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Recovery Potential Modelling of Pugnose Shiner (*Notropis anogenus*) in Canada

Modélisation du potentiel de rétablissement du méné camus (*Notropis anogenus*) au Canada

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ABSTRACT

In 2002, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed the Pugnose Shiner (*Notropis anogenus*) as Endangered in Canada. Here we assess allowable harm, determine a population-based recovery target, conduct long-term projections of population recovery, and quantify habitat requirements in support of a Recovery Potential Assessment (RPA). Our analyses demonstrated that the dynamics of Pugnose Shiner populations are particularly sensitive to perturbations that affect survival in the first two years of life, and the fecundity of first-time spawners. Harm to these characteristics of Pugnose Shiner life history should be minimized to avoid jeopardizing the survival and future recovery of Canadian populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose abundance recovery targets of at least 1,929 adult fish requiring up to 5 ha of habitat. In the absence of mitigative efforts or additional harm, we estimate that a Pugnose Shiner population will reach this recovery target in 17 to 39 years. These recovery times are expected to increase exponentially with additional harm. However, by affecting at least a 14% increase in survival rates, recovery strategies such as habitat rehabilitation or enhancement can reduce the recovery time of a heavily impacted population by half.

RÉSUMÉ

En 2002, le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué que le méné camus (Notropis anogenus) est une espèce en voie de disparition au Canada. Dans le présent document, nous évaluons les dommages admissibles, nous établissons une cible de rétablissement en fonction de la population et nous quantifions les exigences relatives à l'habitat à l'appui d'une évaluation du potentiel de rétablissement. Nos analyses ont démontré que la dynamique des populations de méné camus est particulièrement sensible aux perturbations qui ont des répercussions sur la survie au cours des deux premières années de vie, ainsi que sur la fécondité des géniteurs de premier frai. Il faut minimiser les dommages sur ces caractéristiques de l'historique de vie du méné camus afin d'éviter de mettre en péril la survie et le rétablissement futur des populations du Canada. En fonction d'un objectif de durabilité démographique (c.-à-d., une population autonome à long terme), nous proposons des cibles de rétablissement de l'abondance d'au moins 1 920 poissons adultes nécessitant jusqu'à 5 ha d'habitat. En l'absence de mesures d'atténuation ou de dommages supplémentaires, nous estimons qu'une population de méné camus pourra atteindre cette cible de rétablissement dans une période variant entre 17 et 39 ans. Cette période de rétablissement devrait augmenter exponentiellement dans la perspective de dommages supplémentaires. Cependant, en supposant une hausse d'au moins 14 % du taux de survie, les stratégies de rétablissement, comme l'amélioration ou la remise en état de l'habitat, peuvent diminuer de moitié la période requise au rétablissement d'une population lourdement touchée.

INTRODUCTION

The Pugnose Shiner (*Notropis anogenus*) is a small, omnivorous minnow of the family Cyprinidae (Scott and Crossman 1973). Endemic to North America, this species occurs at low abundance throughout most of Minnesota, Wisconsin, and Michigan, and parts of Illinois and Indiana. Isolated populations also occur in Indiana, on the Minnesota-Iowa border, and on the shores of Lake Huron (one location in Ontario), Lake Erie (three locations in Ontario), Lac St. Claire (one location in Ontario), Lake Ontario, and the upper St. Lawrence (one location in Ontario; COSEWIC 2002). Pugnose Shiner are found in marshes and the still, clear waters of large lakes and rivers (Scott and Crossman 1973), and are strongly associated with aquatic vegetation for the purposes of food, shelter, and reproduction (Becker 1983).

In 2002, the Pugnose Shiner was designated as Endangered in Canada (COSEWIC 2002) over concerns that the recent disappearance of this species from four of six locations is part of a general trend towards decline and extirpation that is being documented in the United States (reviewed by COSEWIC 2002). Although it is not known why the Pugnose Shiner is declining in Canada, evidence from throughout this species' range points to a loss of pristine watercourses and shorelines with good water quality, clean substrates, and macrophytes (Bailey 1959, Trautman 1981, Scott and Crossman 1973), as well as changes in macrophyte, competitor, and (or) predator assemblages (reviewed by COSEWIC 2002).

In accordance with the *Species at Risk Act* (SARA), which mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation in Canada, Fisheries and Oceans Canada has developed the recovery potential assessment (RPA; DFO 2007) as a means of providing information and scientific advice. There are three components to each RPA: an assessment of species status, the scope for recovery, and scenarios for mitigation and alternatives to activities (DFO 2007). This last component requires the identification of recovery targets and timeframes for recovery, and measures of uncertainty associated with the outcomes of recovery efforts. Here, we contribute to components two and three by assessing allowable harm, identifying recovery targets, quantifying habitat requirements for recovery, projecting recovery timeframes and identifying mitigation strategies for Canadian populations of the Pugnose Shiner. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007, 2009a, 2009b), which uses a population-based recovery target, and provides long-term projections of population recovery under a variety of feasible recovery strategies.

METHODS

Our analysis was in four parts. Briefly, we obtained life history data from the relevant literature to determine patterns of growth, reproduction, survival, and fertility. We then used this life history information to develop age-structured projection matrices that represented the Pugnose Shiner life cycle. Third, we used these matrices to conduct a stochastic perturbation to determine allowable harm. This analysis was conducted according to the precautionary approach, and followed Vélez-Espino and Koops (2007, 2009a, 2009b). Finally, we estimated the habitat required to support a recovered population and the effect of both additional harm and potential recovery efforts on the time to recovery of a typical Pugnose Shiner population.

LIFE HISTORY

Most of what we know about Pugnose Shiner life history comes from a few populations in Wisconsin (Becker 1983, but see Table 1 for a summary of all known life history information). Because these populations are at similar latitudes as populations in Canada and probably share a post-glacial evolutionary history (Zhao *et al.* 2008, Ward and McLennan 2009), we consider them to be representative of Canadian populations for the purposes of this recovery assessment.

To describe the general life history of a typical female Pugnose Shiner, we first used minimum and maximum measures of length-at-age to define 'slow' and 'fast' growth trajectories, respectively; we also defined a 'moderate' growth trajectory that was intermediate between these extremes (Figure 1). For all three of these trajectories, we assumed that fish matured after their first year of life, adult growth was linear, and maximum age was three years (see Table 1). We then obtained estimates of egg-number-at-age and an annual instantaneous natural mortality rate for each trajectory as follows. For egg number, we assumed that the largest (1275 eggs) and smallest (530 eggs) observed values were associated with the largest (59 mm) and smallest (20 mm) age-1 females, respectively, and then used linear interpolation (egg number = 19.1 · TL + 146.95) to estimate egg-number-at-age for all other lengths. To estimate annual instantaneous natural mortality rate, we entered length-at-maturity and maximum length into an online life history tool (Froese and Pauly 2009) that was based on equations in Pauly (1980). Assuming a mean annual water temperature of $10^{o}C$, this tool returned annual natural mortality rates of 1.83, 1.76, and 1.72, respectively, for the slow, moderate, and fast growth trajectories.

As described in the next section, life history uncertainty is useful for generating biologically realistic variation in the Pugnose Shiner life cycle. Therefore, in addition to the uncertainty in length-at-age and associated rates of natural mortality that are described above, we allowed the number of clutches per year to vary between 1 and 2. This uncertainty was based on the fact that life history correlates (Winemiller and Rose 1992) predict two clutches per year, but that Canada's relatively short growing season might limit Pugnose Shiner to one clutch per year.

MODELS OF THE PUGNOSE SHINER LIFE CYCLE

We developed 18 post-breeding, age-structured projection matrices (Caswell 2001); one for each combination of growth trajectory (slow, moderate, or fast), annual instantaneous natural mortality rate (1.83, 1.76, or 172), and clutch size (1 or 2) (Figure 2a). The elements of each matrix were the annual survival probability (s_i) and fecundity coefficient (F_i) of an individual in age class i (Figure 2b). For individuals age-1 and older, s_i was based on the annual instantaneous natural mortality rate that was estimated above. For individuals in their first year of life (YOY), we estimated s_i by solving the projection matrix at equilibrium via an iterative process that used elasticities (see below) for a first iteration through direct perturbation of the projection matrices (Vélez-Espino *et al.* 2006). To estimate F_i, we used the equation

$$1) \qquad F_i = m_i \cdot c \cdot \varphi \cdot s_i,$$

where m_i is the number of eggs per clutch at age i, c is the number of clutches in a season, and φ is the proportion of female eggs (assumed to be 0.5). The mean value of each matrix element across all 18 possible matrices is given in Figure 2c.

ALLOWABLE HARM

We assessed allowable harm within a demographic framework following Vélez-Espino and Koops (2007, 2009a, 2009b). Briefly, we focused on estimates of annual population growth rate (λ) as determined by the largest eigenvalue of the projection matrix (Caswell 2001). Setting equilibrium (i.e., $\lambda = 1$) as the minimum acceptable population growth rate, allowable harm (τ_v) and maximum allowable harm ($\tau_{v, max}$) were estimated analytically as:

$$2) \qquad \tau_v \leq (1/\varepsilon_v)\,[(1 - \Lambda)\,/\,\Lambda] \quad \text{and} \quad \tau_{v, max} = (1/\varepsilon_v)\,[(1 - \Lambda)\,/\,\Lambda],$$

where ε_v is the elasticity (a measure of the sensitivity of population growth rate) of vital rate v, and Λ is population growth rate in the absence of additional harm (see below). For projection matrices, the influence of vital rates on the population growth rate was given by the partial derivatives of λ with respect to e_{kl}, the individual elements of the matrix. Elasticities ($\varepsilon_{kl} = \partial \log \lambda \,/\, \partial \log e_{kl}$) represented the sensitivity of population growth rate to vital rate perturbations.

We estimated Λ as the geometric mean of three λ values: (i) Designation population growth rate ($\lambda_{designation}$), as determined by COSEWIC's criterion "A" for the status assessment of species based on observed or inferred rates of population decline. Under this criterion, a species is listed as endangered if there is evidence of a 70% decline over the last 10 years or three generations (3ς) (i.e., $\lambda = 0.3^{1/10}$ or $\lambda = 0.3^{1/3\varsigma}$), whichever is greatest. By incorporating age-at-maturity, egg number-at-age, maximum age, and natural mortality into a life table analysis, we estimated that Pugnose Shiner have a generation time of ~1.2 years, which is similar to Froese and Pauly (2009; see Table 1), and gives a $\lambda_{designation}$ of 0.67. (ii) Maximum population growth rate at low densities (λ_{max}), as estimated by an allometric production equation for riverine fishes (Randall et al. 1995). Assuming that length-at-maturity was 31.5 mm (Figure 1), mass-at-maturity averaged across the three allometric conversion functions in Table 1 was 1.3 g, and, λ_{max} was 1.82. (iii) The population growth rate at equilibrium (1; $\lambda_{equilibrium}$), which is an important dynamic attractor (Turchin 1995). Therefore, the geometric mean of $\lambda_{designation}$, λ_{max}, and $\lambda_{equilibrium}$ (i.e., Λ) was 1.06.

To incorporate variation in vital rates and its effect on population responses to demographic perturbations, we first calculated the mean and variance of s_i and fertility (f_i) across all 18 matrices (Table 2). We calculated f_i as

$$3) \qquad f_i = m_i \cdot c \cdot \varphi.$$

We focused on f_i instead of F_i because it was important to evaluate the elasticities of vital rates individually, not in combination (see equation 1). We then used computer simulations (MATLAB version 7.7; The Mathworks, Inc., Natick, Massachusetts) to (i) generate 1000 matrices of vital rates that were drawn randomly from a uniform distribution (see Vélez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ε_v of s_i and f_i for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. For each vital rate, we then calculated maximum allowable harm for mean, maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on a geometric mean Λ of 1.06.

Because human activities often impact multiple vital rates simultaneously, we also used elasticities to approximate allowable harm to all vital rates of survival or fertility. To estimate harm in this way, we first calculated population growth rate as

$$4) \qquad \lambda \approx \Lambda \cdot \left(1 + \sum_{v=1}^{n} \varepsilon_v \cdot \psi \right),$$

where n is the number of vital rates that are simultaneously harmed, ε_v is the elasticity of vital rate v, and ψ is allowable harm expressed as a single multiplier of all vital rates of interest. We initially assumed that $\psi = 0$ (i.e., no harm to survival or fertility), and then adjusted ψ downwards until $\lambda = 1$.

RECOVERY TARGETS
Consistent with the preconditions of SARA section 73(3), we used demographic sustainability as a criterion to set recovery targets for the Pugnose Shiner. Demographic sustainability is related to the concept of a minimum viable population (MVP; Shaffer 1981), and was defined as the minimum adult population size that results in a 95% probability of persistence over 250 years.

In the absence of an equation to predict MVP in small, short-lived, freshwater fishes, we estimated recovery targets by first generating 3,000 realizations of population size per time step based on the mean (and variance) projection matrix described above. These realizations were then used to generate a cumulative distribution function of extinction probability, where a population was said to be extinct if it was reduced to one adult individual. Next, we incorporated demographic stochasticity and density-dependence in vital rates, together with catastrophic declines in population size, into the population viability analysis software RAMAS (Akcakaya 2002). A catastrophic decline was defined as a 50% reduction in abundance that occurred at a probability (P_k) of either 0.05 or 0.10 per generation. We then used RAMAS to determine the number of adults that were necessary for a 95% probability of persistence over 250 years.

To provide insight on the number of populations that may be needed as part of a distribution target, we estimate the number of populations needed for species persistence. By assuming that populations experience independent and identical catastrophic extirpation risks (Ruckelhaus et $al.$ 2002), we can calculated the probability of persistence for a group of environmentally uncorrelated discrete populations (P_m) as a function of the probability of persistence of individual populations (P_s) and the number of populations (n) as:

$$5) \qquad P_m = 1 - \left(1 - P_s\right)^n$$

where $1-P_s$ represents the probability of extirpation of a single discrete population. Our estimate of the probability of persistence of single populations includes catastrophic events that reduce abundance by 50%, however, we have not included the probability of catastrophic extirpation. Equation 5 can be modified to include the probability of catastrophic extirpation (P_e), yielding:

$$6) \qquad P'_m = 1 - \left(1 - P_s + P_s P_e\right)^n$$

where $1-P'_m$ represents the probability of extinction of the species. Consistent with our criteria for setting the MVP, the probability of persistence of a recovered population (P_s) is 0.95. Based on Reed *et al.* (2003b) the probability of a catastrophic extirpation (P_e), defined as an event that reduces abundance by 95% or more over 250 years, is 0.7.

RECOVERY STRATEGIES AND RECOVERY TIMES
We used recovery targets to determine recovery timeframes of individual populations for six hypothetical recovery strategies. Consistent with the results of the allowable harm analysis (see Results), we focused on positive changes in annual survival probability in the first two years of life (i.e., $s_{1,2}$) and (or) the fertility of first -time spawners (f_2) that might result from specific recovery actions (e.g., the rehabilitation or enhancement of habitat). For each recovery strategy, we adjusted the elements of each of the 18 matrices accordingly.

Because population dynamics were stochastic, we based recovery timeframes on the number of years to achieve a 0.95 probability of reaching the recovery target. The initial size of the adult population ranged from 2 to 20% of the recovery target, and was distributed among age classes according to the stable age distribution. This stable age distribution was represented by the dominant right eigenvector (w) of the original, mean projection matrix (**M** $w = \lambda \cdot w$) (Figure 2c; De Kroon *et al.* 1986). For each initial population size and recovery strategy, we calculated the probability of recovery using Monte Carlo simulations that randomly selected one of the 18 biologically realistic projection matrices, and then increased $s_{1,2}$ and (or) f_2 accordingly. We then used 5,000 realizations of population size to generate a cumulative distribution function for the time to reach the recovery target. The probability of recovery at time t was equal to the proportion of realizations of population size that met or exceeded the recovery target at time t.

MINIMUM AREA FOR POPULATION VIABILITY
Following Vélez-Espino *et al.* (2009), we estimate the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculate MAPV for the adult portion of the population as:

$$7) \qquad MAPV_a = MVP_a \cdot API_a,$$

where MVP_a is the minimum adult population size that results in a 95% probability of persistence over 250 years estimated for the recovery target, and API_a is the area required per adult individual (the inverse of density). We estimate API based on an allometry for lake and river environments from Randall *et al.* (1995) for freshwater fishes:

$$8) \qquad lakes: \ API = e^{-10.37} \cdot TL^{2.58}$$

$$9) \qquad rivers: \ API = e^{-13.28} \cdot TL^{2.904},$$

where TL is the average total length of an adult measured in mm.

To extend the estimate of required habitat to the entire population, we used the stable stage distribution calculated from the model population projection matrix. The API for each stage was estimated from equation 9, an MAPV for each stage was estimated from equation 7, and the MAPV for the entire population was estimated by summing across all life stages.

RESULTS

ALLOWABLE HARM
According to the elasticities of the mean vital rates of the Pugnose Shiner life cycle, population growth rate was most sensitive to perturbations of annual survival probability (s_i) in the first and second years of life, and the fertility (f_i) of first-time spawners (Figure 3). Although the confidence intervals that were associated with these estimates suggest that elasticities of survival were sensitive to variation in clutch size, age at maturity, maximum age, and sex ratio, survival early in life was, on average, more important to population growth rate than survival later in life.

Estimates of the maximum allowable harm to individual vital rates depended on the stochastic element (e.g., mean or upper or lower 95% CL; Table 3). From a precautionary perspective (i.e., assuming an upper 95% CL), our results suggest a maximum allowable reduction of 14% for the survival rate of 1 or 2 year-olds, or 15% for the fertility rate of first-time spawners in individual populations of Pugnose Shiner (Table 3). Similarly, simultaneous impacts on all rates of either survival or fertility (ψ in equation 4) should not exceed 6% or 12%, respectively (Table 3). If human activities are such that harm exceeds just one of these thresholds, the future survival and recovery of individual populations is likely to be compromised.

RECOVERY TARGETS, RECOVERY STRATEGIES, AND RECOVERY TIMES
According to our simulations, MVP was 1,929 adults when the probability of a catastrophic (50%) decline was 0.05, and 14,325 adults when this probability was 0.10. Under current conditions, and in the absence of recovery efforts, a Pugnose Shiner population that was at 10% of either of these MVP values was predicted to take 24 years to reach a 95% probability of recovery (Figure 4). This time to recovery increased exponentially as harm was added simultaneously to all vital rates of either survival or fertility (Figure 5). Conversely, depending on which recovery strategy was applied (Table 4), the time to recovery improved to 10 to 18 years (Figure 6). Not surprisingly, the recovery times associated with each strategy varied with initial percentage of MVP (Figure 7): 15 to 29 years if starting from 2%, and 7 to 13 years if starting from 20%. Regardless of the starting percentage of the population, an increase in $s_{1,2}$ (strategies 1 and 2) had a consistently greater effect on recovery time than an equivalent increase in f_2 (strategies 3 and 4; Figure 7). Efforts to increase $s_{1,2}$ by 20% (strategy 2) were more effective than all other strategies except for strategy 6 (both $s_{1,2}$ and f_2 were increased by 20%). Thus, depending on the initial percentage, the outcome of a strong and proactive recovery strategy (strategies 2 and 6) would have a 95% probability of reaching the recovery target in 7 to 21 years or generations (Figure 7).

The risk of extinction declines exponentially with increasing number of populations recovered to the MVP (Figure 9). The extinction risk associated with 7 recovered populations is 9.5%, but the risk can be reduced to 5% with 9 recovered populations, to 2.5% with 11 recovered populations, and to 1% with 14 recovered populations.

MINIMUM AREA FOR POPULATION VIABILITY
The stable stage distribution for Pugnose Shiner is 98.85% YOY and 1.15% adult individuals. With a target MVP of 1 929 adults under a 0.05 probability of catastrophe per generation, the MAPV in lakes is 0.7 ha and 0.2 ha in rivers (Table 5). With a target MVP

of 14,325 under a 0.10 probability of catastrophe per generation, the MAPV in lakes is 5 ha and 1.5 ha in rivers (Table 5).

DISCUSSION

Our results show that human-induced harm should be minimal to avoid jeopardizing the survival and future recovery of the Pugnose Shiner. Specifically, our modelling suggests that (i) annual survival rate cannot be reduced by >14% for YOY or age-1 individuals, and (ii) fertility cannot be reduced by >15% for first-time spawners. Population decline is also likely if harm reduces the survival of all ages by >6%, or the fertility of all adults by >12%. Any harm beyond just one of these thresholds is expected to compromise the future survival and recovery of a population.

It is important to note that these estimates of allowable harm assume that the Pugnose Shiner is primarily a riverine species. The effect of this assumption is a maximum population growth rate at low densities (λ_{max}) of 1.82, and a population growth rate before harm (Λ) of 1.06. Because Λ > 1 for a typical riverine population, there is some scope for additional harm. However, the Pugnose Shiner also occurs in lakes (COSEWIC 2002), which tend to be less productive than rivers (Randall *et al.* 1995). This reduction in productivity results in a λ_{max} of 1.20, a Λ of only 0.93, and no scope for allowable harm. Although this lack of productivity in lacustrine environments might be offset by the tendency of the Pugnose Shiner to occupy relatively productive littoral habitats and river mouths (COSEWIC 2002), these results suggest that the impacts of additional harm will be greater—and the impacts of restoration efforts lesser—than in river populations.

In addition to providing estimates of allowable harm to riverine (and perhaps lacustrine) populations of Pugnose Shiner, this work also provides recovery targets that were based on the concept of MVP. These targets were estimated at 1,929 to 14,325 adults when the probability of a catastrophic (50%) decline (P_k) was 0.05 to 0.10 per generation. According to Reed *et al.* (2003a), the MVP of vertebrates is 7,316 adults; however, their analysis included only one fish species and ignored catastrophic events, which, in vertebrates, can occur at a probability of up to 0.15 per generation (Reed *et al.* 2003b). Recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery.

In Canada, Pugnose Shiner are present at seven known extant locations and three extirpated locations (Bouvier *et al.* 2010). If the seven known locations are recovered to abundances that meet or exceed the MVP, then the risk of extinction for the species is estimated at 9.5% over 250 years. Re-introduction and recovery of the three extirpated populations, for a total of 10 recovered populations, could reduce the extinction risk to 3.5% over 250 years. For species with a small distribution (COSEWIC criterion B), species can be considered threatened if they are extant at 10 or fewer locations. Recovering Pugnose Shiner at 11 locations would reduce the estimated extinction risk to 2.5% over 250 years. These estimates of extinction risk are based on the assumption that Pugnose Shiner populations are discrete (i.e., there is no dispersal among populations) and

environmentally uncorrelated (i.e., environmental conditions are independent across populations). Meta-population dynamics could be incorporated by evaluating dispersal rates among populations. These rates are particularly important when dispersal between populations is unequal, which can be the case when there are large differences in areas (Ackakaya and Baur 1996). Furthermore, if environmental fluctuations are even partially synchronous among populations, then models like ours that assume independent population dynamics will underestimate extinction risk (Ackakaya 2000).

Estimates of MAPV ranged from 0.2 to 5 ha, and differed from the 0.6-1.1 ha estimated by Vélez-Espino *et al.* (2009). This difference did not result from a difference in methodology for estimating MAPV, as our calculations followed the methodology laid out by Vélez-Espino *et al.* (2009). This difference was also largely independent of our change in the criteria for identifying MVP; using a 95% probability of persistence over 250 years instead of a 99.9% probability of persistence over 40 generations (Reed *et al.* 2003a) had only a small influence on the MVP. However, MAPV was sensitive to changes to some of the life history values that were used in the model. These changes predicted a stable age distribution that included more adults (0.11% in Vélez-Espino *et al.* 2009 versus 1.15% in this study) and, therefore, an increase in the amount of habitat required to protect them. Our estimates of MAPV also included catastrophic events, which greatly increased MVP over the estimate used by Vélez-Espino *et al.* (2009); populations need to be both larger and more widely distributed in space if they are to recover from catastrophic events.

Our analyses show that, in the absence of recovery efforts and harm, a population that is between 2 and 20% of the recovery target in terms of abundance has a 95% probability of reaching that target in 17 to 39 years (Figure 7). This result is independent of the recovery target because we expressed the initial population size as a percentage of MVP (e.g., 2% of 1,929 and 14,325 is 193 and 287, respectively). However, recovery targets do become important when the initial population size is known or can be estimated. For example, in the absence of recovery efforts and harm, the recovery time of a population of ~400 adults is expected to be 17 years if MVP is 1,929, but 36 years if MVP is 14,325 (Figure 8). Additional harm will delay the recovery of a population. For example, recovery times are expected to double at approximately half of maximum allowable harm to composite rates of survival or fertility (Figure 5). To instead reduce recovery times by approximately half, we recommend any recovery actions that increase by >14% the annual survival rate of Pugnose Shiner in their first two years of life; efforts to increase the fertility of first-time spawners are likely to be much less effective.

Finally, we emphasize the need for research on Pugnose Shiner in Canada to determine (i) life history characteristics, (ii) the size and growth rate of populations, and (iii) mechanisms of population decline. In lieu of life history data from populations in Canada, our analysis assumed, on the basis of latitudinal similarity and a shared evolutionary history (Zhao *et al*. 2008, Ward and McLennan 2009), that life history data from populations in Wisconsin were representative. Ideally, especially given that Pugnose Shiner in Canada are at the edge of their range, rare, endangered, and in decline (COSEWIC 2002), recovery modelling should be based on the life history characteristics of the populations to which they are applied. To this end, we recommend research to determine such life-history basics as length- and mass-at-age, age- and size-at-maturity, fecundity, and clutch size. Similarly, although this assessment identifies strategies for Pugnose Shiner recovery (e.g., increased early survival), the fact that both the status and cause(s) of decline in most Canadian populations is unknown (COSEWIC 2002) represents a significant impediment to the implementation of such strategies. For

example, the extent to which $s_{1,2}$ is more likely to respond to changes in habitat or predator abundance is unknown. Therefore, research that identifies those factors that contribute the most to changes in the population growth rate of Pugnose Shiner in Canada, as well as how they impact rates of survival and (or) reproduction, should be a priority for this species.

ACKNOWLEDGEMENTS

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Table 1. Summary of life history information on the Pugnose Shiner (*Notropis anogenus*). SL = standard length, TL = total length, VBL = von Bertalanffy.

Trait	Mean	Min.	Max.	Other	Source
TL (mm)		38	56		Eakins 2009
			60		Eakins 2009
	46				Becker 1983
			58		Froese and Pauly 2009
			56	converted from SL	Bailey 1959
Age-2 TL (mm)		50	55		Etnier and Starnes 1993
Age-1 TL (mm; measured)	42	38	44		Becker 1983 (Aug)
Age-2 TL (mm; measured)	46.3	45	49		Becker 1983 (Aug)
Age-3 TL (mm; measured)	52.5	52	53		Becker 1983 (Aug)
Age-1 TL (mm; estimated)		29			Becker 1983 (May)
Age-2 TL (mm; estimated)		43			Becker 1983 (May)
Age-3 TL (mm; estimated)		57			Becker 1983 (May)
Age-1 TL (mm; estimated)	26	21.5	31.9		Becker 1983 (May/June)
Age-2 TL (mm; estimated)	37.4	29.5	38.3		Becker 1983 (May/June)
Age-3 TL (mm; estimated)	46.5				Becker 1983 (May/June)
VBL asymptotic TL (mm)			62		Froese and Pauly 2009
VBL growth coeff. (/yr)				1.18	Froese and Pauly 2009
VBL t_o				-0.21	Froese and Pauly 2009
TL-SL relationship				SL = 0.852792 * TL	Froese and Pauly 2009
Mass (g)		1	2		Eakins 2009
			2.5		Eakins 2009
TL for a given mass				54.5 mm at 1.905 g	Becker 1983
				55.5 mm at 2.141 g	Becker 1983
				60.0 mm at 2.446 g	Becker 1983
TL-mass relationship				$W = 0.0038 * (TL * 10)^3$	Froese and Pauly 2009 (Notropis spp.)
				$W (g) = -4.75 + 3.53 \log SL$ (mm), n = 100, r^2 = 0.99	Mahon 1976 (cited in Coker *et al.* 2001)
				$W (g) = 10^{2.33C* \log TL \text{ (mm)} - 3.76}$, n = 3, r^2 = 91	Becker 1983 (our calculation)
Condition (K)	1.17	1.02	1.26	n = 10	Becker 1983
Maximum age (yr)			3		Eakins 2009
			3		Froese and Pauly 2009
Age-at-maturity (yr)	1				Eakins 2009
	1				Froese and Pauly 2009
TL-at-maturity (mm)				43	Froese and Pauly 2009
		41	56		Holm and Mandrak 2002
Gonad mass (n = 8)		7	14	% of body mass	Becker 1983
		12.6	16.8	% of body mass	Becker 1983
Egg number			1275		Becker 1983
		530	958	n = 8	Becker 1983
TL for a given egg number				55.5 mm at 1275 eggs	Becker 1983
Egg diameter (mm)		0.5	0.7	Sample mean	Becker 1983
		0.7	1.3	In a single fish	Becker 1983
Spawning periodicity				Mid-may to July	Becker 1983
				Early to mid-June	Holm and Mandrak 2002
				2 clutches/year	Winemiller and Rose 1992
Generation time				1	Froese and Pauly 2009
				2	Holm and Mandrak 2002
Natural mortality (M)				1.96	Froese and Pauly 2009

Table 2. The mean, variance, and range of vital rates across all 18 Pugnose Shiner matrices. These data were used to estimate the mean stochastic elasticity of each vital rate. s_i = annual survival probability at age i and f_i = fertility at stage i.

Statistic	Vital rate					
	s_1	s_2	s_3	f_2	f_3	f_4
mean	0.01138	0.17	0.17	562	712	856
variance	0.00002	$6.26 \cdot 10^{-5}$	$6.26 \cdot 10^{-5}$	58447	72776	94067
maximum	0.02124	0.18	0.18	969	1122	1275
minimum	0.00534	0.16	0.16	265	389	504

Table 3. Summary of maximum allowable harm ($\tau_{v,\ max}$) estimates for individual and combined vital rates of Pugnose Shiner based on a stochastic perturbation analysis and a population growth rate (Λ) of 1.06. s_i and f_i = annual survival probability and fertility at stage i, respectively, and s_n and f_n = annual survival probability and fertility across all ages, respectively. Consistent with the precautionary approach, bold values indicate the maximum allowable harm recommended for management decisions.

Stochastic element	$\tau_{v,\ max}$							
	s_1	s_2	s_3	s_n	f_2	f_3	f_4	f_n
mean	-0.14	-0.14	-0.83	-0.06	-0.17	-0.97	-5.69	-0.14
+95% CL	**-0.14**	**-0.14**	**-0.58**	**-0.06**	**-0.15**	**-0.70**	**-3.04**	**-0.12**
-95% CL	-0.15	-0.15	-1.27	-0.07	-0.20	-1.46	-11.59	-0.17

Table 4. Six hypothetical Pugnose Shiner recovery strategies for representing positive and increasing impacts on the rate of annual survival in the first two years of life ($s_{1,2}$) and (or) the fertility of first-time spawners (f_2) that might result from specific recovery efforts (e.g., the rehabilitation or enhancement of habitat).

Strategy	$s_{1,2}$	f_2
1	10%	0%
2	20%	0%
3	0%	10%
4	0%	20%
5	10%	10%
6	20%	20%

Table 5. Area per individual (API), number of individuals for each stage to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population, under two probabilities of catastrophe per generation (P_k) in lake and river environments.

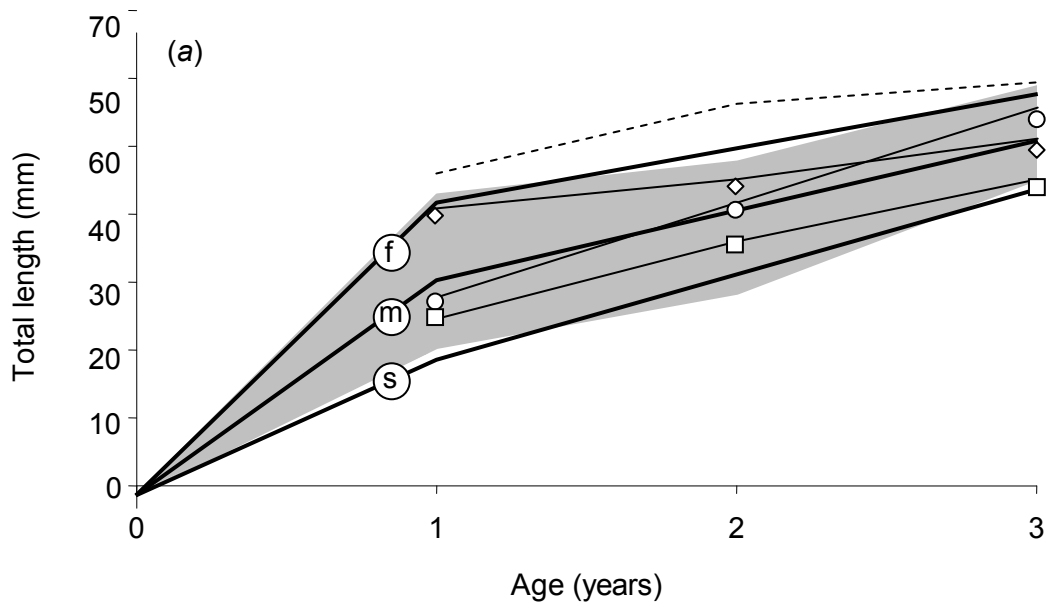| Stage	API (m^2)	$P_k = 0.05$		$P_k = 0.10$	
		MVP	MAPV (m^2)	MVP	MAPV (m^2)
Lake					
YOY	0.02	165 810	3 316.2	1 231 327	24 626.5
Adult	1.80	1 929	3 472.2	14 325	25 785.0
ALL			6 788.4		50 411.5
River					
YOY	0.01	165 810	1 658.1	1 231 327	12 313.3
Adult	0.20	1 929	385.8	14 325	2 865.0
ALL			2 043.9		15 178.3

Figure 1. Fast (f), moderate (m) and slow (s) Pugnose Shiner length-at-age profiles used in this model. The shaded area represents the observed range in length for a given age (see Table 1), the dashed line is predicted length-at-age (Froese and Pauly 2009), and the thin, solid lines are observations from Becker (1983): ◊ (direct measurements), □ (back-calculations from scales collected in May); O (back-calculated from scales collected in late May, early June).

(*a*)

1. Young-of-the-year
2. Age-1+
3. Age-2+
4. Age-3+
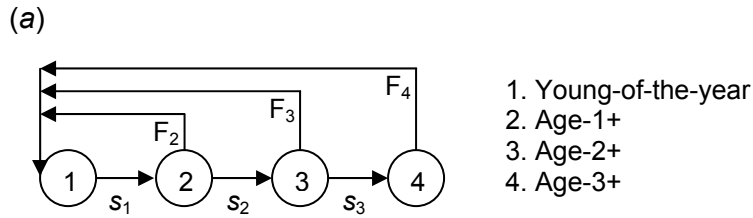
(*b*)

$$\mathbf{M} = \begin{pmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}$$

(*c*)

$$\mathbf{M} = \begin{pmatrix} 0 & 96 & 121 & 146 \\ 0.011 & 0 & 0 & 0 \\ 0 & 0.17 & 0 & 0 \\ 0 & 0 & 0.17 & 0 \end{pmatrix}$$

Figure 2. Generalized life cycle (*a*), corresponding age-structured projection matrices (*b*), and mean values of matrix elements across all 18 possible matrices (*c*) used to model the population dynamics of the Pugnose Shiner. F_i and s_i represent stage-specific fecundity coefficients and annual survival probabilities, respectively.
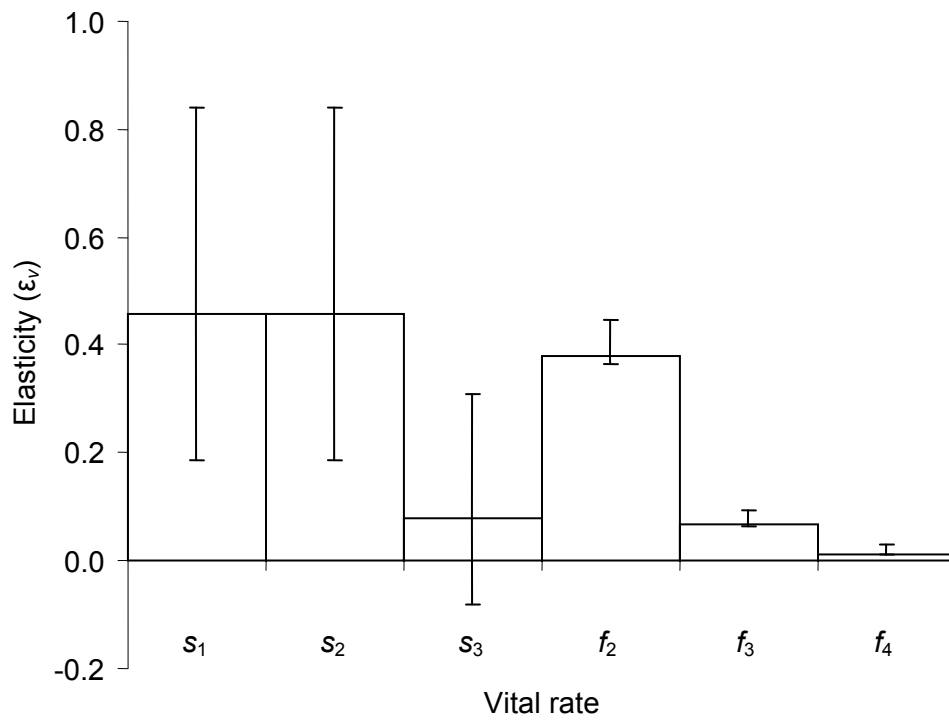
Figure 3. Results of the stochastic perturbation analysis showing elasticities (ε_v) of the vital rates annual survival probability at age i (s_i) and fertility at age i (f_i), with associated 95% CL.
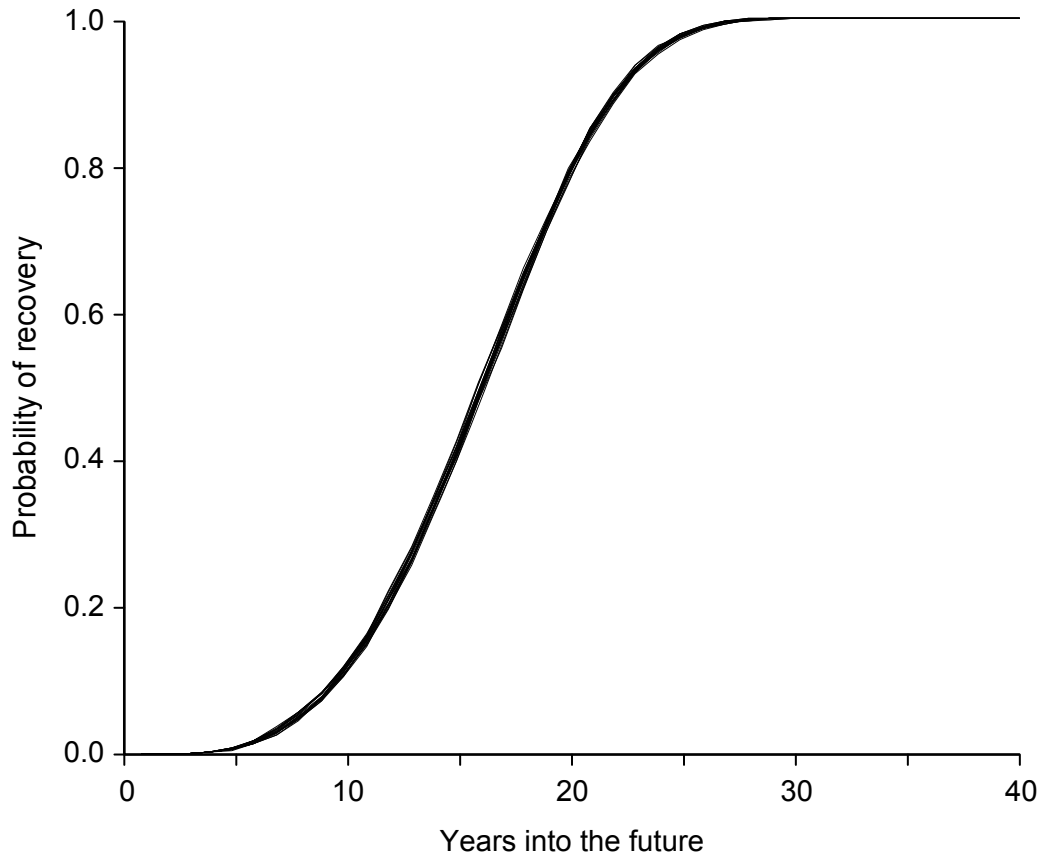
Figure 4. The probability of recovery of 20 simulated Pugnose Shiner populations under status quo conditions based on an initial adult population size that was 10% of a recovery target.
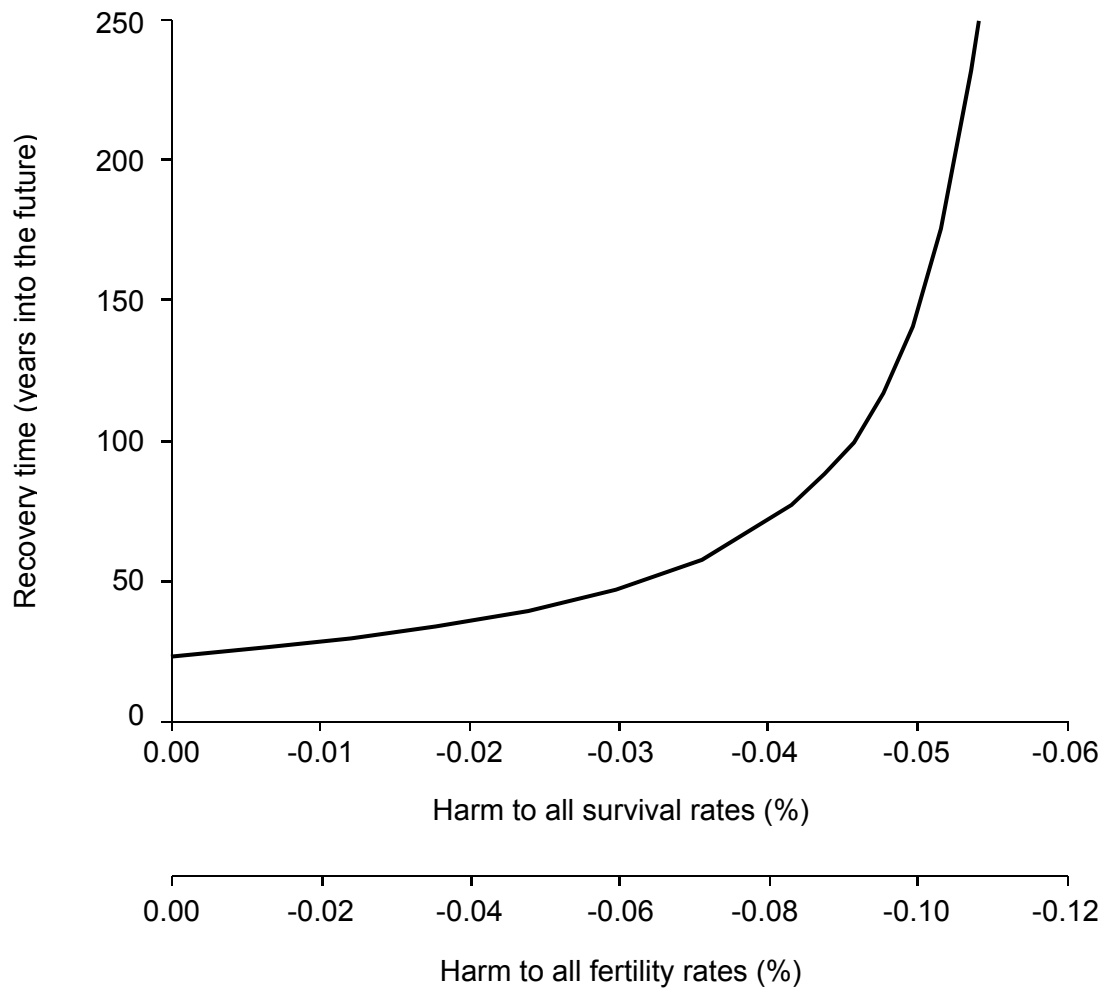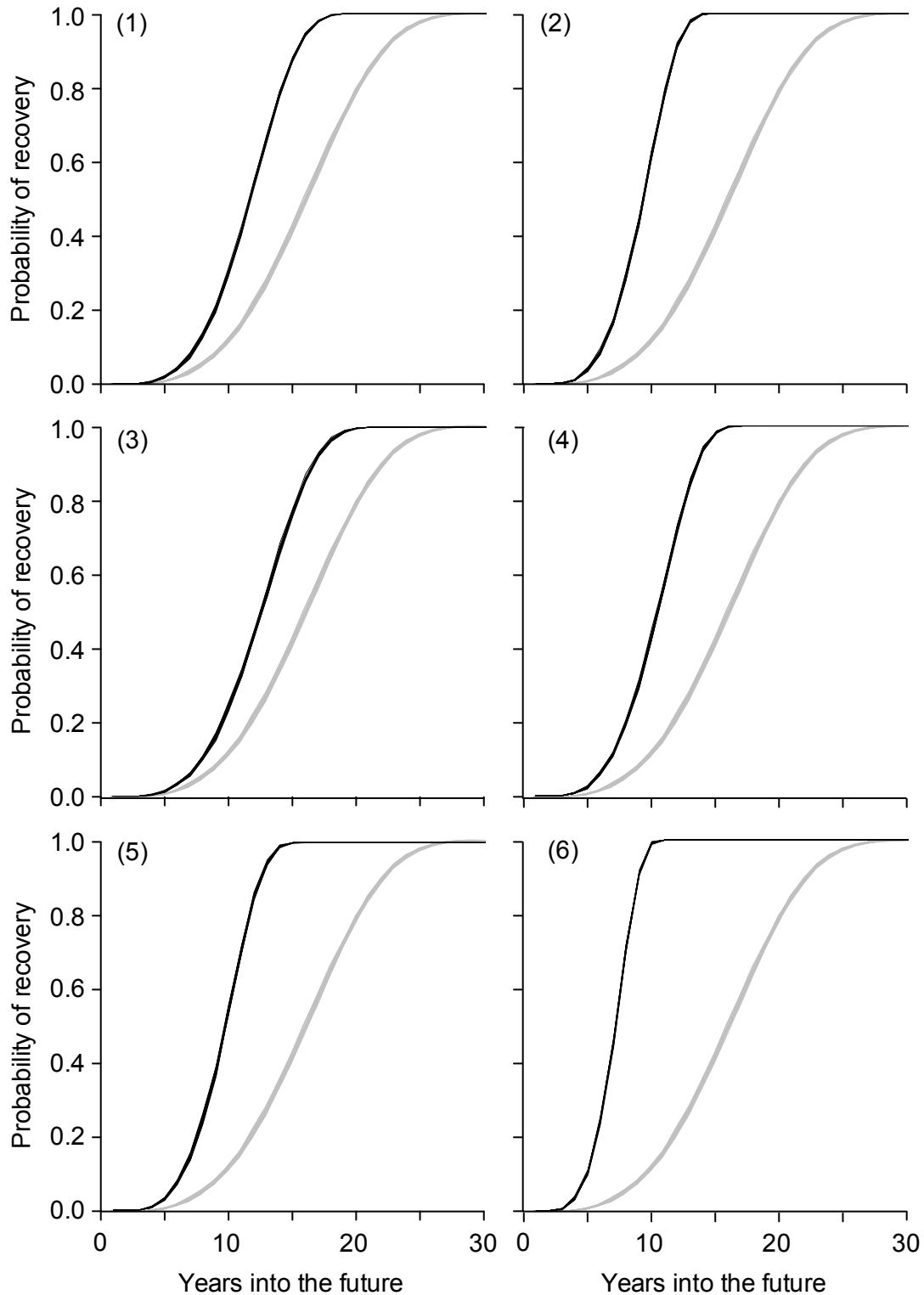
Figure 5. Predicted change in the time to 95% recovery of a Pugnose Shiner population that is experiencing increased harm to composite rates of either survival or fertility.

Figure 6. The probability of recovery of 20 simulated Pugnose Shiner populations under 6 hypothetical recovery strategies based on an initial adult population size that was 10% of a recovery target. Numbered panels correspond to strategies in Table 4 and the grey line shows recovery under status quo conditions (Figure 4).
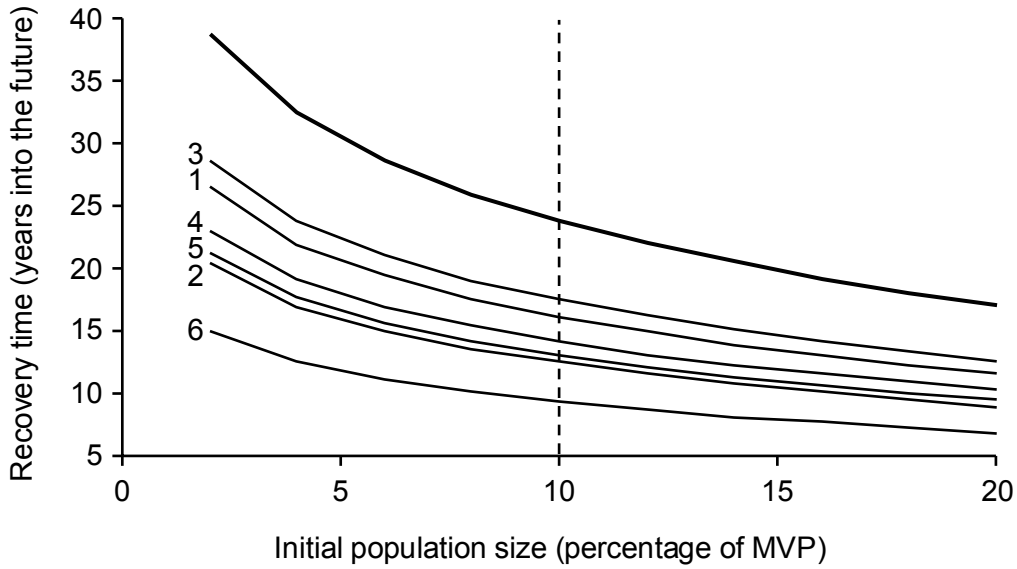
Figure 7. Stochastic projections of mean Pugnose Shiner recovery times over a range of initial population sizes (percentage of a recovery target) for 6 hypothetical recovery strategies. The thick line shows recovery times in the absence of mitigation or additional harm, and numbered lines correspond to strategies in Table 4. Points of intersection with the horizontal dashed line were taken from Figures 4 and 5.
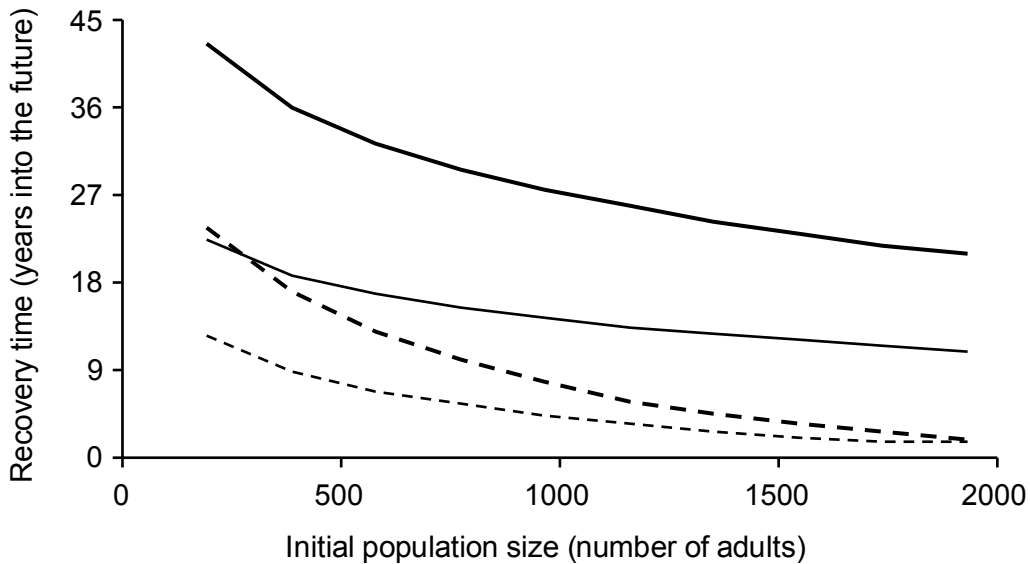

Figure 8. Stochastic projections of mean Pugnose Shiner recovery times over a range of initial population sizes (number of adults) for two recovery targets: 14 325 adults (solid lines) and 1 929 adults (dashed lines). Thick lines show expected recovery times in the absence of mitigation and additional harm, and thin lines show expected recovery times when employing strategy 2 in Table 4.
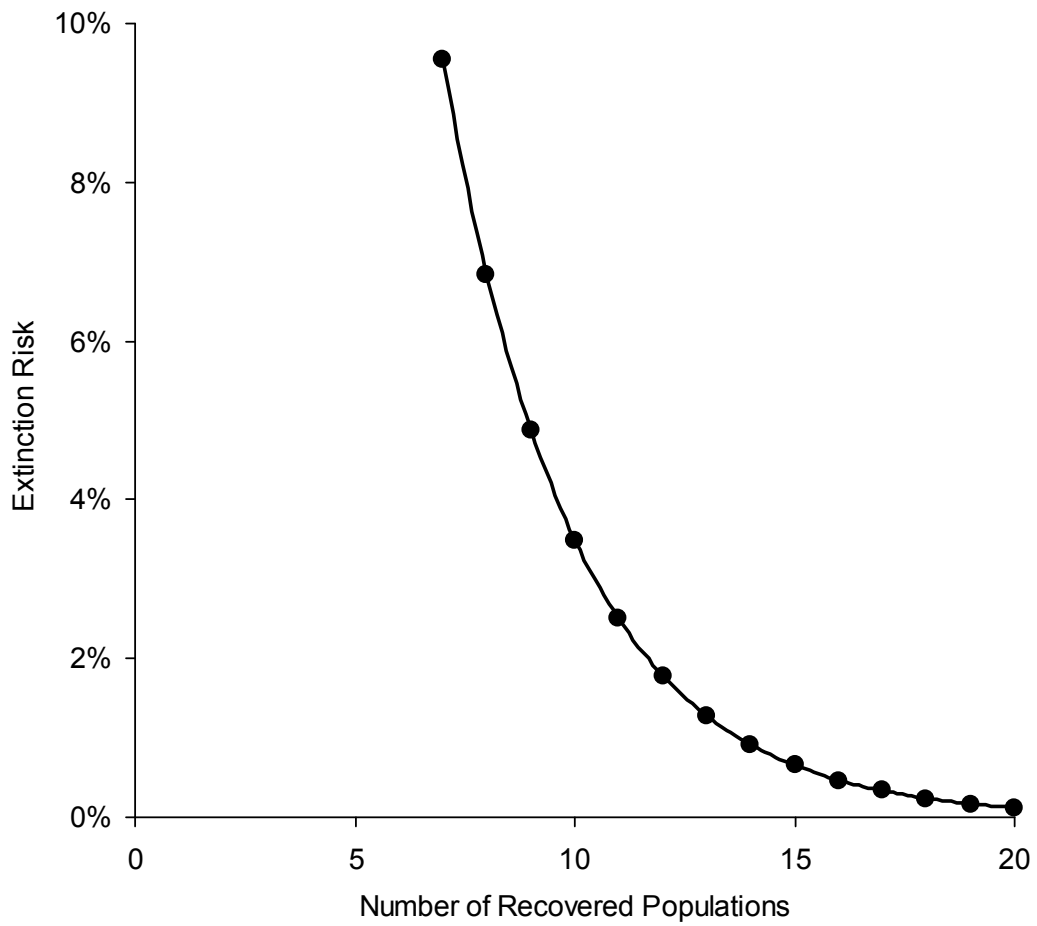
Figure 9. Extinction risk over 250 years as a function of the number of recovered populations of Pugnose Shiner. Curve through the data is described by a negative exponential curve ($y = e^{-0.3355x}$).