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A simulation model of the Devils Hole pupfish population using monthly length-frequency distributions

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Abstract The Devils Hole pupfish, *Cyprinodon diabolis,* is a federally-endangered fish that is endemic to Devils Hole, a discontiguous part of Death Valley National Park in Nye County, Nevada. Due to its status, Devils Hole pupfish monitoring must be non-obtrusive and thereby exclude techniques that require handling fish. Due to a recent decline in pupfish abundance, Devils Hole pupfish managers have expressed a need for a model that describes population dynamics. This population model would be used to identify vulnerable life history stage(s) and inform management actions. We constructed a set of individual-based simulation models designed to explore effects of population processes and evaluate assumptions. We developed a baseline model, whose output best resembled both observed length-frequency data and predicted intra-annual abundance patterns. We then ran simulations with 5 % increases in egg-larval, juvenile, and adult survival rates to better understand Devils Hole pupfish life history, thereby helping identify vulnerable life history stages that should become the target of management actions. Simulation models with temporally constant adult, juvenile, and egg-larval survival rates were able to reproduce observed length-frequency distributions and predicted intra-annual population patterns. In particular, models with monthly adult and juvenile survival rates of 80 % and an egg-larval survival rate of 4.7 % replicated patterns in observed data. Population growth was most affected by 5 % increases in egg-larval survival, whereas adult and juvenile survival rates had similar but lesser effects on population growth. Outputs from the model were used to assess factors suspected of influencing Devils Hole pupfish population decline.

Keywords Conservation · Devils Hole · Elasticity analysis · Endangered species · Population dynamics · Stereovideo

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Introduction

Conservation efforts directed by vague biological data about targeted species are often unlikely to be successful (Tear et al. 1995; Foin et al. 1998; Boersma et al. 2001; Clark et al. 2002; Gerber and Hatch 2002). Understanding population processes is therefore vital for conservation efforts, as basic knowledge about population dynamics can help biologists focus monitoring efforts on evaluating factors likely related to population decline (Campbell et al. 2002). The Devils Hole pupfish, *Cyprinodon diabolis*, is a federally-endangered species endemic to Devils Hole, Nye County, Nevada. Due to their small population size and limited geographic range, there is a general consensus among managers that all sampling of Devils Hole pupfish be non-obtrusive. The Devils Hole pupfish population experienced a dramatic decline in abundance from the mid-1990s to mid-2000s. Consequently, updated information about Devils Hole pupfish population ecology is needed to evaluate management alternatives.

Statistical models describing population dynamics are extensively used in wildlife and fisheries management to identify vulnerable life stages of imperiled populations (Crouse et al. 1987; Doak et al. 1994; Crooks et al. 1998), evaluate mechanisms suspected of influencing species' declines (Lamberson et al. 1992; Fahrig 1997; Huxel 1999; Doubledee et al. 2003), and assess the influence of management alternatives on population dynamics (Heppell et al. 1994). Developing a population model for the Devils Hole pupfish would help increase understanding of Devils Hole pupfish population dynamics and provide a tool to evaluate alternative management strategies. The population model would complement ongoing monitoring efforts for larval and adult Devils Hole pupfish by using population size structure and relative abundance metrics to evaluate traditional beliefs about Devils Hole pupfish population dynamics. For example, observations of postlarvae are few in comparison to prolarvae and adults. As such, biologists are uncertain whether to blame low detectability or low abundance for the small number of postlarvae observations. This problem is exacerbated in winter months, when larval abundance is at its annual low. Thus, the low numbers of postlarvae in early life stage (ELS) surveys in Nov–Jan months could be attributed either to absence or low abundance coupled with low detectability. Overwinter survival of larvae is not well understood and may provide insight as to the cause of the decline in the Devils Hole pupfish population.

Two previous models have described population fluctuations in the Devils Hole pupfish; these models include a density-independent population model developed by Chernoff (1985) and a system dynamics model developed by Graves (2004). While useful, the Chernoff (1985) and Graves (2004) models rely almost entirely on assumptions due to lack of Devils Hole pupfish length-frequency and larval abundance data. In contrast, we constructed a density-independent simulation model, which incorporated data from ongoing adult and larval Devils Hole pupfish monitoring to help guide parameterization of model inputs. Furthermore, to identify vulnerable life history stages (i.e., which survival parameters had the greatest effects on population growth) we compared discrete population growth rates (λ) among simulations with varying larval, juvenile, and adult survival rates. Lastly, we assessed overwinter survival of larval fish by comparing simulation models with and without winter recruitment. Importantly, while a density-dependent model would likely provide a realistic representation of the Devils Hole pupfish population, we had little information about the effect of density on population growth. Furthermore, the current size of the Devils Hole pupfish population is very low compared to its size before 1990 (Graves 2004); thus the population is likely well below its carrying capacity. If true, then using a density-independent model is appropriate for the purposes of this study.

Methods

Study site

Devils Hole is a small limestone cavern located in a discontiguous portion of Death Valley National Park adjacent to Ash Meadows National Wildlife Refuge, Nevada (36°25′N, 116°17′W). For practical purposes, Devils Hole is often divided into two strata: the shallow shelf and the deep pool. The shallow shelf is a 5.5 × 2.0 m boulder ledge submerged under 0.2–0.7 m of water. The depth of the deep pool is unknown, but is >133 m. Devils Hole pupfish population size fluctuates seasonally, historically reaching a maximum of 400–500 fish in early autumn and a minimum of 200–300 fish in mid-spring (Andersen and Deacon 2001). However, population abundance declined in the mid-1990s to mid-2000s, reaching a low of 38 individuals in April 2006 and April 2007.

Study organism

Devils Hole pupfish are omnivorous, feeding mainly upon diatoms that grow on the surface of calcium carbonate crystals (Minckley and Deacon 1975; Wilson 2001). They also feed on amphipods, ostracods, algae, cyanobacteria, beetles, flatworms, and snails (Minckley and Deacon 1975; Wilson 2001). Spawning behavior in Devils Hole pupfish occurs year-round, with peak spawning occurring from mid-February to mid-May (Lyons 2005). Low-frequency disturbance events, such as earthquakes and torrential desert rains, impact nutrient cycling (Wilson and Blinn 2007) and substrate composition of the spawning shelf (Lyons 2005), although the impact of these disturbances on the Devils Hole pupfish population has not been formally examined.

Estimation of length-frequency distributions

Stereo-video technology (SV) presents a powerful tool for non-obtrusively collecting accurate and precise length measurements (Harvey et al. 2002, 2004). For example, length measurements of Saratoga Springs pupfish, *C. nevadensis nevadensis*, generated from a SV system had negligible bias and greater precision compared to visual estimates from SCUBA divers (Bower et al. 2011). We used SV technology to obtain monthly length-frequency distributions of the Devils Hole pupfish population. The SV system consisted of a SeaGIS underwater stereovideo camera system (SeaGIS Pty. Ltd., Bacchus Marsh, Victoria, Australia) equipped with a pair of Canon Vixia HV30 high-definition video cameras (Canon USA, Inc., Lake Success, NY, USA). Cameras settings were set to zero zoom, infinity focus, and an F-stop of 4.8. Detailed information about the SV system is described in Bower et al. (2011).

Stereo-video surveys in Devils Hole were conducted every month from March 2010 to February 2011 to assess dynamics in population size structure. Time intervals between successive SV dives were not uniform and varied from 3 to 6 weeks. Stereo-video surveys were conducted around 9 a.m. by two SCUBA divers; one diver operated the SV system while the other served as the safety diver. Divers first descended approximately 26 m in Devils Hole, waited 5 min, and then began to slowly ascend Devils Hole and videotape fish. Divers followed the same route for each dive and videotaped encountered fish. Importantly, divers were instructed to avoid preferentially sampling larger, more visible fish or large schools of fish. To obtain clear frames of fish images, divers videotaped encountered fish for ~10 s or until a desirable profile shot was obtained. Video processing was completed using the computer program PhotoMeasure (SeaGIS 2009). Processing video requires manual marking of four points on a pair of simultaneous video images. Total length was measured for each fish by manually marking the tip of its snout and the end of its caudal fin. For each fish, three measurements from three different pairs of video frames were measured in PhotoMeasure and the length of each fish was estimated as the mean of the three measurements. If the person processing the video frames was not confident in length measurements for a particular fish (e.g., image was blurry), the fish was excluded from length-frequency distributions. Importantly, estimation of Devils Hole pupfish length-frequency distributions may be subject to error. Despite the video processor's best efforts, it is possible that some fish may have measured twice, although we made every attempt to minimize this problem. Furthermore, stereovideo dives only measured a subset of the Devils Hole pupfish population, which we assumed was representative of the entire population.

Evaluating length-frequency distributions using mixture models

To determine the number of cohorts in each length-frequency distribution, normal and lognormal mixture models were fit to length-frequency distributions from stereo-video surveys using the package MCLUST (Fraley and Raftery 2009) in the statistical computing program R (R Development Core Team 2008). MCLUST fits one to nine normal distributions (i.e., mixtures) with equal and unequal variances, generating a total of seventeen models. The most parsimonious model is then selected using the Bayesian Information Criterion (BIC; Schwarz 1978). Although normal distributions are commonly fit to length-frequency distributions (MacDonald and Pitcher 1979; Fournier et al. 1990, 1998), we also assessed mixture models fitting lognormal distributions due to the observation that the Devils Hole pupfish population exhibits continuous spawning (Gustafson and Deacon 1997; Lyons 2005). We chose to use normal mixture models to describe Devils Hole pupfish length-frequency distributions, because means from normal mixtures conformed better than a lognormal distribution to a von Bertalanffy growth model (see Dzul 2011).

Model construction

In populations that exhibit pulse-reproduction, cohorts may be identifiable in length-frequency distributions by the appearance of separate modes (Petersen 1891; MacDonald and Pitcher 1979). Assuming length distributions within a cohort follow a specified parametric distribution, cohorts can be identified and separated using maximum likelihood (MacDonald and Pitcher 1979; Fournier et al. 1990; Roa-Ureta 2009). Unfortunately, the above-mentioned methods are ill-suited for modeling the Devils Hole pupfish population because following sequential estimates of mean cohort length will result in underestimation of growth in populations which exhibit continuous recruitment (Wang and Somers 1996). Low detectability of small fish further complicates model construction and evaluation because size selectivity can bias growth parameters (Fournier et al. 1990). Our choice to use simulation instead of the above-mentioned methods stems from the difficulty of simultaneously estimating survival, recruitment, and growth from a continuously-reproducing population with only 1 year of length-frequency data. Consequently, we used an individual-based simulation model to describe Devils Hole pupfish dynamics because this approach allowed us to use a wide variety of data sources to estimate population parameters. We used the statistical computing program

R (R Development Core Team 2008) to construct and run the simulation model.

Our model uses a simulation approach which assigns specific functions to population processes and generates monthly length-frequency distributions. Simulation models included four life stages (egg, larval, juvenile, and adult; Fig. 1) and required the following inputs: number of larvae per female, stage-specific survival rates, transition lengths between stages, reproductive length, and growth model(s) (Table 1). When possible, we used current data to describe population processes; however, when current data were unavailable we used data from published studies or long-term (1972–present) monitoring records. Figure 2 provides a simplified schematic illustrating methods used in this study.

Data sources and estimating parameters

Estimating abundance and reproduction

Adult population surveys for Devils Hole pupfish are conducted by SCUBA divers, who count fish as they ascend Devils Hole (for more detailed methods, see Wilson et al. 2009). Adult population surveys commenced in 1972 and continue to present. Currently, surveys for adult abundance occur twice yearly, in late September–early October and in April. In the 1970s and 1980s, adult population surveys occurred more frequently. As such, we assumed current intra-annual adult abundance patterns resembled historic patterns, and predicted monthly adult abundance (N) in 2010 using a linear additive model. This model (hereafter be referred to as the adult abundance model) included two fixed effects, month (α) and year (β), where m and y index month and year, respectively:

$$\ln(N_{m,y}) = \mu + \alpha_m + \beta_y + \varepsilon_i \quad (1)$$

This model was fit to log$_e$-transformed abundance estimates from 1972 to 2010 Devils Hole pupfish adult abundance surveys to determine month and year effects on population abundance. Error was assumed to be normally distributed. Although our intentions were to use the adult abundance model to predict monthly estimates of adult population abundance in 2010, we were unable to do so because adult abundance estimates in 2010 were abnormal. Specifically, population abundance normally fluctuates by almost two-fold between April and October, but in the population estimates the two surveys were similar in 2010 (120 and 118). As such, we used the adult abundance model with population estimates from 2009 to predict monthly population size estimates for 2010. The fit of the adult abundance model was reasonable (residual SE = 0.17; adjusted $R^2 = 0.87$), and examination of residuals suggested that the choice of a linear model was appropriate (not shown). The monthly abundance estimates from adult abundance model exhibit similar patterns to that of Andersen and Deacon (2001).

We estimated total larval abundance by dividing relative larval abundance estimates from ELS surveys by the proportion of shelf sampled; an inherent assumption of this method is that relative abundance estimates from ELS surveys are indicative of total larval abundance. Abundance estimates of prolarvae (4–5 mm larvae) from ELS surveys in 2010 were used to fit a generalized linear model to predict larval abundance (henceforth referred to as the larval abundance model).

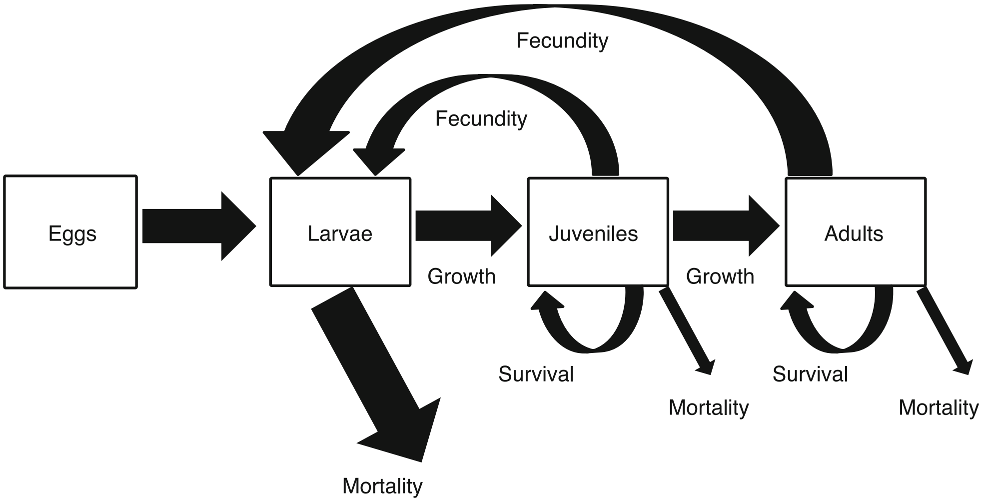

Fig. 1 Diagram of the model describing Devils Hole pupfish *Cyprinodon diabolis* population. Our model included four life stages: eggs, larvae, juveniles, and adults. Egg survival was assumed 100 % due to lack of information about this parameter. Distinctions between juveniles and adults were based on behavioral, not reproductive, characteristics. Devils Hole pupfish are endemic to Devils Hole, a cave in Nye County, NV

Table 1 Descriptions, values, and sources for simulation model parameters for Devils Hole pupfish, *Cyprinodon diabolis*

Parameter	Description
Egg-larval survival	Type I survivorship where mortality occurs during hatch month
Values (%): 7.6, 4.7, 3.4	Source: approximated from simulation model output
Juvenile survival	Type II survivorship where mortality occurs daily
30-day values (%): 70, 80, 86	Source: due to lack of data, set equal to adult survival
Adult survival	Type II survivorship where mortality occurs daily
30-day values (%): 70, 80, 86	Source: approximated from adult abundance model
Larvae per female	Reproduction adjusted for unequal sampling intervals
Values: see Dzul (2011)	Source: estimated from both adult and larval abundance models
Fast growth model	Models growth of fish <15 mm and fish born March–June
Values: $K = 0.0057$; $L_\infty = 41.6$	Source: data from James (1969) fit to a von Bertalanffy model
Slow growth model	Models growth of fish >15 mm and fish born July–February
Values: $K = 0.0025$; $L_\infty = 43.4$	Source: Stereovideo dive data fit to von Bertalanffy model
Juvenile length	Length at which fish enters juvenile stage
Value: 12 mm	Source: Devils Hole pupfish biologists' observations
Adult length	Length at which fish enters adult stage
Value: 18 mm	Source: Devils Hole pupfish biologists' observations
Reproductive length	Length at which female becomes reproductive
Value: 13 mm	Source: Minckley and Deacon (1973)

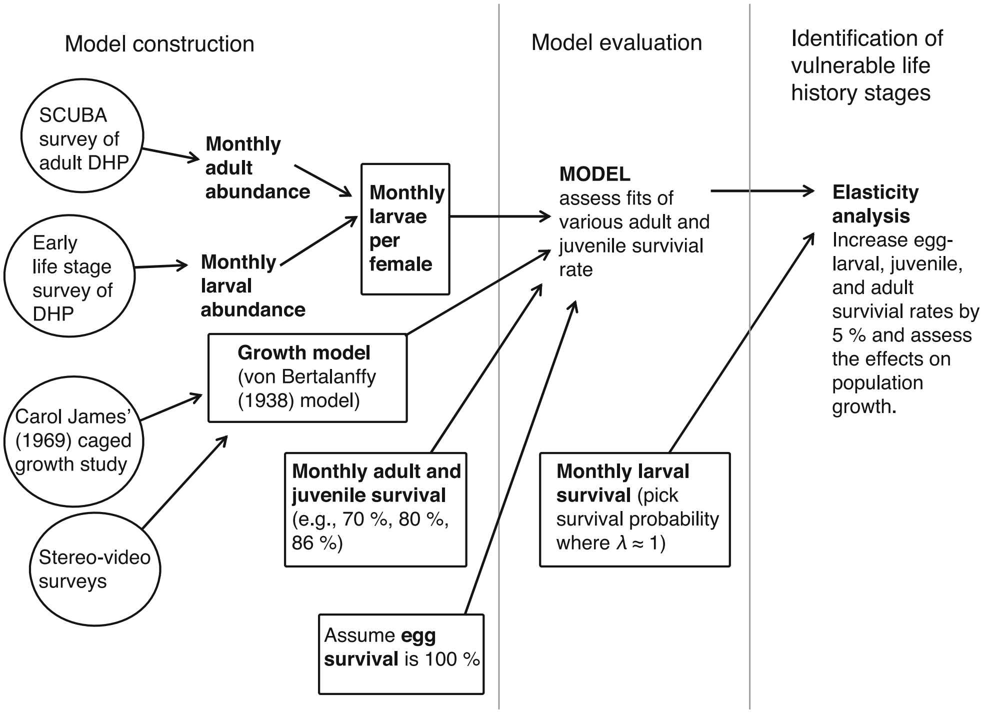

Fig. 2 Schematic representing Devils Hole pupfish (DHP) *Cyprinodon diabolis* population model construction and evaluation, with subsequent identification of vulnerable life-history stages. Sources of data are surrounded by circles and estimated parameters are surrounded by rectangles. Devils Hole pupfish are endemic to Devils Hole, a cave in Nye County, NV

Specifically, the sum of the number of prolarvae observed per event was a Poisson-distributed response variable that was predicted by a polynomial equation with time as the predictor variable (Wood 2006). We fit models with 3–6 degree polynomial terms and selected the best model using BIC. The most competitive model was a 5th degree polynomial equation, with w referring to week number (Jan 1 $= 0$):

$$\int_{t_1}^{t_2} e^{-1.646+1.094w-0.08792w^2+(3.042\times10^{-3})w^3-(4.929\times10^{-4})w^4+(3.087\times10^{-5})w^5}\,dw \tag{2}$$

Comparison of deviances of the best-fit and saturated models showed acceptable model fit ($\chi^2 = 50.7$, $df = 38$, $P = 0.082$). The integral of the larval abundance function was used to predict larval abundance between two time periods (t_1 and t_2). We assumed it took larvae 1 week to grow from 4 to 5.5 mm, which is consistent with the fast growth model.

Spawning behavior in Devils Hole pupfish occurs year-round, with peak spawning occurring from mid-February to mid-May (Lyons 2005). We failed to establish a relationship between female size and fecundity from Minckley and Deacon's (1973) egg counts of 26 wild female Devils Hole pupfish collected during different times of year. Likewise, studies of other pupfishes were unable to establish a relationship between female length and fecundity (Shrode and Gerking 1977; Mire and Millett 1994). Consequently, we assumed all females >13 mm (the minimum length of a reproductive female [Minckley and Deacon 1973]) were reproductive and produced equivalent numbers of larvae and eggs. Furthermore, we assumed sex ratio of 1:1 because correct determination of sex in SV dives is difficult, particularly for small fish. We estimated the number of larvae produced per female by dividing the predicted number of larvae (Eq. 2) by the predicted number of reproductive female pupfish (half the total abundance predicted by Eq. 1) within each interval. Abundances within an interval (i.e., the time between consecutive SV surveys) were estimated by calculating the mean abundance from current and next sampling periods. Importantly, because detection is low for fish <18 mm, this method may over-estimate the number of larvae per female.

Fitting a growth model

The growth model assumes von Bertalanffy growth (von Bertalanffy 1938) and was fit using the Fabens parameterization, which is well-suited for fitting growth curves to mark-recapture of tagged individuals:

$$\Delta L = (L_\infty - L_t)(1 - e^{-K\Delta t}) \tag{3}$$

Equation 3 shows the change in length (ΔL) of an individual fish of length L_t at time t is determined by the asymptotic maximum length (L_∞), the time interval (Δt) and the growth parameter K. Preliminary analyses showed that growth data from individual Devils Hole pupfish (James 1969) were well described by a von Bertalanffy growth model. To portray variability in growth among individuals, a random number was selected from a standard normal distribution ($\mu = 0$; $\sigma^2 = 1$) and added to the predicted growth increment for every individual. Individual fish lengths could not decrease with time; if the length of a fish was smaller in a future interval, the fish's length remained equal to its length during the previous month.

Methods used to fit a growth model to SV survey data required assumptions that resulted in unrealistic model output (Dzul 2011). Specifically, the mean length of the simulated population was much lower than the observed mean length in summer and autumn months, likely due to high population turnover. Consequently, for our simulations we selected a growth model that included two growth curves, hereafter referred to as the 'fast' ($K = 0.005729$; $L_\infty = 41.63$) and 'slow' ($L_\infty = 43.38$; $K = 0.002549$) growth curves. The basis for two growth curves stems from the results of an in situ experimental study of caged Devils Hole pupfish where biologists observed vastly different growth rates for fish with different hatch dates (James 1969). The fast growth curve was used to model all fish from the larval stage until they reached 15 mm. In addition, fish born between March and June also followed the fast growth curve from March to June. Fish >15 mm that were born July through February followed the slow growth curve. The fast growth curve was fit to data from James (1969), which included growth measurements of caged Devils Hole pupfish living in Devils Hole. The slow growth curve was estimated by following estimates of mean length from best-fit normal mixture models in months without substantial recruitment (i.e., October through March) as well as the means of the older cohort from April to June. When estimating the slow growth curve, we assumed neither recruitment nor size-selective mortality occurred between November and March. In addition, for months where the best fit mixture models included two cohorts (i.e., April, May, June), we assumed that neither recruitment nor size-selective mortality occurred into the older cohort.

Estimating survival

Egg, larval, juvenile, and adult survival rates were assigned different parameter values. We assumed egg survival to be 100 %, because we had no information to inform this parameter. As such, larval and egg survival rates are confounded and represented by a single "egg-larval" survival rate. Individuals transitioned between egg-larval and juvenile survival rates when they reached juvenile length (set to 12 mm), and between juvenile and adult survival rates when they reached adult length (18 mm). Adult and juvenile lengths were determined based on their association with notable behavioral changes. Because high mortality at early life history stages is common among fishes, we assumed mortality of larvae occurred within the month of birth. If simulated fish survived their month of birth, their egg-larval survival probability was set to one until they reached juvenile length. Juvenile and adult survival rates were described by a Type II survival curve, which is commonly assumed in fisheries when estimating mortality from catch curves (Haddon 2011). Monthly juvenile and adult survival rates were converted to daily survival rates to adjust for unequal time intervals.

We chose a range of adult survival probabilities because we were uncertain about true adult survival probability. Simulations were run with 30-day adult survival probabilities of 70, 80, and 86 %. We chose 86 % instead of 90 % because the adult abundance model predicts the Devils Hole pupfish population declines by 14 % each month from October to April. Furthermore, juvenile and adult survival rates were considered to be equivalent due to a lack of information on juvenile survival. Egg-larval survival probabilities were selected during simulation runs. Specifically, only within a narrow range of egg-larval survival probabilities (less than 0.1 %) did simulation models result in stable population growth ($\lambda \cong 1$).

Simulated individuals would first grow and subsequently be assigned survival probabilities based on their lengths during the current period and the next period. For example, if an individual was a juvenile during the current period and an adult during the next period, we used the following equation to estimate that individual's survival probability:

$$s_{i,t} = e^{\frac{(l_a - l_{i,t}) r_j + (l_{i,t+1} - l_a) r_a}{l_{i,t+1} - l_{i,t}}} \tag{4}$$

where r_j and r_a are the respective instantaneous survival rates for juveniles and adults, and $l_{i,t}$ and $l_{i,t+1}$ are the respective current and future lengths of individual i. The parameter l_a represents adult length. This equation was also used to estimate the survival probability of individuals transitioning from the egg-larval to juvenile stage, with instantaneous egg-larval and juvenile survival rates replacing instantaneous juvenile and adult survival rates, and juvenile length replacing adult length. Juvenile and adult survival rates were set equal in all models, with the exception of models with 5 % increases in adult and juveniles survival probabilities (see Assessing Elasticity of Model Inputs).

Because data from SV surveys showed lower survival of the older cohort in April–June, our simulation model included a term for decreased survival of fish in the older cohort from April through June. Likewise, all simulated fish >30 mm in length had their survival set to zero in July. Additionally, we assumed adult, juvenile, and egg-larval survival rates were constant for all months. While constant survival may not perfectly reflect population dynamics, assuming constant survival will help interpret deviations of simulated data from observed monthly abundance patterns.

Simulation runs

For the first iteration of each simulation, the initial population was comprised of 108 fish with lengths equal to those observed in the March SV dive. These 108 fish were randomly assigned a sex ("male" or "female") with equal probability. Fish then grew according to the appropriate growth curve and received an individual survival rate based upon their lengths during the current and next intervals. To determine survivorship, simulated fish received a random number drawn from a uniform distribution between zero and one. Only individuals that received a random number less than their survival probability survived to the next sampling period. The number of eggs per sampling period (N_e) was calculated by taking the mean of the numbers of females >13 mm in length (N_f) for the current (m) and the next sampling ($m + 1$) periods, then multiplying it by the fecundity estimate for the particular sampling period (f_m):

$$N_{e,m+1} = f_m \times \frac{N_{f,m} + N_{f,m+1}}{2} \tag{5}$$

The number of eggs was then multiplied by the egg-larval survival rate to obtain the number of larvae which survived the first month post-birth. Upon surviving the first month, larvae were assigned a sex (male or female) with equal probability. They were then randomly assigned a hatch date from a multinomial distribution, with probabilities of hatch dates obtained from the larval abundance function (Eq. 2). Assigning larvae random hatch dates allowed us to use discrete time to realistically depict continuous spawning. Hatch dates were entered into the growth function for each larva to determine its length during the sampling period. We ran simulation models out 120 months and used the first 24 values as burn-in values (i.e., we did not use the first 24 values in calculations because the model was not yet populated).

Simulation models

Choosing a baseline model

Our first task was to select a baseline simulation model that realistically portrayed the Devils Hole pupfish population. Based on its resemblance to observations, this model would help determine realistic values for survival probabilities of Devils Hole pupfish. Regrettably, size selectivity of Devils Hole pupfish SCUBA survey methods hindered direct quantitative comparison of simulations to observations. Consequently, simulation runs were evaluated qualitatively using visualization methods (i.e., we compared plots of simulated and observed data). This approach displays some similarity to pattern-oriented modeling as described by Grimm and Railsback (2012). To account for low detectability of small fish in SCUBA surveys, we only included fish with lengths greater than detection length (set to 18 mm) in comparisons of simulations to observations. Importantly, expressing detection as a function of length would likely be more appropriate; however, we had no data to inform this function.

We ran 2000, 120-month simulations to evaluate model performance and evaluated fit using two different assessments. First, we visually compared intra-annual (monthly) abundance patterns from simulations to estimates predicted by the adult abundance model. Second, we plotted monthly length-frequency probability distributions from one randomly-chosen year from 100 iterations against probability distributions of observed length-frequency from SV dives. We used these two criteria to select a baseline model, which was used in subsequent analyses to assess the effects of model parameters on population growth rates.

Assessing elasticity of model inputs

We ran a total of nineteen simulations (Table 2). Simulations differed in parameter estimates and were comprised of 2,000 iterations. Output from each iteration consisted of monthly adult abundance estimates for a 10 year period. The first 24 months of each iteration were considered burn-in months and were not included in summary statistics. Simulations were summarized by calculating the geometric mean ($\hat{\lambda}$) and standard error of population growth rates from 2,000 iterations, as well as the probability of extinction. Calculation of $\hat{\lambda}$ required first calculating the arithmetic mean abundance for each year within an iteration, then converting mean abundances to finite population growth rates by dividing estimates from consecutive years and calculating the geometric mean. Next, the geometric mean of all 2,000 iterations was calculated to estimate $\hat{\lambda}$. In cases where an iteration resulted in population extinction, we excluded all years post-extinction from the $\hat{\lambda}$ calculation. The probability of extinction was estimated as the proportion of simulations which resulted in a population comprised of <10

Table 2 Discrete population growth rates (λ), extinction probabilities, and elasticity values from simulation models describing population dynamics of Devils Hole pupfish *Cyprinodon diabolis*, living in Nye county, Nevada

	Mean λ	Standard error λ	Extinction probability	Elasticity
Monthly adult survival rate of 80 %				
Baseline model	1.041	0.002	0.015	NA
5 % increase in annual egg-larval survival	1.172	0.002	0.003	1.073
5 % increase in annual juvenile survival	1.061	0.002	0.010	0.971
5 % increase in annual adult survival	1.065	0.002	0.017	0.975
Baseline model (NWR)	1.016	0.002	0.008	NA
5 % increase in annual egg-larval survival (NWR)	1.126	0.002	0.001	1.055
5 % increase in annual juvenile survival (NWR)	1.027	0.002	0.009	0.963
5 % increase in annual adult survival (NWR)	1.054	0.002	0.003	0.988
5 % increase in reproductive length	0.941	0.003	0.075	0.861
5 % increase in juvenile length	1.115	0.002	0.004	1.021
75 % decrease in larvae per female and 400 % increase in annual egg-larval survival	1.033	0.003	0.023	NA
Monthly adult survival rate of 70 %				
Reference model	1.013	0.003	0.062	NA
5 % increase in annual egg-larval survival	1.210	0.002	0.005	1.137
5 % increase in annual juvenile survival	1.055	0.002	0.022	0.992
5 % increase in annual adult survival	1.034	0.003	0.029	0.972
Monthly adult survival rate of 86 %				
Reference model	1.049	0.003	0.021	NA
5 % increase in annual egg-larval survival	1.172	0.002	0.003	1.064
5 % increase in annual juvenile survival	1.075	0.002	0.007	0.976
5 % increase in annual adult survival	1.033	0.002	0.020	0.938

Specifically, annual survival probabilities for adult, juvenile, and egg-larval pupfish were increased by 5 % for simulation models to determine the effect of survival probabilities on the finite population growth rate (λ). Due to uncertainty in survival estimates, simulations with 5 % increases in stage-specific annual survival rates were run for models with 70, 80, and 86 % monthly adult survival rates, as well as for models with an 80 % adult survival rate and no winter recruitment (NWR). Similarly, reproductive length and juvenile length were increased by 5 % in the baseline model to evaluate the response of λ to uncertainty in these parameter estimates. One additional simulation which includes decreased estimates of the number of larvae per female and increased estimates of larval survival probabilities was run to determine response of λ to uncertainty in fecundity estimates. Importantly, because survival of juveniles and adults was modeled as a Type II survival curve, 5 % annual increases in adult and juvenile survival rates corresponds to a 0.4 % (or $1.05^{1/12}$) increase in monthly survival probabilities individuals after 10 years. Notably, estimates of extinction probability and population growth are reported to help illustrate differences between simulation models and not for their (weak) predictive capability. In particular, estimating extinction risk is tenuous, especially with a limited dataset (Fieberg and Ellner 2001).

We conducted an elasticity analysis to assess the influence of model inputs on population growth (de Kroon et al. 1986). Results of elasticity analyses can be used to help evaluate alternative management strategies and determine how uncertainty in parameter estimates will affect estimates of population growth (Morris and Doak 2002). We ran simulations with 5 % increases in annual egg-larval, juvenile, and adult survival rates, as well as 5 % increases in juvenile length and reproductive length. In addition to increasing aforementioned parameters, we ran one simulation which included a fourfold decrease in fecundity coupled with a fourfold increase in egg-larval survival. We included this simulation because we suspected that the baseline model over-estimated fecundity. Importantly, this coupling of egg-larval survival and fecundity parameters did not represent a change in larval abundance values. Rather, we hypothesized differences in pairings of fecundity and egg-larval survival parameters may affect demographic stochasticity, which could in turn affect population growth (Table 2). We will refer to the geometric mean population growth rate of the baseline model as $\hat{\lambda}_.$ and of altered simulations as λ_a, where the difference between the baseline model and altered simulation a is one parameter (referred to as x in the baseline model and x_a in the altered model). We calculated elasticity using the following formula (Morris and Doak 2002):

$$\frac{\hat{\lambda}_a/\hat{\lambda}_.}{x_a/x_.} \tag{6}$$

Whereas stage-specific survival rates may be affected by various management practices, reproductive length and juvenile length are biological characteristics that would likely be unaffected by management alternatives. As such, elasticity values of juvenile length and reproductive length help evaluate how uncertainty in these parameters affects simulation model performance. Because elasticities are calculated at specific parameter estimates (Caswell 1996), we also calculated elasticity values for 2,000 iterations of simulation models with 5 % increases in annual adult, juvenile, and egg-larval survival for models with initial monthly adult survival rates of 70 and 86 %. We calculated elasticities for models with adult survival rates of 70 and 86 % to determine if the relative effects of egg-larval, juvenile, adult survival were similar for various adult and juvenile survival probabilities.

To assess the hypothesis of lower over-winter survival of larvae and juveniles, we ran simulations where no recruitment occurred into the Devils Hole pupfish population in winter months. The no winter recruitment (NWR) simulation model assumed 100 % mortality of all fish with lengths <18 mm from November to January. We included NWR simulation models with an 80 % monthly adult survival rate in the elasticity analysis. Specifically, we increased egg-larval, juvenile, and adult survival rates by 5 % in NWR models to assess whether relative values for elasticities were consistent with those from simulations with winter recruitment. Namely, we expected the relative elasticity of adult survival would be higher in NWR simulations.

Results

Best-fit normal mixture models for April, May, June, and October length-probability distributions were comprised of two mixtures. For all other months, best-fit normal mixture models consisted of a single mixture (Fig. 3). Whereas the choice of adult survival rate had a large effect on intra-annual abundance patterns, egg-larval survival rates primarily affected inter-annual abundance and population growth. When assessing intra-annual patterns, simulations with a monthly adult survival rate of 86 % tended to over-estimate abundance in winter, whereas simulations with a monthly adult survival rate of 70 % tended to result in greater magnitude population fluctuations when compared with the adult abundance model (Fig. 4). The simulation model with a monthly adult survival rate of 80 % produced highly variable estimates in March and April, some of which greatly over-estimated abundance. Nevertheless, simulations with a monthly adult survival probability of 80 % resembled the adult abundance model (Fig. 4). Furthermore, length-probability distributions from simulations with a monthly adult survival rate of 80 % resembled observed length-probability distributions from SV dives from March to February. However, the simulation model under-estimated the proportion of large fish in April and May, suggesting that the model under-estimated growth and(or) over-estimated mortality of large fish during these months (Fig. 5). Length-probability models from simulations with a monthly adult survival rate of 86 % likewise resembled observed length-frequency probabilities. In contrast, length-probability distributions from simulations with a monthly adult survival rate of 70 % tended to under-estimate relative abundance of large fish in July through December. We selected a monthly adult survival rate of 80 % for our baseline model because survival values exhibited the best overall resemblance to the adult abundance model and to length-frequency distributions from SV

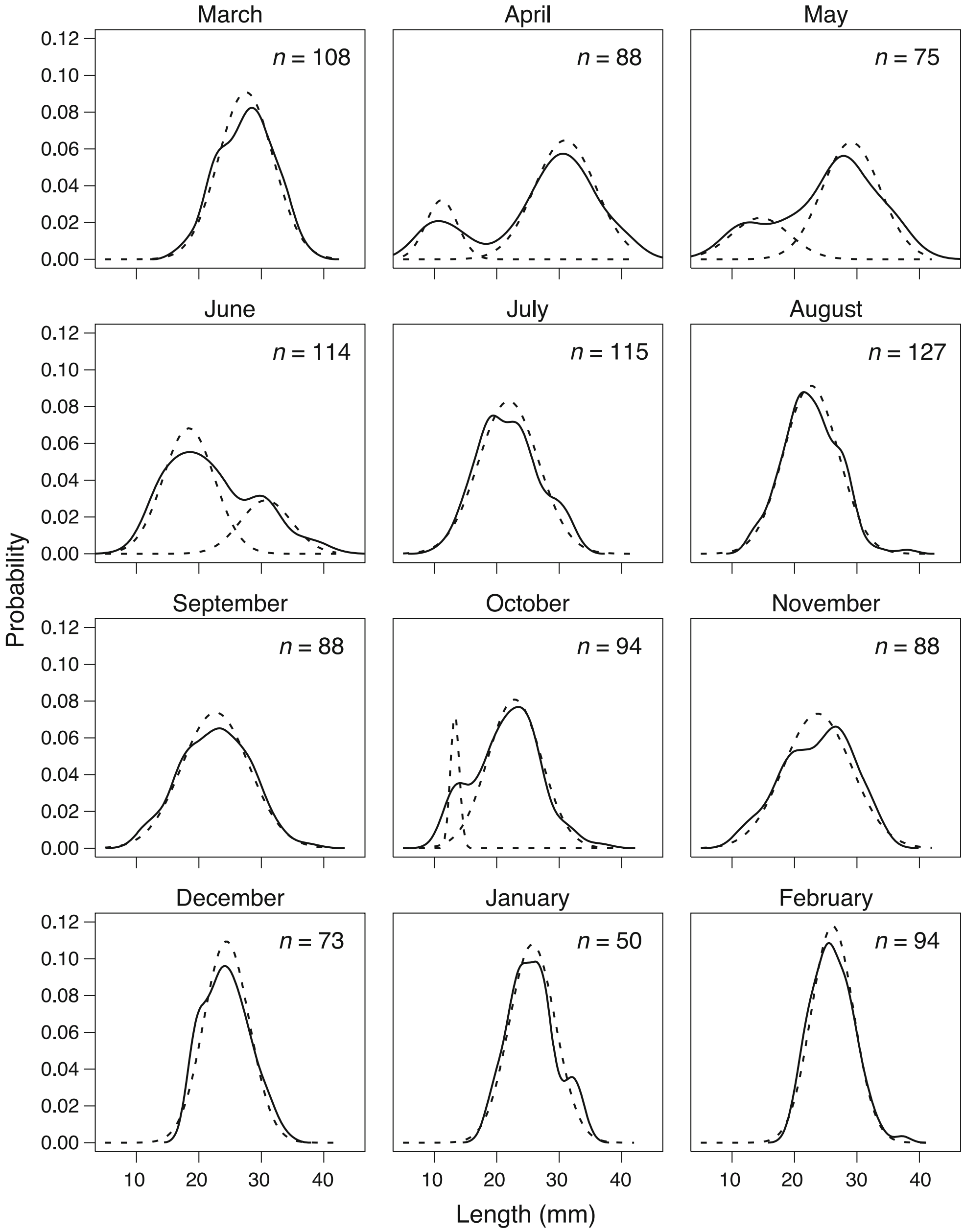

Fig. 3 Mixture models fit to monthly length-probability distributions of the Devils Hole pupfish, *Cyprinodon diabolis*, Devils Hole, Nye County, NV. Observed length-probability distributions from stereo-video surveys (*solid line*) are plotted against best-fit normal mixture models (*broken line*) for March–February. Sample sizes are included in the *upper-right* corner of each *panel*

dives. Corresponding monthly survival probabilities for egg-larvae and juveniles were set to 4.7 and 80 %, respectively.

Iterations within simulations exhibited high variability. Regardless of whether the monthly adult survival rate was set to 70, 80, or 86 %, results of the elasticity analysis indicated that growth of the simulated population was most affected by egg-larval survival. Likewise, elasticity values were highest for egg-larval survival in simulation models without winter recruitment, though the difference between adult and egg-larval elasticity values was lower compared to models with winter recruitment. In all parameterizations, increasing juvenile and adult survival rates had more similar effects on population growth (Table 2; Fig. 6). Furthermore, elasticity values for juvenile length and reproductive length were also relatively high (Table 2). In contrast, assuming larval abundance estimates were similar to those of the baseline model, uncertainty in larvae per female had a negligible effect on population growth rates relative to other sources of uncertainty. For models without winter recruitment, the egg-larval survival rate was increased from 4.7 to 7.2 % to avoid extinction. Simulation models without winter recruitment over-estimated abundance in November and under-estimated abundance from May to August and January to February (Fig. 7). Compared to models with winter recruitment, NWR simulations

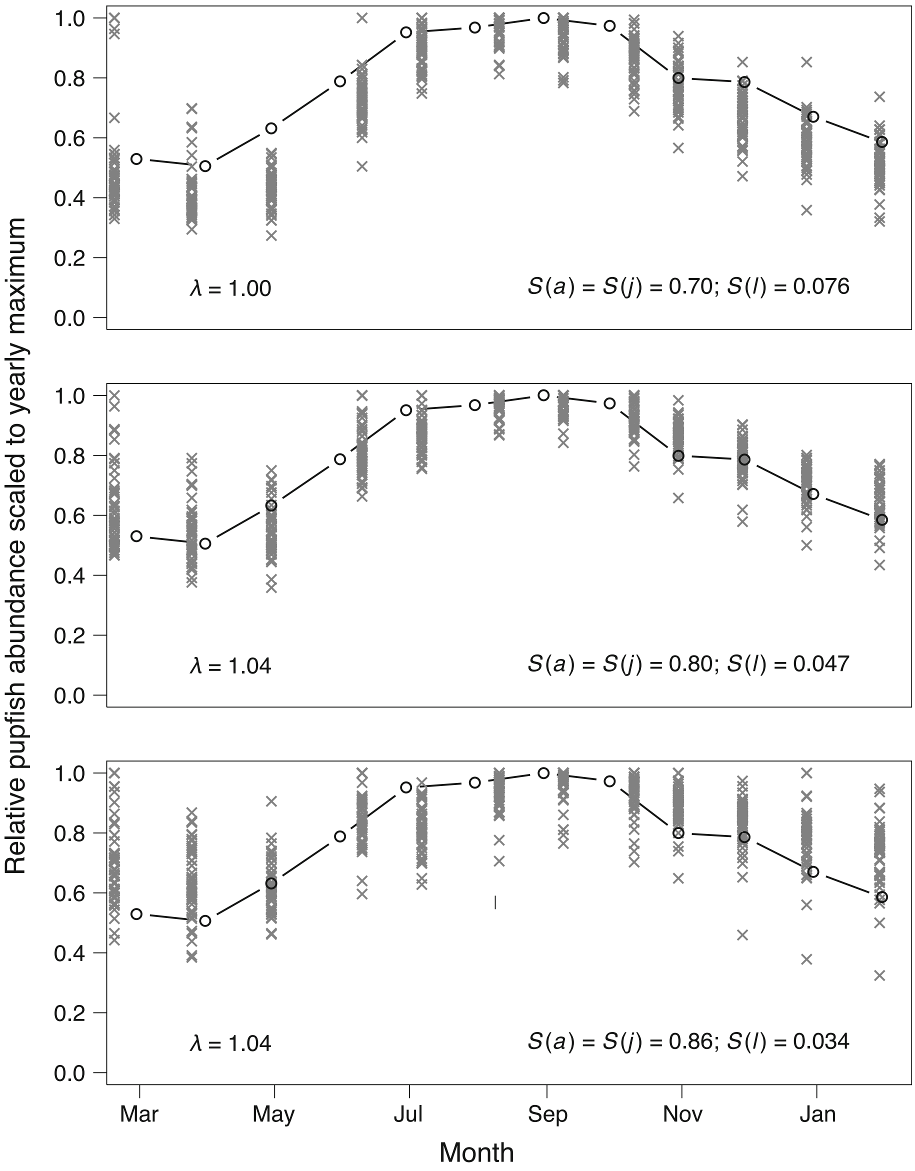

Fig. 4 Intra-annual abundance patterns of Devils Hole pupfish, *Cyprinodon diabolis*, Devils Hole, in Nye County, NV. Simulation models were run with three different monthly adult and juvenile survival probabilities: 70 % (*top*), 80 % (*middle*), and 86 % (*bottom*). Larval survival rates were 7.6 % (*top*), 4.7 % (*middle*), and 3.4 % (*bottom*). All abundance values were scaled by dividing by maximum observed annual abundance. *Lines* represent scaled monthly abundance estimates of Devils Hole pupfish predicted by the adult abundance model. *Crosses* represent scaled abundance (for fish >18 mm total length) from five random iterations of simulation models with different adult survival probabilities

exhibited less resemblance to observed length-probability distributions from SV dives in May and June, and underestimated the relative abundance of large fish in June to September (Fig. 8).

Discussion

Conducting monthly SCUBA dives in Devils Hole was difficult due to the endangered status of the Devils Hole pupfish. Nonetheless, length-frequency distributions from SV dives provided useful information about the population structure in Devils Hole.

Results of best-fit mixture models confirm that the Devils Hole pupfish population experiences a pulse of new recruits from March to June. While the spring pulse in recruitment is well recognized (Gustafson and Deacon 1997; Lyons 2005), a curious finding resulting from SV dives is that the best-fit model describing the October length-frequency distribution included two mixtures. A second peak in Devils Hole pupfish spawning activity was observed in October and November 2010 (A. Chaudoin, personal communication), suggesting that the selection of two cohorts in October might be due to an increase in larval abundance in October.

Results of the population model provided some insight as to the mathematical nature of Devils Hole pupfish population fluctuation. Interestingly, for each estimate of adult survival, there was only a small range of values for egg-larval survival that resulted in stable population growth. Surprisingly, simulation models with constant adult and egg-larval survival rates do resemble observed

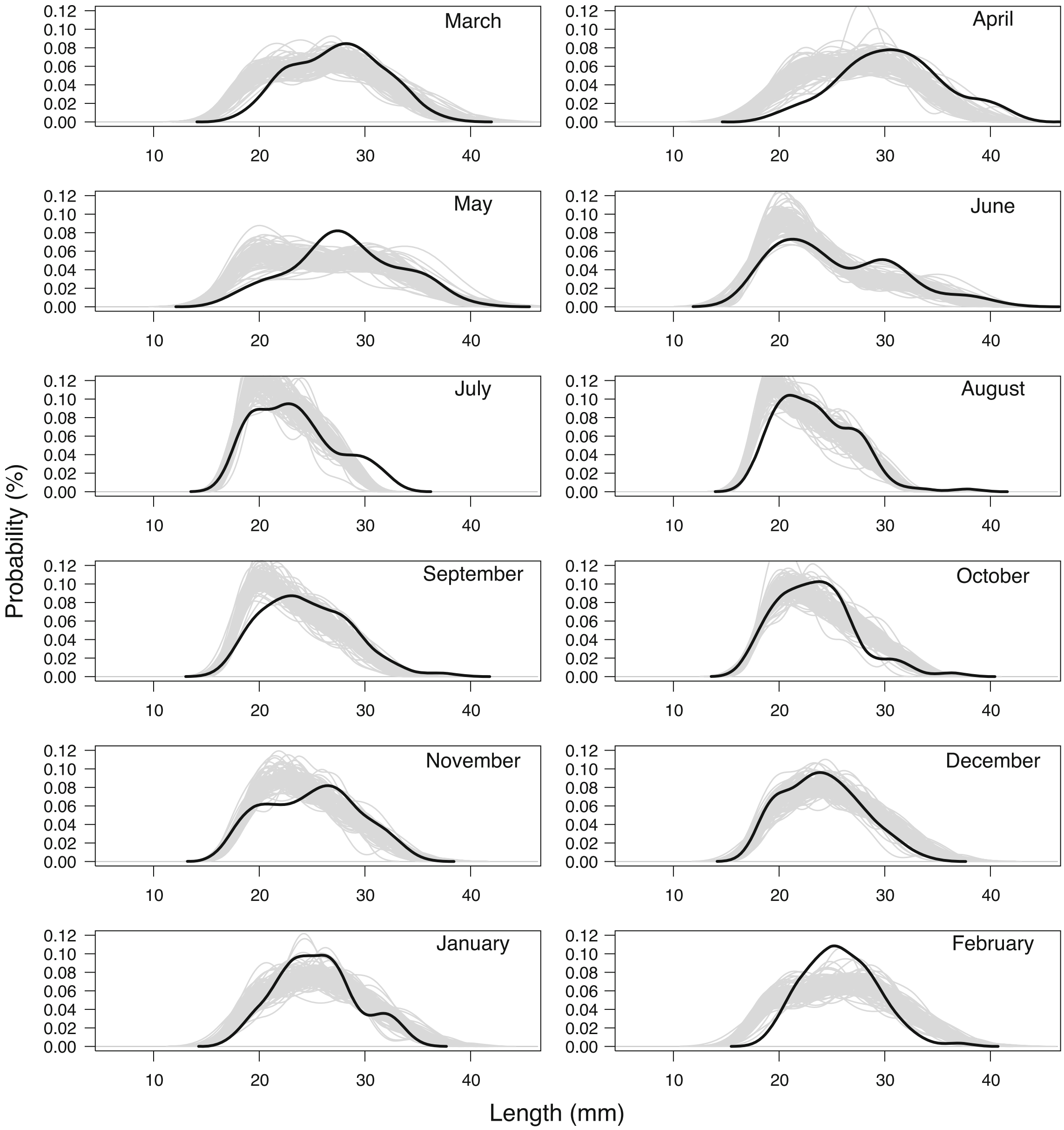

Fig. 5 Simulated and observed length-frequency distributions of the Devils Hole pupfish, *Cyprinodon diabolis*, Devils Hole, Nye County, NV. Length-probability distributions from stereo-video surveys (*black line*) compared to length-probability distributions from 100 randomly-chosen iterations of a simulation model (*grey lines*). To facilitate comparison between stereo-video surveys and the simulation model output, length probability distributions only include fish with lengths >18 mm. The simulation model used monthly adult and juvenile survival probabilities of 80 % and an egg-larval survival rate of 4.7 %

length-frequency distributions as well as intra-annual abundance patterns. While this result does not directly contradict previous studies, constant survival seems incongruent with past findings. For example, Deacon and Deacon (1979) observed a correlation between monthly estimates of Devils Hole pupfish population size and primary production. Similarly, Wilson and Blinn (2007) observed an 80–96 % reduction in carbon sources in Devils Hole during winter months. Both studies suggest Devils Hole pupfish experience a decline in energy availability during winter months, which could plausibly result in lower overwinter survival rates. However, decreases in reproductive activity or slower growth would lower energetic demands of pupfish, which would at least partially counteract the effect of reduced energy availability. Although we are not claiming that the constant survival model is the "true" model, we do believe that it may have some credibility. Furthermore, the simplicity of a constant-survival model facilitates interpretation of model output.

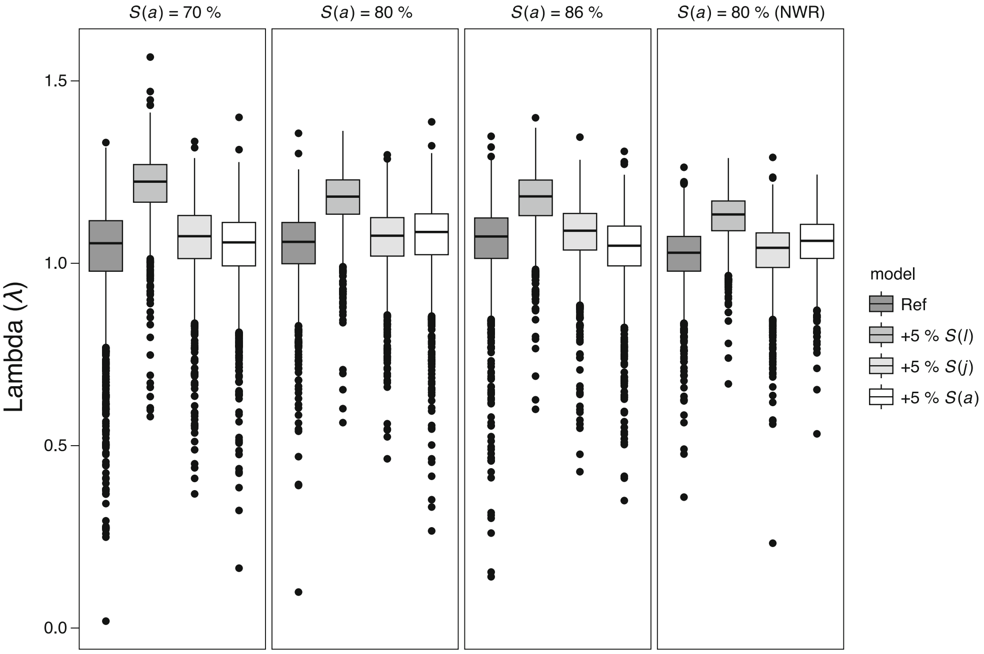

Fig. 6 *Box* and *whisker plots* of discrete population growth rates (λ) from simulation models describing population dynamics of Devils Hole pupfish, *Cyprinodon diabolis*, Devils Hole, in Nye County, NV. *Boxes* represent the interquartile range, and the *horizontal line* in each *box* represents the median. *Vertical lines* extending from *boxes* have length equal to 1.5 multiplied by the interquartile range. *Dots* are datapoints whose values are outside the range designated by *vertical lines*. Distributions include resulting λ's from 2000 iterations within each simulation. Simulation models are grouped by their monthly adult survival rate (*S*(*a*)). In addition, a simulation model with no winter recruitment (NWR) was included due to uncertainty about winter recruitment. Each group includes a reference simulation (Ref) as well as simulations with 5 % increases in annual egg-larval [+5 % *S*(*l*)], juvenile [+5 % *S*(*j*)], and adult survival rates [+5 % *S*(*a*)]

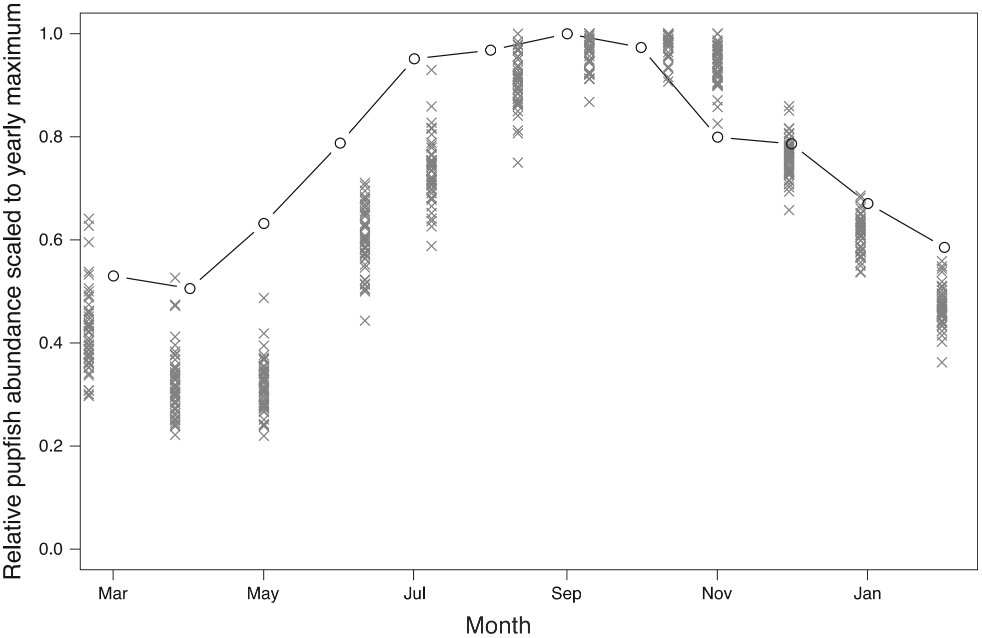

Fig. 7 Intra-annual abundance patterns of a simulation model with zero over-winter survival of eggs, larvae, and juvenile Devils Hole pupfish, *Cyprinodon diabolis*, in Nye County, NV. Monthly adult and juvenile survival rates were set to 80 % and egg-larval survival was set to 7.2 %. All abundance values were scaled by dividing by maximum observed annual abundance. *Lines* represent scaled monthly abundance estimates of Devils Hole pupfish predicted by the adult abundance model. *Crosses* represent scaled abundance (for fish >18 mm total length) of from five random iterations of simulation models with different adult survival probabilities

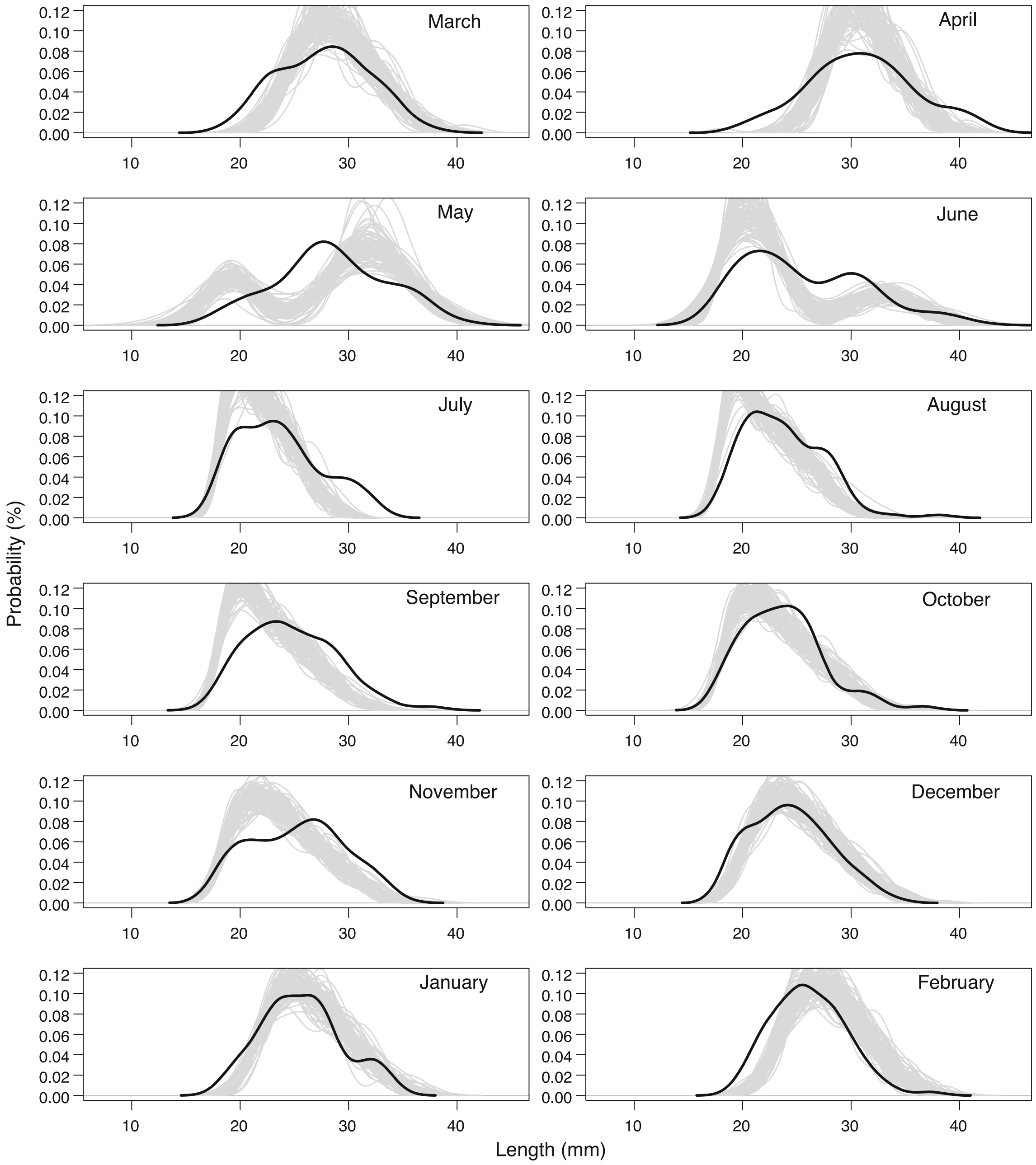

Fig. 8 Simulated and observed length-frequency distributions of the Devils Hole pupfish, *Cyprinodon diabolis*, in Nye County, NV. Length-probability distributions from stereo-video surveys (*black line*) compared to length-probability distributions from 100 randomly-chosen iterations of a simulation model (*grey lines*). To facilitate comparison between stereo-video surveys and the simulation model output, length probability distributions only include fish with lengths >18 mm. The simulation model used monthly adult and juvenile survival probabilities of 80 % and an egg-larval survival rate of 7.2 %. Furthermore, survival probabilities of eggs, larvae, and juveniles were set to 0 from November to January

Our simulation differed from observations and predictions in previous studies. James (1969) observed a caged population of Devils Hole pupfish grow from an initial size of 4 males and 2 females to a final size of 36 from March to July. While this corresponds to 15 individuals per female, our baseline simulation model predicts 5.1 individuals per female. However, in James' (1969) study, many larvae in the caged population grew to lengths >13 mm and could have spawned during the course of the experiment. Furthermore, larval survival rates are suspected of causing the recent decline in the Devils Hole pupfish population (Graves 2004); as such, historic and current larval survival rates may differ. In addition, we obtained a lower estimate of adult survival than Chernoff (1985) who also assumed that a Type II survival curve described adult survival. Chernoff (1985) obtained a monthly adult survival rate of 91 %, from which he estimated the average age of an adult Devils Hole pupfish to be 10 months. In contrast, the adult survival rate used in the current model (80 %) predicts an average age of 4.5 months after fish have reached 18 mm (5.8 months from the larval stage). Importantly, Chernoff (1985) assumed that no recruitment occurs from October to January. Furthermore, one caveat of Chernoff's (1985) model is that adult mortality was partitioned into mortality due to declining primary production (which exhibits a predictable seasonal pattern) and "natural mortality." As such, interpreting Chernoff's (1985) estimate as an "average age" is misleading because it does not incorporate mortality of fish due to seasonal effects. An alternative simulation that assumes constant adult survival is 86 % per month closely resembles the observed length-probability distributions from SV surveys but has poorer fit to the adult abundance model and produces an average age estimate of 7.9 months, which is more similar to Chernoff's estimate.

Length-probability distributions from simulation models with no overwinter recruitment more closely resembled length-probability distributions from the SV dives than the baseline model when fish of all lengths (i.e., including fish with lengths <18 mm) were incorporated into length-probability distributions. Specifically, SV dives in December, January, and February did not detect any fish <17 mm in length. As such, it is not surprising that simulation models without winter recruitment exhibited good fit to SV dives. After accounting for differences in detection by excluding fish with lengths <18 mm from length-probability distributions, the baseline model with winter recruitment better resembled observed data. Interestingly, intra-annual abundance patterns for simulations without winter recruitment exhibited less resemblance to the baseline model. However, such results may arise due to a violation of the assumption of the temporally-constant survival estimates. Specifically, increased egg-larval survival in March–April might result in increased adult abundance from May to July, which would cause the NWR simulations to better resemble observed adult intra-annual abundance patterns.

Despite incorporation of demographically stochastic processes, the current model is partly deterministic because it ignores the effects of environmental variability on population processes. Although the environment in Devils Hole is relatively stable, slight deviances in water temperature, sunlight, or dissolved oxygen concentrations on the shallow shelf may influence pupfish survival and recruitment. Likewise, disturbance events such as earthquakes and rain events may have far-reaching effects. Positive correlation between stage-specific survival rates can increase stochasticity (Fieberg and Ellner 2001). Clearly, there are many uncertainties when using the current simulation model as a predictor of future population trends. Notwithstanding these short-comings, the simulation model can still be used for exploratory analysis to help evaluate mathematical plausibility of various biological scenarios and to compare various management alternatives. Despite uncertainty in model parameters, results of the elasticity analysis were consistent and indicated that increasing egg-larval survival rates had the greatest effect on population growth. Importantly, elasticity values should be put into a realistic context to obtain meaningful results (Morris and Doak 2002). For example, if current adult survival rates are lower than past rates, restoring the population to past conditions may have indirect positive effects (i.e., positive feedback) on larval survival. Uncertainty in juvenile length and reproductive length had substantial effects on population growth estimates (Table 2), suggesting more precise parameter estimates are needed.

Devils Hole pupfish biologists have identified water temperature, dissolved oxygen, sulfide and ammonia concentrations, proportion of fine sediments on the shallow shelf, food availability, inbreeding depression, and disease as factors potentially influencing pupfish abundance (Wilson et al. 2009). Of these factors, those influencing the shallow shelf environment (e.g., water temperature, dissolved oxygen) are thought to exclusively influence egg and larval stages. Experimental studies of *Cyprinodon nevadensis nevadensis* in a laboratory environment showed oogenesis and egg survival were most affected by high temperatures compared to later life history stages (Shrode 1975; Shrode and Gerking 1977). However, results from other laboratory studies indicate that assessing effects of environmental variables in natural environments may be complex. For example, Kinne and Kinne (1962) observed that *Cyprinodon macularis* in freshwater tanks exhibited 100 % egg mortality in treatments with dissolved oxygen levels that were 70 % air saturation at 31 °C but not at 100 % air saturation at 31 °C. This result highlights the importance of considering the interaction between dissolved oxygen and temperature when evaluating their influence on egg survival. Likewise, laboratory studies documented increased thermal tolerance when pupfish eggs were incubated under fluctuating temperatures compared to constant temperatures (Shrode and Gerking 1977). Further complicating assessment of the influences of environmental variables on egg and larval survival is the observation that the shallow shelf in Devils Hole exhibits a gradient of environmental conditions, with shallow areas experiencing more extreme temperatures and higher dissolved oxygen levels than deeper areas (Deacon et al. 1995; Gustafson and Deacon 1997; Lyons 2005). Unfortunately, the simulation model is currently ill-equipped to assess mechanisms associated with egg-larval mortality.

Despite its current limitations, the model is useful in identifying important sources of uncertainty that can help guide future research and management efforts. Given the importance of egg-larval survival in the model, effort should be placed on gathering better estimates of both egg and larval mortality, and describing the mechanisms associated with survival. For instance, biologists could assess temporal patterns of larval mortality by coupling frequent measurements of dissolved oxygen and temperature along the shallow shelf in Devils Hole with laboratory investigations evaluating oxygen sensitivity and thermal tolerance of captive Devils Hole pupfish × Ash Meadows pupfish (C. *diabolis* × *C. nevadensis mionectes*) eggs. Importantly, biologists would first have to determine if(how) the physiology of hybrid fish related to that of Devils Hole pupfish. Not only would such work inform the model with egg survival estimates, but the monthly estimates of egg mortality in Devils Hole could then be entered into the simulation model and used to determine dissolved oxygen and temperature effects on population growth. Because adult abundance surveys represent the most detailed and extensive historic record of biological conditions in Devils Hole, current monthly abundance estimates may also help biologists identify changes in pre- and post-decline population dynamics. If the Devils Hole pupfish population reaches an appropriate size to allow biologists to use wild fish for empirical studies, duplicating James' (1969) experiment of caged fish may provide useful information about current Devils Hole pupfish growth patterns. Experiments assessing detectability as a function of fish length, perhaps conducted with the captive population of hybridized Devils Hole pupfish and Ash Meadows pupfish would further improve future studies. However, the best method to assess population dynamics would be to obtain individual capture histories. Future enhancements in DNA and photo-recognition technologies hold promise as non-obtrusive sampling methods that can be used to obtain individual capture histories.

We believe the limitations imposed by non-obtrusive sampling make our simulation model a particularly useful tool for modeling the Devils Hole pupfish population. Specifically, the simulation approach allows incorporation of data from a wide variety of sources (e.g., ELS surveys, past Devils Hole pupfish studies, studies of other pupfishes). In addition, our simulation model allows comparisons of biological opinions and observed data. However, the simulation model's utility depends on future directions of Devils Hole pupfish research. Accordingly, we emphasize the need for empirical studies of captive hybrid pupfish; additional estimates of growth, adult abundance, and detection; and fine-scale measurements of environmental variables along the Devils Hole shallow shelf. To enable our model to address future questions of interest to Devils Hole pupfish biologists, we have built flexibility into the model's framework by allowing specification of monthly survival and fecundity estimates as new data become available. As such, we hope our simulation model will continue to aid biologists' pursuit of identifying causes of population change of the Devils Hole pupfish.

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