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Recovery Potential Modelling of River Darter (*Percina shumardi*) in Canada

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the River Darter (*Percina shumardi*) as Endangered within the Great Lakes – Upper St. Lawrence Biogeographic Zone (DU3) in Canada. Here we present population modelling to assess the impacts of harm, determine population-based recovery targets, and conduct long-term projections of population recovery in support of a recovery potential assessment (RPA). Limited species-specific data were available for Canadian populations of River Darter and there was much uncertainty in life-history characteristics and vital rate values. Our analysis demonstrated that River Darter population growth was most sensitive to perturbations to young-of-the-year (YOY) survival rate and reproduction. Harm to these aspects of River Darter life-history should be avoided. The risks associated with different levels of stage-specific anthropogenic harm were investigated. Population viability analysis was used to identify potential recovery targets. Demographic sustainability, (i.e., a self-sustaining population over the long term) can be achieved with population sizes of 27,000 to 31,000 adults based on conservative simulation criteria. A population of this size required between 10.6 and 12.1 ha of suitable habitat (assuming densities of 0.25 fish/m^2). Population projections predicted that recovery could occur in 33–35 years with an initial density of 10% of the abundance targets.

INTRODUCTION

Populations of River Darter (*Percina shumardi*) within Designatable Unit 3 (DU3), the Great Lakes – Upper St. Lawrence Biogeographic Zone, have been designated as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The Canadian distribution of River Darter consists of two other DUs in the Saskatchewan – Nelson River Biogeographic Zone (DU1) and the Southern Hudson Bay – James Bay Biogeographic Zone (DU2) which were designated as Not at Risk (COSEWIC 2016). River Darter was previously assessed by COSEWIC as Not at Risk (Dalton 1989). However, at the time it was considered as a single DU. No previous recovery potential modelling exists for River Darter.

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 from Canada, Fisheries and Oceans Canada (DFO) has developed the recovery potential assessment (RPA; DFO 2007a,b) 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 - that are further broken down into 22 elements. This report contributes to components two and three and elements 3, 12, 13, 14, 15, 19, 20, 21, and 22 by assessing allowable harm, identifying recovery targets, and projecting recovery timeframes with associated uncertainty for Canadian populations of River Darter. This work is based on a demographic approach developed by Vélez-Espino and Koops (2009, 2012) and Vélez-Espino et al. (2010) which determines population-based recovery targets based on long-term population projections.

METHODS

Information on vital rates for River Darter was compiled to build projection matrices that incorporate environmental stochasticity and density-dependence. The impact of anthropogenic harm to River Darter populations was quantified with use of elasticity and simulation analyses. Estimates of recovery targets for abundance and habitat were made with estimation of the minimum viable population (MVP) and the minimum area for population viability (MAPV). Finally, simulation analyses were used to project population abundances and make estimates of potential recovery time-frames.

SOURCES

Few studies have been conducted on River Darter and, as a result, species-specific life-history data were sparse. There were no data available from the DU3 populations of River Darter. However, some data were available from other Canadian populations which may be taken as a representation of DU3 River Darter. Targeted River Darter surveys were conducted by Fisheries and Oceans Canada (DFO) at 18 sites in northern Ontario and Manitoba from 2012 to 2014 (Pratt et al. 2016). Sampling utilized mini-Missouri bottom trawls and provided information on length, weight, age, and sex composition. Additional data from incidental captures were available from electrofishing surveys in Rainy River, ON conducted in 2013. Other information required was sourced from the primary literature. All analyses and simulations were conducted using the statistical program R 3.5.0 (R Core Team 2018).

THE MODEL

River Darter life cycle was modeled using a density-dependent, birth-pulse, post-breeding, age-structured matrix model with annual projection intervals (Caswell 2001). Matrix population models use estimates of vital rates (growth, survival, and fecundity) to project age- or stage-specific population sizes. The dominate eigenvalue of the matrix represents the population growth rate (λ) and indicates the long term status of the population based on current conditions (Caswell 2001). A $\lambda > 1$ indicates the population is growing exponentially, a $\lambda = 1$ indicates the population is stable, and a $\lambda < 1$ indicates the population is declining towards 0. The dominant right eigenvector of the matrix represents the stable stage structure of the population and indicates the proportional distribution of individuals among stages/ages. This can be used to estimate the number of individuals in all other stages/ages if one is known, assuming equilibrium.

The matrix structure was defined by River Darter longevity (t_{max}) and age-at-maturity (t_{mat}). It was assumed River Darter live to a maximum age of 4 years and reach maturity at age-1 (COSEWIC 2016). The life cycle of River Darter is represented in Figure 1.

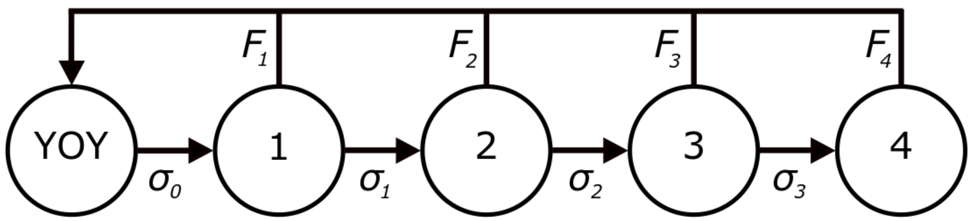

Figure 1. Generalized life cycle used to model the population dynamics of River Darter. F_t represents age-specific annual fertility and σ_t represents the age-specific annual survival.

Elements within the age-structured matrix include age-specific annual survival rate (σ_t) and fertility rate (F_t). Fertility coefficients (F_t) represent the contribution from an adult of age-*t* to the next census of age-0 individuals. Fertility is dependent on: (i) mean age-specific fecundity (f_t) or the mean number of eggs produced per spawning season per individual in age class *t*, (ii) the proportion of offspring that are female (φ), (iii) the proportion of the population that are mature at age-*t* (ρ_t), (iv) spawning periodicity (T) or the number of years between spawning events (1 year for River Darter), and because a post-breeding matrix structure was assumed, (v) the survival coefficient is included to account for mortality between the census and the next spawning event. Fertility is calculated as:

$$F_t = \frac{\varphi \rho_t f_t \sigma_t}{T}. \tag{1}$$

The matrix will have 5 columns representing young-of-the-year (YOY), age-1, age-2, age-3, and age-4 River Darter:

$$\mathbf{B} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 & 0 \\ \sigma_0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 & 0 \\ 0 & 0 & 0 & \sigma_3 & 0 \end{bmatrix}. \tag{2}$$

The matrix is structured as a post-breeding matrix; therefore, the population census occurs just after reproduction. This results in individuals growing and maturing over the course of the year and spawning just prior to the subsequent census. To account for this, the fertility coefficients for age-*t+1* are incorporated into column *t* of the projection matrix (i.e., fertility of age-2 fish is represented in the age-1 column of the matrix). As well, the matrix structure includes a column of 0s to represent age-4 fish. This allows for age-4 fish to exist but not survive to the next census (or spawn as age-5 fish).

Table 1. Values, symbols, descriptions, and sources for parameters used to model River Darter populations. Tables 2, 3, and 4 provide additional river-specific parameters.

	Symbol	Description	Value	Source
Age	t_{max}	Longevity	4	COSEWIC (2016)
	t_{mat}	Age-at-maturity	1	COSEWIC (2016)
	ζ	Generation time	1.8	Estimated
Growth	L_0	Length at hatch	6.15	COSEWIC (2016)
	bp	Break point; age when growth pattern changes	0.25	Fitted / Pratt et al. (2016)
	L_{bp}	Length at break point (mm)	37.1	
	$L\infty$	Asymptotic length (mm)	61.9	
	k	von Bertalanffy growth coefficient	0.31	
Spawning	α_f	Fecundity allometric intercept	197.9	Fitted / Pratt et al. (2016)
	β_f	Fecundity allometric exponent	1	
	sd_f	$\log_e$ standard deviation of fecundity	0.05	
	φ	Proportion female	0.5	Pratt et al. (2016)
	T	Spawning periodicity	1	COSEWIC (2016)
	ρ_0	Proportion reproductive at age-0	0	
	$\rho_{1,\ldots,4}$	Proportion reproductive age-1 to age-4	1	
Weight	α_W	Length-weight allometric intercept	$2.3\text{x}10^{-6}$	Pratt et al. (2016)
	β_W	Length-weight allometric exponent	3.30	
Adult Mortality	M	Instantaneous mortality	0.752	Fitted / Pratt et al. (2016)
	$CV_{M,0}$	Coefficient of variation of YOY mortality	0.1	Mertz & Myers (1995)
	$CV_{M,a}$	Coefficient of variation of adult mortality	0.2	

Parameter Estimates

All model parameters are presented in Tables 1, 2, 3, and 4.

Growth

Length-at-age data were available from otolith-aged River Darter captured from northern Ontario and Manitoba populations (Pratt et al. 2016). River Darter experience very rapid early life growth followed by reduced growth during adulthood (Pratt et al. 2016); similar to related darters (Starnes 1977). Approximately 2/3 of total growth was achieved in the first few months of life. This growth pattern was not well fitted with a simple von Bertalanffy growth curve. Instead, River Darter growth was represented using a biphasic growth model (Lester et al. 2014) consisting of linear early life growth followed by von Bertalanffy growth into adulthood (Figure 2), such that:

$$L_t = \begin{cases} L_0 + \frac{L_{bp}-L_0}{bp}(Age) & if\ Age \le bp \\ L_\infty - \left(L_\infty - L_{bp}\right)e^{-k(Age-bp)} & if\ Age > bp \end{cases}. \quad (3)$$

Where L_t represents length-at-age t, L_0 represents length at hatch, bp represents the break point or age at which the growth pattern changes, L_{bp} represents the length at break point, L_∞ is the asymptotic length, and k is the von Bertalanffy growth coefficient. Length-at-hatch for River

Darter ranges from 5–6.5 mm (COSEWIC 2016); the midpoint, 6.15 mm, was chosen as the value for L_0. The *bp* value was fixed at the median of age-0 aged fish, which was 0.25.

Growth parameters (L_∞, k, and L_{bp}) were fitted as a non-linear mixed model grouped by waterbody with random effects applied to L_∞ and L_{bp}. This allows L_∞ and L_{bp} to vary across waterbodies but holds k constant. Mean growth parameter estimates were: L_∞ = 61.9 mm, k = 0.31, and L_{bp} = 37.1 mm. With growth uncertain for DU3 River Darter populations, analyses were conducted using 3 distinct growth curves from DU1 and DU2 river populations: Assiniboine, English, and Rainy rivers (Table 2). These locations were chosen because their growth curves differed and they were the locations with the largest number of samples, n = 38, 40, and 172 respectively.

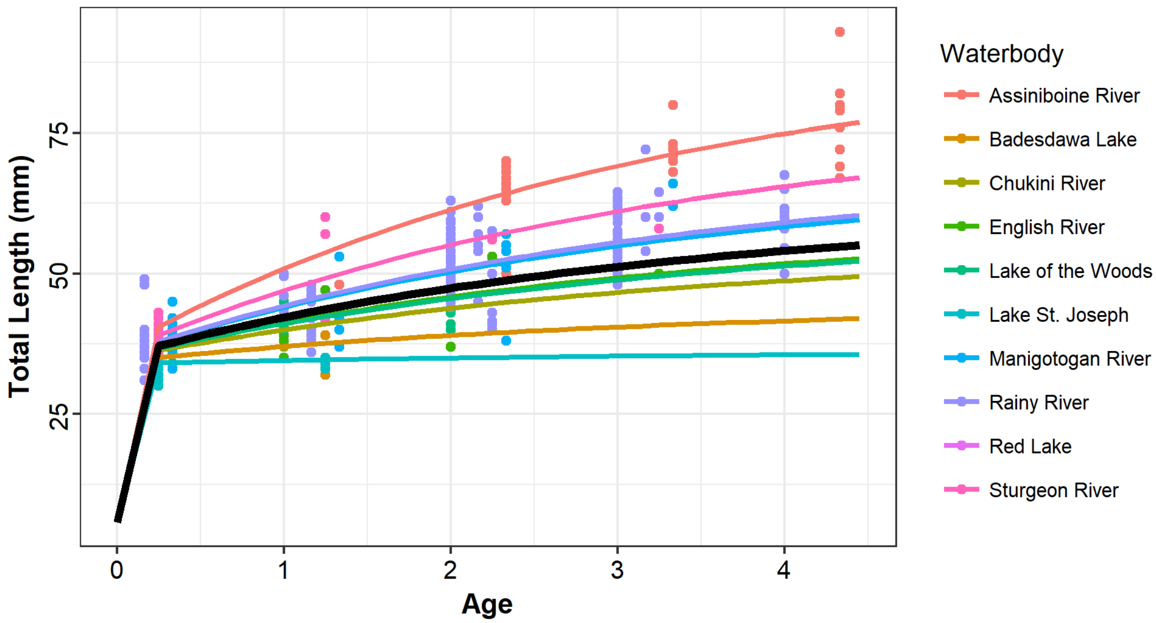

Figure 2. Length-at-age data for River Darter captured in northern Ontario and Manitoba. The black line represents mean growth pattern and the coloured lines represent waterbody-specific growth patterns fit as biphasic growth models.

Table 2. River Darter growth parameters (Equation 3) for the mean and waterbody-specific values used in simulations.

Parameter	Mean	River		
		Assiniboine	English	Rainy
L_∞ (mm)	61.9	90.9	58.7	68.9
k	0.31	0.31	0.31	0.31
bp	0.25	0.25	0.25	0.25
L_{bp} (mm)	37.1	40.5	36.7	37.9

Length-weight data were also available for DU1 and DU2 River Darter (Figure 3). The data were from multiple populations, however, the best model included only fixed effects (ΔAIC > 10). These data were fit as a $\log_e$ transformed linear model (re-transformed as a power curve) to predict the expected weight, in grams, for a given length, in mm, resulting in the relationship:

$$W = 2.30 \times 10^{-6} L^{3.30} \, . \qquad (4)$$

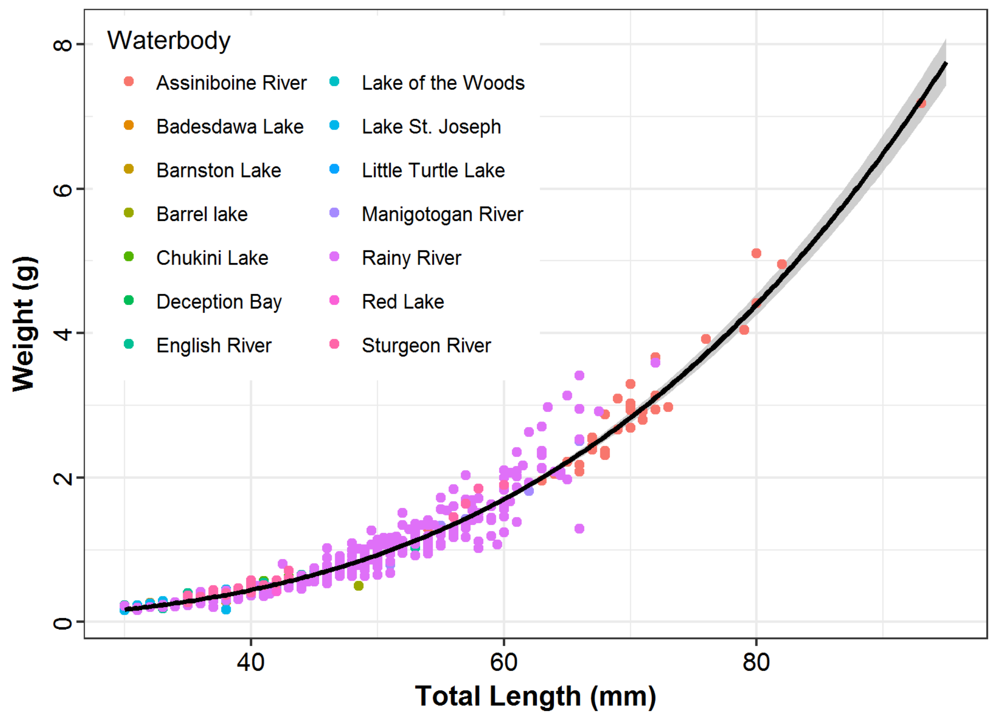

Figure 3. Length-weight data for River Darter captured in northern Ontario and Manitoba. The black line represents the best fit relationship and the grey region represents 95% confidence intervals. $W = 2.30 \times 10^{-6} L^{3.30}$.

Reproduction

Limited data were available relating to River Darter reproduction. River Darter produce multiple clutches during the spawning season which begins in April in southern populations in the United States (Hubbs 1985) but may occur in June and July in Canadian populations (Scott and Crossman 1973). River Darter reproduction was simplified through the use of a birth-pulse matrix model which assumes a single annual reproductive event. This simplification is valid if YOY River Darters experience equal growth and mortality regardless of spawning time.

First spawning typically occurs at age-1 (following the first winter, COSEWIC 2016). It is unclear what proportion of the population become mature at this point but 100% was assumed (ρ_t = 1 for all ages > 0).

Pratt et al. (2016) observed a sex ratio skewed towards females in samples of River Darter from northern Ontario and Manitoba in 2013 and 2014. It is unknown if this was due to the population structure of River Darter or differential vulnerability to the sampling gear (Pratt et al. 2016). Among samples the sex ratio varied significantly from slightly male-skewed (54%) to entirely female (Pratt et al. 2016). Observed sex ratios in other darter species populations were also variable. For example, the observed sex ratio of Channel Darter (*Percina copelandi*) in the Trent River has varied at different times from female skewed (58%; Reid 2004) to male skewed (55 to 58%; Reid et al. 2016). As well, Mathur (1973) observed a sex ratio skewed towards females (58%) in an Alabama population of Blackbanded Darter (*Percina nigrofasciata*). However, in two Florida populations of Blackbanded Darter, Hughley et al. (2012) observed a male-skewed sex ratio (63%). Sex ratio, as incorporated into matrix population models, represents the proportion of females at birth (Caswell 2001). Without a robust biological explanation for a sex ratio divergent from 1:1 it is prudent to assume an equal sex ratio.

Fecundity of darter species may be related to the length of the spawning season with fish in southern populations with warmer temperatures and longer spawning seasons producing more eggs per year than more northern populations (Hubbs 1985). River Darter fecundity is unknown but may be as high as 800 eggs/female/year (Frimpong and Angermeier 2009). River Darter reproduction is likely similar to that of Channel Darter (*Percina copelandi*; Scott and Crossman 1973). Channel Darter fecundity ranges from 350 to 700 eggs/female (COSEWIC 2002). As a result, it is assumed that the fecundity of an age-4 female River Darter has a mean value of 700 and can range to a high of 800. To estimate the fecundity of other age-classes an assumed relationship with weight was used where:

$$f_t = \alpha_f W_t^{\beta_f}. \tag{5}$$

The value of the exponent, β_f, is an indication of the relative influence of maternal body size on egg production (Le Bris et al. 2015). If $\beta_f = 1$, the reproductive output increased linearly with body weight. If, however, $\beta_f > 1$, the relative fecundity of individual females increased with body weight. The simplifying assumption was made that relative fecundity is constant across body sizes by setting β_f to 1. The value of α_f is then solved for such that f_t is 700 at age-4 body weight of a River Darter in Assiniboine River (the largest size). This resulted in a α_f value of 197.9 and was assumed constant across waterbodies.

Mortality

Adult mortality was estimated using catch-curve analysis of age frequencies of otolith-aged fish captured in northern Ontario and Manitoba (Figure 4). Weighted catch curve regression analysis was performed to decrease the bias from rarer, older fish (Maceina and Bettoli 1998). Aggregating all data gives an estimated instantaneous adult mortality of 0.752. The mortality estimates were similar when divided by season (spring/early summer: M = 0.73; late summer/fall: M = 0.77). Mean mortality was assumed constant across adult age-classes (ages 1 to 3) and waterbodies. Young-of-the-year survival (σ_0) was estimated separately by solving for the value that gave a desired population growth rate (λ).

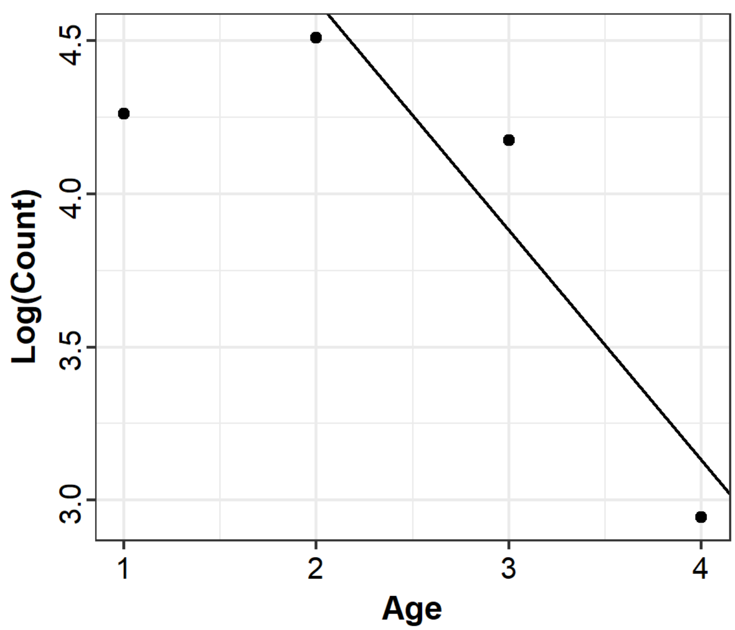

Figure 4. Weighted catch curve analysis of age frequency data of River Darter from northern Ontario and Manitoba. Instantaneous adult mortality was estimated to be 0.752.

YOY survival was estimated to give a variety of population growth rates to represent declining, stable, growing, and booming populations (Table 3). Declining population λ was defined based on COSEWIC criterion A2 for endangered species: a 50% reduction in population size over 10 years or 3 generations, whichever is longer. Generation time (ζ) for River Darter was estimated from the projection matrix to be 1.8 years. From this minimum population growth rate was estimated as: $\lambda_{min} = 0.5^{1/10}$ giving a λ_{min} of 0.93. Stable population λ is equal to 1. Maximum population growth rate (booming populations) was estimated from an allometric relationship (Randall and Minns 2000):

$$\lambda_{max} = e^{2.64W^{-0.35}}, \tag{6}$$

where *W* represents the geometric mean of adult weight (age-1 to 4). As a conservative estimate, the lower prediction intervals from the fitted relationship were used and averaged across waterbodies giving a λ_{max} of 2.49. Growing population λ was estimated through balancing conservative and optimistic estimates of λ by taking the geometric mean of minimum, equilibrium, and maximum λ (Vélez-Espino and Koops 2007). This resulted in a population growth rate of 1.32.

Table 3. River Darter YOY survival rates (σ_0) for various waterbodies under different states of population growth.

State	λ	River		
		Assiniboine	English	Rainy
Declining	0.93	0.0028	0.0073	0.0052
Stable	1	0.0033	0.0084	0.0060
Growing	1.32	0.0059	0.0145	0.0052
Booming	2.49	0.0170	0.0376	0.0287

STOCHASTICITY

Random inter-annual variability was incorporated into simulations to account for environmental stochasticity experienced by populations of River Darter. Variability was incorporated into age-specific fecundity and mortality (Figure 5). Age-specific variables were assumed to vary independently intra- and inter-annually.

Fecundity

In the stochastic simulations random mean population-level fecundity values were generated assuming fecundity has a lognormal distribution. The amount of variation was determined by allowing age-4 fecundity to have a maximum value (approximate upper 99% confidence interval) of 800 eggs. This was produced assuming a lognormal distribution with a log-mean of $\log_e(700)$ and a log-sd of 0.05 (Figure 5 left panel).

Mortality

Inter-annual variability in River Darter mortality was unknown. Bradford (1992) found that across species and life-stages the variance in mortality increases as a function of M ($sd(M) = 0.39M^{1.12}$ or $CV(M) \approx 0.4$). Mertz and Meyers (1995) determined that the variance estimate was likely inflated by error from field estimates of *M* and proposed that inter-annual variability in *M* could be represented by a normal distribution with a constant coefficient of variation (CV_M) of 0.2. A CV of 0.2 applied to YOY mortality rates was determined to result in too much variation, as a result, the CV was halved for YOY River Darter ($CV_{M,0}$ = 0.1).

Stochastic instantaneous mortality rates were generated assuming a normal distribution with CVs of 0.1 for YOY and 0.2 for age-1+ fish (Figure 5 right panel).

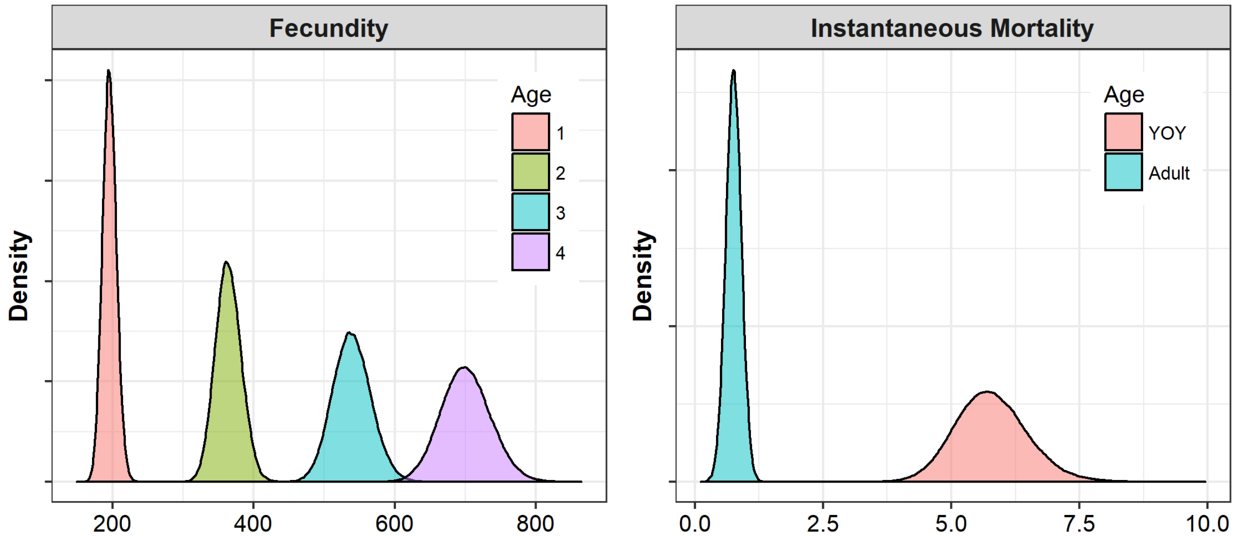

Figure 5. Density graph representing the realized probability distributions for age-specific stochastic parameters (fecundity and instantaneous mortality) incorporated into model simulations. NOTE: age increases along the x-axis from left to right for fecundity but decreased from left to right for mortality.

DENSITY DEPENDENCE

Density-dependence was incorporated into stochastic simulations. It was assumed that density-dependence affects survival in the first year of life (YOY). Density-dependence was represented as a compensatory function of egg density (E_t) using the Beverton-Holt function, such that:

$$\sigma_{0,Et} = \frac{\sigma_{0,max}}{1+\frac{b}{K}E_t}. \qquad (7)$$

Where $\sigma_{0,max}$ is maximum YOY survival rate at 0 density, K is carrying capacity, and b is the density-dependence parameter.

Two levels of maximum population growth were included in simulations, equivalent to booming and growing λ states (λ_{max} = 2.49 or 1.32), to allow for uncertainty in the strength of density-dependence. The density-dependence parameter, *b*, was solved for to give stability (geometric mean population size) at the desired carrying capacity (*K*); giving two unique density-dependence curves for each waterbody (Table 4, Figure 6).

Table 4. River Darter density-dependence parameter, b, values for various waterbodies at different levels of maximum population growth.

State	λ	River		
		Assiniboine	English	Rainy
Growing	1.32	0.0051	0.0109	0.0084
Booming	2.49	0.0285	0.0579	0.0455

Density-dependence was incorporated into population viability analysis and recovery simulations. Density-dependence provides a mechanism for population increase from low density while limiting population size under favourable conditions (Figure 7).

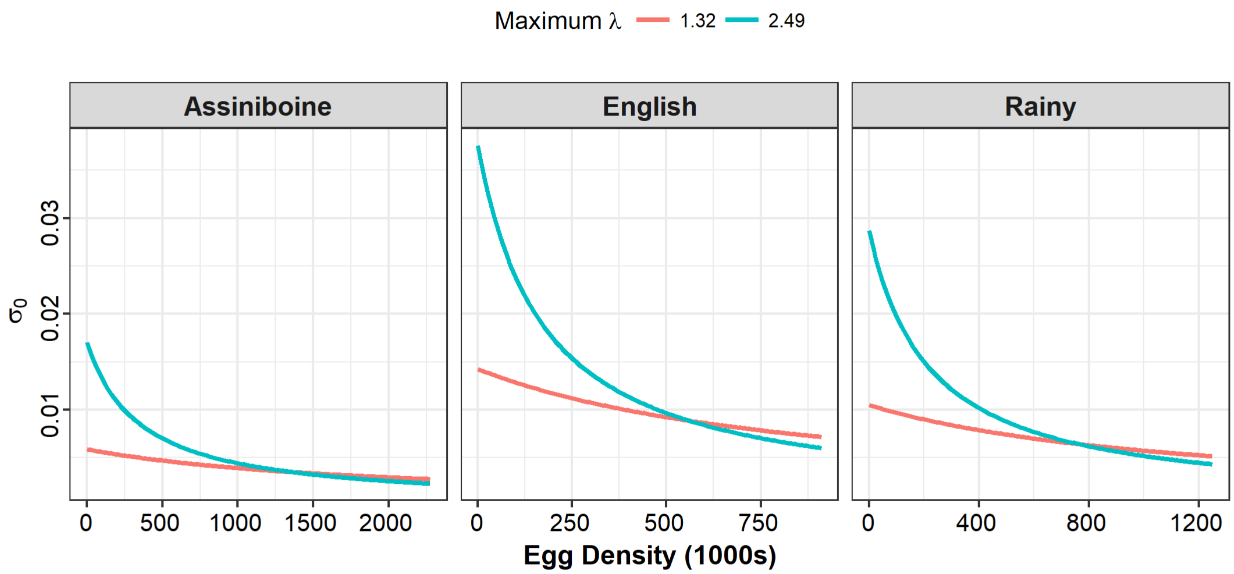

Figure 6. Representation of density-dependence functions incorporated into stochastic simulations for 3 waterbodies at 2 levels of maximum population growth. $\sigma_{0,Et} = \sigma_{0,max}/\left(1+\frac{b}{K}E_t\right)$*; parameter values are listed in Tables 3 and 4.*

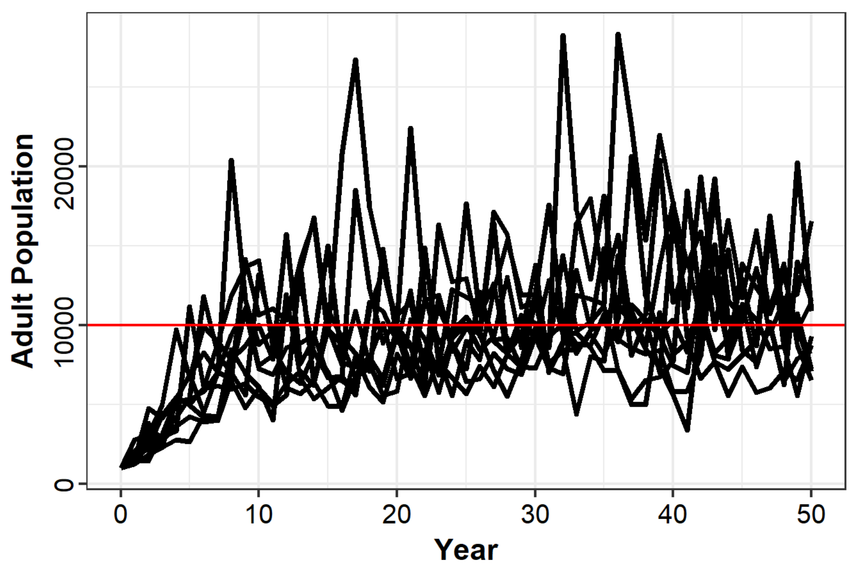

Figure 7. Ten example population trajectories from simulations that include density dependence. Initial population size is 10% of carrying capacity (K = 10,000). Parameter values used were from the Assiniboine River population with a λ_{max} *= 2.49. The red line indicated carrying capacity.*

IMPACT OF HARM

The impact of anthropogenic harm to a River Darter population was assessed with deterministic elasticity analysis of the matrices and stochastic simulations.

Elasticity analysis of matrix elements provides a method to quantify the impact of changes to vital rates on a population. Specifically, elasticities measure the proportional change to population growth rate (λ) that results from a proportional change in a vital rate (*v*). Elasticities

(ε_v) are calculated by taking the scaled partial derivatives of λ with respect to a vital rate (Caswell 2001):

$$\varepsilon_v = \frac{v}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial v} \qquad (8)$$

where a_{ij} is the projection matrix element in row *i* and column *j*.

Elasticity estimates were made deterministically (no stochasticity or density-dependence). Elasticities assume that the change in a vital rate is permanent, that a population is experiencing steady-state conditions and that all other vital rates remain constant. Elasticities are useful because they provide a method to quantify how anthropogenic harm, to specific life-stages, may affect a vulnerable population and identify which life-stages may have the greatest impact on a population when harmed. Vital rates with greater elasticity values have a greater effect on population change and therefore harm to these stages should be considered with care.

Elasticity estimates are influenced by current conditions. Therefore, elasticity values for 4 population states – declining, stable, growing and booming – are provided. When population abundance is increasing (λ > 1) the maximum amount of harm to a specific vital rate that prevents population decline (based on the mean rate) can be estimated as (Vélez-Espino and Koops 2007):

$$\tau_v = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right) \qquad (9)$$

Additionally, simulation analysis was used to investigate the impacts of anthropogenic harm; chronic harm, representing permanent changes to vital rates, and transient harm, representing a one time change in vital rates. Simulations were stochastic but density-independent. Initial, unharmed conditions were those of a population experiencing growing conditions (λ = 1.32). Stage-specific harm (YOY, adult, or all ages) was applied (as deaths per 100 fish per year) ranging between 0 and 99 fish. The change in population size (λ) was estimated over 1 year, 10 years, and 100 years. Simulations were repeated 500 times. This resulted in a distribution of λ values for each level of harm over each time frame. The proportion of observed λs < 1 represent the likelihood of population decline which is used as a proxy for the risk associated with the level of anthropogenic harm (death of fish). The level of risk that is acceptable for a population is a management decision. Harm, as implemented in simulations, was in addition to the mean natural mortality rates of an unharmed population and did not take into account density dependence. Therefore, estimates likely represent 'worst case' scenarios in the absence of compensatory processes. This may be of particular importance in relation to harm to YOY individuals.

This analysis was repeated to assess the impact of transient harm. Here harm is applied in year 1 with the population returned to initial conditions in year 2. Simulations are run for 10 years and replicated 1 000 times. The change in population size from the initial state (year 0) and year 10 was calculated and the probability of population decline (λ < 1) under different levels of harm (death of fish) quantified.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was used to identify potential minimum recovery targets for River Darter. 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 desired probability of persistence over 100 years (~ 55 generations for River Darter). MVP was estimated using simulation analysis which incorporated environmental stochasticity and density-dependence.

Important elements incorporated in population viability analysis include: the choice of time frame over which persistence is determined, the severity and frequency of catastrophic events, and the quasi-extinction threshold below which a population is deemed unviable. The choice of time frame is arbitrary and without biological rationale; however, 100 years (> 50 River Darter generations) is likely reasonable for making management decisions.

The rate and severity of catastrophic events within River Darter populations is unknown. Based on a meta-analysis, Reed et al. (2003) determined that among vertebrate populations, catastrophic die-offs that resulted in a one-year decrease in population size > 50% occurred at a rate of 14%/generation on average. This result was used as a basis within our MVP simulations and used 2 levels of catastrophe rate to allow for uncertainty: 10%/generation and 15%/generation. These rates correspond to a catastrophe frequency of 1 catastrophe every 18 and 12 years, respectively. The impact of catastrophes was drawn randomly from a beta distribution scaled between 0.5 and 1 with shape parameters of 0.762 and 1.5 (Reed et al. 2003; Figure 8).

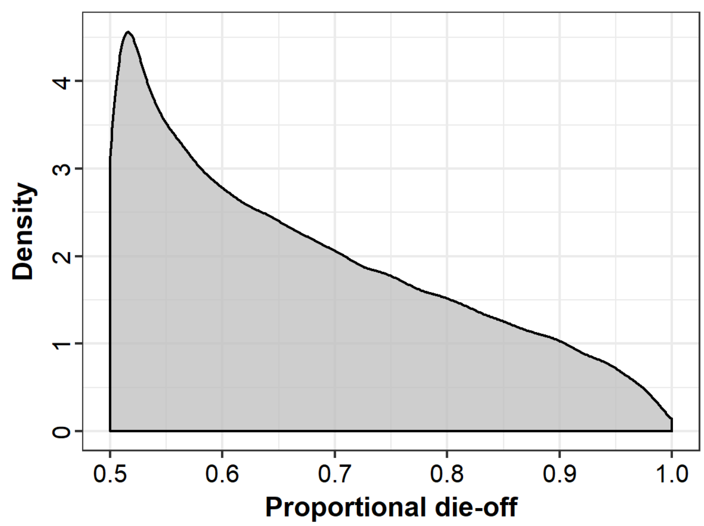

Figure 8. Beta distribution (scaled between 0.5 and 1) use to in stochastic draws of catastrophe impacts. Shape parameters were 0.762 and 1.5.

Quasi-extinction represents the compounding effects of Allee effects, demographic stochasticity and inbreeding depression (Lande 1988, Roberts et al. 2016) leading a population to extinction once the threshold is crossed. The value of the quasi-extinction threshold cannot be empirically measured; therefore, 50 adults was used as a reasonable approximation (Morris and Doak 2002).

Density-dependent, stochastic simulations were conducted for populations of various initial densities (initial density represented carrying capacity, *K*, with λ = 1). Simulations were run for 100 years. Independent simulations incorporated two rates of catastrophes (0.1 and 0.15/generation) and two rates of maximum population growth (1.32 and 2.49) for each waterbody. Each simulation was replicated 3,000 times and the number of quasi-extinctions were counted. The probability of extinction (*P[ext.]*) was modelled as a logistic regression, such that:

$$P[ext.] = \frac{1}{1+e^{-(b_{MVP} log_{10}(N_a)+a_{MVP})}}, \qquad (10)$$

where a_{MVP} and b_{MVP} represent the fitted intercept and slope from the logistic regression. Equation 10 can be rearranged to estimate the required adult population size to give a desired level of population persistence (MVP):

$$MVP = 10^{-\frac{\log\left(1/_{P[ext.]}-1\right)+a_{MVP}}{b_{MVP}}}. \qquad (11)$$

MVP estimates are presented for quasi-extinction probabilities of 5% and 1%.

Habitat: Minimum Area for Population Viability (MAPV)

Minimum area for population viability (MAPV) is defined as the quantity of habitat required to support a population of MVP size (Velez-Espino et al. 2010). MAPV is estimated simply by multiplying population size (MVP) by the area required per individual fish (taken as the inverse of density) :

$$MAPV = MVP/Density. \qquad (12)$$

Density estimates of River Darter populations were available from rivers in northern Ontario (Pratt et al. 2016). As well, fish densities can be estimated from a literature allometry (Randall et al. 1995)

$$Density = 79\,143W^{-0.96}, \qquad (13)$$

where *W* represent mean weight in grams.

RECOVERY TIMES

Time to recovery was estimated using simulation analysis similar to MVP simulations. Simulations began with initial population sizes set to 10% of MVP. Simulations incorporated: stochasticity, density-dependence, and catastrophes in the same manner as MVP simulations. The population was deemed recovered when MVP (1% extinction probability) was reached (MVP was also used as carrying capacity). Simulations were repeated 5,000 times.

RESULTS

IMPACT OF HARM

The impact of anthropogenic harm to a River Darter population was assessed with deterministic elasticity analysis of the matrices and stochastic simulations. Elasticity values were similar across waterbodies (Figure 9). Values were greater for YOY survival rate and fertility than adult survival rate indicating that River Darter populations are likely to be more susceptible to harm to reproduction and early life survival. As population growth rate decreased the sensitivity of adult survival increased though it remained less than YOY survival/reproduction elasticities.

With use of equation 9, these elasticity values were used to estimate the maximum proportional change in vital rates that will still allow for a mean $\lambda \geq 1$ (Table 5). Estimates of harm scale between -1 and 0 and represent proportional decreases in a vital rate. Values < -1 indicate that the vital rate would need to decline more than 100% to cause population decline. This, however, assumes other vital rates remain constant, for example, reproduction continues despite 0 surviving adults. This is clearly an underestimate of the impact of adult mortality which can be better quantified through simulations. These estimates of harm only apply when initial $\lambda > 1$. When $\lambda < 1$ there is no scope for harm as any additional harm would jeopardize population survival.

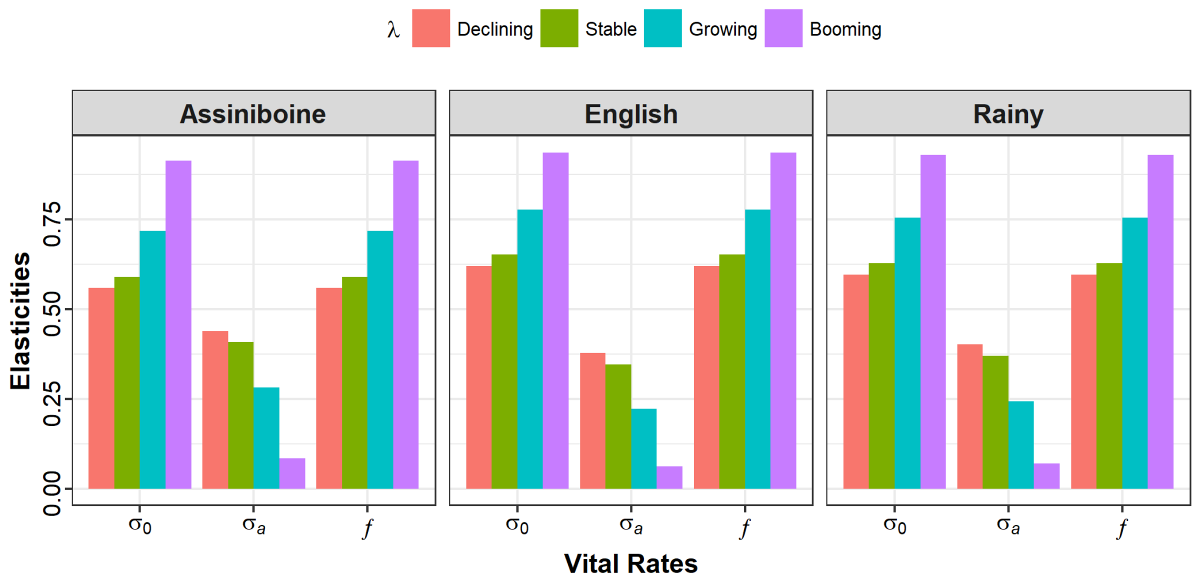

Figure 9. Elasticity analysis results for 3 River Darter populations under 4 population states: declining (orange), stable (green), growing (blue), and booming (purple) (c.f. Table 3).

Table 5. Maximum harm estimates for River Darter populations. The greatest proportional change in vital rates that maintains mean λ > 1. Estimates were based on elasticity estimates (Figure 9).

River	Population Growth Rate (λ)	Vital Rate σ_y / f	σ_a	σ
Assiniboine	1.32	-0.341	-0.867	-0.245
	2.49	-0.654	< -1	-0.598
English	1.32	-0.315	< -1	-0.245
	2.49	-0.639	< -1	-0.598
Rainy	1.32	-0.324	< -1	-0.245
	2.49	-0.644	< -1	-0.598

The results from maximum harm analysis indicated that under growing conditions (λ = 1.32) populations could maintain a mean λ > 1 with mortalities of 31.5 to 34.1% to the YOY stage (or equivalent decline in reproduction) or a 24.5% mortality to all life stages. These values increased to 63.9 to 65.4% and 59.8%, respectively when the population was booming (λ = 2.49). Generally, River Darter populations were not susceptible to mortality to the adult stage based on this method of evaluation and results from simulation analyses should be considered.

Simulation analysis was employed to examine the impacts of chronic and transient harm (in the form of mortalities per 100 individuals) to River Darter populations. Simulations assumed density-independence and a population under growing conditions; therefore unharmed populations would maintain a mean λ of 1.32. Harm (in the form of mortalities) applied reduces mean λ. Simulations incorporated environmental stochasticity leading to a distribution of realized population change (λ) over different time scales (Figure 10). The proportion of realized λ < 1 provides an estimated of the likelihood of observing population decline under current conditions. As the level of harm increases the distribution of realized λ shifted leftward and the likelihood of population decline increases. The probabilities of population decline over three time-frames (1 year, 10 years, and 100 years) for harm (0 to 100 deaths per 100 individuals) affecting YOY, adult or all ages for three waterbodies are estimated (Figure 11).

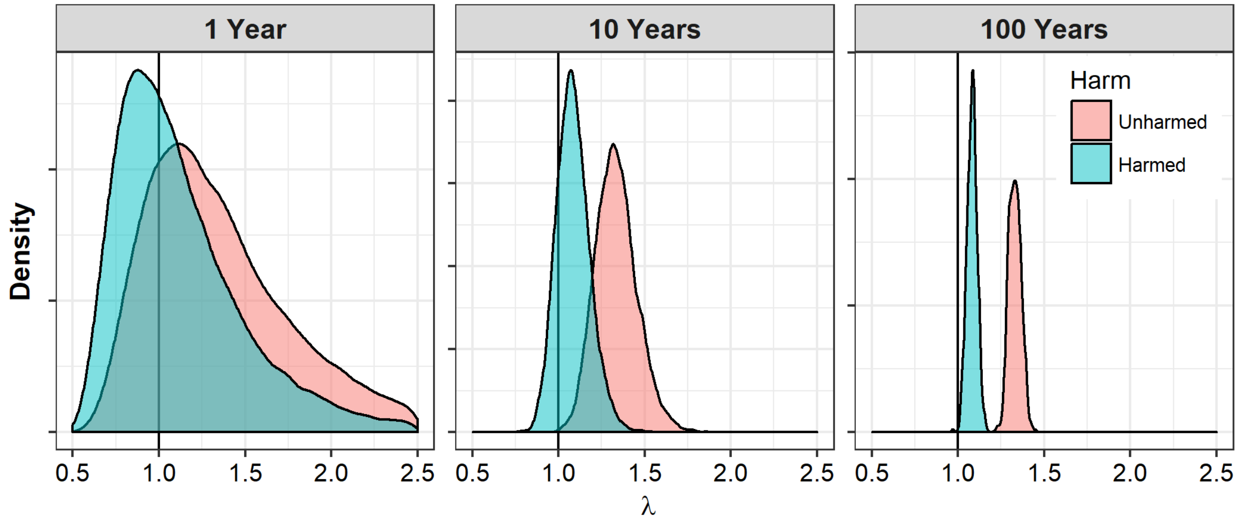

Figure 10. Examples of distributions of population growth rates (λ) from stochastic simulations of River Darter populations over 1 year, 10 years and 100 years when unharmed (average λ = 1.32) and experiencing maximum harm (Table 5; λ ≈ 1).

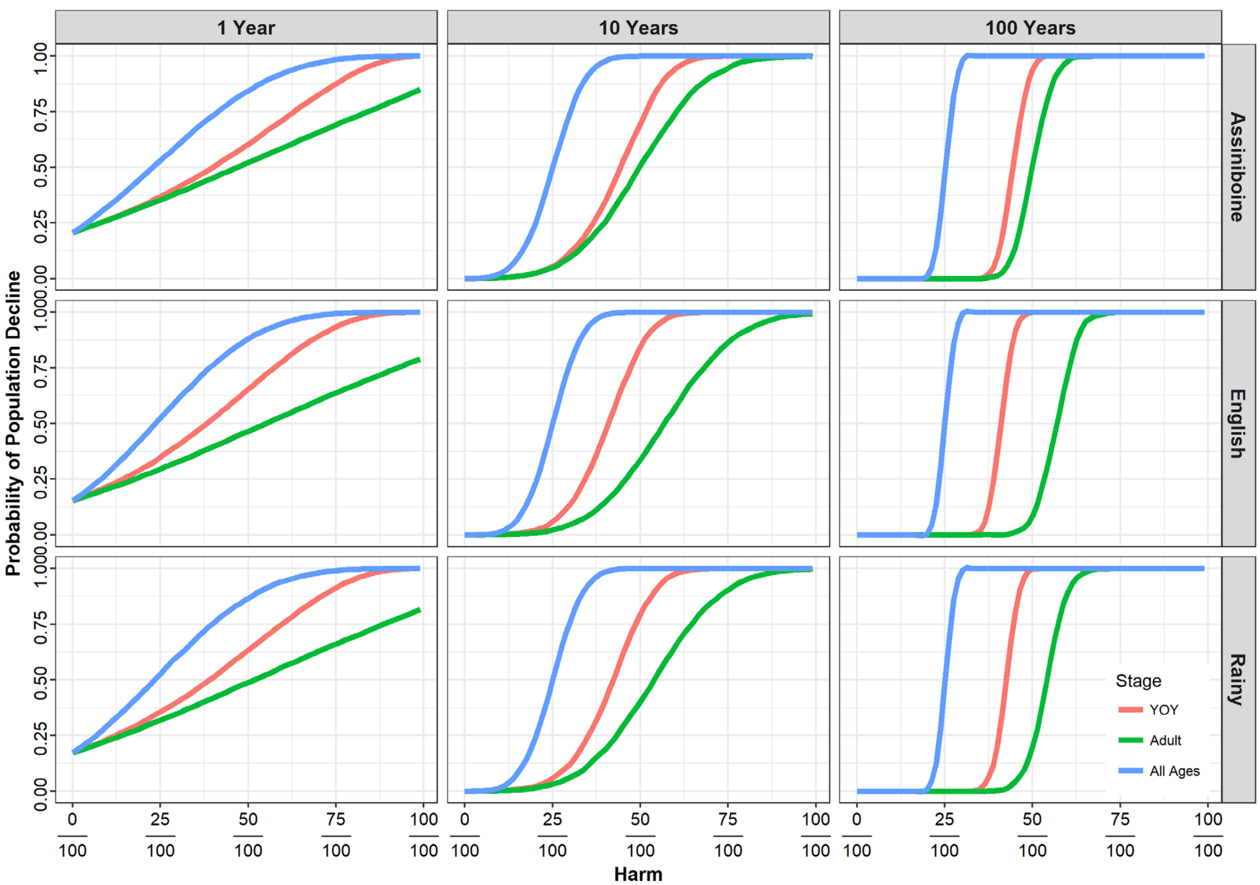

Figure 11. The probability of River Darter population decline (λ < 1) for various levels of harm (deaths per 100 fish) to different life stages (YOY, adult, or all ages) over 3 time periods (1 year, 10 years, and 100 years).

There was a 15.4–20.7% probability of observing population decline annually for an unharmed River Darter population with a mean λ = 1.32. Over 10 or 100 years the probability of observing decline was 0%. The probability of decline increased with increased harm. Congruent to elasticity analysis, the probability of decline increased most rapidly when all life stages were harmed, followed by harm to YOY darters, then harm to adults. The risk (chance of population decline) associated with different levels of harm can be estimated from Figure 11. The results presented (Figure 11) are specific to the initial assumed population growth rate (λ = 1.32). At lower growth rates the risk of decline at equivalent levels of harm will be greater and vice versa for larger λs.

Transient harm was assessed similarly, however, harm was only applied once over a 10 year period (Figure 12). Large impacts of one time harm were only observed when all life stages were affected and when harm exceeded 30 mortalities per 100 individuals. These estimates are specific to a one time event given the initial assumed λ and will increase as harm frequency increased and/or λ decreases.

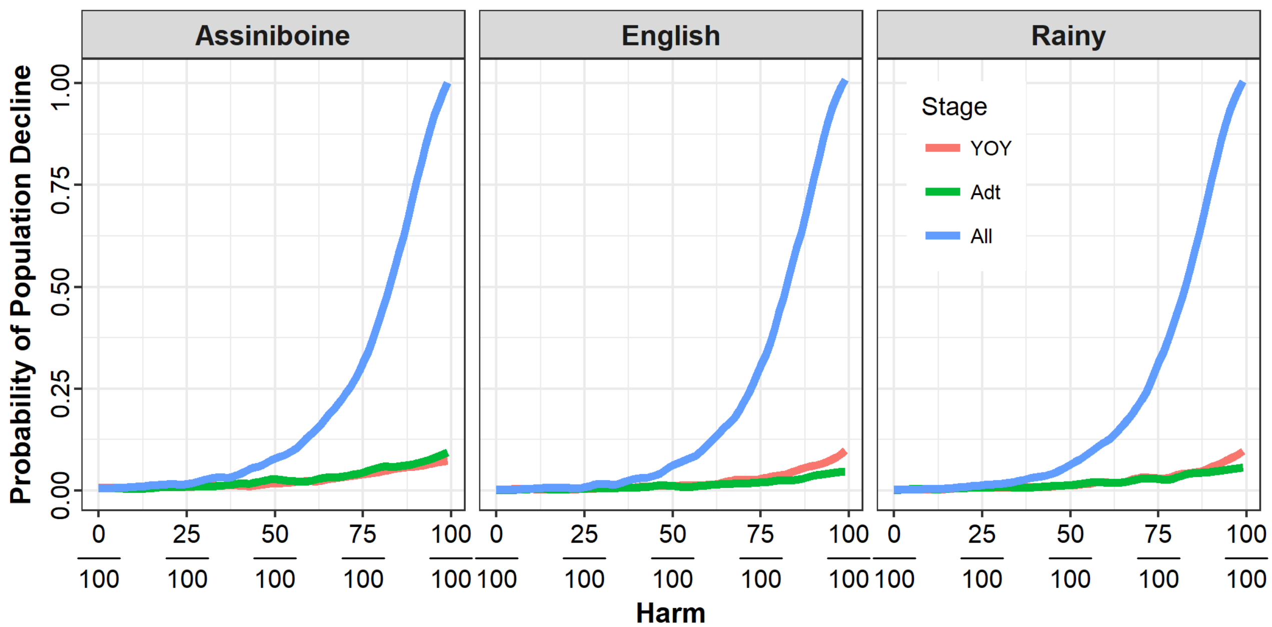

Figure 12. The effects of transient harm (a 1-time death) as the probability of observing population decline over a 10 year time period for three waterbodies and 3 stages impacted by harm.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was assessed using stochastic, density-dependent population simulations. Simulation outputs, binomial quasi-extinctions (1:extinct; 0: extant) were fitted using a logistic regression (Table 6; Figure 13).

Recovery target abundances that provide a 5% and 1% probability of quasi-extinction over 100 years are presented (Table 7). Additional targets, those with different extinction risks, can be estimated with use of Equation 10. Estimates of MVP were highly dependent on the assumed catastrophe rates, maximum population growth rate, and desired level of persistence. Assuming a 1% extinction probability over 100 years and a λ_{max} of 2.49 MVP estimates ranged across rivers from 12,850 to 15,234 with a 10%/generation catastrophe rate. With a 15%/generation catastrophe rate, MVP estimates ranged from 27,097 to 30,910. If λ_{max} was only 1.32 MVP estimates were as high as 223,698 adults.

Table 6. Parameter values for the extinction probability relationships (Equation 10) used to estimate minimum viable population (MVP, Table 7).

River	λ	Catastrophe Rate	a_{MVP}	b_{MVP}
Assiniboine	1.32	0.10	6.818	-2.438
		0.15	6.973	-2.174
	2.49	0.10	7.483	-2.888
		0.15	8.583	-2.973
English	1.32	0.10	7.377	-2.609
		0.15	6.808	-2.136
	2.49	0.10	8.189	-3.111
		0.15	8.273	-2.883
Rainy	1.32	0.10	7.375	-2.614
		0.15	6.758	-2.122
	2.49	0.10	8.065	-3.079
		0.15	8.209	-2.852

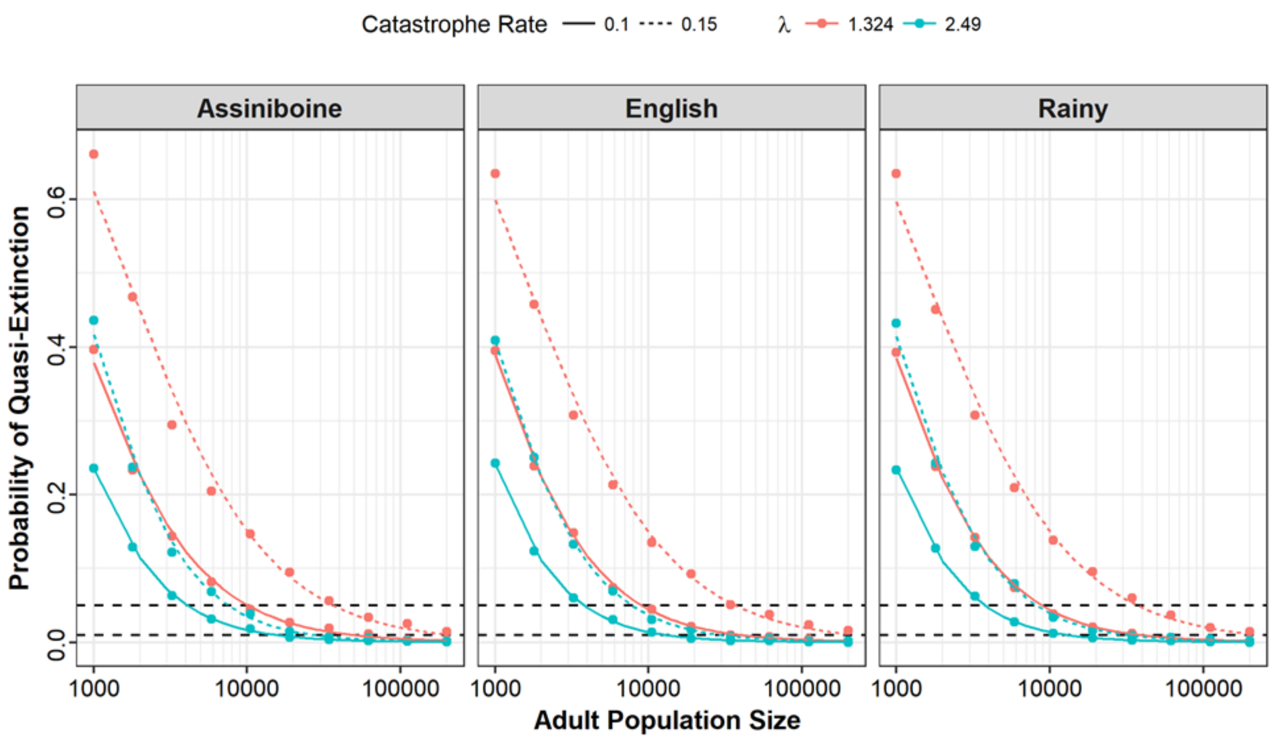

Figure 13. The probability of population quasi-extinction from recovery target simulations. Results are presented for MVP scenarios with a probability of catastrophe of 0.1 and 0.15/generation and maximum growth rates of 1.32 and 2.49.

Habitat: Minimum Area for Population Viability (MAPV)

River Darter density estimates were available for northern Ontario populations. Sample estimates of density (fish/m^2) appeared to decrease with area sampled (Figure 14). A relationship was fitted between density and area. Both density and area were log-transformed to normalize the data and area was centred to reduced correlations in the model fit ($centred\ \log(area) = \log(area) - \log(190.5)$) . The relationship is fitted with ordinary least squares (OLS) and quantile regression (at the 75th quantile). A quantile regression based on the assumption that higher density values are more reflective of carrying capacity than low density values was used. There was no impact of waterbody when incorporated as a random effect (AIC ~ -2).

Table 7. Estimates of the adult minimum viable population (MVP) for River Darter populations and a 5% and 1% probability of extinction. Simulations were conducted for three waterbodies, using two levels of maximum population growth rate and two rates of catastrophes.

River	λ	Catastrophe Rate	MVP	
			***P[ext]* = 5%**	***P[ext]* = 1%**
Assiniboine	1.32	0.10	10,095	47,992
		0.15	36,421	209,213
	2.49	0.10	4,085	15,234
		0.15	7,545	27,097
English	1.32	0.10	9,020	38,707
		0.15	36,859	218,524
	2.49	0.10	3,788	12,850
		0.15	7,781	29,085
Rainy	1.32	0.10	8,860	37,919
		0.15	37,313	223,698
	2.49	0.10	3,769	12,955
		0.15	8,152	30,910

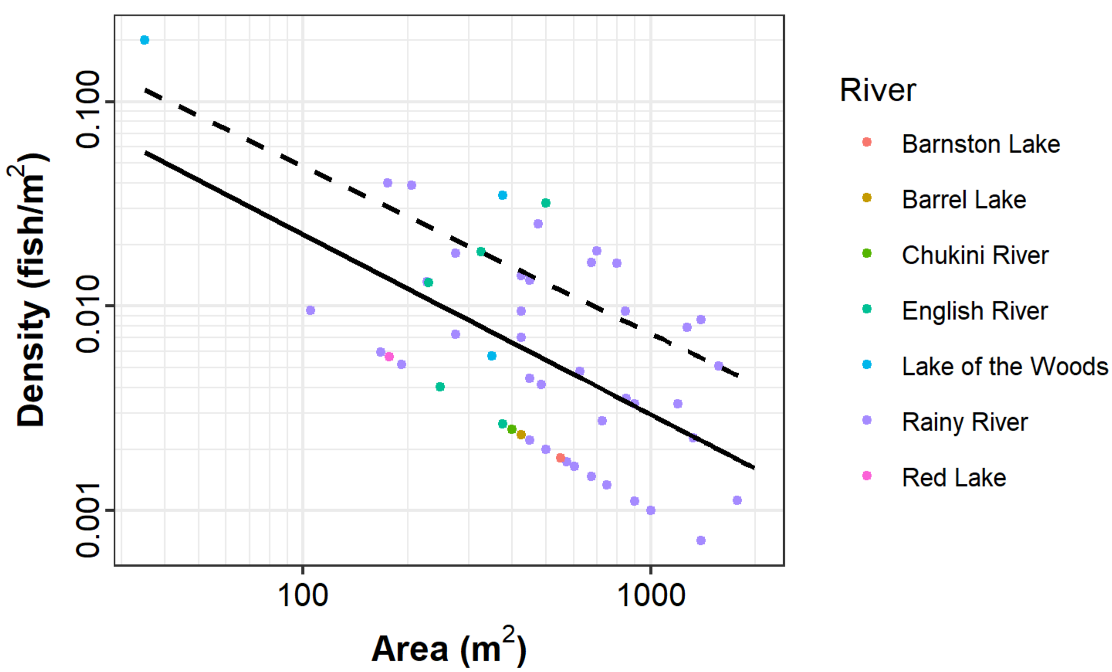

Figure 14. The relationship between area sampled (m²) and River Darter density (fish/m²) from mini-Missouri trawls in northern Ontario (Pratt et al. 2016). The solid line represents an OLS regression ($log(Density) = 0.89 - 0.88\ log(Area)$) and the dashed line represents a 75th quantile regression ($log(Density) = 1.69 - 0.82 log(Area)$).

The estimates of River Darter density at mean effort were 0.013 and 0.029 fish/m^2 from OLS and 75th quantile regression, respectively (Figure 14). Using equation 13, River Darter maximum densities can be estimated based on mean adult weight (1.31, 0.56, and 0.75 g in the Assiniboine, English, and Rainy rivers) giving estimated densities of 6.1,13.6, and 10 fish/m^2. It is likely that the observed low densities of River Darter in habitat where they are not at risk was due to low catchability. Estimates of MAPV for River Darter are provided using the observed density (OLS and quantile regression) adjusted for low catchability with assumed catchability between 0.5 and 10%. MAPV is estimated simply as: $MAPV = MVP/Density$ and assumes early life stages share habitat with sampled adults (Figure 15).

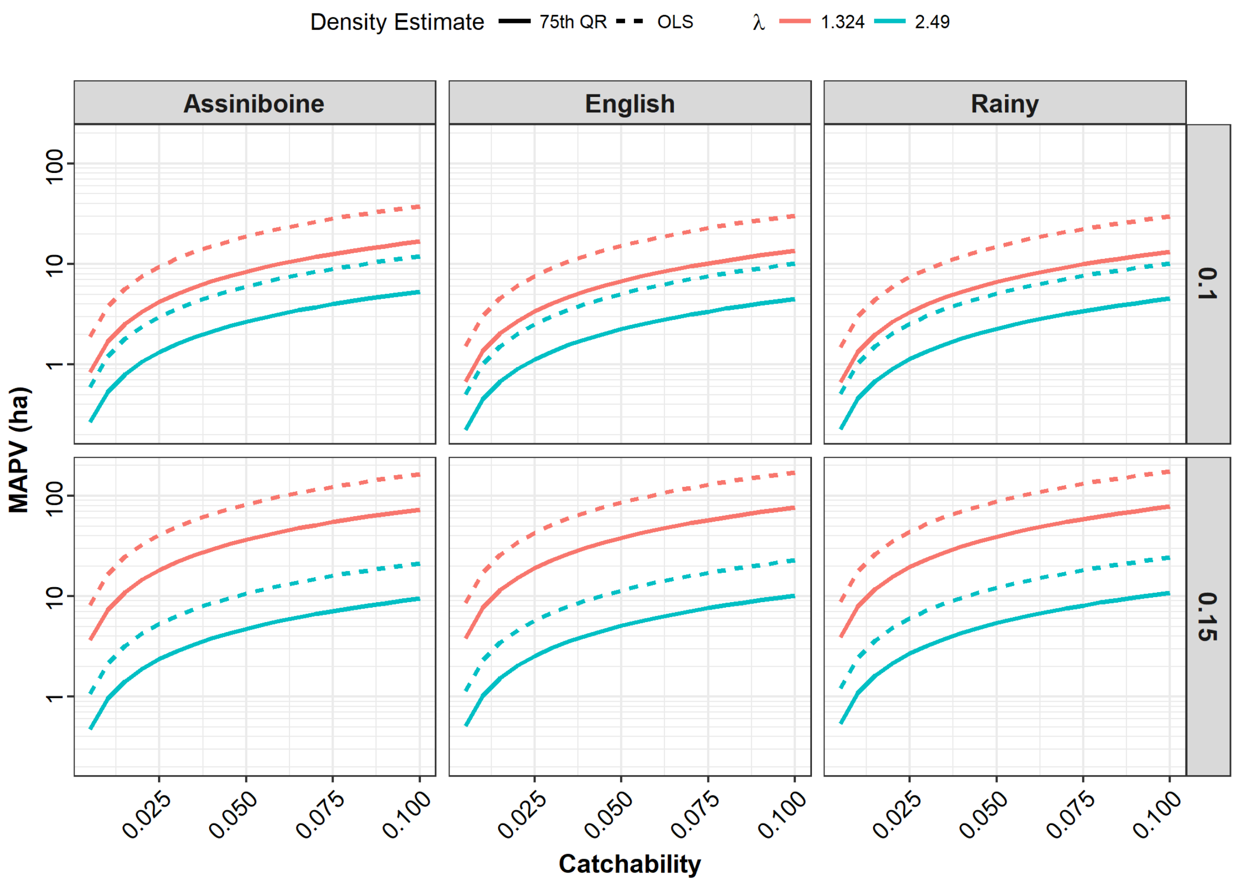

Figure 15. Estimates of MAPV for River Darter populations bases on standardized density estimates (from OLS and 75th quantile regression) adjusted by various rates of catchability. Results are presented for three waterbodies, two rates of catastrophe (0.1 and 0.15/generation), and two levels of maximum population growth rate.

Assuming a 5% catchability gives density estimates of 0.25 and 0.57 adult River Darter per m^2 based on OLS and quantile regressions, respectively. A population with a λ_{max} of 2.49, experiencing catastrophes at a rate of 15%/generation with a 1% extinction probability would require between 10.6 and 12.1 ha (1 ha = 10,000 m^2) with a density of 0.25 fish/m^2 or between 4.7 and 5.4 ha with a density of 0.57 fish/m^2. In the Thames River, River Darter are found between Little John Rd. and Kent Bridge, ON (Jason Barnucz, DFO, pers. comm.) which, represents an approximately 28.7 km length of river and 109 ha of wetted area. If this stretch of river is equally suitable as River Darter habitat 272,500 or 621,300 adult River Darter could be sustained, assuming maximum densities of 0.25 and 0.57, respectively. While this likely over-estimates the carrying capacity of this habitat it does demonstrate that achieving MVP population size in inhabitable portions of the Thames River is possible. The average density required to reach recovery targets of 31,000 adult River Darter in this stretch of the Thames River was 0.028 fish/m^2 which is close the standardized mean density from the 75th quantile regression.

RECOVERY TIMES

Time to recovery was estimated with simulation analysis. Initial population size was set to 10% of MVP. Simulations were run to determine the time to reach MVP population size (MVP also acted as carrying capacity). These simulations reflect an increase in available habitat or a reduction in threats such that vital rates return to a pre-threat state allowing population size to increase towards carrying capacity.

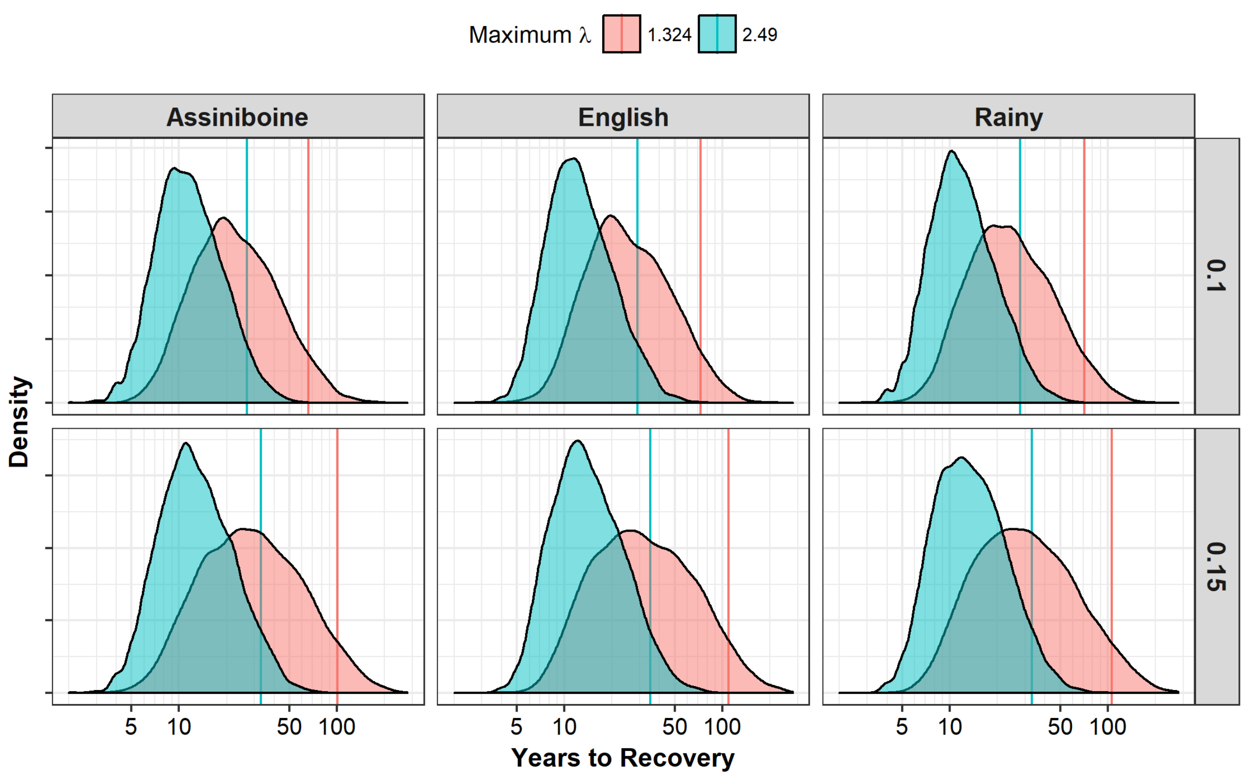

Figure 16. The distributions of recovery time-frames for River Darter populations given a recovery target of MVP (1% $P_{[ext.]}$) an initial abundance of 10% of MVP. Results are presented for three waterbodies, two rates of catastrophe (0.1 and 0.15/generation), and two levels of maximum population growth rate. The reference lines represent the 95th percentiles of recovery.

Simulation replicates resulted in a distribution of recovery times (Figure 16). Estimates of recovery time as the 95th percentile of simulations are presented. Therefore, 95% of simulations experience recovery by the recovery time estimate (Table 8). Recovery occurred quicker with larger maximum growth rates and more infrequent catastrophes, between 27 and 29 years. Populations with slower growth and more frequent catastrophes, however, took between 101 and 109 years to reach recovery targets.

Table 8. Time required (in years) for a population to have a 95% probability of reaching recovery targets (MVP; Table 7) given a recovery target of MVP (1% $P_{[ext.]}$) an initial abundance of 10% of MVP.

Population Growth Rate	Catastrophe Rate	Years to Recovery		
		Assiniboine	English	Rainy
1.32	0.1	66	73	71
	0.15	101	109	106
2.49	0.1	27	29	28
	0.15	33	35	33

DISCUSSION

ELEMENTS

Element 3: Estimate the current or recent life-history parameters for River Darter

The best available data were assembled to provide life-history parameters for River Darter. The value for each life-history parameter used in modelling is presented in Tables 1, 2, 3, and 4. Details regarding how the parameters were estimated and source data used are outlined in the Methods section of this report.

Element 12: Propose candidate abundance and distribution target(s) for recovery

Abundance targets were estimated using population viability analysis and estimates of minimum viable population (MVP). Simulations incorporated density-dependence, environmental stochasticity, and random catastrophes. Targets varied depending on the desired persistence probability, catastrophe rate, and maximum population growth rate (Table 7).

Conservative estimates of MVP utilize a 1% quasi-extinction probability and a catastrophe rate of 0.15/generation. Maximum growth rate for River Darter populations at low density is unknown. The value of 2.49 was taken from an allometry (Randall and Minns 2000) based on the lower prediction interval and is therefore potentially conservative; 1.32 may be overly pessimistic. Therefore, MVP estimates in the range of 27,000 to 31,000 is recommended.

It is emphasized that recovery targets based on MVP can be easily misinterpreted 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. It is stressed that these MVP targets refer to adult numbers only. If juveniles are being included in abundance or density estimates, then the MVP must include these age-classes as well.

Additionally, MVP estimates for River Darter were made using a post-breeding matrix model. This means that abundance estimates were made directly after spawning has occurred and before age-specific mortality has acted. Therefore abundance estimates from MVP analysis represent maximum annual abundances for a given population. When compared to field observations of abundance, sampling date relative to spawning date should be considered and the expected mortality rate over this time period accounted for.

Element 13: Project expected population trajectories over a scientifically reasonable time frame (minimum 10 years), and trajectories over to the potential recovery target(s), given current River Darter population dynamics parameters

Current population abundances and trajectories are unknown for DU3 River Darter. Simulations were conducted for River Darter populations with an initial abundance of 10% of MVP and projected time to recovery where recovery is MVP (MVP was also set as carrying capacity). Assuming a maximum growth rate of 2.49 and a catastrophe rate of 15% per generation, River Darter had a 95% chance of reaching these recovery targets after 33–35 years.

Element 14: Provide advice on the degree to which supply of suitable habitat meets the demands of the species both at present and when the species reaches the potential recovery target(s) identified in element 12

GIS software (ESRI ArcGIS 10.6.1) was used to quantify the available habitat (as wetted area) in the Thames River, bounded by locations where River Darter have been sampled. This totalled a 28.7 km length of river and an area of 109 ha of potential habitat. Assuming this is all usable habitat, MVP abundances (31,000 adults) can be achieved with densities of 0.028 fish/m^2. It is unlikely that the entirety of this stretch of river is suitable habitat for River Darter, however, densities greater than 0.028 fish/m^2 are likely achievable. If one assumed catchability of River Darter was 5%, standardized mean densities of River Darter in northern Not At Risk populations were estimated to be 0.25 or 0.57 fish/m^2. Using these densities, MVP abundances required between 10.6 and 12.1 ha or between 4.7 and 5.4 ha of suitable habitat. Therefore, there is likely sufficient habitat in the Thames River to meet the needs of a sustainable River Darter population. The quantity of habitat in other inhabited areas of DU3 (i.e., Sydenham River) have not been calculated.

Element 15: Assess the probability that the potential recovery target(s) can be achieved under the current rates of population dynamics, and how that probability would vary with different mortality (especially lower) and productivity (especially higher) parameters

See element 13.

Element 19: Estimate the reduction in mortality rate expected by each of the mitigation measures or alternatives in element 16 and the increase in productivity or survivorship associated with each measure in element 17

No clear links have been identified between the mitigation measures and River Darter mortality rates or productivity.

Element 20: Project expected population trajectory (and uncertainties) over a scientifically reasonable time frame and to the time of reaching recovery targets, given mortality rates and productivities associated with the specific measures identified for exploration in element 19. Include those that provide as high a probability of survivorship and recovery as possible for biologically realistic parameter values

Without a direct link between mitigation measures and River Darter mortality rates or productivity, this information cannot be provided.

Element 21: Recommend parameter values for population productivity and starting mortality rates and, where necessary, specialized features of population models that would be required to allow exploration of additional scenarios as part of the

assessment of economic, social, and cultural impacts in support of the listing process

The parameter values presented in Tables 1, 2, 3, and 4 are based on the best available data for this population and should be used for any future population modelling.

Element 22: Evaluate maximum human-induced mortality and habitat destruction that the species can sustain without jeopardizing its survival or recovery

The maximum anthropogenic harm that can be applied to a River Darter population without causing population decline was estimated (Table 5). These values represent the maximum proportional changes to vital rates, in the absence of any other harm, that prevent mean population growth rate (λ) being < 1. Estimates were taken from elasticity analysis, assuming density-independence and are specific to assumed rates of population growth (1.32 and 2.49). Elasticity analysis revealed that River Darter populations are most sensitive to perturbations to YOY survival rates and fertility. Harm to these aspects of life history should be avoided. Decreases in YOY-survival or reproductive success greater than 31 to 34% may result in population decline. Perturbations greater than 24.5% affecting all age-classes may also cause population decline. Relationships between anthropogenic activities and changes in vital rates have not yet been established and require future research.

Simulation analysis was also used to investigate the impact of harm (Figures 10 and 11). Again, these simulations were conducted assuming density-independence and were specific to an initial (unharmed) mean λ = 1.32. These results demonstrate the risks associated with various levels of harm to River Darter populations. Risk was quantified as the probability of population decline (λ < 1) under harm to different life-stages over 3 time-frames: 1 year, 10 years and 100 years (i.e., what is the likelihood of having fewer River Darter than was started with if one were to return after 1, 10 or 100 years). Initially, due to environmental stochasticity, there was an approximately 21% chance of observing population decline annually, although, the risk was 0% over 10 and 100 years. As harm was increased the risk of population decline also increased. At our estimate of maximum harm (24% for all ages) there was approximately a 51%, 44%, and 32% probability of population decline over 1, 10, and 100 years, respectively. The time-frame of interest and level of acceptable risk will have to be determined.

Similarly, the impact of transient harm was estimated (Figure 12). This measures the risk of population decline over 10 years after a one time death of fish event. Stage-specific effects were small but with all ages impacted, the effects at high rates (> 75%) of harm were significant. These results are specific to an assumed density-independent λ of 1.32 and to harm occurring no more than once every 10 years. As the frequency of harm increases, the results will begin to approximate those of chronic harm (Figure 11).

UNCERTAINTIES

Limited data were available to parameterize the River Darter population model. Data were available from DUs 1 and 2, which were deemed Not at Risk in the most recent COSEWIC assessment. It is unknown what differences may exist between DU1 and 2 versus DU3 River Darter. As well, information on population trajectory and abundance were unavailable. Where necessary, assumptions were made about population growth rate and density. More information relating to population trajectories from multiple sites, which would require long abundance time series, would help refine estimates of λ and better inform harm and recovery estimation.

There was also little empirical data related to important vital rates such as survival and fecundity. A single estimate of adult mortality was available and its estimation may have violated the assumptions of catch-curve analysis (e.g., constant year class strength and equal vulnerability to sampling gear). As well, no data were available on the survival of younger age classes. Instead estimates of YOY survival were solved for using an optimization procedure and an assumed population growth rate, which may not reflect realized population growth. It is unknown whether the survival rates incorporated into the simulation model reflect mean trends experienced by DU3 River Darter. Less information was available to inform parameter values related to fecundity. Estimates of fecundity were based on a number of assumptions. First, it was assumed that River Darter reproduction and fecundity is similar to that of Channel Darter in Canada (Scott and Crossman 1973). This assumption was used to define the range of fecundity values for age-4 River Darter but this is un-validated. Second, it was assumed the relative influence of maternal body size was constant across age classes ($\beta_f = 1$). The effect of maternal body size on fecundity in DU3 or any River Darter population is unknown; however, as River Darter growth as adults is limited it is unlikely that this assumption would have a large impact on model results.

Inter-annual variability in vital rates was also largely unknown. The variation in fecundity incorporated into stochastic simulations was based on an assumed maximum value (Fringpong and Angermeier 2009). It is not clear what River Darter population this estimate is from. Darter populations in southern locations experience longer spawning seasons and, as a result, can produce more eggs per year (Hubbs 1985); therefore, it is possible that this is an over-estimate of maximum fecundity for DU3 River Darter resulting in an over-estimate of variability and an under-estimate of MVP. Increases in the variation of fecundity included in stochastic simulations tend to result in lower MVP estimates (Vélez-Espino and Koops 2012). As well, variability in survival rate was entirely unknown. A constant coefficient of variation of 0.2 was assumed and applied to adult mortality (Bradford 1992; Mertz and Meyers 1995) and 0.1 applied to YOY mortality. It is unknown how well these assumptions approximate variation in River Darter mortality. Simulation results have shown an exponential increased in MVP with increased standard deviation of YOY survival rate (Vélez-Espino and Koops 2012). This assumption should be considered when applying abundance targets based on MVP values with future estimates adjusted as more information on vital rate variability becomes available.

Pratt et al. (2016) reported a female-skewed sex ratio among populations of River Darter in northern Ontario and Manitoba; however, no mechanism to cause this result was given and the ratio was variable among sampling locations. It is possible that this result was due to gear selectivity. Other explanations are differential survival between sexes or an unequal number of male and female offspring produced; however, no supporting evidence was available. The sex ratio, as incorporated into matrix models, represents the proportion of females at birth. Simulations assuming an equal sex ratio were conducted. Preliminary analysis with a skewed sex ratio produced qualitatively similar results. As no data were available to define sex-specific survival rates, this scenario was not explored in simulations and it is not known what impact this may have on model outputs. More data on the sex composition of River Darter populations in Canada is required to definitively determine the natural sex ratio; if a skewed ratio is found, a mechanism for this result must be established.

Final, the frequency and impacts of catastrophic events for River Darter were unknown. According to Reed et al. (2003), catastrophic events (a one-time decline in abundance of 50% or more) occur at a probability of 0.14/generation in vertebrates. It is uncertain at what frequency catastrophic events occur for River Darter populations. Therefore, modelling of recovery targets assuming a stable population with the most conservative catastrophe scenario, based on Reed et al. (2003), of 15% was included. The choice of catastrophe frequency had a large impact on MVP estimates. Research that identifies the magnitude and frequency of catastrophic events at the population level would greatly reduce uncertainty in estimates of MVP size, and is recommended for the conservation of River Darter.

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