens treefrog (*Hyla andersonii*), and southern leopard frog (*Lithobates sphenocephalus*), because they commonly breed in Pinelands ponds (Bunnell and Zampella 1999, Zampella and Bunnell 2000) and each exhibits a different breeding phenology (Figure 4). The southern leopard frog and spring peeper are among the first species to begin breeding each year, but the southern leopard frog continues to breed well after the spring peeper stops. In contrast, the Pine Barrens treefrog, which is a species of conservation concern in New Jersey, South Carolina, Florida, and Alabama, is a relatively late-breeding frog. The varied breeding phenology of these three species allowed us to determine the relative vulnerability of each to potential changes in pond hydroperiod.

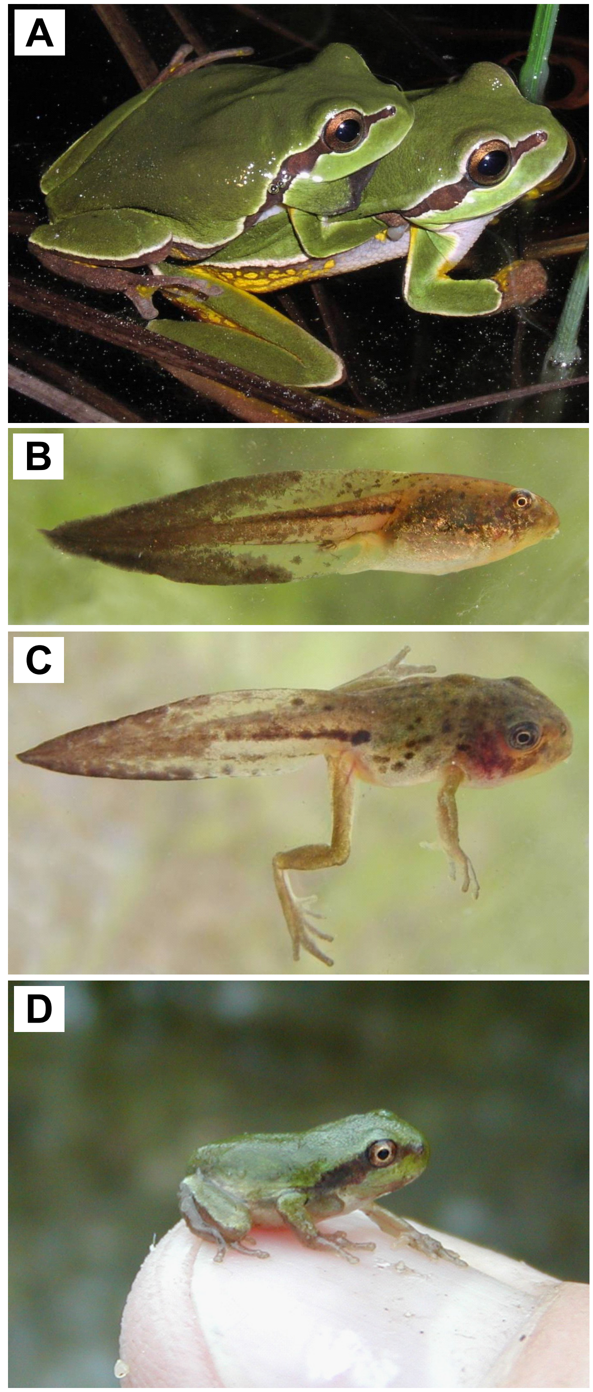

Figure 3. Pine Barrens treefrogs in amplexus preparing to deposit eggs (A), treefrog larva (B), treefrog pre-metamorph (C), and treefrog metamorph (D).

Pond Hydrology

From 1996 to 2006, we measured water depth

Table 1. The percentage of the total number of years in which each of nine anuran species was heard vocalizing at three Pinelands ponds. The three focal species are indicated with asterisks. Letters indicate the year in which larvae were present for that species during 2005 (a) and 2006 (b). Mean hydroperiod for both survey periods is based on monthly water-depth measurements. The year 2000 was excluded due to incomplete water-depth data.

	2005 to 2006 Survey Period			1996 to 2004 Survey Period		
Species	Chew	Hampton	Furnace	Chew	Hampton	Furnace
Pine Barrens treefrog (*Hyla andersonii*) *	100 ab	100 ab	100 ab	100	100	89
Spring peeper (*Pseudacris c. crucifer*) *	100 ab	100 ab	100 ab	100	89	100
Southern leopard frog (*Lithobates utricularius*) *	100 ab	100 ab	100 ab	100	100	89
Green frog (*Lithobates clamitans*)	100 ab	50	50 ab	78	78	33
Carpenter frog (*Lithobates virgatipes*)	-	100 ab	50 b	-	67	22
New Jersey chorus frog (*Pseudacris triseriata kalmi*)	100	-	-	100	-	-
Wood frog (*Lithobates sylvatica*)	100	-	50	33	11	11
Northern gray treefrog (*Hyla versicolor*)	50	-	-	44	11	11
Fowler's toad (*Anaxyrus fowleri*)	-	-	-	22	22	11
Mean (±1 SD) hydroperiod (d)	308 ± 58	290 ± 76	290 ± 76	261 ± 74	253 ± 78	270 ± 83

monthly at the three ponds with a staff gage located in the deepest part of each pond. In addition to these monthly readings, we measured water depth at each pond weekly or biweekly during each larval-sampling event in 2005 and 2006. Using the weekly/biweekly and monthly measurements, we determined the hydroperiod of each pond as the number of days when standing water was present from January 1 to the date of first drying.

To determine whether water-depth fluctuations were similar among the three ponds, we used Spearman rank correlation to relate water depth among ponds on the individual sample dates in 2005 and 2006. To assess the relationship between pond hydroperiod and precipitation in 2005 and 2006, we obtained daily precipitation data from the National Oceanic and Atmospheric Administration (http://www.ncdc.noaa.gov/oa/climate/) for the Indian Mills, NJ weather station and from the U. S. Geological Survey (http://waterdata.usgs.gov/nj/nwis/) for the Albertson Brook near Hammonton, NJ and the Greenwood Branch at New Lisbon, NJ stations (Figure 1). We averaged daily precipitation values from the three weather stations, summed the mean values between sampling events, and compared precipitation amounts with pond hydrographs graphically.

Many Pinelands ponds, including the three study ponds, are embedded in an upland pine-oak

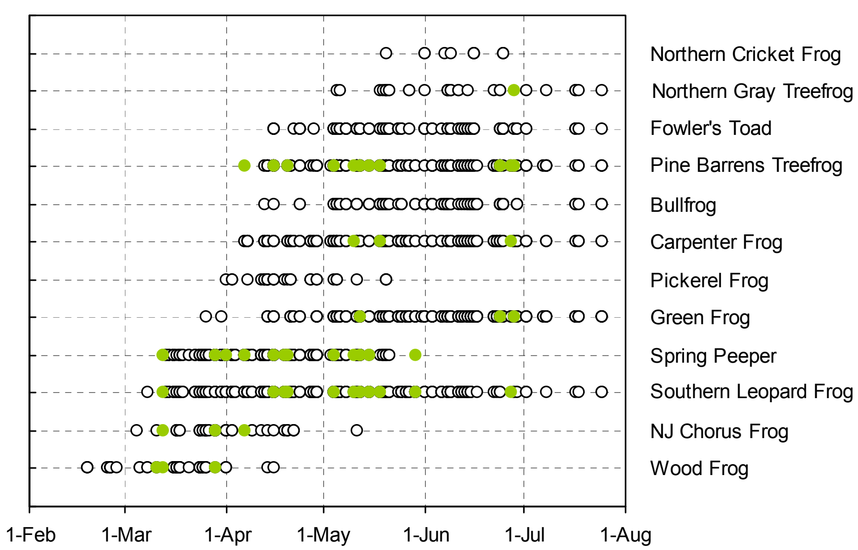

Figure 4. Breeding phenology of Pinelands anurans. Filled circles indicate that a species was heard during vocalization surveys conducted at three Pinelands ponds in 2005 and 2006. Open circles indicate that a species was heard during surveys completed at 227 Mullica River watershed sites in 1993 and 1996 to 1999. See Zampella et al. (2001b) for details regarding Mullica River watershed surveys.

or pitch pine lowland forest matrix (Zampella and Laidig 2003). To evaluate the relationship between water-level fluctuations in ponds and forests of the region, we used Spearman rank correlation to relate the water depths of each of the three ponds to the water depths of shallow wells installed in a pitch pine lowland and a pine-oak upland forest plot. The two adjacent forest plots were 19 km from Hampton and Furnace and 30 km from Chew (Figure 1). Water-level values from three wells in each forest plot were averaged for a single monthly value for each plot. The water-level data were a subset of the data used in Zampella et al. (2001a). Although pond and well water levels were both collected monthly during the 1996 - 2006 period, we excluded dates when the ponds were dry or frozen and dates when the pond and well measurements were more than two days apart. This resulted in 49, 50, and 51 dates (Furnace, Chew, and Hampton, respectively) for relating water levels of the three ponds to those for each forest plot.

Climatic Conditions

We obtained long-term stream-discharge and precipitation data from nearby stations to assess climatic conditions during the 1996 - 2006 study period. Daily stream-discharge data were obtained from the U. S. Geological Survey for the McDonalds Branch at Brendan T. Byrne State Forest gaging station (Figure 1). The McDonalds Branch station represents a minimally impacted hydrologic-benchmark site (Mast and Turk 1999). Daily precipitation data were acquired for the Indian Mills, Albertson Brook near Hammonton, and the Greenwood Branch at New Lisbon stations (Figure 1). To determine whether overall climatic conditions were similar during each year of the 1996 - 2006 study period, we compared total monthly precipitation values and mean monthly stream-discharge values between years using Kruskall-Wallis ANOVA tests. Post hoc comparisons were completed using multiple comparisons of mean ranks (Siegel and Castellan 1988).

Short-term Simulations

To simulate the potential impact of groundwater withdrawals on pond hydroperiod over a short-term (two-year) period, we created ten water-depth-reduction scenarios by subtracting from 5 to 50 cm (in 5-cm increments) from each weekly or biweekly water-depth value measured at the three study ponds in 2005 and 2006. For each pond and year, we determined the date of initial pond drying based on actual water-depth measurements and for the ten water-depth-reduction scenarios. Drying dates were used to determine pond hydroperiods. We determined which scenarios would have induced pond drying prior to the earliest egg-deposition date for each focal species at a pond. We also calculated the percentage of the total number of larvae, pre-metamorphs, and metamorphs that would have occurred on the drying dates for each focal species present at a pond.

Long-term Simulations

To simulate the potential impact of groundwater withdrawals on pond hydroperiod over a long-term (ten-year) period, we subtracted from 5 to 50 cm (in 5-cm increments) from each monthly water-depth value measured at the three ponds from 1996 - 1999 and 2001 - 2006. We excluded 2000 because water-depth measurements were missing for June, July, and August of that year. The date of initial drying was determined for each pond in each year based on actual water-depth measurements and for the ten water-depth-reduction scenarios. For each scenario, we determined the percentage of the ten years that each pond dried prior to the earliest date in which eggs were found during the two-year period and prior to the date in which we first observed pre-metamorphs and metamorphs for each focal species at a pond during the two-year period.

We also applied the long-term-hydroperiod reductions to southern leopard frog metamorph production. This analysis was limited to leopard frogs because metamorph sample size was the greatest for this species. Because the window of metamorphosis for leopard frogs varied somewhat among ponds and between 2005 and 2006, we chose the year with the longest metamorphic window for each pond and calculated the percentage of the total number of metamorphs collected on each sample date. We used linear interpolation to estimate the percentage values for individual dates between sample dates, which resulted in a continuous timeline of cumulative metamorph production for the leopard frog at each pond. Using the drying dates from each reduction scenario and the metamorph-production timelines, we estimated the percentage of leopard frog metamorphs produced at each pond during each of the ten years.

Some pond water-depth values were missing from the long-term record for the months of October - March due to factors such as staff-gage vandalism and frozen-pond conditions. Missing water-depth values did not affect the results of the long-term analyses because none of the reduction scenarios induced pond drying as early as March and the frog data that were applied to the long-term period were collected during the months of March - August of 2005 and 2006, which brackets the earliest and latest dates for oviposition, pre-metamorphs, and metamorphs for all three species.

Results

Pond Hydrology

Water-depth fluctuations were strongly correlated among ponds during the 2005 - 2006 period, with fluctuations most similar between Hampton and Furnace (Hampton vs Furnace, r = 0.95, Hampton vs Chew, r = 0.82, Chew vs Furnace, r = 0.80, n = 45 and $p < 0.001$ for all three ponds). Water-depth fluctuations at each of the three ponds were strongly related to water-depth fluctuations in the pitch pine lowland forest plot (r = 0.85 and $p < 0.001$ for all three ponds) and the pine-oak upland forest plot (r = 0.83 for Furnace, r = 0.84 for Hampton and Chew, $p < 0.001$ for all three ponds).

Water depth at the three ponds varied with precipitation (Figure 5). In 2005, Hampton and Furnace dried in early August, partially refilled, and dried again in early September (Figure 5). Chew also dried in early September. All three ponds remained dry until early October 2005. In 2006, Chew dried in late August, whereas Hampton and Furnace came close to drying, but did not dry.

In both years, the hydroperiod for Hampton and Furnace was about the same when based on weekly/biweekly versus monthly water-depth values (both ponds were 216 vs 215 d in 2005 and 365 vs 365 d in 2006). For Chew, the hydroperiod using the weekly/biweekly and monthly values was identical in 2005 (250 d), but was much shorter in 2006 when using the weekly/biweekly values (236 d) compared to the monthly values (365 d). Based on monthly water-depth measurements, the mean hydroperiod for each of the three ponds was greater in the 2005 - 2006 period compared to the

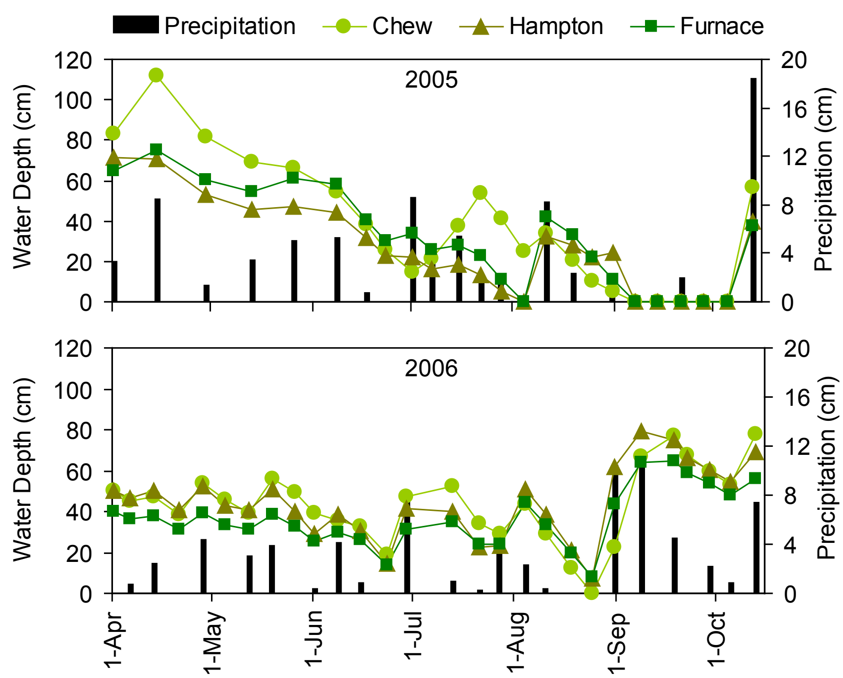

Figure 5. Hydrographs for three Pinelands ponds in 2005 and 2006. Mean daily precipitation values from three weather stations were summed between pond water-depth dates.

1996 - 2004 period (Table 1).

Climatic Conditions

There was no overall difference in total monthly precipitation between years from 1996 - 2004 (ANOVA, $p = 0.270$). There was a difference in mean monthly stream discharge between years from 1996 - 2004 (ANOVA, $p < 0.001$). Mean monthly discharge for 2002 was lower than that for 1996 ($p < 0.001$), 1998 ($p = 0.012$), 2003 ($p = 0.005$), 2004 ($p < 0.001$), 2005 ($p = 0.003$), and 2006 ($p = 0.022$). No other pair wise comparisons were different, indicating that climatic conditions in 2005 and 2006 were similar to conditions for all but one of the other eight years.

Breeding and Oviposition

We heard eight frog species calling at the three ponds in 2005 and 2006 (Table 1). With the exception of the Fowler's toad, anuran species heard during the 2005 - 2006 survey period were the same as those heard at the ponds during the 1996 - 2004 survey period (Table 1). In 2005 and 2006, species were heard calling on dates that corresponded to their documented breeding phenology for the region (Figure 4).

During 2005 and 2006, eggs were found only for the three focal species (spring peeper, southern leopard frog, and Pine Barrens treefrog). The southern leopard frog deposited eggs first, followed by the spring peeper, and then the Pine Barrens treefrog (Table 2). Southern leopard frog egg masses were found in all three ponds in both years and during a greater number of sampling dates in each year (3 dates in 2005, 10 dates in 2006) compared to the spring peeper (1 date in 2005, 4 dates in 2006) and Pine Barrens treefrog (1 date in 2006). Early season leopard frog egg masses were absent only from Furnace in 2005. Late-season leopard frog egg masses were usually found when a pond partially refilled after it either dried or came close to drying.

Larval Development

We collected and staged 4,545 larvae, pre-metamorphs, and metamorphs from the three ponds in 2005 and 2006. Five species were represented, including the carpenter frog (224 individuals), spring peeper (290), green frog (478), Pine Barrens treefrog (1,251), and southern leopard frog (2,302). We found carpenter frog larvae in Hampton in 2005 and Hampton and Furnace in 2006 and green frog larvae in Chew and Furnace in both years (Table 1). Carpenter frog and green frog larvae appeared in ponds relatively late in the season (late July for both years) and neither species was able to complete larval development prior to pond drying. Carpenter frog larvae were observed at developmental stage 28 in 2005 and stages 25 - 33 in 2006. Green frog larvae were found at stages 25 - 27 in 2005 and stages 25 - 40 in 2006

Spring peeper, Pine Barrens treefrog, and southern leopard frog larvae were present in all three ponds in 2005 and 2006. The abundance of larvae and pre-metamorphs varied widely among the three focal species and three ponds (Table 3).

Based on size and developmental stage, almost all of the southern leopard frog larvae captured in Furnace in 2005 and a few of the leopard frog larvae collected from Hampton in 2005 hatched during the previous year and spent the winter of 2004/2005 in the ponds. Leopard frogs did not overwinter in Chew in the 2004/2005 season or in any pond in the 2005/2006 season. Spring peepers and Pine Barrens treefrogs did not overwinter in any pond during the study.

Unlike the spring peeper, low numbers of Pine Barrens treefrog and southern leopard frog larvae were often present during the sampling event prior to a pond drying. Almost all of the larvae present during sampling events after a pond dried and

Table 2. Dates in which eggs were found for three frog species in three Pinelands ponds in 2005 and 2006.

Year	Pond	Spring peeper	Pine Barrens treefrog	Southern leopard frog
2005	Chew	-	-	4/14
	Hampton	4/29	-	4/14, 8/11
	Furnace	-	-	8/11, 8/19
2006	Chew	4/28, 5/5	6/1	3/31, 4/21, 5/19, 7/27, 8/10, 8/31, 9/22
	Hampton	4/6, 4/13, 5/5	-	3/31, 4/6, 4/13, 4/21
	Furnace	4/13, 4/28	-	4/6, 4/13, 6/1, 8/31

Table 3. Number of larvae, pre-metamorphs, and metamorphs collected for three frog species from three Pinelands ponds in 2005 and 2006. Frog larvae were staged according to Gosner (1960). Developmental stages 25 - 38 were considered larvae, 39 - 41 were pre-metamorphs, and 42 - 46 were metamorphs.

	2005			2006		
Species	Chew	Hampton	Furnace	Chew	Hampton	Furnace
Spring Peeper						
Larvae	70	18	27	31	51	58
Pre-mets.	10	-	2	-	7	11
Mets.	4	-	-	-	-	1
Pine Barrens Treefrog						
Larvae	337	20	100	312	86	159
Pre-mets.	77	6	24	49	16	22
Mets.	29	1	-	11	-	2
Southern Leopard Frog						
Larvae	220	221	204	143	426	708
Pre-mets.	61	25	54	2	47	43
Mets.	29	16	54	2	21	26

partly refilled were from the southern leopard frog, although some Pine Barrens treefrog larvae were occasionally present. This indicated that both of these species were capable of breeding relatively late in the season.

Metamorphosis

In each year, spring peeper metamorphs were found in one pond, Pine Barrens treefrog metamorphs at two ponds, and southern leopard metamorphs at all three ponds. Similar to the larvae and pre-metamorphs, the number of metamorphs collected also varied among species and ponds (Table 3).

With three exceptions, metamorphosis for the three focal species began on June 23 of each year. The exceptions were southern leopard frog (June 17) and Pine Barrens treefrog (July 15) in Hampton in 2005 and Pine Barrens treefrog (July 13) in Furnace in 2006. With one exception, metamorph production for the focal species appeared to stop from two to six sampling events (13 - 41 d, mean ± 1 SD of 20 ± 11 d) prior to a pond drying. The exception was Chew in 2006, where we collected metamorphs during the sampling event prior to the pond drying.

Short-term Simulations

The first two water-depth-reduction scenarios (5 and 10 cm reductions) would have resulted in little or no change to the hydroperiods of the three ponds in 2005 and Chew in 2006 (Figure 6). For Hampton and Furnace in 2006, the first reduction scenario would not have caused either pond to dry and the second scenario would have resulted in both ponds drying at 237 d (August 24, Figure 6). This was the same hydroperiod for Chew in 2006 based on actual water-depth measurements and from the first two scenarios.

The first two reduction scenarios would have

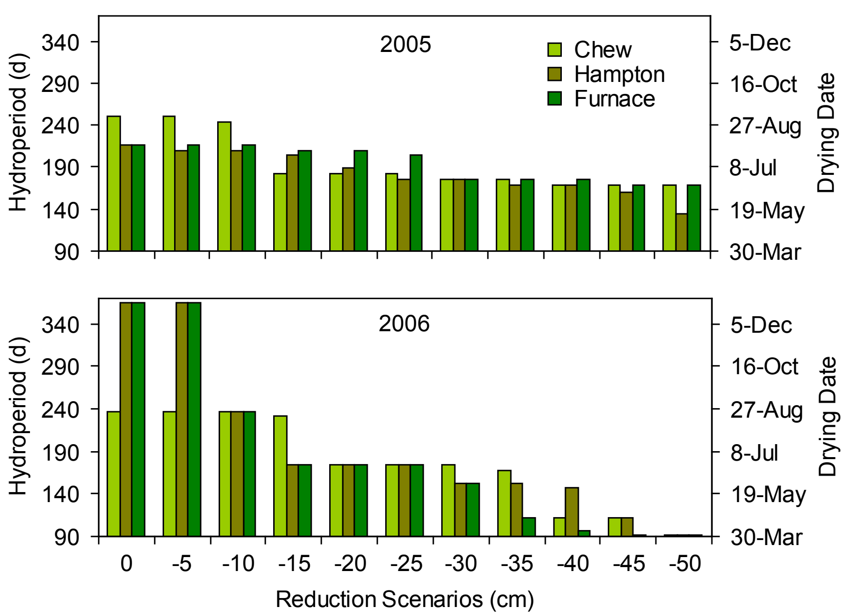

Figure 6. Hydroperiods for three Pinelands ponds in 2005 and 2006 for the actual water-depth measurements and for water depths reduced by 5 to 50 cm.

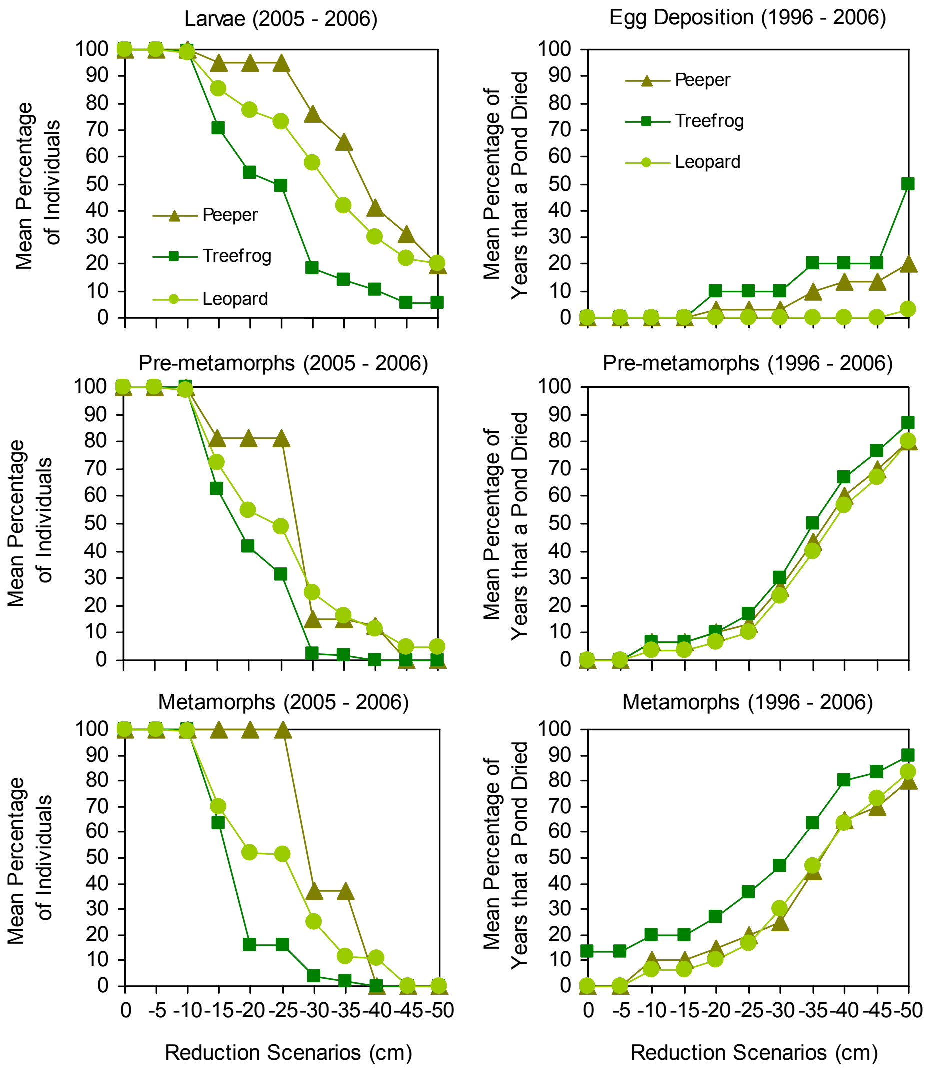

Figure 7. Mean percentage of individual larvae, pre-metamorphs, and metamorphs that occurred on drying dates for 2005 - 2006 and mean percentage of years from 1996 - 2006 in which three Pinelands ponds dried prior to the date of initial egg deposition and appearance of the first pre-metamorphs and metamorphs for the actual water-depth measurements and for water depths reduced by 5 to 50 cm.

also resulted in little or no impact to the percentages of larvae, pre-metamorphs, or metamorphs that occurred for the three focal species (Figure 7). In contrast, some of the larger water-depth reductions would have shortened pond hydroperiods in both years to the point where relatively few or no larvae and pre-metamorphic larvae were present and metamorph production had not yet begun. The 45 and 50-cm scenarios in 2005 would have induced pond drying sometime between mid-May and mid-June and the 35, 40, 45, and 50-cm scenarios in 2006 indicated that the ponds would have dried between early April and early June (Figure 6). None of the ponds was estimated to produce metamorphs for any species under these six scenarios.

Simulated pond drying would have affected initial oviposition only in 2006. The greatest effects were observed for Chew, where the 40, 45, and 50-cm scenarios would have resulted in pond drying prior to the date of first oviposition for the spring peeper and Pine Barrens treefrog. As mentioned previously, Pine Barrens treefrog eggs were observed on only one date (Table 2). The 50-cm scenarios would have induced pond drying prior to the date of first oviposition for all ponds in which spring peeper eggs were observed. For the southern leopard frog, the 50-cm scenarios would have caused Furnace to dry prior to the date of first oviposition and would have induced Chew and Hampton to dry one day after the date of first oviposition. Overall, the effects of simulated water-depth reductions on hydroperiod, oviposition, larval development, and metamorphosis were estimated to be greater in 2006 compared to 2005 probably because ponds started out with less water in 2006 (Figure 5).

Long-term Simulations

Over the ten-year period, pond hydroperiod (drying date) based on the actual water-depth measurements ranged from 190 d (July 8) to 365 d (i.e., not drying at all). The 5-cm and 10-cm reduction scenarios would have had no effect on pond hydroperiod during eight and five of the ten years, respectively, whereas the 50-cm reductions would have resulted in hydroperiods that ranged from 96 d (April 5) in 2006 to 239 d (August 26) in 1996.

None of the ponds would have dried prior to the date of initial egg deposition for any species based on the actual water-depth measurements and for the first three reduction scenarios (Figure 7). Effects on initial spring peeper and Pine Barrens treefrog oviposition were estimated to occur for reductions of ≥20 cm. For Pine Barrens treefrog oviposition, which only occurred on one date at Chew (Table 2), the 50-cm reduction scenario would have caused Chew to dry prior to the date of first egg deposition during five of the ten years (Figure 7). For the spring peeper, the 50-cm scenario would have caused Hampton, Furnace, and Chew to dry prior to first oviposition during one, two, and three of the ten years, respectively. The simulations showed the greatest estimated impact on the first date of oviposition for the Pine Barrens treefrog compared to the spring peeper. Simulated pond drying was estimated to have little effect on the first date of oviposition for the southern leopard frog (Figure 7).

With one exception, based on the actual water-depth measurements, none of the ponds would have dried prior to the appearance of the first pre-metamorphs and metamorphs for any of the three focal species (Figure 7). The exception was that Hampton and Furnace would have dried before the first Pine Barrens treefrog metamorphs in 2001 and 2004. On average, estimated impacts to the date of the first pre-metamorphs and metamorphs began at reductions of 10 - 15 cm and increased more sharply for reductions ≥20 cm. The 50-cm scenarios would have resulted in the ponds drying prior to the first pre-metamorphs and metamorphs during 80 - 90% of the years.

Although the differences were not dramatic, the reduction scenarios showed the greatest average impact for pre-metamorphs and metamorphs of the Pine Barrens treefrog compared to the spring peeper and southern leopard frog (Figure 7). The lack of major differences among species for the estimated impact of hydroperiod reductions on pre-metamorphs and metamorphs was due to the similarity in the timing of metamorphosis among species and ponds.

The separate analysis on southern leopard frog metamorph production showed that long-term mean metamorph production for this species decreased with each successive water-depth-reduction scenario (Figure 8). For each scenario, variation in long-term mean metamorph production within and among ponds was due to different annual hydroperiods for each pond over the ten-year period and the different pond-specific leopard frog metamorph-production timelines used. Declines in long-term metamorph production for the leopard frog were more pronounced for reductions of ≥30 cm, especially for Hampton, which was estimated to produce very few metamorphs for the 50-cm reductions. Hampton displayed the lowest mean

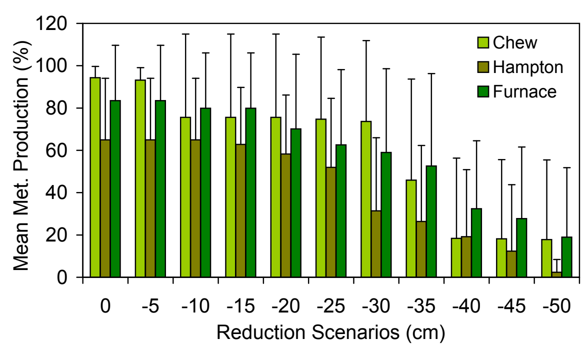

Figure 8. Long-term mean (1 SD) metamorph production for southern leopard frogs for three Pinelands ponds for the actual water-depth measurements and water depths reduced by 5 to 50 cm. Means represent an average of ten annual values from 1996 - 2006. The year 2000 was excluded due to incomplete hydroperiod data.

metamorph production for almost every scenario because it was slightly shallower than Furnace and Chew.

Discussion

Our results show how water-depth reductions that may result from groundwater withdrawals have the potential to reduce pond hydroperiods and lead to impacts on the various life stages of frogs. For the long-term analysis, the actual and reduced hydroperiods were determined from monthly water-depth measurements, but ponds may have actually dried at some point between those monthly readings, which would have resulted in a shorter hydroperiod. Inflated hydroperiods derived from monthly readings would result in overestimated metamorph production and underestimated impacts to the first date of encountering eggs, pre-metamorphs, and metamorphs. This indicates that our long-term results are likely somewhat conservative. Compared to the long-term analysis, the results of the short-term simulations were probably more accurate due to the use of hydroperiods derived from biweekly/weekly water-depth values and because we estimated impacts during the period when we actually collected the frog life-stage data.

Water-depth reductions that resulted in pond drying prior to the date of the initial appearance of pre-metamorphs, metamorphs, and eggs were striking because of the consequences of the total lack of recruitment for those scenarios. Our analysis did not incorporate the cumulative effects of water-depth reductions or reduced or failed recruitment in successive years. While the threshold at which persistently low metamorph production would cause a species to decline at any particular pond is not known, the combined effect of low metamorphic success, reduced larval development, and the lack of water for oviposition would magnify the probability of decline or even extirpation at a pond. Although long-term hydroperiod reductions may be particularly detrimental to relatively short-lived frog species due to the cumulative effect of reduced juvenile recruitment each year and the relatively few number of times that a short-lived species may be capable of breeding (Berven 1990), pond-breeding amphibian populations appear fairly resilient to the effects of multiple years of low metamorphic success due to short (≤100 d) hydroperiods (Semlitsch et al. 1996) and even several years of no water from prolonged droughts (Gibbons et al. 2006).

Our analysis did not include the possibility of acceleration of larval development in response to pond drying (Denver 1997). While acceleration has been shown for several amphibian species, acceleration often results in fewer individuals reaching metamorphosis (Parris 2000, Ryan and Winne 2001, Ryan 2007) and individuals that metamorphose are usually smaller (Crump 1989, Denver et al. 1998, Ryan and Winne 2001), which may (Berven 1990) or may not (Boone 2005) affect juvenile survival. Increased larval density as a pond dries may even extend larval period and delay metamorphosis (Leips et al. 2000). Although we found no studies on acceleration for the spring peeper or Pine Barrens treefrog, acceleration in southern leopard frogs can range from 2 d (Parris 2000) to 15 d (Ryan and Winne 2001). Although it is possible that some focal-species larvae could accelerate development, acceleration values for frogs are relatively short and our results showed that relatively few or no pre-metamorphic larvae were present and ready to metamorphose when a pond was estimated to dry.

Early breeding and oviposition may provide an advantage for the spring peeper and southern leopard frog over the Pine Barrens treefrog. For the spring peeper, the relatively low abundance of larvae, pre-metamorphs, and especially metamorphs at the study ponds during 2005 and 2006 suggested that peepers may constitute a relatively minor component of total annual metamorph production for Pinelands ponds. The spring peeper constituted a relatively small proportion of the number of metamorphs collected from a coastal plain pond in South Carolina (Gibbons et al. 2006) and seven woodland vernal pools in Rhode Island (Paton and Crouch 2002). Unlike the spring peeper, the propensity for the southern leopard frog to deposit egg masses very early and periodically throughout the season and the ability of the larvae to overwinter in a pond likely contributed to its relatively high larval, pre-metamorph, and metamorph abundance at the ponds. Southern leopard frogs have been observed to be a dominant component of the metamorphs that emerged from a South Carolina coastal plain pond (Gibbons et al. 2006).

Like our study, late-season oviposition by the southern leopard frog has been observed in several other regions of the United States (Wright and Wright 1949, Martoff et al. 1980, Caldwell 1986) and, similar to what we noted, appears to be related to precipitation events (McCallum et al. 2004). Late-season breeding for the southern leopard frog and the Pine Barrens treefrog may provide an opportunity for both species to exploit ponds that dry and refill late in the season, which would reduce or eliminate aquatic predators and competitors (Morin et al. 1990, Semlitsch et al. 1996). Late-season breeding is more likely to benefit the leopard frog because of the ability of the larvae to overwinter. In any case, premature pond drying associated with groundwater pumping may eliminate the possibility of larvae overwintering for any species. The lack of early season leopard frog egg masses in Furnace in 2005 may have been due to the presence of large leopard frog larvae that overwintered from the previous season because they can prey upon freshly deposited anuran eggs and recent hatchlings (Faragher and Jaeger 1998).

Our findings that the Pine Barrens treefrog was the most vulnerable to water-depth reductions and the spring peeper the least vulnerable must be interpreted with some caution because peeper and treefrog pre-metamorphs and metamorphs were not found in all ponds and sample size was low at some ponds. Despite small sample sizes, the trends were similar to those with larger sample sizes. The single date of June 1 in which we observed treefrog eggs seemed a little late for this species because treefrogs typically begin vocalizing in mid- to late-April (Figure 4) and have been observed in amplexus and depositing eggs in late-April/early May (JFB, personal observation). Nonetheless, the June 1 date falls between the mid-May and mid-June breeding pulses reported for Pinelands ponds in Morin et al. (1990) and the estimated impacts of water-level reductions on oviposition would have been similar even if we used an early May egg-deposition date.

The lack of complete larval development for the carpenter frog and green frog indicated that these two species require a longer hydroperiod than the three focal species. Both species can be heard vocalizing from temporary and permanent-water habitats in the Pinelands (Zampella and Bunnell 2000, Bunnell and Zampella 2008) and elsewhere (Werner and McPeek 1994, Werner et al. 1995, Otto et al. 2007). Although both species can develop and metamorphose if eggs are deposited early enough in the year, they typically spend one winter as larvae and metamorphose the following season (Martof 1956, Standaert 1967). In our study, larvae of both species were still developing in Furnace in mid-October 2006, which indicated that larvae probably overwintered into 2007. Groundwater withdrawals that cause early pond drying every year would likely eliminate these species because of their long larval periods, which is particularly important for the carpenter frog because of its conservation status in New Jersey, Delaware, Maryland, and Virginia.

Although adults were heard calling, the absence of eggs and larvae for the New Jersey chorus frog, northern gray treefrog, and wood frog may be due to the low pH of the ponds. Although these non-Pinelands species can occasionally be heard calling from Pinelands ponds (Zampella and Bunnell 2000), the environmental resistance associated with the low pH of Pinelands wetlands may prevent acid-sensitive non-native species from reproducing successfully (Gosner and Black 1958, Bunnell and Zampella 1999, Bunnell and Zampella 2008).

Management Applications

Although we only collected complete ontogeny data for three frog species at three intermittent ponds, several factors increase the general transferability of our results to other ponds in the region. First, the three species that we focused on are widely distributed in the Pinelands (Conant 1979), all three species commonly breed in natural and artificial Pinelands ponds (Zampella and Bunnell 2000), and all three species are often the most abundant species heard vocalizing (Bunnell and Zampella 1999). Secondly, the three focal species covered a range of breeding phenologies allowing us to assess the potential impacts of hydrologic alterations on frogs that breed early, late, and fairly continuously. Third, although variability associated with field studies can be high, we monitored hydrology and anuran ontogeny under natural conditions at real ponds, rather than in a laboratory or semi-natural setting, so that our results would be more applicable to ponds in the landscape. Lastly, the three artificial ponds that we studied were well-developed ponds more than 50 years old and supported similar anuran assemblages and exhibited comparable hydrologic regimes to natural Pinelands ponds (Table 1, Bunnell and Zampella 1999, Zampella and Laidig 2003).

Several findings indicate that 2005 and 2006 were fairly representative years for pond hydrology and anuran ontogeny. First, the similarity in precipitation and stream discharge over the ten-year period indicated that climatic conditions were similar during each year and the hydrology data collected during 2005 and 2006 was representative of the longer hydrologic record for the region. Secondly, the timing of the breeding calls heard for each species during the vocalization surveys in 2005 and 2006 corresponded with documented breeding phenologies for species from numerous sites in the Pinelands (Figure 4). Lastly, we evaluated development data over two anuran-breeding seasons and metamorphosis for all three focal species generally began around the same time in each year.

The strong relationships for water levels among the ponds and between the ponds and distant forest plots emphasized the linkage between groundwater and pond-water levels and indicated that hydrologic patterns for ponds and forests were similar across the region. Zampella et al. (2001a) found that groundwater levels in Pinelands forest plots mirrored reference-forest sites regardless of whether they were proximate or distant. Like Carolina Bays, which are also found in coastal plain soils, Pinelands ponds appear to represent a "surface expression of the water table" (Lide et al. 1995). Variations in pond-water levels reflect groundwater, which, in the highly permeable sand and gravel sediments of the region, are responding directly to precipitation (Rhodehamel 1979a).

The impact of long-term hydrologic alterations on anurans may become increasingly important in the future due to increased groundwater withdrawals in human-dominated regions and greater variability in future weather patterns predicted in climate-change models (IPCC 2001, Hulme et al. 2002). Our results can be used to assess the potential impacts of groundwater withdrawals on the various life stages of pond-breeding frogs. Although different measures were used for the short-term and long-term simulations, the results of all simulations indicated that impacts would generally begin to occur at water-depth reductions of 10 to 15 cm. For all simulations, successively greater reductions would have caused increasing impacts that varied by species and pond, with the 50-cm reductions shortening pond hydroperiods enough to practically eliminate the possibility of larval development and metamorphosis for all three species.

Our results can be used in conjunction with watershed-wide hydrologic models that were developed as part of the larger Kirkwood-Cohansey Project (Pinelands Commission 2003). These models will be used to estimate the potential effects of groundwater pumping on various hydrologic and ecological attributes of Pinelands wetlands and to help determine the optimum location, depth, and pumping rate for water-supply wells. Some of the general well-siting criteria determined from the Kirkwood-Cohansey project may also be applicable to other coastal plain regions.

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