SUSTAINABILITY MANAGEMENT OF SHORT-LIVED FRESHWATER FISH IN HUMAN-ALTERED ECOSYSTEMS

BY

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CHAPTER ABSTRACTS

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CHAPTER ABSTRACTS

CHAPTER 1 ABSTRACT - SUSTAINABILITY MANAGEMENT OF SHORT-LIVED FRESHWATER FISH IN HUMAN-ALTERED ECOSYSTEMS SHOULD FOCUS ON ADULT SURVIVAL

Evidence is presented that fish populations globally are susceptible to endangerment through exploitation and habitat loss. Theoretical simulations are presented to explore how reduced adult survival (age truncation) might affect short-lived freshwater fish species in human-altered contemporary environments. Simulations evaluate two hypothetical "average fish" and five example fish species of age 1 or age 2 maturity. From a population equilibrium baseline representing a natural, unaltered environment we impose systematic reductions in adult survival and quantify how age truncation affects the causes of variation in population growth rate. Estimates are presented of the relative contributions to population growth rate arising from simulated temporal variation in age-specific vital rates and population structure. At equilibrium and irrespective of example species, population structure (first adult age class) and survival probability of the first two adult age classes are the most important determinants of population growth. As adult survival decreases, the first reproductive age class becomes increasingly important to variation in population growth. All simulated examples show the same general pattern of change with age truncation as known for exploited, longer-lived fish species in marine and freshwater environments. This implies age truncation is a general potential concern for fish biodiversity across life history strategies and ecosystems. Managers of short-lived, freshwater fishes in contemporary environments often focus on supporting reproduction to ensure population persistence. However, a strong focus on water management to support reproduction may reduce adult survival. Sustainability management needs a focus on mitigating adult mortality in human-altered ecosystems. A watershed spatial extent embracing land and water uses may be necessary to identify and mitigate causes of age truncation in freshwater species. Achieving higher adult survival will require paradigm transformations in society and government about water management priorities.

CHAPTER 2 ABSTRACT – MITIGATION OF RECURRENT PERTURBATIONS IS AN IMPORTANT GOAL FOR CONSERVATION OF FRESHWATER FISHES

Human perturbations affect many aquatic ecosystems globally. I use matrix population models to explore the effects of environmental perturbations on population growth rates using short-lived freshwater fish species as examples. Estimates of annual flow intermittence frequency and average annual spatial extent of flow intermittence were used to approximate how contemporary hydrologic conditions may vary over time and space and affect population growth for the endangered Rio Grande silvery minnow (*Hybognathus amarus*). Deterministic calculations indicate that a single occurrence of flow intermittence may require 20 or more years for recovery to an initial population equilibrium baseline. Perturbation that reduces only juvenile survival has a shorter recovery time to initial population size and greater resilience of population growth than when adult survival is reduced. Consecutive occurrences of perturbation lengthen recovery time nonlinearly, more notably when adults experience perturbation mortality. I illustrate with an example how managers could identify multiple options to mitigate recurrent ecosystem perturbations by reducing perturbation frequency and/or mitigating perturbation mortality. When life history data are unavailable or uncertain for a specific species of concern, our simulations suggest parameter approximations for a hypothetical species of comparable size and lifespan would provide a useful general frame of reference for conservation assessments aimed at informing management measures needed to mitigate recurrent perturbations.

CHAPTER 3 ABSTRACT – MANAGEMENT OF WATER SUPPLY AND WATER SHORTAGES TO SUSTAIN AN ENDANGERED FISH SPECIES

Arid and semi-arid landscapes globally represent significant challenges to develop and manage regional water resources for human uses while simultaneously sustaining aquatic ecosystems. There is a pressing need for conservation initiatives that limit or mitigate the extent of human perturbations to aquatic ecosystems. However, little theory exists to effectively manage scarce water resources to support an environmental state that sustains aquatic species and water resources while limiting the cost of that protection to existing water uses.

Results of demographic analyses along with statistical characterizations of flow intermittence, are used to identify how changing patterns of habitat size, flow continuity, and consecutive years of flow intermittence operate to shape population growth rates of the Rio Grande silvery minnow (*Hybognathus amarus*), a small-bodied endangered fish species endemic to the Rio Grande Basin of North America. The joint effects of demographic and hydrologic factors provide a logical basis to estimate limits of river drying to avoid levels of environmental mortality that threaten the capacity of *H. amarus* to sustain a positive capacity for population growth.

I explore how demographic characteristics of *H. amarus* relates to water demand for species conservation, and how consideration of this need can be integrated into procedural conventions of water management. The analytic framework presented provides a structured context for integrated resource planning to identify promising combinations of management actions to restrict flow intermittence for conservation purposes, possibly including water supply augmentation and options for least-cost water shortage management under conditions of time and space variant flow intermittence.

Keywords: matrix population model, transient population growth simulation, age truncation, conservation planning, Cypriniformes, fish life history

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CHAPTER 1 – SUSTAINABILITY MANAGEMENT OF SHORT-LIVED FRESHWATER FISH IN HUMAN-ALTERED ECOSYSTEMS SHOULD FOCUS ON ADULT SURVIVAL

Introduction

Despite a 450 million-year evolutionary history punctuated with global climate fluctuations and mass extinctions, contemporary biodiversity exceeds 35000 species of fish (Fricke et al., 2019), more than one-half of all vertebrates. However, in the Anthropocene (http://quaternary.stratigraphy.org/working-groups/anthropocene/, accessed 11 February 2020) numerous fish species globally have declined severely from over-exploitation (Botsford et al., 1997) and habitat modification by humans (Kominoski et al., 2017). Continued human population growth should be expected to increase direct impacts on harvested fish stocks and indirect impacts on all fishes with modifications to the waters they occupy. A transition in policy (Gleick, 2018) is urgently needed to confront growing human needs for freshwaters while also recognising and mitigating indirect ecological effects on freshwater biota.

Managers of fish species for recreational, subsistence or commercial pursuits commonly regulate harvest aiming to reduce adult mortality, a general affirmation that adult survival is important for sustainable use (Lande et al., 1995). In contrast, with nongame fish species the management focus is often on supporting successful reproduction in hopes of facilitating species' survival (George et al., 2009; Day et al., 2017). A focus on reproduction implies that adult survival may be less important for conservation of endangered freshwater fish species, or that improving reproduction will offset the adult mortality the species experiences in its contemporary environment. Prior work on the relative importance of adult survival for freshwater fish populations is contradictory. Velez-Espino et al. (2006) suggested that juvenile survival and fecundity were more important than adult survival for short-lived freshwater fishes.

In contrast, Wang et al. (2017) reported that population growth was generally more dependent on juvenile and adult survival and reproductive output was of minor importance. Is adult survival important for conservation of short-lived freshwater fishes? We use a matrix population model to explore what happens to a population when adult survival declines.

Reconciling the shortcomings of asymptotic theory of population ecology with the reality of unstable, altered environments occupied by endangered species is a contemporary problem in conservation. The inadequacy of asymptotic theory for endangered species can include probable lack of a stable population structure, survival probabilities that vary across years and erratic habitat conditions that contribute additional mortality in some years (Hastings, 2004; Wolkevich et al., 2014). Although it relies on a single life history of vital rates, an asymptotic perspective has been commonly applied to conservation including numerous applications to fish conservation (Wang et al., 2017; Bajer & Wildhaber, 2010; Durham & Wilde, 2009; Jaric´ et al., 2010). The asymptotic approach assumes equilibrium conditions with a stable population structure in a stationary environment. Stochastic variation in vital rates driven by fluctuations in the environment is ignored in the asymptotic approach and as a result, an asymptotic approach can fail to identify key factors contributing to population growth rate and can promote ineffective conservation when environmental conditions are variable in time.

It would be naïve to suggest there is a single asymptotic set of vital rates that are valid over all habitat conditions (Koons et al., 2017) because environmental stochasticity can affect age-specific survival and reproductive potential. Temporal variation in vital rates introduces variation in population structure that can have a large effect on population growth, especially for life histories with low juvenile survival probability (Koons et al., 2016). Generally in fishes, juvenile survival rates are low and they vary inversely with fecundity (Moyle & Cech, 2004). Although an investigator can obtain sample estimates of survival probabilities for an endangered species, samples in different years or locations are likely to yield different estimates. It can be difficult to know exactly which set of estimates is appropriate for use in an asymptotic analysis of matrix population models. As a consequence, a transient approach may be superior to an asymptotic perspective in addressing the question of the relative importance of adult survival for short-lived fish species. Life table response experiments (LTREs) using controlled perturbations (Caswell, 2001) are not likely to be permitted or practical for an endangered species. The inevitable uncertainty in estimates of vital rates for an endangered species led us to use simulated transient LTREs (Koons et al., 2016) to evaluate the effects of perturbations to vital rates on population growth rate.

Here we use simulations of temporal variation in vital rates and retrospective transient LTREs to explore how fish populations might respond to environmental variation that reduces adult survival. Reduced adult survival can drive rapid change in fish populations with high natural predation (Reznick et al., 1997) or strong exploitation (Biro & Post, 2008). The manifestation of reduced adult survival in fish populations has been variously called age truncation (Ottersen et al., 2006), juvenescence (Stenseth & Rouyer, 2008), longevity overfishing (Beamish et al., 2008), recruitment overfishing (Hilborn & Walters, 1992; Smith et al., 2018) and growth overfishing (Seibert et al., 2018). Irrespective of its cause, age truncation occurs when reduced adult survival probability causes a decline in the mean age of adults and decreases the population's future reproductive potential (Rouyer et al., 2011), while also shortening a species' effective life span as older adults become rarer.

In this study, we develop a fecundity equation for an iteroparous "average fish" and a hypothetical equilibrium baseline from which to simulate demographic effects of age truncation.

For comparative purposes, we further mimic the life history of five freshwater fish species (Order Cypriniformes) (Tan & Armbruster, 2018) from three continents that differ variously in life span, growth rate, maximum size, age at maturity and age-specific fecundity (Fig 1, Table 1): Marico barb (*Enteromius motebensis*; Family Cyprinidae: Smiliogastrinae), Rio Grande silvery minnow (*Hybognathus amarus*; Leuciscidae: Pogonichthyinae), western silvery minnow (*Hybognathus argyritis*; Leuciscidae: Pogonichthyinae), boga portuguesa (*Iberochondrostoma lusitanicum*; Leuciscidae: Leuciscinae) and Burchell's redfin (*Pseudobarbus burchelli*; Cyprinidae: Smiliogastrinae). These example species are broadly representative of iteroparity, the most common reproductive strategy among ray-finned fishes (Actinopteryi), which comprise about two-thirds of all fish species (Fricke et al., 2019). We had access to more information for *H. amarus*, a local species in the Rio Grande Basin. The additional example species had sufficient published information to approximate their life history. We chose these species and the comparable-sized hypothetical "average fish" to address the question: "Is there similarity or dissimilarity across different life histories in how the drivers of variation in population growth respond to age truncation in short-lived fish species?"

Methods

Terms and symbols used in this paper are defined in Appendix Table S1. An archive of all simulation scripts and results is available in Dryad (https://doi.org/10.5061/dryad.69p8cz8z7).

Our approach to study age truncation in short-lived freshwater fishes involved these aspects: (1) development of a theoretical equilibrium population baseline, (2) compilation of published fecundity and body length data for 33 freshwater cypriniform species, and Bayesian meta-analysis to enable prediction of fecundity at-age, (3) simulation of temporal variation in fecundity and survival at four levels of adult survival, (4) retrospective analysis of simulations to infer relative contributions of each vital rate and component of population structure to population growth rate and (5) comparison of simulation results across example species.

Implementation of a Matrix Population Model

We use a single matrix population model that accommodates life spans of age 4+ and age 5+. We assume the last age class is composed of age 5 and older individuals, of which there is a non-zero probability of occurrence even with adult survival for an age 2 longevity. An age class model is preferred to a juvenile-adult stage-based model because many fish species have a strongly allometric increase in fecundity with body length (and age) that exceeds the slope of the relationship between fecundity and body mass (Dick et al., 2017; Barneche et al., 2018); a stage-based model may not accurately represent the contribution of fecundity from older females with disproportionately higher fecundity.

The vital rate parameters (eq. 1) in the simulated post-breeding birth-pulse female transition matrix include age-specific survival probability (S_i) and fecundity (number of eggs; F_i). We assumed density independence because other species with similar life histories have conformed poorly to models of density dependence (Winemiller, 2005). Note that the age-specific number of individuals (n_i) in the population vector are additional model parameters in transient LTREs (Koons et al., 2016). We assume that $S_1 = \ldots = S_5$ in the starting transition matrix for each simulation scenario; for simulations of delayed maturity $F_1 = 0$.

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_t = \begin{bmatrix} 0 & S_1F_1 & S_2F_2 & S_3F_3 & S_4F_4 & S_5F_5 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_4 & S_5 \end{bmatrix}_t \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t-1} \qquad (1)$$

To facilitate simulating age truncation, we develop a hypothetical "natural equilibrium" view of a species in its natural environment wherein adult survival probability determines approximate natural lifespan. We assume for a natural equilibrium that a species' fecundity at size and age is a result of selection in the natural environment. If juvenile mortality is a stochastic determination of the environment, then a species that persists in the natural environment must have fecundity at-age high enough to compensate for juvenile mortality.

In this hypothetical context, a species would have population growth rates close to equilibrium ($\lambda \cong 1$) and the population would have an equilibrium age-class structure after some generations in the natural environment. A natural equilibrium perspective is helpful for simulations because there is inevitable uncertainty about true values of vital rates in contemporary, perturbed environments, and secondly, it provides a convenient frame of reference that can be developed for any species. With limited data it is possible to approximate aspects of life history sufficiently to define a natural equilibrium baseline for each example species. We simulate age truncation for age 1 and age 2 maturities because some fish species delay reproduction and attain larger body size and reproductive potential. We next describe how values for survival probabilities and fecundity were derived for the study species.

Adult Survival

We used a theoretical context to derive the adult survival probability. Prior meta-analysis (Kenchington, 2014) and application (Horswill et al., 2019) establish that natural mortality (M) in fishes is best approximated as $M = 4.3/T_{max}$, where T_{max} is the species' life span (years) in an unperturbed natural environment (see Table 1 and Appendix Fig S1). The adult survival probability necessary for this longevity is $S_1 = ... = S_5 = e^{-M}$. For exploited fish populations adult survival probability is commonly estimated as $S_1 = ... = S_5 = e^{-(E+M)}$, where natural mortality (M) is augmented by E, which represents mortality from environmental sources.

We begin simulations at an adult survival necessary for the assumed life span for each species. The estimated values of adult survival using the equation given by (Kenchington, 2014) for natural mortality are 0.34 and 0.42 for life spans of four and five years, respectively. In simulations we use adult survival values of 0.35 and 0.45 to represent life spans of ages 4+ and 5+, respectively. From this hypothetical baseline, we conducted simulations systematically at values of adult survival of 0.15, 0.25, 0.35 and 0.45, while holding S_0 at its equilibrium value. Note that adult survival values of 0.25 and 0.15 in our simulations are equivalent to age-truncated life histories of age 3+ and 2+, respectively. We calculate a value of *E*, environmental mortality, at each reduced level of adult survival. Notice that $e^{-(E+M)} = e^{-E}$ x e^{-M} where e^{-E} represents survivorship to environmental mortality and e^{-M} is survivorship to natural mortality.

Age 0 Survival (S_0)

We obtain an equilibrium estimate (Vaughn & Saila, 1976) of the survival probability of age 0 using species-specific values of fecundity at-age and the adult survival necessary for its approximate life span in an unperturbed natural environment. This equilibrium estimate of S_0 (Appendix Table S2), given a species' fecundity at-age and natural life span, yields a stable population at equilibrium with its environment ($\lambda_1 = 1$) as the frame of reference in simulations for each species.

For a comparison with equilibrium estimates of S_0, we used previously unpublished data for *H. amarus* from a laboratory experiment on larval survival using four replicate microcosms. Additional details are given in Appendix Table S3. The geometric mean daily survival probability was calculated for each microcosm and an annual estimate of age 0 survival probability was obtained using the geometric mean daily survival probability across replicates.

Age-specific Fecundity

We used Bayesian meta-analysis of 119 marine and freshwater fish species to estimate fecundity at-age for each species in the simulations. There is compelling evidence for a hyperallometric relationship between fecundity and body size in almost all fish species (Barneche et al., 2018). We downloaded supporting data (Barneche et al., 2018) for 342 marine species in 15 orders and to this dataset we added fecundity-body length data extracted from published literature for 33 species of freshwater fish (Order Cypriniformes, n = 1359), thus adding a 16th order to the dataset. A list of the cypriniform species is given in Appendix Table S4. Fecundity and length data were extracted from tables or digitized from published figures; thus, data from figures are an approximation of the original values. On a logarithmic scale we assume approximation errors are independent and small.

We inspected a scatterplot of the data (Appendix Fig S2) and elected to use a hierarchical modeling framework to assess the relationship between fecundity (Y) and length (X). Both variables were transformed using a logarithmic scale. In the analysis we excluded species with less than 10 observations, yielding data for 119 species (33 freshwater and 86 marine species) and a total of 7721 observations. We fitted a model with species-specific intercept and a common slope for all species (eq. 2) to predict fecundity:

$$\log(Y_{ij}) = \beta_{0(j)} + \beta_1 \log(X_{ij}) + \varepsilon_{ij}, \quad i = 1, 2, \ldots, 7721; \; j = 1, 2, \ldots, 119 \qquad (2)$$

$$\beta_{0(j)} \sim N(\beta_0, \sigma_b^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$$

where Y_{ij} and X_{ij} are the fecundity and length of the i^{th} individual of species j, respectively, $\beta_{0(j)}$ is the intercept for species j (i.e. species-specific intercept), β_0 and β_1 are the mean intercept and common slope, respectively, ε_{ij} is the residual, and σ_b^2 and σ_ε^2 are the variances for the random intercept and residuals, respectively.

We specified non-informative priors for all model parameters ($\beta_0 \sim Normal(0, 0.001)$, $\beta_1 \sim Normal(0, 0.001)$, $\sigma_b \sim Uniform(0,100), \sigma_\varepsilon \sim Uniform(0,100)$) and ran three independent MCMC chains of 5000 iterations with a burn-in of 2000 iterations to obtain posterior estimates of model parameters. We assessed convergence using the Brooks-Gelman-Rubin diagnostic statistic ($\hat{R}$; Brooks & Gelman, 1998) and by visually inspecting the trace plots. The trace plots for all parameters showed a good mixing and the $\hat{R}$ values for all parameters were below 1.1, indicating there was no lack of convergence. We implemented the Bayesian meta-analysis in JAGS (Plummer, 2003) using the 'jagsUI' (Kellner, 2016) package in R (R Core Team, 2017).

Results from the Bayesian meta-analysis was used to predict fecundity at mean length at-age for an "average fish" of age 1 or age 2 maturity using the mean intercept and common slope from Bayesian meta-analysis. For each example species we estimated fecundity using the species-specific intercept and common slope. For *E. motebensis*, *H. argyritis*, *I. lusitanisum* and *P. burchelli*, we obtained or inferred mean size at-age from published literature. For *H. amarus*, mean size at age was estimated from a large sample of *H. amarus* (N = 2423) collected in May 2009 (Hatch & Gonzales, 2009); data are provided in Dryad (https://doi.org/10.5061/dryad.69p8cz8z7). Individual age was estimated using a modelled age-length key (Ogle, 2016); additional details are given in Appendix Table S5.

Simulation Details

Our approach to study age-truncation involved retrospective analysis of simulated transient variation in vital rates and population structure using transient LTREs (Koons et al., 2016). For each simulation we generated random values of vital rates for 25 time steps (Koons et al., 2016) At each time step, survival probabilities were drawn from a beta distribution with expected value equal to the starting value in the transition matrix and shape parameters *a* and *b* chosen for a coefficient of variation (CV) of 0.2. The effect of different levels of CV were evaluated at CV = 0.05, 0.1, 0.2 and 0.3. Random deviates for fecundity were drawn from a lognormal distribution with expected value equal to the logarithm of predicted fecundity and standard deviation (estimated from Bayesian analysis) equal to the standard deviation of the species-specific intercept divided by the square root of the sample size, an approximate standard error for mean fecundity at-age. Notice that a random transition matrix is generated each simulation time step using the starting transition matrix as the expected values for vital rates.

The stochastic realisation of the transition matrix at each time step (t) was used to calculate the realised population growth rate ($\lambda_t = N_t/N_{t-1}$), where population structure (n_i) is normalized at time $t-1$ (Koons et al., 2016). The variance of realised population growth rate ($\sigma^2_{\lambda t}$) was decomposed into a proportional contribution for each parameter in the matrix population model using the example of Koons et al. (2016). The estimation of parameter contributions involved calculation of sensitivities to changes in vital rates and population structure, and temporal covariances among these parameters (Koons et al., 2016). Each simulation scenario was replicated 100 times and mean contributions were obtained for each vital rate and component of population structure. Transient LTRE results were summarized for each species by plotting the mean proportional contribution for each vital rate contributing at least 10% of $\sigma^2_{\lambda t}$ at each level of adult survival. All simulations were conducted in R (R Core Team, 2017) following the example of Koons et al. (2016).

Results

Values used in simulations for age at maturity and age-specific length (L_i) and fecundity (F_i) are shown in Table 2. Species simulated with age 1 maturity (age 4+ life span) had smaller adult body size and lower fecundity than did the species in simulations of age 2 maturity (age 5+). The F_i shown in Table 2 were calculated using the results from Bayesian meta-analysis of fecundity-body length (Appendix Table S6). The slope (3.447) and mean intercept over all species (-8.101) were used to compute fecundity at-age for a hypothetical "average fish" of age 1 or age 2 maturity, given an approximately scaled length at-age (Table 2). The Bayesian estimates of species-specific intercept (Appendix Table S6) were used to calculate fecundity for each example species (Table 2).

Equilibrium estimates of S_0 (Appendix Table S2) ranged from 4.562×10^{-4} to 4.911×10^{-3}. The equilibrium value of $S_0 = 7.008 \times 10^{-4}$ for *H. amarus* was two orders of magnitude smaller than survival estimated from the laboratory experiment where $S_0 = 3.046 \times 10^{-2}$ (Appendix Table S3).

In simulations varying the CV for survival, values of CV < 0.2 resulted in slightly greater importance of fecundity (Appendix Fig S3) to variation in population growth rate. However, in all transient LTREs for example species (Appendix Figs S4-S10) fecundity was consistently a minor contributor to population growth. An archive of all simulation scripts and results is available in Dryad (https://doi.org/10.5061/dryad.69p8cz8z7).

The results of transient LTREs at CV = 0.2 and adult survival values of 0.15, 0.25, 0.35 and 0.45 are summarised by example species and grouped by age 1 or age 2 maturities. Full LTRE results are shown in Appendix Figs S4-S10. For species with age 1 maturity (Fig 2), the primary drivers of variation in population growth rate are n_1, S_1 and S_2. With reduced adult survival the proportional contributions of n_1 and S_1 increased whilst that of S_2 decreased for all species. The reductions of adult survival to 0.25 and 0.15 represented increases in environmental mortality (E) that augment natural mortality (M); respective calculated values of E were 0.3365 and 0.8473 with respective survivorship to environmental mortality (e^{-E}) of 0.71 and 0.43. For all example species with age 2 maturity, the main drivers of variation in population growth rate were n_2, S_2, and S_3 (Fig 3) and reduced adult survival similarly increased the proportional contributions to population growth rate from the number and survival of the first reproductive age class. However, the effect of reduced adult survival was greater with delayed maturity (compare Figs 2 and 3). The calculated values of E for age 2 maturity at adult survival values of 0.35, 0.25 and 0.15 were 0.2513, 0.5878 and 1.0986, respectively, with survivorship to E of 0.78, 0.56 and 0.33, respectively.

Discussion

Our simulations of a hypothetical "average fish" suggest that iteroparous fishes may share a common risk of endangerment from age truncation in human-altered environments. Across species there appears to be similarity in how drivers of fish population growth respond to age truncation. All the short-lived freshwater species and the hypothetical representations of "average fish" in our simulations responded to age truncation as documented elsewhere for longer-lived and exploited species (Ottersen et al., 2006; Hilborn & Walters, 1992). As adult survival decreased, the number of individuals and survival of the first reproductive age class became progressively more important in determining variation in population growth. The results indicated that population growth rate is driven by a combination of adult survival probability and population structure, especially the number and survival probability of the first reproductive age class. Mean fecundity at-age is not an important contributor to variance of population growth and results are consistent across species in our simulations. These findings agree with observations on 83 fish species of the Yangtze River (Wang et al., 2017), where juvenile and adult survival were more important than reproductive output. The importance of fecundity for short-lived freshwater fishes has been further questioned recently (Hitt et al., 2020). Simulation results suggest that irrespective of their fecundity, short-lived fish species are susceptible to age truncation.

Have the freshwater species in our simulations undergone age truncation? All five example species range in status (IUCN) from near threatened to critically endangered and they share threats from water extractions and exotic predatory species (Table 1). For *H. amarus*, Horwitz et al. (2018) suggest contemporary adult survival probability from different samples is about 0.1, which is consistent with strong age truncation reducing effective life span from age 4+ to about age 2. Erratic temporal abundance of the species (U.S. Fish and Wildlife Service, 2016) is also consistent with age truncation driving erratic variation in population size (Stenseth & Rouyer, 2008). Although we lack sufficient detailed information for the other example species, we suggest it may be possible to detect age truncation in a large sample.

Caveats and Alternate Models

With their high biodiversity globally, the rich evolutionary elaboration of fish life histories precludes any single model from accurately representing all species. Details of life history are important for a matrix population model to accurately represent a species' population growth under specific environmental conditions. We focused narrowly on a systematic exploration of the process of age truncation and comparing simulations within and between species. Our population model mimics an iteroparous life history with reproduction in multiple years after reaching maturity, which is typical for a majority, but not all, freshwater and marine fishes.

There are many possible variations and extensions of our model. For example, fishes with a semelparous life history such as off-shore spawning capelin (*Mallotus villosus*) cannot retain older repeat spawners as represented in our transition matrix, whereas nearshore spawning iteroparous individuals can (Christiansen et al., 2008). As a second example, the effects of reduced adult survival on short-lived marine fish species under commercial exploitation, such as Peruvian anchoveta (*Engraulis ringens*), will require model refinements to simulate its life history. This migratory, pelagic species can spawn throughout the year but exhibits two spawning peaks annually and age classes can be comprised of 2 cohorts a year of different sizes and ages (http://www.fao.org/fishery/species/2917/en, accessed 20 February 2020).

Additional model refinements ought to be examined for individual species in a particular environment. For example, only a fraction of individuals may be reproductively mature at younger adult ages in some species (Bronte et al., 1991; Diana, 1983; Lorenzoni et al., 2011). A maturation parameter for the first or several adult age classes could be included in the transition matrix, or, a model of density dependence could be informative with larger body size freshwater fishes. We predict that with partial maturation at age 1, reduced adult survival would yield a population response intermediate to our simulations of age 1 and age 2 maturities. Although we simulate a model of density independence, additional work is needed to clarify how density dependence might affect a population's response to age truncation.

Environmental perturbations such as river intermittency associated with water extractions or drought, as occurs with four of the five simulated example species, can be included in the population model as a stochastic environmental source of reduced survival. Simulations of alternate models of transient mortality caused by river drying, for example, could be compared to discern the relative importance of juvenile versus adult mortality associated with river intermittency.

Detecting Age Truncation

We began modelling work with *H. amarus*, a local species in the Rio Grande Basin. Initially, we attempted to estimate age-specific adult survival rates (results not shown) with a large sample dataset (Dryad https://doi.org/10.5061/dryad.69p8cz8z7) but not all were estimable and temporal variation in survival was indicated. This further implied a likely non-equilibrium population structure and conveyed uncertainty about values of survival rates in the contemporary environment. The important question for us became "how might one develop a frame of reference to evaluate contemporary disturbances to a species?" This led to the development of a hypothetical equilibrium baseline for a species in an unperturbed natural environment.

How might a manager detect age truncation in a population? Although manifestation of age truncation may be noticeable through increased fluctuations in population size over time (Stenseth & Rouyer, 2008), it may be difficult to identify if age truncation is the cause when we only have data on fluctuations in population size. We suggest that a simple binomial proportion (eq. 3) can be calculated on a sufficiently large, unbiased sample and compared with an equilibrium expectation to test for age truncation:

$$\theta_A = \left(\sum_{i=2}^{k} n_i\right) / \left(\sum_{i=1}^{k} n_i\right) \tag{3}$$

where θ_A represents the fraction of adults older than the first reproductive age divided by the total number of adults across all *k* ages. The binomial proportion θ_A is the converse of Heinke's method (Miranda et al., 2007). At the natural equilibrium adult survival rate, and at stable population structure, $\theta_A = 0.349$ for an age 4+ lifespan, and $\theta_A = 0.427$ for an age 5+ lifespan. The sample data for *H. amarus* (Dryad https://doi.org/10.5061/dryad.69p8cz8z7) yields an estimate of $\theta_A = 0.258$ (95% confidence limit: $0.24 \leq \theta_A \leq 0.28$), which can be calculated from (Appendix Table S5). In R, the probability of the observed sample given the expected equilibrium value of θ_A [*pbinom*(573,2215,0.349)] is 4.1×10^{-20}, evidence of significant age truncation. We caution that analysis of a single sample should not be construed as proof of age truncation, but rather that the proposed metric θ_A should be examined in additional sufficiently large samples over time and space because, for example, an event of strong recruitment to the first reproductive age class will also result in a lower value of θ_A. Likewise, if strong recruitment events are associated with augmentation of the population from captive production or translocation (George et al., 2009; Day et al., 2017), then inference of significant age truncation could be incorrect. Clearly it is important to consider the life span of a species and the contemporary historical (temporal) context for a sample to use θ_A as a test of age truncation. For our example species, a simple application of θ_A could be to use mean size at age of the second reproductive age class to assign individuals in a sample to first or later adult age classes.

Identifying Causes of Age Truncation

Although one can test for age truncation, identifying the causes of adult mortality in contemporary environments may be difficult. There are many possible causes of reduced adult survival in fish populations, which may vary across species or across populations of the same species in different environments. As opposed to fishing being a primary cause of age truncation in the marine environment, there are multiple possible contributors to increased adult mortality of freshwater fishes. Direct exploitation of wild populations can drive age truncation for many short-lived freshwater fish species in the ornamental fish trade (Rahel, 2002). However, for many fish species, especially those in rivers, causes of reduced adult survival may be indirect, arising from multiple factors and hence more difficult to quantify.

The wide-spread introduction of exotic predatory fish species for sport fishing has led to homogenization of freshwater fish communities over large spatial extents (Rahel, 2002). In four of the simulated examples, seasonal low river flows are thought to facilitate increased predation mortality by introduced exotic fishes (Cambray & Stuart, 1985; Cowley et al., 2006; Kimberg et al., 2014; Magalhaes et al., 2003). Additionally, over-utilization of freshwater resources and river flow regulation for hydropower or irrigation are important global drivers of population declines in freshwater fish populations (Kominoski et al., 2017; Worthington et al., 2018). For example, water diversions for irrigation can cause seasonal occurrences of river intermittence that dries habitat and kills fish (Cowley, 2006).

As a second example, a primary emphasis of conservation for *H. amarus* has sought to manage water resources to encourage spawning (U.S. Fish and Wildlife Service, 2003, 2016) and thereafter habitats can be depleted or dried through irrigation withdrawals. The emphasis on successful spawning involves early season water releases from upstream reservoirs, an irreversible commitment of water resources during drought. This management choice can reduce the water available to promote survival after spawning and it can maintain or increase age truncation if it reduces later supply of water to support survival. Our results point directly to the importance of adult survival, not fecundity, for population growth of short-lived, iteroparous species like *H. amarus*. This implies that during water shortage, reduced water investment for spawning may be necessary to achieve increased adult survival.

Other human activities may reduce adult survival with indirect and subtle effects because freshwater ecosystems are imbedded in discrete watersheds of the terrestrial landscape. Each watershed is a spatial mosaic of influences from geology, climate and landform coupled with human-mediated ecosystem perturbations through uses of terrestrial and aquatic resources.

Landscape impacts to river networks can be cumulative because of the directional topology of rivers. These effects can be subtle but important determinants of species' distribution and abundance. For example, the spatial extent of agricultural and urban areas in a watershed can be important influences on freshwater invertebrates and fish when analysed with a spatial stream network model (Lois & Cowley, 2017). Spatial stream network models (Peterson et al., 2013) offer an important analytic advancement that may facilitate identifying drivers of age truncation in contemporary freshwater environments. One approach, of perhaps several, would be to use θ_A as a response variable in a spatial stream network model, where θ_A has been estimated at many times and places.

Implications for Biodiversity Conservation

Reductions in adult survival are important potential concerns for thousands of fish species that share a common age-structured life history of iteroparity and an indeterminate lifespan dependent on adult survival. Extinction risk increases under age truncation because a population becomes more dependent on the first reproductive age class. As a result, population growth becomes highly sensitive to very small random fluctuations in juvenile survival (Stenseth & Rouyer, 2008). For example, an age-truncated population is vulnerable to rapid declines in population size with successive years of lower juvenile survival such as might occur with drought. Managing habitats for increased adult survival would buffer temporal variation in juvenile survival (Rouyer et al., 2011) and generally improve reproductive resilience of fish populations. Captive breeding or translocation (George et al., 2009; Day et al., 2017) could be used to accomplish short-term increases in population size; however, the activity contributes nothing to alleviating the ecosystem level causes of age truncation.

To achieve sustainable fisheries one must consider the sensitivity of fish populations to environmental changes that reduce adult survival. Successful conservation programs for freshwater biota may depend on accommodating local prevailing cultural and social values (Peterson et al., 2013), which can present significant impediments to ecosystem restoration and biodiversity conservation (Cowley, 2006). A proposed emergency recovery plan (Bennett et al., 2017) identified six global action priorities to stem the loss of freshwater biodiversity. All of these global action priorities (Bennett et al., 2017) are consistent with strategies to alleviate adult mortality in human-altered environments.

Water management is a global concern with freshwater fishes whose riverine habitats are fragmented by dams that regulate flows, diminished in quality by introduction of exotic species and depleted by water extractions for human use (Kominoski et al., 2017; Worthington et al., 2018). As an example, a primary emphasis of conservation for *H. amarus* has sought to manage water resources to encourage spawning (U.S. Fish and Wildlife Service, 2016; Tickner et al., 2020) and thereafter habitats can be depleted or dried through irrigation withdrawals. The emphasis on successful spawning involves early season water releases from upstream reservoirs, an irreversible commitment of water resources during drought. This management choice can reduce the water available to promote survival after spawning and it can maintain or increase age truncation if it reduces later supply of water to support survival. Our results point directly to the importance of adult survival, not fecundity, for population growth of short-lived, iteroparous species like *H. amarus*. This implies that during water shortage, a reduced water investment for spawning may be necessary to achieve increased adult survival.

Conclusions

Managers may fail to recognize the importance of adult survival for short-lived freshwater fish species when contemporary environmental conditions reduce a species' lifespan. Although managing reproduction is a likely short-term necessity, a strong focus on water management to support reproduction may further reduce adult survival. Achieving sustainable freshwater fish populations seems unlikely to be achieved with a focus on supporting reproduction because this activity does not address the ecosystem problems caused by human uses of water and watersheds. Sustainability management requires a holistic view of impacts to freshwater ecosystems caused by humans at local to watershed spatial extents and its aim should be managing human uses of land and water in ways that enable restoration of watershed-scale ecological systems (Cowley, 2006). Achieving higher species survival will require paradigm transformations at societal and governmental levels regarding water management priorities and legal accommodations that provide environmental flows of water needed to sustain aquatic ecosystems and their biota (Bennett et al., 2017). Alleviating human impacts to freshwaters is urgently needed for conservation of freshwater biodiversity.

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Tables

Table 1 (Chapter 1). A synopsis of study species and data sources.

Species[a]	**Loc**[b]	**Mat**[c]	**Age**[d]	**Threats**	**Status**[e]	**Refs**
Enteromius motebensis	SA	1	4+	Pollution, water extractions, exotic predatory fishes	NT	[Kimberg et al., 2014; Kindler, 2015]
Hybognathus amarus	USA	1	4+	Dams, water extractions, exotic predatory fishes, intermittency	E	[Cowley et al., 2006, 2007; Caldwell et al., 2019]
Hybognathus argyritis	CA	2	5+	Water extractions, climate change	NT	[COSEWIC, 2008; Young & Koops, 2013]
Iberochondrostoma lusitanicum	PT	2	5+	Exotic predatory fishes, intermittency	CE	[Magalhaes et al., 2003]
Pseudobarbus burchelli	SA	2	5+	Exotic predatory fishes	CE	[Cambray & Stuart, 1985]

[a] Species common names given in text

[b] Country locations (Loc) are shown in Fig 1: South Africa (SA), United States of America (USA), Canada (CA), Portugal (PT)

[c] Age (yr) at sexual maturity (Mat)

[d] Approximate life span (yr) assumed in simulations

[e] IUCN categories: near threatened (NT), endangered (E), critically endangered (CE)

Table 2 (Chapter 1). Age of maturity and values of length and fecundity used in simulations of age truncation.

		Length (mm) at Age					**Fecundity (eggs) at Age**[a]				
Species	**M**[b]	**L_1**	**L_2**	**L_3**	**L_4**	**L_5**	**F_1**	**F_2**	**F_3**	**F_4**	**F_5**
"ave. fish"[c]	1	50	65	75	80	85	218	538	881	1101	1357
"ave. fish"[c]	2	45	75	90	108	120	0	881	1652	3097	4454
E. motebensis	1	50	65	75	80	85	683	1688	2764	3451	4255
H. amarus[d]	1	51	61	69	74	82	1830	3392	5187	6602	9405
H. argyritis	2	50	81	105	118	130	0	3273	8008	11975	16721
I. lusitanicum	2	45	75	95	115	125	0	1505	3399	6567	8753
P. burchelli	2	45	75	85	100	115	0	1125	1732	3032	4909

[a] Age-specific fecundity was calculated using the overall slope (3.447) and species-specific intercept (Appendix Table S6) from Bayesian meta-analysis.

[b] M denotes age of maturity used in simulation.

[c] Fecundity for "average fish" was calculated using the overall slope (3.447) and mean intercept (-8.101).

[d] Fecundity data were from captive fish, which may or may not be accurate for wild fish.

Figures

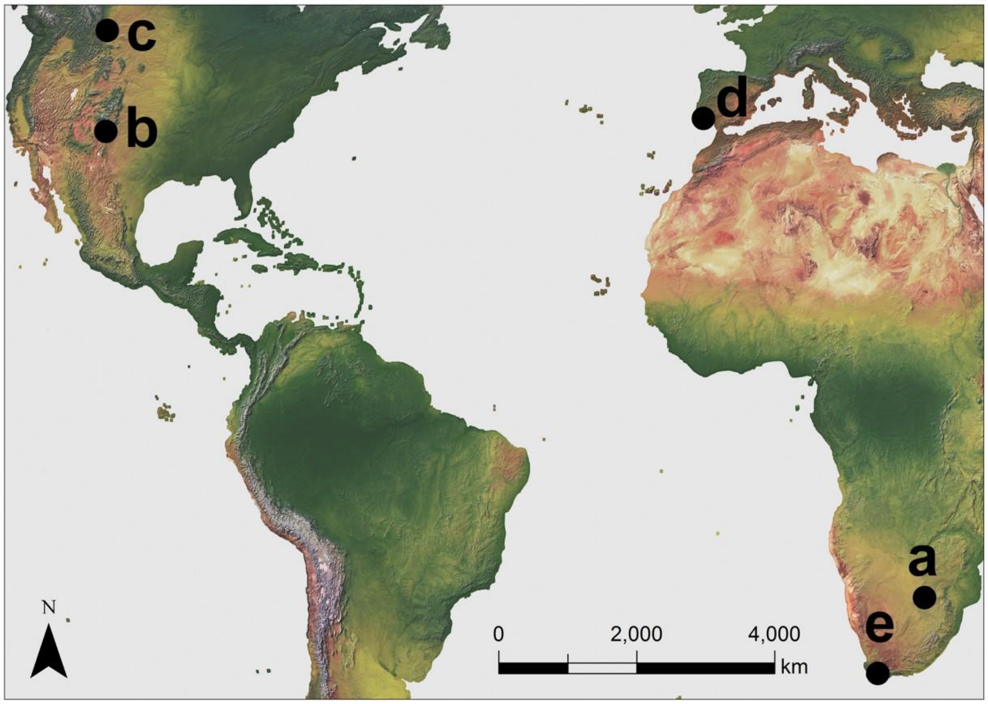

Figure 1 (Chapter 1). Locations of example species used in simulations of age truncation.

Locations of example species used in simulations of age truncation (a) *Enteromius motebensis*, Marico River, South Africa; (b) *Hybognathus amarus*, Rio Grande, New Mexico, USA; (c) *Hybognathus argyritis*, Milk River, Alberta, Canada; (d) *Iberochondrostoma lusitanicum*, Torgal Rivulet, Portugal; (e) *Pseudobarbus burchelli*, Breede River, South Africa; Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

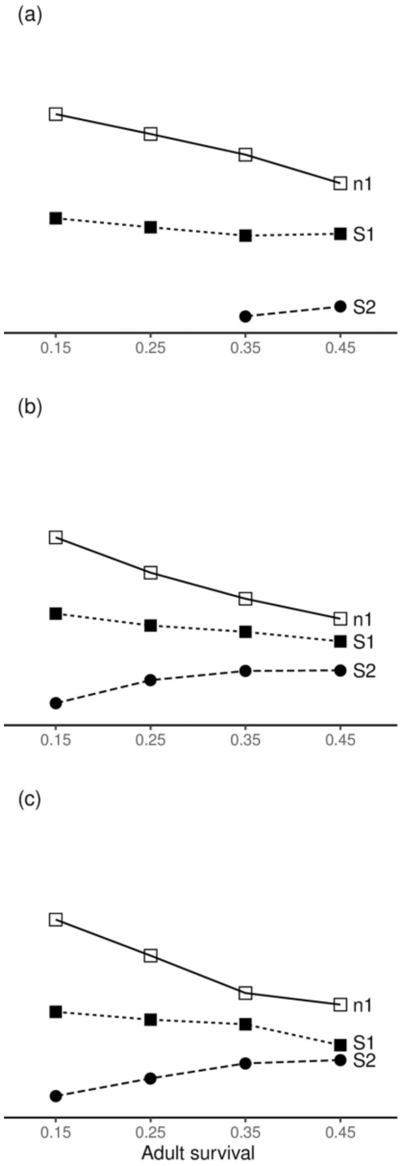

Figure 2 (Chapter 1). Simulations of age truncation for species with age 1 maturity. Simulations of age truncation for species with age 1 maturity: (a) *H. amarus*, (b) a hypothetical species "average fish", (c) *E. motebensis*; proportional contributions exceeding 0.1 of $\sigma^2_{\lambda t}$ are shown: *n*1 is number of age 1 fish, *S*1 and *S*2 are survival probabilities for ages 1 and 2, respectively. A bar plot showing the contribution from each model parameter for each transient LTRE is provided in (Appendix S4–S6 Figs) for each species.

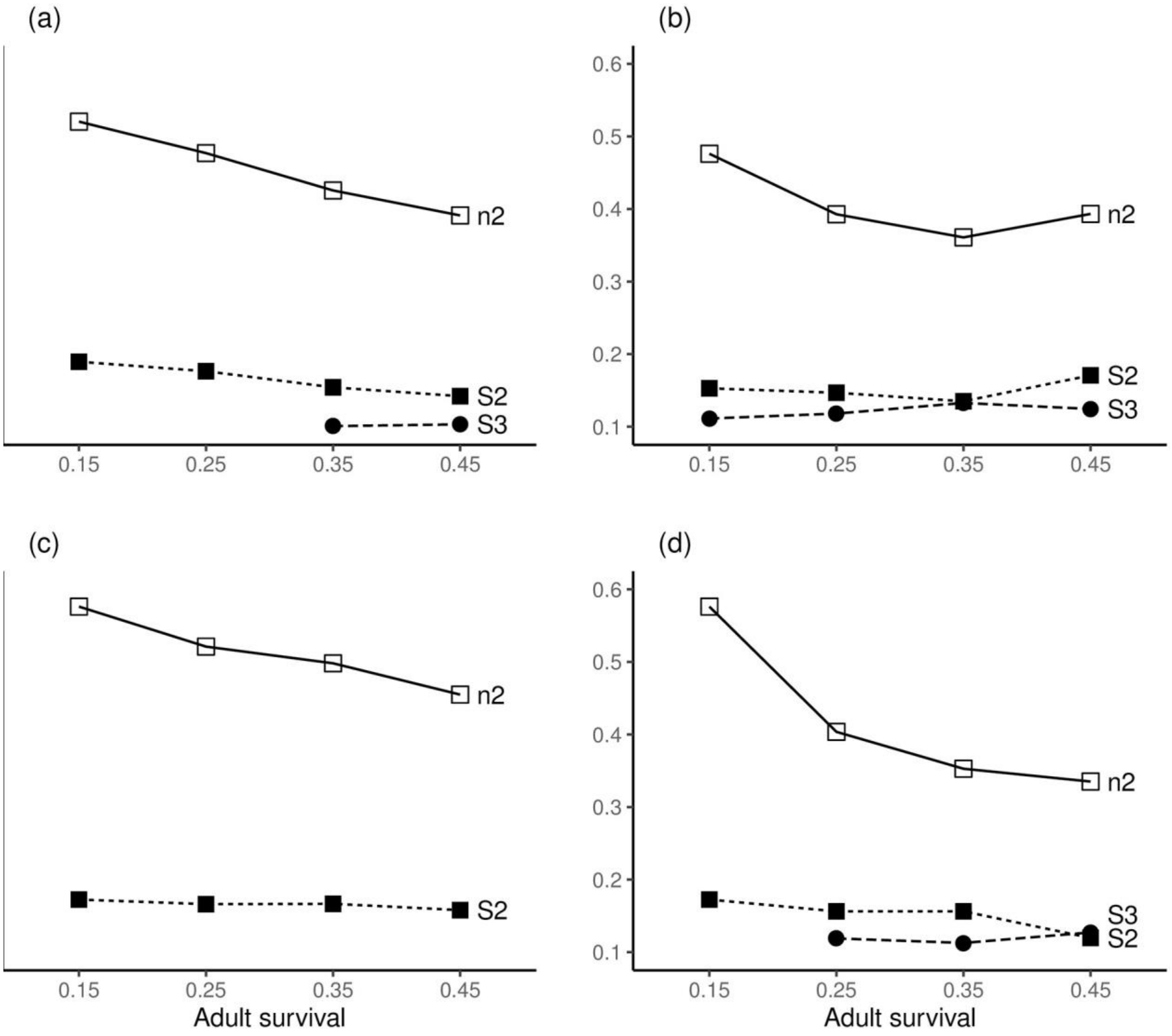

Figure 3 (Chapter 1). Simulations of age truncation for species with age 2 maturity.

(a) a hypothetical species "average fish", (b) *H. argyritis*, (c) *P. burchelli*, (d) *I. lusitanicum*; proportional contributions exceeding 0.1 of $\sigma^2_{\lambda t}$ are shown: n2 is number of age 2 fish, S2, and S3 are survival probabilities for ages 2 and 3, respectively. A bar plot showing the contribution from each model parameter for each transient LTRE is provided in (Appendix S7–S10 Figs) for each species.

Chapter 1 Appendix

SUSTAINABILITY MANAGEMENT OF SHORT-LIVED FRESHWATER FISH IN HUMAN-ALTERED ECOSYSTEMS SHOULD FOCUS ON ADULT SURVIVAL

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S1 Fig. The general relationships in fishes between life span and (a) M = 4.3/maximum age and (b) $S = e^{-M}$.

S2 Fig. Fish fecundity (eggs) and body length data for 33 freshwater species (order Cypriniformes, black symbols, data in Appendix S2 Fig) and 342 marine species from 15 orders (gray symbols, data source [30] in main text).

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S6 Fig. Transient LTREs for *Hybognathus amarus*, age 1 maturity. (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

S7 Fig. Transient LTREs for "average fish", age 2 maturity. (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

S8 Fig. Transient LTREs for *Hybognathus argyritis*, age 2 maturity. (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

S9 Fig. Transient LTREs for *Iberochondrostoma lusitanicum*, age 2 maturity. (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

S10 Fig. Transient LTREs for *Pseudobarbus burchelli*, age 2 maturity. (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

CHAPTER 1 - SUPPORTING TABLES

Table S1. Terms, symbols and definitions

age truncation	mortality of adults in a population that reduces mean age of breeders and diminishes future reproductive potential, also known as juvenescence or longevity overfishing
asymptotic	the theoretical demographic conditions attained when vital rates and the environment are stationary
E	environment-caused mortality that augments natural mortality
F_i	age-specific fecundity, number of eggs
iteroparity	an adult reproducing in multiple years
λ_1	the leading eigenvalue of the transition matrix, the asymptotic population growth rate under stationary conditions
λ_t	the observed (realised) population growth rate at each time-step in a simulation ($\lambda_t = N_t/N_{t-1}$)
$\sigma^2_{\lambda t}$	variance of realised population growth rate
life span	an approximate number of years; it is indeterminate in many fishes because life span depends on adult survival probability
LTRE, LTREs	life table response experiment(s) in which vital rates are varied stochastically in simulations and the relative contributions to population growth rate are deduced
M	natural mortality
n_i	age-specific abundance in a population vector, or the relative abundance when population size is normalized ($\sum n_i = 1$)
normalised	in calculating realised population growth rate, N_{t-1} is normalised ($\sum n_i = 1$)
population structure	the relative fraction of the population in each age class
predicted fecundity	age-specific fecundity predicted from posterior estimates of a species' intercept and the overall slope in Bayesian meta-analysis of fecundity-body length data
retrospective	simulation of a life history and using stochastic values observed to deduce drivers of population growth
S_i	age-specific survival probability of reaching the next age class
S_E	survival rate to environmental mortality, a multiplier of natural mortality
stable age distribution	an asymptotic stable condition in population age structure that will be attained when vital rates and the environment are stationary
stationary	no change in variation over time
transient LTRE	a transient life table response experiment in which the variance of λ_t is decomposed into fractions attributable to each parameter in the matrix population model; a retrospective analysis of simulated vital rate variation
transient variation	random variation in vital rates caused by fluctuations in the environment
vital rates	age-specific survival rates and age-specific fecundities

Table S2 Asymptotic estimates of S_0.

Fecundity Schedule	**Maturity**	**S_0**	**a**	**b**
"average fish"	1	4.911E-3	24.8726	5051.1682163265
Enteromius motebensis	1	1.566E-3	24.59284	1545.8311702171
Hybognathus amarus	1	7.008E-4	24.981779	35622.534202535
"average fish"	2	1.858E-3	24.951692	13404.376618010
Hybognathus argyritis	2	4.562E-4	24.988144	54773.573259508
Iberochondrostoma lusitanicum	2	9.567E-4	24.975118	26072.326867271
Pseudobarbus burchelli	2	1.665E-3	24.95671	14964.058305015

Estimate obtained using the adult survival probability necessary for an age 4+ (maturity age 1) or 5+ (maturity age 2) lifespan; "a" and "b" denote shape parameters for a beta distribution from which stochastic values were drawn in simulations.

Table S3 Age 0 survival of *H. amarus* in laboratory microcosms.

Microcosm	**Survival Probability Mean Daily**[†]	**S_0**
A	0.9797	5.610E-4
B	0.9942	1.197E-1
C	0.9945	1.336E-1
D	0.9936	9.599E-2
Geometric Mean		
A, B, C, D	0.9905	3.046E-2

[†] value shown is the geometric mean of n=57 values of daily survival rate for each microcosm

The number of live *H. amarus* was counted daily in each of four microcosms (38 L, filled with 30 L water). Aerated well water maintained at 20˚C, a salinity of 0.4 ppt and propagation in an environmental chamber with a 12h light:12h dark photoperiod approximated ambient river conditions. Juvenile *H. amarus* were fed nauplii of brine shrimp (*Artemia salina*). To initiate replicates, fertilized eggs were obtained from eight captive parental pairs that were injected with carp pituitary extract to induce spawning. Eggs were transported to an environmental chamber on day 1 and 700 randomly selected eggs were added to each microcosm. Egg hatching occurred two to three days after fertilization; our estimate of daily survival in each microcosm began with the number of larvae counted on day 4. Daily counts of survival up to day 58 post-hatch were used to calculate daily survival for each microcosm. Data are available in Dryad (https://doi.org/10.5061/dryad.69p8cz8z7).

Table S4 List of cyprinid species included in Bayesian analysis of fecundity-length.

Species	n	Reference
Alburnoides bipunctatus	13	Polacik, M, Kovác,V. Folia Zool. 2006;55:399-410
Alburnoides bipunctatus	39	Patimar, R et al. Turk J Zool. 2012; 36:383-393
Alburnoides sp.	22	Seifali, M et al. Iran J Sci Technol. 2012;A2:181-187
Alburnus chalcoides	188	Patimar, R et al. Turk J Fish Aquat Sci. 2011;10: 277-285
Barbus strumicae	19	Sapounidis, A et al. NW J Zool. 2015;11:331-341
Enteromius humilis	19	Dejen, E et al. Neth J Zool. 2003;52:281-299
Enteromius motebensis[a]	26	Kindler, D. MSc Thesis, U Johannesburg. 2015
Enteromius tanapelagius	20	Dejen, E et al. Neth J Zool. 2003;52:281-299
Pethia pookodensis	37	Jacob, E. PhD Thesis, Mahatma Ghandi U. 2013
Pethia ticto	59	Hossain, M et al. J Appl Ichthyol. 2017; doi:10.1111/jai.13427
Pseudobarbus burchelli	17	Cambray, J, Stuart, C. S Afr J Zool. 1985;20:155-165
Puntius sophore	74	Hossain, M et al. J. Appl Ichthyol. 2012;28:818-822
Schizothorax plagiostomus	30	Jan, M et al. J Threat Taxa. 2014;6:5375-5379
Sahyadria denisonii	11	Solomon, S et al. J Threat Taxa. 2011;3:2071-2077
Capoeta trutta	140	Patimar, R, Farzi. S. Folia Zool. 2011;60:153-158
Carassius auratus	20	Amin, R et al. J Agric Vet Sci. 2013;3:36-41
Carassius gibelio	113	Tarkan, A et al. J Freshw Ecol. 2007;22:11-17
Labeo horie	66	Dadebo, E et al. Afr J Ecol. 2003;41:31-38
Chondrostoma regium	65	Mahboobi Soofiani, N et al. Iran J Fish Sci. 2014;13:810-822
Chrosomus tennesseensis	19	Hamed, M et al. Am Midl Nat. 2008;160:289-299
Dionda argentosa	23	McMillan, S MSc Thesis, Tx St U-San Marcos. 2011
Dionda diaboli	35	McMillan, S MSc Thesis, Tx St U-San Marcos. 2011
Hybognathus placitus	28	Taylor, C. MSc Thesis, Oklahoma State U. 1988
Hybognathus argyritis	11	Young, J, Koops, M. Can Sci Advis Secretariat, Doc. 2013/084, Ottawa: 2013
Hybognathus amarus	20	Caldwell, C et al. N Am J Aquac. 2019;81:47-54
Iberochondrostoma lusitanicum	22	Magalhaes, M et al. J Fish Biol. 2003;63:300-317
Notropis rafinesquei	50	Haag, W et al. Am Midl Nat. 2007;158:306-320
Notropis simus pecosensis	13	Hatch (unpubl. data, Dryad (https://doi.org/10.5061/dryad.69p8cz8z7)
Phoxinus phoxinus	19	Mills, C, Elorant, Ann Zool Fenn. 1985;22:1-12
Rhinichthys cataractae	18	Roberts, J, Grossman, G. Ecol Freshw Fish. 2001;10:184-190
Rhinichthys cobitis	14	Britt, K MSc Thesis, New Mexico State U. 1982
Rutilus kutum	48	Keivany, Y et al. Res Zool. 2012;2:7-14
Squalius squalus	25	Lorenzoni, M et al. Knowl Manag Aquat Ecosyst 2011;403:09,doi:10.1051/kmae/2011069
Squalius torgalensis	27	Magalhaes, M et al. J Fish Biol. 2003;63:300-317

Table S5 Mean size at age for *H. amarus* collected from the Isleta Reach of the middle Rio Grande of New Mexico in 2009.

Age	n	SL[a]	StdDev	StdErr
0	222	43.9	2.639	0.177
1	1642	51.3	3.405	0.084
2	173	61.3	2.492	0.189
3	241	68.8	2.530	0.163
4	148	73.7	2.735	0.225
5	11	81.2	1.888	0.569

[a] mean standard length (mm)

To develop an age-length key for *H. amarus* we used an aged sample comprised of 12 observations of standard length (SL) and age estimated from scale annuli from specimens collected in 1874 [1], augmented by two additional observations from the 2009 sample data. For age 0, we included a SL of 37 mm, which was in the left tail of the frequency distribution of the 2009 sample. For age 1, we included a SL of 52 mm, which was the highest and first peak in the frequency distribution of the 2009 sample data. We fitted a multinomial logistic regression model [2] on 5 mm length intervals of the aged sample using 'nnet' [3] in R [4]. We estimated age [5] for each fish in the sample using the modelled age-length key and the 'alkIndivAge' function in package 'FSA' in R [6](Ogle, 2016). The total fish assigned to each age class was obtained and used to calculate mean length at age. Mean size-at-age values were used to calculate age-specific fecundity values for simulations of age truncation; values are given in Table 2 of the main text. Notice that with this large sample it is not possible to calculate a valid estimate of all age-specific survival probabilities (n_{i+1}/n_i).

CHAPTER 1, Table S5 – SUPPORTING REFERENCES

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[6] Ogle, D.H. Introductory Fisheries Analyses with R. CRC Press, UK. 2016.

Table S6. Results of Bayesian analysis of fecundity-body length.

Species	**Estimate**	**SD**	**2.5%**	**97.5%**	**System**	**Rank**
- "average fish" -						
overall slope	3.447	0.030	3.388	3.506		
mean intercept	-8.101	0.202	-8.495	-7.711		
- species-specific intercepts -						
Acanthochromis polyacanthus	-10.758	0.182	-11.12	-10.401	Mar.	117
Alburnoides bipunctatus	-7.547	0.141	-7.819	-7.271	Fre.	37
Alburnoides sp.	-8.152	0.162	-8.47	-7.834	Fre.	65
Alburnus chalcoides	-9.221	0.16	-9.53	-8.907	Fre.	97
Amblygaster sirm	-7.527	0.176	-7.87	-7.176	Mar.	34
Aphanopus carbo	-11.66	0.243	-12.134	-11.191	Mar.	118
Archosargus rhomboidalis	-6.365	0.175	-6.705	-6.022	Mar.	9
Atherina presbyter	-7.581	0.156	-7.89	-7.274	Mar.	40
Balistes capriscus	-6.621	0.177	-6.962	-6.273	Mar.	14
Barbus strumicae	-9.774	0.188	-10.138	-9.409	Fre.	108
Canthigaster valentini	-6.689	0.13	-6.942	-6.433	Mar.	15
Capoeta trutta	-9.691	0.166	-10.011	-9.364	Fre.	106
Carassius auratus	-6.76	0.175	-7.104	-6.419	Fre.	18
Carassius gibelio	-9.098	0.169	-9.426	-8.766	Fre.	95
Caulolatilus microps	-8.218	0.202	-8.606	-7.825	Mar.	68
Centropomus undecimalis	-8.296	0.231	-8.752	-7.843	Mar.	71
Cephalopholis cruentata	-6.575	0.204	-6.974	-6.174	Mar.	12
Chondrostoma regium	-9.052	0.156	-9.353	-8.743	Fre.	94
Chrosomus tennesseensis	-7.006	0.15	-7.297	-6.712	Fre.	23
Cynoscion regalis	-8.579	0.208	-8.985	-8.165	Mar.	83
Dionda argentosa	-9.447	0.154	-9.75	-9.146	Fre.	101
Dionda diaboli	-8.935	0.139	-9.205	-8.662	Fre.	93
Elagatis bipinnulata	-8.39	0.212	-8.804	-7.976	Mar.	72
Engraulis anchoita	-7.809	0.154	-8.111	-7.509	Mar.	52
Engraulis mordax	-7.015	0.169	-7.348	-6.683	Mar.	24
Engraulis ringens	-7.746	0.156	-8.048	-7.438	Mar.	48
Enteromius humilis	-7.426	0.16	-7.737	-7.109	Fre.	29
**Enteromius motebensis*	-6.958	0.15	-7.252	-6.663	Fre.	21
Enteromius tanapelagius	-8.071	0.158	-8.371	-7.762	Fre.	64
Epinephelus aeneus	-7.765	0.209	-8.18	-7.354	Mar.	51
Ethmalosa fimbriata	-8.804	0.183	-9.165	-8.441	Mar.	89
Gadus morhua	-8.559	0.204	-8.957	-8.156	Mar.	82
Gasterosteus aculeatus	-8.513	0.126	-8.756	-8.264	Mar.	78
Genyonemus lineatus	-9.242	0.172	-9.573	-8.9	Mar.	98
Hippoglossoides platessoides	-7.262	0.166	-7.581	-6.937	Mar.	27
Hoplostethus atlanticus	-9.883	0.181	-10.234	-9.526	Mar.	111
**Hybognathus amarus*	-6.041	0.159	-6.353	-5.729	Fre.	5
Hybognathus placitus	-7.489	0.148	-7.779	-7.2	Fre.	32
**Hybognthus argyritis*	-7.054	0.189	-7.423	-6.685	Fre.	25

Species	**Estimate**	**SD**	**2.5%**	**97.5%**	**System**	**Rank**
**Iberochondrostoma lusitanicum*	-7.556	0.161	-7.87	-7.243	Fre.	38
Labeo horie	-9.419	0.202	-9.816	-9.027	Fre.	99
Larimus fasciatus	-5.229	0.154	-5.526	-4.925	Mar.	2
Lates calcarifer	-7.615	0.223	-8.047	-7.18	Mar.	43
Lutjanus carponotatus	-7.456	0.173	-7.795	-7.117	Mar.	30
Mallotus villosus	-7.862	0.167	-8.184	-7.538	Mar.	58
Merlangius merlangus	-6.838	0.177	-7.182	-6.493	Mar.	20
Merluccius hubbsi	-8.601	0.192	-8.974	-8.226	Mar.	84
Merluccius merluccius	-9.834	0.193	-10.209	-9.455	Mar.	109
Micropogonias furnieri	-8.861	0.202	-9.251	-8.471	Mar.	92
Mugil cephalus	-6.277	0.175	-6.615	-5.934	Mar.	8
Notropis rafinesquei	-7.474	0.122	-7.711	-7.238	Fre.	31
Notropis simus pecosensis	-6.965	0.17	-7.3	-6.635	Fre.	22
Odontesthes argentinensis	-9.926	0.187	-10.286	-9.554	Mar.	112
Oxylebius pictus	-7.598	0.176	-7.941	-7.257	Mar.	42
Paralichthys dentatus	-7.414	0.192	-7.782	-7.038	Mar.	28
Paralichthys patagonicus	-10.066	0.206	-10.464	-9.657	Mar.	114
Paralonchurus brasiliensis	-7.949	0.193	-8.329	-7.571	Mar.	61
Pethia pookodensis	-6.725	0.135	-6.986	-6.456	Fre.	17
Pethia ticto	-5.708	0.135	-5.97	-5.442	Fre.	4
Phoxinus phoxinus	-8.832	0.156	-9.139	-8.529	Fre.	90
Planiliza subviridis	-5.253	0.187	-5.623	-4.891	Mar.	3
Pleuronectes platessa	-8.785	0.182	-9.138	-8.424	Mar.	88
Pomacentrus coelestis	-5.057	0.124	-5.299	-4.815	Mar.	1
Pomatoschistus minutus	-6.717	0.151	-7.012	-6.424	Mar.	16
**Pseudobarbus burchelli*	-7.857	0.171	-8.194	-7.523	Fre.	56
Pseudopleuronectes americanus	-6.57	0.203	-6.966	-6.17	Mar.	11
Puntius sophore	-6.266	0.137	-6.531	-5.998	Fre.	7
Reinhardtius hippoglossoides	-12.202	0.201	-12.591	-11.804	Mar.	119
Rhinichthys cataractae	-8.427	0.165	-8.745	-8.11	Fre.	74
Rhinichthys cobitis	-8.845	0.164	-9.167	-8.517	Fre.	91
Rhomboplites aurorubens	-8.249	0.194	-8.624	-7.867	Mar.	69
Rutilus kutum	-9.85	0.195	-10.228	-9.465	Fre.	110
Sahyadria denisonii	-9.44	0.189	-9.804	-9.066	Fre.	100
Sardinops sagax	-8.034	0.157	-8.339	-7.728	Mar.	62
Schizothorax plagiostomus	-10.68	0.19	-11.047	-10.308	Fre.	116
Scomber scombrus	-7.22	0.196	-7.599	-6.833	Mar.	26
Scomberomorus cavalla	-8.75	0.213	-9.161	-8.324	Mar.	87
Sebastes alutus	-9.577	0.183	-9.934	-9.215	Mar.	102
Sebastes atrovirens	-7.542	0.201	-7.934	-7.148	Mar.	36
Sebastes auriculatus	-8.545	0.194	-8.919	-8.163	Mar.	80
Sebastes carnatus	-7.625	0.213	-8.049	-7.213	Mar.	44
Sebastes caurinus	-8.49	0.19	-8.858	-8.121	Mar.	76
Sebastes chlorostictus	-7.761	0.18	-8.109	-7.411	Mar.	50
Sebastes constellatus	-7.945	0.195	-8.327	-7.564	Mar.	60

Species	**Estimate**	**SD**	**2.5%**	**97.5%**	**System**	**Rank**
Sebastes crameri	-8.718	0.219	-9.143	-8.292	Mar.	86
Sebastes dallii	-7.823	0.17	-8.155	-7.491	Mar.	53
Sebastes diploproa	-7.914	0.202	-8.304	-7.519	Mar.	59
Sebastes elongatus	-7.84	0.188	-8.204	-7.467	Mar.	54
Sebastes entomelas	-8.184	0.193	-8.558	-7.808	Mar.	67
Sebastes flavidus	-8.152	0.195	-8.53	-7.773	Mar.	66
Sebastes goodei	-8.405	0.192	-8.774	-8.03	Mar.	73
Sebastes hopkinsi	-8.452	0.173	-8.787	-8.11	Mar.	75
Sebastes jordani	-9.214	0.213	-9.629	-8.8	Mar.	96
Sebastes levis	-8.614	0.211	-9.03	-8.204	Mar.	85
Sebastes melanops	-7.517	0.184	-7.874	-7.155	Mar.	33
Sebastes mentella	-10.292	0.179	-10.64	-9.942	Mar.	115
Sebastes miniatus	-8.048	0.195	-8.423	-7.663	Mar.	63
Sebastes mystinus	-7.749	0.175	-8.093	-7.414	Mar.	49
Sebastes norvegicus	-9.607	0.192	-9.977	-9.228	Mar.	105
Sebastes paucispinis	-8.558	0.198	-8.941	-8.171	Mar.	81
Sebastes pinniger	-7.85	0.23	-8.3	-7.398	Mar.	55
Sebastes rosaceus	-7.655	0.183	-8.01	-7.297	Mar.	45
Sebastes rosenblatti	-7.709	0.178	-8.058	-7.358	Mar.	47
Sebastes rufus	-8.506	0.201	-8.898	-8.104	Mar.	77
Sebastes saxicola	-7.581	0.171	-7.915	-7.247	Mar.	41
Sebastes semicinctus	-7.859	0.166	-8.183	-7.534	Mar.	57
Sebastes serranoides	-8.529	0.187	-8.892	-8.167	Mar.	79
Sebastes viviparus	-9.604	0.179	-9.947	-9.251	Mar.	104
Seriphus politus	-7.529	0.155	-7.832	-7.221	Mar.	35
Siganus canaliculatus	-6.602	0.186	-6.966	-6.239	Mar.	13
Solea solea	-7.568	0.178	-7.915	-7.22	Mar.	39
Spratelloides gracilis	-6.059	0.157	-6.362	-5.755	Mar.	6
Squalius squalus	-9.98	0.189	-10.352	-9.606	Fre.	113
Squalius torgalensis	-8.287	0.156	-8.595	-7.987	Fre.	70
Stegastes fuscus	-6.378	0.171	-6.71	-6.041	Mar.	10
Stellifer rastrifer	-7.682	0.168	-8.013	-7.356	Mar.	46
Thalassoma bifasciatum	-6.817	0.132	-7.076	-6.559	Mar.	19
Thunnus alalunga	-9.731	0.213	-10.14	-9.317	Mar.	107

Each species in our simulations (*) is in the upper one-half of intercepts for all 119 species, and three of the five examples are in the upper one-quarter of relative fecundity. Species' ranks from highest fecundity to lowest were: *H. amarus* (captive stock; 5 of 119), *E. motebensis* (21), *H. argyritis* (25), *I. lusitanicum* (38) and *P. burchelli* (56).

CHAPTER 1 - SUPPORTING FIGURES

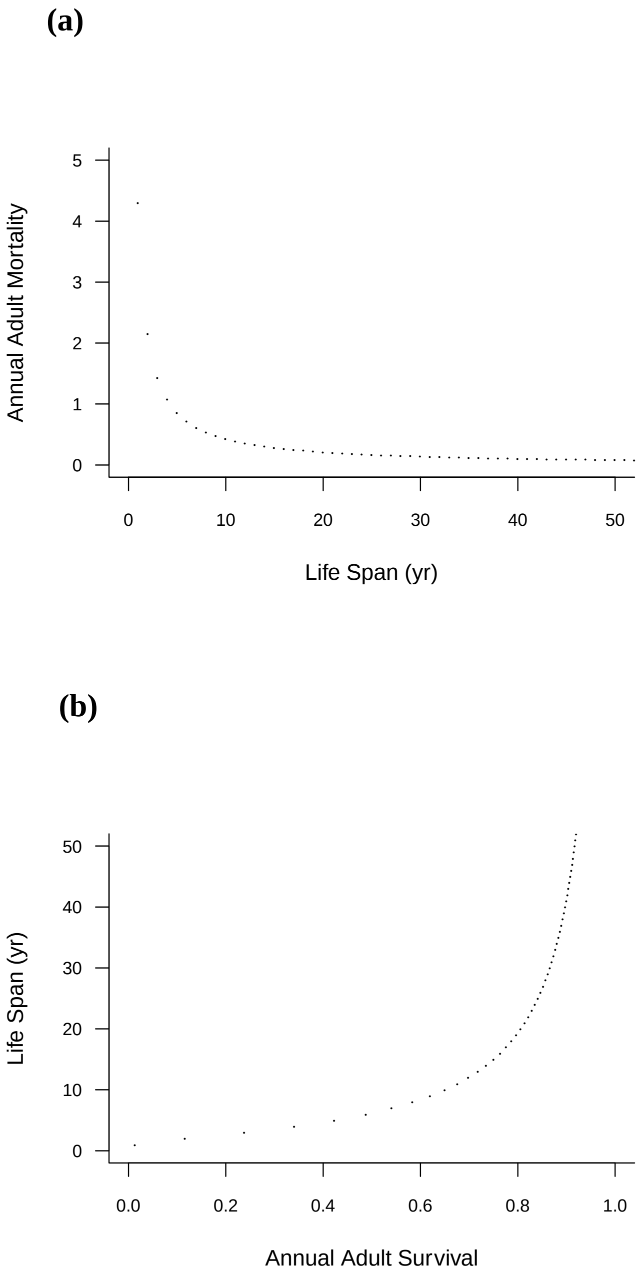

Figure S1. The relationship between life span and (a) natural adult mortality and (b) natural adult survival rate (i.e., the general relationships in fishes between life span and (a) M = 4.3/maximum age and (b) S = e^{-M}).

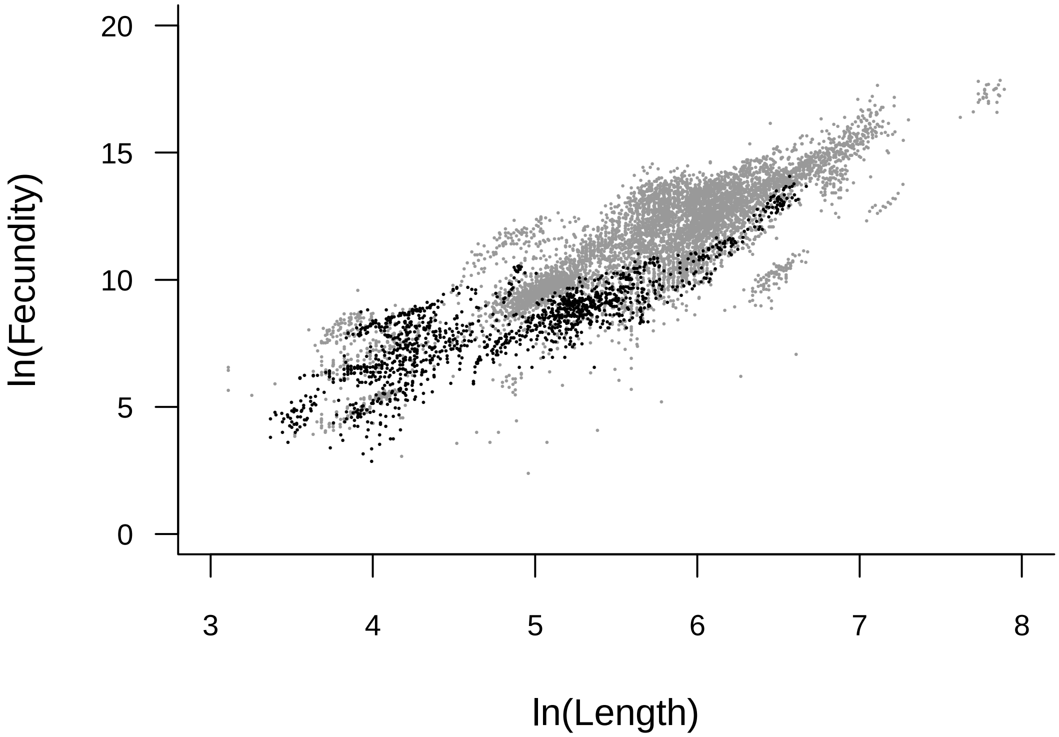

Figure S2. Fish fecundity (eggs) and body length data for 33 freshwater cypriniform species (black, and marine species from 15 Orders (gray) [1].
Data: Dryad https://doi.org/10.5061/dryad.69p8cz8z7.

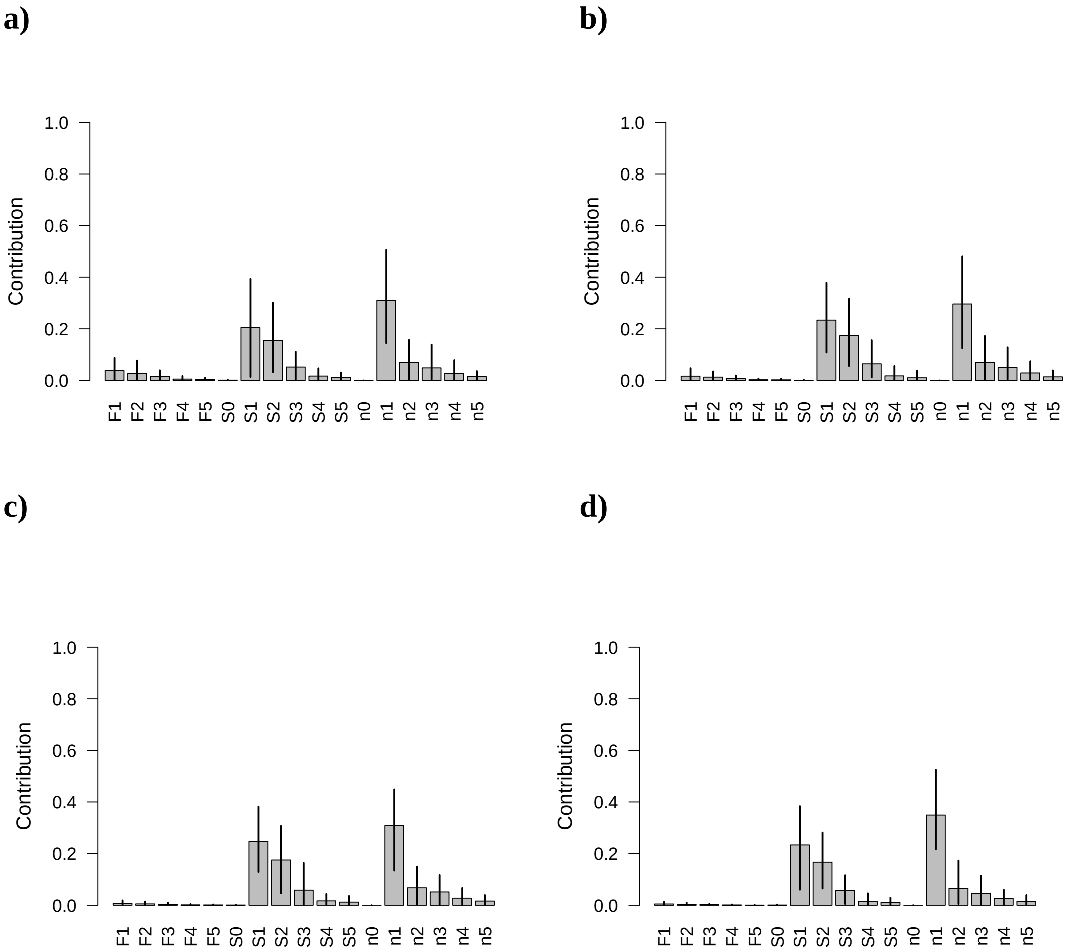

Figure S3. Transient LTREs at four levels of CV for survival probabilities.
Transient LTREs were obtained using the "average fish" fecundity schedule at age 1 maturity referenced in Table 3 of the main text. In each panel, the vertical axis is the proportional contribution to variance of population growth rate ($\sigma^2_{\lambda t}$): F_i denotes fecundity, S_i is survival and n_i represents fraction of the population at the i^{th} age. Simulations in each panel represent a life span of age 4+ with adult survival = 0.35; a) CV = 0.05, b) CV = 0.1, c) CV = 0.2 and d) CV=0.3.

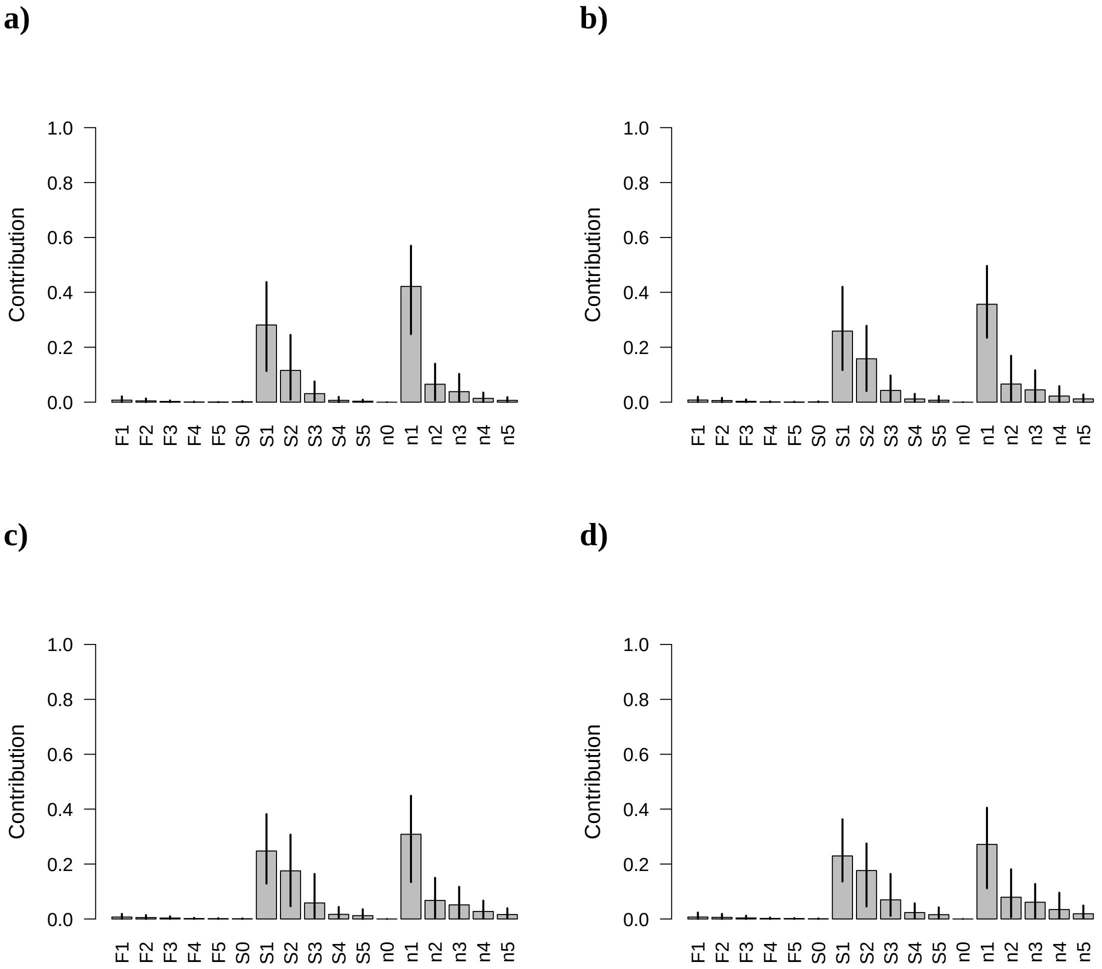

Figure S4. Transient LTREs for "average fish", age 1 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

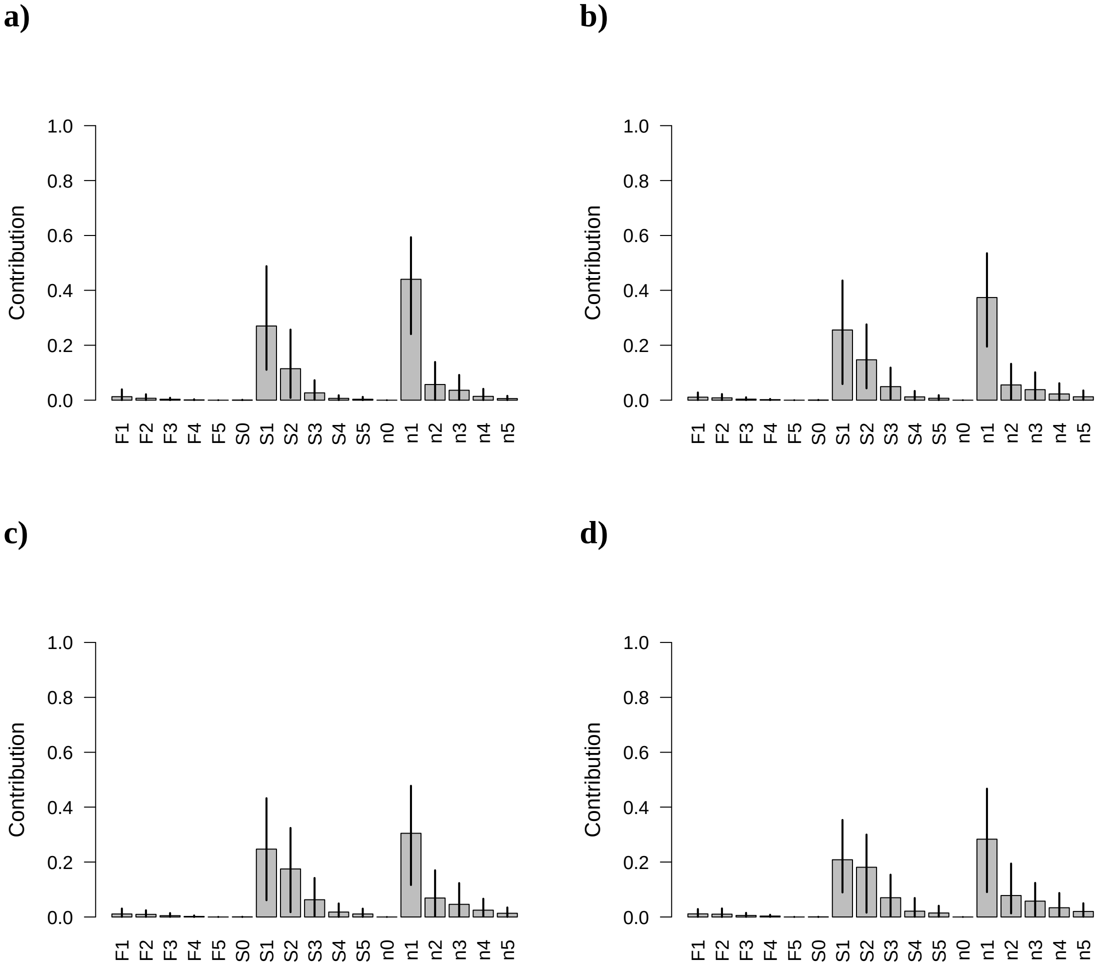

Figure S5. Transient LTREs for *Enteromius motebensis*, age 1 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

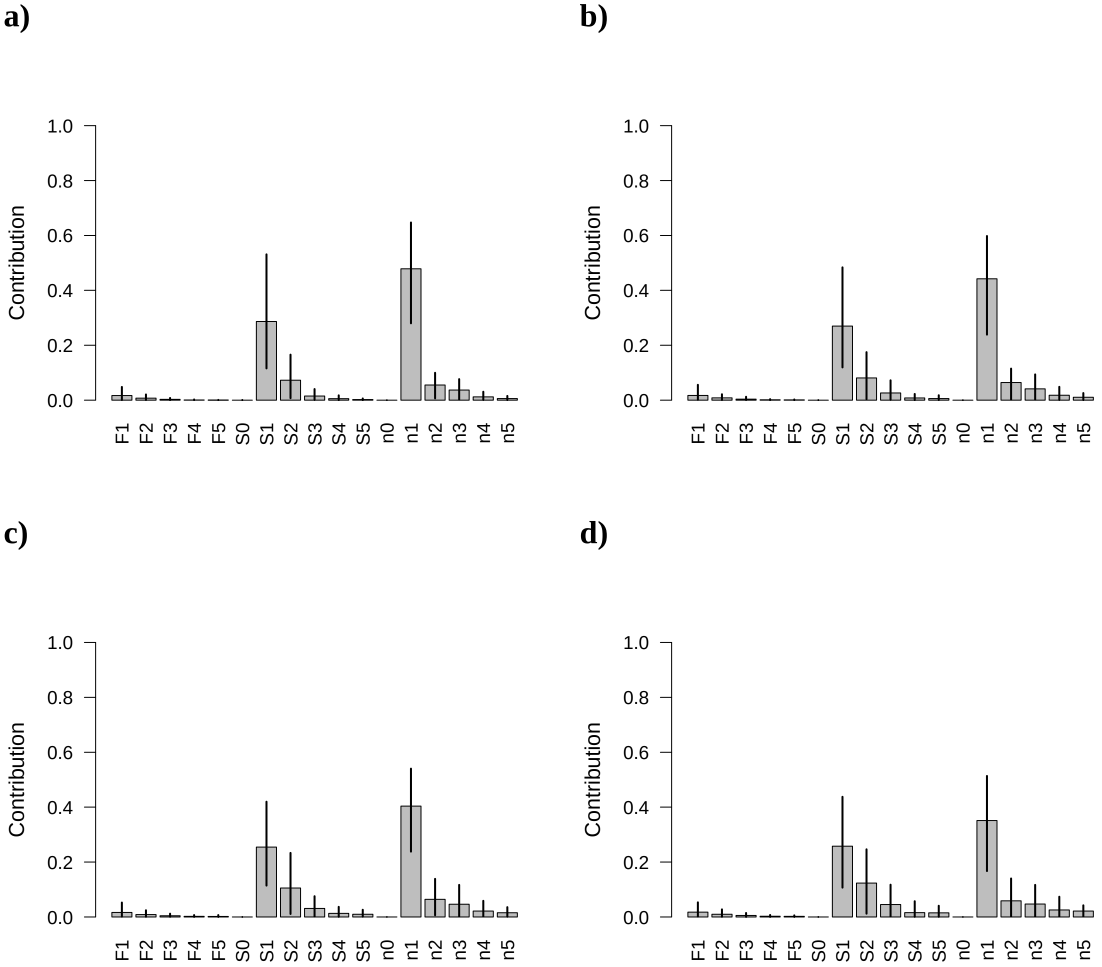

Figure S6. Transient LTREs for *Hybognathus amarus*, age 1 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

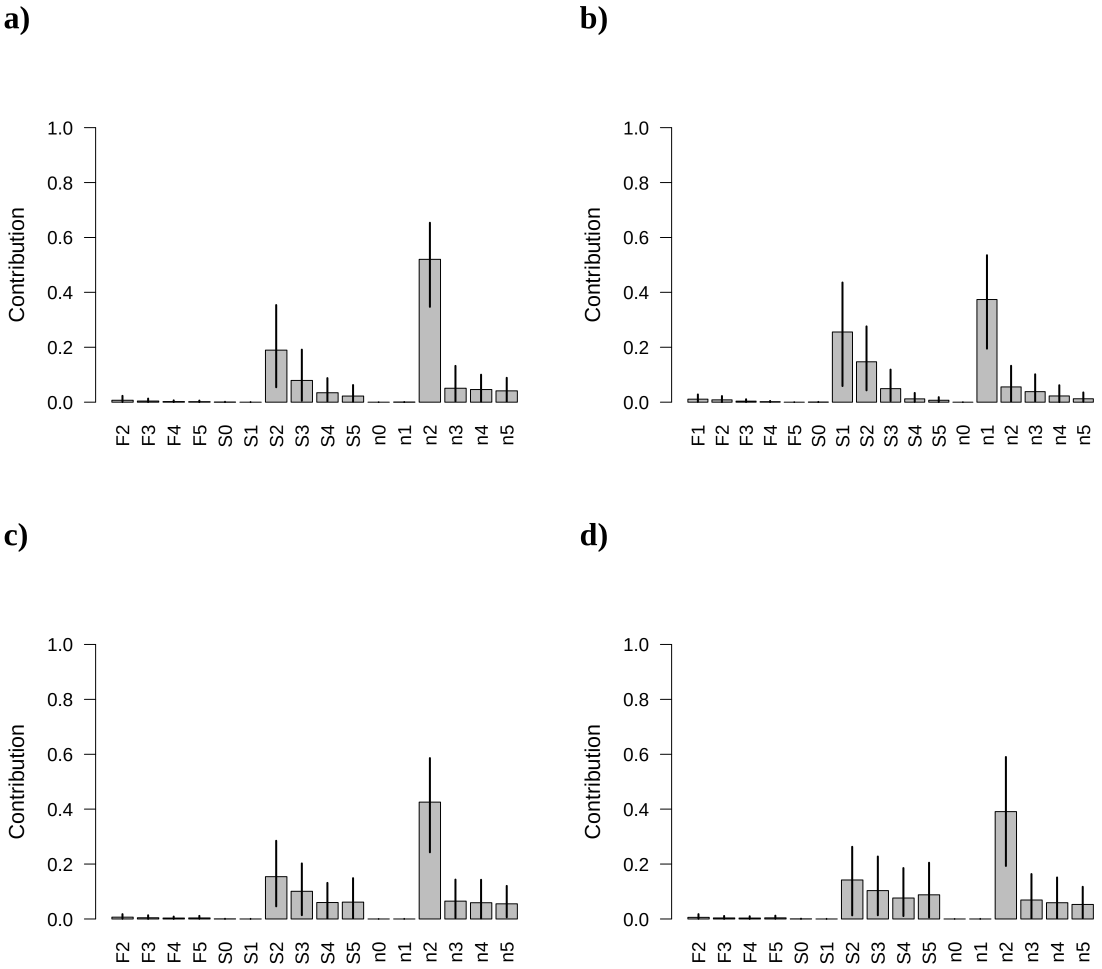

Figure S7. Transient LTREs for "average fish", age 2 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

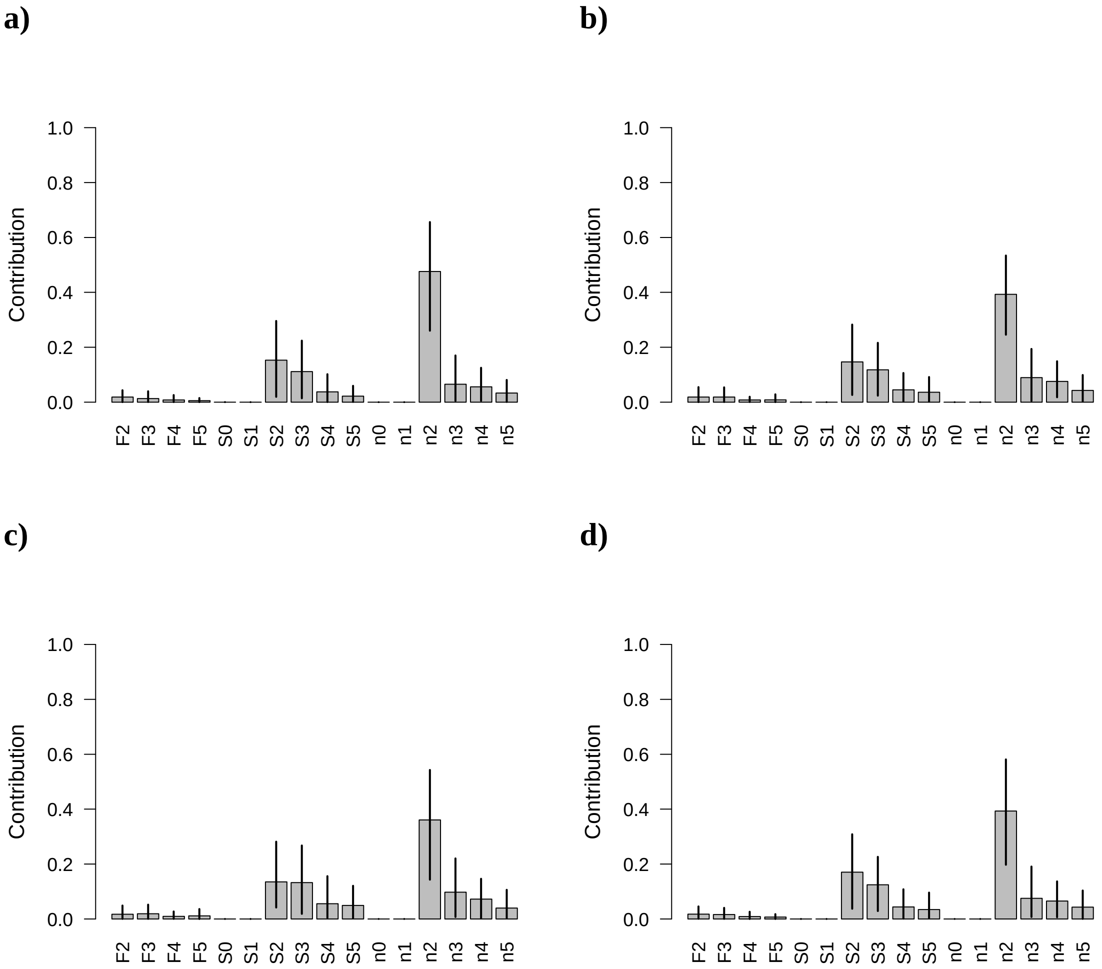

Figure S8. Transient LTREs for *Hybognathus argyritis*, age 2 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

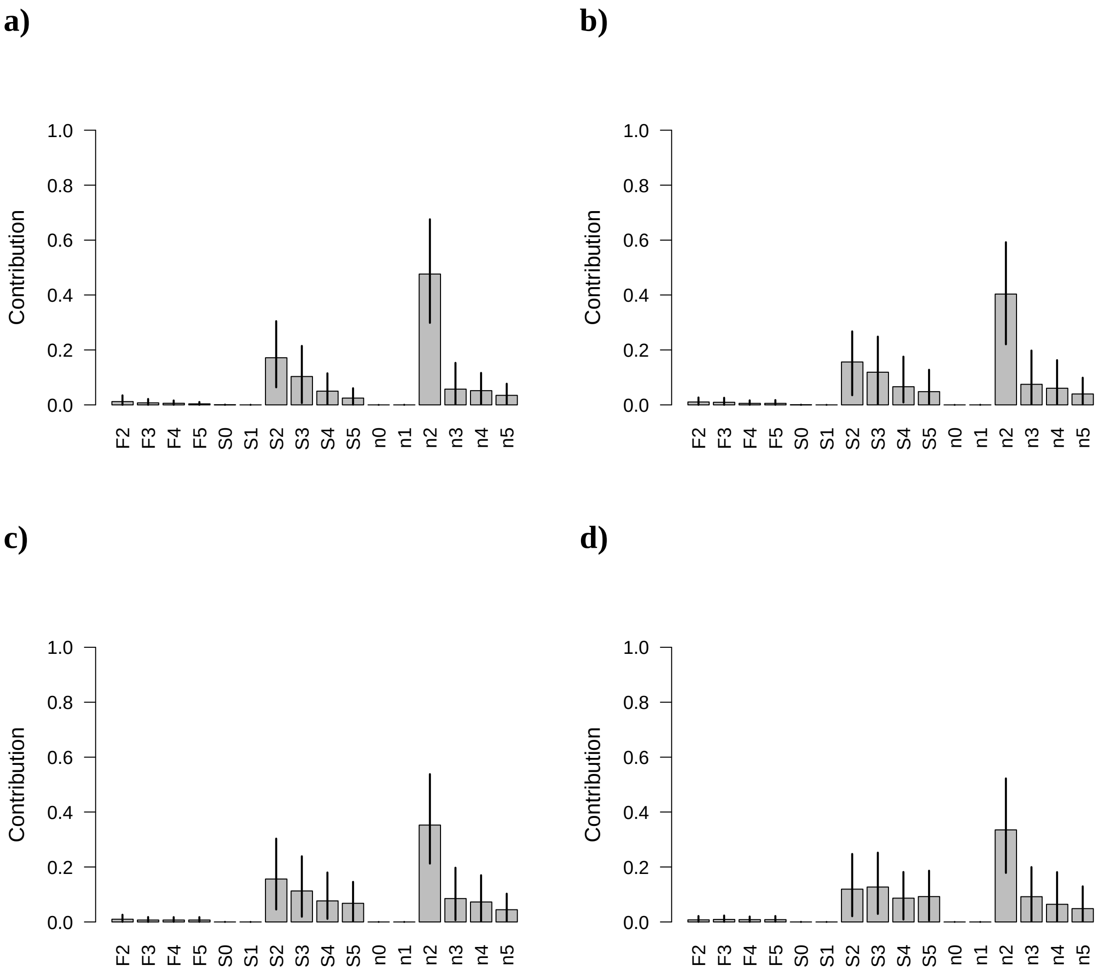

Figure S9. Transient LTREs for *Iberochondrostoma lusitanicum*, age 2 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

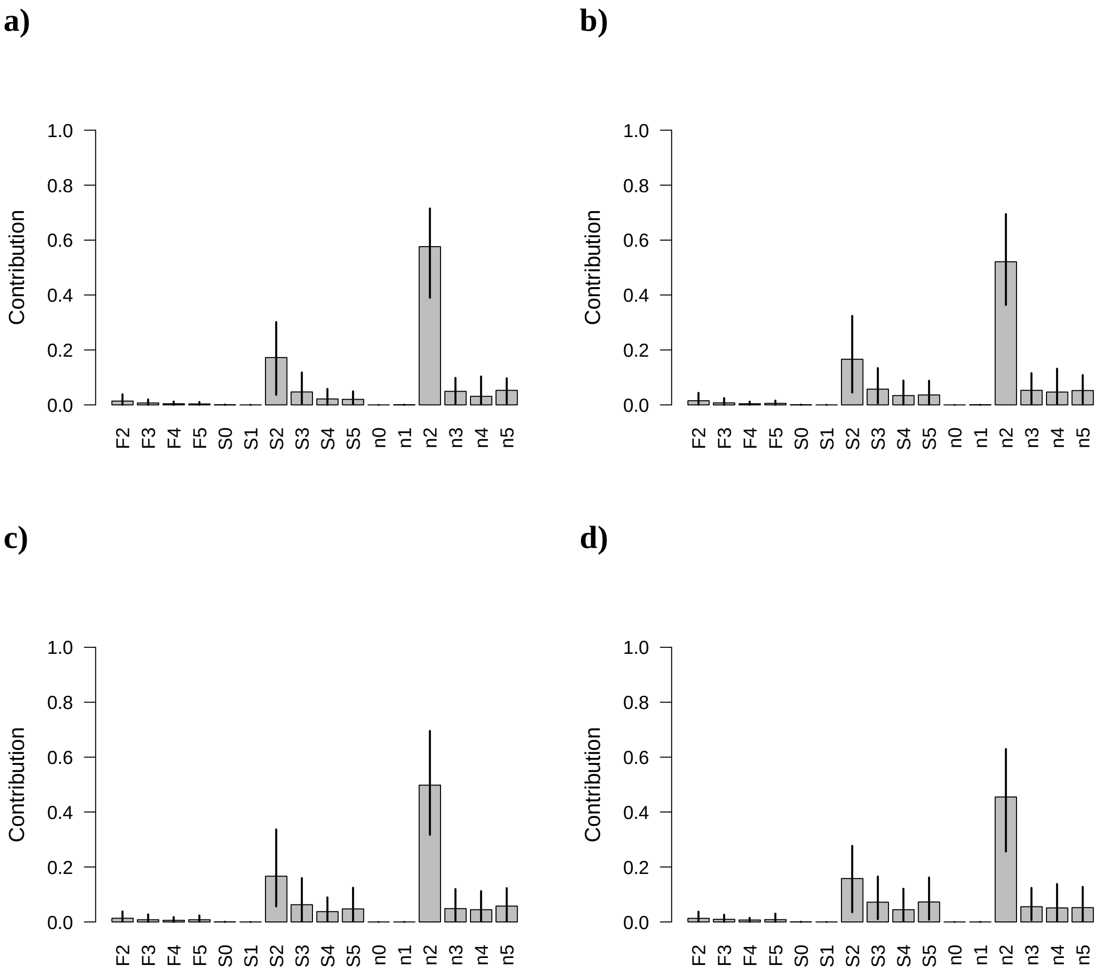

Figure S10. Transient LTREs for *Pseudobarbus burchelli*, age 2 maturity: (a) adult survival = 0.15, (b) 0.25, (c) 0.35 and (d) 0.45.

CHAPTER 2 – MITIGATION OF RECURRENT PERTURBATIOS IS AN IMPORTANT GOAL FOR CONSERVATION OF FRESHWATER FISHES

Introduction

Human-mediated perturbations to freshwater ecosystems have been implicated in widespread declines of short-lived freshwater fishes (Kominoski et al., 2017; Worthington et al., 2018; Tickner et al., 2020). Some example perturbations that are persistent or recurrent include flow regulation, water diversion, river intermittence, introduction of exotic species, fishing, altered biophysical processes from human uses of watersheds, and uncoupling of floodplains and river networks (Cowley, 2006; Cowley et al., 2007; Heino et al., 2015; Lois & Cowley, 2017; Worthington et al., 2018; Hatch et al., 2020).

The demographic effects of such human-associated perturbations are often temporally and spatially variable (Reznick, 1993; Trippel, 1995; Hamel et al., 2020), which contribute to erratic population dynamics and can drive rapid declines in fish populations. The potential for rapid declines in fish populations creates a pressing need for conservation initiatives that avoid or mitigate recurrent human-driven perturbations to aquatic ecosystems (Ruhí, 2016; Palmer & Ruhi, 2019). Perturbations that change the flow regime of running-water ecosystems have generally been insufficiently considered in conventional conservation strategies (Tickner et al., 2020), notably involving regulated rivers in basins vulnerable to climate stressed water shortages, where water resources are fully appropriated, and where demand for water often exceeds the supply.

How species-specific fitness characteristics contribute to population sustainability in habitats subject to perturbation may depend on the spatial extent and recurrence interval of mortality-causing flow intermittence. Factors such as species' age at maturity, lifespan, and population structure affect the relative sensitivity of population growth rate to recurrent mortality-causing habitat perturbations (Hatch et al., 2020). Such life history information is generally incomplete or uncertain for most species (Shenton et al., 2012; Koons et al., 2017), notably including species of conservation concern in contemporary environments that are highly perturbed by human uses of water and watersheds. However, Hatch et al. (2020) showed it is possible and appropriate for management purposes to approximate a species' life history for demographic simulations aimed at understanding possible consequences of environmental change. Likewise, it is possible to analyze through simulation multiple interacting demographic processes across a plausible parameter space. Knowledge of how population growth rates diminish with greater intermittence frequency and intensity (Poff et al., 2010; Shenton et al. 2012; Davies et al., 2014) can aid in establishing limits of flow intermittence to constrain perturbation mortality to levels sufficient to sustain a population's future capacity for growth.

I use matrix population models to explore several aspects of species' demography in time-variant freshwater environments. First, I simulate long-term stochastic population growth rates across a bivariate parameter space of perturbation frequency (annual) and perturbation intensity (mortality rate) to determine how recurrent perturbations might affect population growth rate of a freshwater fish species. I summarize simulations as a generalized population fitness surface with respect to recurrent habitat perturbations that cause mortality. Second, I compare simulation results for two example species to inquire if different species' life histories might respond similarly to human-mediated perturbations. Third, I conduct deterministic calculations of population dynamics following single or successive years (2, 3) of mortality-causing perturbation to estimate recovery time in years to a population equilibrium baseline. Finally, I use independent sets of simulations to assess the relative importance of juvenile versus adult mortality occurring with perturbations.

Methods

Matrix projection models are used, along with deterministic and stochastic simulation methods, to explore aspects of population growth of short-lived freshwater fish species in time-variant habitats (Caswell, 2001). I developed a matrix population model incorporating perturbation mortality, (2) implemented stochastic simulations to estimate long-term stochastic population growth with results summarized as a population fitness (growth rate) surface, (3) made deterministic calculations to estimate post-perturbation time to recovery of population size, and (4) developed a management example to illustrate how mitigation of perturbations might be accomplished.

Matrix Population Model with Perturbations

Hatch et al. (2020) demonstrated demographic simulation can yield insight into a population's potential fate relative to a "natural" population equilibrium baseline. A natural (pre-perturbation) baseline is a convenient and general way to consider a fish species' life history and it enables comparisons between simulations parameterized for different life histories. I summarize key aspects of long-term stochastic population growth to emphasize the importance of a frame-of-reference for simulations of a species' population dynamics in a variable environment. Briefly, I assume a species can be considered in a natural environment where variable adult survival probability determines its natural lifespan. Given an approximate lifespan and age-specific fecundity, one can obtain an analytic estimate of juvenile survival probability necessary for the population growth rate (λ) to be stable (λ very close to one), which implicitly assumes a species' fecundity is sufficient to offset juvenile mortality (Hatch et al., 2020). In this paper I use a hypothetical, natural population equilibrium baseline in applications of matrix population models to explore demographic effects of human-associated perturbations that may cause mortality.

I use variations of a post-breeding birth pulse female transition matrix (eq. 1) with six age classes for simulations. Terms and symbols used in this paper are defined in Appendix Table S1.1. Equation 1 expresses the relationship between number of individuals in age class i at time t as a function of the number of individuals in the previous generation (t-1). I use a subscript "M" to denote a survival rate in a hypothetical unperturbed natural environment and a subscript "E" to denote a survival rate to environmental perturbation; numerals denote age classes. Parameters in the transition matrix include age-specific natural adult survival rate (S_{Mi}), fecundity (F_i), and survivorship after environmental perturbation (S_{Ei}). For clarity, S_{Ei} is equivalent to 1-d_i, where d_i represents the perturbation mortality rate. I assume the last age class is composed of age 5 and older individuals. Notice that if perturbation has no effect on survival, all of the S_{Ei} equal one.

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_t = \begin{bmatrix} 0 & S_{E1}S_{M1}F_1 & S_{E2}S_{M2}F_2 & S_{E3}S_{M3}F_3 & S_{E4}S_{M4}F_4 & S_{E5+}S_{M5+}F_5 \\ S_{E0}S_{M0} & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{E1}S_{M1} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{E2}S_{M2} & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{E3}S_{M3} & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{E4}S_{M4} & S_{E5+}S_{M5+} \end{bmatrix}_t \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t-1} \qquad (1)$$

I assume density independence in this annual time step model, although I acknowledge that seasonal fluctuations in habitats can increase susceptibility to competition or predation in a density dependent way. High environmental variability, as I evaluate here, tends to decrease the influence of density dependence on extinction probability (Henle et al., 2004) and it is generally more important than vital rates (Lande, 1993). I used the model to explore the problem of identifying management options when populations are generally in a perpetual transient state (Rose et al., 2001; Rotella et al., 2009).

The matrix population model shows perturbation effects on age-specific survival and fecundity through multiplicative effects in the transition matrix (see the S_{Ei} in eq. 1). Three scenarios of perturbation mortality were evaluated in separate simulations: (a) all age classes are affected equally, i.e., $S_{E0} = ... = S_{E5}$; (b) only adult age classes are affected, $S_{E0} = 1$, $S_{E1} = ... = S_{E5}$; (c) only juveniles are affected, $S_{E1} = ... = S_{E5} = 1$.

Example Species and Study Area

I use as an example the Rio Grande silvery minnow (Cypriniformes: Leuciscidae: *Hybognathus amarus*). For comparisons of the effects of perturbation on population growth across taxa, I use a second example – a hypothetical "average fish" – with the same lifespan but lower age-specific fecundity than *H. amarus* (Hatch et al., 2020).

Hybognathus amarus is an endangered fish species (U.S. Department of Interior, 1994) endemic to the Rio Grande Basin that has been described as the most climate stressed river system in North America, U.S.A. (Dettinger et al., 2015). Additionally, the regulation of flow in the Rio Grande for agricultural, industrial, or domestic uses of scarce water resources has altered patterns of river flow that has negatively impacted aquatic life in the basin (Sublette et al., 1990; Ward et al., 2001; Cowley, 2006; Ward et al., 2019; Hatch et al., 2020).

Hybognathus amarus is an iteroparous (reproduction in multiple years), small-bodied freshwater fish species with maturation at age 1, maximum age of 5 (Cowley et al., 2006) and low juvenile survival rate (Hatch et al., 2020). Large transient changes in *H. amarus* population size (U.S. Fish and Wildlife Service, 2016) may be driven by recurrent river intermittence that is known to have occurred with water diversions since at least the late 1800s (Cowley, 2006). The species' contemporary distribution is confined mostly to the Rio Grande of New Mexico, U.S.A., from Angostura Diversion Dam (north of Albuquerque) to Elephant Butte Reservoir, a distance of approximately 241 km. Here, as an example, I consider how river intermittence, driven largely by water extractions, affects the demography of *H. amarus* in the Isleta Reach of the Rio Grande, New Mexico, U.S.A. This reach is an 85.5 km river segment bounded by diversion dams at Isleta (upstream) and San Acacia (downstream).

There are no published fecundity estimates for wild *H. amarus*. For this reason, Hatch et al. (2020) conducted a Bayesian meta-analysis of fecundity at-age to derive fecundity estimates for use in simulations of population dynamics under natural conditions. For this, I compiled published mean size at age and fecundity at body length data for 119 marine and freshwater fish species, including 33 freshwater cypriniform species (Hatch et al., 2020). Of particular relevance to this study is the inclusion of data for three congeners: wild *Hybognathus placitus* (plains minnow), wild *Hybognathus argyritis* (Western silvery minnow), and captive *H. amarus* (Caldwell et al., 2019). I used the Bayesian meta-analysis results to estimate fecundity at-age for each species in simulations as previously described by Hatch et al. (2020). Mean size at age was modelled from an age-length key estimated from a large sample of *H. amarus* (N = 2423); additional details are given in the aforementioned paper.

Long-term Stochastic Population Growth Rate with Perturbations

I simulated stochastic population growth (Caswell, 2001) using alternate transition matrices for equilibrium (all $S_{Ei} = 1$ in eq. 1) and perturbation ($0.4 \leq S_{Ei} \leq 1$) scenarios, initiating each simulation with the asymptotic stable-age population vector for the equilibrium baseline. Population growth was simulated for 50,000 time steps to ensure unbiased estimation of long-term stochastic population growth (λ). At each time step, either the equilibrium transition matrix or the perturbation transition matrix was chosen randomly to simulate population growth. The probability of selecting each matrix was determined by the annual frequency of perturbation. Applications of this simulation strategy have been used in other studies (e.g., Caswell, 2001; Caswell & Kaye, 2001; Tuljapurkar et al., 2003).

From the simulated sequence, I calculated long-term stochastic population growth rate using the "*stoch.growth.rate*" function from the "*popbio*" package in R (Stubben & Milligan, 2007), and the results were summarized using "*ggplot2*" in R (Appendix S1.6). To obtain a view of population growth rates across the model parameter space, I conducted this simulation process at all 24000 pair-wise combinations of values of perturbation annual frequency ranging from 0 to 1 in increments of 0.005, and perturbation mortality ranging from 0 to 0.6 in increments of 0.005. Three sets of 24000 pair-wise simulations were conducted to evaluate how population growth responds to perturbation mortality: a) all ages have the same mortality, b) only adult survival is affected by perturbation, and c) mortality only affects juveniles (Table 2; appendices S1.2 and S1.3).

Deterministic Evaluation of Recovery Time

I conducted deterministic calculations of population growth beginning with an equilibrium population and a stable-stage population vector. For this, I use a prospective analytic approach (Caswell, 2001; Caswell & Kaye, 2001; Morris & Doak, 2002) to estimate recovery times of population size from single or serial occurrences of perturbations. These calculations were initiated by one, two or three successive years of intermittence disturbance, and thereafter applied the equilibrium transition matrix. I considered three years a relevant time span for managers of water and fishery resources to utilize knowledge of past species demographic performance and future water resource availability to guide adaptive management strategies to achieve species conservation. I observed the time for the population to recover from perturbation and I evaluated the three scenarios of perturbation mortality. Results were summarized to compare single versus serial occurrences of perturbation.

River Intermittence from Water Extraction as an Example Perturbation

To provide a context for considering the potential effects of perturbations on population growth, I used data on river intermittence in the Isleta Reach. I compiled a contemporary 12-year (2004-2015) record of flow intermittency (Appendix S1.4) and calculated the annual rate at which river drying occurred by dividing the number of years with drying by 12. For each year in the data, I divided the length dried by the reach length (85.5 km) to obtain the proportion of the Isleta Reach that dried each year. I considered the mean fraction of river dried to represent the perturbation mortality rate, which subtracted from one, yielded a survival rate after drying (1-proportion dry; i.e. the S_{Ei} elements of the transition matrix in equation 1). I calculated the annual frequency of intermittency over the 12-year period and the geometric mean perturbation mortality to illustrate possible management options.

Also for comparative purposes, I identified 10 unique transition matrices for the 12-year period of Isleta Reach intermittence (Appendix S1.5). Two years had no drying and represented equilibrium conditions (frequency 2/12). Of the remaining nine transition matrices, two years had identical drying (each with frequency = 2/12) whereas the remaining transition matrices occurred at frequency = 1/12. I then calculated long-term stochastic population growth rate from simulations with random time-step selections of a transition matrix from the set of ten matrices where the probability of selection was determined by the annual frequency of each perturbation. Finally, I compared simulation results at the geometric mean annual proportion of river reach intermittence.

Results

The estimated fecundity at age for captive *H. amarus* was judged atypical as a consequence of a high intercept rank (rank 5 of 119 species) relative to wild *H. argyritis* (rank 25 of 119 species) and wild *H. placitus* (rank 32 of 119 species). For this reason, I elected to use the estimated intercept for *H. argyritis* at the mean length at age as estimated for *H. amarus* by Hatch et al. (2020, see their Appendix Table S6). The common slope (3.447) and mean intercept over all species (-8.101) were used to compute fecundity at-age for a comparably-sized hypothetical "average fish" of age 1 maturity (Table 1). Additional details are given in Hatch et al. (2020).

I use values of age-specific adult survival of 0.35 for *H. amarus* and "average fish" (Table1), which approximates an age 4+ lifespan (Hatch et al., 2020). Species-specific equilibrium values of S_0 were obtained, given each species' fecundity at age, by adapting the algorithm of Vaughn & Saila (1976) for my post-breeding census model. Note that the hypothetical "average fish" is distinguished from *H. amarus* by lower age-specific fecundity and a higher juvenile survival rate at population equilibrium (Table 1).

Long-term stochastic population growth rate at different combinations of annual frequency and perturbation mortality is summarized for *H. amarus* (Figs. 1a-c) and for the hypothetical "average fish" (Figs. 1d-f). Note that all examples in Fig. 1 are relative to a hypothetical natural population equilibrium. Population growth rate is resilient to perturbations across a range of perturbation frequencies and intensities, as indicated by the blue zone in each graph in Fig. 1. Results show that relative resilience in population growth rates varies with perturbation frequency and perturbation mortality. Importantly, notice the panels in Fig. 1 show fitness surfaces that decline toward the upper right of each figure. The results further show that perturbation affecting only adults decreases long-term population growth rates more than when mortality is confined to juveniles. The results are visually consistent between *H. amarus* and the hypothetical "average fish" (Fig. 1).

Assuming a population equilibrium baseline, deterministic projections of population growth following perturbation are summarized in Fig. 2 for one, two, and three consecutive years of perturbation. Attenuation of population growth becomes progressively more severe with consecutive years of perturbation.

In my example, the observed geometric mean annual proportion of reach dried (when drying occurred) was 0.23 and intermittence survival (S_{1E}) = 0.77 (i.e., 1.0 – 0.23). The annual frequency of intermittence was 0.83 (Appendix S1.4). The long-term stochastic population growth rate at these values was equal to 0.79 (see Fig. 3 at point x = 0.23, y = 0.83). In contrast, long-term stochastic population growth rate was substantially lower (0.68) when simulations mimicked the observed 12-year period of river drying in the Isleta Reach using 10 transition matrices.

Discussion

Simulations presented here demonstrate that recurrent environmental perturbations can strongly depress short- and long-term population growth rates (Lande et al., 2003; Horne et al., 2019). Simulations of long-term stochastic population growth rates imply there are limits to the annual perturbation frequency and perturbation mortality if a positive capacity for population growth is to be maintained (e.g., population loss restricted to less than 5% per year; $\lambda \geq 0.95$). Similarity of fitness surfaces in my examples suggest that frequent perturbation mortality, such as flow intermittence, likely reduces survival and population growth (Jaeger et al., 2014; Ruhí et al., 2016) for an iteroparous freshwater fish species like *H. amarus*. Perturbation mortality causes a steeper decline in population growth rate when it affects adults as opposed to juveniles, which is inconsistent to contemporary management emphasis on captive propagation and stocking of juvenile fish for *H. amarus* conservation (U.S. Fish and Wildlife Service, 2016). Results here and elsewhere (Hatch et al., 2020) suggest that long-term sustainability management in time-variant habitats requires management strategies that improve adult survival.

Consecutive annual occurrences of perturbation mortality lengthen recovery time nonlinearly, especially when perturbations cause adult mortality (Koons et al., 2007; Ezard et al., 2010). This implies that species conservation plans for unstable environments need dual strategies. Firstly, managers may need to use aggressive population support, such as stocking hatchery-produced fish, to ensure short-term population persistence. Secondly, long-term sustainability management requires implementing strategies to improve adult survival (Wang et al., 2017; Hatch et al., 2020).

I demonstrate that the geometric mean value of perturbation mortality may seriously under-estimate long-term population growth rate, and hence, fail to recognize true extinction risk. Long-term stochastic population growth rate is more realistically estimated from an observed series of annual perturbation mortality. Assuming the extent of river intermittence in my example is a reasonable surrogate of perturbation mortality for *H. amarus*, the estimate of long-term stochastic population growth rate (0.68) under the 12 year record of intermittence for the Isleta Reach is consistent with age truncation of the species as inferred by Hatch et al. (2020). These results highlight the importance of adult survival relative to juvenile survival – a finding that should be emphasized in management efforts to mitigate recurrent perturbations to freshwater ecosystems.

Although I used data on river intermittence to illustrate how recurrent perturbation in the middle Rio Grande may affect *H. amarus* population growth, I acknowledge there are no field estimates of mortality caused by flow intermittence (Archdeacon, 2016). Likewise, there are no field survey estimates of age-specific *H. amarus* survival to recurrent perturbations in the middle

Rio Grande. Although, I used the fraction of habitat dried as a proxy for perturbation mortality on an annual basis, perturbation mortality could be higher than the proportion of habitat dried. I suggest that additional sources of adult mortality for *H. amarus* beyond river drying should be considered. For example, a persistent low flow period preceding intermittence could increase predation mortality (Cowley et al., 2007; Hatch et al., 2020) that is not represented by the spatial extent of intermittence.

Thresholds of probable concern for mitigating perturbation mortality

Contours of population growth with recurrent perturbation indicate progressive reduction in population resilience with increasing perturbation frequency and increasing perturbation mortality. These contours can be used to define progressively harsh "thresholds of probable concern" (Biggs & Rogers, 2003; Rogers et al., 2013) that can guide managers in conservation efforts to avoid, limit, or mitigate perturbation mortality.

When water shortages occur, managers may find it necessary to support a minimum short-term population growth rate, which will likely fail to sustain the species over long time periods. However, such a strategy over short time periods could be employed to limit declines in population size. As an example, a manager could adopt a short-term species conservation objective to restrict population loss to less than 5% per year ($\lambda \geq 0.95$). An objective such as this could facilitate least-cost water shortage management strategies applied to short-term species conservation and that operate to minimize impacts to existing water uses.

Several example alternative strategies for restricting population loss to less than 5% per year are depicted in Fig. 3, where $\lambda \geq 0.95$ is illustrated by a thin black line. Obviously a different value might be used in a specific application and my example is intended to illustrate possible management alternatives. These scenarios, and other scenarios with similar restrictive effects on intermittence frequency or extent, should receive consideration for incorporation in an adaptive decision-making process involving options most appropriate for the uncertainties of recent past and present hydrologic conditions along with recent histories of demography (Polasky et al., 2011).

Alternative strategies illustrated in Fig. 3 are represented by arrows that originate at $\lambda = 0.68$, i.e., my estimate of long-term stochastic population growth rate under the 12 year record of intermittence for the Isleta Reach. With regard to my example of river intermittence, a manager could consider options of reducing perturbation mortality while not attempting to reduce annual frequency of intermittence (Fig. 3, arrow a, left-pointing). Conversely, the right-diagonal arrow (Fig. 3, arrow c) illustrates a scenario of reducing annual frequency of intermittence with no focus on perturbation mortality. A combination of reducing annual frequency of intermittence and perturbation mortality is illustrated by the middle diagonal arrow (Fig. 3, arrow b). Although each management alternative depicted in Fig. 3 represents an equally effective approach to species conservation, each alternative will likely have unique implications for the estimated amount of water needed to supplement in-channel flow to achieve this objective.

Sustainability management of short-lived freshwater fish species needs to adjust adaptively to limit mortality caused by recurrent perturbations in human-altered ecosystems. The opportunities for mitigation of human-mediated perturbations such as recurring flow intermittence will depend on factors such as climate, hydrology, species-specific life histories, and the availability of water for environmental flow. Inevitably, conservation of freshwater fish species requires water, which for my Rio Grande example, is over-allocated to human extractive uses.

Considerations of management strategies for mitigating flow intermittence mortality is an important element of conservation planning, including the formulation of conservation goals that are measurable, time and space delimited, and easily monitored (Lindenmayer & Likens 2009, 2010; Shenton et al., 2012; Kaplan et al., 2019). In this regard and as I demonstrate by example, a natural (pre-perturbation) baseline is an informative perspective of a fish species' life history for establishing management goals for species conservation. Early in this diagnostic process, it is important to identify demographic factors that are the most important determinants of population growth (Koons et al., 2016; Hatch et al., 2020), and to subsequently direct management efforts at maximizing the effects of those determinants to positively affect population growth. For example, as adult survival decreases, resulting in age-truncation, the first reproductive age class becomes increasingly important to variation in population growth (Hilborn, 1992; Ottersen et al., 2006; Wang et al., 2017; Hatch et al., 2020).

Limiting mortality caused by flow intermittence may require increasing stream flow (Acreman et al., 2014) or reductions in diverted water for consumptive uses. Water shortages can be addressed by demand regulation of consumptive uses, conjunctive use of irrigation infrastructure and irrigation water excesses, water reuse, or short- and long-term supply-related solutions such as water leases, appropriation, and transfers of existing rights (e.g., Ward et al., 2001, 2019). All of these approaches to water shortage management should be evaluated for application in the middle Rio Grande.

Environmental flow shortages can be partially addressed by measures to enhance riverine geomorphic processes (Petts & Gurnell, 2013; Yarnell et al., 2015; Palmer & Ruhi, 2019), perhaps utilizing flow-deflecting objects such as large woody debris (Bond & Lake, 2005; Howson et al., 2009; Howson et al., 2012; Dunkerley, 2014) or other revetment structures

(Kinzli & Myrick, 2009) that can enhance habitat complexity at smaller spatial scales. Such geomorphic processes can create scour pools that alter surface water/groundwater connections and river base flows, which often represent a large component of total river discharge (Miller et al., 2016; Rumsey et al., 2020).

A proposed emergency recovery plan (Tickner et al., 2020) identified six global action priorities to stem the loss of freshwater biodiversity. All of these global action priorities are consistent with strategies to mitigate the effects of recurrent perturbations. Further, such strategies are equally necessary to alleviate age truncation caused by reduced adult survival (Hatch et al., 2020). By integrating hydrologic and demographic analyses, it is possible to quantify how changing patterns in habitat size, flow continuity, and consecutive years of perturbation can affect growth rates of fish populations. Knowledge of how population growth rates diminish with greater intermittence frequency and intensity (Poff et al., 2010; Shenton et al. 2012; Davies et al., 2014) can aid in establishing limits of flow intermittence to reduce environmental mortality to levels sufficient to sustain a population's future capacity for growth.

Future climate change imposes further challenges to develop and manage regional water resources for human uses while simultaneously sustaining aquatic ecosystems (Vivoni et al., 2009; Dominguez et al., 2012; Elias et al., 2015). Climate stressed water shortages raise the importance of water delivery efficiency to satisfy the diversity of needs for scarce water supplies (Habteyes & Ward, 2020). Efficiency in water transport and water use can extend the economic productivity of scarce water supplies and limit potential adverse impacts on farmers from changes in water supply and water allocation (Linstead, 2018). Similarly, in fully appropriated basins and where water demands exceed supplies, it may become economically productive to augment regulated stream flow and improve delivery efficiency of water to limit the incidence of mortality-causing flow intermittence. Where water resources are already over appropriated, efficiency in consumptive water use can effectively contribute to environmental flow only if it results in overall reduction in consumptive use and is joined by measures to prevent expansion or intensification of consumptive use (Linstead, 2018).

The potential adverse effects of recurrent perturbations on a fish species' population growth show the need for transformations in environmental management of freshwater social-ecological systems (Gleick, 2018). Sustainability management of fish populations requires consideration of watershed scale factors in addition to water availability from upstream sources. I acknowledge there are diverse and substantial constraints to adjusted patterns of consumptive water use to accomplish sustainability goals for humans and freshwater biota (Ward et al., 2019). Much of these constraints originate from water law that governs the allocation of scarce water supplies among prospective water rights claimants and the failure of that system to prevent over consumption of water and to balance private and public interests in the use of water (Falkenmark & Rockstrom, 2004; Ward et al., 2019). As practiced in New Mexico and many other prior appropriation states, state water law has minimized risk of capital investment for private stakeholders (DuMars and Tarlock, 1989; Johnson and DuMars, 1989). Water resources allocated under the prior appropriation doctrine are rarely managed efficiently or consumed in response to the highest market demand (Ward et al., 2019). Such water resources are generally undervalued and over-consumed, often generating external costs (Laitos, 2002) that are typically absorbed or ignored by society.

My results illustrate how demographic characteristics of an endangered fish species relate to environmental flow needed for species conservation, and how consideration of this need can be integrated into conventions of water management. Irrespective of the intervention approach to provide environmental flows, mitigation of perturbation mortality should incorporate safeguards that involve multiple ecosystem processes where possible. A single intervention strategy may be inefficient in its individual effect, but multiple intervention measures managed concurrently may yield a more robust solution (Frissell et al., 1986).

My results indicate two principal avenues of intervention to mitigate flow intermittence perturbation: reducing annual frequency and/or reducing perturbation mortality. The option to reduce annual frequency of river intermittence requires greater foresight of expected water supply, greater investment in planning, and greater commitment of water resources to environmental flow. The option to reduce perturbation mortality is better suited to management responses to unforeseen environmental conditions and is more dependent on adaptive adjustments in water management operations based on monitoring and evaluation of dynamic river conditions.

My work suggests that many fish species could reasonably be expected to respond similarly to human-mediated perturbation mortality. My observations are relevant globally for many short-lived, small-bodied freshwater fish species that have iteroparous life histories, an indeterminate lifespan dependent on adult survival, high fecundity, and low juvenile survival. In mitigating perturbations fishery managers should be less concerned with the species-specific details of life history and more focused on how an "average fish" of comparable size and lifespan would be expected to respond to environmental perturbation.

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Tables

Table 1 (Chapter 2). Equilibrium baseline parameter values used in projections of population growth.

Parameter	*H. amarus*[a]	"average fish"
$S_{(M0)}$	1.929E-3	4.911E-3
$S_{(M1)} \ldots S_{(M5)}$	0.35	0.35
F_1	665	218
F_2	1232	538
F_3	1884	881
F_4	2397	1101
F_5	3415	1357

[a] fecundity at length for *H. argyritis* is used as a proxy estimate of fecundity for wild *H. amarus.*

Table 2 (Chapter 2). *H. amarus* perturbation survival rates (S_{Ei}).

Scenario	S_{E0}	$S_{E1} = \ldots = S_{E5}$
Equilibrium	1	1
All ages affected equally	(0.4, 1)[a], 0.77[b]	(0.4, 1)[a], 0.77[b]
Only adult ages affected	1	(0.4, 1)[a], 0.77[b]
Only juveniles affected	(0.4, 1)[a], 0.77[b]	1

[a] inclusive range of parameter values used to estimate stochastic population growth rates at various combinations of perturbations defined by annual frequency and mortality.

[b] value used in deterministic projections to represent the Isleta Reach of the middle Rio Grande.

Figures

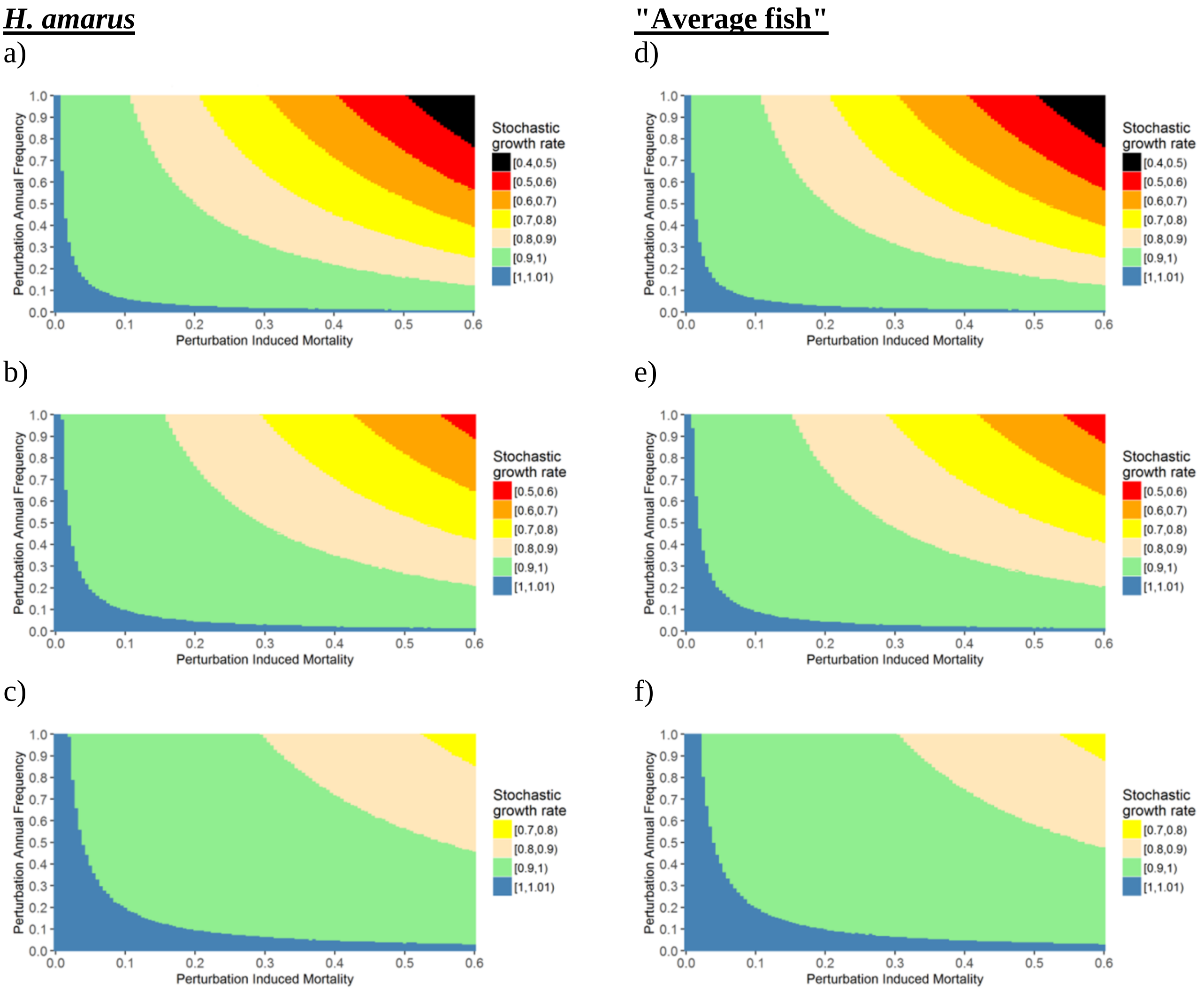

Figure 1 (Chapter 2). Stochastic long-term population growth rate of *H. amarus* and a hypothetical "average fish".

Stochastic long-term population growth rate of *H. amarus* (a-c) and a hypothetical "average fish" (d-f) as a function of perturbation frequency and mortality for three alternative scenarios of perturbation: all age classes affected equally (a, d), only adult age classes affected equally by perturbation (b, e), and only juveniles have mortality from perturbation (c, f).

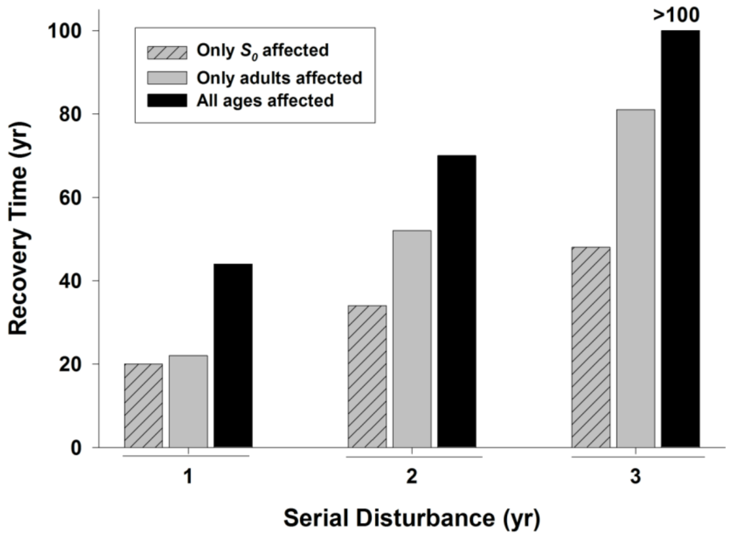

Figure 2 (Chapter 2). ***H. amarus*** **recovery time (yr) from one to three serial perturbations.** Recovery time (yr) from one to three serial perturbations to an equilibrium population; example uses *H. amarus* and the geometric mean proportion of its habitat dried as a perturbation mortality rate.

H. amarus

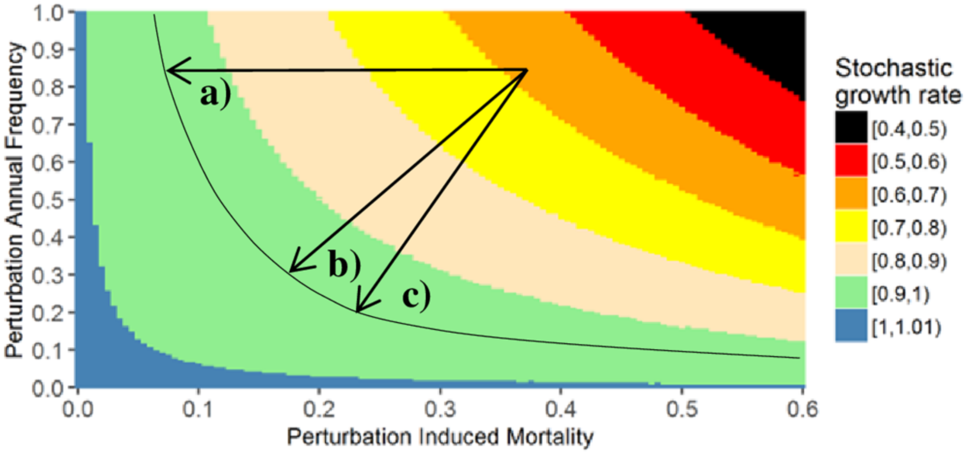

Figure 3 (Chapter 2). Example management alternatives to mitigate flow intermittence.

The overlay arrows represent scenarios in which the contemporary flow intermittence rate and extent (originating at $\lambda = 0.68$) are adjusted to restrict declines in population growth rates to < 5% per year (i.e., $\lambda \geq 0.95$).

Scenarios:

a) annual freq. unchanged (0.83), $S_{(E)} \approx 0.08$.

b) annual freq. reduced to ≈ 0.3, $S_{(E)} \approx 0.17$.

c) annual freq. reduced to ≈ 0.2, $S_{(E)}$ unchanged (0.23).

Chapter 2 Appendix

MITIGATION OF RECURRENT PERTURBATIOS IS AN IMPORTANT GOAL FOR CONSERVATION OF FRESHWATER FISHES

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S1.4. A 12-year record of the spatial extent of river drying, survival to river drying ($S_{Ei,}$), and intermittence mortality (*E*) in the Isleta Reach.

S1.5. Ten matrices representing a 12-year record of flow conditions in the Isleta Reach.

S1.6. Example R code to calculate the stochastic growth rate. (DOCX; R code)

S1.1 Table. Terms, symbols and definitions.

age truncation	mortality of adults in a population that reduces mean age of breeders and diminishes future reproductive potential, also known as juvenescence or longevity overfishing.
asymptotic	the theoretical demographic conditions attained when vital rates and the environment are stationary.
E	environment-caused mortality that augments natural mortality.
F_i	age-specific fecundity, number of eggs.
flow intermittence	the cessation of flow in a running-water ecosystem.
Isleta Reach	A segment of the Rio Grande, New Mexico, U.S.A. This reach is an 85.5 km river segment bounded by diversion dams at Isleta (upstream) and San Acacia (downstream).
λ_1	the leading eigenvalue of the transition matrix, the asymptotic population growth rate under stationary conditions.
λ_t	the observed population growth rate at each time-step in the simulations ($\lambda_t = N_t/N_{t-1}$).
M	natural mortality.
middle Rio Grande	as used herein, that portion of the Rio Grande of New Mexico, USA, extending downstream from Angostura Diversion Dam (north of Albuquerque) to the head of Elephant Butte Reservoir, a distance of approximately 241 km.
n_i	age-specific abundance in a population vector, or the relative abundance when population size is normalized ($\sum n_i = 1$).
perturbation	a deviation of a system from its normal state caused by an outside influence.
perturbation mortality	mortality associated with a perturbation.
prospective simulation	prospective demographic simulation is conducted independent of patterns of variation. Prospective demographic simulation employs deterministic calculations of population growth, typically beginning with a stable-stage population vector at equilibrium.
population structure	the relative fraction of the population in each age class.
retrospective simulation	retrospective demographic simulation looks back on an observed set of matrices to determine how much the variance in a parameter value contributed to the variance in λ. In this study, retrospective demographic simulations utilize a time-variant, age-based, post-breeding, birth-pulse, density independent model.
S_i	age-specific survival probability of reaching the next age class
S_E	survival rate to environmental mortality, a multiplier of natural mortality
stable age distribution	an asymptotic stable condition in population age structure that will be attained when vital rates and the environment are stationary.
stationary	no change in variation over time.
transient variation	random variation in vital rates caused by fluctuations in the environment.
vital rates	age-specific survival rates and age-specific fecundities.

S1.2 Table. "Natural" baseline transition matrix (matrix A1; perennial conditions) for six age classes at $T_{max} = 4$. The average adult survivorship rate employed in baseline simulations was 0.35, which coincides with an approximate maximum longevity of age 4+.

Transition matrix A1 – no river drying.					
Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
0	0.35 • 665	0.35 • 1232	0.35 • 1884	0.35 • 2397	0.35 • 3415
0.001929	0	0	0	0	0
0	0.35	0	0	0	0
0	0	0.35	0	0	0
0	0	0	0.35	0	0
0	0	0	0	0.35	0.35

S1.3 Table. Transition matrices (A2, A3, and A4) for six age classes at $T_{max} = 4$ used to simulate different age-specific responses to river drying. Note: The average annual rate at which river drying occurred in the Isleta Reach was 0.83. The average mean proportion of the reach that dried was 0.23; survival rate after drying 1-0.23 = 0.77. This figure can be found in calculations for hypothetical scenario-specific transition matrices.

Transition matrix A2 – river drying affects all age classes equally					
Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
0	0.77 • 232.75	0.77 • 431.2	0.77 • 659.4	0.77 • 838.95	0.77 • 1195.25
0.001485	0	0	0	0	0
0	0.77 • 0.35	0	0	0	0
0	0	0.77 • 0.35	0	0	0
0	0	0	0.77 • 0.35	0	0
0	0	0	0	0.77 • 0.35	0.77 • 0.35

Transition matrix A3 – river drying only affects adults					
Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
0	0.77 • 232.75	0.77 • 431.2	0.77 • 659.4	0.77 • 838.95	0.77 • 1195.25
0.001929	0	0	0	0	0
0	0.77 • 0.35	0	0	0	0
0	0	0.77 • 0.35	0	0	0
0	0	0	0.77 • 0.35	0	0
0	0	0	0	0.77 • 0.35	0.77 • 0.35

Transition matrix A4 – only age 0 affected by river drying.					
Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
0	232.75	431.2	659.4	838.95	1195.25
0.001485	0	0	0	0	0
0	0.35	0	0	0	0
0	0	0.35	0	0	0
0	0	0	0.35	0	0
0	0	0	0	0.35	0.35

S1.4 Table. A 12-year record of the spatial extent of river drying, survival to river drying ($S_{Ei,}$), and intermittence mortality (E) in the Isleta Reach. Simulated annual time step rate of 0.833 and a mean annual proportion of reach drying (when drying occurs) of 0.231.

Year	**Length Dry (km)**	**Proportion Dry (PD)**	S_{Ei} **(1.0 - PD)**	**Intermittence mortality** (*E*)**;** –*ln* (S_{Ei})
2004	49.89	0.584	0.4160	0.8770
2005	9.66	0.113	0.8870	0.1199
2006	15.29	0.179	0.8210	0.1972
2007	15.29	0.179	0.8210	0.1972
2008	0.00	0.000	1.0000	0.0000
2009	0.00	0.000	1.0000	0.0000
2010	14.97	0.175	0.8250	0.1924
2011	21.24	0.249	0.7510	0.2863
2012	37.30	0.436	0.5640	0.5727
2013	17.69	0.207	0.7930	0.2319
2014	5.54	0.065	0.9350	0.0672
2015	10.30	0.121	0.8790	0.1289

S1.5 Table. Ten matrices representing a 12-year record of flow conditions in the Isleta Reach. NOTE: the following ten matrices represent unique transition matrices for the 12-year period of Isleta Reach intermittence. Two years (2008-2009) had no drying and represented equilibrium conditions (frequency 2/12). Of the remaining nine transition matrices, two years (2006-2007) had identical drying (frequency = 2/12) whereas other transition matrices occurred at frequency = 1/12.

Transition matrix A_2004					
Age 0	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 5+**
0	33.8884	62.78272	96.00864	122.15112	174.0284
0.001929188	0	0	0	0	0
0	0.1456	0	0	0	0
0	0	0.1456	0	0	0
0	0	0	0.1456	0	0
0	0	0	0	0.1456	0.1456

Transition matrix A_2005					
Age 0	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 5+**
0	72.2572375	133.86604	204.71073	260.4520275	371.0653625
0.001929188	0	0	0	0	0
0	0.31045	0	0	0	0
0	0	0.31045	0	0	0
0	0	0	0.31045	0	0
0	0	0	0	0.31045	0.31045

Transition matrix A_2006_07					
Age 0	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 5+**
0	66.8807125	123.90532	189.47859	241.0722825	343.4550875
0.001929188	0	0	0	0	0
0	0.28735	0	0	0	0
0	0	0.28735	0	0	0
0	0	0	0.28735	0	0
0	0	0	0	0.28735	0.28735

Transition matrix A_2008_09_equilibrium					
Age 0	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 5+**
0	232.75	431.2	659.4	838.95	1195.25
0.001929188	0	0	0	0	0
0	0.35	0	0	0	0
0	0	0.35	0	0	0
0	0	0	0.35	0	0
0	0	0	0	0.35	0.35

Transition matrix A_2010

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5+
0	66.33375	122.892	187.929	239.10075	340.64625
0.001929188	0	0	0	0	0
0	0.285	0	0	0	0
0	0	0.285	0	0	0
0	0	0	0.285	0	0
0	0	0	0	0.285	0.285

Transition matrix A_2011

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5+
0	61.1783375	113.34092	173.32329	220.5180075	314.1714625
0.001929188	0	0	0	0	0
0	0.26285	0	0	0	0
0	0	0.26285	0	0	0
0	0	0	0.26285	0	0
0	0	0	0	0.26285	0.26285

Transition matrix A_2012

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5+
0	61.1783375	113.34092	173.32329	220.5180075	314.1714625
0.001929188	0	0	0	0	0
0	0.26285	0	0	0	0
0	0	0.26285	0	0	0
0	0	0	0.26285	0	0
0	0	0	0	0.26285	0.26285

Transition matrix A_2013

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5+
0	64.5997625	119.67956	183.01647	232.8505725	331.7416375
0.001929188	0	0	0	0	0
0	0.27755	0	0	0	0
0	0	0.27755	0	0	0
0	0	0	0.27755	0	0
0	0	0	0	0.27755	0.27755

Transition matrix A_2014

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5+
0	76.1674375	141.1102	215.78865	274.5463875	391.1455625
0.001929188	0	0	0	0	0
0	0.32725	0	0	0	0
0	0	0.32725	0	0	0
0	0	0	0.32725	0	0
0	0	0	0	0.32725	0.32725

Transition matrix A_2015					
Age 0	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 5+**
0	71.6055375	132.65868	202.86441	258.1029675	367.7186625
0.001929188	0	0	0	0	0
0	0.30765	0	0	0	0
0	0	0.30765	0	0	0
0	0	0	0.30765	0	0
0	0	0	0	0.30765	0.30765

S1.6. Example R code to calculate the stochastic growth rate

```
#***************************************************************
#R code to calculate the stochastic growth rate
#under different river drying and annual frequency scenarios
#Case 2: River drying affects all ages equally
#Baseline: No river drying
#***************************************************************

#********************
#Load packages
#********************
library(popbio)
library(ggplot2)
library(gridExtra)

#***************************************
#Annual frequency with river drying
#***************************************
f <- seq(0, 1, by = 0.005)

#***************************************************
#Case 2: River drying affects all ages equally
#d: Mean proportion of river reach dried
#***************************************************
d0 <- seq(0, 0.60, by = 0.005)

#*******************************************
#Create all combinations of f and d0
#*******************************************
fd <- expand.grid(f=f, d0 =d0)
fd$d1 <- fd$d0
#***********************************************
```

```
#Store results (stochastic growth rates)
#***********************************************
sg_sim <- sg_app <- matrix(NA, nrow = nrow(fd), ncol = 1)
out_sim <- out_app <- matrix(NA, nrow = nrow(fd), ncol = (ncol(fd)+1))

#************************************************************
#User-defined function
 #Calculates the stochastic growth rate for each scenario
 #saves the outputs in CSV file format
#************************************************************
sg <- function(S0=S0, S1=S1, S2=S2, S3=S3, S4=S4, S5=S5,
               rho1=rho1, rho2=rho2, rho3=rho3, rho4=rho4,
               rho5=rho5, fd = fd){
for(i in 1:nrow(fd)){

  params <- data.frame(S0=S0, S1=S1, S2=S2, S3=S3, S4=S4, S5=S5 , rho1=rho1, rho2=rho2,
                       rho3=rho3, rho4=rho4, rho5=rho5, d0=fd[i,2], d1=fd[i,3])

  #A projection matrix with no river dying (d0 = d1 = 0)
  A1 <- expression(0, S1*rho1, S2*rho2, S3*rho3, S4*rho4, S5*rho5,
                               S0, 0, 0, 0, 0, 0,
                               0, S1, 0, 0, 0, 0,
                               0, 0, S2, 0, 0, 0,
                               0, 0, 0, S3, 0, 0,
                               0, 0, 0, 0, S4, S5)

  #A projection matrix With river drying effect
  A2 <- expression(0, (1-d1)*S1*rho1, (1-d1)*S2*rho2, (1-d1)*S3*rho3, (1-d1)*S4*rho4, (1-
d1)*S5*rho5,
                   (1-d0)*S0, 0, 0, 0, 0, 0,
                               0, (1-d1)*S1, 0, 0, 0, 0,
                               0, 0, (1-d1)*S2, 0, 0, 0,
```

```
                              0, 0, 0, (1-d1)*S3, 0, 0,
                              0, 0, 0, 0, (1-d1)*S4, (1-d1)*S5)

  A1_1 <- sapply(A1,eval,params)
  A2_1 <- sapply(A2,eval,params)

  #Create a list of the 2 matrices
  A12 <- list(A1_1,A2_1)

  #Calculate the stochastic growth rate
  sg12 <- stoch.growth.rate(A12, prob=c(1-fd[i,1],fd[i,1]))

  #Extract the results
  sg_sim[i,] <- round(exp(sg12$sim),3) # based on the simulation
  sg_app[i,] <- round(exp(sg12$approx),3) # based on the Tuljapurkar's approximation method

  #Create a dataframe with f, d1 and sg
  out_sim[i,] <- cbind(fd[i,1], fd[i,2], fd[i,3], sg_sim[i,1])
  out_app[i,] <- cbind(fd[i,1], fd[i,2], fd[i,3], sg_app[i,1])
  }
  colnames(out_sim) <- colnames(out_app) <- c("f", "d0", "d1", "stoc_gr")
  print(out_sim)
  print(out_app)

  #Save the outputs
  write.csv(out_sim, file="out_sim_river_drying_all_age.csv")
  write.csv(out_app, file="out_app_river_drying_all_age.csv")
}#End function

#****************************************************
#Run the function with specified parameter values
#****************************************************
```

```
start <- Sys.time()
sg(S0 = 0.001929, S1 = 0.35, S2 = 0.35, S3 = 0.35, S4 = 0.35,
          S5 = 0.35, rho1 = 665, rho2 = 1232,
          rho3 = 1884, rho4 = 2397, rho5 = 3415,
          fd = fd)

end <- Sys.time()

print(difftime(end, start, units  = "mins"))

#*****************************************
#Load the output and produce a heatmap
#*****************************************
sg_df <- read.csv("out_sim_river_drying_all_age.csv")
sg_df$stoc_gr1 <- cut(sg_df$stoc_gr,breaks = c(0.4, 0.5, 0.6, 0.7, 0.8, 0.9,
1,max(sg_df$stoc_gr)+0.001),right = FALSE)
tiff("fig_river_drying_all_age.tiff", width = 6.18, height = 3, units = "in", pointsize = 10,
compression=c("lzw"), bg = "white", res = 300)
f1 <- ggplot(sg_df, aes(d0,f))
f1 <- f1 + xlab("Perturbation Induced Mortality") + ylab("Perturbation Annual Frequency")
f1 <- f1 + ggtitle("All age classes affected equally") + geom_tile(aes(fill = stoc_gr1))
f1 <- f1 + scale_fill_manual(values=c("black", "red","orange", "yellow", "wheat1", "lightgreen",
"steelblue"), name="Stochastic\ngrowth rate")
f1 <- f1 + theme(plot.title = element_text(hjust = 0.5,size=10))
f1 <- f1 + theme(panel.background = element_rect(fill = "transparent", colour = "NA"))
f1 <- f1 + theme(axis.text=element_text(size=10), axis.title=element_text(size=10))
f1 <- f1 + scale_y_continuous(breaks=seq(0,1,0.1), expand = c(0, 0)) +
scale_x_continuous(breaks=seq(0,0.6,0.1), expand = c(0, 0))
f1
dev.off()
################## END #########################################
```

CHAPTER 3 – MANAGEMENT OF WATER SUPPLY AND WATER SHORTAGES TO SUSTAIN AN ENDANGERED FISH SPECIES

Introduction

The regulation of river flows for agricultural, industrial, or domestic uses produces altered patterns of flow that can negatively impact aquatic life (Poff, 1997; Bunn & Arthington, 2002; Poff et al., 2010; Januchowski-Hartley et al., 2016; Reid et al., 2019; Bonada et al., 2020). Flow regulation changes water quality, and alters the quantity, timing, continuity, and variability of runoff (Blythe & Schmidt, 2018; Palmer & Ruhi, 2019.). Out-of-channel diversion of water contributes to the accumulation of sediments in the river channel by decreasing discharge, and diversion dams influence river slope and hydraulic head (Padilla & Young, 2006). Importantly, water storage, flow regulation, and out-of-channel water diversion can increase the incidence, extent, and annual sequencing of mortality-causing flow intermittence (Horne et al., 2019; Chapter 2, this dissertation). This problem is amplified where barriers to the movement of fish effectively prevent their ability to escape mortality-causing flow intermittence or other impaired habitat conditions (Lennox et al., 2019).

Flow intermittence affects many freshwater lotic habitats globally (Hamilton et al., 2005; Larned et al., 2010; Leigh & Daltry, 2017), notably including rivers in arid mid-latitude, Mediterranean, and semi-arid climatic regions (Tockner et al., 2009; Larned et al., 2010; Skoulikidis et al., 2011, 2017; Stubbington et al., 2018). This perturbation, often seasonal in timing and duration, is projected to become more common with diminished stream flow and drier surface conditions that are forecast for many arid and semi-arid regions as a consequence of consumptive demand for water and reduced water supply linked to climate change (Mu &

Ziolkowska, 2018; Tickner et al., 2020; Pusey et al., 2020; Padron et al. 2020; Erb et al., 2020; Townsend & Gutzler, 2020; Arthington, 2021).

Climate stressed water shortages raise the importance of water delivery efficiency to increase productivity in irrigated agriculture (Habteyes & Ward, 2020). Efficiency in water use can extend the economic productivity of scarce water supplies and limit potential conflict between competing interests in how scarce water resources are managed and allocated (Linstead, 2018). Similarly, in fully appropriated basins and where water demands exceed supplies, it may become economically productive to augment regulated stream flow and improve delivery efficiency of water to limit the incidence of mortality-causing flow intermittence on freshwater biota.

Economic efficiency in water delivery for environmental flow was investigated by Ward et al. (2006), reporting that flow requirements of an endangered fish species can have considerable impacts on agricultural and municipal uses of water from the Rio Grande. Application of crop irrigation technology to improve delivery efficiency of water for environmental flow is not without precedence; such technology has been applied recently to the Rio Grande and Pecos rivers of New Mexico to conserve endangered species (U.S. Bureau of Reclamation, 2006; Tetra Tech, 2014).

Often, water management policy and operations are considered mainly in the narrow context of economic development (Opperman et al., 2020). Historically, incorporating provisions for environmental flow into regional water operations has been difficult to justify economically, leaving the majority of the world's rivers with few environmental flow provisions (Poff et al., 2010). I address this problem by describing an analytic process that integrates demographic data for an endangered fish species, hydrologic data for a river segment with high frequency of seasonal flow intermittence, and cost-effectiveness metrics for alternate water management strategies to achieve an environmental objective. The integrated analyses of demographic and hydrologic data serve to assess how changing patterns in habitat size and flow continuity can affect fish population growth. I also examine how economic productivity of scarce water supplies varies with management adjustments to frequency and extent of flow intermittence utilizing different water transport infrastructure. This integrated analysis offers the potential for systematic examination of a range of possible problem-solution sets for the management of scarce water resources to support an environment that sustains aquatic species and water resources while limiting the economic impacts of that protection to existing water uses.

Original Contribution

Herein, I apply knowledge of how fish population growth rates diminish with greater flow intermittence frequency and extent (Poff et al., 2010; Shenton et al., 2012; Davies et al., 2014; Chapter 2, this dissertation) to establish limits to this form of perturbation that reduce environmental mortality to levels sufficient to sustain a population's short-term capacity for population growth. I also quantify the water-saving potential of water transport technology to maintain environmental flow over a distance determined to be critical for species conservation. Finally, I estimate the water budget of a number of water management alternatives to achieve a species conservation objective over a practical range of flow intermittence conditions to estimate alternative-specific water budgets and cost-efficiency of each alternative.

Example Species and Study Area

I use the Rio Grande silvery minnow (Cypriniformes: Leuciscidae: *Hybognathus amarus*) as an example of a small-bodied, short-lived iteroparous fish species to show how greater flow intermittence frequency and intensity affect population dynamics. This follows Chapter 2 of this dissertation where I indirectly analyze the effects of flow intermittence on *H. amarus* population growth rate by approximating a species natural life history, estimate effective limits of environmental stochasticity, and analyze through simulation many interacting demographic processes within these limits. Herein, I expand upon that work and that of Hatch et al. (2020) by presenting an analytic process that integrates hydrologic and demographic factors to estimate the amount of water needed to supplement in-channel flow to maintain surface water conditions adequate to achieve population growth minimally needed for short-term species survival.

Hybognathus amarus is an endangered fish species (U.S. Department of Interior, 1994) endemic to the Rio Grande Basin of North America (Sublette et al., 1990). The species reaches maturity at age 1 and has a maximum age of 5 in the wild (Cowley et al., 2006), with juvenile survival rates notably lower than adult survival (Chapter 2, this dissertation). The species most commonly occupies potamonic running water ecosystems with moderately variable environmental conditions (Archdeacon et al., 2020) and exhibits physiologic flexibility sufficient to survive some notable physiochemical stressors (e.g., high nutrient loads, late afternoon summer water temperatures exceeding 30C, and summer pre-dawn near-anoxic conditions).

The contemporary distribution of *H. amarus* is confined mostly to the Rio Grande of New Mexico downstream of Angostura Diversion Dam (north of Albuquerque) to Elephant Butte Reservoir, a distance of approximately 150.0 mi. (241.5 km). Large transient changes in *H. amarus* population size (U.S. Fish & Wildlife Service, 2016) have likely been driven in part by recurrent river intermittence since at least the late 1800s (Cowley, 2006). Historians and hydrologists document the ephemeral nature of the Rio Grande in the Mesilla Valley during the late 1800's, 37 years before river flow was regulated by large dams (Lee, 1907; Baldwin, 1938).

Here, I consider the effects of river intermittence on *H. amarus* demography within the Isleta Reach of the Rio Grande, a 53.13 mi. (85.5 km) river reach bounded by cross-channel irrigation diversion dams at Isleta (upstream) and San Acacia (downstream). I assume the effects of flow intermittence on *H. amarus* population growth rates accrue within the Isleta Reach, although with adequate overland (river channel) flow following periods of flow intermittence, significant effects can extend to downstream populations as a consequence of fish transport affected by directional surface water flow.

Methods

While *H. amarus* life history, regional hydrology, and water laws of the Rio Grande may be unique, the methods developed for this study can be applied to other basins and species. Terms and symbols used in this chapter are defined in Appendix Table S1.1.

Assessing Conservation Water Needs

I compiled records of the annual number of days a given 0.5 mile (0.805 km) river segment was observed dry for a six year subset of records of flow intermittency for the Isleta Reach (2009-2014). From this compilation, I estimated the number of days a given 0.5 mile river segment is known to go dry. Maximum and percentile estimates (50th and 75th) were estimated for days that a given 0.5 mile river segment was observed dry. I interpret these statistics as incremental spatial indices of flow intermittence severity that are used in estimates of water volumes needed to supplement in-channel flow to achieve a conservation objective under different severities of flow intermittence. This water volume is expected to vary as a function of annual intermittence frequency and extent of flow intermittence (i.e., environmental mortality). It will also vary by age-specific perturbation scenario. I note that the extent of drying has been found to be a good proxy for an areal measure of river drying (Yu et al., 2019).

To establish a long-term minimal overland (river channel) flow threshold needed to maintain wetted habitat in the Isleta Reach, I examined gaged records of average daily flow (ft^3/sec) from

Bosque Farms (USGS 08331160) and Highway 346 (USGS 8331510) for 2008 and 2009 when there was continuity of surface flow. From these data, and for the period's prevailing climatic and hydrologic conditions, I determine an average daily flow (ft^3/sec) minimally sufficient to avert flow intermittence over most historical seasonal periods of low flow. Likewise, dynamics of river channel rewetting following periods of flow intermittence were used to obtain a point-specific perspective of the flow needed to maintain flow continuity over a given distance. Estimates of the amount of water needed to supplement in-channel flow to achieve my example conservation objective was derived by summing daily volumes of supplemental water needed over all point locations of water input, multiplied by the number of days supplemental water is needed at a given point as determined by intermittence severity spatial profiles.

Demographic Effects of Flow Intermittency

I follow Hatch et al. (2020) and Chapter 2 of this dissertation in using matrix projection models and stochastic methods to explore the effects of environmental perturbations on population growth rates for *H. amarus*. Briefly, Hatch et al. (2020) and Chapter 2 of this dissertation used values of age-specific adult survival of 0.35, which approximates a species with an age 4+ lifespan, whereas a species-specific equilibrium value of S_0 was obtained, given its fecundity at age, by adapting the algorithm of Vaughn and Saila (1976) for a post-breeding census. For additional details see Hatch et al. (2020) and Chapter 2 of this dissertation.

My analysis of transient *H. amarus* population dynamics is founded on a contemporary baseline geometric mean of the annual proportion of river reach dried (0.23) and the annual frequency of flow intermittency (0.83). The contemporary long-term stochastic population growth rate for this combination of perturbation mortality and frequency is 0.68 when estimated from an observed 12-year period in the Isleta Reach (2021). This estimate is consistent with the age truncation of contemporary *H. amarus* populations inferred by (Hatch et al., 2020) and it is consistent with recent observed episodic annual declines in *H. amarus* abundance (USFWS, 2016).

The estimated amount of water needed to supplement in-channel flow to achieve a conservation objective will vary by water transport losses, water transport methods, and age-specific perturbation scenario. In my analysis I assume that all age classes are equally affected by river drying. This scenario poses a significant risk to species resilience and places populations at greater risk of extinction than adult- or juvenile-specific perturbation scenarios (Hatch et al., 2020; Chapter 2, this dissertation), therefore representing a "worst case" scenario. All analyses are conducted for an annual time step and at the river reach scale. I note that long-term species' needs for running-water habitat cannot be met if management efforts are directed exclusively at short time horizons and at the microhabitat scale when environmental stressors, such as flow intermittence, represent system-level factors operating hierarchically at greater temporal and spatial scales (Frissell et al., 1986).

Short-term Management Objective

When demand for extractive water use exceeds water supply, and under conditions of moderate to severe drought that leads to flow intermittence, species sustainability is likely to be attained only when adequate environmental flows are provided and legally protected. But many forces exist for conservatism in the management of scarce water resources – for maintaining the status quo for out-of-channel water use. This is principally because any possibility of reductions in water supply represents heightened risk to the sustainability of rural agriculture-based economies, although possibilities exist to reduce this risk with added provisions for efficiency in water transport and out-of-channel applications of water. Meanwhile, until environmental flows are provided and legally protected, species conservation strategies will generally remain reliant on short-term minimalist strategies to stem the loss of population size for a species like *H. amarus*. Implementation of short-term solutions, such as evaluated here, are imperative because finding equitable long-term social-ecological solutions for environmental flow will fall to the future, likely following a complex and lengthy process of social, economic, and political transformation.

When water shortages occur, managers may find it necessary to support minimum short-term population growth rates at levels that are intended only to sustain the species over short time periods. For example, limiting short-term declines in stochastic *H. amarus* population growth rates to <5% loss per year (i.e., $\lambda \geq 0.95$) would not sustain the species over the long-term, but would maintain, in the short-term, a relatively robust capacity for future population growth except for circumstances of critically low population abundance. An objective such as this could facilitate least-cost water shortage management strategies applied to short-term species conservation that operate to minimize marginal tradeoff adjustments between economic sectors dependent on water extraction and water applied to ecosystem services uses (Hulsmann et al., 2019).

Alternate Water Management Scenarios

With sufficient water resources, overland (river channel) water transport is well suited to restrict annual frequency and extent of river drying to achieve conservation objectives. Where and when water resources are limiting, efforts to achieve management objectives may benefit from more efficient methods of water transport that result in reduced environmental demand for supplemental water. Herein, I explore the efficiency and practicality of utilizing a water-conserving lined canal to transport water with multiple lateral branches along the canal that provide spatial options for supplemental water input to augment flow in intermittent river segments (King et al., 2006). Many management options exist that employ lined canals for water transport. Herein, I focus on options that maximize the use of water reclaimed following other beneficial uses to minimize marginal tradeoff adjustments needed between existing water rights claimants.

As examples, I present management options to adjust λ to ≥ 0.95 that involve two water transport options: 1) overland (river channel) delivery, and 2) water transport using a lined main canal (King et al., 2006) with multiple, strategically spaced, lateral points of water input to the river. My analysis of management scenarios that incorporate lined canals for water transport includes four combinations of constraints on annual frequency and extent of flow intermittence to sufficiently limit added mortality from flow intermittence to achieve the example management objective.

In my analysis, average water demand, economic damage, water savings, and equivalent annual costs are compared across water management scenarios. I assume $990.56 per acre-foot of water savings (King et al., 2006) and $50 per acre-foot economic damage per acre foot of reduced flow for consumptive use (Ward et al., 2006). This example involves an endangered fish species having no commercial value; hence, there is no economic damage associated with the loss of fish due to flow intermittence.

The quantity of water saved is the primary benefit of channel lining. Assessments of its value must be considered against its cost. For my example, I use the cost estimate of lined canals presented in King et al. (2006) based on typical lining thickness, reinforcing-steel, and labor costs typical for the general area of Las Cruces, New Mexico and El Paso, Texas. King et al. (2006) present a high estimated cost of $41/ linear ft. For my example addressing the need for wetted habitat to conservation goals for *H. amarus* in the Isleta Reach, the practical limits of a lined canal for efficient transport of supplemental water for environmental flow is 7.0 miles (11.27 km; extending roughly from just downstream of Isleta diversion dam to one river mile downstream of Los Lunas at NM Hwy 49), with multiple lateral branches (piped conveyances), extending the lined canal distance by approximately a mile, for a total estimated cost of $1,731,840.

The scope of analysis of water management scenarios is summarized in Table 1. These scenarios are examples of an infinitely broad set that reflect variable combinations of hydrologic conditions and demographic histories that present different management challenges and opportunities for adaptive approaches for *H. amarus* conservation. Management scenarios are illustrated on the heat map of stochastic long-term population growth rate of *H. amarus* (Fig. 1), which is described in greater detail in Chapter 2 (this dissertation). The overlay arrows represent scenarios in which the contemporary flow intermittence rate and extent (originating at $\lambda = 0.68$) are adjusted to restrict declines in population growth rates to < 5% per year (i.e., $\lambda \geq 0.95$). Each management scenario has unique implications for the estimated amount of supplemental water needed to achieve the management objective.

Incorporation of capital investment and periodic maintenance costs are needed for a comprehensive analysis of management options utilizing efficient water transport infrastructure to restrict annual frequency and extent of river drying. Such costs can be incorporated in analyses using equivalent annual cost accounting methods (Ward et al., 2019) that reflect initial capital investment in water transport infrastructure, longevity of beneficial effects, and investment in water resources for each management scenario. In my annual cost accounting analysis of lined canal water transport scenarios, I assume water transport in a 7-mile canal, multiple short lateral canals totaling 1.0 mile to convey water from the main canal to the river, 6% discrete compound interest, and 50 year productive use of the lined canal system.

Results

Two widely separated river segments in the Isleta Reach, separated by about 11 miles (18 km), have high annual probabilities of drying. Each segment has a characteristic pattern of flow intermittence that gradually increases in duration with distance downstream to a maximum point, and then resumes perennial flow relatively abruptly (Fig. 2, panels a and b). Illustrated are estimates of days a given 0.5 mile river segment has been observed dry (i.e., flow intermittence severity). These estimates vary seasonally, with greater estimated flow intermittence severity during July and August, correlating with greater rates of evaporation and transpiration, compared to September and October when reduced rates of evaporation and transpiration prevail.

The pattern of flow intermittence in the Isleta Reach appears to vary with the elevation of the streambed relative to that of adjacent segments of drain canals that parallel the river. Differences in streambed and adjacent drain canal elevations appear to establish a hydraulic gradient that directs subsurface flow toward the lower elevation (Fernald et al., 2010; Wondzell, 2011; Godsey & Kirchner, 2014). I speculate that subsurface transport capacity and flow direction depends on the extent and permeability of river and riparian sediments, hydraulic conductivity of sediments, as well as the local hydraulic gradient (Prancevic & Kirchner, 2019; Fetter, 2001). Given this, it would be reasonable to expect that flow intermittence may be increased when local hydraulic gradients move away from the river channel. Flow intermittence severity is expected to change as these parameters vary spatially. As the prevailing hydraulic gradient slopes toward the river, it has been my observation that perennial river flow prevails.

To establish a long-term minimal overland (river channel) flow needed to maintain wetted habitat in the Isleta Reach, I examined gaged records of average daily flow (ft^3/sec) for 2008 and 2009 when there was continuity of surface flow in the Isleta Reach. From these records I estimate that an average daily flow of 150 ft^3/sec (approximating the 10th percentile), over an average period of 109 days/year (average of maximum annual duration of flow intermittence), to be minimally sufficient to avert flow intermittence over most historical seasonal periods of low flow in the upper Isleta Reach. Over an annual cycle, this totals 32,430 ac-ft/yr for the reach.

In the lower Isleta Reach, I estimate an average daily flow of 50 ft^3/sec (approximating the 10th percentile), is required over an average period of 89 days/year (average of maximum annual duration of flow intermittence) to be minimally sufficient to avert flow intermittence over most historical seasonal periods of low flow in the lower Isleta Reach. Over an annual cycle, this totals 8,826 ac-ft/yr. Total estimated average overland (river channel) flow needed under contemporary conditions to maintain wetted habitat in the Isleta Reach (upper and lower segments subject to flow intermittence) is 41,256 ac-ft/yr.

I examine if a correlation exists between an upstream two-day moving average of increasing flow (ft^3/sec) measured at the USGS Bosque Farms gauge and a three-day delayed record of the downstream length of river that was rewet. These dynamics were used to obtain an estimate of the flow needed to maintain overland (river channel) flow over short-spatial and temporal scales. Although a broad confidence interval exists for this relationship (Appendix Fig. S1), I infer that 10.0 ft^3/sec will marginally sustain wetted habitat over a 1.0 mile river segment (Appendix Fig. S1). In practice, this relationship would be more accurately determined by site-specific field trials.

Among the management scenarios, water resources needed for environmental flow is greatest for overland (river channel) water delivery at all levels of intermittence severity (Fig. 3). For management scenarios that utilize lined canals (Fig. 3; scenarios 2a-2d), water resources needed for environmental flow increase with decreased frequency of flow intermittence, with concurrent flow intermittence adjusted to restrict declines in population growth rates to $< 5\%$ per year (i.e., $\lambda \geq 0.95$).

Among the management scenarios, annual water savings increase with decreasing extent of flow intermittence, decrease with decreasing frequency of flow intermittence, and increase proportionately with increasing severity of flow intermittence (Appendix Fig. S2). Benefits of water savings increase with decreasing extent of flow intermittence, increase inversely with frequency of flow intermittence, and increase with severity of flow intermittence (Appendix Fig. S2). Among lined canal scenarios, the potential for water savings are greatest for scenario 2a involving the highest annual frequency of flow intermittence (0.83) reflective of contemporary conditions, but involving the lowest extent of flow intermittence ($S_{(E)} \approx 0.08$; flow intermittence extent of 4.25 mi [6.84 km]).

Among management scenarios involving lined canals, estimates of equivalent annual costs increase with increasing annual frequency of river drying and the lowest extent of flow intermittence (Appendix Fig. S3, scenario 2a). The opposite hydrologic conditions result in lower equivalent annual costs (Appendix Fig. S3, scenario 2d).

I use equivalent annual costs minus economic damage as an expression of net costs (Fig. 4). According to the basic rule of benefit maximization, in which increasing the total value of scarce resources is presumed desirable, management action should be undertaken if the equivalent annual cost is less than or equal to the average economic damage (Ward, 2002). Among management scenarios involving lined canals, the difference between equivalent annual costs and average economic damage is greatest (Fig. 4) at all levels of intermittence severity for management scenario 2d (the lowest frequency of flow intermittence, and the highest extent of flow intermittence). The difference between equivalent annual costs and average economic damage is smallest (Fig. 4) at all levels of intermittence severity for management scenario 2a (the highest frequency of flow intermittence, but the lowest extent of flow intermittence).

Discussion

An analytic process is presented that integrates demography and hydrology to quantify how changing patterns in habitat size and flow continuity operate to affect growth rates of fish populations (Chapter 2, this dissertation). This process is extended to incorporate economic evaluators to reveal cost-effectiveness of a number of water management strategies. The integration of these three perspectives of impacts of unstable hydrologic conditions can aid managers in establishing limits of flow intermittence to reduce associated fish mortality to levels sufficient to sustain a population's future capacity for growth while limiting the impacts of that protection to existing water uses.

In my example, I examine a practical range of water management alternatives that limit flow intermittence frequency and extent sufficiently to restrict declines in stochastic *H. amarus* population growth rates to <5% loss per year (i.e., $\lambda \geq 0.95$). Whereas limiting short-term declines in stochastic population growth rates to this level would not sustain a species over the long-term, it would maintain, in the short-term, a relatively robust capacity for future population growth. Achievement of this objective in the Isleta Reach of the middle Rio Grande would require improved timing, placement, and quantity of water to mitigate the effects of contemporary levels of flow intermittence.

Study results suggest different management approaches to limit flow intermittency that vary with methods of water transport and severity of flow intermittency. Even with these variable circumstances, distinct patterns in problem-solution sets are evident in the study results that provide managers with much-needed insight to plan effective and flexible management responses to challenges arising from an unstable environment.

For the Isleta Reach of the Rio Grande, the water needed for environmental flow is greater for overland (river channel) transport of water compared to water transported in lined canals. This need increases with intermittence severity and, for overland (river channel) transport scenarios, will often exceed the water supply. In contrast, the demand for water for all management scenarios involving lined canals is estimated to be less than that of overland (river channel) transport, but progressively increases with decreased frequency of flow intermittency with concurrent increased extent of flow intermittency (e.g., Fig. 3, scenario 2d). The possibilities for water savings from lined canal transport are greatest in circumstances of higher intermittence frequency with concurrent decreased extent of river drying (e.g., Fig. 3, scenario 2a).

For management scenarios involving lined canal water transport, the equivalent annual cost is greatest with higher annual frequencies of flow intermittency joined with lower extents of river drying. Net costs (i.e., equivalent annual costs minus economic damage) are lowest for overland (river channel) water transport because there is no infrastructure cost. However, reliance on overland (river channel) water transport may be risky for species conservation because demand for water, including high water transport losses, will often exceed water supply. Among management scenarios involving lined canals, equivalent annual costs are lowest relative to economic damage for scenario 2a, i.e., for higher annual frequencies of flow intermittency coupled with lower extents of river drying (Fig. 4).

Over the period of 2003-2012, the U.S. Bureau of Reclamation has annually applied an average of 37,182 AF of water to environmental flow in the middle Rio Grande (Tetra Tech, 2014). This approximates my slightly higher estimates of the amount of water needed to address all but the most extreme needs for a specific management objective to conserve *H. amarus* in the Isleta Reach. I observe that the water applied by the Bureau of Reclamation in the past to limit the impacts of flow intermittency has primarily been used to regulate the rate of river recession over two river reaches of the middle Rio Grande. Whereas regulating river recession rates can influence immediate incidence of *H. amarus* mortality, the inter-annual impacts of this action on population dynamics seem uncertain since water so applied generally reduces the amount of water ultimately needed later in the year to maintain the most important determinants of population growth, namely a strong first adult age class and high survival of the first two adult age classes (Hatch et al., 2020). Short-term aggressive management strategies, such as timed water releases from upstream reservoirs conducive to spawning, along with aquaculture-based strategies to supplement cohort abundance, may be necessary periodically to ensure species persistence in unstable environments (Chapter 2, this dissertation).

Opperman et al. (2019) address system-scale policy and management of large-scale water storage and transport infrastructure to provide environmental flows. Likewise, selected aquifer protection measures are reviewed by Ward et al. (2019). Water shortages can be addressed by demand regulation (e.g., water use conservation, cutbacks, and limits on irrigated crop demands for water), conjunctive use of irrigation infrastructure and irrigation water excesses, coordination among water users, water reuse, or short- and long-term supply-related solutions (e.g., water leases, appropriation, and transfers of existing rights). Where legally authorized, storage of water reserved for environmental flow would greatly expand options for managers to adapt to unpredictable environmental conditions (Ackerman et al., 2014; Habteyes & Ward, 2020). All of these approaches to water shortage management should be evaluated for application in the middle Rio Grande.

Economic impacts of tradeoff adjustments between water applied to environmental flow and traditional out-of-channel consumptive purposes is problematic because formal markets do not regulate citizen accrual of benefits from most environmental flow programs – they represent extra-market outcomes. In this sense, water resources that may be applied to environmental purposes lack profit margin criteria that are commonly used by managers to evaluate market activities in the private sector. Still, the economic principles underlying water policy decisions are often founded on fundamental concepts of benefits and costs (Ward & Michelsen, 2002).

A major challenge in the management of scarce water resources is the reduction of opportunity costs of instream flow reservations. Efficiency in water use and water transport can extend the economic productivity of scarce water supplies (Ward & Michelsen, 2002) and limit potential adverse impacts on an aquatic biota from the allocation of water resources to out-of-channel uses. For benefit maximization, management action should be undertaken if the equivalent annual cost is less than or equal to the average economic damage (Ward & Michelsen, 2002). See, for example, scenario 2d, Fig. 4 at all levels of intermittence intensity.

When preferred water management options involve tradeoff adjustments between economic sectors, optimization modeling can be employed to identify water use restrictions that minimize economic losses among consumptive interests in the use of scarce water resources (Baah-Kumi et al., 2020). However, in my example, non-equilibrium conditions of transient fish population growth rates in response to time-varying hydrologic conditions, along with variable impacts of water shortages to different economic sectors, create ill-defined, often short-term and dynamic management situations. Such circumstances may practically preclude optimal mathematical solutions (Arthur, 2021) to the management challenge of allocating scarce water resources to maintain an environmental state adequate for sustaining aquatic species while limiting the impacts of that protection to existing water uses. In contrast, study results presented here reveal the possibility of multiple options for least-cost water shortage management under conditions of time variant flow.

Environmental Flow Under Existing Regulatory Authorities and Practices

Water resource management in New Mexico has evolved under a regulatory-intensive design that incorporates elements of common law, state regulations and statutes, federal statutes, and federal compacts and treaties that govern how water resources in basins bisected by geopolitical lines are shared between competing water rights claimants, and between states and nations, including tribal lands. Significant among federal laws that may affect the management of water resources is the Endangered Species Act (ESA; 16 U.S.C. §1531 et seq.), which provides substantive protections to any species listed by the federal government as endangered or threatened.

The Rio Grande bisects international and interstate boundaries, including those of Colorado, New Mexico, Texas, and Mexico. As an international river, the Rio Grande is subject to terms of an international treaty agreement established in 1906 between the United States and Mexico that specifies how the basin's annual water resources will be apportioned between the countries. As an interstate river, the Rio Grande is also subject to terms of the Rio Grande Compact, an agreement between the states of Colorado, New Mexico, and Texas to stabilize the water allocation pattern in the upper Rio Grande as it existed in 1929 (Hinderlider et al., 1938; Clark, 1987; Ingram, 1990; King & Maitland, 2003; Ward et al., 2006), the year that a preliminary agreement had been reached between the states about the interstate allocation of waters of the Rio Grande. This agreement was made, perhaps under the mistaken presumption that the hydrologic record at that time adequately represented hydrologic stochasticity observed or possible in the system, including the effect of future anthropogenically altered flows in downstream river reaches, that variance would remain stationary around the reference hydrologic time series, and that future water supplies would be similar to those of the past (Milly et al., 2008; Peel, 2015; Erb et al., 2020; Townsend & Gutzler, 2020).

The flow regime of the middle Rio Grande has been profoundly altered under the terms of the Rio Grande Compact, including by consumptive water use in Colorado and New Mexico (Townsend & Gutzler, 2020) and by efforts of New Mexico to meet downstream water delivery obligations to Elephant Butte Reservoir, principally to benefit irrigators of southern New Mexico (principally the Mesilla Valley of New Mexico) and northern Texas (the ninety-mile-long El Paso-Juárez Valley). Given these circumstances, a logical question is if the burden of environmental flows for an endangered species should be distributed equitably amongst the parties that contribute to the problem of species endangerment linked to water shortages, and that share in the benefits of the Compact.

As practiced in New Mexico and many other prior appropriation states, state water law has minimized risk of capital investment for private stakeholders (DuMars & Tarlock, 1989; Johnson & DuMars, 1989). But the system possesses only modest self-regulating mechanisms of competitive private enterprise (Laitos, 2002), or even that of a positive feedback monopoly, in which managers seek to maximize profit margins. Water resources are rarely managed efficiently or consumed in response to the highest market demand. These resources are often undervalued and over-consumed, which can generate external costs (Laitos, 2002) that are typically absorbed or ignored by society.

Water for environmental flow could be partially met by reclaiming some of the irrigation water excesses that infiltrate soils and collect in drain canals adjacent to the river channel, where, in conflict with state water law, there is no immediate or proximal benefit to agricultural interests (see generally Brown, 2000). Interception of irrigation water excesses in drain canals that closely parallel the river can profoundly alter surface-water / groundwater connections and river base flows, often representing a large component of total river discharge (Miller et al., 2016; Rumsey et al., 2020). I caution that where water resources are already over appropriated, efficiency in consumptive water use can contribute to environmental flow only if it results in a reduction in consumptive use and is joined by measures to prevent future expansion or intensification of consumptive use (Linstead, 2018).

Agricultural demand for water is tied to the growing season for crops and directly contributes to seasonal water shortages for environmental purposes. The time and spatial frames of reference normally useful in establishing the long-term water supply used for planning consumptive water needs is generally mismatched to time and space scales appropriate for planning environmental flow needs. Planning for environmental flow needs involves system-level factors operating at spatial extents of river reaches and for time frames minimally defined in terms of a species' natural lifespan. These differences in frames of reference for problem solving and planning are difficult to reconcile, and can impede adoption of effective strategies to meet the plurality of water needs for consumptive and environmental flow purposes.

Conclusions

The problems that managers of water-deficient aquatic systems face are highly variable and it is rarely possible to provide simple prescriptive guidance for matching specific management techniques (alternatives) to certain types of problems or conditions. As I identify in Chapter 2 (this dissertation) it's possible that alleviating intermittence may not fully mitigate perturbation mortality. A manager should be cognizant of all possible sources of perturbation mortality, such as additional mortality during persistent periods of low flows that isn't accounted for by the extent of intermittence (e.g., elevated predation risk, altered physicochemical features like oxygen, temperature). In these circumstances, program monitoring is necessary to determine whether management actions have placed aquatic species and water resources on a trajectory towards agreed-upon desired future conditions. Assessments of management programs may help to reveal information deficits and technical problems that directed research may be able to rectify. Likewise, program monitoring and evaluation, when focused on problem identification, can reveal limiting factors that underlie fish communities that fail to achieve their full potential (e.g., Hatch et al., 2020). Finally, monitoring and evaluation of contemporaneous dynamic variables is required to adapt management practices to new circumstances. Without monitoring, innovation is discouraged, new knowledge is applied too slowly, and inefficiencies persist to the detriment of aquatic biota, water resources, and the public good.

Sustainability management of short-lived iteroparous fish species in habitats periodically subject to flow intermittence depends on limiting out-of-channel uses of water (Richter et al., 2003) in ways that result in relatively robust rates of fish population growth and that incorporate consideration for financial, hydrologic, technical, and legal constraints that are inherent in contemporary water resource management (DuMars & Tarlock, 1985; Richter, 2010; Poff et al., 2010; Habteyes & Ward, 2020). Selection of effective management strategies requires an interdisciplinary and integrated assessment (Arthington, 2021) to discover the mix of management elements that best address the plurality of needs (Oldekop et al., 2016) of the aquatic biota, in addition to the needs of water users that deplete or impair river ecosystems.

Integrating considerations of species' demography and hydrology, along with implications of water management for a regional irrigated agriculture-based economy is necessary for species' conservation and for sustainability management of freshwater social-ecological systems. My work shows several things. First, there are many ways that resource managers can mitigate recurrent sources of perturbations that harm a species of concern. Second, sustainability management of aquatic species and water resources are problems of natural and economic sciences; both are concerned with intertemporal choices in the usage of scarce and universally vital natural resources. Third, in periods of water shortage, management strategies should include considerations of equitable allocation of water deficits amongst beneficiaries of water use that enable river flows that sustain the biota (Hahn, 2021). Finally, avenues to the sustainable management of water resources and aquatic biota can be obtained through intensive conservation and reclamation efforts, but societal and legal transformations (Gleick, 2018) may be necessary before the decision-making process in the allocation of water resources routinely includes considerations of environmental needs, incorporates considerations of equity into cost-benefit analysis of management options (Hahn, 2021), and extends through phased processes of new or adapted policy as needs arise.

Achievement of management objectives where water resources are limiting may benefit from improved transport efficiency, timing, placement, and quantity of water to mitigate the effects of contemporary flow intermittence. Canal lining is well suited for these purposes (King et al., 2006; Habteyes & Ward, 2020). The quantity of water saved is the primary benefit to canal lining. Efficiency of water transport can increase the amount of environmental flow and improve timing of water delivery to river segments judged critical for long-term species survival. Likewise, storage of water for environmental flow in existing upstream reservoirs could be used to mitigate adverse impacts of future water shortages (Ackerman et al., 2014; Habteyes & Ward, 2020).

Many management opportunities exist for sustainable human uses of water that simultaneously sustain the aquatic ecosystem upon which people depend. Where water resources are effectively fully appropriated, additional demands for water applied to new uses like environmental flow can only be accommodated by transfers from existing water rights claimants, forbearance of consumptive uses, conjunctive use of irrigation infrastructure and irrigation water excesses, coordination among water users, water reuse, and water conservation, joined by measures to prevent expansion or intensification of consumptive uses (Linstead, 2018; Ward et al., 2001, 2019). During periods of hydrologic abundance, storage of water for environmental flow in existing upstream reservoirs could be used to mitigate adverse impacts of future water shortages. Where alternatives exist for the management of water resources and its multiple uses, a pattern of coexistence must be negotiated that protects aspects of the qualities that each person values. Compromise is necessary if legal mandates, private demands and public support for government action are to be reconciled and combined to produce policy outputs that ensure the long-term sustainability of freshwater social-ecological systems.

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Tables

Table 1 (Chapter 3). Hypothetical water management scenarios.

Hypothetical water management scenarios that restrict declines in stochastic population growth rates to <5% loss per year (scenarios assume all ages are equally affected by flow intermittence).

Water Delivery Method	**Scenario**	**Annual Frequency of River Drying**	**Annual Mean $S_{(E)}$**	**Length of River Drying**
Overland (river channel) transport – continuous flow	1	0	0	0
Lined canal water transport				
	2a	0.83 (unchanged)	0.08	4.25 mi (6.84 km)
	2b	0.50	0.11	5.84 mi (9.405 km)
	2c	0.30	0.17	9.03 mi (14.54 km)
	2d	0.20	0.23 (unchanged)	12.219 mi (19.665 km)

Figures

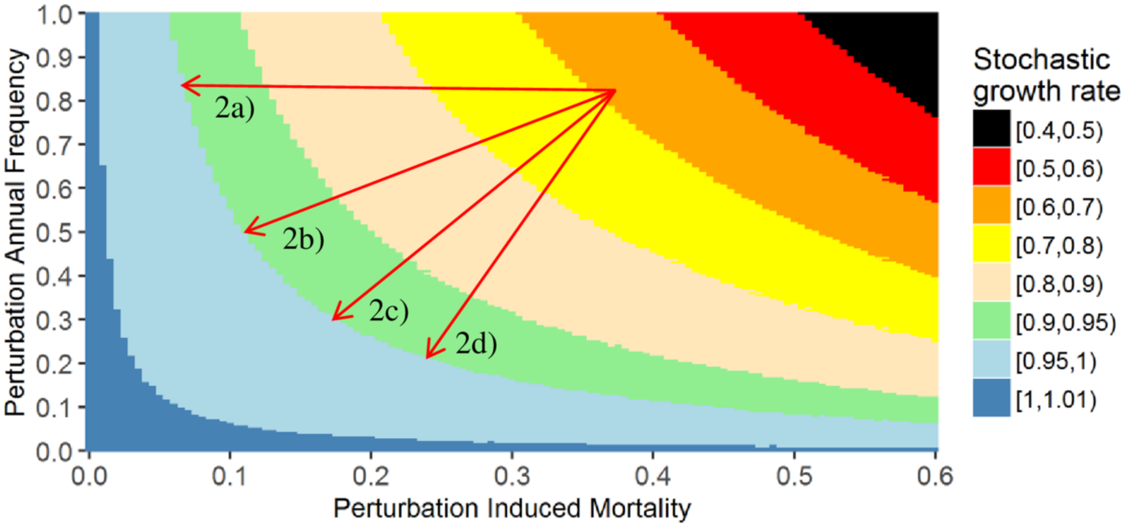
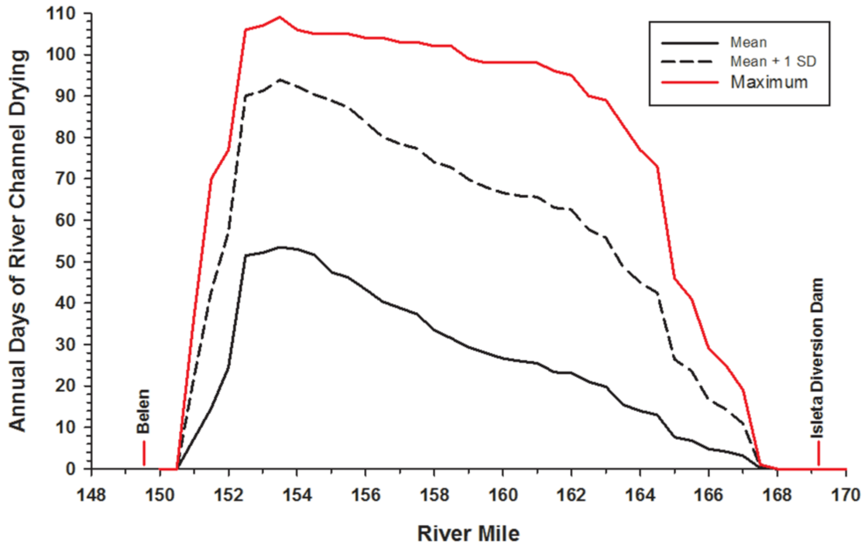


Figure 1 (Chapter 3). Example management alternatives to mitigate flow intermittence (assume all ages are equally affected by flow intermittence).

The overlay arrows represent scenarios in which the contemporary flow intermittence rate and extent (originating at $\lambda = 0.68$) are adjusted to restrict declines in population growth rates to < 5% per year (i.e., $\lambda \geq 0.95$).

a)



b)

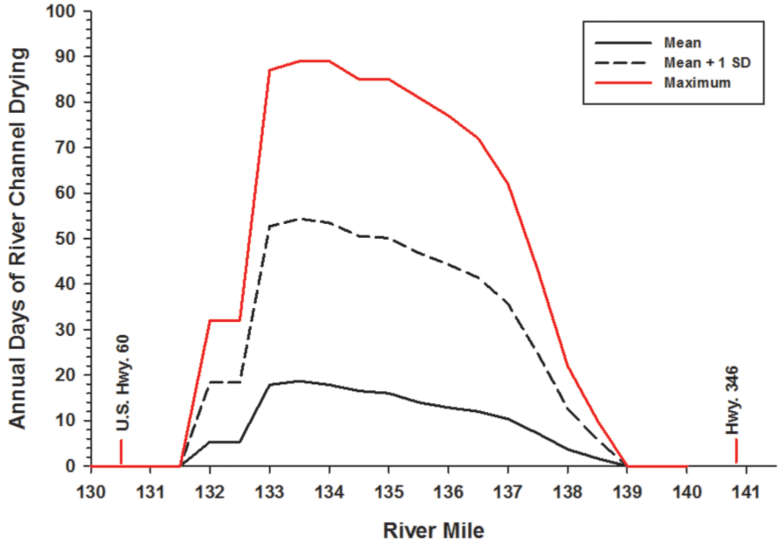


Figure 2 (Chapter 3). The annual number of intermittent flow days (river flow right to left).

The annual number of intermittent flow days observed for half-mile segments of the upper Isleta Reach (pannel a) and lower Isleta Reach (pannel b) at different levels of flow intermittence severity.

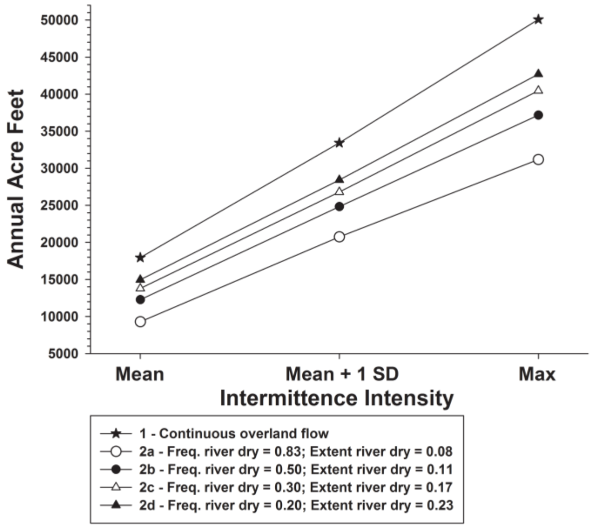


Figure 3 (Chapter 3). Estimates of water demand for management scenarios.

Estimates of water demand for management scenarios that restrict declines in stochastic population growth rates to <5% loss per year utilizing lined water transport infrastructure. See Table 1 for details of water management scenarios.

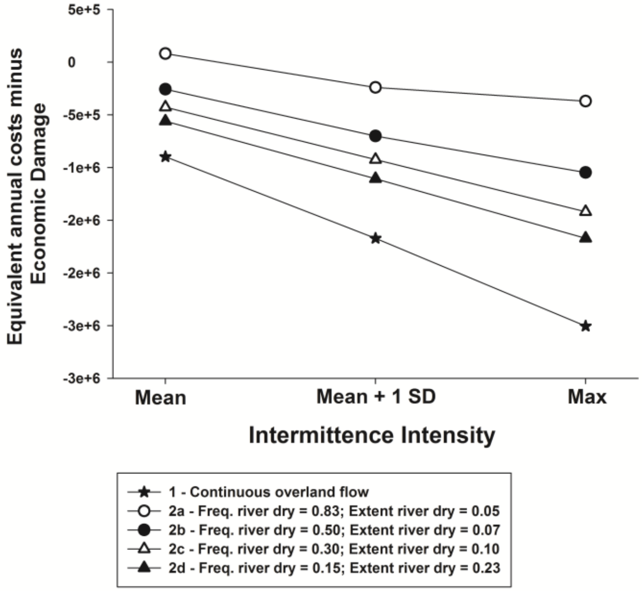


Figure 4 (Chapter 3). Equivalent annual costs minus economic damage (i.e., net costs).

Chapter 3 Appendix

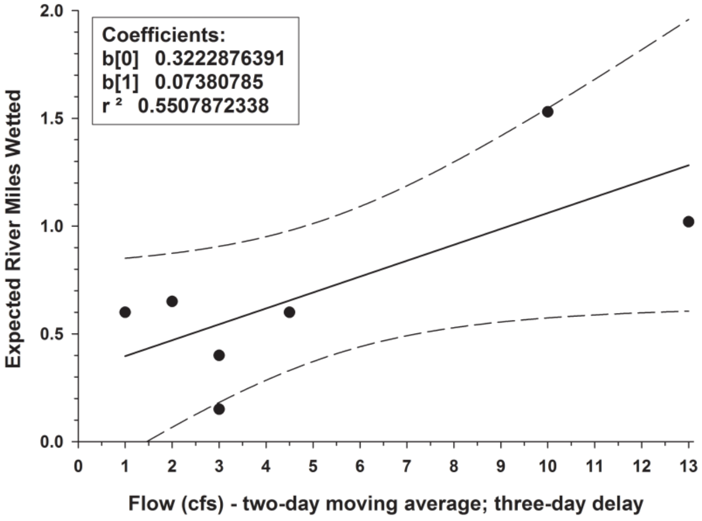
MANAGEMENT OF WATER SUPPLY AND WATER SHORTAGES TO SUSTAIN AN ENDANGERED FISH SPECIES

Appendix Contents List

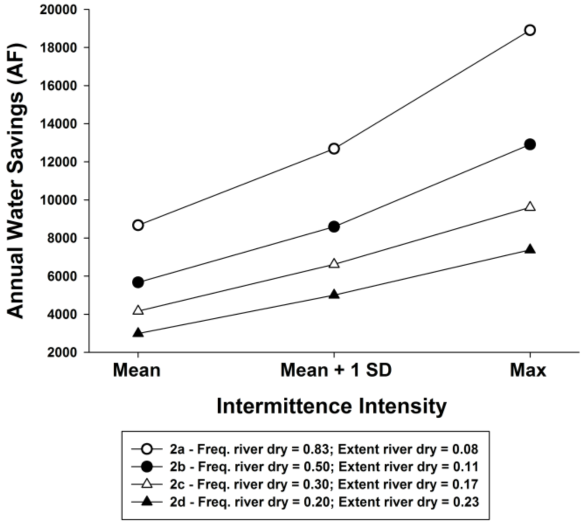
S1.1 Table. Terms, symbols and definitions.

age truncation	mortality of adults in a population that reduces mean age of breeders and diminishes future reproductive potential, also known as juvenescence or longevity overfishing.
conjunctive water use	alignment of water uses to benefit two or more purposes at the same point in time and space (e.g., river channel water transport for ultimate application in crop irrigation that also supports aquatic biota).
economic damage	a monetized per acre foot expression of reduced flow available for consumptive use.
equivalent annual costs	the annual cost of owning, operating, and maintaining an asset over its entire life.
extra-market	formal markets do not regulate citizen accrual of benefits.
flow intermittence	the relatively brief cessation of flow in an otherwise running-water ecosystem.
Isleta Reach	a segment of the Rio Grande, New Mexico, U.S.A. This reach is an 85.5 km river segment bounded by diversion dams at Isleta (upstream) and San Acacia (downstream).
λ (lambda)	the observed population growth rate at each time-step in the simulations ($\lambda_t = N_t/N_{t-1}$).
Middle Rio Grande	as used herein, that portion of the Rio Grande of New Mexico, USA, extending downstream from Angostura Diversion Dam (north of Albuquerque) to the head of Elephant Butte Reservoir, a distance of approximately 241 km.
opportunity cost	the potential benefits foregone when choosing one alternative over another.
natural lifespan	the lifespan reflective of survival rates in an unperturbed natural environment.
perturbation	a deviation of a system from its normal state caused by an outside influence.
perturbation mortality	mortality associated with a perturbation.
population structure	the relative fraction of the population in each age class.
potamon	the warmer and lower gradient portion of a river. Unaltered, the potamon is characterized by slower currents, fine substrate materials, and variety of features of river channel morphology, including large river channels, oxbows, sloughs, and habitats of the floodplain. Autochthonous inputs of organic materials support a preponderance of detritivores, herbivores, and planktivores.
prior appropriation doctrine	the basis for water rights administration in New Mexico, as it is in most other western states. The principal of "priority" in the doctrine's title implies that the water rights claimant with the senior right for "beneficial use" has the superior right to those junior in time. The doctrine is specifically designed to grant usufructuary rights to appropriate water for beneficial purposes. In theory, superiority in right provides an aspect of security for capital investment during

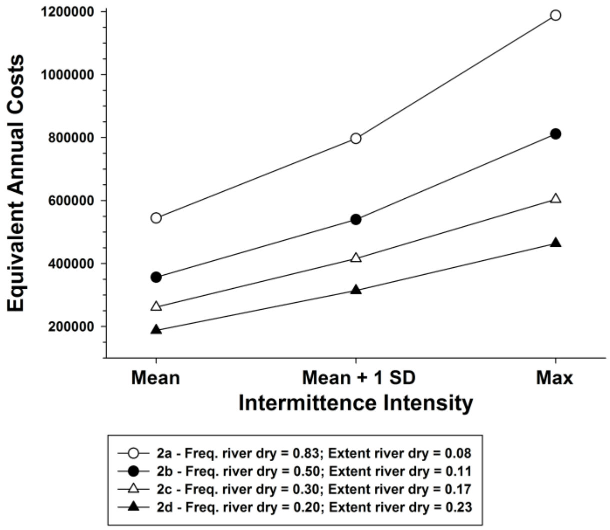
	periods when water demands exceed supplies.
S_i	age-specific survival probability of reaching the next age class.
stationary	no change in variation over time.
stationary time series	time series data in which the probabilistic behavior of every collection of values is identical to that of the time shifted set (i.e., the mean value function is constant and does not depend on time). Stationarity requires regularity in the mean and autocorrelation functions so that these quantities may be estimated by averaging. The variance with strictly stationary data is also stationary. Time series must be stationary so that averaging lagged products over time will be a sensible thing to do. It would be difficult to measure the dependence between successive values of a time series if the dependence structure is not regular.
threshold of probable concern	low lambda values that indicate an impaired capacity for population growth.
transient variation	random variation in vital rates caused by fluctuations in the environment.
vital rates	age-specific survival rates and age-specific fecundities.



Appendix Figure S1. The correlation between an upstream two-day moving average of increasing flow (ft^3/sec) and a three-day delayed record of the downstream length of river that was rewet (linear regression - solid line; 95% confidence interval - dashed lines).



Appendix Figure S2. The estimates of water savings for each lined canal water transport scenario. Water savings represent the differences in water needed for the overland (river channel) transport scenario and the water needed for each lined canal scenario. See Table 1 for details of water management scenarios.



Appendix Figure S3. Equivalent annual costs for each lined canal water transport scenario.