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Authors: Luhring, Thomas M., Wszola, Lyndsie S., Connette, Grant M., and Schalk, Christopher M.

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Thomas M. Luhring,[1,2,7,8] Lyndsie S. Wszola,[3,7] Grant M. Connette,[4,5] and Christopher M. Schalk[6]

[1]*Biological Sciences, Wichita State University, Wichita, Kansas, USA 67260*
[2]*Savannah River Ecology Laboratory, University of Georgia, Aiken, South Carolina, USA 29802*
[3]*Biological Sciences, University of Nebraska, Lincoln, Nebraska, USA, 68588*
[4]*Working Land and Seascapes, Conservation Commons, Smithsonian Institution, Washington DC, USA, 20013*
[5]*Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, Virginia, USA, 22630*
[6]*Arthur Temple College of Forestry and Agriculture, Stephen F. Austin University, Nacogdoches, Texas, USA, 75962*

ABSTRACT.—Many aquatic organisms are experiencing increasingly severe and frequent droughts and drying events. Simultaneously, drought effects are carrying over to nondrought years as ecosystems remain in incomplete states of recovery. Aquatic organisms are thus faced with fewer sequential years under degraded environmental conditions to prepare for increasingly severe droughts and potential drying events. We assessed the effect of droughts and sex on the growth, mass, and mass-dependent estivation potential of long-lived aquatic salamanders (Greater Sirens, *Siren lacertina*) that estivate during drying events brought on by severe droughts. We calculated growth rates of *S. lacertina* based on mark–recapture data spanning 11 yr of a severe drought local minimum (of past 50 yr) in the southeastern United States. Sirens showed a distinct seasonal gain in body length and mass from March through September and little growth for the rest of the year. Gains during the growth season were strongly reduced by drought conditions. Although male and female sirens were predicted to reach a similar maximum body size, females grew much slower. Recruitment into drying event "size refugia" is constrained by drying event severity (determines minimum size required), frequency (determines available time between events to grow), and environmental conditions between drying events (determines the rate of growth). Thus, increases in drying event severity and frequency will require faster growth to a larger body size for successful recruitment into a size class that is resistant to drying events. The slower growth of females and reduction of growth during suboptimal years (mild to moderate droughts) suggest that the life history strategy of Greater Sirens for persisting through drying events potentially increases their demographic susceptibility to the predicted effects of climate change.

Anthropogenic climate change continues to increase the frequency and severity of climatic events (IPCC, 2014), leading to globally pervasive alterations of organismal ecology and evolution (Parmesan and Yohe, 2003; Scheffers et al., 2016). Drier and warmer conditions are increasing the global footprint of ecosystems in a chronic state of incomplete drought recovery (Schwalm et al., 2017). Despite potential ambiguity in global drought patterns (Sheffield et al., 2012; Trenberth et al., 2014), certain regions of the world are projected to experience further increases in both drought severity and frequency (Overpeck and Udall, 2010; Cook et al., 2015; Touma et al., 2015). In aquatic habitats, droughts (periods of below average rainfall) often lead to drying events (lack of surface water). Wetlands naturally experience cycles of inundation and drying, which is a dynamic to which many animals have adapted (Gehlbach et al., 1973; Buhlmann et al., 2009; Winne et al., 2010). However, emerging drought patterns of increased duration and severity are increasingly divergent from species' evolutionary history, posing a novel challenge for strategies evolved over long timespans in dynamic wetland systems. Although there are myriad studies on the acute effects of drying events or periodic droughts on vertebrates, the chronic effects of repeated droughts on the capacity of estivating vertebrates to persist through drying events are largely unknown.

The demographic resilience of organisms to drought—the ability of a population to grow or maintain itself at a sustainable size under increasing climate stress—is shaped by their life history and past evolutionary responses to localized climatic regimes. As droughts intensify and local resources dwindle, organisms with higher motility and desiccation resistance can potentially disperse over land to other aquatic habitats (Gibbons et al., 1983; Willson et al., 2006; Luhring et al., 2011; Boersma and Lytle, 2014). However, those reliant on aquatic corridors for dispersal (e.g., Schalk and Luhring, 2010) become isolated in drying pools and depend on physiological mechanisms to survive drying events (Willson et al., 2006; Luhring and Holdo, 2015; Vogrinc et al., 2018; Hopper et al., 2020).

Several aquatic vertebrates estivate underground to cope with periodic short-term drying events (Gehlbach et al., 1973; Fishman et al., 1986; Buhlmann et al., 2009; Luhring and Todd 2010). However, prolonged drying events cause mortality that is often predictably linked to traits such as body size (Winne et al., 2010; Luhring and Holdo, 2015). Both droughts and drying events generally shift body size distributions to smaller individuals by selecting against the higher total metabolic costs of larger individuals (Buhlmann et al., 2009; Winne et al., 2010; Sheridan and Bickford, 2011). Alternatively, larger body size can be advantageous if the higher metabolic demand is outpaced by added energetic reserves (Etheridge, 1990; Luhring and Holdo, 2015). Because ectotherms rely entirely on stored energy reserves and are unable to accrue more resources during torpor (Gehlbach et al., 1973; Fishman et al., 1986; Etheridge, 1990; Staples, 2016), their ability to survive for some period of time in estivation depends upon their condition entering the drying event.

Greater Sirens, *Siren lacertina*, are long-lived large aquatic salamanders found throughout the southeastern United States that reach high population densities and are well-adapted to persisting in semipermanent wetlands (Snodgrass et al., 1999; Sorensen, 2004; Luhring 2008; Schalk et al., 2010). These aquatic

salamanders lack a terrestrial life stage and are poor overland dispersers even under ideal conditions (Schalk and Luhring, 2010). Thus, they persist through wetland drying events by estivating underground (Gehlbach et al., 1973). In *S. lacertina*, increased body size coincides with a higher proportion of body mass allocated to endogenous energy reserves (lipids) used to persist during estivation (Etheridge, 1990). Small sirenids can estivate through shorter drying events (Luhring and Todd, 2010) but are extirpated during prolonged drying events (Luhring and Holdo, 2015). Larger sirens enter "size refugia"—a range of body sizes above the threshold required to estivate through a given drying event—upon accruing enough mass (Luhring and Holdo, 2015). Field-estimated growth rates indicate that the minimum size threshold for severe drying events requires multiple years of growth (Luhring and Holdo, 2015). In this study, we investigated the effects of drought on individual growth rates in a population of Greater Sirens. The study period included over 11 yr characterized by droughts and drying events of varying severity, including one of the longest and most severe local droughts on record. We leverage drought-informed models of siren growth to project the consequences of drought severity on sex-specific recruitment into size classes that can survive periodic drying events.

MATERIALS AND METHODS

Study Site.—Sirens were collected as part of an ongoing long-term mark–recapture study at Dry Bay, a hydrologically isolated 5-ha Carolina bay depressional wetland, located on the United States Department of Energy's Savannah River Site (SRS) in Aiken County, South Carolina (Luhring, 2008; Luhring and Holdo, 2015). Dry Bay is one of the most permanent Carolina bays on the SRS and retains water year-round except during severe droughts (Luhring and Holdo, 2015).

Sampling and Marking.—Sirens were sampled with five types of passive sampling traps to facilitate capturing individuals of a variety of sizes without damaging their habitat (Luhring 2008; Luhring and Jennison, 2008; Luhring et al., 2016). Although these traps individually have strong size biases, their combined use results in the capturability of all but the smallest individuals (<~80 mm snout–vent length [SVL]) (Luhring et al., 2016). After capture, all sirens were taken to the lab, measured, weighed, marked, and returned to their place of capture within the same day (details in Luhring, 2008). Sirens greater than ~185 mm SVL were marked by injecting a sterile passive integrative transponder (PIT) tag into the ventral region of the tail posterior to the vent (Luhring, 2009).

Growth Analysis.—We fit a hierarchical growth model to simultaneously assess changes in individual length and mass during both drought and nondrought periods. Growth models generally predict length or mass as a function of time *t* (e.g., size at age *t*). Fitting these models requires individual measurements of length at known ages. Because there are no available methods for determining the chronological age of captured sirens, we instead implemented a mark–recapture growth model. The mark–recapture growth model predicts the change in length over time of a marked individual (of known size but unknown age) between trapping surveys. Because sampling surveys did not occur during regular intervals, this model portrays time as intervals of summer (April–September) and winter (October–March, when growth was near 0) days (each parameterized for specific growth rates) rather than a linear representation of age. This approach yields required parameter values to predict long-

term growth in variable environments (e.g., seasonality and drought conditions) while a facilitating statistical analysis of marked individuals at unknown ages.

We represented changes in length over time using an individual growth model fit to SVL measurements taken during repeated captures of individual sirens (Fabens, 1965). The basic mark–recapture formulation of the growth function followed the form

$$L_{i,t} = L_{i,t-1} + (L\infty - L_{i,t-1}) \times (1 - \exp[-K \times \Delta_t]) \qquad (1)$$

where $L_{i,t}$ represents the length of individual *i* at survey *t*, $L_{i,t-1}$ represents the individual's length at survey $t - 1$, and Δ_t represents the elapsed time between surveys *t* and $t - 1$ (Equation 1). The asymptotic size parameter, $L\infty$, represents the maximum length that individuals approach as they age, whereas the growth coefficient, *K*, governs how quickly individuals approach asymptotic size. Similar to Muñoz et al. (2016) and Rose et al. (2018a), we modified this basic growth function to allow for variation in asymptotic size and growth coefficients in relation to modeled covariates. We modeled growth trajectories as a function of sex, season, and drought conditions

$$L_{i,t} = L_{i,t-1} + (L\infty_{Sex}i - L_{i,t-1})$$
$$\times \left(1 - \exp\left[-Ks_{i,t} \times \left\{\frac{\Delta s_t}{365}\right\} - Kw \times \left\{\frac{\Delta w_t}{365}\right\}\right]\right) \qquad (2)$$

where Δs_t represents the number of summer (active season) days and Δw_t represents the number of winter (inactive season) days between surveys *t* and $t-1$ (Equation 2). We accounted for differences in asymptotic length between males and females by incorporating sex-specific asymptotic size parameters, using Bayesian interpolation to impute the sex for individuals of unknown sex while accounting for uncertainty (e.g., Rose et al., 2018b). We also assumed the summer growth coefficient, $Ks_{i,t}$, varies in relation to both the sex of individual *i* and the Palmer Drought Severity Index (PDSI) at survey *t*

$$Ks_{i,t} = \alpha_0 + \alpha_1 \times Sex_i + \alpha_2 \times PDSI_t \qquad (3)$$

but treated winter growth as constant because it is expected to be near zero with little or no detectable difference in relation to sex or drought (Equation 3). Because PDSI is available on a monthly basis and reflects longer-term drought conditions, we assume that PDSI at survey *t* is a reasonable approximation for relative aquatic resource availability in our system over the interval between surveys *t* and $t - 1$. Finally, we assumed normal random error in observed SVL measurements to account for both measurement error and individual-level deviations in length from the population-level mean, where σ^2 represents the variance in length (Equation 4).

$$SVL_{i,t} \sim Normal(L_{i,t}, \sigma^2) \qquad (4)$$

We then modeled individual body mass (g) by using the log transformation of a basic allometric scaling function, $W = a \times L^b$ (Le Cren, 1951), where *W* represents weight, *L* indicates length, and *a* and *b* are the scaling constant and exponent, respectively (Equation 5).

$$\log(W_{i,t}) = \log(a_{i,t}) + b \times \log(L_{i,t}) \qquad (5)$$

We estimated effects of sex and drought on body condition by modeling the allometric scaling constant, *a*, as a log-linear function of sex and drought (PDSI) (Equation 6).

TABLE 1. Parameter means and 95% credible intervals from our Greater Siren, *Siren lacertina*, growth model for length (SVL, mm) and mass (g). Prob(X > 0) gives the proportion of the marginal posterior distribution for a given parameter that is greater than 0. Values close to 0 and 1 indicate high probabilities of nonzero effects. τ is precision, equal to $1/$variance. T(0,) indicates truncation to only values >0, and T(0.0001,) indicates truncation to only values >0.0001. Note that PDSI scales positively with α_2 values because positive values represent wetter years and negative values are drier years.

Parameter	Prior	Mean	2.5% CI	97.5% CI	Prob(X > 0)
Female asymptotic length ($L\infty_{Female}$)	Normal($\mu = 450, \tau = 0.0001$)T(0,)	511.85	467.80	577.86	
Male asymptotic length ($L\infty_{Male}$)		511.04	491.55	536.98	
Effect of sex (male) on asymptotic length ($L\infty_{Male} - L\infty_{Female}$)	Normal($\mu = 0, \tau = 0.0001$)	−0.81	−73.22	47.69	0.45
Female summer growth intercept (α_0)	Normal($\mu = 0.2, \tau = 0.01$)	0.37	0.27	0.48	
Effect of sex (male) on summer growth (α_1)	Normal($\mu = 0, \tau = 0.01$)	0.22	0.13	0.32	1.00
Effect of PDSI on summer growth (α_2)	Normal($\mu = 0, \tau = 0.01$)	0.15	0.09	0.21	1.00
Winter growth (K_w)	Normal($\mu = 0.1, \tau = 0.01$)T(0,)	0.06	0.01	0.13	
Residual error for length ($1/\sigma^2$)	Gamma($r = 1, \lambda = 0.001$)	0.14	0.12	0.17	
Log-scale female mass intercept (β_0)	Normal($\mu = -10, \tau = 0.01$)	−13.05	−13.37	−12.74	
Effect of sex (male) on log-scale mass (β_1)	Normal($\mu = 0, \tau = 0.01$)	0.10	0.08	0.13	1.00
Effect of PDSI on log-scale mass (β_2)	Normal($\mu = 0, \tau = 0.01$)	0.01	−0.01	0.02	0.85
Residual error for log-mass ($1/\gamma^2$)	Gamma($r = 1, \lambda = 0.001$)	84.60	72.92	97.47	
Length-mass allometric scaling exponent (b)	Normal($\mu = 3, \tau = 0.01$)T(0.0001,)	3.22	3.17	3.29	

$$\log(a_{i,t}) = \beta_0 + \beta_1 \times Sex_i + \beta_2 \times PDSI_t \qquad (6)$$

Thus, drought may affect body mass both indirectly through its effect on length and directly through its effect on body condition (i.e., mass per unit length). Finally, we assumed that measured (log-scale) mass includes normal random error with variance γ^2 (Equation 7).

$$\log(Mass_{i,t}) \sim Normal\left(\log(W_{i,t}), \gamma^2\right) \qquad (7)$$

We performed a Bayesian analysis of this hierarchical model using Markov chain Monte Carlo simulation, assuming non-informative or weakly informative priors for all model parameters (Table 1). All models were fit in the JAGS software using the jagsUI package in the R statistical environment (Plummer, 2003; Kellner, 2019; R Core Team, 2020). We estimated parameter means and credible intervals (CIs) by using 7,500 draws from the joint posterior distribution. We evaluated model convergence by using the Gelman-Rubin statistic ($\hat{R}<1.1$; Brooks and Gelman, 1998). We summarized model results by using the mean and 95% credible intervals. We then estimated estivation potential using a deterministic function per Etheridge (1990) as

$$P_{i,t} = 145.63 + 0.3701 \times W_{i,t} + 0.0002 \times W_{i,t}^2 \qquad (8)$$

to generate corresponding estimates for the number of dry days individuals can survive based on their mass.

To project the effects of moderate droughts (those not leading to a drying event) on survival during prolonged drying events, we simulated the accrual of estivation potential (number of days an individual could survive given their current body mass) for individuals across a continuum of drought patterns. PDSI over the course of the study (September 2006–January 2016) ranged from −4.7 to 3.8 (−0.7 ± 1.6, mean ± SD) (Fig. 1). Out of the 113 mo, 40 were nondrought months (PDSI > 0) and 73 were drought months (PDSI < 0) with an average drought month having a PDSI of −1.7 ± 1.0. We projected daily sex-specific age-length, age-mass, and age-estivation potential relationships across 10 yr for sirens experiencing a continuum of recurring drought durations (0, 30, 60, 90, 120, or 150 drought days) during the growing season (214 days; March–September). We used moderate drought (−2 PDSI) values for drought days because Dry Bay held water under these conditions, but siren growth was reduced relative to nondrought years. All non-drought days during the growing season were set to conditions of an average year (0 PDSI). Although PDSI values were dynamic across time (Fig. 1), the static PDSIs in the projection model created a gradient of growth curves that encapsulate a range of responses across 10 consecutive years without a drying event. The 10-yr cutoff for simulations reflects that drying events occur on an approximately decadal basis at Dry Bay (Luhring and Holdo, 2015). We simulated length, mass, and estivation potential on each day by calculating daily growth as a function of sex, drought conditions (PDSI = 0 on a nondrought day and −2 on a drought day), and season-specific length and mass coefficients. Drought days occurred at the beginning of each summer growth season. We estimated somatic growth trajectories for all ages and model iterations and then extracted means and 95% credible intervals of length, mass, and estivation potential on each day to ensure the appropriate propagation of uncertainty.

RESULTS

Captures.—We recorded 827 total captures with a mean (SD) SVL of 330 mm (84.9) and mass of 388.2 g (306.8). Data from 430 total captures of 138 recaptured individuals were used for mark–recapture growth rate analysis. Of these individuals, 9 were identified as female and 19 as male through dissection, deposition of eggs in captivity, or definitive secondary sexual characteristics (large males have enlarged masseters and broad tail fins). The mean (SD) SVL and mass of recaptured individuals used in the analyses were 347.4 mm (75.9) and 422.0 g (293.9). The smallest recorded reproductive female was 273 mm in SVL and had an estimated age of 3.0 yr (CI = 2.4, 3.8) according to the growth model (see *Simulated Projections* and supplementary tables).

Age-Specific Length, Mass, and Estivation Potential.—Males grew more quickly than females but were predicted to have roughly the same asymptotic size (Table 1). Both sexes grew more quickly in the summer months than in the winter months and under nondrought conditions (PDSI ≥ 0) than in drought conditions (PDSI < 0) (Table 1).

Simulated Projections.—The overall slower growth rates of females were further depressed by increasingly severe droughts (periods of reduced rainfall and suboptimal aquatic conditions, not necessarily leading to drying events) (Fig. 2b, d). The
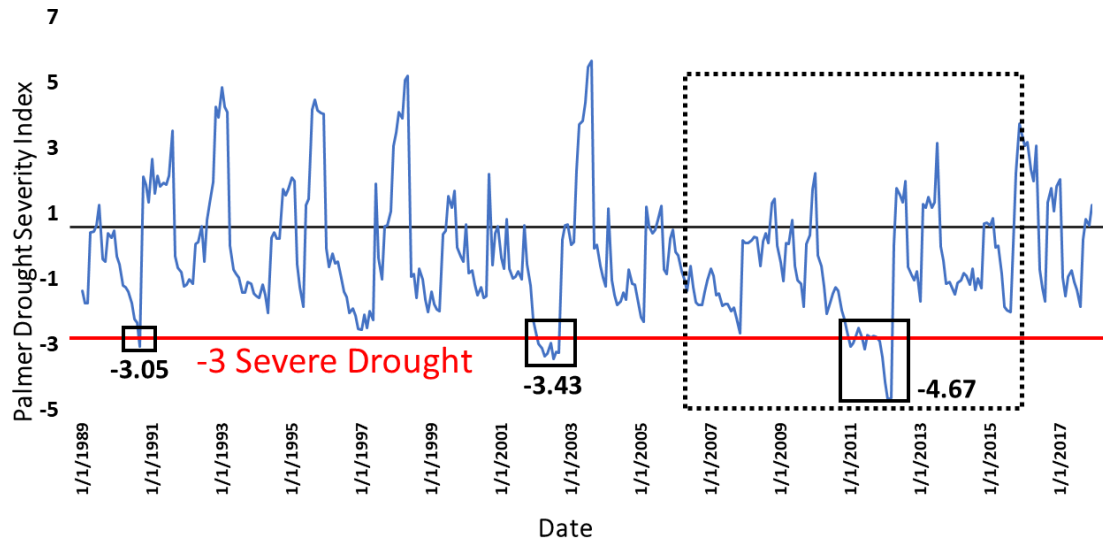
FIG. 1. Palmer Drought Severity Index (PDSI) values encompassing three severe droughts that led to known drying events at Dry Bay. PDSI values of −3 (red line) or lower are associated with known drying events (roughly enclosed by black boxes) at Dry Bay. Growth data used for the model were collected during the time period enclosed in the dashed box.

consequences of drought-induced reductions in annual growth and subsequent reductions in mass accrual and estivation potential were readily apparent for males and females (Fig. 2). However, the effects of sex and drought on growth rate, mass, and subsequent estimated estivation potential were particularly severe in females (Fig. 2). For example, a 6-yr-old male siren that had lived its life completely under average conditions (PDSI = 0) would be an estimated 456.9 mm (CI = 444.2, 467.9) SVL, 900.2 g (CI = 816.9, 975.2), and have an average estivation potential of 640.8 days (CI = 581.4, 696.8) (Supplemental Table S1). In contrast, a 6-yr-old female siren that had lived every growing season of its life under mild drought conditions (PDSI = −2) would be an estimated 269.8 mm (CI = 233.0, 300.3) SVL, 150.5 g (CI = 92.1, 210.5) mass, and an estivation potential of 205.8 days (CI = 181.4, 232.4) (Supplemental Table S2). This estivation potential would be well short of the last three decadal drying events at Dry Bay that lasted from 1.25 to 1.6 yr (Luhring and Holdo, 2015).

DISCUSSION

Although mild-to-moderate droughts may not dry out more permanent wetlands, they increase the demographic vulnerability of *S. lacertina* to future drying events by lowering somatic growth rates and the accrual of endogenous energetic reserves. Moreover, sexually dimorphic growth rates (not maximum size) exacerbate negative effects of drought on females by increasing the time needed to accrue enough mass to survive through a given drying event (Fig. 3). Males growing under nondrought conditions are projected to recruit into size refugia big enough to survive a 1.5-yr drying event in approximately 5 yr. Females growing under the same conditions would take approximately 9 yr to reach the same minimum size (Fig. 3). Drought conditions are highly dynamic across time (Fig. 1), and projections of individual growth across time with a static PDSI value are overly simplistic. Rather, projections of constant conditions (e.g., Fig. 2, 3) serve as reference lines for potential outcomes under poorer conditions during years without drying events. Although moderate droughts may not lead to drying events, they still reduce the amount of growth and potential demographic

resilience of populations that rely on accrued endogenous resources to estivate. These reduced growth rates are especially concerning for females (e.g., females under drought conditions would not recruit to a 1.5-yr drying event size refugium within the 9-yr interval last experienced at Dry Bay) (Fig. 3). Growing larger to persist through episodic environmental selective events is a successful strategy under climatic regimes experienced in recent evolutionary history. However, giving up near-term reproductive opportunities to invest in long-term survival is a gambit that depends on the relative success of future reproductive output. Consequently, populations that delay maturation become increasingly sensitive to lowered juvenile survivorship (Congdon et al., 1993). If increasingly longer drying events select for accruing more energetic reserves and delaying maturation, the number of uninterrupted sequential growth years required to recruit into a larger size refugia will subsequently increase. Given the expected increase in both drought frequency and severity in many parts of the world (Overpeck and Udall, 2010), this strategy faces a sort of ecological catch-22—becoming more resilient to increasingly severe drying events necessarily increases demographic vulnerability to increasing drying event frequency.

Ecosystem resilience and recovery time from drought conditions further compound the linked constraints imposed by drought frequency and severity. Although droughts that result in wetland drying represent spatiotemporally acute events from the perspective of the population, the conditions in the intervening time between drying events are essential for animals to accrue resources and recruit into drought-resistant states (e.g., condition, age, and mass). Given increasing recovery times from droughts and decreased time between them, ecosystems are increasingly operating at an incomplete state of recovery characterized by reduced gross primary productivity (Overpeck and Udall, 2010; Cook et al., 2015; Touma et al., 2015; Schwalm et al., 2017). In the years between drying events, *S. lacertina* growth rates (and thus accumulated estivation potential) changed with regional drought indices. In years with less optimal conditions, growth rates were lower, and this corresponded to especially severe reductions in female estivation potential (Fig. 2; supplemental Tables S1, S2). The length of
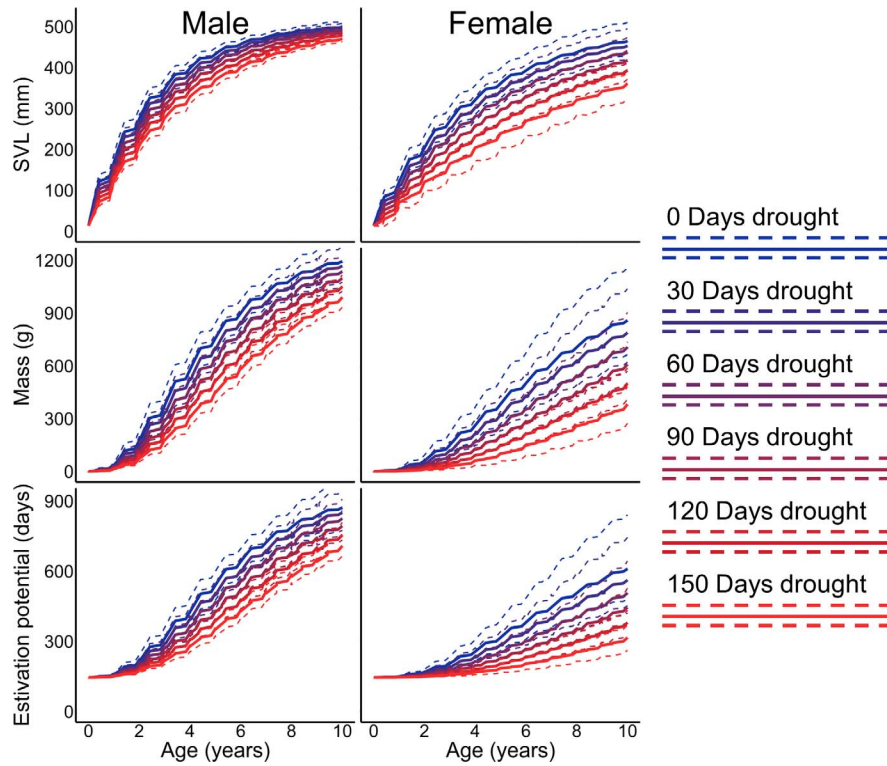
FIG. 2. Projections of male (left) versus female (right) age-length, age-mass, and age-estivation potential relationships for Greater Siren, *Siren lacertina*, growing on an annual cycle with between 0 and 150 days of moderate drought (–2 PDSI) during the growing season (1 March–31 September, 214 days), with all nondrought days set at 0 PDSI. Estimates of annual accrued length, mass, or estivation potential (solid lines) and 95% credible intervals (dashed lines) are shown based on data from *Siren lacertina* at Dry Bay collected from 2006 to 2016.

time required to reach a given level of estivation potential is extended by a reduction of growth in intervening years. Thus, reductions in ecosystem function because of incomplete recovery from droughts reduce organisms' adaptive capacity to increasingly frequent and severe droughts.

Evolution and phenotypic plasticity shape the capacities of organisms to adapt to changing climate regimes (Seebacher et al., 2015; De Meester et al., 2018; Luhring et al., 2019). Body size evolution in sirens appears to be driven by the joint selection pressures of drying events and sexual selection. Drying event severity may select for species-level differences in maximum body size and sexual dimorphism in growth rate or asymptotic size within each species. Greater Sirens are found most often in isolated wetlands that experience longer
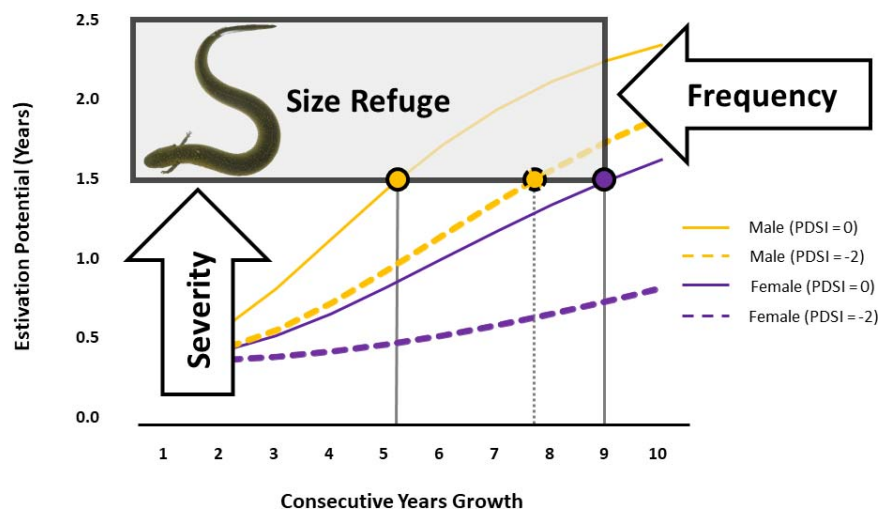

FIG. 3. Conceptual figure depicting sex-specific consequences of drying event frequency and severity coupled with droughts. Only Greater Siren, *Siren lacertina*, reaching a minimum size quickly enough (within the size refuge) persist through drying events. Recruitment of newly hatched individuals into the size refuge requires consecutive years of growth uninterrupted by major drying events. Males (orange lines) grow faster than females (purple) and both grow faster under average (PDSI = 0, solid line) versus moderate drought conditions (dashed lines). Increased drying event severity (arrow) increases the lower bounds of the size refuge, and increased drying event frequency (arrow) decreases the number of sequential years available for growth and accrual of estivation potential. Only growth trajectories reaching size refuge parameter space recruit into the population. The last drying event at Dry Bay lasted 1.6 yr and was only 9 yr after the previous drying event. Growth trajectories are model projections incorporating sex and growing season PDSI.

periodic drying events, whereas the smaller Lesser Sirens (*Siren intermedia*) are found in contiguous permanent bodies of water (Snodgrass et al., 1999). The larger size of Greater Sirens gives them an advantage in persisting through longer drying events, albeit at the cost of delayed age of first reproduction (Luhring and Holdo, 2015). Sexual selection in sirens is apparent in larger maximum male size of Lesser Sirens (Gehlbach and Kennedy, 1978; Hampton, 2009) and the accelerated growth rate in male Greater Sirens (this study). Male sirens aggressively protect nests of externally fertilized eggs (Reinhard et al., 2013), and larger males are typical of amphibian species with male–male combat (Shine, 1979). Although female Greater Sirens grow more slowly than males, their similar asymptotic size may reflect selection to reach an optimal size to persist through regional historic drying events. Future studies linking maximum size and mass–length relationships of siren populations to their local historic drought regimes (or contemporary plastic responses) may provide insight into the ability of organisms to fine-tune life history characteristics to climate-related selection pressures.

Our study focused on the effects of droughts and drying events, and these events are occurring within the context of phenotypically plastic responses to a warming world. Warming, through its relatively stronger effect on maturation rate versus growth rate, frequently leads to maturation at a smaller size and smaller size at adulthood (Atkinson and Sibly, 1997; Atkinson et al., 2003; Luhring et al., 2018). Given the tendency of warming to reduce body size, it may potentially counter or at least constrain evolutionary shifts toward positive size selection. Experiments using species with short generation times could be useful for understanding the constraints imposed by warming on phenotypically plastic or evolutionary responses that would otherwise lead to larger size at maturation. Additionally, the need to use minimally invasive sampling methods on a long-lived species means that we were able to identify sex for relatively few Greater Sirens ($n = 28$). Although we did not find support for differences in asymptotic length between sexes, a model with a larger sample size may find additional or diverging evidence on this point. More broadly, the role of sexual dimorphism in population responses to warming and drought merits further attention. Our 11 yr of observed in situ growth rates suggest that the adaptations large ectotherms have long used to survive severe, infrequent drying events may be unsuited to a future with longer and more frequent droughts.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/21-084.S1