Technical Note Regarding Demographic Processes of Fish Species in Cienega Creek, Arizona. [Mike Hatch, February 16, 2015]

Introduction

Multiple independent contemporary surveys for fish in Cienega Creek, some dating back to 1989 (Young 1995), have documented the occurrence of three native fish species, including: Gila Chub (*Gila intermedia*), Gila Topminnow (*Poeciliopsis occidentalis occidentalis*), and Longfin Dace (*Agosia chrysogaster*). Although sample sites differ among independent studies, they can be partitioned into two distinct sampling segments. The upper sampling segment of Cienega Creek varies between 1.05 to 1.60 miles long, located upstream of Spring Water Canyon, whereas the lower sampling segment varies between 2.20 to 4.00 miles long, located downstream of Spring Water Canyon. The surveys conducted by Simms and Ehret (2014) were conducted to yield species-specific census counts that have been standardized by sample effort to yield "catch per effort" (CPE) statistics. Surveys of Gila Topminnow conducted by Bodner et al. (2007) were conducted to yield census counts that have been standardized by sample area to yield density estimates (fish per m^2). Surveys of Gila Chub conducted by Foster and Simms (2005) were conducted during 2005 to estimate species abundance derived from a Lincoln-Peterson model.

Time sequences of census data can be used to estimate inter-annual population growth rates as long as the sampling protocol is standardized to repeatedly sample the same sites at the same time of year, employ the same sample gear, survey sites that are representative of perennial habitats, and are conducted to insure that the portion of the population observed is a relatively constant fraction of the whole. Of the available data sets, the annual autumn counts of fish conducted by Simms and Ehret (2014) is best suited for examining species-specific inter-annual population growth rates for the fish species known from Cienega Creek.

Population growth rate is a key unifying variable linking various facets of population ecology. Population growth rate is important in the identification of factors that regulate species abundance and density, notably including response rates to environmental stressors. Estimates of population growth rate are important to management because they enable qualified projection of future population sizes and provide insight into how managers can most effectively intervene to leverage critical biological processes to have the desired impact on the population. Population growth rate describes the per capita rate by which population size increases per year, conventionally expressed as $\lambda = N_{t+1}/N_t$, where lambda (λ) is the annual population multiplication rate, expressing population size (N) in year $t+1$ as a multiple of the preceding year's number, N_t.

Typically, count data do not increase or decrease smoothly over time, but instead vary around a long-term trend due to demographic and environmental stochastic processes. Because stochastic processes are inherently unpredictable, it is impossible to predict with certainly future patterns of demographic fluctuations. As a consequence, even if we know the current size of a population and both the average value and variability in the rate of population growth, only probabilistic statements can be made about the number of individuals the population will include at some time in the future.

In the temporally varying environment of Cienega Creek, the long-run population growth rate governs the vulnerability of a population to extirpation[1]. This concept is expressed mathematically as $r - Ve / 2$, where r is the intrinsic rate of population growth and Ve is the between-generation variance of population growth rate (National Research Council 1995). When $Ve / 2 > r$, the population will decline toward extirpation deterministically. The expected time to population extirpation will vary with population size, depending on the ratio of the mean to the variance of the rate of population growth: $\sim r / Ve$ (National Research Council 1995). As a general rule of conservation biology, the greater the environmentally driven fluctuations in population growth rate, the greater the risk of extirpation at early time horizons (Morris et al. 1999).

Data Sets and Data Analysis

This analysis uses species-specific census counts presented by Simms and Ehret (2014). This data set was chosen because it is representative of contemporary conditions and satisfies the sampling criteria stated earlier, i.e., that the sampling protocol was standardized to repeatedly sample the same sites at the same time of year, employ the same sample gear, and are conducted to insure that the segment of the population observed can be standardized to reflect a relatively constant fraction of the whole. The data set used in this analysis includes annual autumn counts over four years (2005, 2008, 2011 and 2012) in upper Cienega Creek, and annual autumn counts over five years (2005, 2007, 2008, 2011, and 2012) in lower Cienega Creek (Simms and Ehret, 2014). All species except Longfin Dace were present in upper and lower Cienega Creek; Longfin Dace was not found in upper Cienega Creek.

All fish sampling was conducted by Simms and Ehret (2014) employed hoop nets that were 4.5 foot long, 20-inch diameter, double-throated, with 1/8-inch green netting, and baited with dog food (Simms and Ehret, 2014). Hoop nets were generally fished horizontally, although nets were occasionally set vertically. There were more nets employed in 2005 than in other years, but the catch data employed in this analysis was standardized by the number of "net days" (24 hours ± 1-2 hours).

From computer simulations of demographic processes we find that the endpoints of multiple independent realizations of population growth will lie approximately along a log-normal probability distribution (Dennis et al. 1991; Morris et al. 1999). This result means that we can use linear regression analysis of a time sequence of species-specific counts to calculate a single best estimate of the mean (μ) and variance (σ^2), which together describe how the normal distribution of the log of population size will change over the period of census. The regression approach requires that inter-census time intervals are square-root transformed and counts are log transformed to permit the use of linear regression to calculate the long-term mean and variance of the rate of population change. The mean and variance of population growth can then be used to model species-specific demography and generate various quantitative and probabilistic expressions of demography useful for species conservation planning. Noteworthy among these outputs is the between-generation variance of population growth rate (Ve), calculated as the average of the variance over the number of census counts times the number of inter-census counts minus 1 (used in calculations of extirpation probabilities), and the average population growth rate (λ), calculated as the base of natural logarithms, e, raised to the power $\mu + \frac{1}{2} \sigma^2$.

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[1] Extirpation is the condition in which a species ceases to exist in a specific geographic area of study, though it still exists elsewhere.

Using linear regression to describe how the normal distribution of the log of population size will change with time, the slope of the regression line is an estimate of μ and the regression's error mean square is an estimate of σ^2. Confidence intervals (95%) for μ and σ^2 were calculated to specify upper and lower bounds on the true value of each parameter, thereby providing a context in which confidence in these parameters can be assessed. When μ is positive, population trajectories tend to increase; when μ is negative population trajectories tend to decrease. In instances in which the lower bound of the confidence interval for μ is negative, the real possibility of long-term population decline cannot be ruled out, even when the regression slope estimate of μ is positive.

The long-term mean and variance of the rate of population change was calculated in Excel as was the demographic model from which various demographic statistics were derived, including: r – the intrinsic rate of population growth, Ve – the between-generation variance of population growth rate, and λ – the average finite rate of population increase. Mean time to population extirpation was not calculated because the single best estimates of μ were positive for all species and therefore it is unlikely that an estimate of mean time to population extirpation would apply to every population realization.

A test was not preformed to determine if mean and variance of species-specific rates of population change differed statistically over the short period of census count records because evidence of catastrophes or bonanzas were not apparent and further partitioning of the existing small data sets would impart little statistical power to detect simple trends over time. Normality (Shapiro-Wilk) and equal variance tests were performed in SigmaPlot in the process of performing species-specific one way analyses of variance (ANOVA). For all species-specific data sets, the data matched the pattern expected if the data was drawn from a population with a normal distribution. Equal valiance tests for all species except Longfin Dace indicated the differences in the mean values among the treatment groups were not great enough to exclude the possibility that the difference is due to random sampling variability; there was no statistically significant difference. For Longfin Dace, the ANOVA equal variance test failed (P < 0.050). For this reason, a Kruskal-Wallis One Way Analysis of Variance on Ranks was performed in which the differences in the median values among the treatment groups were not great enough to exclude the possibility that the difference is due to random sampling variability; there was not a statistically significant difference (P = 0.200).

Results

Species-specific regression results are presented in the following series of tables (Tables 1-5). Result parameters that are used in the model (μ and σ^2; highlighted in yellow) appear in the Analysis of Variance table associated with the regression. The calculated intercept coefficient should be "0" indicating the analysis forced the y-intercept to be zero, enforcing the rule that there can be no change in population size if no time has elapsed. The "X variable 1" coefficient provides an estimate of μ; the mean squared residual (MS residual) is an estimate of σ^2. It should be noted that the regression analyses are generally non-significant (i.e., p>0.05). This is unimportant to this analysis because we are not conducting a test of a hypothesis; instead, we are using linear regression to find the best-fit values of the parameters μ and σ^2 given the data.

Table 1. Regression Analysis of Counts of Gila Chub from Upper Cienega Creek.

Gila Chub - Upper Cienega Creek

CPU Data

Year	x= sqrt(t(j)-t(i))	CPE	y=ln(N(j)/N(i))/x
2005		5.5	
2008	1.732050808	17	0.651519717
2011	1.732050808	3	-1.001472386
2012	1	27.8	2.226423732

CPE DATA
SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.242372619
R Square	0.058744487
Adjusted R Square	-0.441255513
Standard Error	1.733398389
Observations	3

ANOVA

	df	SS	MS	F	Significance F
Regression	1	0.375047567	0.375047567	0.1248216	0.783795976
Residual	2	6.009339949	3.004669975		
Total	3	6.384387517			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.231469704	0.655163009	0.353300936	0.7576274	-2.587469203	3.05040861

$t_{0.05,2}$ = 4.30265273   95 % confidence iInterval around μ (regression slope) = -2.587469203 , 3.05040861132729
$X^2_{0.025, 2}$ = 11.98292909   95 % Confidence Interval around $σ^2$ (MS) = 0.501491739 , 118.678124759828
$X^2_{0.975, 2}$ = 0.050635616

Table 2. Regression Analysis of Counts of Gila Chub from Lower Cienega Creek.

Gila Chub - Lower Cienega Creek

CPE Data

Year	x= sqrt(t(j)-t(i))	CPE	y=ln(N(j)/N(i))/x
2005		16.1	
2007	1.414213562	14.7	-0.064326761
2008	1	17.6	0.180051408
2011	1.732050808	1.9	-1.285207689
2012	1	25	2.577021939

CPE Data
SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.057630678
R Square	0.003321295
Adjusted R Square	-0.330012038
Standard Error	1.663499631
Observations	4

ANOVA

	df	SS	MS	F	Significance F
Regression	1	0.027664253	0.027664253	0.009997	0.929475657
Residual	3	8.301693066	2.767231022		
Total	4	8.329357319			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.062865222	0.628743761	0.09998544	0.926663	-1.938078038	2.063808482

$t_{0.05,3}$ = 3.182446305   95 % confidence iInterval around μ (regression slope) = -1.938078038 , 2.0638084820692
$X^2_{0.025, 3}$ = 9.348403604   95 % Confidence Interval around $σ^2$ (MS) = 0.888033232 , 38.4702249503285
$X^2_{0.975, 3}$ = 0.215795283

Table 3. Regression Analysis of Counts of Gila Topminnow from Upper Cienega Creek.

Gila Topminnow - Upper Cienega Creek

CPE Data

Year	x= sqrt(t(j)-t(i))	CPE	y=ln(N(j)/N(i))/x
2005		1.7	
2008	1.732050808	55.4	2.011460246
2011	1.732050808	76.3	0.184805979
2012	1	168.7	0.793449051

CPE
SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.800711572
R Square	0.641139022
Adjusted R Square	0.141139022
Standard Error	0.919272231
Observations	3

ANOVA

	df	SS	MS	F	Significance F
Regression	1	3.019564096	3.019564096	3.57318885	0.309774795
Residual	2	1.69012287	0.845061435		
Total	3	4.709686966			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.65678482	0.347452244	1.890288034	0.199288428	-0.838181528	2.1517512

$t_{0.05,2}$ = 4.30265273   95 % confidence iInterval around μ (regression slope) = -0.838181528 , 2.15175116746185
$X^2_{0.025, 2}$ = 7.377758908   95 % Confidence Interval around $σ^2$ (MS) = 0.229083505 , 33.3781437685145
$X^2_{0.975, 2}$ = 0.050635616

Table 4. Regression Analysis of Counts of Gila Topminnow from Lower Cienega Creek.

Gila Topminnow - Lower Cienega Creek

CPE Data				CPE						
Year	x= sqrt(t(j)-t(i))	CPE	y=ln(N(j)/N(i))/x	SUMMARY OUTPUT						
2005		16.5								
2007	1.414213562	6.2	-0.692123958	*Regression Statistics*						
2008	1	8.8	0.350202429	Multiple R	0.011590931					
2011	1.732050808	3.32	-0.562793501	R Square	0.00013435					
2012	1	17.5	1.662236098	Adjusted R Square	-0.333198984					
				Standard Error	1.107692509					
				Observations	4					
				ANOVA						
					df	*SS*	*MS*	*F*	*Significance F*	
				Regression	1	0.000494601	0.000494601	0.000403	0.985804544	
				Residual	3	3.680948085	1.226982695			
				Total	4	3.681442686				
					Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
				Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A
				X Variable 1	0.008405786	0.418668416	0.02007743	0.985242	-1.323983966	1.340795538

$t_{0.05,3}$ = 3.182446305   95 % confidence iInterval around μ (regression slope) = -1.32398397 , 1.34079553787081

$X^2_{0.025, 3}$ = 9.348403604   95 % Confidence Interval around σ^2 (MS) = 0.393751515 , 17.0575929219249

$X^2_{0.975, 3}$ = 0.215795283

Table 5. Regression Analysis of Counts of Longfin Dace from Lower Cienega Creek.

Longfin Dace - Lower Cienega Creek

CPE Data				CPE Data						
Year	x= sqrt(t(j)-t(i))	Count	y=ln(N(j)/N(i))/x	SUMMARY OUTPUT						
2005		6.1								
2007	1.414213562	3.2	-0.456181427	*Regression Statistics*						
2008	1	14.4	1.504077397	Multiple R	0.295794507					
2011	1.732050808	56.45	0.78873384	R Square	0.08749439					
2012	1	27.1	-0.733821563	Adjusted R Square	-0.245838943					
				Standard Error	1.050913588					
				Observations	4					
				ANOVA						
					df	*SS*	*MS*	*F*	*Significance F*	
				Regression	1	0.31768736	0.31768736	0.287651	0.645400537	
				Residual	3	3.313258106	1.104419369			
				Total	4	3.630945466				
					Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
				Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A
				X Variable 1	0.213034994	0.397208	0.536331075	0.628949	-1.051058139	1.477128127

$t_{0.05,3}$ = 3.182446305   95 % confidence iInterval around μ (regression slope) = -1.051058139 , 1.4771281268388

$X^2_{0.025, 3}$ = 9.348403604   95 % Confidence Interval around σ^2 (MS) = 0.354419668 , 15.3537096152917

$X^2_{(0.975, 3)}$ = 0.215795283

Discussion

Estimates of μ for all fish species in Cienega Creek were positive, although only marginally so for lower Cienega Creek populations of Gila Chub and Gila Topminnow (Table 6). However, the lower bound of the confidence interval for μ is negative for all species except the upper Cienega Creek population of Gila Topminnow. Populations with negative values for the lower bound of the confidence interval have a real possibility of long-term population decline, especially during sequential years of mortality-causing environmental stress that results in population-wide age-class failures (i.e., circumstances in which individuals fail to recruit from a pre-reproductive stage to a reproductive stage), or with declining environmental trends that exceed the limits of historic precedence.

Upper and lower Cienega Creek populations of Gila Chub exhibit relatively high variance values compared to populations of Gila Topminnow and Longfin Dace. The upper Cienega Creek population of Gila Chub appears to be at a reduced risk of extirpation compared to the lower Cienega Creek population of the species as indicated by their respective probabilities of reaching

the extirpation threshold of 1 CPE (Table 6). To persist, populations that exhibit higher between-generation variance in growth, like Gila Chub, require relatively higher intrinsic rates of population growth.

The Lower Cienega Creek population of Gila Topminnow exhibits only slightly positive μ values but a sufficiently low σ^2 to avoid extirpation in the near term. Nonetheless, this population appears to be at high risk of extirpation; it exhibits the highest observed probability that the extirpation threshold (1 CPE) is reached (Table 6). The persistence of Gila Topminnow in Lower Cienega Creek through the census period is likely attributable to the species' early age at maturity, physiological flexibility, and its capacity to produce multiple broods of young within a given year. These same life history characteristics afford the Gila Topminnow population in upper Cienega Creek, the sampling segment with apparent improved environmental conditions, the lowest observed probability that the extirpation threshold (1 CPE) is reached (Table 6).

Lambda (λ) values for all fish species are relatively high, a characteristic common to short-lived species that mature at an early age and that have a high reproductive potential. With cyclic fluctuations in carrying capacity, caused in Cienega Creek by fluctuating hydrologic conditions, the time delay of the response of a population to the environmental conditions relative to the period of the environmental cycle becomes critical in the ability of a species to persist. Survival and fecundity are basic components of demography that most profoundly operate to define the time delay of the response of the population to the environmental conditions. When the response is relatively fast, as would be the case for late to mature species, population size will closely track environmental variation and periodically approach low levels at which extirpation due to demographic stochasticity becomes more likely. When the response is slow, as would be true for the early to mature fish species found in Cienega Creek, fluctuations in species abundance will tend to be moderate and the risk of extirpation due to demographic stochasticity less likely.

The foregoing analysis and discussion assumes that the species-specific mean and variance of the log population growth rates are constant. However, in reality it is more likely that μ and σ^2 will change over time as a consequence of density dependence, demographic stochasticity, and temporal trends in environmental conditions. The major determinants of variability in population size are stochasticity in population growth rate and the strength of density-dependent population regulation (Lande et al. 2003).

Census counts presented in Simms and Ehret (2014) are standardized by "net days"; these data cannot be standardized by area sampled to yield density estimates (e.g., fish per m^2). As such, it is impossible to investigate the possible link between density and population growth rate. Management of declining fragmented fish populations in Cienega Creek might advocate protecting or restoring habitat (e.g., drought refugia) to increase carrying capacity (*K*). Future research might focus on the role of asymptotic scaling of mean time to extirpation as a function of *K* for different stochastic factors.

With a prospect of future declining environmental trends, the equilibrium population size is expected to decline faster than the amount of suitable habitat, which occurs because the equilibrium population size is proportional to the product of the amount of suitable habitat and the equilibrium occupancy of it (Lande et al. 2003). Additionally, researchers might consider investigating the log-log bivariate plot of species abundance and area to determine if the relationship is linear, indicating a power relationship between variables. This would suggest that size of water catchments that might serve as drought refugia is more important than the length of river with continuity of flow so long as water quality is not impaired. One possible empirical expression of species-habitat relationships is represented by the following general density model (adapted from Donovon and Weldon 2002):

$$N_i = dp_i{}^z$$

where:

- N_i represents density.
- d represents the maximum carrying capacity for habitat i, which will change with varying hydrologic conditions.
- p_i represents the proportion in habitat i.
- z represents the sensitivity for species i to the total amount of habitat for the species. Realistically, we lack a robust explanation for observed differences in demography that focuses on the link between one or more causal factors and rates of population growth. Because of the eurytopic habits of fish species in Cienega Creek, it may be difficult to find compelling distinguishing predictor variables of population growth that account for a significant amount of variation in the response variable and that may ultimately enable researchers/managers to discriminate among competing hypotheses about system behavior.

Critical biological processes (e.g., birth, localized recruitment, death, and survival) are known to vary with environmental conditions. Environmental conditions in running water systems tend to be autocorrelated as are environmentally-linked population dynamics. Population synchrony strongly influences regional population dynamics and the risk of regional extirpation. Synchronous population dynamics can vary with such things as the degree to which portions of the river go dry, along with habitat size and maximum carrying capacity for a given habitat type. Short-term spatial scale of population synchrony will be greatly affected by dispersal of eggs and larvae (passive downstream drift) and other transport processes. However, high environmental stochasticity often contributes to chaotic oscillations of abundance, characterized at times by exponential population growth in a single time step during periods of relative hydrologic abundance. Such oscillations in rates of population growth can result in large overshoots of long-term carrying capacity and are often followed by periods of steep population decay during periods of hydrologic scarcity, often accompanied by heightened probability of year class failure.

Table 6. Demographic Parameters for Fish Species in Upper and Lower Segments of Cienega Creek Based on an Analysis of Catch Per Effort Data Presented in Simms and Ehret (2014).

PARAMETER	Gila Chub (Upper Cienega Creek)	Gila Chub (Lower Cienega Creek)	Gila Topminnow (Upper Cienega Creek)	Gila Topminnow (Lower Cienega Creek)	Longfin Dace (Lower Cienega Creek)
μ (95% confidence interval)	0.23147 ($-2.5875 \le \mu \le 3.0504$)	0.0629 ($-1.9381 \le \mu \le 2.0638$)	0.6568 ($0.8382 \le \mu \le 2.1518$)	0.0084 ($-1.3240 \le \mu \le 1.34080$)	0.2130 ($-1.0511 \le \mu \le 1.4771$)
σ^2 (95% confidence interval)	3.0047 ($0.5015 \le \sigma^2 \le 118.6781$)	2.7672 ($0.8880 \le \sigma^2 \le 38.4702$)	0.8451 ($0.2291 \le \sigma^2 \le 333.3781$)	1.2270 ($0.3938 \le \sigma^2 \le 17.0576$)	1.1044 ($-1.0511 \le \sigma^2 \le 15.3537$)
r (95% confidence interval)[2]	1.7380 ($-1.6656 \le r \le 5.1332$)	1.4465 ($-1.2047 \le r \le 4.0977$)	1.0793 ($-0.1444 \le r \le 2.3030$)	0.6199 ($-0.7609 \le r \le 2.0006$)	0.7652 ($-0.5113 \le r \le 2.0417$)
Ve [3]	2.0031	2.0754	0.5634	0.9202	0.8283
$Ve/2$ [4]	1.0016	1.0377	0.2817	0.4601	0.4142
$r - Ve/2$ [5]	0.7365	0.4088	0.7976	0.1598	0.3511
r / Ve [6]	0.8677	0.6970	1.9158	0.6736	0.9239
λ (95% confidence interval)	5.6622 ($0.1891 \le \lambda \le 169.5564$)	4.2814 ($0.2998 \le \lambda \le 60.1992$)	2.9427 ($0.8656 \le \lambda \le 10.0041$)	1.8587 ($0.4673 \le \lambda \le 7.3938$)	2.1495 ($0.5997 \le \lambda \le 7.7040$)
Probability extirpation threshold (1 CPE) is eventually reached	0.4637	0.8228	0.0000064156	0.9609	0.1832

[2] r is the intrinsic rate of population growth.

[3] Ve is the between-generation variance of population growth rate.

[4] Values near zero suggest relative population stability; relative instability increases progressively with values larger than zero.

[5] Small positive values suggest modest but relatively stable population growth; higher values suggest greater population growth potential.

[6] The expected time to extirpation will vary with population size, depending on the ratio of the mean to the variance of the rate of population growth. Values that closely approximate 1.0 suggest stability; values significantly <1 are at heightened risk of extirpation.

Assumptions of Data Analysis and Interpretation

Prospective analytical approaches to demographic analysis for any species will be constrained by the type of data available. Ideally, an age-based model (Caswell, 2001) could be developed to simulate species-specific demography for the purpose of predicting the future fates of fish populations in the spatially subdivided habitats of Cienega Creek where a large fraction of fish populations regularly occurs in spatially and temporally variable "sink" habitats characterized by within-habitat reproduction that is insufficient to balance local mortality. Unfortunately, age-based demographic data do not exist for any of the fish species present in Cienega Creek. Only a small series of species counts exist for native fish species in Cienega Creek on which to describe past observed demography and to gain a qualified understanding of local species-specific demographic processes.

As has already been stated, environmental and demographic stochastic processes are inherently unpredictable, and therefore it is impossible to predict with certainly future patterns of demographic fluctuations. Only probabilistic statements can be made about the number of individuals the population will include at some time in the future. Nonetheless, the analytic approach taken in this report provides an objective method to obtain quantitative measures of species status and fitness given the array of within-generation mortality-causing factors characteristic of Cienega Creek. Still, users of this analysis should be aware of the real limitations of this approach when underlying assumptions are violated. The assumptions of analysis and interpretation are explicit and provide a context for qualified interpretation.

The following bulleted list represents an annotated discussion of key assumptions of the count-based analysis presented in this report. This discussion, like the analysis, is generally adapted from Morris and Doak (2002) and Morris et al. (1999). The statement of key assumptions are preceded by a solid "black" circle, whereas related annotations are indented and preceded by an open circle.

- The mean and variance of population growth rate remain constant over time.

  - The analysis and discussion presented in this document assumes that the species-specific mean and variance of the log population growth rates are constant. In reality it is more likely that μ and σ^2 will change over time as a consequence of density dependence, demographic stochasticity, and temporal trends in environmental conditions.

- Population growth rate is density independent.

  - Populations cannot grow indefinitely because of carrying capacity constraints, and density does not drop to levels that result in Allee effects, characterized by lower rates of population growth from depressed birth rates or elevated rates of death at low densities.

  - In times of drought and spatial subdivision of the population, species persistence can be dependent on maintaining a minimum area of suitable habitat that can sustain an isolated population in the face of random individual dispersal into surrounding regions of intermittent suitability. Future research should explore the role of asymptotic scaling of mean time to extinction as a function of carrying capacity.

o Often, regression analysis can be used to evaluate the relationship between flow attributes and fish density. An assumption of prominent concern inherent with linear regression analysis involving a time series of census data (i.e., repeated measurements on sampling units) concerns independence between successive observations. The assumption in regression analysis is that the *Y*-values and error terms are independent of each other, i.e., that the *Y*-value for any x_i does not influence the *Y*-values for any other x_i. Unfortunately, a common occurrence in wildlife census data in general is a positive relationship between error terms and census values from adjacent samples through time (i.e., the data are "autocorrelated"). The degree of autocorrelation is the correlation coefficient between successive error terms. Further, small sample sizes sometimes unevenly represent the ranges of response or covariate variables, which can lead to biased regression results. In such cases, apparent outlier values should be evaluated in terms of whether they exert undue influence on estimated parameters.

o An additional concern about the Cienega Creek data pertains to the fidelity[7] of remotely measured predictor values (i.e., flow gauge sites) with conditions at the location where the response variable is measured. As such, the record of flow at the Cienega Creek gauges may not accurately reflect the flow regime at the fish sample sites without a complex accounting of water loss in transit over the distance between water gauge sites and fish sample sites. Failure to account for the disparity in flow that must exist between gauge sites and fish sample sites represents a sampling error in the predictor variable.

• There are no temporal environmental trends.

o Increasing spatial scale of environmental autocorrelation increases the spatial scale of population synchrony, which increases regional extirpation risk. This risk depends primarily on the magnitude of local population fluctuations and their synchrony resulting from the net influence of density dependence, spatial environmental autocorrelation, and individual dispersal (Lande et al. 2003).

• Census counts represent a relatively constant fraction of the whole and there are enough years of data to be representative of the types and severity of environmental stochasticity common to the system.

o Morris and Doak (2002) suggest ten census counts are necessary to adequately represent species-specific demographic oscillations attributable to a given system. However, they acknowledge that ten census counts is not an explicit requirement and that adequate sample size is dependent on environmental stability and sample error. In the case of Cienega Creek, census counts do not document catastrophes or bonanzas and base flow is low but relatively stable, with short-term high discharge disturbance limited to occasional monsoon storm-water runoff.

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[7] As used, "fidelity" refers to the degree to which something matches or copies something else.

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