Seasonal Climate Trends, the North Atlantic Oscillation, and Salamander Abundance in the Southern Appalachian Mountain Region

ROBERT J. WARREN II AND MARK A. BRADFORD

School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut

(Manuscript received 15 March 2010, in final form 18 May 2010)

ABSTRACT

The North Atlantic Oscillation (NAO) is a large-scale climate teleconnection that coincides with worldwide changes in weather. Its impacts have been documented at large scales, particularly in Europe, but not as much at regional scales. Furthermore, despite documented impacts on ecological dynamics in Europe, the NAO's influence on North American biota has been somewhat overlooked. This paper examines long-term temperature and precipitation trends in the southern Appalachian Mountain region—a region well known for its biotic diversity, particularly in salamander species—and examines the connections between these trends and NAO cycles. To connect the NAO phase shifts with southern Appalachian ecology, trends in stream salamander abundance are also examined as a function of the NAO index. The results reported here indicate no substantial long-term warming or precipitation trends in the southern Appalachians and suggest a strong relationship between cool season (November–April) temperature and precipitation and the NAO. More importantly, trends in stream salamander abundance are best explained by variation in the NAO as salamanders are most plentiful during the warmer, wetter phases.

1. Introduction

Increased radiative heating at the earth's surface is driving the mean global temperature upward nearing a rate unseen in 10 000 years (Pachauri and Reisinger 2007). The warming trend explains current large-scale ecological patterns and may also foreshadow what is to come (Root et al. 2003; Walther et al. 2002). However, there exists an enormous discrepancy between mean warming trends at global and regional scales (Hurrell 1995; Pachauri and Reisinger 2007; Parry et al. 2007; Smith et al. 2007). Contributing to this variance are teleconnections: fluctuations in atmospheric circulation patterns that impact multiple regions concurrently (proximate and distant). The El Niño–Southern Oscillation (ENSO) is a well-known teleconnection that incurs worldwide synchronized impacts. These linkages dictate that warming in one region corresponds with cooling in another (Hurrell and Dickson 2004).

The North Atlantic Oscillation (NAO) is a recurrent teleconnection influencing weather throughout western Europe and eastern North America and as far as eastern Asia (Durkee et al. 2008; Hurrell 1995; Hurrell and Dickson 2004). The NAO, which is particularly robust in the Northern Hemisphere winter, is named for the distribution of atmospheric pressure between the Arctic (polar low) and mid-Atlantic (subtropical high) regions. The NAO oscillates between positive and negative phases (corresponding to relative pressure differentials) and the variation in the strength of these lows and highs influences oceanic wind strength and direction, heat and moisture transport, and storm paths and intensities (Durkee et al. 2008; Hurrell and Dickson 2004). These phases vary greatly within and across seasons yet often persist over multiple consecutive years. Since the 1970s, the NAO has tended toward the positive phase, resulting in warmer, wetter winters in northern Europe and eastern North America and colder, drier conditions in southern Europe and North Africa (Durkee et al. 2008; Hurrell 2008; Hurrell and Dickson 2004). Whereas these impacts are well described for European ecology (Stenseth et al. 2002), the NAO influence on North American ecology is relatively unknown.

Teleconnections set up an intriguing conundrum for those interested in explaining and forecasting ecological responses to historical and future climate variation. In looking to explain biological trends, researchers may focus on climate signal trends, but failure to connect

Corresponding author address: Robert J. Warren II, Room 107, 370 Prospect Street, New Haven, CT 06511.
E-mail: hexastylis@gmail.com

DOI: 10.1175/2010JAMC2511.1

ecological and weather patterns may reflect the comprehensive effect of teleconnections (Stenseth et al. 2002) rather than a lack of biological climate response. Variation in the NAO corresponds with variation in the population dynamics of many terrestrial and marine species (see Stenseth et al. 2002 and references therein). The southern Appalachian Mountain region contains a high degree of salamander diversity and biomass, most notably lungless (plethodontid) salamanders (Petranka 1998). What most distinguishes plethodontid salamanders from other salamander families, and amphibians as a whole, is their complete dependence upon cutaneous respiration (i.e., absorption of oxygen via moist skin; Feder and Burggren 1985; Whitford and Hutchinson 1967). Plethodontid salamanders are often the dominant vertebrates in the mesic forests of the eastern United States. (Hairston 1987; Jaeger 1979; Petranka and Murray 2001), with abundance and biomass that equals or surpasses that of small mammals and birds (Burton and Likens 1975). They are sensitive to desiccation caused by low moisture and/or high temperature (Bernardo and Spotila 2006; Bernardo et al. 2007; Feder and Londos 1984; Jaeger 1980; Spotila and Berman 1976; Tilley and Bernardo 1993).

This study examines seasonal variation in temperature and precipitation from 1931 to 2004 in the southern Appalachian region of North Carolina (Southern Blue Ridge physiographic area). The objectives in this paper are to investigate the long-term trends in regional temperature and precipitation and assess the correspondence between southern Appalachian climate trends and the NAO index. The study also examines whether a link exists between variation in the NAO index and local stream salamander abundance.

2. Methods

The southern Appalachian region is the site of a National Science Foundation (NSF) Long-Term Ecological Research (LTER) site (i.e., Coweeta Hydrological Laboratory) and receives the highest precipitation levels in the eastern United States. It is characterized by high endemic diversity and functions as a water source for widespread human development in the surrounding lowlands. Understanding climate patterns and drivers is therefore important both for preserving diversity and assuring water quantity and quality in the region.

a. Climate data

Annual mean monthly temperatures and precipitation totals for the years 1931–2004 were gathered from monthly readings at 11 weather stations located within a 21 000 km^2 area in the southern Appalachian Mountains of North Carolina (Table 1). The climate data for these stations are compiled by the National Climatic Data Center (NCDC; data available online at www.ncdc.noaa.gov), managed by the National Oceanic and Atmospheric Administration (NOAA), and were accessed via the Coweeta LTER Program (data available online at http://coweeta.ecology.uga.edu/ecology/climate/climate.html). Whereas there are more than 11 weather stations within the target area, only those selected had complete temperature and precipitation data for the years 1931–2004. Climate trends were analyzed using temperature and precipitation anomalies from the mean of the base period, 1951–80. The use of anomalies rather than means corrects for spatial variance between weather stations as well as confounding effects from variations in weather station methodology, vegetation, and urbanization (Hansen et al. 1999). To ensure that individual stations did not follow different long-term trends than others within the target region, we analyzed the coefficient of variation between stations as a function of time (1931–2004) and found no trends in temperature or precipitation variance.

Annual climate measures were divided into two seasons—the Northern Hemisphere ''cool season'' (November–April) and ''warm season'' (May–October)—which reduces the impact of weather noise inherent in three-month periods and the impact of seasonal autocorrelation between climate variables and allows the investigation of the influence of large-scale climate drivers such as the North Atlantic Oscillation (sensu Hansen et al. 1999). The NAO index is a dimensionless measure of strength of the North Atlantic Oscillation. It is calculated from the difference between the normalized sea level pressure over Gibraltar and the normalized sea level pressure over southwest Iceland. Monthly NAO index values for the years 1931–2004 were downloaded from the Internet (available online at http://www.cru.uea.ac.uk/cru/data/nao/).

TABLE 1. Southern Appalachian weather stations (North Carolina) used for regional trend analysis.

Station	County	Elev (m)
Andrews	Cherokee	533
Banner Elk	Avery	1142
Boone	Watauga	988
Brevard	Transylvania	674
Cullowhee	Jackson	668
Hendersonville	Henderson	658
Highlands	Macon	1016
Hot Springs	Madison	426
Marshall	Madison	610
Swannanoa	Buncombe	1317
Waynesville	Haywood	810

The salamander abundance data (1976–2007) were collected near Ball Creek (elevation 686 m) at the U.S. Forest Service's Coweeta Hydrologic Laboratory (35°00′N, 83°30′W) and downloaded from the Internet (http://www.unc.edu/~rhwiley/salamandertrends). Four species of *Desmognathus* salamanders (*D. quadramaculatus*, *D. monticola*, *D. ocoee*, and *D. aeneus*) were collected and identified twice per year beginning in 1976. Abundance was estimated as the number of salamanders surveyed per person in 1.5 h of searching from the creek and upslope. See Hairston and Wiley (1993) for more information on methods. Annual (or seasonal average) surveys are reasonable estimates of relative abundance if standardized protocols are used (Smith and Petranka 2000; Welsh and Droege 2001). Whereas these *Desmognathus* species are stream salamanders, making hydroperiod the intuitive direct climate-driven effect (Camp et al. 2007), stream salamanders forage terrestrially (Hairston 1987), the extent of which is governed by temperature and moisture (Camp and Lee 1996; Feder and Londos 1984; Moore and Sievert 2001; Petranka and Smith 2005; Petranka et al. 1994).

b. Data analysis

Time series of seasonal (warm and cool) southern Appalachian temperature and precipitation were analyzed to determine long-term (74 year) trends. The data were modeled using Box–Jenkins autoregressive moving average (ARMA) models (Box et al. 1994) using the R software package (available online at http://www.r-project.org/) to account for the autocorrelation between observations inherent in time series analysis. The autoregressive portion resembles a linear regression of the current time series value against one or more previous values; the moving average is essentially a filtering function that compares the current value against random error in previous values (Shumway and Stoffer 2006). Generalized least squares (GLS) regressions with maximum likelihood were used to analyze the models. The GLS model assumes that errors are correlated and may have unequal variances without assuming linearity in the data. The model order (degree of autocorrelation) was selected based on the autocorrelation (ACF) and partial autocorrelation (PACF) functions (Shumway and Stoffer 2006). The Akaike information criterion (AIC) was used to select models where indications were ambiguous. First- and second-order polynomials were included in the time series models to account for nonlinear, long-term trends. Southern Appalachian temperature, precipitation, and salamander abundance trends as a function of NAO also were modeled using ARMA models.

3. Results

Climate patterns, drivers, and ecological response

Statistically significant, long-term trends in southern Appalachian cool and warm season temperature anomalies were observed (Figs. 1a,b). Relative to the mean of the base period (1951–80), cool season temperatures decreased considerably between 1931 and the 1960s (coefficient = −2.45, standard error SE = 1.2, $t = -2.1$, and $p < 0.05$) and then increased slightly between the 1960s and 2004 (coefficient = 0.006, SE = 0.003, $t = 2.1$, and $p < 0.05$). A similar pattern was observed during the warm season as temperatures decreased significantly between 1931 and the late 1950s (coefficient = −2.36, SE = 0.5, $t = -4.8$, and $p < 0.001$) and then increased slightly between the 1960s and 2004 (coefficient = 0.0006, SE = 0.0003, $t = 4.8$, and $p < 0.001$). The slope coefficients indicate that the cooling trends were far greater than the warming, and cool and warm season temperatures in the latter half of the 1931–2004 study period do not exceed those at the beginning. Interannual variation in cool season temperature anomalies appeared more pronounced than interannual variation in warm season anomalies, which was emphasized by the magnitude of the fluctuations in the 5-yr running means (Figs. 1a,b). In contrast to temperature, there were no long-term trends in precipitation during the 1931–2004 period (Figs. 1c,d). There were no significant temporal trends in precipitation in either cool (coefficient = 1.27, SE = 2.5, $t = 0.5$, and $p > 0.05$) or warm (coefficient = −0.1, SE = 2.1, $t = -0.51$, and $p > 0.05$) seasons as compared with the mean of the base period (1951–80).

Variation in southern Appalachian temperatures varied significantly with the NAO index during the cool season (coefficient = 0.58, SE = 0.1, $t = 4.8$, and $p < 0.001$) (Fig. 2a) but not during the warm season (coefficient = −0.33, SE = 0.4, $t = -0.8$, and $p > 0.05$) (Fig. 2b). As with temperature, southern Appalachian precipitation trends also varied significantly with the NAO index during the cool season (coefficient = 0.72, SE = 0.3, $t = 2.3$, and $p < 0.05$) but not during the warm season (coefficient = −0.47, SE = 0.5, $t = 0.9$, and $p > 0.05$). The correspondence between southern Appalachian temperature and precipitation and shifts in the NAO index also appeared to impact salamander (*Desmognathus* sp.) abundance during the cool season (coefficient = 0.76, SE = 0.4, $t = 1.9$, and $p < 0.05$) but not during the warm season (coefficient = −0.1, SE = 0.5, $t = -0.2$, and $p > 0.05$) (Fig. 3).

4. Discussion

We find that long-term trends in southern Appalachian cool and warm season temperatures are biased

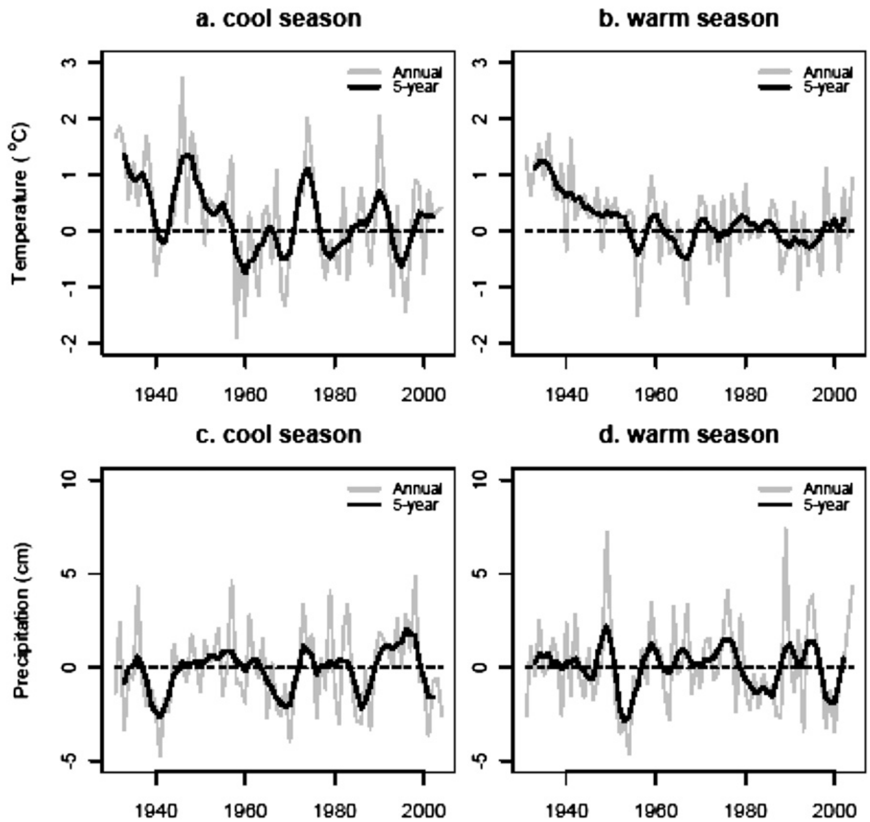

FIG. 1. Southern Appalachian region (top) temperature and (bottom) precipitation trends by cool (left) (November–April) and warm (right) (May–October) seasons. The trends are represented by annual means (gray line) and center-weighted 5-yr means (black line) of southern Appalachian mean temperature and precipitation anomalies (1931–2004). The climate anomalies are the difference between the yearly means and the mean for the base period 1951–80.

toward cooler temperatures since 1931 with a slight leveling in recent decades (Fig. 1). In particular, there is no evidence for an overall warming trend (Figs. 1 and 2). Variation in the southern Appalachian cool season temperature from 1931 to 2004 is significantly related to the decadal oscillations of the NAO index (Fig. 2). During the cool season, when the atmospheric influence of the NAO is strongest, southern Appalachian temperatures rise and fall with atmospheric pressure discrepancies in the North Atlantic summarized as the NAO index. During the warm season, when the influence of the NAO is weak, southern Appalachian temperatures do not correspond with the NAO index. The full impact of this on ecological response is unknown, but only cool season NAO indices statistically correspond with stream salamander abundance (Fig. 3).

Despite pronounced interannual variability in cool and warm season precipitation anomalies, no long-term trends in southern Appalachian precipitation are apparent. Given that increased temperature speeds up the hydrologic cycle, and there is evidence of increased precipitation in the United States that may be linked with global trends (Easterling et al. 2000), this may change in the next century. Cool season precipitation is statistically linked with the NAO index, suggesting that effective prediction of change in this teleconnection may facilitate robust projection of southern Appalachian cool season climate. Variation in the NAO appears to be driven by sea surface temperatures, particularly in tropical waters (Hurrell 2008). A definitive link with anthropogenic climate forcing has not been found, although NAO trends may reflect mean global temperatures (Goodkin et al. 2008). Indeed, as with the unprecedented spike in the rate of global warming, evidence suggests that atmospheric circulation drivers of climate variability (e.g., the NAO) are also beginning to reach intensities anomalous in the long term (Jones and Mann 2004). Positive NAO phases have dominated the oscillation since 1980 at a magnitude unprecedented in the observational and paleoclimatic record (see Hurrell and Dickson 2004),

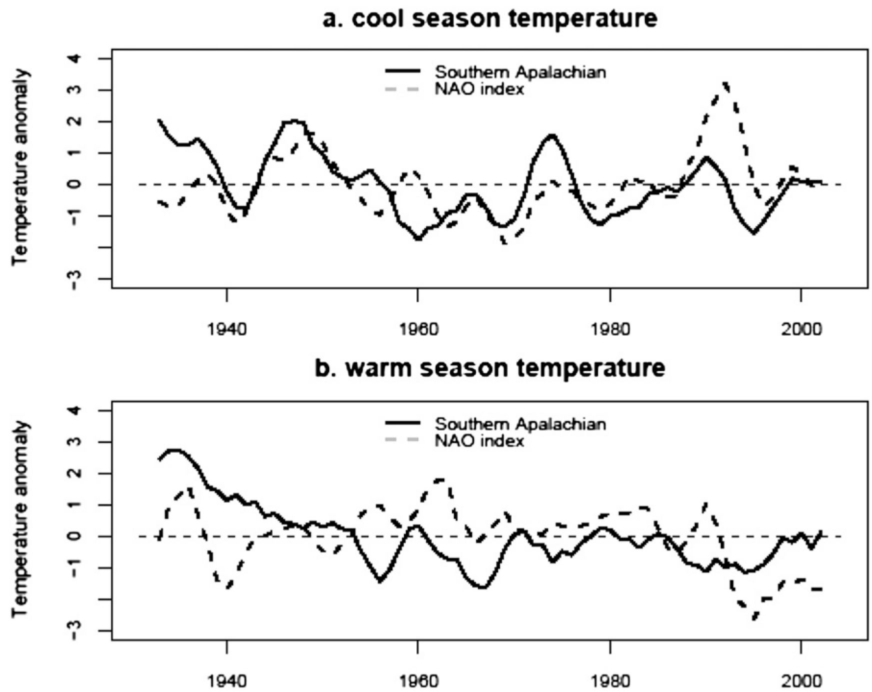

FIG. 2. Standardized anomalies for southern Appalachian (solid line) and NAO index (dashed line) for the years 1931–2004 by (top) cool (November–April) and (bottom) warm (May–October) seasons. The climate anomalies are the difference between the 5-yr weighted means and the weighted mean for the base period 1951–80. The anomalies were standardized to a normal distribution with mean = 0 and standard deviation = 1 to illustrate disparate trends at the same scale.

and this has been linked with warming tropical ocean waters (Hoerling et al. 2001). The uncertainty in whether there will be reinforcement or weakening of this oscillation trend means that ecologists need to consider multiple climate change scenarios to facilitate projection of possible ecological response in the southern Appalachians, as well as other regions around the world where climate is strongly influenced by teleconnections.

That stream salamander abundance in the southern Appalachians corresponds with variation in the NAO highlights the possibility that changes in the frequency and amplitude of the NAO have profound impacts on southern Appalachian biota, as it does on biota throughout the North Atlantic basin (Stenseth et al. 2002). Salamander abundance likely responds positively to positive NAO anomalies because warmer and wetter cool seasons facilitate overwintering survival and/or increase spring foraging (Bernardo and Spotila 2006; Bernardo et al. 2007; Camp et al. 2007; Marshall and Camp 2006). Walls (2009) attempted to correlate statistically (without accounting for temporal autocorrelation) southern Appalachian terrestrial plethodontid salamander hybrid zone data with annual regional temperature trends, but only found a weak temperature correlation with the high elevation species and not its putative hybrid. In doing so, this may obscure actual seasonal trends driven by regional climate within the context of teleconnection oscillations. The period observed by Walls (2009), 1974–90, coincides with a particularly biased phase of the NAO, and thus a species shift may actually reflect any or all of the multiple climate variables that shift in concert with the NAO (Huntley et al. 1995).

The 2007 IPCC synthesis report (Pachauri and Reisinger 2007) states that ecological impact research is hampered by uncertainties surrounding regional projections of climate change. The uncertainty concerning climate drivers has a substantial impact on climate projection. Indeed, a dizzying selection of climate prediction models outline scenarios for future climate (Parry et al. 2007), and selection of the climate projection is critical in assessing the potential impact on species (Beaumont et al. 2008). For the southeastern U.S. region, not enough of the global climate models predict congruent precipitation patterns to estimate reliably future patterns (Pachauri and Reisinger 2007). The southern Appalachian region has yet to experience the recent, pronounced warming trend exhibited at the global scale, and predicted outcomes for this region vary greatly per model. Thus,

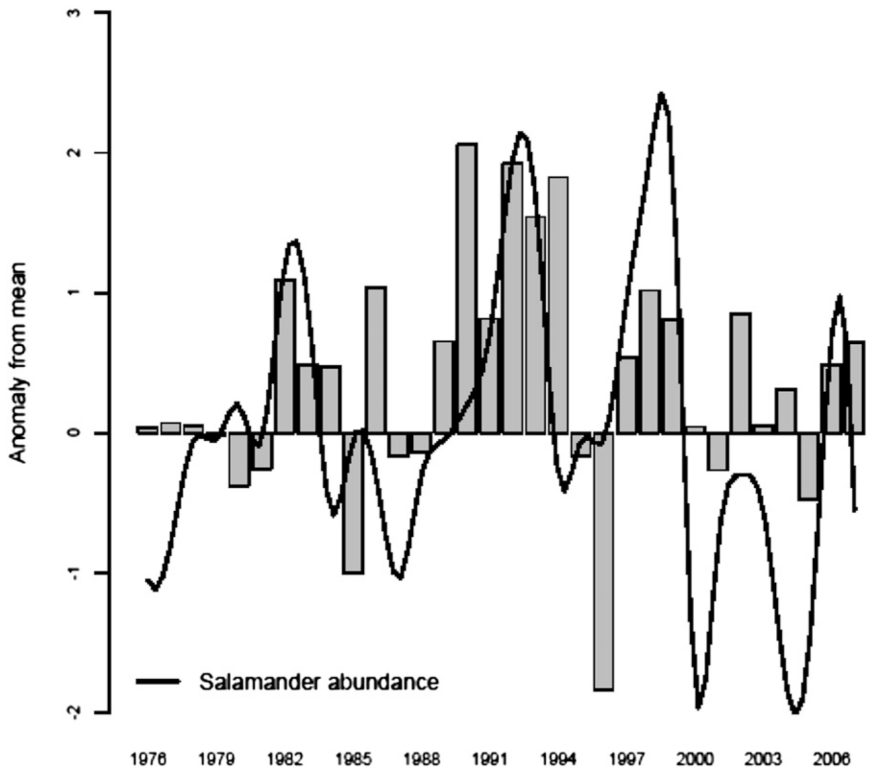

FIG. 3. NAO index phase anomalies (bar plots) overlain by anomalies in southern Appalachian plethodontid abundance (line). The NAO index and salamander abundance anomalies are the difference between the yearly means and overall means. Positive NAO index anomalies are associated with warmer, wetter winters in the eastern United States.

models that project rapid warming and drying by the end of the century may better fit global than southern Appalachian trends.

Acknowledgments. Publication was based on research conducted in or near the Coweeta Basin and used datasets whose collection was supported by National Science Foundation grants to the Coweeta LTER program, under which the current work was performed. We thank the National Climatic Data Center, the Coweeta Long Term Ecological Research (LTER) Program, the Climatic Research Unit of the University of East Anglia, and Haven Wiley for making public the data used for this research.

REFERENCES

Beaumont, L. J., L. Hughes, and A. J. Pitman, 2008: Why is the choice of future climate scenarios for species distribution modelling important? *Ecol. Lett.,* **11,** 1135–1146.

Bernardo, J., and J. R. Spotila, 2006: Physiological constraints on organismal response to global warming: Mechanistic insights from clinally varying populations and implications for assessing endangerment. *Biol. Lett.,* **2,** 135–139.

——, R. J. Ossola, J. Spotila, and K. A. Crandall, 2007: Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: Validation of an intrinsic determinant of macroecological and phylogeographic structure. *Biol. Lett.,* **3,** 695–698.

Box, G. E. P., G. M. Jenkins, and G. C. Reinsel, 1994: *Time Series Analysis: Forecasting and Control*. 3rd ed. Prentice Hall, 598 pp.

Burton, T. M., and G. E. Likens, 1975: Salamander populations and biomass in Hubbard Brook Experimental Forest, New Hampshire. *Copeia,* **1975,** 541–546.

Camp, C. D., and T. P. Lee, 1996: Intraspecific spacing and interaction within a population of *Desmognathus quadramaculatus*. *Copeia,* **1996,** 78–84.

——, D. L. Huestis, and J. L. Marshall, 2007: Terrestrial versus aquatic phenotypes correlate with hydrological predictability of habitats in a semiterrestrial salamander (Urodela, Plethodontidae). *Biol. J. Linn. Soc.,* **91,** 227–238.

Durkee, J. D., J. D. Frye, C. M. Fuhrmann, M. C. Lacke, H. G. Jeong, and T. L. Mote, 2008: Effects of the North Atlantic Oscillation on precipitation-type frequency and distribution in the eastern United States. *Theor. Appl. Climatol.,* **94,** 51–65.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns, 2000: Climate extremes: Observations, modeling, and impacts. *Science,* **289,** 2068–2074.

Feder, M. E., and P. L. Londos, 1984: Hydric constraints upon foraging in a terrestrial salamander, *Desmognathus ochrophaeus* (Amphibia: Plethodontidae). *Oecologia,* **64,** 413–418.

——, and W. W. Burggren, 1985: Cutaneous gas exchange in vertebrates: Design, patterns, control and implications. *Biol. Rev.,* **60,** 1–45.

Goodkin, N. F., K. A. Hughen, S. C. Doney, and W. B. Curry, 2008: Increased multidecadal variability of the North Atlantic Oscillation since 1781. *Nat. Geosci.,* **1,** 844–848.

Hairston, N. G., 1987: *Community Ecology and Salamander Guilds.* Cambridge University Press, 230 pp.

——, and R. H. Wiley, 1993: No decline in salamander (Amphibia: Caudata) populations: A twenty-year study in the Southern Appalachians. *Brimleyana,* **18,** 59–64.

Hansen, J., R. Ruedy, J. Glascoe, and M. Sato, 1999: GISS analysis of surface temperature change. *J. Geophys. Res.,* **104,** 30 997–31 022.

Hoerling, M. P., J. W. Hurrell, and T. Y. Xu, 2001: Tropical origins for recent North Atlantic climate change. *Science,* **292,** 90–92.

Huntley, B., P. M. Berry, W. Cramer, and A. P. McDonald, 1995: Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J. Biogeogr.,* **22,** 967–1001.

Hurrell, J. W., 1995: Decadal trends in the North Atlantic Oscillation—Regional temperatures and precipitation. *Science,* **269,** 676–679.

——, 2008: Decadal climate prediction: Challenges and opportunities. *J. Phys.,* **125,** 12–18.

——, and R. R. Dickson, 2004: Climate variability over the North Atlantic. *Marine Ecosystems and Climate Variation: The North Atlantic: A Comparative Perspective,* N. C. Stenseth et al., Eds., Oxford University Press, 15–32.

Jaeger, R. G., 1979: Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. *Herpetologica,* **35,** 90–93.

——, 1980: Microhabitats of a terrestrial forest salamander. *Copeia,* **1980,** 265–268.

Jones, P. D., and M. E. Mann, 2004: Climate over past millennia. *Rev. Geophys.,* **42,** RG2002, doi:10.1029/2003RG000143.

Marshall, J. L., and C. D. Camp, 2006: Environmental correlates of species and genetic richness in lungless salamanders (family *Plethodontidae*). *Acta Oecol.,* **29,** 33–44.

Moore, M. M., and L. M. Sievert, 2001: Temperature-mediated characteristics of the dusky salamander (*Desmognathus fuscus*) of southern Appalachia. *J. Therm. Biol.,* **26,** 547–554.

Pachauri, R. K., and A. Reisinger, Eds., 2007: *Climate Change 2007: Synthesis Report*. IPCC, 104 pp. [Available online at http://www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_synthesis_report.htm.]

Parry, M. L., O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, Eds., 2007: *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Cambridge University Press, 992 pp.

Petranka, J. W., 1998: *Salamanders of the United States and Canada*. Smithsonian Institute Press, 587 pp.

——, and S. S. Murray, 2001: Effectiveness of removal sampling for determining salamander density and biomass: A case study in an Appalachian streamside community. *J. Herpetol.,* **35,** 36–44.

——, and C. K. Smith, 2005: A functional analysis of streamside habitat use by southern Appalachian salamanders: Implications for riparian forest management. *For. Ecol. Manage.,* **210,** 443–454.

——, M. P. Brannon, M. E. Hopey, and C. K. Smith, 1994: Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *For. Ecol. Manage.,* **67,** 135–147.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds, 2003: Fingerprints of global warming on wild animals and plants. *Nature,* **421,** 57–60.

Shumway, R. H., and D. S. Stoffer, 2006: *Time Series Analysis and its Applications: With R Examples*. Springer, 575 pp.

Smith, C. K., and J. W. Petranka, 2000: Monitoring terrestrial salamanders: Repeatability and validity of area-constrained cover object searches. *J. Herpetol.,* **34,** 547–557.

Smith, D. M., S. Cusack, A. W. Colman, C. K. Folland, G. R. Harris, and J. M. Murphy, 2007: Improved surface temperature prediction for the coming decade from a global climate model. *Science,* **317,** 796–799.

Spotila, J. R., and E. N. Berman, 1976: Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comp. Biochem. Physiol.,* **55,** 407–411.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima, 2002: Ecological effects of climate fluctuations. *Science,* **297,** 1292–1296.

Tilley, S. G., and J. Bernardo, 1993: Life history evolution in Plethodontid salamanders. *Herpetologica,* **49,** 154–163.

Walls, S. C., 2009: The role of climate in the dynamics of a hybrid zone in Appalachian salamanders. *Global Change Biol.,* **15,** 1903–1910.

Walther, G. R., and Coauthors, 2002: Ecological responses to recent climate change. *Nature,* **416,** 389–395.

Welsh, H. H., and S. Droege, 2001: A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conserv. Biol.,* **15,** 558–569.

Whitford, W. G., and V. H. Hutchinson, 1967: Body size and metabolic rate in salamanders. *Physiol. Zool.,* **40,** 127–133.