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Simulated developmental and reproductive impacts on amphibian populations and implications for assessing long-term effects

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Abstract

Fish endpoints measured in early life stage toxicity tests are often used as representative of larval amphibian sensitivity in Ecological Risk Assessment (ERA). This application potentially overlooks the impact of developmental delays on amphibian metamorphosis, and thereby reduced survival, in amphibian populations constrained by habitat availability. Likewise, the effects of reduced productivity or altered sexual development as a result of chemical exposure are not presented in terms of lower population fecundity in these surrogate tests. Translating endpoints measured in toxicity tests to those that are more representative of amphibian ecology and population dynamics provides a means of identifying how developmental effects result in long-term impacts. Here we compare effects of developmental delay on metamorphosis success in six anuran species and simulate population-level impacts of subsequent reductions in larval survival as well as potential reductions in fecundity as a result of developmental impacts. We use deterministic matrix models to compare realistic combinations of amphibian demographic rates and relative impacts of reduced growth on larval survival and subsequently on population growth. Developmental delays are less detrimental in species with longer and less synchronous larval periods. All six species were most sensitive to changes in first-year survival, and damping ratios were generally a good indicator of resilience to perturbations in both larval survival and fecundity. Further identification of species and population-level vulnerabilities can improve the evaluation of sublethal effects in relevant context for ERA.

Keywords

ecological risk assessment; comparative matrix model; aquatic toxicology

1. Introduction

In response to a deficit of standardized toxicological data for amphibian species, empirical data for the most representative species are often substituted in Ecological Risk Assessment (ERA). Typically, early life stage fish tests (e.g., OECD 1992) are substituted for the aquatic phase of the amphibian life cycle prior to metamorphosis, and the terrestrial stages are represented by bird or small mammal data. Although some studies have assessed chemical

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toxicity to various amphibian species (Berrill et al. 1998, Bridges and Semiltsch 2000, Howe et al. 2004, Jones et al. 2009, Relyea and Jones 2009, Hua and Relyea 2014), data are generally limited in chemical diversity and often focus on high profile pesticides (e.g., endosulfan, carbaryl, atrazine, glyphosate). While these studies provide additional context about species sensitivity and population vulnerability, they do not follow a uniform approach for comparison among a variety of amphibian species and compounds. When amphibian data are available for newer or less studied chemicals they are generally limited in taxonomic diversity or represent invasive model species (e.g., bullfrog, *Xenopus* spp.). These species are easily bred in the laboratory and ample genetic data are available for identification of molecular-level impacts (Harland and Grainger 2011, Hammond et al. 2017); however, they differ from many native amphibian species in their sensitivity to toxicants (Birge et al. 2000, Mann and Bidwell 2000, Fort et al. 2006) as well as their demography and habitat. Use of surrogates in general introduces uncertainty since species sensitivity and population-level effects of chemical exposure can vary even between closely related species (Bridges and Semiltsch 2000, Banks et al. 2014) or among populations of the same species (Bridges and Semiltsch 2000, Cothran et al. 2013, Hua et al. 2013). Likewise, various exposure pathways and diverse life history strategies of amphibians are inadequately captured by their proxies (Johnson et al. 2017).

While larval fish are often sufficiently sensitive to be considered conservative and protective surrogates in both acute and chronic toxicity evaluations using organism-level endpoints (Weltje et al. 2013), these endpoints do not represent long-term effects associated with the unique life cycle and plasticity of amphibian development. In addition to size-based measurements being poor representation of effects on metamorphosis, the most commonly used metrics of chronic toxicity tests are hypothesis test-based endpoints such as No Observed Adverse Effect Concentration (NOAEC) and the Lowest Observed Adverse Effect Concentration (LOAEC). NOAECs and LOAECs are criticized because of their lack of confidence limits, dependence on selected test concentrations, and use of statistical hypothesis testing to determine “no-effect” (Crane and Newman 2000). Additionally, studies that report only point estimates such as NOAECs and LOAECs are inadequate to estimate toxicity effects in population models, whereas dose-response functions of toxicity effects present this relationship with continuous variables that can be used for model simulations of long-term effects (Kramer et al. 2011). These shortcomings in existing data necessitate approaches to improve population-level assessments of chemical exposure, particularly to amphibians with few representative model species and endpoints. Test protocols that include time to metamorphosis and relevant endpoints for amphibians improve upon data limitations (OECD 2009, OECD 2015). Extrapolation methods based on quantitative adverse outcome pathways could use these endpoints in conjunction with molecular data to estimate toxicity to a variety of species with minimal animal testing. Finally, a framework for population-level assessment (Raimondo et al. in review) would facilitate incorporation of these endpoints in appropriate ecological and management contexts.

Although complex endocrine cues are responsible for developmental processes in both fish and amphibians (Fort et al. 2007, Terrien and Prunet 2013), mechanisms vary among aquatic taxa (Duarte-Guterman et al. 2014). Evidence of low-dose effects and nonmonotonic response in amphibian species suggest pathways might be affected differently by endocrine

disruption (Hinther et al. 2010, Vandenburg et al. 2012, Stark et al. 2015). In some cases, developmental processes might be sufficiently altered such that some tadpoles are unable to metamorphose, with sublethal developmental effects effectively resulting in mortality. Wilbur and Collins (1973) describe the probability of metamorphosis as a function of the size and recent growth rate of a tadpole as well as the environmental variability under which the species has persisted. Implicit in this scenario is a range of masses in which metamorphosis will occur and the assumption that below the minimum threshold, transition to the terrestrial juvenile stage is unlikely. Proximate causes of metamorphosis and its plasticity are hormone-driven (Denver 1997) such that chemical impacts on corticotropin-releasing or thyroid hormones could alter development within environmentally restricted periods. Time to metamorphosis, which may be a function of habitat availability, density dependence, and/or chemical exposure, is the metric we focus on in this study to interpret growth effects in terms of survival and transition to the juvenile stage.

Estimation of growth effects in developing tadpoles is further complicated by habitat constraints (Indermaur et al. 2010) and developmental plasticity of species that are dependent upon ephemeral breeding ponds being inundated for sufficient duration to allow metamorphosis. The duration of the larval stage varies in response to annual precipitation and hydroperiod in some species (Denver et al. 1998, Perotti et al. 2011, Amburgey et al. 2016, cf. Amburgey et al. 2012). Reduced hydroperiod can accelerate development but often with carryover effects of reduced mass, survival, or reproduction (Chelgren et al. 2006, cf. Green and Bailey 2015). Within a brood, accelerated development has limited compensatory effect for reduced survival associated with shortened hydroperiod (Ryan and Winne 2001, Amburgey et al. 2016). Repercussions of accelerated development could be seen in reduced survival (Goater 1994), smaller size at maturity (Smith 1987), or lower fecundity in smaller females (Woolbright 1983, Elmberg 1991).

Endocrine disrupting compounds that affect gonadal development and effectively alter sex ratios (e.g., Hogan et al. 2008) in breeding amphibian populations could also reduce fecundity (Kloas and Lutz 2006), especially in species for which explosive breeding episodes require parity in operational sex ratio and breeding frequency (Alho et al. 2008). Disparities in maturation time can also contribute to male-biased sex ratios associated with declining amphibian populations (Swannack and Forstner 2007), although female-biased sex ratios have also been associated with vulnerable populations of amphibians (DiMinin and Griffiths 2010). In response to observed effects of endocrine-disrupting compounds on clutch size, sexual differentiation, and gonadal development (Orton and Tyler 2015), we also simulate reduction in reproductive potential and the population-level impacts.

For larval amphibians developing in an ephemeral habitat, growth and survival are density dependent (Wilbur 1977, Vonesh and De la Cruz 2002, Schiesari et al. 2007, Rogers and Chalcraft 2008), and ecological and demographic factors unique to different species can influence long-term effects of stressors (Lips et al. 2003). As multiple stressors contribute to amphibian population declines (Grant et al. 2016), ecologically relevant risk assessment methods are necessary to present variable long-term effects of habitat availability and chronic pesticide exposure (Bruhl et al. 2011, Weir et al. 2016, Willson et al. 2012). One objective of this study is to demonstrate the influence of delayed tadpole development on

reduced survival. We also compare the resulting mortality and reduced fecundity in species of amphibians with different life histories to further explore population-level vulnerabilities. We expand on a simple, stage-based comparative matrix model approach advocated elsewhere (Biek et al. 2002, Weir et al. 2016) for initial evaluation of population sensitivity and offer perspectives on differential species sensitivity for consideration in population-level ERA.

2. Methods

2.1 Larval period estimation

The time to metamorphosis ranges were used to develop cumulative distribution functions (CDF) of metamorphosis during a standard larval period for six amphibian species (western toad, *Anaxyrus boreas*; southern toad, *A. terrestris*; southern leopard frog, *Lithobates sphenoccephalus*; common frog, *Rana temporaria*; northern red-legged frog, *R. aurora*; California red-legged frog, *R. draytonii*). These species were selected because they are frequently studied and adequate demographic data existed in the literature for subsequent population modeling (discussed below). Their life cycles include terrestrial juvenile and adult stages, unlike aquatic model species. In addition to these six species, we also developed CDF for one aquatic species commonly used in toxicity testing (African clawed frog, *Xenopus laevis*). The range of time to metamorphosis data used to develop the CDFs were obtained from AmphibiaWeb (AmphibiaWeb 2017), Encyclopedia of Life (Encyclopedia of Life 2017), or published literature (Beck and Congdon 1999). Estimates for *X. laevis* were based on laboratory observations (unpublished data) which were similar to standard protocol guidelines (OECD 2015). For each CDF, the inflection point (e) represents the approximate median age at which metamorphosis occurs and the slope (b) represents the rate at which larvae for each species transition. Steeper slopes represent species with smaller estimated time ranges during which they undergo metamorphosis. The slope values were determined iteratively using a log-logistic function so that 5-95% metamorphosis fell within the published ranges:

$$S_l = S_{max}(\exp(-\exp(b(\log(x) - \log(e))))$$

2.2 Delayed development as larval mortality

To simulate delays in development, we shifted the inflection point of the curve, or the point at which 50% of the population reaches metamorphosis, to the right by 1-15 days while keeping the slope constant. Exposure to some pesticides can delay metamorphosis by weeks or cause cessation of development (Howe et al. 2004). Most pesticide-induced developmental delays tend to be more modest, on the order of a few to several days (Sullivan and Spence 2003, Yahnke et al. 2017). We chose this range of developmental delays to be broad yet representative of potential impacts. We then estimated the proportion of the population to undergo metamorphosis over time for each species with and without developmental delays. By comparing percent metamorphosis at a given time for each curve, we were able to infer potential larval mortality attributed to delayed larval development, assuming habitat constraints limited the larval period and death is the only alternative to

metamorphosis. The hypothetical delay in development could be a function of chemically induced impacts or density-dependent effects. Chemically induced acceleration in development would be unlikely to result in additional mortality under these assumptions, and therefore was not considered here. For this comparison, we did not quantify any potential compensatory effects of accelerated development in response to drying habitat or contaminant exposure. We then compared the percent metamorphosis at the original inflection point in the curve (median time to metamorphosis), to the percent metamorphosis at the same time point for the curves with developmental delays. The reduction in percent metamorphosis was used as reduced larval survival in our population models.

2.3 Simulated reductions in fecundity

Chemical-induced impacts on amphibian reproduction vary widely (Orton and Tyler 2015), and environmental stochasticity also contributes to variation in reproductive success, including years with complete reproductive failure (Salice 2012). Rather than systematically replicating environmental or pesticide-specific effects over time, we evaluated the relative contribution of breeding success on population dynamics by manipulating this parameter across the entire range of potential variability. Reduced fecundity (10-90%) was simulated for each species to determine relative population-level effects between species and in relation to larval survival effects. Proportional reduction in PGR in response to reduced fecundity was calculated.

2.4 Population sensitivities to perturbations

We used a three-stage, female-only, matrix model in which the amphibian life cycle was divided into larval-metamorph, juvenile, and adult stages, with an annual time step and post-breeding census (Figure 1). We used published demographic estimates (Table 1; Biek et al. 2002, Gray 2009, Weir et al. 2016), to construct deterministic matrix models for the six anuran species. Fecundity (F) was calculated as the product of probability of annual survival for that stage, probability of breeding, sex ratio (initially assumed to be even for all species), and clutch size. The fecundity estimates for the juvenile stage (F_j) account for the proportion of individuals that may transition from juvenile to adult within the time step. Survival (P) of juvenile and adults was calculated as the probability of annual survival and probability of remaining in that stage. Growth (G) is expressed as the probability of transition to the next stage. Growth in the first stage (G_1) is the product of embryo, larval, and metamorph survival rates if these three estimates were reported independently (*A. boreas*, *R. aurora*, *R. temporaria*, *A. terrestris*, *L. sphenoccephalus*) or estimates of first year survival rates (*R. draytonii*).

Chemical exposure effects resulting from developmental delays were simulated as percent reductions in first year survival (G_1) from the baseline model. By using a post-breeding census, any chemical impacts to hatching success or larval survival are represented by this parameter. To explore the relative effects of larval mortality throughout a range of developmental delays (1-15 days), we reduced larval survival for each of the six species based on estimated reductions in percent metamorphosis and assuming failure to metamorphose resulted in mortality, based on hypothetical hydroperiod limitations. Population growth rates (PGR) were calculated based on the estimated reduction of larval

survival for the corresponding developmental delay. Under post-breeding census model structure, reproductive effects associated with reduced clutch size, biased sex ratio, or probability of breeding are included in fecundity estimates, which were reduced 10-90% in separate simulations, and PGR was also calculated for reduced fecundity matrices.

Sensitivity and elasticity were analyzed for each baseline species model. For each species, we also calculated the damping ratio, the ratio of the first two eigenvalues, which is a measure of intrinsic resilience. This value indicates how quickly a population can recover following a disturbance; higher ratios indicate a population can recuperate from a perturbation more quickly than those with smaller ratios.

3. Results

3.1 Metamorphosis rates

A narrow range of metamorphosis was reported for most species, with the exception of *R. draytonii* (Figure 2). The laboratory data for model species *X. laevis* was most similar to the brief and more synchronous larval period of *A. boreas*. For species that began metamorphosis at approximately the same age, the slope of the CDF shows differing rates of metamorphosis between species (Figure 2). Steeper slopes occur where individuals in the larval cohort undergo metamorphosis at approximately the same time.

Shifting the CDFs to simulate delays in development produced proportional reductions in metamorphosis at a given time point (Figure 3), resulting in potential reductions in larval survival where development is limited by habitat constraints (i.e., hydroperiod). Species with longer larval periods that are less synchronous (greater range of time to metamorphosis as denoted by a shallower slope; e.g., *R. draytonii*) experienced relatively less impact on percent metamorphosis with the simulated shifts in time than species with shorter, synchronous larval periods (Table 2).

3.2 Population modeling

For all six species, PGR was most sensitive to the matrix element representing survival in the first year (Table 1). Relative sensitivity to first-year survival was indicative of population-level impact of reduced larval survival (Table 1). For example, reducing larval survival to 27% of the original value produced a PGR that was 76% of the original PGR in *R. aurora* and 65% of the original PGR in *R. temporaria*. (Table 2). Original range of time to metamorphosis distinguished the relative severity of developmental delays on larval survival, and hence PGR (Figure 4a). For example, a two-day delay in metamorphosis resulted in a 10% reduction of in *R. draytonii* larval survival and 50% in *A. terrestris*, with corresponding reductions of 3% and 20% in PGR, respectively. Neither the sensitivity of first year survival nor adult survival were correlated to the slope or inflection point of the metamorphosis CDF curves.

Damping ratios were highest in populations with relatively greater sensitivity to adult survival, indicating that these populations will recover from perturbations more quickly (*A. boreas*, *R. aurora*; Table 1). Conversely, amphibian species that are more sensitive to first-year survival had lower damping ratios, are less resilient, and population impacts will

require longer time for recovery (*R. temporaria*, *A. terrestris*, *L. sphenoccephalus*). Damping ratios were also a good indicator of the populations that were most sensitive to reductions in fecundity, as measured by the summed elasticity values of fecundity parameters: those with the lowest damping ratios had relatively greater reductions in PGR when fecundity is reduced (*R. temporaria*, *A. terrestris*, and *L. sphenoccephalus*, Table 1, Figure 4b). Relative population impacts of the two parameters manipulated in this study varied by species (Figure 4).

4. Discussion

The simulations presented here demonstrate that developmental delays in amphibians can have direct implications on survival, the long-term consequences of which may vary among species based on population dynamics. Developmental effects that impact gonad development, produce intersex individuals, skew the operational sex ratio, or otherwise reduce the reproductive success can also cause reductions in fecundity. In the species represented here, impacts on first-year survival and recruitment were relatively more influential than impacts on reproductive parameters, corroborating similar population simulations (Salice 2012). The common practice of reporting growth effects in terms of size differences fails to capture impacts in amphibians with developmental plasticity and a range of potential sizes at which transition into the next life stage can occur (Awkerman et al. in prep). Nonmonotonic responses to endocrine disruption likewise are not adequately represented by NOAEC or LOAEC values that assume linear relationships between dose and response (Welshons et al. 2003). In response to habitat constraints or chemical influence, faster development can yield smaller individuals (Rudolf and Rodel 2007), which often produce smaller clutches, so trade-offs between size and developmental stage are not captured by measuring mass or length. Reduced growth is often accompanied by possible carryover effects on age at maturity, juvenile survival rate, or productivity that are difficult to quantify or identify with consistency (Boone 2005, Distel and Boone 2009, Green and Bailey 2015, Earl and Whiteman 2015). Likewise, effects on sex differentiation and intersex individuals can be difficult to estimate in terms of altered sex ratio, reduced egg production, or breeding frequency.

While time to metamorphosis is subject to plasticity, the cumulative metamorphosis distribution provides a useful population-level function as an indicator of transition to terrestrial life stages. This habitat-dependent transition is a potential bottleneck for species using ephemeral ponds for breeding (Wang et al. 2011), and this estimate translates sublethal impacts on development to reductions in larval survival, the parameter to which species in this study were most sensitive. Development rates and time to metamorphosis for the aquatic model species, *X. laevis*, are similar to some native species, although population dynamics are likely to differ from those with terrestrial juvenile and adult stages. Nonetheless, the use of an amphibian surrogate that can capture changes in metamorphosis is more relevant to amphibian species than size metrics and effect concentrations used in early life-stage fish tests. The process of metamorphic transition from an aquatic larval stage to a terrestrial life stage and the plasticity of this response to environmental and anthropogenic stressors suggest that *X. laevis* is a more suitable model species for amphibian assessment than fish species. Many studies have evaluated the relative sensitivity of *Xenopus* spp. compared to

other amphibians and demonstrate the chemical-dependent species sensitivities (Birge et al. 2000, Mann and Bidwell 2000, Fort et al. 2006). The time necessary to observe developmental effects through metamorphosis might be cost-prohibitive, in which case, identifying key molecular events associated with delayed development could greatly facilitate use of existing toxicological data to extrapolate effects in other species. Additional information on receptor homology between species could improve toxicity extrapolation techniques for chemicals with a common adverse outcome pathway and empirical data available for model species.

The extent to which sublethal impacts are considered in an ERA can be subject to debate, with a recent report published by the National Academy of Sciences determining that sublethal effects are only adverse to the degree at which it affects an organism's survival and reproductive success (NRC 2013). For fish, the relationship between size and fecundity is linear and direct correlations between reduced growth and reproductive success can be made. Amphibians diverge from this model through their process of metamorphosis, but here we demonstrate the relationship between reduced growth rate and survival for these taxa. For ERAs that weigh heavily on impacts to survival and reproduction, the presented model translates reduced development directly to altered survival. As demonstrated here, delays in time-dependent metamorphosis can be expressed as a proportional reduction of larval survival in ERAs for evaluating population-level consequences to chemically induced developmental delays. Time to metamorphosis, in conjunction with information on typical hydroperiod for the species' range, could be used in probabilistic evaluations of developmental effects to capture the impacts of not reaching metamorphosis. Failure to complete larval development should be considered in addition to any lethal effects caused by chemical exposure. Estimating developmental effects on reproductive potential is more difficult, requiring phenotypic classification (e.g., altered gonadal development) to be linked to population-relevant endpoints associated with productivity (e.g., biased sex ratio, smaller clutch size, lower breeding propensity). Identifying molecular events associated with disruptions of key endocrine processes is a starting point for anticipating significant reproductive effects associated with developmental impacts.

Delayed development has a relatively greater impact on larval survival in species with shorter, less synchronous larval periods where habitat availability is constrained by hydroperiod. Species with longer larval periods breed successfully in areas with more consistent precipitation, less selective pressure for developmental plasticity, and less dramatic results of slight delays in development. Faster larval development in some species is likely an adaptation of developmental plasticity to ephemeral and variable conditions during the larval period (Wilbur and Rudolf 2006) and could imply additional capacity to accelerate metamorphosis that was not included in our simulations. The proximal causes of metamorphosis and developmental plasticity are endocrine driven (Boorse and Denver 2003). Inhibition of stress-induced responses by endocrine disruption could produce delays like those simulated here, without the potential compensatory effects of accelerated development in response to pond drying. Developmental delays resulting from chemical exposure tend to be less than the 15-day maximum in this study (e.g., Sullivan and Spence 2003, Yahnke et al. 2017) such that interspecific differences to chemical-induced developmental delays might be less dramatic than those simulated here.

In addition to potential differences in species' physiological responses, population dynamics differ according to life history strategies and ecology such that similar effects at the organismal level could have different implications across species for long-term developmental impacts. The anuran species modeled here were relatively similar in terms of life history strategies in the context of the diverse amphibian species that exist. The sensitivity to first-year survival in all species was reflected in the proportional population-level response to larval mortality, although the duration of the larval period determined the relative severity of delayed development (Table 1). In our model, first-year survival incorporates the most significant morphological changes in the amphibian life cycle and includes early survival in both aquatic and terrestrial environments. Further evaluating differential sensitivities to model parameters could identify variable chemical impacts across species. For species with the available estimates of embryo, tadpole, and metamorph survival, sensitivity to these three parameters will likely vary based on differences in species ontogeny (e.g., Biek et al. 2002).

Differences in population response to larval mortality also demonstrates taxonomic distinctions between *Bufonidae* and *Ranidae* (Figure 4) that could help identify vulnerable species. The distinctions in the relative severity of reduced larval survival demonstrates slight differences in life history strategies related to tradeoffs in survival and reproduction (Table 1). Higher damping ratios in species with greater sensitivity to adult survival suggests these populations will more quickly converge on a stable stage distribution and be more resilient to perturbations. For species without estimates of stage-specific demographic rates to develop population models and obtain this metric, the relative placement along the "fast-slow continuum" could be used; a species' placement on this continuum with respect to productivity and life span is indicative of population vulnerability of the species to extrinsic mortality. For example, the *Ranid* species modeled here, with larger clutches and fewer reproductive years, typify potential for faster population increase. The *Bufonid* species with longer lifespans exemplify the "slow" strategy of lower risk in stochastic environments (Allen et al. 2017). These differences are slight, however, and within-species variance can also demonstrate different selective pressures. For example, increasing altitudinal gradients can push life history strategies toward the "slow" end of the spectrum (Morrison and Hero 2003).

In all species, survival to the juvenile stage is determined by stage-specific survival rates of embryos, larvae, and metamorphs, which are low and highly variable and contribute to population fluctuations. Likewise, reproductive success can vary greatly depending on environmental conditions as well as population dynamics. Stressor-induced reductions of these rates reduce the probability of "boom" years and increase the probability of "bust" years, making populations less resilient. Simulating population dynamics with realistic environmental stochasticity and stressor effects could determine cumulative impacts of biotic and abiotic influences as well as any interactions between chemical-induced growth effects and potential compensatory mechanisms, such as accelerated development and density dependence (Willson et al. 2012). The deterministic matrices developed here do not include a full range of environmental and demographic variability, nor should they be considered a definitive evaluation of the species or their population status. Rather, they provide realistic combinations of demographic rates with which to compare life histories and

sensitivities to altered amphibian development. Stressors contributing to amphibian population decline vary regionally in their impacts (Grant et al. 2016), and the life history and environment of some species put them at a higher risk (Sodhi et al. 2008). Identifying inherent species sensitivity, population vulnerabilities, and likely local stressors would be a useful starting point for improvements in ERA in addition to using endpoints informative for the taxa of concern.

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Figure 1.
Amphibian life cycle stages and parameters used in matrix models.

Figure 2.
Estimated baseline cumulative distribution curves of metamorphosis times in seven different species.

Figure 3. Percent metamorphosis cumulative distribution functions for a) southern toad (*Anaxyrus terrestris*) and b) California red-legged frog (*Rana draytonii*) with delayed metamorphosis up to fifteen days.

Figure 4.

Proportional reductions in population growth rate (PGR) as a result of reductions in larval survival due to delayed growth and metamorphosis (a) and for reduced fecundity (b) for six amphibian species. Y-axes are the same scale.

Table 1

Life history characteristics, parameters, elasticity values, and damping ratios for matrices in baseline population models for six species. SVL = snout to vent length; TTM = time to metamorphosis; F_j = the reproductive contribution of juveniles; F_a = the reproductive contribution of adults; G_j = the transition probability from embryo to juveniles; G_j = the transition probability of juveniles to adults; P_j = survival probability of juveniles; P_a = survival probability of adults.

Life history characteristic	<i>A. boreas</i>	<i>A. terrestris</i>	<i>R. aurora</i>	<i>R. draytonii</i>	<i>L. sphenoccephalus</i>	<i>R. temporaria</i>
Length (SVL, mm)	56-125	42-92	51-133	116-138	51-127	75-80
Clutch size	5200-12000	2500-4000	530-830	300-5000	1200-1500	670-4500
Age at maturity (yrs)	3	2.5	3	2.5	2.5	3
Longevity (yrs)	11.5	10	15	10	NA	14
TTM (days)	33-55	54-63	107-143	105-210	53-80	80-119
Parameter						
F_j	24.72	69.30	27.27	67.50	59.17	52.00
F_a	1377.48	485.10	209.07	375.00	520.73	279.50
G_j	0.029	0.019	0.015	0.006	0.006	0.019
G_j	0.26	0.20	0.26	0.26	0.05	0.25
P_j	0.01	0.10	0.09	0.09	0.10	0.08
P_a	0.78	0.70	0.69	0.50	0.44	0.43
Elasticity						
F_j	0.129	0.197	0.106	0.159	0.121	0.250
F_a	0.160	0.149	0.158	0.147	0.195	0.119
G_j	0.289	0.345	0.265	0.307	0.316	0.369
G_j	0.065	0.048	0.077	0.102	0.017	0.085
P_j	0.160	0.149	0.158	0.147	0.195	0.119
P_a	0.198	0.112	0.236	0.136	0.157	0.057
Damping ratio	3.81	2.24	5.67	3.71	2.48	2.04

¹Biek et al. 2002

²Weir et al. 2016

³Licht 1974, Doubledee 2003, Gray 2009

Table 2

Proportional values of larval survival associated with delays in the baseline 50% metamorphosis and reduced population growth rate (PGR), assuming that failure to metamorphosis resulted in mortality.

Delay (days)	<i>A. terrestris</i>		<i>A. boreas</i>		<i>R. aurora</i>		<i>R. draytonii</i>		<i>L. sphenoccephalus</i>		<i>R. temporaria</i>	
	Larval Survival	PGR	Larval Survival	PGR	Larval Survival	PGR	Larval Survival	PGR	Larval Survival	PGR	Larval Survival	PGR
1	0.808	0.930	0.794	0.938	0.923	0.979	0.943	0.982	0.910	0.971	0.891	0.959
2	0.499	0.799	0.622	0.879	0.803	0.945	0.901	0.969	0.767	0.921	0.801	0.923
3	0.283	0.683	0.475	0.824	0.689	0.911	0.861	0.956	0.634	0.871	0.715	0.886
4	0.152	0.592	0.356	0.773	0.584	0.877	0.821	0.942	0.517	0.822	0.634	0.849
5	0.080	0.529	0.263	0.729	0.490	0.844	0.781	0.929	0.415	0.775	0.558	0.813
6	0.042	0.487	0.193	0.692	0.407	0.813	0.743	0.916	0.330	0.730	0.489	0.778
7	0.022	0.462	0.141	0.661	0.335	0.785	0.706	0.902	0.261	0.690	0.426	0.744
8	0.011	0.448	0.103	0.636	0.274	0.758	0.670	0.889	0.205	0.654	0.370	0.712
9	0.006	0.440	0.075	0.616	0.223	0.735	0.635	0.876	0.160	0.621	0.321	0.681
10	0.003	0.435	0.055	0.601	0.181	0.714	0.601	0.863	0.125	0.593	0.277	0.651
11	0.002	0.433	0.040	0.589	0.147	0.695	0.568	0.850	0.098	0.568	0.238	0.623
12	0.001	0.432	0.030	0.580	0.118	0.679	0.537	0.837	0.076	0.547	0.205	0.598
13	0.001	0.431	0.022	0.574	0.095	0.666	0.506	0.824	0.059	0.529	0.176	0.573
14	0.000	0.431	0.016	0.568	0.077	0.654	0.478	0.812	0.046	0.514	0.151	0.551
15	0.000	0.430	0.012	0.565	0.062	0.644	0.450	0.800	0.036	0.501	0.129	0.530