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Climate change is linked to long-term decline in a stream salamander

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ABSTRACT

Amphibian declines have been documented worldwide and several have been linked to climate change, but the long-term data needed to detect declines are largely restricted to pond-breeding species. This limits our knowledge of population trends in other major groups of amphibians, including stream salamanders, which have their greatest diversity in North America. I hypothesized that increasing air temperature and precipitation in northeastern North America caused abundance of the stream salamander *Gyrinophilus porphyriticus* in a New Hampshire population to decline between 1999 and 2010. I found a significant decline in abundance of *G. porphyriticus* adults over this 12-year period, and no trend in larval abundance. Adult abundance was negatively related to annual precipitation, which is predicted to increase further in the Northeast due to climate change. Analysis of a 6-year capture–mark–recapture data set for the same population showed no temporal variation in larval and adult detectability, validating the abundance data, and no variation in larval and adult survival. However, survival during metamorphosis from the larval to adult stage declined dramatically. These results suggest that increasing precipitation is causing a decline in adult recruitment, which, if it persists, will lead to local extinction. A likely mechanism for the decline in adult recruitment is mortality of metamorphosing individuals during spring and fall floods, which have increased in volume and frequency with the increase in precipitation. More broadly, this study presents strong evidence that the amphibian decline crisis extends to North America's stream salamanders, and shows the critical need to collect population data on these species.

1. Introduction

Amphibian declines are occurring worldwide (Alford and Richards, 1999; Houlahan et al., 2000; Stuart et al., 2004), and recent studies suggest that climate change is contributing to these declines (e.g., Pounds et al., 2006; Whitfield et al., 2007; Bombi and D'amen, 2009; Griffiths et al., 2010). It is clear that long-term data are invaluable for detecting these declines and identifying their underlying causes (Pechmann et al., 1991; Skelly et al., 1999; Green, 2003). However, long-term data sets (>10 years) are largely restricted to pond-breeding species, limiting our knowledge of population trends and response to environmental change in other major groups of amphibians, including terrestrial and stream-associated species (Corn et al., 2003; Lannoo, 2005; Wake and Vredenburg, 2008). This bias in long-term data may prevent us from understanding the true scope of amphibian declines and identifying those regions and habitats where conservation efforts are most needed.

Stream-associated species account for approximately 35% of total amphibian diversity in the United States (Davic and Welsh, 2004), and up to 45% of all salamander species rely on streams for part or all of their life cycle (Lannoo, 2005). Most stream-associated salamanders belong to the family Plethodontidae, the lungless salamanders, and have complex life cycles where aquatic larvae metamorphose into aquatic or terrestrial adults (Petranka, 1998; Duellman, 1999). Stream plethodontids have their greatest species diversity in headwater areas of North America (Duellman, 1999; Milanovich et al., 2010), where they represent a valuable resource for scientific discovery and for increasing public awareness of native biodiversity (Hairston, 1987; Bruce et al., 2000; Stein et al., 2000). Understanding population trends in these species is especially critical now that headwater streams are at risk of losing protection under the US Clean Water Act (Meyer et al., 2003; Nadeau and Rains, 2007).

Green (2003) estimated that local extinction rates are near zero for stream-associated amphibians, and that populations of these species are more stable than those of pond-breeding amphibians. But the only published long-term study of stream plethodontids – Hairston and Wiley (1993) – lacks the standardized survey methods crucial to assessing population trends (Bailey et al., 2004a; Schmidt, 2004). Short-term studies show that stream plethodontids are sensitive to natural and anthropogenic disturbance (e.g., Welsh and Droege, 2001; Lowe and Bolger, 2002; Willson and Dorcas, 2003), and Grant et al. (2010) found that dispersal facilitates persistence in these species. However, our understanding of how gradual

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environmental change is affecting stream plethodontids, and the demographic mechanisms underlying these effects, is severely limited by a lack of long-term population data.

Climate models predict substantial changes in temperature and precipitation in northeastern North America that are likely to have profound effects on stream ecosystems (Meyer et al., 1999; Brooks, 2009; Rodenhouse et al., 2009). Hayhoe et al. (2007) predict that mean annual temperature in the Northeast will increase by 2.9–5.3 °C by the end of the century. Precipitation is predicted to increase by 7–14% in the same period, and the variability of weather is predicted to increase, resulting in higher frequencies of flood and drought events (Huntington, 2003; Hayhoe et al., 2007). A 100-year data set on climate in New Hampshire shows a clear increase in annual precipitation over the last 20 years (www.nhclimateaudit.org), and mean annual temperature in the northeastern United States increased by 0.75 °C between 1970 and 2000 (Hayhoe et al., 2007). But despite this evidence that changes in temperature and precipitation are underway, there is little research assessing the effects of climate change on native species of the Northeast (Rodenhouse et al., 2009).

I used 12 years of data to assess population trends in the stream salamander *Gyrinophilus porphyriticus* (Plethodontidae) and to test whether these trends were related to annual climatic variation. *G. porphyriticus* is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama to southern Quebec (Petranka, 1998). The larval period is estimated to be 3–5 years (Bruce, 1980), and maximum age is estimated to be 14 years. During the day, larvae and adults are found under rocks and wood in the stream channel, but adults can leave the channel at night to forage for terrestrial invertebrates in the riparian zone (Burton, 1976; Greene et al., 2008). From 1999 to 2010, I conducted standardized surveys of Merrill Brook, a 1-km headwater stream in northern New Hampshire, to generate annual estimates of larval and adult *G. porphyriticus* abundance. I then tested for trends in salamander abundance over the 12-year sampling period, and for effects of annual variation in air temperature and precipitation on abundance. To assess changes in population size structure that might be related to trends in abundance (Caswell, 2001; Mills, 2007), I also tested for trends in the mean size (snout-vent length [SVL]) of larvae and adults over the 12-year sampling period.

I hypothesized that increasing air temperature and precipitation in northeastern North America have caused *G. porphyriticus* abundance in Merrill Brook to decline over the 12-year sampling period. Air temperature and precipitation may have complex effects on amphibian populations resulting from interactions with each other and with other biotic and abiotic variables (Corn, 2005; Pounds et al., 2006; McCaffery and Maxell, 2010). For example, if increased precipitation caused soil moisture to increase, the precipitation trend could benefit *G. porphyriticus* and offset negative effects of increasing air temperature (Feder and Burggren, 1992; Grover, 2000). But increased precipitation in the Northeast has not produced significant increases in soil moisture, likely because evapotranspiration has also increased (Hayhoe et al., 2007; Huntington et al., 2009). Therefore, I expected the negative effect of increasing air temperature to be caused primarily by increased evaporative water loss by *G. porphyriticus* adults during terrestrial foraging bouts, resulting in physiological stress, reduced prey intake, and increased mortality (Spight, 1968; Feder and Burggren, 1992). I expected the negative effect of increasing precipitation to be caused primarily by higher and more flashy flood events (Huntington, 2003; Hayhoe et al., 2007), resulting in increased mortality of *G. porphyriticus* individuals in the stream channel (Baumgartner et al., 1999; Barrett et al., 2010). Merrill Brook receives significant groundwater inputs that prevent extensive dewatering in the summer, and likely mitigate the effects of drought.

Temporal variation in detectability can bias amphibian survey data (Schmidt, 2003; Bailey et al., 2004b; Mazerolle et al., 2007). I addressed this crucial issue with intensive capture–mark–recapture data from the first 6 years of this study (1999–2004). Specifically, I used multistate capture–mark–recapture modeling to test for variation in capture probabilities of *G. porphyriticus* larvae and adults that could bias annual abundance data (White and Burnham, 1999; Lebreton et al., 2009). These capture–mark–recapture analyses also allowed me to evaluate demographic mechanisms underlying trends in abundance (Lebreton et al., 1992; White and Burnham, 1999; McCaffery and Maxell, 2010).

2. Methods

2.1. Study site

The study site was Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, located in northern New Hampshire. Merrill Brook flows into the fourth-order Dead Diamond River; a wetland at the confluence serves as a barrier to brook trout (*Salvelinus fontinalis*) that might enter Merrill Brook from the larger river. Sampling occurred throughout a 1-km long section of Merrill Brook that started at the confluence with the outflow wetland and ended 1000 m upstream of that point, encompassing the perennial portion of the stream.

Undistured headwater streams in New Hampshire are characterized by low conductivity (12.0–15.0 µS cm^{-1}), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation), and moderate mid-day temperatures in the summer (13.0–17.0 °C) (Likens and Bormann, 1995). Sampling throughout Merrill Brook matched these data. Other salamanders encountered in Merrill Brook were *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae).

2.2. Survey methods

I conducted capture–mark–capture surveys of Merrill Brook during 3-day periods in mid-June, mid-July, and mid-August of 1999–2004. A cover-controlled, active search sampling method was used (Heyer et al., 1994). Moving upstream, I turned rocks within the channel and along the edge measuring 64–256 mm in diameter (cobble); surveys continued until 1200 rocks had been turned. The even distribution of cobble allowed me to standardize sampling effort at just over one rock per meter of stream length. An aquarium dip-net was used to capture salamanders, including those flushed by the current.

All unmarked *G. porphyriticus* larvae and adults encountered were individually marked by subcutaneous injection of flourescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). Retention of these marks is high throughout the life of the animals, and marks have no effect on individual survival or behavior (Grant, 2008). The length (SVL, mm) and life history stage (larva vs. adult) of all individuals encountered were recorded. The distinction between larvae and adults was based on the presence of external gills in larvae (Bishop, 1941; Brandon, 1966). I continued annual abundance surveys of Merrill Brook in mid-July of 2005–2010. Methods were identical to those used in the capture–mark–capture surveys, but I did not examine animals for existing marks and no new animals were marked.

2.3. Long-term trends in salamander abundance

I used the count data from surveys in July of 1999–2010 to test for trends in *G. porphyriticus* abundance across the 12-year sampling period. My index of relative abundance in the 1-km study

stream was number of salamanders encountered in each effort-standardized survey. I used capture–mark–capture models described in the next section to test for variation in capture probabilities that could have biased this index of relative abundance. To assess long-term trends in larval and adult *G. porphyriticus* abundance, I used nonparametric Mann–Kendall tests for trend, which control for temporal autocorrelation in the dependent variable (Gilbert, 1987). I also used Mann–Kendall tests to assess trends in the mean size (SVL, mm) of *G. porphyriticus* larvae and adults.

I used linear regression analysis to test whether larval or adult *G. porphyriticus* abundance in July of year t was related to mean annual air temperature (August$_{t-1}$–July$_t$, °C) and cumulative annual precipitation (August$_{t-1}$–July$_t$, mm). Temperature and precipitation data were obtained from the NOAA National Climate Data Center (www.ncdc.noaa.gov/oa/ncdc.html) and were specific to New Hampshire Climate Division 1, which covers the northern portion of the state. I deliberately chose these large-scale, integrated measures of air temperature and precipitation to assess population response to broader climatic trends in the study region, and to avoid problems of multicollinearity among climatic variables (Graham, 2003). Abundance data were log-transformed for regression analyses. To ensure that this analysis was not confounded by multicollinearity of predictors, I also tested for temporal trends in mean annual air temperature and cumulative annual precipitation using Mann–Kendall tests, and for correlation between mean annual air temperature and cumulative annual precipitation using Pearson product-moment correlation analysis.

2.4. Capture–mark–recapture modeling

I had two objectives for the capture–mark–capture modeling used in this study. My first objective was to test for variation in capture probabilities of *G. porphyriticus* larvae and adults that could bias the long-term data on abundance (Schmidt, 2003; Bailey et al., 2004b). My second objective was to derive estimates of larval and adult survival probabilities, and larva → adult transition probabilities (i.e., metamorphosis probabilities), that might explain long-term trends in abundance.

Yearly survival (S) and capture (p) probabilities of *G. porphyriticus* larvae and adults, and yearly transition probabilities from the larval to the adult stage ($\psi^{\text{larva}\rightarrow\text{adult}}$) were estimated for 1999–2004 with a multistate model using the MARK computer program (White and Burnham, 1999; Lebreton et al., 2009). In this analysis, observations from the three surveys each summer were collapsed into a single annual observation. This allowed me to derive yearly parameter estimates and, relative to models where all 18 surveys were included, reduced the number of estimated parameters, increasing accuracy and precision of the parameters of interest (e.g., Grant et al., 2010).

Survival probability represents the probability that an animal alive at time t in one state (i.e., life history stage) will be alive at time $t + 1$, independent of state at $t + 1$. With two states, the transition probability is the conditional probability that an animal in one state at time t will be in the other state at $t + 1$, given that the animal is alive at $t + 1$. Transition probability estimates are based on the assumption that survival from time t to $t + 1$ does not depend on state at $t + 1$. Capture probability is the probability that a marked animal at risk of capture at time t is captured at t, conditional on being alive and available for capture.

Estimates of survival probability (S) confound mortality with permanent emigration from the population. However, *G. porphyriticus* larvae and adults exhibit upstream-biased dispersal (Lowe, 2003), no individuals were found in yearly sampling of the outflow wetland and upper ephemeral portion of Merrill Brook, and extensive overland dispersal is unlikely considering the highly-aquatic habits and morphology of *G. porphyriticus* adults (Brandon, 1966;

Petranka, 1998; Greene et al., 2008). These observations indicate that the study section encompassed all available habitat and that the population was largely closed with regard to emigration. Because the nearest occupied stream was 3 km away, I assumed that immigration did not occur at a demographically significant rate.

Survival, capture, and transition probabilities were modeled as constant or variable over time (year). Because transitions from the adult to larval stage are impossible, $\psi^{\text{adult}\rightarrow\text{larva}}$ was fixed at 0. Estimates of S^{larva} and $\psi^{\text{larva}\rightarrow\text{adult}}$ were used to calculate yearly survival–transition probabilities ($\phi_t^{\text{larva}\rightarrow\text{adult}}$), representing the probability of a larva surviving from t to $t + 1$ and metamorphosing to an adult (e.g., $\phi_t^{\text{larva}\rightarrow\text{adult}} = S_t^{\text{larva}} \psi_t^{\text{larva}\rightarrow\text{adult}}$).

I used Akaike's information criterion, or AIC (Akaike, 1973), to identify the model that represented the data adequately with as few parameters as possible. Models were ranked by second-order AIC (AIC$_c$) differences (ΔAIC$_c$; Burnham and Anderson, 2002). Relative likelihood of each model in the candidate set was then estimated with AIC$_c$ weights (Buckland et al., 1997). I ran the set of 32 candidate models that included all combinations of time-invariant and time-variant survival (S), capture (p), and transition probabilities ($\psi^{\text{larva}\rightarrow\text{adult}}$). Prior to model selection, I used program U-CARE (Choquet et al., 2003) to perform goodness-of-fit tests on the saturated multistate model (i.e., with time-variant S^{larva}, S^{adult}, p^{larva}, p^{adult}, and $\psi^{\text{larva}\rightarrow\text{adult}}$).

3. Results

3.1. Long-term trends in salamander abundance

Between 1999 and 2010, the number of *G. porphyriticus* larvae encountered in July surveys of Merrill Brook ranged from 20 to 47; the number of adults ranged from 18 to 70. There was no trend in larval abundance over the 12-year sampling period (Mann–Kendall $Z = 0.00$, $P = 0.95$; Fig. 1A), but adult abundance declined significantly ($Z = -0.66$, $P < 0.01$; Fig. 1B). Mean SVL of larvae ranged from 45 to 58 mm; mean SVL of adults ranged from 78 to 85 mm. There was no trend in mean SVL of larvae ($Z = 0.09$, $P = 0.74$), but mean SVL of adults increased significantly ($Z = 0.46$, $P = 0.04$).

Abundance of *G. porphyriticus* adults was negatively related to cumulative annual precipitation over the 12-year sampling period ($F_{1,10} = 7.52$, $r^2 = 0.43$, $P = 0.02$; Fig. 2) and unrelated to mean annual temperature ($F_{1,10} = 0.30$, $r^2 = 0.03$, $P = 0.59$). Larval abundance was unrelated to cumulative annual precipitation ($F_{1,10} = 2.93$, $r^2 = 0.23$, $P = 0.12$; Fig. 2) and unrelated to mean annual temperature ($F_{1,10} = 0.22$, $r^2 = 0.02$, $P = 0.65$). The precipitation × temperature interaction was not significant in multiple regression models of adult and larval abundance ($P > 0.8$). There was no temporal trend in mean annual temperature or cumulative annual precipitation over the sampling period (temperature: $Z = -0.25$, $P = 0.30$; precipitation: $Z = 0.42$, $P = 0.06$), and no correlation between mean annual temperature and cumulative annual precipitation ($r = -0.08$, $n = 12$, $P = 0.8$).

3.2. Capture–mark–recapture modeling

None of the five lack-of-fit tests performed on the saturated capture–mark–recapture model with program U-CARE were significant, indicating that the multistate framework in program MARK was appropriate for the data set (Choquet et al., 2003). The best multistate model had time-invariant larval and adult survival and capture probabilities ($S^{\text{larva}}, S^{\text{adult}}, p^{\text{larva}}, p^{\text{adult}}$), and time-variant larva → adult transition probabilities ($\psi^{\text{larva}\rightarrow\text{adult}}$; Table 1). This model fit the data approximately four times as well as the second best fitting model.
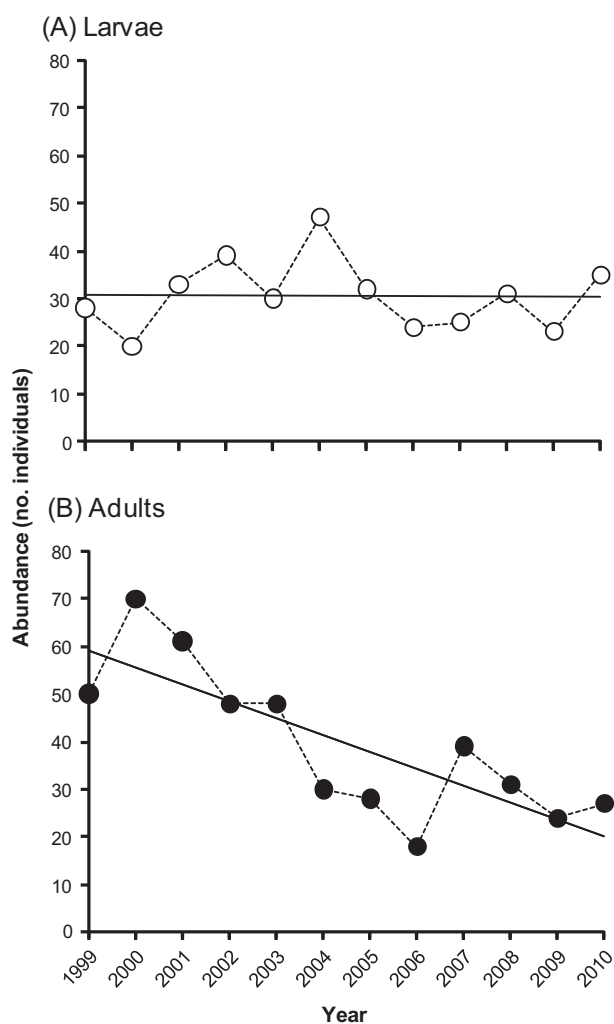
(A) Larvae

(B) Adults

Fig. 1. Trends in abundance of *G. porphyriticus* larvae (A) and adults (B) over the 12-year study period, from 1999 to 2010. Linear regression lines are plotted.
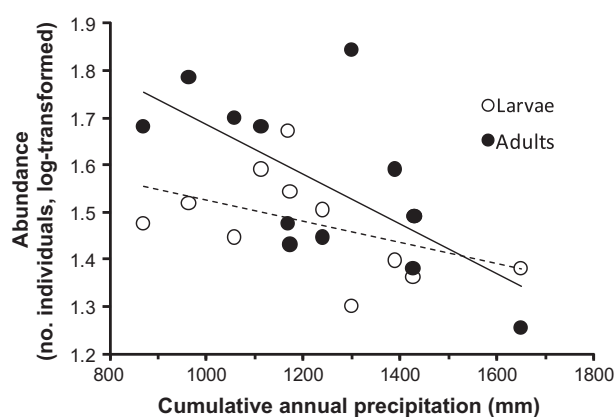

Fig. 2. Linear regression of larval and adult *G. porphyriticus* abundance with cumulative annual precipitation.

Larval and adult capture probabilities were constant across years in the best multistate model ($p^{larva} \pm 1$ SE = 0.07 ± 0.01; p^{adult} = 0.15 ± 0.02; Table 1), indicating that temporal variation in detectability did not bias abundance data (Fig. 1). Larval and adult survival probabilities were also constant across years ($S^{larva} \pm 1$ SE = 1.00 ± 0.00; S^{adult} = 0.71 ± 0.05), so cannot explain the decline

in adult abundance. However, yearly survival–transition probabilities ($\phi_t^{larva \rightarrow adult}$), the probability of larvae surviving from year t to $t+1$ and metamorphosing to the adult stage, showed a striking downward trend from 2000 to 2003 (Fig. 3).

4. Discussion

My data show a significant decline in adult *G. porphyriticus* abundance over the 12-year study period, and no trend in larval abundance (Fig. 1). Capture probabilities of *G. porphyriticus* larvae and adults did not vary between 1999 and 2004 (Table 1), validating abundance data for that period. I cannot analyze capture probabilities for 2005–2010, but considering the range of abundances in 1999–2004 (Fig. 1) and support for the top capture–mark–recapture model (Table 1), it is unlikely that capture probabilities changed enough to offset overall trends in abundance. The lack of trend in larval abundance is consistent with previous evidence that larval recruitment is partially independent of adult density (Lowe et al., 2004), likely due to the species' long lifespan and iteroparous reproduction (Cole, 1954; Mills, 2007). However, a rapid decline in larval abundance is expected once the adult population reaches a minimum threshold for larval recruitment (Caswell, 2001; Biek et al., 2002). The coefficient of variation (CV) for total *G. porphyriticus* abundance (0.25) was lower than the mean CVs for all amphibian groups analyzed by Green (2003), but it is clear that this lack of variability in abundance does not imply population stability (Fig. 1).

Over the 12-year study period, adult *G. porphyriticus* abundance was negatively related to cumulative annual precipitation (Fig. 2). Annual precipitation is already showing a strong positive trend in the Northeast (www.nhclimateaudit.org) and predicted to increase further with climate change (Hayhoe et al., 2007). However, there was no temporal trend in annual precipitation in northern New Hampshire during the study period. This suggests that the relationship between adult *G. porphyriticus* abundance and annual precipitation was not simply an artifact of temporal trends in those two variables (Graham, 2003), and instead that adult recruitment from July of year $t-1$ to July of year t was reduced by precipitation during the same period.

Capture–mark–recapture modeling revealed a demographic mechanism for the downward trend in adult abundance: a steep decline in the probability of successful metamorphosis (Fig. 3). The probability of larvae surviving metamorphosis to the adult stage ($\phi_t^{larva \rightarrow adult} \pm 1$ SE) dropped from 0.20 (±0.13) in 1999 to 0.00 (±0.00) in 2003 (Fig. 3). If fewer larvae were initiating metamorphosis, then, because larval survival was constant over the first 6 years of the study (Table 1), I would expect larval abundances to increase. But there was no trend in larval abundance (Fig. 1A). Therefore, these results indicate that larvae were initiating metamorphosis, but with increasing probability of dying during transformation (Fig. 3), leading to a decline in recruitment of adults (Fig. 1B). Furthermore, mean adult size increased over the 12-year study period, consistent with reduced recruitment of smaller adults via metamorphosis, and an aging adult population.

Metamorphosis is a vulnerable stage in amphibian life history, when the transition from larval to adult morphology increases susceptibility to biotic and abiotic sources of mortality (Wilbur and Collins, 1973; Wilbur, 1980; Werner, 1986). Recent studies suggest that metamorphosing individuals are most susceptible to infection and mortality by the chytrid fungus *Batrachochytrium dendrobatidis*, which has been implicated in widespread amphibian declines (Briggs et al., 2010; Rosenblum et al., 2010). But extensive sampling by Hossack et al. (2010) showed low prevalence of *B. dendrobatidis* in headwater amphibians, including *G. porphyriticus*. There is little published information on metamorphosis in *G. porphyriticus*

Table 1

Multistate capture–mark–recapture models of yearly larval and adult survival probabilities (S^{larva}, S^{adult}), capture probabilities (p^{larva}, p^{adult}), and larva → adult transition probability ($\psi^{larva \rightarrow adult}$) for *G. porphyriticus* in Merrill Brook, based on data from 1999 to 2004. I compared 32 candidate models and show the 10 best-fitting models here (AIC weight > 0.005).

Model	AIC_c	ΔAIC_c	AIC weight	K
$S^{larva}(\cdot)$, $S^{adult}(\cdot)$, $p^{larva}(\cdot)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(t)$	1367.87	0.00	0.47	9
$S^{larva}(t)$, $S^{adult}(\cdot)$, $p^{larva}(t)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(\cdot)$	1370.57	2.70	0.12	13
$S^{larva}(\cdot)$, $S^{adult}(\cdot)$, $p^{larva}(t)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(t)$	1370.66	2.80	0.12	13
$S^{larva}(\cdot)$, $S^{adult}(\cdot)$, $p^{larva}(t)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(\cdot)$	1371.11	3.25	0.09	5
$S^{larva}(t)$, $S^{adult}(\cdot)$, $p^{larva}(\cdot)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(t)$	1371.64	3.77	0.07	13
$S^{larva}(\cdot)$, $S^{adult}(t)$, $p^{larva}(\cdot)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(t)$	1372.93	5.07	0.04	13
$S^{larva}(t)$, $S^{adult}(\cdot)$, $p^{larva}(\cdot)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(\cdot)$	1373.31	5.44	0.03	9
$S^{larva}(\cdot)$, $S^{adult}(\cdot)$, $p^{larva}(\cdot)$, $p^{adult}(t)$, $\psi^{larva \rightarrow adult}(t)$	1373.77	5.91	0.02	13
$S^{larva}(\cdot)$, $S^{adult}(\cdot)$, $p^{larva}(\cdot)$, $p^{adult}(t)$, $\psi^{larva \rightarrow adult}(\cdot)$	1375.74	7.88	0.01	9
$S^{larva}(\cdot)$, $S^{adult}(t)$, $p^{larva}(t)$, $p^{adult}(\cdot)$, $\psi^{larva \rightarrow adult}(t)$	1375.77	7.91	0.01	17

Notes: Second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), AIC_c weights, and number of estimable parameters (K) are provided for all models. Parameterization for S, p, and ψ is in parentheses: "·" = constant by time (survey year), "t" = variation by time.
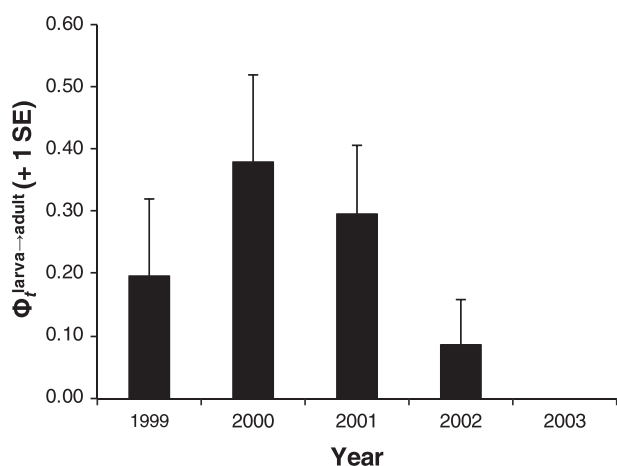

Fig. 3. Capture–mark–recapture estimates of yearly survival–transition probabilities ($\phi_t^{larva \rightarrow adult}$), representing the probability of larvae surviving from year t to year $t + 1$ and metamorphosing to the adult stage.

(Petranka, 1998). However, Bishop (1941) reported that larvae in New York populations transformed from March through October, whereas larvae in southern populations transform during a narrower interval, from late June through late August (Bruce, 1972, 1978, 1980). In Merrill Brook, I captured individuals in both early and middle stages of metamorphosis in June, July, and August of 1999–2004, consistent with Bishop's (1941) observation that metamorphosis can occur in spring through fall in northern populations.

This extended period of metamorphosis in northeastern North America may make *G. porphyriticus* especially vulnerable to mortality from increased precipitation and associated flood events. Recent climatic trends and model predictions for the Northeast indicate that the greatest increases in precipitation will occur in spring and fall, with more frequent floods in headwater systems where precipitation is transmitted rapidly to the stream channel (Post and Jones, 2001; Huntington, 2003; Hayhoe et al., 2007). The recent flooding caused by Hurricane Irene, in September of 2011, underscores this trend. Metamorphosing individuals may be unable to exploit flood-avoidance strategies used by larvae and adults (e.g., burrowing in the stream bed vs. moving to terrestrial refugia, respectively), leading to increased mortality during spring and fall floods, and reducing adult recruitment. My results establish a clear link from survival during metamorphosis to the decline in adult abundance (Figs. 1 and 3), but further work is needed to test this and alternative hypotheses for the steep decline in survival during metamorphosis.

This study assesses long-term population trends in a stream salamander with data from standardized surveys, and with explicit analyses of detection and demography. I found significant declines in recruitment and abundance of *G. porphyriticus* adults that, if they persist, are likely to lead to local extinction. These results also link population decline in *G. porphyriticus* to climate change in the northeastern United States, where increasing precipitation appears to be disrupting hydrologic conditions in the headwater systems that most stream salamanders rely on (Figs. 2 and 3; Petranka, 1998; Meyer and Wallace, 2001). More broadly, this study shows the critical need to expand the taxonomic scope of long-term data on amphibians (Pechmann et al., 1991; Alford and Richards, 1999; Green, 2003). It is sobering to think that North America's stream salamanders may be experiencing gradual declines that, ultimately, will be just as significant as other high-profile amphibian declines (e.g., Lips et al., 2006; Pounds et al., 2006; Wake and Vredenburg, 2008), but are obscured by a lack of data and the secretive habits of these species.

Acknowledgments

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