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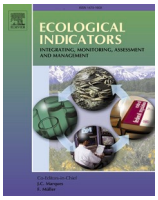

Importance of local weather and environmental gradients on demography of a broadly distributed temperate frog

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ABSTRACT

Amphibian populations are sensitive to environmental temperatures and moisture, which vary with local weather conditions and may reach new norms and extremes as contemporary climate change progresses. Using long-term (11–16 years) mark-recapture data from 10 populations of the Columbia spotted frog (*Rana luteiventris*) from across its U.S. range, we addressed hypotheses about how demographic relationships to weather depend upon a population's position along climate gradients. We estimated the effect of seasonal weather on annual survival probability and recruitment rates both within populations and across the species' range from subalpine forests to semi-arid deserts. We calculated population-specific weather variables that captured seasonal temperature and precipitation between summer sampling events, both for periods when frogs were active (spring to fall) and inactive (winter). Across all populations, we marked 15,885 adult frogs, with 33% of frogs recaptured at least once. Population demography varied with seasonal weather across the species' range. Annual adult survival probability and recruitment rates of each population were influenced by a unique set of seasonal temperature and precipitation variables, particularly in winter and spring. Hence, adult survival varied with local conditions but, when analyzed across all populations, was predictable along a species-environment response curve associated with the timing of snowmelt and spring moisture. In contrast, recruitment rates for each population peaked at different values along an environmental gradient associated with the amount of snow during winter, and fall temperature and moisture levels, suggesting that recruitment may be responding to local conditions independently within each population. These findings highlight that sampling across the environmental (i.e., elevational and meteorological) gradients within a species range is necessary to predict species-level responses to regional climate change. This study also provides evidence of the importance of winter conditions on the demography of temperate amphibians, conditions that are already responding to climate change. Finally, this study further emphasizes that local context and spatiotemporal scale of inquiry remain paramount to understanding and potentially managing for climate effects on populations of amphibian species with broad geographic ranges.

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1. Introduction

Short-term (i.e., daily, seasonal) changes in temperature and precipitation, as well as other measures of local weather, may affect survival, reproduction, migration, and other aspects of life history (e.g., Nouvellet et al., 2013; Le Corre et al., 2017; Neilson et al., 2020). A considerable challenge in understanding how climate change will affect species is addressing the spatial and temporal scales at which weather affects population demography (Grosbois et al., 2008; Knape and de Valpine, 2011). This is a particular challenge for species with broad geographic distributions. Broadly distributed species experience different weather in different parts of their range, both within and across years, and any changes in climate are unlikely to be uniform across geographies (e.g., latitudes) or topographies (Li et al., 2016). Thus, studies from different locations across a species' range may produce different or even conflicting responses to meteorological variation, which complicates conservation planning for climate risk and mitigation (Muths et al., 2017).

In temperate regions, climate change is expected to alter seasonal temperature and precipitation patterns and further increase seasonal and inter-annual variability in weather. Climates in inland areas of the western U.S. are predicted to shift towards warmer, wetter winters and warmer, drier summers (Intergovernmental Panel on Climate Change (IPCC), 2021). This is already observable as higher nighttime temperatures, reduced snowpack, earlier spring snowmelt, higher peak stream flows, and increasing extreme weather events. Weather extremes, such as droughts, deluges, heat waves, deep freezes, and false springs, are occurring more frequently (Crockett and Westerling, 2018). There is increasing concern that effects of climate change, when combined with other stressors (e.g., land use change), will lead to wildlife population declines and local extirpation (Newbold, 2018).

Among temperate vertebrates, amphibians are experiencing relatively high rates of decline in recent decades (Leung et al., 2017) and are expected to be particularly vulnerable to climate change (Araújo et al., 2006; Foden et al., 2013; Mims et al., 2018). Seasonal changes in temperature or precipitation as well as extreme weather events may affect amphibian populations by altering survival, breeding, and recruitment, or displacing individuals (McCaffery et al., 2012; Li et al., 2013; Walls et al., 2013). As ectotherms, temperate amphibian life history is highly influenced by seasonal temperatures (Abram et al., 2017; Cayuela et al., 2021a). With their thin skin and mostly external fertilization, frogs are also particularly dependent on moist habitats for survival and reproduction. Most frogs also move through and forage in terrestrial environments, which requires careful timing, selection of microhabitats, behaviors, or physiological mechanisms to conserve water (Lertzman-Lepofsky et al., 2020; Bartelt et al., 2022). Climate change is likely to alter the thermal and moisture conditions that frogs experience, potentially with consequences for populations (Miller et al., 2018). These environmental changes will be strongly influenced by changing seasonal and inter-annual weather patterns. This may be particularly problematic for temperate pond-breeding frogs that already experience wide fluctuations in seasonal temperature and precipitation resulting in changes in surface water availability, hydroperiods, soil moisture, and vegetation (McCaffery et al., 2014; Kissel et al., 2019; Pilliod et al., 2021). Alternatively, frogs in these locations may be better able to handle new weather patterns and extremes because of learned or innate behaviors, genetic adaptations, or phenotypic plasticity (Storey and Storey, 2012).

To better understand how climate change may affect different populations of a broadly distributed amphibian, we investigated the effects of local weather conditions on demography of Columbia spotted frogs (*Rana luteiventris*) at multiple locations across the species' range in the U.S. Specifically, we modeled demographic responses of frog populations as a function of seasonal temperature and precipitation, as well as extreme weather events that occur over days (e.g., cold snaps) or weeks to months (e.g., droughts). For this analysis, we took advantage of 10 long-term (11–16 years) mark-recapture datasets. This analysis allowed us to test for similarities in demographic responses within and among populations of a species across a range of habitats, elevations, and latitudes.

We considered two competing hypotheses for effects of seasonal weather variables on frog survival and recruitment (Fig. 1). Under the species-trait hypothesis (Fig. 1A), there is a temperature or precipitation optimum for the species regardless of its position within its range. Populations that are in areas with lower temperature or precipitation than optimal (e.g., population Q) would exhibit a positive interannual association with increasing temperature or precipitation until the optimum is reached, with potential decreases in performance during droughts or cold snaps. Conversely, populations that are in areas where temperature and precipitation are higher than optimal (e.g., population S) would exhibit a positive interannual association with decreasing temperature or precipitation until the optimum is reached, with potential decreases during deluges or heat waves. Populations located at the temperature or precipitation optimum (e.g., population R) would exhibit a Gaussian relationship with local weather variables, unless they only experienced near optimal conditions, in which case there would be no detectable relationship with the weather variable. Under the context-dependent hypothesis (Fig. 1B), each of the three populations would respond independently to its local temperature and precipitation conditions and each would exhibit its own Gaussian relationship with temperature or precipitation. Under this scenario, we might expect to see multiple, population-specific Gaussian response curves along a gradient and possibly two populations responding in different directions (i.e., discordance) to the same range of values for a given weather variable (Fig. 1B).

2. Materials and methods

2.1. Study species

The Columbia spotted frog is a pond-breeding anuran that has one of the largest ranges of any amphibian in western North America. Although considered secure in the northern portions of its range, southern populations tend to be physically and genetically isolated from each other within a vast, arid landscape (Funk et al., 2008; Pilliod et al., 2015; Robertson et al., 2018). Successful reproduction is dependent upon the availability of lentic wetlands with relatively long hydroperiods, emergent vegetation, and few aquatic predators (Pearl et al., 2007; Hossack et al., 2013). Tadpoles do not overwinter. Post-metamorphic juvenile and adult frogs overwinter in ponds, streams, and springs (Bull and Hayes, 2002; Pilliod et al., 2002). Many of the populations in the southern end of the species' range persist solely along streams and spring-fed stock ponds (Arkle and Pilliod, 2015). In most populations, individuals move among different wetlands seasonally (Pilliod et al., 2002; Bull and Hayes, 2001) or as interacting subpopulations within a metapopulation (e.g., Murphy et al., 2010).

2.2. Study area

We compiled Columbia spotted frog capture-recapture data from 10 study areas, each representing a single population in Idaho, Nevada, Montana, or Oregon (Fig. 2). The two most northerly populations inhabit multiple lakes and ponds scattered throughout montane basins with occasional use of intervening small streams and flooded meadows (Pilliod et al., 2002; McCaffery et al., 2014). Moving southward, populations inhabit complexes of wetlands (i.e., ponds, seasonally inundated pools, and beaver dam complexes) in grasslands, shrublands, aspen woodlands, and mixed coniferous forests, and along streams and adjacent meadows (Arkle and Pilliod, 2015). Hydroperiods of these wetlands ranged from seasonal pools that dry in most years to permanent ponds. Study areas ranged in elevation from 1,195 to 2,485 m.

2.3. Data collection

Frog population data were collected in June, July, or August of each year over a 11–16-yr period (depending on study sites) between 1997 and 2015. Each study area was surveyed annually during 2–5 capture events (most sites had 3 capture events per year), where all observed frogs were captured by hand or net, measured, marked, and released. These capture events were usually conducted on consecutive days to approximate a closed population within the annual survey periods. Surveys were conducted by 2–8 observers each year, depending on study area complexity and availability of personnel. At initial capture, frogs were either injected subcutaneously with a 12-mm passive integrated transponder (PIT) tag or toe-clipped with a unique pattern (LIRO only, through 2012). Although juveniles were captured and marked in some populations, we only include data from adult frogs in this analysis. We defined adults as individuals with a snout-to-vent length (SVL) of > 45 mm.

We divided the time interval between our annual summer sampling events into three seasonal activity periods for frogs: late summer and fall (hereafter fall), winter, and spring and early summer (hereafter spring). The fall period varied by site and year, as it spanned from the annual date of last capture (i.e., July or August) to the first occurrence of a three consecutive day period when maximum daily temperature was < 10C and minimum daily temperature was ≤ 0 C (occurred in the late fall or early winter). The winter period at each site and year lasted from the end of fall (defined above) to the first occurrence of a three consecutive day period when maximum daily temperature was ≥ 10C and minimum daily temperature was > 0 C (occurred in the spring). This period was intended to span the time when frogs were inactive and overwintering. Longitudinal analyses of temperate amphibians have found that winter-related covariates are good predictors of survival and recruitment, especially for frogs (Muths et al., 2017). The spring period at each site and year spanned from the end of winter (defined above) to the date of first capture of the next survey, which was typically in July.

We compiled weather data for each year for each study population from 1995 to 2015 to derive variables used in demographic models. Our selection of weather variables (Table 1) was based on the literature pertaining to frog biology and the environments occupied by this species as well as the availability of relevant weather data across all sampled sites. Daily temperature and precipitation were derived from a single point representing each population using Daymet, an interpolated gridded (1-km resolution) weather product (Thornton et al., 2014). This point was centered on the location where most frogs in a population were captured. If two locations were needed for a population (because of a large area relative to the Daymet pixel resolution), the weather data were compiled for both and then averaged by day. Each variable represented an average, cumulative (sum), or extreme in temperature or precipitation over a seasonal activity period (Table 1).

We represented longer duration moisture trends using the Palmer Hydrological Drought Index (PHDI; www.ncdc.noaa.gov), a gridded (2.5 km scale) measure of cumulative hydrological drought and wet conditions (Quiring, 2009). Because PHDI is calculated monthly, we used the following time periods to approximate our seasons: fall (August – October); spring (May – June). PHDI values are relative to location and drought is considered severe when PHDI values are ≤ 2 (www.ncdc.noaa.gov). We examined correlations between all variables prior to analysis (Figs. S1–S6), but we did not remove correlated variables from our analyses because models were either performed univariately (i.e., mark-recapture) or the modeling process (i.e., non-parametric multiplicative regression; NPMR) allows for correlated variables as NPMR selects the variable that has more explanatory power of two correlated predictors and the second of the two correlated predictors would not improve model fit enough to meet the improvement criterion threshold (discussed below). Thus, only one of two (or potentially more) correlated variables will be included in a final model. To help us visualize the environmental gradients across the species' range, we further examined multivariate relationships among predictor variables across populations using non-metric multi-dimensional scaling (NMS; McCune and Mefford, 2011; Fig. S7).

2.4. Data analysis

Using the capture histories of individually-marked frogs within each population, we first analyzed the relationship between weather variables and adult survival probability or recruitment rates in Program MARK (White and Burnham, 1999) using the *f*-parameterization of the Pradel model (Pradel, 1996; Williams et al., 2002). The Pradel model includes a parameter for capture probability, p_t, which is defined as the probability an individual is captured during the sampling period in year *t*. The demographic parameters in the Pradel model are apparent survival probability, Φ_t (hereafter, survival probability) and adult recruitment rate, f_t, where *t* indexes year.

Survival probability, Φ_t, is the probability an individual survives and remains in the study area from sampling in year *t* to sampling in year $t + 1$ (Fig. 3). Although we cannot differentiate emigration from mortality, we assumed that Φ_t primarily reflected survival probability because movements out of our designated metapopulations into surrounding areas were extremely low, where documented. Recruitment rate, f_t, is the number of adults added to the population from sampling in year *t* to sampling in year $t + 1$ per adult in the population during sampling in year *t* (Fig. 3). We defined population-level recruitment rates as the recruitment of unmarked adult (>45 mm SVL) frogs into the marked

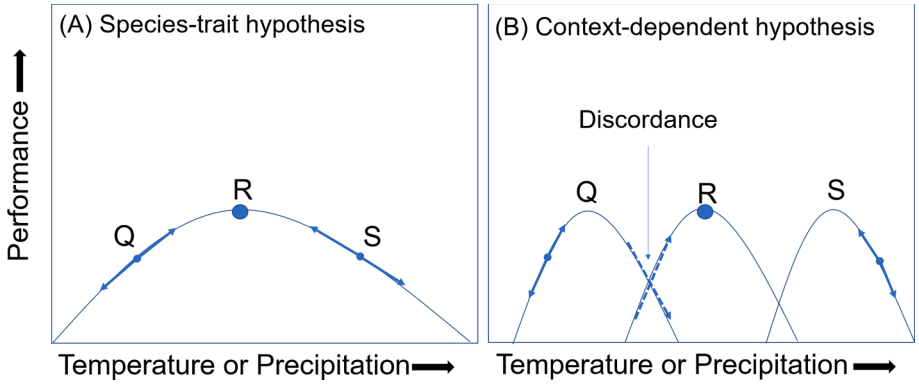

Fig. 1. Hypothesized relationships between environmental variables, in this case temperature or precipitation, and performance at the population level (e.g., survival, recruitment). The weather conditions at three populations (Q, R, and S) in different locations across a species' range are identified. Under the species-trait hypothesis (A), all three populations are adapted to the same environmental conditions but occur at different positions along the environmental gradient. Inter-annual changes in survival probability, for example, depend upon the weather conditions for a given year at a specific location, but responses (denoted as arrows) are predictable in relation to an optimum survival probability for the species. Under the context-dependent hypothesis (B), each population responds independently to local weather conditions resulting in different optimum performance along an environmental gradient. This would be observed as discordance between population responses to changing weather conditions, such as observed between populations Q and R at a specific temperature or precipitation level.

adult population. In other words, newly recruited adults were mostly unmarked juvenile frogs the previous year that had reached sexual maturity (or at least have a SVL > 45 mm; Fig. 3). Although we focus on weather effects on adult recruitment from our survey period in year t to year $t + 1$, we acknowledge that this recruitment rate is also influenced by processes that affect different life stages over 1–3 years (Fig. 3). For simplicity, we only included lag effects of seasonal weather on recruitment rates (and adult survival probability) in our range-wide population analysis (see below).

Each model that we fit to the data included a sub-model for capture probability, survival probability and recruitment rate. We fit models to the data in three steps and used ΔAIC_c values and Akaike weights (w_i, where i indexes model) to evaluate models at each step in the analysis (Burnham and Anderson, 2002). We considered models with ΔAIC_c values ≤ 7 to contain meaningful information and considered individual variables in those models to be important if their 95% confidence intervals did not overlap zero (Arnold, 2010; Morin et al., 2020).

In the f-parameterization of the Pradel model, imposing a structure on annual survival probability might influence the recruitment rate structure that is best supported in a step-wise approach (Williams et al., 2002). Therefore, constraints on annual survival probability could affect estimates of recruitment rate and vice versa (Franklin, 2001). To avoid unanticipated effects of constraining survival probability on estimates of recruitment rate (and vice versa), we only evaluated sub-models for recruitment rate by combining them with the sub-model for survival probability with full time-dependence (Morin et al., 2020). Similarly, to evaluate sub-models of survival probability, we combined them with the fully time-dependent sub-model of recruitment rate.

2.4.1. Weather effects on frog demography within populations

In the first step of model fitting for the population-specific models, we evaluated two sub-models of capture probability: the null model and time-dependent model. Sub-models for capture probability that include effects of year allowed us to account for differences in the number and composition of surveyors, as well as account for unmeasured characteristics of the survey year that might have influenced capture rates. The sub-models for annual survival probability and recruitment rate during this step included full time-dependence.

In the second step of model fitting for the population-specific models, we evaluated 21 sub-models for survival probability, Φ_t. In this step, we used the fully time-dependent sub-models of capture probability and recruitment rate in all sub-models of survival probability. Sub-models for survival probability included the fixed effect of year, a model of no annual variation (i.e., constant survival), and models where survival probability is a univariate function of season-specific weather covariates (Table 1). Preliminary examinations of sub-models with linear versus quadratic relationships between survival probability and each covariate indicated that linear trends were far more typical for these frog populations. Similarly, preliminary examinations of differences in survival between males and females indicated that including this covariate in the sub-models did not improve model fit or relationships with weather variables. Therefore, our model set focused on linear relationships and did not include sex-specific estimates of survival.

We evaluated 21 sub-models for recruitment rate and used a similar approach to model specifications as we used for sub-models of survival probability. We used the fully time-dependent sub-models of capture probability and survival probability in all sub-models of recruitment rate. As described above for survival models, sub-models for recruitment rate included fixed effects of year, a model of no annual variation (i.e., constant recruitment), and models where recruitment is a univariate function of season-specific weather covariates.

We used model-averaging (Burnham and Anderson, 2002) to generate annual estimates of survival probability and recruitment rate. For some combinations of sub-models in the Pradel model, parameters are confounded with one another. Therefore, we do not report the first and last estimates of capture probability, the last estimate of survival

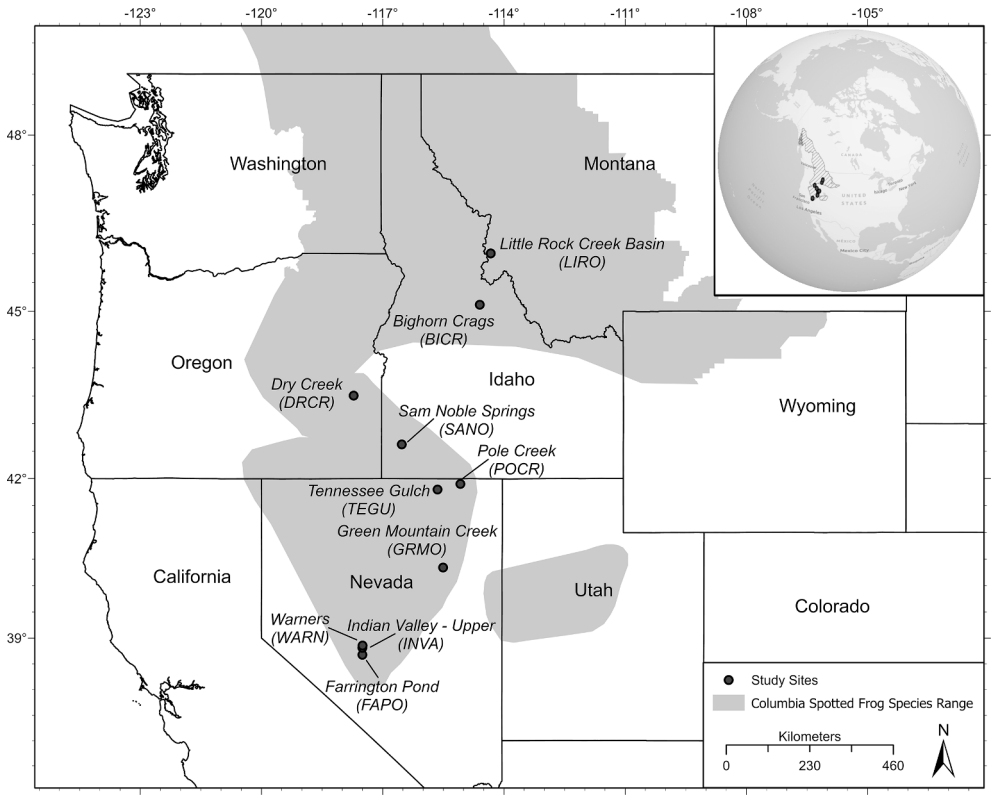

Fig. 2. Map of study region, showing the location of each population of Columbia spotted frog used in the analysis. Gray shading indicates range of the Columbia spotted frog (IUCN NatureServe 2014).

Table 1
Definition of average, cumulative, and extreme weather variables used in models. Temperature variables are listed before precipitation variables for each season. See text for season definitions.

Season and Variable	Definition
Fall	
ave.max.temp.fall	Average daily maximum temperature during the late summer and fall
ave.min.temp.fall	Average daily minimum temperature during the late summer and fall
gdd.fall	Cumulative number of days during the late summer and fall when the maximum temp was ≥ 10 °C
precip.fall	Cumulative precipitation during the late summer and fall
phdi.fall	Average Palmer Hydrological Drought Index (PHDI) for August–October, a measure of cumulative moisture relative to average conditions
Winter	
ave.max.temp.winter	Average daily maximum temperature during the winter
ave.min.temp.winter	Average daily minimum temperature during the winter
3 day.min.temp.winter	Average daily minimum temperature during the coldest 3-d period during the winter
var.min.temp.winter	Number of days during the winter when the minimum temperature goes from above freezing one day to below freezing the next or below freezing one day to above freezing the next
precip.winter	Cumulative precipitation during the winter
max.swe	Maximum snow-water equivalent (SWE) during the winter
day.0.swe	Ordinal day of the last snow on the ground when SWE = 0 or the first capture date of spring, whichever comes first
winter.length	Number of days classified as winter using inactive season rules
Spring	
ave.max.temp.spring	Average daily maximum temperature during the spring and early summer
ave.min.temp.spring	Average daily minimum temperature during the spring and early summer
gdd.spring	Cumulative number of days during the spring and early summer when the maximum temp was ≥ 10 °C
spring.cool.days	Cumulative number of days during the spring and early summer when the maximum temp was < 10 °C and the minimum temperature was ≤ 0 °C
precip.spring	Cumulative precipitation (mm) for the spring and early summer
phdi.spring	Average PHDI for May–June

probability, and the first estimate of recruitment rate from each population (Williams et al., 2002).

2.4.2. Weather effects on frog demography across populations

We used non-parametric multiplicative regression (NPMR) in HyperNiche 2.30 (McCune and Mefford, 2009) to model survival probability and recruitment rates as functions of multiple, interacting weather variables, without specifying *a priori* response shapes (McCune, 2011). Response variables were generated from the mark-recapture time-varying "t" models, which provided an estimate for each year for each population. The first and last estimate in each population's time series were not included for reasons previously described. We acknowledge that treating parameter estimates generated from the *f*-parameterization of the Pradel model as response values ignores the measure of precision around each of those estimates. Although this modeling approach is a bit unconventional, it allowed us to test our hypotheses about species-trait versus context-dependent demographic responses to temperature and precipitation across the range of the species.

We included all predictor variables, plus 1- and 2-year time lags of each variable, in the pool of potential variables available for the final models. For each analysis, we used a local linear model with Gaussian weighting functions to carry out free-search iterations of predictor variables and their associated tolerances (tolerance = SD of Gaussian weighting function) such that the fit of each candidate model was maximized, while minimizing overfitting. Model fit was assessed with cross-validated R^2 (xR^2) and overfitting was controlled through minimum average neighborhood size, minimum data-to-predictor ratio, and "leave-one-out" cross validation of xR^2.

For each response variable, all combinations of the 18 predictor variables (plus their 1- and 2-year lags) were run, and models were identified with the greatest fit for each number of included predictor variables. The final model for each response variable met an improvement criterion of having a fit at least 5% better than the best model with one fewer predictor variable. We quantified the stability of each final model to the inclusion of particular sample units in the dataset by conducting bootstrap resampling (each dataset was resampled, with replacement, 100 times) and reporting the average xR^2 (±SE) of the 100 resulting bootstrapped models. For each final model, we also reported the average neighborhood size (N*, the average number of sample units contributing to the estimate of the response at each point on the modeled surface) and Monte Carlo randomization results (to provide a measure of fit by using 100 free-search iterations with randomly shuffled response values). For each predictor included in a final model, we report a sensitivity value, which indicates the relative importance of the predictor to the response value. High sensitivity values (i.e., those close to or greater than one) indicate that a change in the predictor value by anywhere from −5% to + 5% of its range results in a change of equal magnitude in the predicted response value (i.e., ±5%; McCune, 2011).

After fitting final models for survival and recruitment, we plotted: 1) "global" response curves for each predictor variable, intended to show the overall relationship between all populations and the response variable (i.e., species-trait hypothesis), and 2) simple linear or quadratic functions for each population's interannual relationship between the predictor variable and the response, intended to examine population-level variation (i.e., context-dependent hypothesis). For the latter, we first removed sample units identified as multivariate outliers (i.e., >2 SD from the mean of either predictor or response variables) to ensure that no individual points had disproportionate influence on response curves. We calculated traditional R^2 values to describe the fit between each NPMR model estimates and "observed" (i.e., program MARK estimated) survival or recruitment across years for each population, and similar scores for each population's inter-annual correlation with each predictor variable. Because sample sizes for these population-level functions were limited to 9–14 sample units (i.e., years with demographic estimates for each population), we did not perform statistical tests on these relationships, but use R^2 values to demonstrate the relative strength of patterns and to highlight the number of populations that conform to expected trends.

3. Results

3.1. Weather effects on frog demography within populations

The number of individuals captured and marked in each population varied from 305 to 3,817 (Table 2). We recaptured 33.5% of marked individuals at least once, which ranged from 9% at the lowest elevation to 52–53% at the highest latitudes. The sub-model of capture probability with year effects had the lowest AIC_c value in 9 of the 10 populations (all but BICR), compared to a model with a constant capture probability.

The effects of weather on adult survival probability (Φ_t) varied by population, with little consistency among populations (Table S1). The lowest elevation population (DRCR) had the lowest average survival probability (Φ_t = 0.294 ± 0.124 SD), whereas average survival was highest in the population at the highest elevation (BICR: Φ_t=0.818 ± 0.018 SD; Fig. 4A). Three populations had nearly invariant survival probabilities across years and two of these had the highest average survival of all 10 populations (Fig. 4A). The other seven populations had considerable inter-annual variability in survival. The top model selected within a population had a fully time-dependent structure (i.e., Phi[t]) in half the populations (Table S1). For the other half, there was either considerable model uncertainty (BICR, TEGU) or one weather covariate

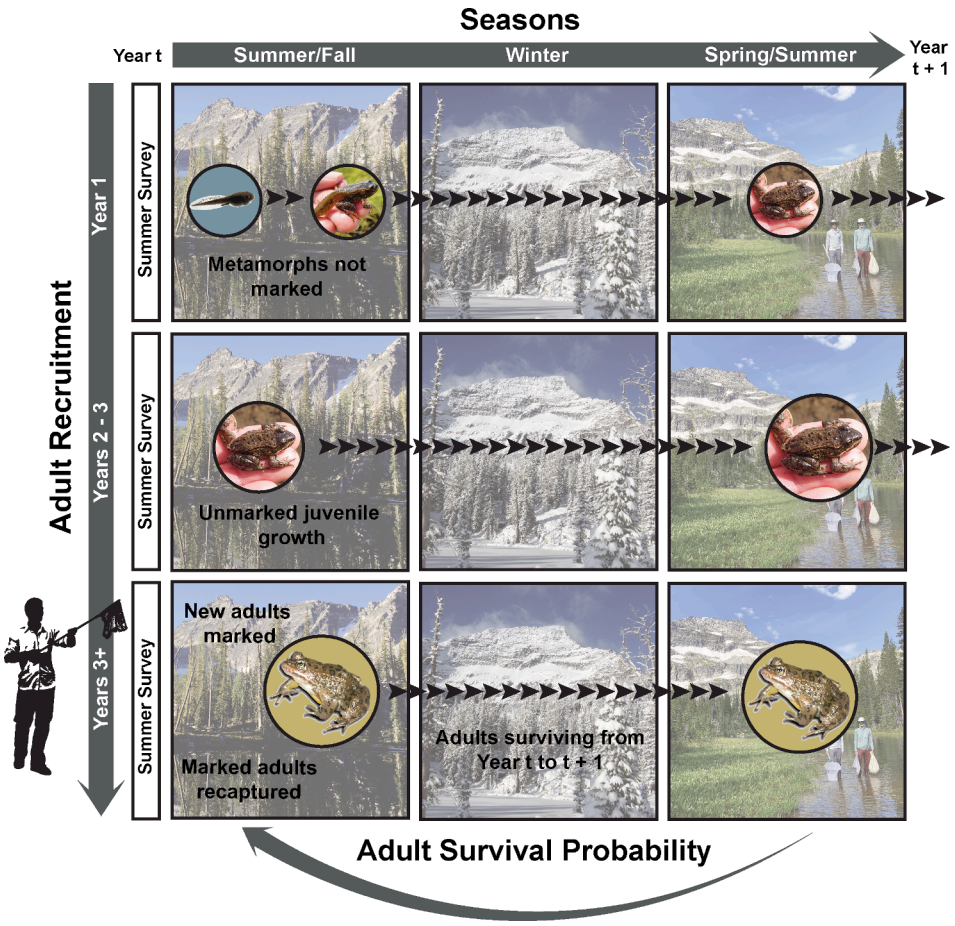

Fig. 3. Conceptual diagram of the life history of the Columbia spotted frog in relation to summer surveys. We modeled the effect of seasonal weather variables on adult survival probability and recruitment rates, which span the period from the last day a frog was captured during the summer survey in year t to the first day a frog was captured in year t + 1. Only adult frogs > 45 mm were marked and included in our analyses.

explained most of the variation in adult survival (phdi.spring in DRCR; max.swe in POCR; ave. min.temp.winter in WARN; Table S1). Overall, average seasonal temperatures and growing degree days were the strongest predictors of adult survival probability in four of the ten populations, with both positive and negative effects (Table 3). Seasonal precipitation, in general, was a weak predictor of adult survival, except at: DRCR where survival was negatively associated with more spring moisture (positive values of phdi.spring); INVA where survival was negatively associated with worsening drought (negative values of phdi. spring, particularly below −2); and POCR where survival was negatively associated with more or wetter snow (max.swe; Table 4).

The effects of weather on recruitment rates (*f*) also varied by population, with little consistency among populations (Table S2). Recruitment rates ranged from 0.058 to 1.435 across populations (Fig. 4B). The populations with the highest median recruitment also had the greatest variability in recruitment (Fig. 4B). The remainder of the populations tended to have relatively low interannual variability in recruitment. The lowest elevation population (DRCR) had substantially greater recruitment across years than other populations (Fig. 4B), but experienced near-complete recruitment failure in two very wet springs (high values of precip.spring; Table 5) that coincided with high peak flow events (Fig. S8). The model that had a fully time-dependent structure (i.e., Phi [t]) and no weather covariates was the best model of recruitment in half of the populations (Table S2). For the other half, there was either considerable model uncertainty (DRCR, GRMO, POCR, TEGU) or one weather covariate explained most of the variation in recruitment (ave. max.temp.spring in WARN; Table S2). Overall, average temperatures best explained recruitment rates at four of 10 populations, with recruitment increasing with warmer daily high temperatures (ave.max. temp) in all seasons, particularly in the spring (Table 3). Growing degree days in spring (gdd.spring) were also positively associated with recruitment in two populations, whereas one population had lower recruitment in springs with more unusually cold days (spring.cool.days; Table 5). Two populations had higher recruitment when winter cold snaps were less severe (higher values of 3 day.min.temp.winter; Table 5). Seasonal precipitation was a useful predictor of recruitment, especially in 3 of the populations (Table 3).

3.2. *Weather effects on frog demography across populations*

Examinations of interactive effects of temperature and precipitation on adult survival probability across the species' range revealed patterns that were distinct from the population-level analyses. Across all sites and years, survival was best predicted by an interaction among three variables: day.0.swe (1-yr lag), phdi.spring, and population ($xR^2 = 0.68$; $p < 0.005$; $N^* = 5.6$; bootstrap average +/- 1 SE = 0.80 +/- 0.03; Sensitivity: day.0.swe = 0.66, phdi.spring = 0.32). This model fit was 8% greater than the best two-predicter model and fit well to each population (R^2 of observed versus modeled survival averaged 0.65 ± 0.07 across sites; R^2 range = 0.41–0.98; Table S3; Fig. S9). Populations in locations where snowpack persisted later in the spring (higher values of day.0. swe) had higher survival probabilities than populations where melt-out was earlier, although this effect plateaued after 29–30 May (day 150; Fig. 5A). The relationship between survival and snowmelt timing within a population, however, was strongest in locations with lower snowpacks, where adult survival responded positively to increasing values of

Table 2
Summary of adult captures at 10 populations of Columbia spotted frogs across the species' range. Populations are arranged north to south, by state.

Population	State	Elevation (m)	Years Sampled	Number of Years	Frogs Marked
Little Rock Creek Basin (LIRO)	Montana	2,138	2000–2015	16	2,134
Bighorn Crags (BICR)	Idaho	2,485	2005–2015	11	1,590
Sam Noble Springs (SANO)	Idaho	1,774	1997–2012	16	1,243
Dry Creek (DRCR)	Oregon	1,195	2001–2015	15	3,795
Tennessee Gulch (TEGU)	Nevada	2,247	2004–2015	12	818
Pole Creek (POCR)	Nevada	2,241	2005–2015	11	376
Green Mountain Creek (GRMO)	Nevada	2,341	2004–2015	12	305
Warners (WARN)	Nevada	2,182	2004–2015	12	1,367
Indian Valley - Upper (INVA)	Nevada	2,231	2004–2015	12	3,817
Farrington Pond (FAPO)	Nevada	2,086	2004–2015	12	440
Total					15,885

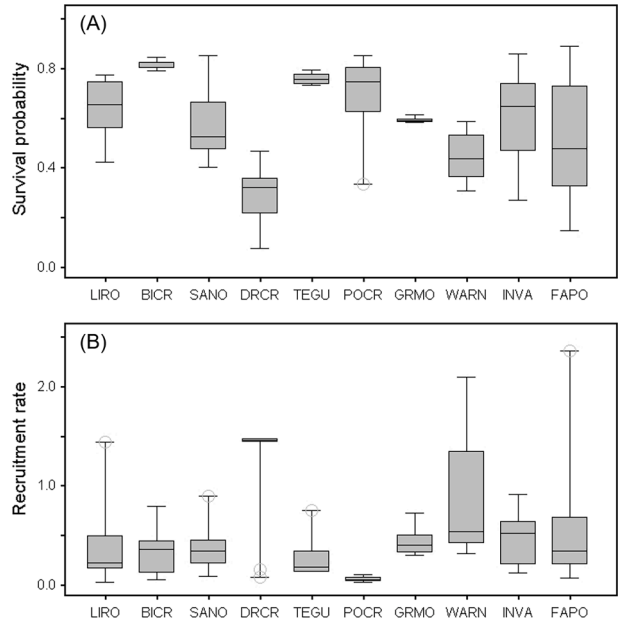

Fig. 4. Box plot of estimated annual adult survival probability (A) and recruitment rate (B) for 10 Columbia spotted frog populations showing median, 25%, and 75% quartiles. Whiskers show 5th and 95th percentiles. Outlier years are indicated by a circle and defined as any value>1.5 times the interquartile range for that population.

day.0.swe. In contrast, sites at the snowier end of the sampled gradient exhibited no correlation with day.0.swe and the population with the latest snowmelt, LIRO, exhibited a negative, albeit weak ($R^2 = 0.07$), relationship with survival. Fits for individual populations' modeled survival probabilities to day.0.swe were generally strong (R^2 average $\pm$ 1 SE $= 0.60 \pm 0.09$), except for the four populations with slopes near zero (R^2 average $\pm$ 1 SE $= 0.04 \pm 0.01$) near the peak of the global curve. Besides day.0.swe, spring moisture (phdi.spring) was also an important predictor of survival, but populations had differing relationships to this variable (Fig. 5B). Fits for individual populations' modeled survival probabilities to phdi.spring were fairly strong (R^2 average $\pm$ 1 SE $= 0.60 \pm 0.08$), including the five populations with slopes near zero.

Table 3
Seasonal temperature and precipitation variables that had the greatest effects on adult survival probability or recruitment rates of Columbia spotted frogs at 10 populations across the species' range. Effects are identified by population and direction of effect. Blank cells indicate variable not relevant to that season.

	Survival			Recruitment		
Variables	Fall	Winter	Spring	Fall	Winter	Spring
Temperature						
ave.max.temp	BICR (-)	BICR (+)	FAPO (-)	TEGU (+)	TEGU (+); POCR (+)	FAPO (+); WARN (+)
ave.min.temp	BICR (-); SANO (+)	WARN (-)	FAPO (-)	None	None	POCR (+)
gdd	None		BICR (-)	None		LIRO (+); SANO (+); INVA (-)
3 day.min. temp.winter		LIRO (+)			GRMO (+); POCR (+)	
var.min.temp. winter		None			None	
winter.length		None			None	
spring.cool. days			None			POCR (-)
Precipitation						
precip	None	None	None	FAPO (-)	GRMO (+)	DRCR (-)
phdi	None		DRCR (-); INVA (+)	None		None
max.swe		POCR (-)			None	
day.0.swe		None			None	

Recruitment rates across the species' range were related to different temperature and precipitation variables than were identified in population-level analyses and different than (but related to) variables associated with survival probabilities. Across all populations and years, recruitment was best predicted by an interaction among four variables: max.swe, gdd.fall (1-yr lag), phdi.fall, and population ($xR^2 = 0.61$; $p < 0.009$; $N^* = 1.5$; bootstrap average +/- 1 SE = 0.72 +/- 0.09; Sensitivity: max.swe = 2.49, gdd.fall (1-yr lag) = 1.33, phdi.fall = 0.57). This model fit was 6.7% greater than the best three-predictor model and fit well to each population (R^2 of observed versus modeled recruitment averaged 0.88 +/- 0.05 across sites; R^2 range = 0.60–0.98; Table S4; Fig. S10). In general, recruitment was negatively related to max.swe, especially values between 0 and 300 kg/m^2 (Fig. 6A). Thus, populations in locations with less snow (lower max.swe) had higher recruitment rates than populations where the snowpack tended to be high (higher max.swe), although above 300 kg/m^2, max.swe had little effect on recruitment rates. However, each population exhibited a Gaussian curve in a localized portion of the max.swe gradient. Populations in snowier portions of the gradient tended to have lower recruitment peaks, but also much wider tolerance to a range of max.swe values, whereas populations on the least snowy portion of the gradient tended to have greater peak recruitment and far less tolerance to years with relatively high max.swe.

Table 4
Estimated covariate effects on annual survival probability for 10 Columbia spotted frog populations from models with ΔAICc < 7 (see Table S1) and 95% confidence limits on the model estimates that did not overlap zero. See Table 1 for covariate definitions. Populations are arranged north to south, by state.

Population	Covariate	Estimated Regression Coefficient	LCL (95%)	UCL (95%)
LIRO	3 day.min.temp. winter	0.409	0.291	0.527
BICR	ave.max.temp. fall	−0.380	−0.670	−0.090
	ave.min.temp. fall	−0.170	−0.300	−0.050
	ave.max.temp. winter	0.190	0.040	0.340
	gdd.spring	−0.190	−0.340	−0.040
SANO	ave.min.temp. fall	0.288	0.184	0.392
DRCR	phdi.spring	−0.807	−0.987	−0.627
TEGU	ave.max.temp. fall	0.870	0.480	1.250
	ave.max.temp. winter	0.790	0.500	1.070
POCR	max.swe	−0.720	−0.940	−0.510
GRMO	none selected	–	–	–
WARN	ave.min.temp. winter	−0.561	−0.862	−0.261
INVA	phdi.spring	2.028	1.801	2.255
FAPO	ave.max.temp. spring	−0.632	−0.886	−0.377
	ave.min.temp. spring	−0.540	−0.760	−0.320

Table 5
Estimated covariate effects on annual recruitment rates for 10 Columbia spotted frog populations for models with ΔAICc < 7 (see Table S2) and 95% confidence limits on the model estimates that did not overlap zero. See Table 1 for covariate definitions. Populations are arranged north to south, by state.

Population	Covariate	Estimated Regression Coefficient	LCL (95%)	UCL (95%)
LIRO	gdd.spring	0.774	0.666	0.883
BICR	none selected	–	–	–
SANO	gdd.spring	0.380	0.220	0.550
DRCR	precip.spring	−0.676	−0.824	−0.527
TEGU	ave.max.temp. fall	0.870	0.480	1.250
	ave.max.temp. winter	0.790	0.500	1.070
POCR	3 day.min.temp. winter	0.930	0.170	1.690
	ave.max.temp. winter	0.900	0.160	1.640
	spring.cool.days	−0.910	−1.790	−0.030
	ave.min.temp. spring	1.220	0.030	2.410
GRMO	precip.winter	0.700	0.090	1.300
	3 day.min.temp. winter	0.410	0.000	0.810
WARN	ave.max.temp. spring	0.659	0.546	0.772
INVA	gdd.spring	−0.591	−0.649	−0.533
FAPO	precip.fall	−0.594	−0.827	−0.362
	ave.max.temp. spring	0.561	0.392	0.730

Model fits for individual populations' modeled recruitment to max.swe were generally good (R^2 average ± 1 SE = 0.36 ± 0.06).

Overall, recruitment was greater in populations with warmer fall seasons the year prior (gdd.fall with a 1-yr lag), especially where values were>100 growing degree days (Fig. 6B). However, each population exhibited a Gaussian relationship with gdd.fall. Populations in portions of the gradient with cooler falls tended to have lower recruitment peaks,

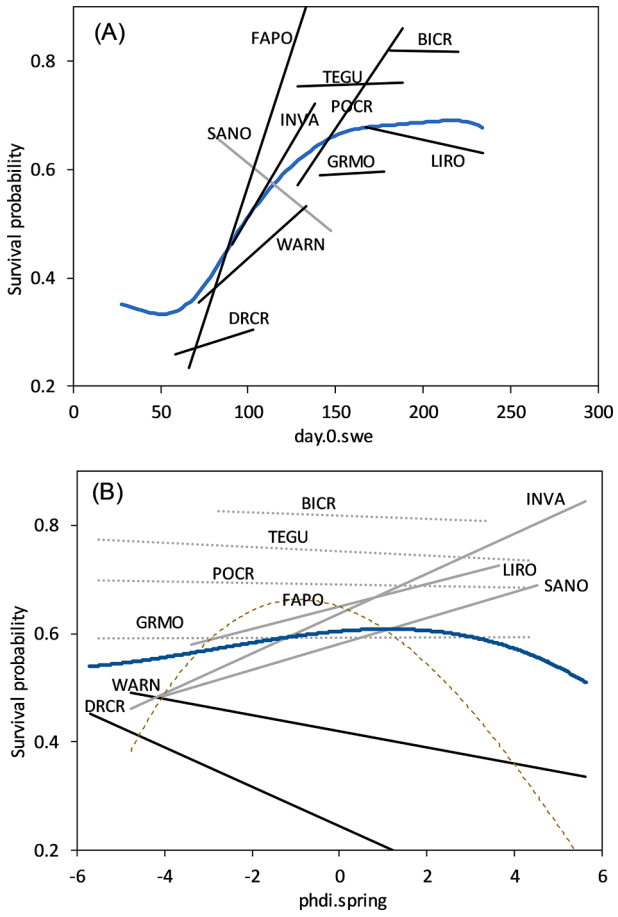

Fig. 5. NPMR estimated survival probability versus (A) day.0.swe (1-yr lag) and (B) phdi.spring across years for 10 Columbia spotted frog populations. Day.0.swe is the day of year that snow-water equivalent at a location reaches zero the previous year. Phdi.spring is a unitless measure of the average Palmer Hydrological Drought Index for May and June. The blue line shows the overall response of survival to each variable. For day.0.swe (A), black lines show each population's interannual association with this variable and the gray line indicates one population that did not follow the expected pattern. For phdi.spring (B), black solid lines show populations with negative correlations, gray solid lines show populations with positive correlations, gray dotted lines show populations with no correlation, and the dashed line shows one population with a Gaussian correlation to this variable. Population abbreviations are given near the high point of each corresponding line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

whereas populations on the portion of the gradient with warmer falls tended to have greater peak recruitment. The dip in the global curve between days 50–70 reflects years on the warm end of the gradient for BICR and LIRO and on the cool end of the gradient for TEGU, SANO, and POCR. Fits for individual populations' modeled recruitment to gdd.fall (with a 1-yr lag) were generally strong (R^2 average ± 1 SE = 0.53 ± 0.09). Finally, recruitment rates were generally greater with increasing fall moisture (phdi.fall), although populations also tended to exhibit somewhat independent relationships to this variable (Fig. 6C). Fits for individual populations' modeled recruitment to phdi.fall were generally good (R^2 average ± 1 SE = 0.39 ± 0.09).

4. Discussion

Understanding the effects of weather on population demography is a critical first step in evaluating risks associated with rapidly changing climates and developing climate mitigation strategies. For amphibian

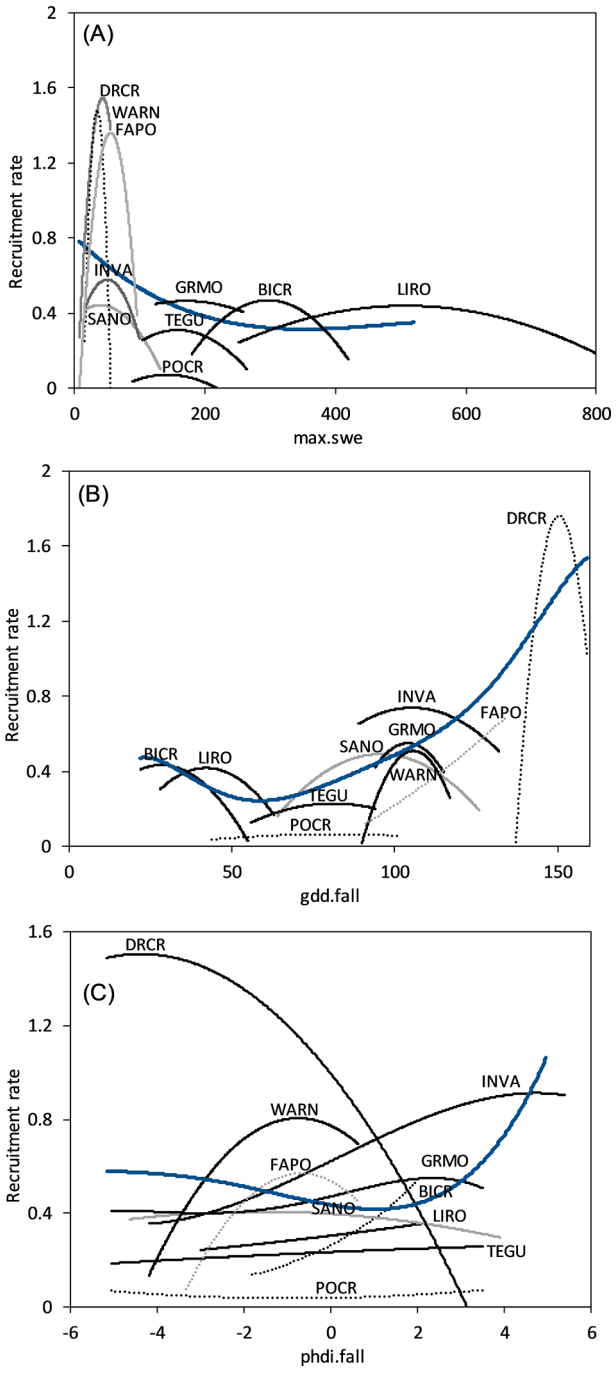

Fig. 6. NPMR estimated recruitment rates versus (A) max.swe, (B) gdd.fall (1-yr lag), and (C) phdi.fall across years for 10 Columbia spotted frog populations. Max.swe is the maximum snow-water equivalent (kg/m^2) reached at a location in a winter. Gdd.fall (1-yr lag) is the cumulative number of days where the maximum temperature was $\geq$ 10 °C in the previous summer/fall active season. Phdi.fall is a unitless measure of the average Palmer Hydrological Drought Index for August to October. For each panel, the blue line shows the overall response of recruitment to each variable. Black, gray, and dashed lines show each populations' interannual correlation to response variables, with different line types used simply to assist in distinguishing populations from one another. Population abbreviations are given near the high point of each corresponding line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

populations, most research has focused on the stability and continued availability of breeding habitats in relation to warming and shifting patterns of precipitation and wetland or stream hydrology. Ultimately, however, effects of drying will manifest in changes in demography, such as reduction or absence of recruitment. For species that occupy large ranges, sampling across environmental gradients is necessary to better understand and predict responses to regional climate change, because large-range species experience greater variability in temperature and precipitation across their ranges than small-range species (Li et al., 2016). Further, individual populations of large-range species may experience unique local weather and some may have adapted to those environmental conditions. Indeed, when we examined demographic responses within each of the ten geographically separated populations, we found that effects of seasonal temperatures and precipitation were conditional on location. Variation in adult survival probability among populations, however, was predictable based on where a population fell along a species-environment response curve. In contrast, maximum recruitment rates for each population peaked at different values along an environmental gradient, suggesting that recruitment may be most influenced by, or perhaps adapted to, local conditions. Although we did not examine demographic responses in relation to habitat changes, local (i.e., population-specific) differences in recruitment may have been influenced by the stability or sensitivity of breeding, rearing, or juvenile frog overwintering habitats to seasonal and interannual changes in temperature and precipitation. Although other studies have documented adaptive responses of amphibians to climate along spatial gradients (Urban et al., 2014), our findings suggest that those responses may differ by demographic process and our understanding of those relationships varies with scale of inquiry (i.e., individual population versus range-wide). These findings have implications for understanding climate change effects on the demography, conservation, and management of this and other broadly-distributed temperate anuran species.

4.1. *Weather effects on frog demography within populations*

Our analysis of the effects of seasonal temperature and precipitation on individual Columbia spotted frog populations revealed some consistent patterns amongst considerable variation. Temperature variables were generally better predictors of annual adult survival probability than seasonal precipitation variables within individual populations. We also found that recruitment rates were positively influenced by years with warmer daytime high temperatures in all seasons and more warm days in the spring. While our analysis cannot assess causal relationships, warm temperatures can facilitate increased activity and growth directly through increased metabolism (Abram et al., 2017), and indirectly through increased food resources (e.g., insects, spiders; Blaustein et al., 2010). Although years with warm, dry conditions may decrease available surface water and shorten wetland hydroperiods (Kissel et al., 2019), warm, wet years are often ideal for temperate frogs (Yu et al., 2018). Changes in wetland hydroperiods associated with shifting climates and weather extremes (e.g., drought) are worrisome for amphibian biologists because pond drying can eliminate entire cohorts and cause population declines (Hossack et al., 2013; Ray et al., 2016).

Our results add to a growing body of research investigating the effects of weather and climate on temperate anuran populations. First, other studies have explored weather effects on a subset of Columbia spotted frog populations included in this study, though the number of years in the dataset and the specific weather covariates in each study have differed. In some cases, our findings have generally been consistent with previous studies. For example, Muths et al. (2017) found that the best predictor of survival in BICR was warm days during hibernation, and one of the better predictors of BICR frog survival in our study was average maximum winter temperature. In both cases, warmer winters had a positive effect on this high elevation, northern population. In other cases, different weather covariates were important to survival and

recruitment among analyses of the same populations (e.g., SANO: Pilliod and Scherer, 2015, Muths et al., 2017, and this study; LIRO: Muths et al., 2017; McCaffery and Maxell, 2010, and this study), which may be a function of both study length and the selection and quantification of covariates hypothesized to be important to the populations. For other species, we also see contrasts in modeled responses within the same population. For example, Kissel et al. (2019) found that longer winters and wetter summers were associated with increased survival in the Cascades frog (*Rana cascadae*), whereas Muths et al. (2017) found that unusual hot events in the summer best predicted adult survival in this same population. These comparisons across studies highlight how covariate selection, study length, which years are included, and other factors can challenge our understanding of weather and climate drivers in amphibian populations, even in the same well-studied systems (Winter et al., 2016).

Efforts to synthesize weather drivers of demographic rates and population growth across populations and species have generally concluded that effects are context-dependent and population specific. Whether within (Cayuela et al., 2016, Amburgey et al., 2018, Muths et al., 2018) or across (Muths et al., 2017) species, no individual weather covariate has shown consistent patterns with a given demographic variable. Variation and idiosyncratic responses appear to be the most consistent pattern, as we found in our analyses of individual Columbia spotted frog populations. Intrinsic factors like life history traits (Muths et al., 2017), age structure (Cayuela et al., 2016), or density dependence (Pellet et al., 2006; Cayuela et al., 2020), and extrinsic factors such as local habitat conditions or predators may be as important as weather in regulating demography or may interact in complex ways with weather to affect populations (Urban et al., 2014). Furthermore, microhabitats where frogs spend their time may have more stable temperature (e.g., Scheffers et al., 2014a,b) and moisture (e.g., Long and Prepas, 2012; Lannoo and Stiles, 2017) than measured weather variables, potentially buffering individuals from some variation in seasonal weather.

4.2. Weather effects on frog demography across populations

Despite the apparent idiosyncratic nature of demographic studies, we found some interesting trends in adult survival and recruitment across all populations when temperature and precipitation were allowed to interact and local responses were put into the context of environmental gradients across the species range. Variation in adult survival across all populations was best explained by two variables that represent an interaction of temperature and precipitation: timing of snowmelt (day.0.swe) and spring moisture (phdi.spring). The effect of snowmelt timing was most predictive with a 1-yr time lag, suggesting that adult survival may result from carryover effects over multiple years. The timing of snowmelt, in particular, provided support for our species-trait hypothesis, whereby populations occur at different points along a common response curve based on their local weather. Predictable variation in adult survival across this species' range was also reported by Cayuela et al. (2021b) who found lower survival in locations with warmer mean annual (1990–2019) temperatures (i.e., lower elevations and southern latitudes). Clearly, both temperature and precipitation are important predictors of Columbia spotted frog survival, but they interact in complex ways and their influence on survival may depend upon a given population's position along a temperature - precipitation gradient, as depicted in Fig. 1A.

Much like survival, snow (max.swe) was one of the most important variables for recruitment across all populations. Specifically, populations that experienced less snow (lower max.swe) had greater recruitment rates than sites with more snow. In contrast to survival, we found that this relationship supported our context-dependent hypothesis whereby each population exhibited a Gaussian curve in a localized portion of the max.swe gradient. Essentially, there appeared to be an optimum amount of snow for each population, and years with more or less snow than that optimum had reduced recruitment. We suspect that more snow provides more moisture in the spring while providing insulation for overwintering frogs. Too little snow may result in dry conditions in the spring for these snow-dominated hydrologic regimes, or may expose overwintering frogs to higher mortality risk from cold snaps, at least for frogs overwintering in shallower locations (e.g., streams, undercut banks). This relationship was less apparent at the lowest end of the snow gradient, perhaps because these areas have so little snow that other factors are more important. Other variables influencing recruitment, such as moisture (phdi.fall) and growing degree days (gdd.fall) in the fall did not appear to have as strong a local effect as snow.

Our results contribute to a growing body of evidence that snow and winter conditions are important to the demography of temperate amphibians, even though they are inactive during this time of year (e.g., Corn, 2003; McCaffery et al., 2012; O'Connor and Rittenhouse, 2016). A time series *meta*-analysis of 31 populations across 11 temperate amphibian species revealed that winter-related covariates, such as winter length, winter severity (number of particularly cold days), and timing of the onset of winter, were some of the most important predictors of survival and recruitment (Muths et al., 2017). Similar to our findings, they found that the direction and magnitude of response to winter covariates varied by population and was thus context dependent. Based on our findings, this could be due to populations' positions along environmental or weather gradients.

The importance of snow to these and other populations of temperate amphibians is concerning given the expected decline in snowpack in the western United States over the coming decades (Siler et al., 2019; Siirila-Woodburn et al., 2021). This change is happening now. Mote et al. (2018) reported that over 90% of snow monitoring sites with long records across the western US show declines, especially in the spring in locations with milder winters. Increasing winter snowmelt, which is highly sensitive to temperature, was evident at 34% of those snow monitoring stations (Musselman et al., 2021). These locations fall toward the lower end of our max.swe gradient, which could be problematic for adult survival and recruitment in some of our Columbia spotted frog populations without management intervention (Pilliod et al., 2021).

5. Conclusions

Understanding the relative influence of changing temperature and precipitation regimes on population demography can ultimately help determine management options for maintaining amphibian populations into the future. Our findings highlight the importance of quantifying population demography across environmental gradients for broadly distributed species, like the Columbia spotted frog. Populations experience unique local weather at different locations across a species' range, and the conditions that are favorable for one population may be detrimental to another. Variable population demography among populations, however, can be good from a conservation perspective. Among-population variability might foster asynchronous population dynamics across a species' range, which can reduce extinction risk and increase opportunities for local adaptation (Liebhold et al., 2004). Our results have important implications for species conservation, but also put more onus on resource managers to monitor and understand factors influencing local population cycles and extinction risk. For broadly distributed species, climates that are becoming too warm and dry for one population, may be becoming too cool or wet for others. In other words, timely responses to climate-related population declines or development of effective climate mitigation strategies, such as habitat restoration or facilitated dispersal, may need to be largely based on local- or population-level information.

CRediT authorship contribution statement

David S. Pilliod: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision,

Visualization, Writing – original draft. **Rebecca M. McCaffery:** Investigation, Project administration, Writing – review & editing. **Robert S. Arkle:** Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. **Rick D. Scherer:** Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. **Jacqueline B. Cupples:** Investigation, Project administration. **Lisa A. Eby:** Writing – review & editing, Supervision. **Blake R. Hossack:** Investigation, Project administration, Writing – review & editing. **Hallie Lingo:** Investigation, Project administration. **Kristin N. Lohr:** Investigation, Project administration. **Bryce A. Maxell:** Investigation, Project administration. **Megan J. McGuire:** Investigation, Project administration. **Chad Mellison:** Investigation, Project administration. **Marisa K. Meyer:** Investigation, Project administration. **James C. Munger:** Investigation, Project administration. **Teri Slatauski:** Investigation, Project administration. **Rachel Van Horne:** Investigation, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108648.

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