Craig O’Neill

ESM 211

Winter 2018

Prioritized Assisted Repopulation Efforts for Sierra Nevada Yellow-legged Frogs

# Summary

Despite a century of decline in population numbers and geographic extent, recent long-term survey results have shown that the endangered population of the Sierra Nevada Yellow-legged Frog (*Rana sierrae*) has been undergoing an overall increase in population sizes within Yosemite National Park over the past twenty years (Knapp, et al., 2016). This increase in population is occurring despite ongoing and multiple stressors afflicting the species, including persistent disease and invasive fish predators. While this increase in population counts is encouraging it is likely not sustainable without management intervention. At minimum, to secure population growths for this species continued fish removals from lakes are suggested as well as strategic translocation of adult frogs to extirpated water bodies.

# Species Background and Ecology

Amphibians are considered one of the most threatened animal groups in the world, with a significant proportion of species considered as a risk for extinction worldwide. Reasons for amphibian declines include anthropogenic habitat loss, introduction of invasive species, and disease (Skerratt, et al., 2007).

Once a common site amongst the lakes and riparian zones in the Sierra Nevada mountain range, the Sierra Nevada Yellow-legged Frog (*Rana sierrae*) has seen its population counts decrease dramatically since the beginning of the 20th century, making it a model species for the overall trend of amphibians worldwide.

The Sierra Nevada Yellow-legged Frog was formerly recognized as part of the same species as the Mountain Yellow-legged Frog (*Rana mucosa*). Research into separate populations of *R. muscosa* has indicated significant genetic differences, indicating that these populations comprised of two distinct species rather than distinct populations of the same species (Vredenburg, et al., 2007). Due to the recent distinction between the two species, and similar morphology and ecology of the two species, data, and studies for *Rana muscosa* will often be used to compliment information on the Sierra Nevada Yellow-legged Frog.

#### Species Status

The Sierra Nevada Yellow-Legged Frog is a species of great conservation concern in California. Considered endangered by the IUCN Red List of Threatened Species (Hammerson, 2008), the species was formally listed as a federally protected species under the Endangered Species Act as of 4/25/14 (Nafis, 2018). Approximately two years after the listing, the U.S. Fish and Wildlife Service designated 1.8 million acres of protected critical habitat for the Sierra Nevada Yellow-Legged Frog. This protected habitat was also designated to help other threatened and endangered amphibians including the Southern Mountain Yellow-Legged Frog (*Rana muscosa*) and the Yosemite Toad (*Anaxyrus canorus*) (Miller, 2016).

#### Morphology

The Sierra Nevada Yellow-Legged Frog is approximately 1.5 to 3.25 inches on average and is classified as a medium-sized amphibian. Like most anurans, the female Yellow-Legged Frog is typically larger than the males (U.S. Fish & Wildlife Service, 2017).

Coloration of the frogs can vary, though adults tend to have a mix of brown and yellow coloration on the dorsal side of the body. The common-name for Rana sierrae comes from the coloration of the underside of the back legs which are a distinctive yellow or light orange. Tadpoles grow up to 2 inches long and are brown with flecks of gold (Nafis, 2018).

#### Ecology and Life History

The Yellow-Legged Frog is mostly found near persistent pools of water and does not forage far from their initial breeding lakes. It eats a variety of terrestrial and aquatic invertebrates and tadpoles and may also consume dead frogs and its own eggs (Nafis, 2018).

Unlike other species of frogs found in California, the Yellow-Legged Frog is active mostly during the day. During the height of winter, the species is assumed to live at the bottom of frozen lakes and will not reemerge until shortly after the beginning of snowmelt. It rarely occurs where predatory fishes have been introduced (U.S. Fish & Wildlife Service, 2017).

Reproduction is aquatic and follows a reproductive cycle like most other frogs and toads in California. The Yellow-legged frog comes into maturity after approximately 4 years, though food availability can alter the length of the juvenile life-stage. Adult males will produce a mating call after at the beginning of breeding season, which typically occur after April, to attract females.

Fertilization is external, and is done in amplexus, with the male grasping the back of the female and releasing sperm as the female lays her eggs. Females lay eggs in large clusters and are often attached to underwater vegetation. Entire egg clusters have the approximate mass of a tennis ball (Stebbins, 2003).

The eggs hatch into tadpoles which feed in the water and eventually grow four legs, lose their tails and emerge onto land where they disperse into the surrounding territory (Nafis, 2018). Yellow-legged frog tadpoles often overwinter 2-3 times before metamorphosing into juveniles (Vrendenburg, Fellers, & Davidson, 2005).

Juvenile and adult Yellow-legged frogs are considered highly aquatic, rarely found more than a few meters from a source of water (Vrendenburg, Fellers, & Davidson, 2005). These frogs are opportunistic feeders and consume both aquatic and terrestrial invertebrates. Adult Yellow-Legged frogs are expected to live up to 20 years old (Matthews & Miaud, 2007).

Yellow-legged frogs have no natural aquatic predators, other than an occasional cannibalism. Introduced trout species to naturally fish-free lakes and streams in high elevation regions of California are considered the main reason of the species decline (U.S. Fish & Wildlife Service, 2017), followed by the subsequent introduction of a fungal pathogen, *Batrachochytrium dendrobatis*, that has been linked to global declines in amphibian populations (Skerratt L. , et al., 2007).

#### Range and Habitat

The historical range of the Sierra Nevada Yellow-Legged Frog (R. sierra) extended throughout California and parts of Nevada. The historical range is bounded by the Diamond Mountains in Plumas County at the Northwest; Mount Rose, located in Washoe County, Nevada, to the Northeast; the Middle and South Fork of the Kings River, located in Fresno County, California, to the Southwest; and the Glass Mountains, located in Mono County, California, to the Southeast. Rana sierrae is now extirpated from Nevada and from large portions of the historical range in the Sierra Nevada of California (Hammerson, 2008).

#### Population Data

The population of this species that I will be looking at is located within Yosemite National Park and includes studies of species across several geographically distinct lakes found within that park (Knapp, et al., 2016). Surveys were conducted for 2,154 distinct water bodies within Yosemite National Park over a period of 20 years. Not all water bodies were surveyed every year, and some sites were surveyed multiple times within a same year. In total 7,678 frog population count surveys were conducted for this population (Knapp, et al., 2016).

# Conservation Problem

The decline in population counts for the Sierra Nevada Yellow-legged frog is due to many stressors. Initial declines began due to the introduction of nonnative fish to formerly fishless lakes in the early 20th century. Fish introductions have ceased within Yosemite National Park, though are still common outside of the park. Additionally, while the artificial stocking of fish has ceased within Yosemite National Park, populations of fish still exist in most of the lakes from which they were introduced to.

Efforts to remove non-native fish have been tested using sinking monofilament gill nets. Initial efforts have shown some success in eradicating non-native fish populations from oligotrophic lakes in the Sierra Nevada region (Knapp & Kathleen, 1998), though remain a time intensive and expensive endeavor.

Experiments conducted on populations of Mountain Yellow-legged Frogs in the Humphreys Basin and LeConte Basin, both located in the southern Sierra Nevada region (Sierra National Forest and Kings Canyon National Park respectively) have shown drastic increases in population sizes immediately following the removal of non-native trout species (Knapp, Boiano, & Vredenburg, Removal of nonnative fish results in population expansion of a declining amphibian mountain yellow-legged frog, Rana muscosa, 2007).

In addition to population pressures that are the result of introduced, and persisting, populations of non-native fish, the spread of the chytrid fungus into Yosemite National Park starting in the 1970s has caused additional declines in frog populations. The presence of chytrid is considered ubiquitous within Yosemite National Park, with infected frogs likely to exist at all surveyed populations, however, data containing information on infection loads were not collected during the surveys used for this project. Lab research done in conjunction with these population surveys, however, indicate that mortality due to chytrid, measured via infection intensities, is lower for frogs from populations that have persisted with chytrid in the environment (Knapp, et al., 2016).

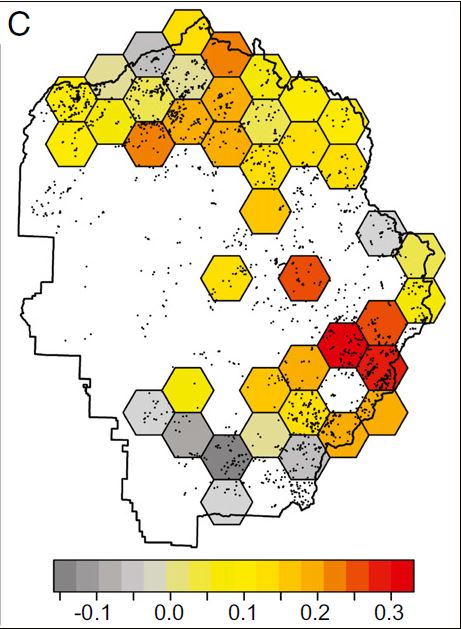


Figure 1. **Spatial variation in population growth rates from 1993 to 2012.** The intrinsic rates of growth are mapped on the color scale at the bottom of this image and applied to the spatially distinct hexagonal grid cells throughout Yosemite National Park. The above result come from the results of Knapp, et al., 2016’s paper from which the population survey data for this paper was extracted from. Values greater than 0 indicate that positive population growth occurred on average for the bodies of water found within that hexagonal cell.

Analyses of this data have shown an overall positive intrinsic growth rate for the Yosemite National Park (Figure 1) ( (Knapp, et al., 2016) population of Yellow-legged Frogs, though recovery of the species is far from complete. Part of this is that despite population counts of frogs at a single lake are growing, there is little movement towards reestablishing areas where the species was extirpated from.

To facilitate the growth of the Yosemite National Park population of Sierra Nevada Yellow-legged frogs I am proposing a management decision to artificially transplant individuals to suitable lakes in the area. Since this type of artificial transplanting of individuals is time intensive, expensive, and potentially risky for an endangered species such as the Yellow-legged Frog, I will be utilize a series of population models to determine the environmental characteristics of a lake that make for the most suitable growth rate and the life stage of the individuals that have the greatest impact on increasing the asymptomatic growth rates for the species. Using the population survey count data, along with recorded environmental characteristics of each of the survey sites, can identify key indicators for places to artificially reestablish native populations.

The first set of models used will be a life stage demographic model that has been conducted via literature review. The usage of this model will allow us to detect the life stages that have the greatest potential for increasing the growth rate of the species. Once this is determined, population trend analyses will be preformed for individuals in that life stage across all the surveyed sites to determine the characteristics that are most suitable for increasing that life stage’s population growth. The combination of these two models will provide management decisions not only where to transplant frogs within Yosemite National Park, but also for what life stage.

# Demographic Analysis

A demographic stage analysis was conducted using literature reviewed information to assume life stage survivorship rates for the Sierra Nevada Yellow-legged Frog. Due to the Sierra Nevada Yellow-legged Frog’s recent designation as a distinct species from the Mountain Yellow-legged Frog, a lot of the details about life stage survivorship was derived from research conducted on the latter species. Additional assumptions based on generalized amphibian studies were also used to estimate the survivorship for each of the life cycle stages.

For this analysis five distinct age classes were used. An individual remains in each age class for one year, though certain age classes can by skipped entirely due to the life history of this species. These classes are defined as below:

* Tadpole1. The Tapole1 stage refers to tadpoles that have survived one overwintering. These are tadpoles which have hatched from eggs in the previous year (spring to early fall) and survived through the winter.
* Tadpole2. The tadpole2 stage refers to tadpoles who overwinter for a second time, while remaining as tadpoles.
* Subadult1. This life stage refers to any individual who has metamorphized but is not yet to breeding size (40 mm snout/vent length)
* Subadult2. This life stage occurs if an individual remains too small to breed for a second consecutive year.
* Adult. Adults are individuals that have reached breeding size and are assumed to be breeding annually thereafter.

A life stage demographic table (Table 1) displays the survival probabilities for an individual. These probabilities were determined using best estimates from literature review. This analysis is based upon a pre-breeding assumption.

Table 1. **Life Stage Demographic Table.** The probabilities for survival and transition to the next life stage for an individual female Sierra Nevada Yellow-legged frog are shown in the below table. Fecundity rates, measured as the number of viable female tadpoles a single breeding adult is expected to produce annually is shown in the first row of the table. Each life stage represents 1 year or survivorship. Due to the life history and distinct life stages of the species, some individuals may skip certain life stages, for example, a tadpole may remain a tadpole for two years, or after one year metamorphize into a subadult. Female adults are defined as having a snout/ventral length of greater than 40mm and are expected to breed annually.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Tadpole1 | Tadpole2 | Subadult1 | Subadult2 | Adult |
| Tadpole1 | 0 | 0 | 28.5 | 15 | 105 |
| Tadpole2 | 0.095 | 0 | 0 | 0 | 0 |
| Subadult1 | 0.001 | 0.095 | 0 | 0 | 0 |
| Subadult2 | 0 | 0 | 0.1 | 0 | 0 |
| Adult | 0 | 0 | 0.19 | 0.1 | 0.7 |

#### Reproduction Rates

Reproduction only occurs in the adult stage (snout/vent length > 40mm). Breeding occurs within a distinct seasonal period and female frogs only lay one egg mass per year. Egg masses on average contain 150 to 300 eggs (Nafis, 2018). For this assessment I have assumed that 300 eggs on average are laid.

Breeding is constrained by the number of available females, so therefore this demographic analysis will only be looking at female population numbers. The sex ratio for this frog has been observed as 1:1 (Bonham, 2011), and I have found no indication that environmental factors contribute to whether or not an egg is female or not, so therefore I have assumed that half of the laid eggs will be female (150). A personal conversation with a herpetologist confirmed that for this species that would be a decent enough estimation (E., Wilson, Personal Conversation on February 26, 2018).

Fecundity rates for this model considers survivorship from an egg being laid, to egg hatching, and the tadpole surviving the first year. Studies have shown that a significantly large portion (99-98%) of fertilized eggs hatch into tadpoles after 18-20 days and survive the first winter (Vrendenburg, Fellers, & Davidson, 2005).

Since this is a pre-breeding model, three life stages can possible contribute to the next generation of tadpoles: Surviving adults, Subadult1’s that survive and transition directly to the adult stage, and Subadult2 that survive and transition directly to the adult stage. As indicated by Table 1, the number of expected tadpoles that survive from egg to the first year of survey from each life stage are 105 for adults, 15 from subadult2, and 28.5 from subadult1.

#### Tadpole Survivorship

Tadpole metamorphosis occurs between 1-2.5 years, or 2-3 overwinters (Vrendenburg, Fellers, & Davidson, 2005). Information is lacking regarding the probability that a tadpole metamorphizes after the second or third overwinter. Literature for higher elevation Mountain Yellow Legged Frogs, which would include the population of Sierra Nevada Yellow-legged Frogs located in Yosemite National Park, suggest that they tend to take overwinter 3 times.

Studies also indicate that survivorship of tadpoles into subadults is relatively low. I could not find specific numbers for the Mountain Yellow-Legged Frogs, however found studies indicating that approximately 1-5% of tadpoles survive metamorphosis and become subadults across a variety of frog species (Calef, 1973). For this analysis, I am assuming the lowest survivorship rate of 1% for all tadpoles to reach the subadult life stage.

Using this information, I have assumed that the cumulative probability of tadpole1 and tadpole2 stages reaching the subadult1 stage is equal to 0.1. This cumulative probability is the probability of surviving a year multiplied by the probability of transitioning to the next life stage, either tadpole2 or subadult1 plus the probability that a tadpole2 survives multiplied by it’s probability of transitioning to a subadult1. Figure 2 details the exact equation used. This assumption presumes that annual survivorship for tadpole1 and tadpole2 is equal. This may not be the case, as it is possible that a larger tadpole2 may have greater survivorship compared to a more recently born tadpole1, however since that data is lacking I feel that this assumption is relevant. Any demographic related managerial decisions based upon either tadpole1 or tadpole2 survivorship rates will likely affect all tadpoles equally.

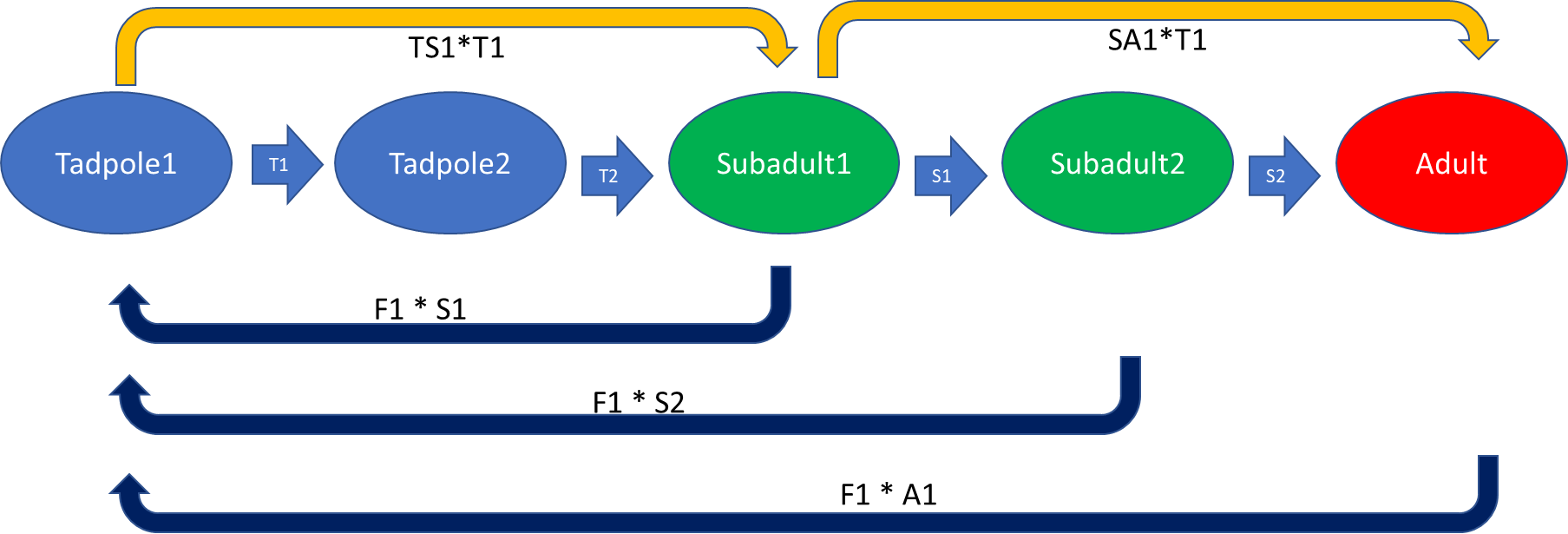


Figure 2. **Life Stage Diagram.** The 5 life stages of an individual frog are designated by the circles in the above diagram. Each stage lasts for 1 year, and survivorship to the next life stage is designated by the arrows between the circles. T1 refers to the probability of surviving a year by a Tadpole 1 (0.095). The yellow arrows above the circles represent the possibility for an individual to skip a life stage. The probability that a Tadpole1 becomes a Subadult 1 is listed at TS1 (0.001, the probability that it will skip at life stage) multiplied by the annual survivorship (T1, or 0.095). Not listed in this diagram is the annual adult survivorship, which is 0.7. The purple arrows at the bottom represent fecundity rates. The number of female offspring that a female adult produce is listed as F1 (150 tadpoles). This rate is multiplied by the annual survivorship rate for each age class (S1 for 1st year subadults, S2 for second year subadults, and A1 for adult survivorship). Below is the sample equation used to derive survivorship rates for the Tadpoles based on the overall stat that only 1% of all tadpoles survive metamorphosis. I can’t figure out how to put a caption for this equation.

Observations of the species have observed that higher elevation Mountain Yellow Legged Frogs typically spend 2 years as tadpoles (3 overwinters), I am presuming that only 0.1% of 1-year old tadpoles become subadults in year 2 and survive. The probability for a tadpole1 in year 1 to survive and become a year 2 tadpole2 is presumed to be 9.5%. This creates a cumulative survivorship for tadpoles to subadults to be the probability of Tadpole1 becoming Subadult1 (0.001) plus the probability of a tadpole in year 1 remaining a tadpole in year 2 (0.095) multiplied by the probability of a tadpole in year 2 surviving and becoming a subadult (0.095) which equals 0.01, or 1% of tadpoles reach the life stage of a subadult (Figure 2).

#### Subadult Survivorship

Subadult individuals are any individuals which have metamorphized from a tadpole but are still too small to breed. Typically, an individual will progress into breeding adults after 1 year, however some may remain as subadults for a second year, likely due to environmental effects. Like tadpoles, studies are not conclusive regarding the proportion of subadults that reach breeding size after one year or not, so some assumptions were made based upon the overall survivorship of all subadults into adults.

Mortality of subadults is observed to be high, with only approximately 20% reaching the adult stage (Bonham, 2011), this is likely due to how metabolically expensive it is for the tadpole to complete metamorphosis, and the risk associated with being a smaller frog.

Literature suggest that usually subadults become breeding adults after one year, so I have assumed a very small (10%) proportion of subadult1 transition into subadult2, while a relatively larger proportion go straight to the adult stage (19%). The same proportion of subadult2 frogs (10%) are expected to transition into breeding adults.

#### Adult Survivorship

Adult, in comparison, have been found to have high estimates for survivorship. One assessment claims that over 90% of adults survive year to year, with other estimates suggesting between 56% and 86% (Bonham, 2011) (Briggs, Knapp, & Vredenburg, 2010). For this project I took an estimated median value of 70%.

# Demographic Analysis

To determine the stable stage proportion for this species I used initial population counts from a site 1764. This site is a highly surveyed site that frequently contained high numbers of frogs. The data for this analysis does not breakdown the proportions of tadpoles and subadults that fall within the tadpole1/tadpole2 and subadult1/subadult2 respectively, so some assumptions were made for this analysis.

The stable stage proportion for this species was found to be approximately 90% tadpole1, 9% tadpole2, and less than 1% for the remaining life stages (Table 2) (Figure 3). This highly skewed stable stage proportion towards tadpoles is expected due to the high observed mortality found in tadpoles.

Table 2 **Stable Stage Distribution.** When the population reaches stable stage distribution the vast majority of individuals will be tadpoles. This is the result of the high fecundity rates of adults and high mortality rates of tadpoles for the species. The asymptotic growth rate for this species was calculated to be approximately 1, indicated that the species is stable.

|  |  |
| --- | --- |
| **Life Stage** | **Proportion** |
| Tadpole | 89.88% |
| Tadpole2 | 8.53% |
| Subadult1 | 0.90% |
| Subadult2 | 0.09% |
| Adult | 0.60% |

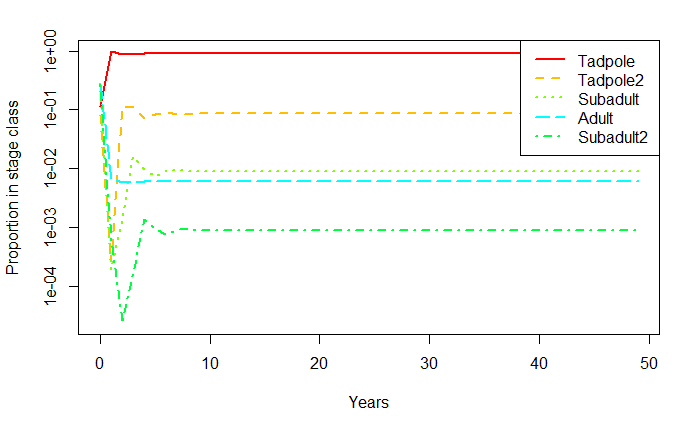


Figure 3. **Stable Stage Distribution Projection.** Using population counts from site 1764 I plotted the estimated time until stable stage distribution is met. For most sites that had established populations of the frog, the stable stage distribution was met in less than 10 years.

The asymptomatic growth rate for this species showed stable to very slight increase in population size with a lambda of 1.000473.

A sensitivity analysis detailed that the most sensitive life stage for the frogs exist for tadpoles becoming subadults. Both tadpole1 becoming subadult1 and tadpole2 becoming subadult1 returned the highest sensitivity numbers. Putting in management efforts to increase survivorship of this transition would have the greatest effect on the asymptomatic growth rate for the species (Table 3).

Table 3. **Sensitivity Analysis Results.** A sensitivity analysis showed that increasing tadpole survivorship to subadults (metamorphizing) had the greatest impact in increasing the asymptomatic growth rate for the species. Increasing the number of first year tadpoles to become a subadult had the greatest impact. Increasing the value may have management implication via reducing predatory pressures on tadpoles by removing non-native trout from the region.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Tadpole1** | **Tadpole2** | **Subadult1** | **Subadult2** | **Adult** |
| **Tadpole1** |  |  | 0.001897025 | 0.000189613 | 0.001262663 |
| **Tadpole2** | 1.7955719 |  |  |  |  |
| **Subadult1** | 18.9096944 | 1.79557192 | 0.189399469 |  |  |
| **Subadult2** |  |  | 0.094701972 |  |  |
| **Adult** |  |  | 0.662913807 | 0.06626005 | 0.441236629 |

However, when we looked at the proportional effect that increasing survivorship has on increasing the asymptomatic growth rate using an elasticity analysis has shown that increasing adult survivor ship will have the greatest impact. My assumption of this related to the biology of the species: The number of eggs and tadpoles produced by each adult female, and the extreme levels of tadpole mortality, increasing the number of breeding adults would have the greatest effect (Table 4).

Table 4. **Elasticity Analysis Results.** Contrary to Table 3’s Sensitivity results, increasing adult survivorship rates has a more relative impact on increasing the asymptomatic growth rate. Adult survivorship may be impacted in certain lakes due to density dependence. Increasing adult survivorship and thus the number of adults, has the greatest impact.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Tadpole1** | **Tadpole2** | **Subadult1** | **Subadult2** | **Adult** |
| **Tadpole1** | 0 | 0 | 0.05404 | 0.002843 | 0.132517 |
| **Tadpole2** | 0.170499 | 0 | 0 | 0 | 0 |
| **Subadult1** | 0.018901 | 0.170499 | 0 | 0 | 0 |
| **Subadult2** | 0 | 0 | 0.009466 | 0 | 0 |
| **Adult** | 0 | 0 | 0.125894 | 0.006623 | 0.30872 |

#### Demographic Analysis Limitations

Some limitations of this demographic analysis include a lack of control for density dependence. While density dependence is not likely to be an issue for frog populations located in lakes where population counts are kept low due to predation by invasive fish species, it will likely affect the survivorship rates in some of the more populated lakes.

Additionally, these survivorship rates are based on generalized predictions for the species and do not reflect the actual difference in survivorship between lakes of different environmental stressors. Egg masses, tadpoles, and subadults, for example, would likely have higher mortality rates in lakes which still contain remaining fish populations as these fish are likely to predate upon the more aquatic life stages of this species.

Environmental stochasticity is missing from this model, which greatly impacts the frog's development and survival. Multiple "good" years could create a natural scenario where subadult survivorship grows, drastically increasing lambda for the population. Environmental stochasticity is most likely to impact the early life stages which would be particularly vulnerable to increased streamflow (which may cause increased mortality to eggs or tadpoles due to egg masses being scoured from the lakes or streams, though my population is in a lake so probably not that big of a deal). Extreme cold winters would likely affect all populations equally if the cold weather is able to freeze the lake solid, preventing the frogs of all life stages from finding and hibernating in the refuge beneath the lake.

# Population Trend Analysis

The results of the demographic analysis show that increasing adult frog survivor ship has the greatest relative impact on increasing the asymptomatic growth rate. Using this insight, and the results from 20 years of surveys across thousands of lakes in Yosemite National Park, a population trend analysis was preformed to determine what characteristics are most conducive to increasing adult populations. After determining these characteristics, a prioritization schema can be constructed which prioritizes which lakes and water bodies have the greatest potential to accept transplanted adult frogs and provide the greatest opportunity for overall increases in the metapopulation of the species.

A stochastic exponential growth model was used on surveyed sites to determine mean growth rates (mu) for all surveyed sites which had at least 4 year’s worth of surveys conducted across the 20-year survey period. Any surveys which found zero adult frogs were ignored for this function and assumed to be attributed to sampling error at the time of the survey. This assumption is done so that mathematically a mean growth rate can be conducted and to also account for observational error.

Mean growth rates for each surveyed site were analyzed using a linear regression model to predict which of the following environmental characteristics best predicted the mean growth rate:

* Depth. The maximum depth of the water body at the survey site. The values for this measurement were standardized so that the mean maximum depth of all surveyed water bodies was equal to 0.
* Elevation. The elevation above sea level. The elevation was standardized so that the mean elevation of all surveyed water bodies was equal to 0.
* Cell. A hexagonal cell was overlaid across the extent of Yosemite National Park for spatial groupings of surveyed waterbodies. Each waterbody was assigned to a single hexagonal cell; however, I do not have a map of where these cells exist within Yosemite National Park.
* Fish. The presence, absence, and removal of non-native trout from the lakes were also denoted. Lakes are either denoted as never having introduced non-native trout (“No”), introduced and persisting populations of non-native trout (“SF”), or introduced but now extirpated populations of non-native trout (“SFL”)

Mean growth rates were weighted by the square root of the standard error for the mean growth rate as calculated by the stochastic exponential growth model. A linear regression model was conducted independently for each of the three statuses of fish in the waterbodies.

#### Linear Regression Results

Since some sites were surveyed more than once per year, the average number of adults found per year were used for each site.

The overall results from the linear regression analysis showed that cell, fish status, and maximum depth significantly predicted the mean growth rate for the species across all sites (p-value < 0.0001, R2 = 0.8072).

Lakes in which non-native fish populations were removed was shown to have a significantly higher mean growth rate compared lakes which never had introduced fish. This is likely due to the lakes which never had fish introduced are closer to a carrying capacity compared to the newly opened habitat in the SFL lakes due to the removal of the invasive predatory pressures.

Spatially, it appears that Cell 60 had a significant negative impact on mean growth rate, indicating that lakes in this area may not be as useful for repopulation compared to lakes within cells 66, 76, 113, and 135 compared to cell 31. Full details and statistically significance of each variables can be seen in Table 5.

Table 5. **Regression Analysis Results.** A linear regression analysis was preformed to predict the mean annual growth rate of a water body based upon the depth (standardized so that a depth of 0 is mean depth of all lakes), geographic location (cell numbers), and fish status of the lake. Additional variables, basin origin and elevation, were tested but proved either insignificant or highly correlated. The overall model statistically predicted the average growth rate (p-value < 0.001, alpha = 0.05, R2 = 0.8089)

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Estimate** | **Std.** | **Error** | **tvalue** | **Pr(>|t|)** |
| **(Intercept)** | -0.030521 | 0.057733 | -0.529 | 0.5982 |  |
| **depth** | 0.007676 | 0.011971 | 0.641 | 0.5229 |  |
| **fishSF** | -0.180945 | 0.140932 | -1.284 | 0.2021 |  |
| **fishSFL** | 0.059713 | 0.03432 | 1.74 | 0.085 | . |
| **cell32** | -0.041931 | 0.079056 | -0.53 | 0.597 |  |
| **cell36** | -0.06609 | 0.162625 | -0.406 | 0.6853 |  |
| **cell37** | -0.019024 | 0.062632 | -0.304 | 0.7619 |  |
| **cell38** | 0.096993 | 0.061569 | 1.575 | 0.1183 |  |
| **cell41** | 0.039173 | 0.078305 | 0.5 | 0.618 |  |
| **cell43** | -0.113761 | 0.110366 | -1.031 | 0.3051 |  |
| **cell47** | -0.143259 | 0.085551 | -1.675 | 0.0971 | . |
| **cell54** | 0.13242 | 0.142408 | 0.93 | 0.3547 |  |
| **cell55** | 0.103389 | 0.082066 | 1.26 | 0.2107 |  |
| **cell60** | -0.343667 | 0.061044 | -5.63 | 1.66E-07 | \*\*\* |
| **cell66** | 0.167369 | 0.064828 | 2.582 | 0.0113 | \* |
| **cell72** | 0.164549 | 0.103662 | 1.587 | 0.1156 |  |
| **cell76** | 0.234038 | 0.108567 | 2.156 | 0.0335 | \* |
| **cell83** | 0.093965 | 0.154705 | 0.607 | 0.545 |  |
| **cell104** | 0.117273 | 0.081496 | 1.439 | 0.1533 |  |
| **cell107** | -0.015148 | 0.177116 | -0.086 | 0.932 |  |
| **cell108** | 0.111301 | 0.341223 | 0.326 | 0.745 |  |
| **cell112** | 0.030073 | 0.145827 | 0.206 | 0.837 |  |
| **cell113** | 0.155752 | 0.092534 | 1.683 | 0.0955 | . |
| **cell114** | -0.095159 | 0.080894 | -1.176 | 0.2423 |  |
| **cell117** | -0.108697 | 0.062967 | -1.726 | 0.0874 | . |
| **cell118** | 0.041098 | 0.074486 | 0.552 | 0.5823 |  |
| **cell119** | 0.030645 | 0.187663 | 0.163 | 0.8706 |  |
| **cell123** | 0.017155 | 0.079078 | 0.217 | 0.8287 |  |
| **cell124** | 0.086478 | 0.058928 | 1.468 | 0.1454 |  |
| **cell125** | -0.00958 | 0.081946 | -0.117 | 0.9072 |  |
| **cell129** | -0.039472 | 0.058032 | -0.68 | 0.498 |  |
| **cell130** | 0.039247 | 0.097002 | 0.405 | 0.6866 |  |
| **cell135** | 0.278751 | 0.162471 | 1.716 | 0.0893 | . |

# Recommendations and Conclusions

The success in removing non-native trout from lakes has repeatedly been shown to benefit population growth rates for this endangered frog. However, this action is not only costly and time consuming, but often causes issues with recreational fishing enthusiasts and creates a potentially undesirable public battle between conservationists and the public.

While it is still recommended that fish removal efforts take place, an alternative way to assist in the landscape scale recovery of the Yellow-legged Frog is to reintroduce adult frogs to a prioritized set of lakes. These prioritized lakes should be found within cells 66, 76, 113, and 135 of Yosemite National Park (the collected survey data from Knapp, et al., 2016 includes the cell number for all of the surveyed lakes, including those which no frogs were ever observed) and prioritize for deeper bodies of water. Elevation and watershed basin did not appear to have any affect on population growth rates, though the impact of these factors may be included in the hexagonal cell designation of the park.

# References

Bonham, C. (2011). *A Status Review of the Mountain Yellow-Legged Frog (Rana sierrae and Rana muscosa).* State of California, Department of Fish and Game. Natural Resources Agency.

Briggs, C. J., Knapp, R. A., & Vredenburg, V. T. (2010, May 25). Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *PNAS, 107*(21), 9695-9700.

Calef, G. W. (1973, July 1). Natural Mortality of Tadpoles in a Population of Rana Aurora. *Ecology, 54*(4), 741-758.

E., Wilson, Personal Conversation on February 26, 2018. (n.d.).

Hammerson, G. (2008). *Rana sierrae*. Retrieved from The IUCN Red List of Threatened Species 2008: e.T136114A4240654: http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T136114A4240654.en

Hammerson, G. (2008). *Rana sierrae*. Retrieved from IUCN Red List of Threatened Species: http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T136114A4240654.en

Knapp, R. A., Boiano, D. M., & Vredenburg, V. T. (2007). Removal of nonnative fish results in population expansion of a declining amphibian mountain yellow-legged frog, Rana muscosa. *Biological Conservation*(135), 11-20.

Knapp, R. A., Fellers, G. M., Kleeman, P. M., Miller, D. A., Vredenburg, V. T., Rosenblum, E., & Briggs, C. J. (2016, October). Large-scale recovery of an endangered amphibian despite ongoing exposure to multiple stressors. *Proceedings of National Academy of Sciences, 42*(113), 11889 - 11894.

Matthews, K. R., & Miaud, C. (2007). A skeletochronological study of the age structure, growth, and longevity of the mountain yellow-legged frog, Rana muscosa, in the Sierra Nevada, California. *Copeia*, 986-993.

Miller, J. (2016, August 25). *1.8 Million Acres of Sierra Nevada Habitat Protected for Imperiled Frogs, Toads*. Retrieved from Center for Biological Diversity: http://www.biologicaldiversity.org/news/press\_releases/2016/sierra-nevada-amphibians-08-25-2016.html

Nafis, G. (2018). *Sierra Nevada Yellow-legged Frog - Rana sierrae*. Retrieved from CaliforniaHerps.com: http://www.californiaherps.com/frogs/pages/r.sierrae.html

Skerratt, L. F., Berger, L., Speare, R., Cashins, S., McDonald, K. R., Phillott, A. D., . . . Kenyon, N. (2007). Spread of Chytridiomycosis Has Caused Rapid Global Decline and Extinction of Frogs. *EcoHealth, 4*(2), 125-134.

Skerratt, L., Berger, L., Speare, R., Cashins, S., McDonald, K., Phillott, A., . . . Kenyon, N. (2007). Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth*, 125-134.

Stebbins, R. C. (2003). *A field guide to western reptiles and amphibians.* (Third edition ed.). Boston, Massachusetts: Houghton Mifflin Company.

U.S. Fish & Wildlife Service. (2017, November 30). *Species Information Sierra Nevada Yellow-legged Frog*. Retrieved from U.S. Fish & Wildlife Service: https://www.fws.gov/sacramento/es\_species/Accounts/Amphibians-Reptiles/sn\_yellow\_legged\_frog/

Vredenburg, V. T., Bingham, R., Knapp, R., Morgan, J., Moritz, C., & Wake, D. (2007, April). Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. *Journal of Zoology, 271*(4), 361-374. doi:10.1111/j.1469-7998.2006.00258.x

Vrendenburg, V. T., Fellers, G. M., & Davidson, C. (2005). The mountain yellow-legged frog (Rana muscosa). In *Status and Conservation of U.S. Amphibians* (pp. 563-566). Berkeley, California: University of California Press.

# Appendix A

R Code Used for population trend analysis

library(tidyverse)

library(PVA)

## Getting the Data

KnappsYLFData <- read\_csv("KnappsYLFData.csv") #original Dataset

Lakes\_Adult <- aggregate(adult~site, KnappsYLFData, sum) %>%   
 subset(adult != 0)  
  
Adult\_vec <- Lakes\_Adult$site #List of sites with at least 1 frog found  
  
FrogLake <- KnappsYLFData[KnappsYLFData$site %in% Lakes\_Adult$site,]  
  
FrogLake\_agg <- aggregate(adult~ year+site, data = FrogLake, mean) # Aggregate the surveys to account for multiple surveys for the same lake in the same year. We are taking the average counts for adults when this occurs.  
  
Fish\_Status <- KnappsYLFData %>%   
 select(site, fish) %>%   
 subset(!duplicated(site))

## Calculated Mu using SEG

R\_Adults <- FrogLake\_agg %>% #Select the FrogLake\_Agg  
 subset(adult != 0) %>% #Remove any datapoints where no frogs were found  
 group\_by(site) %>% #group by the site (lake)  
 filter(n() > 2) %>% #Remove any sites which were surveyed for 2 or less years times during the 20 years  
 summarise(mu = estimate\_SEG\_params(adult, year)$mu, #calculate the mu for adults  
 SE = sqrt(estimate\_SEG\_params(adult, year)$sigma2/(n()-1))) #calculate the standard error for adults for each site

R\_Adult\_Lake <- merge.data.frame(KnappsYLFData, R\_Adults, by = "site") #Remerge dataframe so I can get the other lake qualities  
  
  
Adult\_LakeSummary <- R\_Adult\_Lake %>% #Group and summarize per lake  
 mutate(Weight = 1/(SE^2)) %>%   
 group\_by(site) %>%   
 summarise(mu = mean(mu),  
 depth = mean(depth),  
 elev = mean(elev),  
 basin = mean(basin),  
 SE = mean(SE),  
 cell= mean(cell),  
 Weight = mean(Weight))  
  
Adult\_LakeSummary <- merge.data.frame(Fish\_Status, Adult\_LakeSummary, by = "site") #Add back in the fish status for each lake  
  
Adult\_LakeSummary$basin <- as.factor(Adult\_LakeSummary$basin) #set basin to factor  
Adult\_LakeSummary$cell <- as.factor(Adult\_LakeSummary$cell) #set cell to factor  
Adult\_LakeSummary$site <- as.factor(Adult\_LakeSummary$site) #set site to factor  
  
Adult\_LakeSummary <- Adult\_LakeSummary %>%   
 subset(Weight != "Inf") #remove inf weights

## Linear Regression Characteristics to Mu

R1 <- lm(data = Adult\_LakeSummary, mu ~ depth + fish + cell, weights=Weight) #LM on the growth rate of frogs based on lake characteristics, weight is 1/SE^2 as suggested by Bruce. This is th  
  
summary(R1)

##   
## Call:  
## lm(formula = mu ~ depth + fish + cell, data = Adult\_LakeSummary,   
## weights = Weight)  
##   
## Weighted Residuals:  
## Min 1Q Median 3Q Max   
## -1.8906 -0.1048 0.0000 0.1951 0.8608   
##   
## Coefficients:  
## Estimate Std. Error t value Pr(>|t|)   
## (Intercept) -0.030521 0.057733 -0.529 0.5982   
## depth 0.007676 0.011971 0.641 0.5229   
## fishSF -0.180945 0.140932 -1.284 0.2021   
## fishSFL 0.059713 0.034320 1.740 0.0850 .   
## cell32 -0.041931 0.079056 -0.530 0.5970   
## cell36 -0.066090 0.162625 -0.406 0.6853   
## cell37 -0.019024 0.062632 -0.304 0.7619   
## cell38 0.096993 0.061569 1.575 0.1183   
## cell41 0.039173 0.078305 0.500 0.6180   
## cell43 -0.113761 0.110366 -1.031 0.3051   
## cell47 -0.143259 0.085551 -1.675 0.0971 .   
## cell54 0.132420 0.142408 0.930 0.3547   
## cell55 0.103389 0.082066 1.260 0.2107   
## cell60 -0.343667 0.061044 -5.630 1.66e-07 \*\*\*  
## cell66 0.167369 0.064828 2.582 0.0113 \*   
## cell72 0.164549 0.103662 1.587 0.1156   
## cell76 0.234038 0.108567 2.156 0.0335 \*   
## cell83 0.093965 0.154705 0.607 0.5450   
## cell104 0.117273 0.081496 1.439 0.1533   
## cell107 -0.015148 0.177116 -0.086 0.9320   
## cell108 0.111301 0.341223 0.326 0.7450   
## cell112 0.030073 0.145827 0.206 0.8370   
## cell113 0.155752 0.092534 1.683 0.0955 .   
## cell114 -0.095159 0.080894 -1.176 0.2423   
## cell117 -0.108697 0.062967 -1.726 0.0874 .   
## cell118 0.041098 0.074486 0.552 0.5823   
## cell119 0.030645 0.187663 0.163 0.8706   
## cell123 0.017155 0.079078 0.217 0.8287   
## cell124 0.086478 0.058928 1.468 0.1454   
## cell125 -0.009580 0.081946 -0.117 0.9072   
## cell129 -0.039472 0.058032 -0.680 0.4980   
## cell130 0.039247 0.097002 0.405 0.6866   
## cell135 0.278751 0.162471 1.716 0.0893 .   
## ---  
## Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1  
##   
## Residual standard error: 0.4683 on 100 degrees of freedom  
## Multiple R-squared: 0.8552, Adjusted R-squared: 0.8089   
## F-statistic: 18.46 on 32 and 100 DF, p-value: < 2.2e-16

# Appendix B

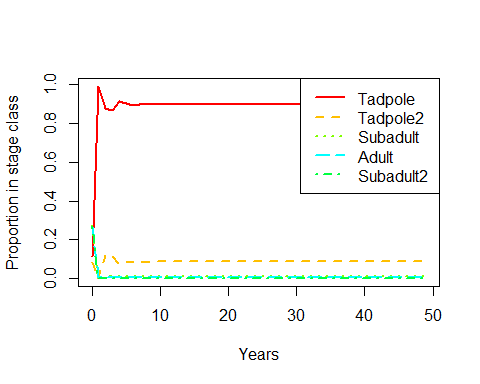
R code used for Demographic Analysis

class\_names <- c( "Tadpole", "Tadpole2", "Subadult", "Subadult2", "Adult")  
A <- matrix(c( 0, 0, 28.5, 15, 105,  
 0.095, 0, 0, 0, 0,  
 0.001, 0.095, 0, 0, 0,  
 0, 0, 0.1, 0, 0,  
 0, 0, 0.19, 0.1, 0.7 ),  
 nrow = 5, ncol = 5, byrow = TRUE, dimnames = list(class\_names, class\_names))

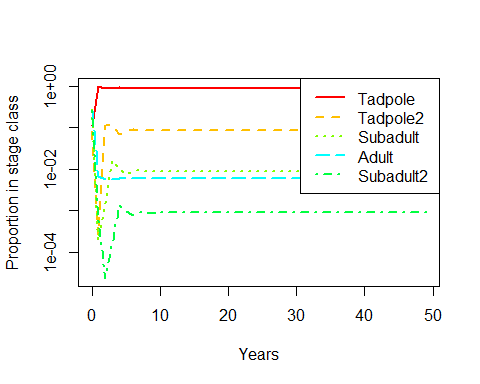
n\_0 <- c(278, 96, 200, 670, 670) #Site 1764  
n\_0 <- c(35, 25, 86, 83, 83) #Site 1634  
time <- 50  
  
pop <- pop.projection(A, n\_0, iterations = time)  
pop

## $lambda  
## [1] 1.000473  
##   
## $stable.stage  
## Tadpole Tadpole2 Subadult Subadult2 Adult   
## 0.8987641969 0.0853422444 0.0090020208 0.0008997766 0.0059917613   
##   
## $stage.vectors  
## 0 1 2 3 4 5  
## Tadpole 35 12411.000 8885.38500 6586.100437 8074.85843 8306.87884  
## Tadpole2 25 3.325 1179.04500 844.111575 625.67954 767.11155  
## Subadult 86 2.410 12.72687 120.894660 86.77670 67.51441  
## Subadult2 83 8.600 0.24100 1.272687 12.08947 8.67767  
## Adult 83 82.740 59.23590 43.907336 53.83239 55.37919  
## 6 7 8 9 10  
## Tadpole 7869.141063 7923.370937 8029.036965 7994.441477 7981.340188  
## Tadpole2 789.153490 747.568401 752.720239 762.758512 759.471940  
## Subadult 81.182476 82.838723 78.942369 79.537460 80.456500  
## Subadult2 6.751441 8.118248 8.283872 7.894237 7.953746  
## Adult 52.460940 52.822473 53.526913 53.296277 53.208935  
## 11 12 13 14 15  
## Tadpole 7999.25457 8003.901425 8003.806978 8008.330617 8012.939187  
## Tadpole2 758.22732 759.929184 760.370635 760.361663 760.791409  
## Subadult 80.13117 80.030850 80.197174 80.239017 80.242689  
## Subadult2 8.04565 8.013117 8.003085 8.019717 8.023902  
## Adult 53.32836 53.359343 53.358713 53.388871 53.419595  
## 16 17 18 19 20  
## Tadpole 8016.332582 8020.008346 8023.931626 8027.722983 8031.485651  
## Tadpole2 761.229223 761.551595 761.900793 762.273504 762.633683  
## Subadult 80.288123 80.333109 80.367410 80.404507 80.443706  
## Subadult2 8.024269 8.028812 8.033311 8.036741 8.040451  
## Adult 53.442217 53.466722 53.492878 53.518153 53.543238  
## 21 22 23 24 25  
## Tadpole 8035.292334 8039.098232 8042.895625 8046.698042 8050.504126  
## Tadpole2 762.991137 763.352772 763.714332 764.075084 764.436314  
## Subadult 80.481686 80.519450 80.557612 80.595757 80.633831  
## Subadult2 8.044371 8.048169 8.051945 8.055761 8.059576  
## Adult 53.568616 53.593988 53.619304 53.644654 53.670028  
## 26 27 28 29 30  
## Tadpole 8054.310709 8058.118931 8061.929330 8065.741480 8069.555347  
## Tadpole2 764.797892 765.159517 765.521298 765.883286 766.245441  
## Subadult 80.671954 80.710110 80.748273 80.786453 80.824654  
## Subadult2 8.063383 8.067195 8.071011 8.074827 8.078645  
## Adult 53.695405 53.720793 53.746196 53.771610 53.797036  
## 31 32 33 34 35  
## Tadpole 8073.371052 8077.188575 8081.007890 8084.829011 8088.651942  
## Tadpole2 766.607758 766.970250 767.332915 767.695750 768.058756  
## Subadult 80.862872 80.901108 80.939362 80.977635 81.015925  
## Subadult2 8.082465 8.086287 8.090111 8.093936 8.097763  
## Adult 53.822474 53.847924 53.873386 53.898860 53.924346  
## 36 37 38 39 40  
## Tadpole 8092.476681 8096.303227 8100.131582 8103.961749 8107.793726  
## Tadpole2 768.421935 768.785285 769.148807 769.512500 769.876366  
## Subadult 81.054234 81.092560 81.130905 81.169268 81.207649  
## Subadult2 8.101593 8.105423 8.109256 8.113091 8.116927  
## Adult 53.949845 53.975355 54.000877 54.026412 54.051958  
## 41 42 43 44 45  
## Tadpole 8111.627515 8115.463117 8119.300532 8123.13976 8126.980808  
## Tadpole2 770.240404 770.604614 770.968996 771.33355 771.698277  
## Subadult 81.246049 81.284466 81.322901 81.36136 81.399827  
## Subadult2 8.120765 8.124605 8.128447 8.13229 8.136136  
## Adult 54.077517 54.103087 54.128670 54.15427 54.179872  
## 46 47 48 49  
## Tadpole 8130.823670 8134.668349 8138.514845 8142.363161  
## Tadpole2 772.063177 772.428249 772.793493 773.158910  
## Subadult 81.438317 81.476825 81.515352 81.553897  
## Subadult2 8.139983 8.143832 8.147683 8.151535  
## Adult 54.205491 54.231122 54.256766 54.282421  
##   
## $pop.sizes  
## [1] 312.000 12508.075 10136.634 7596.287 8853.237 9205.562 8798.689  
## [8] 8814.719 8922.510 8897.928 8882.431 8898.987 8905.234 8905.737  
## [15] 8910.340 8915.417 8919.316 8923.389 8927.726 8931.956 8936.147  
## [22] 8940.378 8944.613 8948.839 8953.069 8957.304 8961.539 8965.777  
## [29] 8970.016 8974.258 8978.501 8982.747 8986.994 8991.244 8995.495  
## [36] 8999.749 9004.004 9008.262 9012.521 9016.783 9021.047 9025.312  
## [43] 9029.580 9033.850 9038.121 9042.395 9046.671 9050.948 9055.228  
## [50] 9059.510  
##   
## $pop.changes  
## [1] 40.0899840 0.8104072 0.7493895 1.1654690 1.0397962 0.9558015  
## [7] 1.0018218 1.0122286 0.9972449 0.9982584 1.0018639 1.0007020  
## [13] 1.0000564 1.0005169 1.0005698 1.0004374 1.0004566 1.0004861  
## [19] 1.0004738 1.0004692 1.0004735 1.0004736 1.0004725 1.0004727  
## [25] 1.0004730 1.0004729 1.0004728 1.0004729 1.0004729 1.0004728  
## [31] 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729  
## [37] 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729  
## [43] 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729 1.0004729  
## [49] 1.0004729

stage.vector.plot(pop$stage.vector)



stage.vector.plot(pop$stage.vector, log = "y")



Sensitivity

S <- DemoInfo(A)  
S

## $lambda  
## [1] 1.000473  
##   
## $SSD  
## [1] 0.8987641969 0.0853422444 0.0090020208 0.0008997766 0.0059917613  
##   
## $RV  
## [1] 1.000000 9.480343 99.840271 49.921315 349.449207  
##   
## $Sensitivities  
## [,1] [,2] [,3] [,4] [,5]  
## [1,] 0.1893995 0.01798445 0.001897025 0.0001896128 0.001262663  
## [2,] 1.7955719 0.17049871 0.017984446 0.0017975946 0.011970479  
## [3,] 18.9096944 1.79557192 0.189399469 0.0189309953 0.126064629  
## [4,] 9.4550706 0.89780718 0.094701972 0.0094657214 0.063033804  
## [5,] 66.1854943 6.28465025 0.662913807 0.0662600495 0.441236629  
##   
## $Elasticities  
## Tadpole Tadpole2 Subadult Subadult2 Adult  
## Tadpole 0.00000000 0.0000000 0.054039654 0.002842848 0.1325170  
## Tadpole2 0.17049871 0.0000000 0.000000000 0.000000000 0.0000000  
## Subadult 0.01890076 0.1704987 0.000000000 0.000000000 0.0000000  
## Subadult2 0.00000000 0.0000000 0.009465721 0.000000000 0.0000000  
## Adult 0.00000000 0.0000000 0.125894094 0.006622873 0.3087197  
##   
## $PPM  
## Tadpole Tadpole2 Subadult Subadult2 Adult  
## Tadpole 0.000 0.000 28.50 15.0 105.0  
## Tadpole2 0.095 0.000 0.00 0.0 0.0  
## Subadult 0.001 0.095 0.00 0.0 0.0  
## Subadult2 0.000 0.000 0.10 0.0 0.0  
## Adult 0.000 0.000 0.19 0.1 0.7