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Recovery Potential Modelling of Kidneyshell (*Ptychobranchus fasciolaris*) 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 Kidneyshell (*Ptychobranchus fasciolaris*) in Canada as Endangered. Sampling data provided by the UMBO (Unionid Monitoring and Biodiversity Observation) network was analyzed to estimate abundance and population growth for Kidneyshell populations in the Ausable and Sydenham Rivers. Population modelling is presented to assess the impacts of harm and estimate abundance and habitat requirements to support viable populations in support of a recovery potential assessment (RPA).

The model incorporated parameter uncertainty, environmental stochasticity, and density-dependence into population projections. The Ausable River population in the sample sites has a projected adult abundance of 1,129 (95% CI 933–1,360) and an estimated population growth rate of 1.07 (95% CI: 1.02–1.13). The Sydenham River population in the sample sites has a projected adult abundance of 6,949 (95% CI 5,371–9,059) and an estimated population growth rate of 1.13 (95% CI: 1.11–1.15). These abundance estimates are minimum estimates since Kidneyshell can be found outside the sample sites. The population model analysis demonstrated that Kidneyshell populations were most sensitive to perturbations to adult survival under most circumstances. Estimates of the maximum sustainable level of harm (i.e., harm that would not reduce population growth rate to less than 1) were estimated for populations in the Ausable and Sydenham Rivers. Population viability analysis was used to identify requirements for population viability. Demographic sustainability (i.e., a self-sustaining population over the long term) can be achieved with an adult population size of ~ 5,250 (CI: 2,250–9,750) at a 99% probability of persistence over 100 years. Based on current population densities, such a population would require ~ 260 ha (CI: 105–680) in the Ausable River and ~ 50 ha (CI: 22–113) in the Sydenham River. Based on extrapolated population densities at carrying capacity, the population would require ~ 108 ha (CI: 4.7–5,100) in the Ausable River and ~ 10 ha (CI: 0.62–109) in the Sydenham River. The Sydenham River population in the sample sites currently exceeds this estimate of minimum viable population size (MVP). At current population growth rates, the Ausable River population within the sample sites can reach the MVP in 52 years (CI: 22–167).

INTRODUCTION

The Kidneyshell (*Ptychobranchus fasciolaris*) is a medium to large freshwater mussel historically found in Lake St. Clair and Lake Erie, and in the Grand, Thames, Sydenham, Ausable, Niagara and Detroit River systems in Canada. However, it has been extirpated from most of its historical range and is currently only found in the Ausable River, the East Sydenham River and in portions of the St. Clair River delta. The mussel is usually found in small to medium-sized rivers and streams and in shallow areas with gravel and sand substrates and clear, swift-flowing water (COSEWIC 2003).

This species was assessed as Endangered in May 2003 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). It was re-assessed and the status confirmed in May 2013. A recovery strategy was developed for this species in 2006 (Morris 2006) and subsequently revised in 2013 (DFO 2013). This Recovery Potential Assessment (RPA) is being produced to incorporate new information and new modelling and analysis techniques to support future management actions.

The *Species at Risk Act* (SARA) mandates the development of recovery strategies for the protection and recovery of species that are at risk of extinction or extirpation from Canada. In response, Fisheries and Oceans Canada (DFO) has developed the RPA (DFO 2007a,b) as a means of providing information and scientific advice. This report contributes to the RPA through the use of statistical analyses and population modelling to assess current population status, the impact of anthropogenic harm to populations, and identifying abundance and habitat requirements with associated uncertainties. This work is based on a demographic approach developed by Vélez-Espino and Koops (2009, 2012) and Vélez-Espino et al. (2010).

FIELD SAMPLING ANALYSIS

DATA

Data from the Unionid Monitoring and Biodiversity Observation (UMBO) network (Metcalfe-Smith et al. 2007, Sheldon et al. 2020) for locations in the Sydenham and Ausable Rivers were analysed to estimate Kidneyshell density, population trajectory, and various life-history parameters.

The UMBO network is a collaborative monitoring program between DFO and regional conservation authorities used to track the status of unionid species in Southern Ontario. Index sites were identified in each system using prior knowledge to target areas of greater mussel density and species at risk (SAR) occurrence. Survey methods used a systematic sampling design where sites were divided into approximately 25 blocks, each measuring 3 x 5 m. Three randomly selected 1 m^2 quadrats within each block were hand-excavated to approximately 10 cm. Species were identified, counted and measured (maximum length) (Sheldon et al. 2020).

Ten sites in the Sydenham River have been sampled at least twice and are within the expected distribution of Kidneyshell. Sites were sampled the first time between 1999 and 2003, resampled between 2012 and 2015, and in 2022 four sites were sampled for a third time. Sydenham River sampling was conducted by Environment Canada in the first sampling period and then subsequently by DFO.

Five sites in the Ausable River have been sampled three times and are within the expected distribution of Kidneyshell. Sites were initially sampled in 2006, sampled a second time in 2011 and sampled a third time between 2018 and 2019. Ausable River sampling was conducted primarily by the Ausable Bayfield Conservation Authority.

Spent shells encountered during a targeted study in 2012 and 2013 on the Ausable River were collected by DFO and used for aging.

ANALYSIS

Population density and trajectory were estimated by fitting statistical models to the quadrat data with separate models for the Sydenham and Ausable Rivers. The models were constructed as generalized linear mixed models (GLMM) and fit using INLA (Integrated Nested Laplace Approximation; Rue et al. 2009). INLA is a method for making fast and accurate Bayesian approximations and provides greater flexibility in model formation than many frequentist methods and quicker model fitting than Markov Chain Monte Carlo methods.

Models were fit with a variety of probability distributions and random effect structures with each model following the structure:

$$\log_e(\mu_{ij}) = \alpha + \beta_1 \cdot year + \beta_{2\ldots n} \cdot covariates_{2\ldots n} + z_j. \tag{1}$$

Where μ_{ij} is the mean expected value for observation (count of live mussels) i at site j, α is the intercept, β are fixed effects coefficients and z_j are the random effects. The various probability distributions explored were all capable of handling positive discrete data and included: Poisson, Negative Binomial (NB), Tweedie, and Zero-inflated Poisson (ZIP) (Table 1). The random effect structures explored related to site effects and included: no random effects ($z_j = 0$), site as a random intercept ($z_j = site_j$), and site as a random intercept and slope for year ($z_j = site_j + \gamma_j \cdot year$) with the intercept and year random effects treated as either independent or correlated parameters. The random errors were assumed to be independent and identically distributed (iid) where $e_j \sim N(0, \sigma_j^2)$.

Table 1. Parameterization of prospective probability distributions used in quadrat count models.

Distribution	Parameterization	Definition
Poisson	$y_i \sim Poisson(\mu_i)$ $E(y_i) = \mu_i$ $var(y_i) = \mu_i$	μ_i = mean
Negative Binomial	$y_i \sim NB(\mu_i, \mathrm{k})$ $E(y_i) = \mu_i$ $var(y_i) = \mu_i + \frac{{\mu_i}^2}{\mathrm{k}}$	μ_i = mean k = size
Tweedie	$y_i \sim Tweedie(\mu_i, p, \phi)$ $E(y_i) = \mu_i$ $var(y_i) = \phi \cdot {\mu_i}^p$	μ_i = mean p = Tweedie power parameter ϕ = dispersion parameter
Zero-inflated Poisson	$y_i \sim ZIP(\mu_i, \pi)$ $E(y_i) = (1-\pi) \cdot \mu_i$ $var(y_i) = (1-\pi) \cdot (\mu_i + \pi \times {\mu_i}^2)$	μ_i = mean π = proportional zero inflation

The fixed effects incorporated into the model included year, which because of the log-link function (Equation 1) represents the instantaneous rate of population increase, r, and, therefore can give population growth rate as $\lambda = e^r$. In addition, depth and percent sand and gravel substate were included as potential covariates because these characteristics may influence Kidneyshell density (COSEWIC 2003).

The ‘best’ fit model was assessed with Bayesian p-values of fit statistics, DHARMa residuals (Hartig 2022), and Watanabe-Akaike information criterion (WAIC; Watanabe 2010).

Bayesian p-values compare the proportion of fit statistics estimated from simulated data generated from the model that exceed the fit statistic estimated from the observed data. Values close to 0.5 indicate good fit. Three fit statistics were used: sum of squared estimates (SSE), where:

$$SSE = \sum \left[\frac{y_i - E(y_i)}{\sigma_y{}^2}\right]^2, \qquad (2)$$

Residual variance, where:

$$residual\ variance = var(y_i - E(y_i)), \qquad (3)$$

and the proportion of zeros, where the number of observed zeros was compared to those generated across simulations.

DHARMa residuals use a simulation-base approach to generate interpretable residuals for GLMMs. The residuals are scaled between 0 and 1 and describe the proportion of simulated data points above or below the observed value. The residuals should follow a uniform distribution, assessed with a Kolmogorov-Smirnov test, with no obvious trend when plotted against the rank order-transformed fitted values, assessed visually.

Once the 'best' model was selected, giving the preferred probability distribution and random effect structure, a step-wise procedure was used to reduce the fixed effects based on parameter significance and ΔWAIC, covariates were removed when they had a non-significant parameter and its removal did not worsen WAIC by more than two.

Penalised complexity priors were used for random effects hyperparameters (Simpson et al. 2017), with a u parameter of three times the standard deviation of y with respect to the potential random effect and $\alpha = 0.01$; indicating that there is a 1% probability of the random effect σ being greater than three times the standard deviation.

Growth of Kidneyshell were assessed using analyses applied to age data from spent shells collected at sample sites in the Ausable River in 2012 and 2013. Growth was assumed to follow the von Bertalanffy growth function (VBGF) where:

$$L_t = L_\infty(1 - e^{-kt}). \qquad (4)$$

Where L_t is length at age t, L_∞ represents asymptotic length, and k is the growth coefficient.

The frequency distributions of Kidneyshell in the Sydenham and Ausable Rivers were compared across sampling periods with ridge plots (Wilke 2022). Putative juveniles were identified based on an estimate of length-at-maturity derived from the fitted VBGF (Equation 4) and a predictive relationship for age-at-maturity based on the growth coefficient k: $T_{mat} = 0.69k^{-1.031} - 1$ (Haag 2012).

RESULTS

749 and 506 Kidneyshell were encountered in the Sydenham and Ausable Rivers, respectively. Mean density was similar between the two rivers, 0.417 mussels/m^2 in the Sydenham River and 0.450 mussels/m^2 in the Ausable River (Table 2). In the Sydenham River, density has increased throughout the survey; 0.094 mussels/m^2 in the first sample period (1999–2003), 0.622 mussels/m^2 in the second sample period (2012–2015); and 0.72 mussels/m^2 in the partial third sample period (2022). Density in the Ausable River was more variable but has increased overall, 0.375 mussels/m^2 in the first sample period (2006), 0.269 mussels/m^2 in the second sample period (2011), and 0.706 mussels/m^2 in the third sample period (2018–2019). All sites in the Sydenham River increased in density between the first and second/third samples. In the Ausable River, four sites increased in mean density between the first and third samples;

however, one of those four sites decreased between samples 1 and 2, and one site decreased between samples 1 and 3 (Table 2).

The best fit models for quadrat count used the Negative Binomial probability distribution with the intercept and slope for year random effect structure for both rivers, where the slope and intercept random effects were treated as uncorrelated parameters (Tables 3 and 4). Both models produced adequate fit statistics and there were no patterns in the residuals plots (Figure 1). Residuals were examined using semi-variogram to check for possible spatial correlations.

Table 2. Summary of sample data for Kidneyshell (KS); SE is standard error.

River	Site	Latitude	Longitude	Year	# of Blocks	# of Quadrats	# of KS Collected	Mean Density (#/m^2)	SE
Sydenham River	SR-01	42.86	-81.79	2002	24	72	2	0.03	0.003
				2012	24	72	5	0.07	0.004
				2022	25	75	36	0.48	0.01
	SR-02	42.806	-81.847	2003	26	78	1	0.01	0.001
				2013	25	75	8	0.11	0.005
	SR-03	42.779	-81.835	1999	23	69	7	0.1	0.004
				2012	23	69	12	0.17	0.006
				2022	25	75	54	0.72	0.012
	SR-05	42.651	-82.01	2003	23	69	8	0.12	0.005
				2015	25	75	69	0.92	0.014
	SR-06	42.604	-82.072	2002	26	78	10	0.13	0.004
				2012	25	75	35	0.47	0.01
				2022	25	75	82	1.09	0.015
	SR-07	42.697	-81.99	2003	27	81	2	0.02	0.002
				2013	25	75	4	0.05	0.003
	SR-10	42.846	-81.825	2001	25	75	10	0.13	0.006
				2013	25	75	20	0.27	0.007
	SR-12	42.589	-82.126	1999	26	78	13	0.17	0.005
				2015	25	75	147	1.96	0.02
	SR-17	42.679	-82.017	2001	27	81	7	0.09	0.004
				2012	25	75	54	0.72	0.012
				2022	25	75	45	0.6	0.012
	SR-19	42.626	-82.023	2002	25	75	11	0.15	0.005
				2013	25	75	107	1.43	0.018
Ausable River	AR-12	-	-	2006	25	75	3	0.04	0.003
				2011	32	96	4	0.05	0.002
				2019	28	84	17	0.22	0.006
	AR-13	-	-	2006	25	75	0	0	0
				2011	27	81	0	0	0
				2018	30	90	1	0.01	0.001
	AR-24	-	-	2006	25	75	93	1.24	0.019
				2011	27	81	64	0.85	0.015
				2019	27	81	212	2.83	0.034
	AR-7	-	-	2006	23	69	36	0.52	0.012
				2011	26	78	28	0.37	0.009
				2018	30	90	13	0.17	0.005
	AR-8	-	-	2006	25	75	6	0.08	0.004
				2011	26	78	6	0.08	0.003
				2018	28	84	23	0.3	0.007

Table 3. Sydenham River quadrat count model fit statistic comparison across various random effects structures and probability distributions. The fits include the complete suites of potential fixed effect covariates. The selected model is indicated in bold. NB is negative binomial, ZIP is zero-inflated Poisson. SSE is sum of squared estimates, KS is Kolmogorov-Smirnov, and WAIC is Watanabe-Akaike information criterion.

		Bayesian p-values				
Random effects	Distribution	SSE	Residual Variance	# of Zeros	KS Test	WAIC
Intercept and slope - independent	**NB**	**0.428**	**0.534**	**0.586**	**0.204**	**2,470.5**
Intercept and slope – independent	ZIP	0.306	0.228	0.630	0.168	2,476.7
Intercept and slope – independent	Poisson	0.206	0.040	0.842	0.183	2,477.2
Intercept	NB	0.316	0.505	0.595	0.508	2,496.3
Intercept	ZIP	0.364	0.214	0.973	0.108	2,505.0
Intercept	Poisson	0.094	0.013	0.896	0.987	2,508.2
Intercept and slope – independent	Tweedie	0.701	0.997	0.308	0.326	2,523.7
Intercept	Tweedie	0.590	0.988	0.338	0.002	2,546.2
Intercept and slope – correlated	NB	0.000	0.470	0.761	0.214	2,649.2
Intercept and slope – correlated	ZIP	0.000	0.142	0.764	0.422	2,661.3
Intercept and slope – correlated	Poisson	0.000	0.002	0.978	0.290	2,667.8
Intercept and slope – correlated	Tweedie	0.010	0.969	0.509	0.265	2,689.9
None	NB	0.381	0.657	0.510	0.307	2,749.3
None	ZIP	0.453	0.172	1.000	0.000	2,788.3
None	Tweedie	0.589	0.689	0.545	0.619	2,790.3
None	Poisson	0.000	0.000	0.998	0.005	2,838.4

Table 4. Ausable River quadrat count model fit statistic comparison across various random effects structures and probability distributions. The fits include the complete suites of potential fixed effect covariates. The selected model is indicated in bold. NB is negative binomial, ZIP is zero-inflated Poisson. SSE is sum of squared estimates, KS is Kolmogorov-Smirnov, and WAIC is Watanabe-Akaike information criterion.

		Bayesian p-values				
Random effects	Distribution	SSE	Residual Variance	# of Zeros	KS Test	WAIC
Intercept and slope – independent	**NB**	**0.515**	**0.484**	**0.710**	**0.671**	**1,449.0**
Intercept and slope – independent	ZIP	0.388	0.008	0.664	0.433	1,483.0
Intercept	NB	0.533	0.462	0.698	0.679	1,488.1
Intercept and slope – independent	Poisson	0.138	0.000	0.994	0.006	1,510.9
Intercept	ZIP	0.557	0.010	0.999	0.040	1,525.9
Intercept and slope – independent	Tweedie	0.431	0.647	0.885	0.539	1,526.4
Intercept	Tweedie	0.372	0.551	0.921	0.819	1,560.3
Intercept	Poisson	0.096	0.000	1.000	0.002	1,566.8
Intercept and slope – correlated	NB	0.246	0.538	0.704	0.650	1,773.9
None	NB	0.381	0.527	0.649	0.585	1,804.6
Intercept and slope – correlated	Tweedie	0.010	0.110	0.984	0.205	1,828.6
Intercept and slope – correlated	ZIP	0.020	0.004	0.555	0.314	1,843.5
None	ZIP	0.272	0.094	1.000	0.000	1,880.1
None	Tweedie	0.044	0.009	0.994	0.243	1,889.1
Intercept and slope – correlated	Poisson	0.000	0.000	1.000	0.000	2,014.3
None	Poisson	0.000	0.000	1.000	0.000	2,206.7

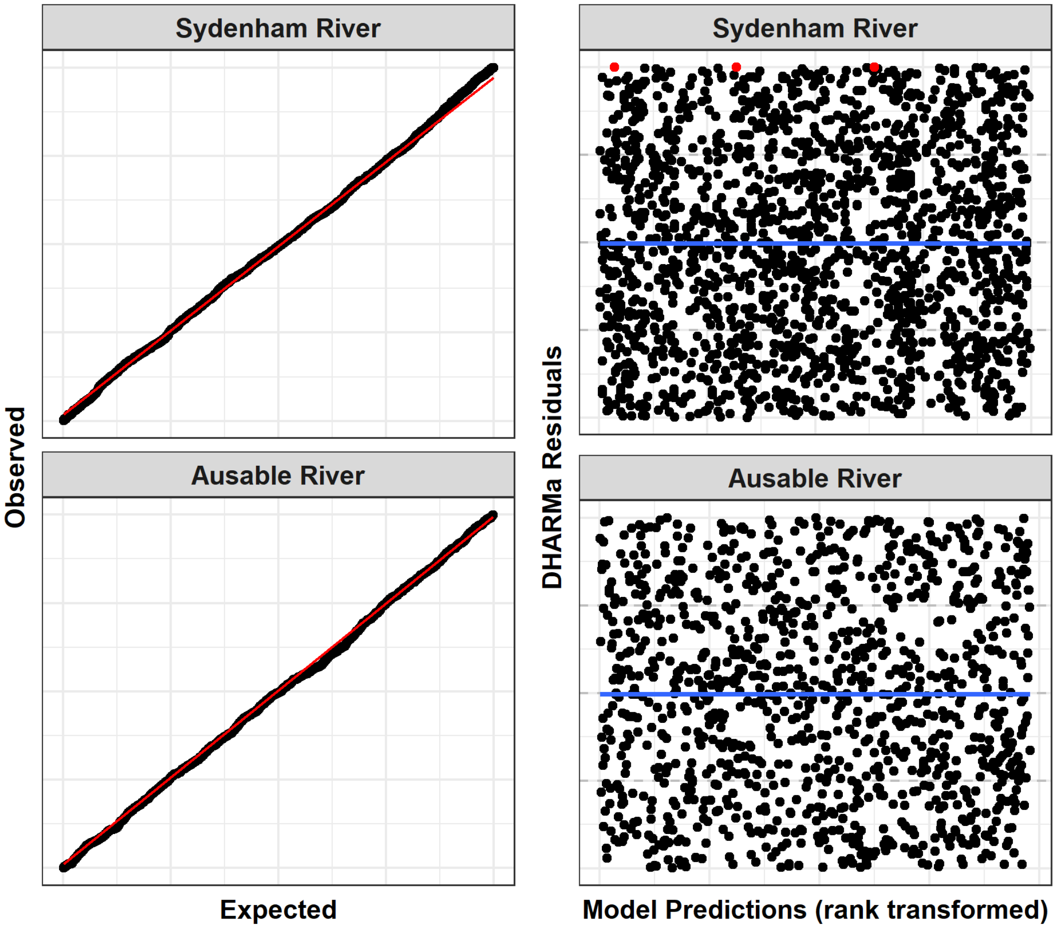

Figure 1. DHARMa residual plots for quadrat count models. Plots on the left are quantile-quantile plots comparing the distribution of the DHARMa residuals to a uniform distribution; the red line is a 1:1 reference line. The plot on the right are the DHARMa residuals plotted against the rank transformed model predictions; the blue line is a smoothed trend line and the red points represents potential outliers.

Significant increases in quadrat count were estimated across years for both rivers (Table 5, Figure 2). In the Sydenham River the rate of increase was slightly lower when the partial third sample was included in the model compared to when it was excluded. For the Sydenham River, between 1999 and 2022, the estimated population growth rate was 1.13 (95% CI: 1.11–1.15), which indicates a 1,732% (95% CI: 1,112–2,745) increase over the 23 year time series. All site-specific estimates of population growth rate were > 1 (Table 6). For the Ausable River, between 2006 and 2019, the estimate of population growth rate was 1.07 (95% CI: 1.02–1.13), which indicates a 238% (95% CI: 130–466) increase over the 13 year time series. Three of the five site-specific estimates of population growth rate were > 1, one was neutral, and one site showed a significant decrease in density.

Percent sand and gravel substrate was retained in the Sydenham River model as an important covariate and percent sand and gravel substrate and depth were retained in the Ausable River model as important covariates (Table 5). Count increased with the covariates, however, the effect sizes were small. Between 0 and 100% sand and gravel substrate, the mean quadrat count increased by 2.31 times in the Sydenham River and 3.87 times in the Ausable River. Across the range of depths sampled in the Ausable River (2–52 cm) the mean count was predicted to increased by 4.46 times.

Table 5. Parameter estimates for quadrat count models for the Sydenham and Ausable Rivers. Included is the fit to Sydenham River data with sampling from 2022 excluded (each site sampled twice). LCI is the lower credible interval and UCI is the upper credible interval, k is the size parameter for the Negative Binomial distribution, σ_{site} is the standard deviation for the random intercept by site, and $\sigma_{site,year}$ is the standard deviation for the random slope for year by site.

Parameters	**Mean**	**SD**	**LCI**	**UCI**
Sydenham River				
Fixed Effects				
Intercept	-1.448	0.07	-1.585	-1.313
Year	0.124	0.01	0.105	0.144
Sand & Gravel	0.188	0.046	0.098	0.278
Hyperparameters				
k	8.964	4.863	3.608	21.713
σ_{site}	1.053	0.258	0.655	1.662
$\sigma_{site,year}$	0.046	0.015	0.024	0.082
Sydenham River – 2022 excluded				
Fixed Effects				
Intercept	-1.45	0.076	-1.601	-1.302
Year	0.137	0.014	0.11	0.163
Sand & Gravel	0.2	0.059	0.084	0.315
Hyperparameters				
k	21.642	24.104	4.595	82.717
σ_{site}	1.107	0.269	0.686	1.736
$\sigma_{site,year}$	0.046	0.018	0.019	0.089
Ausable River				
Fixed Effects				
Intercept	-2.114	0.176	-2.479	-1.788
Year	0.067	0.025	0.02	0.118
Sand & Gravel	0.321	0.081	0.162	0.48
Depth	0.174	0.069	0.039	0.308
Hyperparameters				
k	1.841	0.414	1.187	2.799
σ_{site}	1.884	0.616	0.993	3.388
$\sigma_{site,year}$	0.114	0.043	0.054	0.221

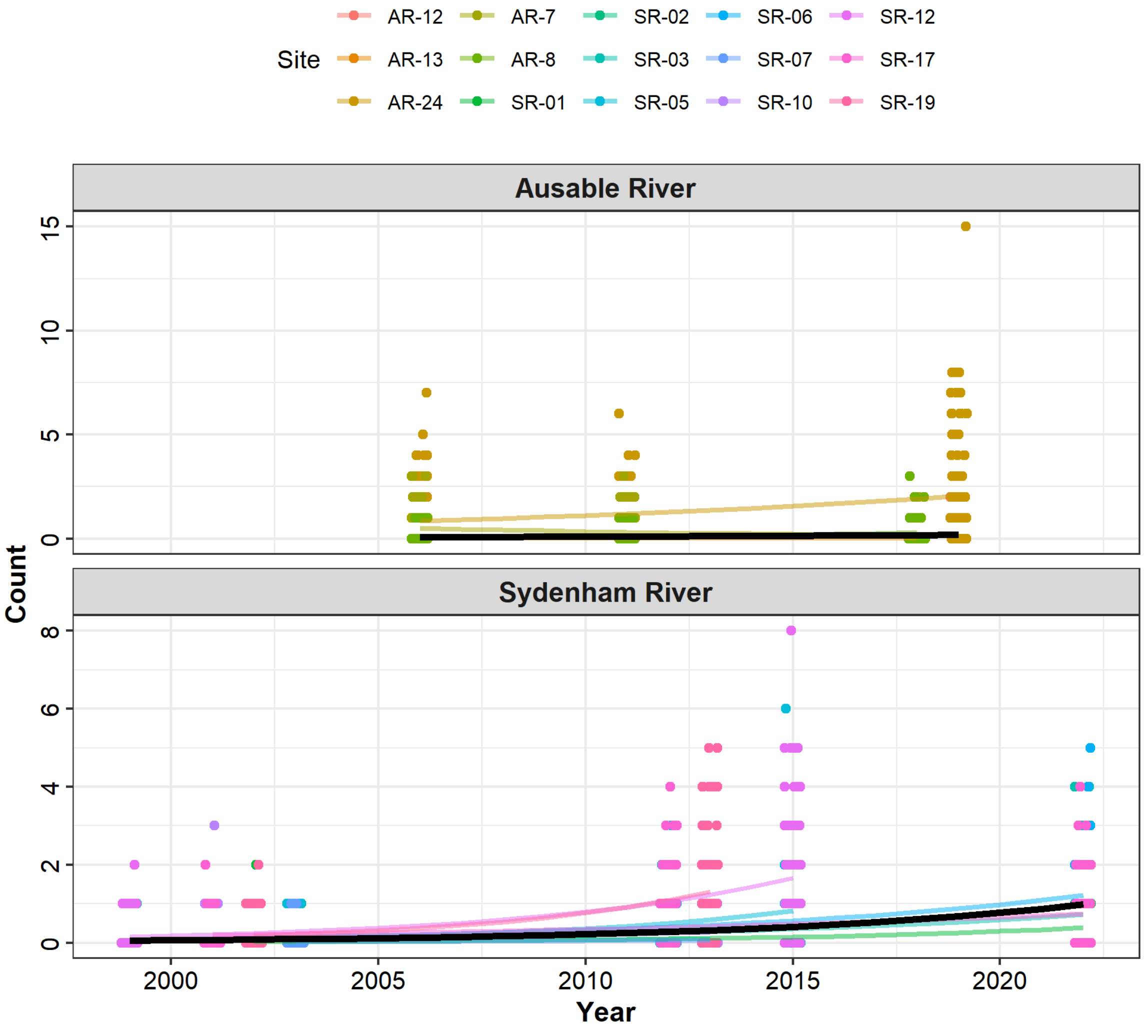

Figure 2. Quadrat counts data (mussels/m^2) of Kidneyshell collected at the UMBO sample sites in the Ausable and Sydenham River over time. Each dot represents a sample data point. Colour indicates the sampled site and the lines represent the estimated trends through time (Table 5) with the black line indicating the site-combined trend and the coloured lines showing site-specific trends.

Table 6. River and site-specific population growth rate (λ) estimates from the quadrat count models. LCI and UCI are the lower and upper credible intervals.

Site	Median	LCI	UCI
Sydenham River			
SR-01	1.150	1.097	1.209
SR-02	1.149	1.062	1.262
SR-03	1.107	1.070	1.144
SR-05	1.173	1.118	1.239
SR-06	1.115	1.086	1.146
SR-07	1.118	1.022	1.215
SR-10	1.088	1.025	1.148
SR-12	1.160	1.123	1.201
SR-17	1.067	1.040	1.095
SR-19	1.195	1.140	1.261
Total	1.132	1.110	1.155
Ausable River			
AR-12	1.134	1.046	1.232
AR-13	1.100	0.922	1.365
AR-24	1.071	1.043	1.099
AR-7	0.908	0.859	0.960
AR-8	1.145	1.066	1.232
Total	1.069	1.020	1.126

Mean density and abundance within UMBO sample sites was projected using the quadrat count models for the Sydenham and Ausable Rivers, predictions assumed mean values for covariates. Predicted density within sample sites in the Sydenham River in 2022 was 0.98 mussels/m^2 (95% CI: 0.78–1.23) and projected abundance was 6,949 (95% CI: 5,371–9,059). At the sample sites in the Ausable River, predicted density in 2019 was 0.19 mussels/m^2 (95% CI: 0.12–0.28) and projected abundance was 1,129 (95% CI: 933–1,360); approximately 74% of the population was located at site AR-24. Estimated site-specific and site-total abundance with 95% credible intervals are depicted on Figure 3. These abundance estimates apply only to the sample sites. Since Kidneyshell can be found in other locations in both rivers, the total river-wide abundance would be higher.

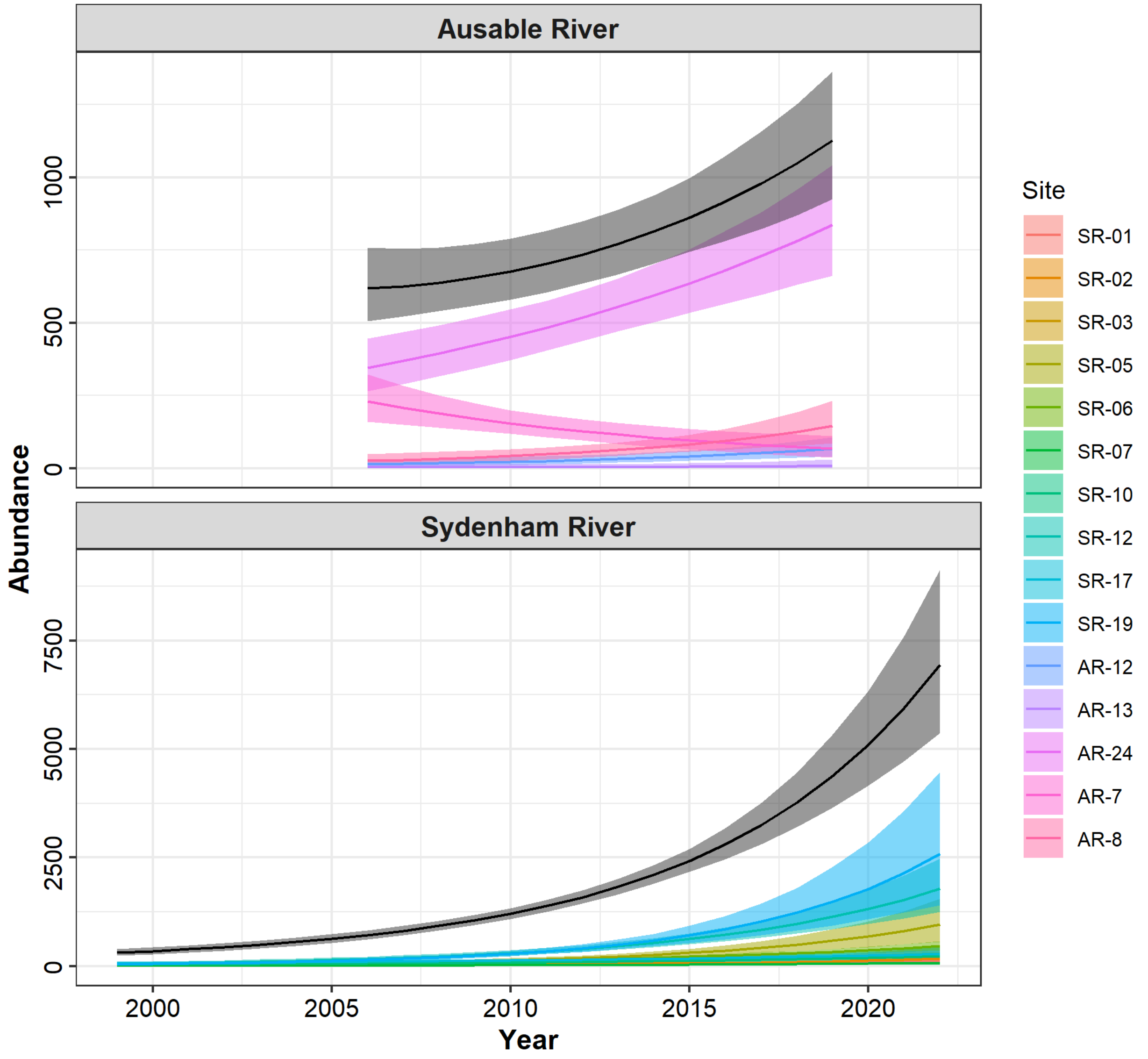

Figure 3. Abundance estimates of Kidneyshell population at the sample sites in the Ausable and Sydenham River over time. Coloured lines represent the estimated mean abundance through time with the lighter region around the line representing the 95% credible interval. The black line indicates the site-total abundance and the coloured lines show site-specific abundance.

The length frequency distributions followed fairly similar trends for both rivers (Figure 4). Mean size decreased slightly across sample periods; in the Sydenham River 82.3 mm in sample 1, 69.4 mm in sample 2 and 74.3 mm in sample 3 (only 4 of 10 sites having been sampled); in the Ausable River 76.1 mm in sample 1, 74.7 mm in sample 2, and 64.6 in sample 3. Small individuals were classified as putative juveniles based on length and their abundance as a proportion of the overall population was examined. The proportion of juveniles declined significantly in the Sydenham River ($logit(P_{juv.}) = -0.07year - 2.55; (95\%CI: -0.11\ to - 0.026)$) but remained stable in the Ausable River ($logit(P_{juv.}) = -0.007year - 2.78; (95\%CI: - 0.05\ to\ 0.06)$).

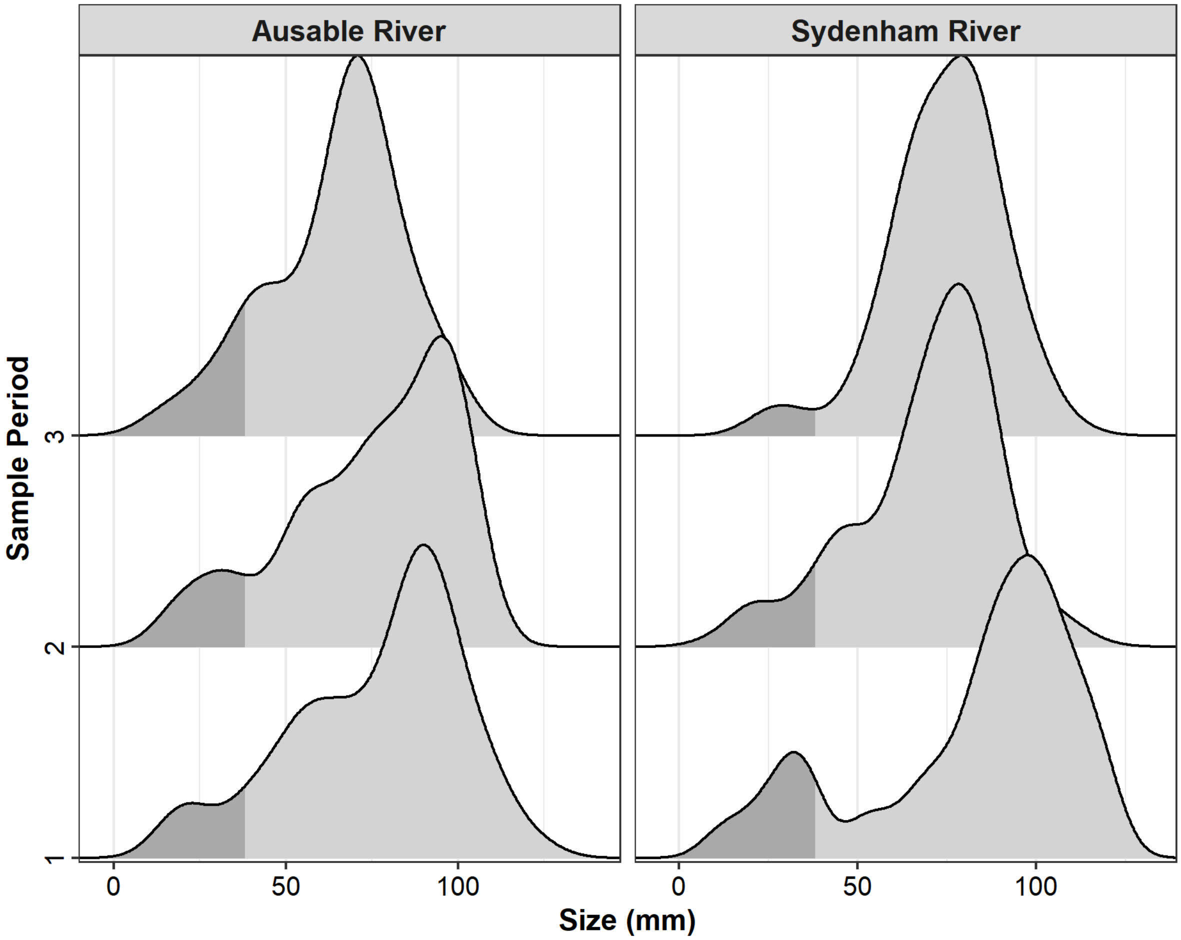

Figure 4. Length frequency density plots by sample period for Kidneyshell in the Sydenham and Ausable Rivers. The dark grey indicates putative juveniles. Sample periods for the Sydenham River represent years: 1–1999 to 2003, 2–2012 to 2015, 3–2022 (partial sample). Sample periods for the Ausable River represent years: 1–2006, 2–2011, 3–2018 to 2019.

POPULATION MODELLING

METHODS

Information on vital rates was compiled to build projection matrices that incorporated parameter uncertainty, environmental stochasticity and density-dependence. The impact of anthropogenic harm to populations was quantified with the use of elasticity and simulation analyses. Estimates of abundance and habitat requirements for population viability were made with estimation of the minimum viable population (MVP) and the minimum area for population viability (MAPV). All analyses and simulations were conducted using the statistical program R 4.2.1 (R Core Team 2022).

THE MODEL

The Kidneyshell life cycle was modelled using a female only, density-dependent, birth-pulse, pre-breeding, stage-structured matrix population model with an annual projection interval (Caswell 2001, Figure 5). The projection matrix represents a series of linear equations describing survival through stages, transitions to subsequent stages, and reproduction. The projection matrix can be multiplied by an abundance vector (representing abundance in each stage) to predict future abundances.

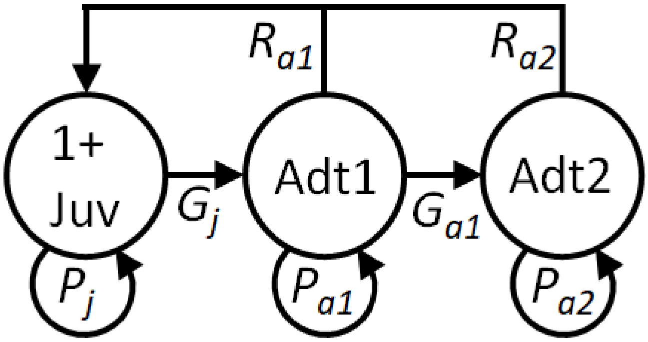

Figure 5. Generalized life cycle used to model the population dynamics of Kidneyshell. 1+ Juv represents the juvenile life-stage after age-1, Adt1 represents the young adult stage and Adt2 represents the old adult stage. R_i represents stage-specific annual recruitment, P_i represents the probability of surviving and remaining in stage i, and G_i represents the probability of surviving and moving to stage i+1 each year.

The projection matrix consisted of three stages (Figure 5) representing age-1+ juveniles, young adults and old adults. The 1+ juvenile stage represents immature Kidneyshell, from age-1 to the age-of-maturity (T_{mat}). The adult stage was divided into young and old adults based on expected annual somatic growth. The young adult stage represented mature individuals that continued to put resources toward somatic growth; the old adult stage represented individuals that express minimal somatic growth. The amount of growth, in mm, was estimated from the von Bertalanffy growth function (VBGF, see Equation 4). The division was set to the age where annual growth becomes less than 1 mm (age-14). The oldest Kidneyshell identified from the sampling data was 33 years old. Therefore, stage-1 includes ages 1 to T_{mat} which represented 2 to 4 age classes depending on the values of T_{mat} (see below); stage-2 includes ages T_{mat} to 14 which represents 10 to 12 age-classes; and stage-3 includes ages > 14 which represents at least 19 age-classes.

The projection matrix **A** is the product of the transition matrix **B**, which contains the life-history parameters, and the density-dependence matrix **D** (see Equation 15 below) which represents the density-dependent effects.

$$\boldsymbol{B} = \begin{bmatrix} P_j & R_{a1} & R_{a2} \\ G_j & P_{a1} & 0 \\ 0 & G_{a1} & P_{a2} \end{bmatrix} \qquad (5)$$

and:

$$\mathbf{A} = \mathbf{B} \circ \mathbf{D}, \qquad (6)$$

where the symbol ∘ represents the Hadamard product or the element by element multiplication of the matrices. Stage-specific abundance, $\boldsymbol{n}$, each year, y, is calculated from:

$$\boldsymbol{n}_{y+1} = \mathbf{A}_{n,y}\boldsymbol{n}_y, \qquad (7)$$

where $\boldsymbol{n}$ is a vector of stage-specific abundance and the population projection matrix **A** varies among years due to environmental conditions and population size impacting vital rates.

Stage-based matrix models incorporate estimates of R_i, stage-specific recruitment, P_i, the probability of survival and remaining in stage *i*, and G_i, the probability of surviving and moving to the next stage. Recruitment, R_i, represents the number of age-1 female offspring produced per adult female annually and includes all reproductive and subsequent survival parameters. P_i and G_i are both a function of stage-specific survival (σ_i) and stage-specific transition probabilities (τ_i) describing the likelihood of moving from stage i to $i+1$, where:

$$P_i = \sigma_i(1 - \tau_i) \text{ and} \qquad (8)$$

$$G_i = \sigma_i \tau_i. \qquad (9)$$

The stage transition probability (τ_i) describes the proportion of individuals in stage i that will move to stage $i+1$, which can be estimated from (Caswell 2001):

$$\tau_i = \frac{{\sigma_i}^{T_i} - {\sigma_i}^{(T_i - 1)}}{({\sigma_i}^{T_i} - 1)}. \qquad (10)$$

Where T_i represents the stage duration in years. Equation 10 describes the oldest individuals in stage i moving to stage $i+1$ the following year.

PARAMETERIZATION

The understanding of many important characteristics of the life-history and population ecology of Kidneyshell is incomplete. When possible, model parameters were estimated directly from field data. When this was not possible parameters were estimated from generic relationships or solved for to provide a certain population state (e.g., population growth rate (λ) = 1). When a parameter was not directly estimated from Kidneyshell population, specific data uncertainty was incorporated into model runs by drawing the unknown parameter from a specified probability distribution providing a range of plausible values. This allows different model runs to incorporate different parameter combinations and provides results that span the full extent of the uncertainty. Parameter values incorporated into the population model are listed in Table 7.

Age and Growth

Growth and mortality of Kidneyshell were assessed using analyses applied to age data from spent shells collected at sample sites in the Ausable River in 2012 and 2013. Growth was assumed to follow the von Bertalanffy growth function (VBGF; see equation 4). 120 Kidneyshell shells were collected for aging, 119 from the Ausable River and 1 from the Sydenham River. The lone shell from the Sydenham River was removed for consistency in the data analysis. A consensus age could not be reached for 21 Ausable shells with 98 shells retained for analysis.

Shell lengths ranged from 34.4 mm to 121.1 mm (mean: 81.2) and ages ranged from 1 to 33 (mean: 11.3). Shell lengths of live collected Kidneyshell ranged from 6 to 121 mm in the Sydenham River and 12 to 125 mm in the Ausable River. The VBGF fitted to the length-at-age data shows a relationship (Figure 6) where:

$$L_t = 98.36(1 - e^{-0.23t}) \tag{11}$$

Based on the sample data, the maximum age of Kidneyshell was assumed to be 33 years.

Table 7. Parameter definitions and values used in the population model describing Kidneyshell.

Parameter	Definition	Value
Fixed parameters		
M_a	Adult instantaneous mortality rate	0.1242
σ_a	Adult annual survival rate (e^{-M_a})	0.8832
CV_M	Coefficient of variation for *M*. Used to describe inter-annual variation in survival.	0.15
L_∞	Asymptotic length (mm)	98.36
k	Growth coefficient	0.23
T_a	Age division between young adult and old stages	14
ζ	Generation time	10.7 years (calculated)
Uncertain parameters		
T_{mat}	Age-at-50%-maturity	3–5
σ_j	Annual survival rate for age-1+ juveniles	0.794 (95%CI: 0.49–0.97)
R	Recruitment	Solved for (Figure 8)
CV_R	Coefficient of variation for R. Used to describe inter-annual variation in recruitment.	0.15–0.5
α	Relative recruitment between young and old adults	0.5–2.0
λ_{max}	Maximum population growth rate	1.1–1.4

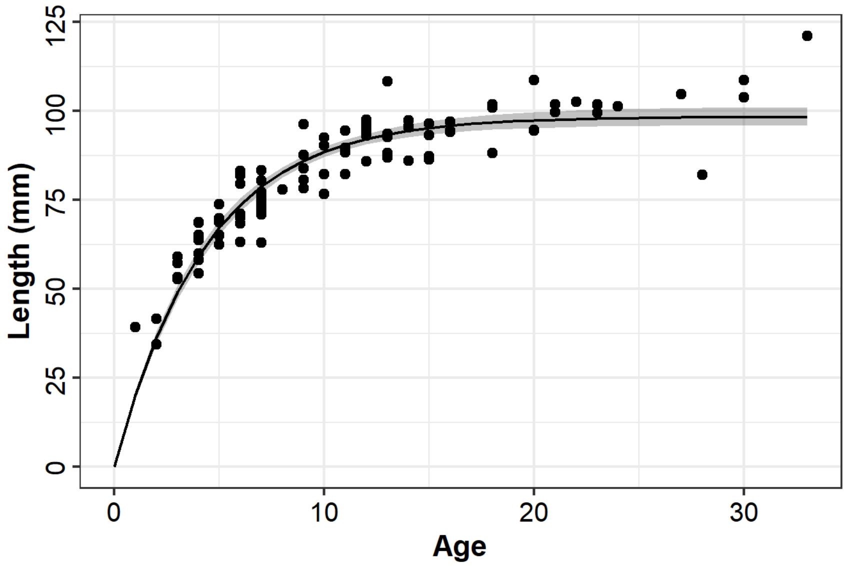

Figure 6. Length-at-age data of spent Kidneyshell shells collected in the Ausable River (n = 98). The solid line represents a fitted von Bertalanffy growth function ($L_t = 98.27(1 - e^{-0.23t})$) and the grey region represents the 95% credible intervals estimated via bootstrapping.

Mortality

Mortality was estimated using a Chapman-Robson catch curve analysis (Smith et al. 2012), where survival rate, S, is estimated based on the assumption that the duration of life follows a geometric distribution:

$$\hat{S} = \frac{\bar{T}}{1+\bar{T}-\frac{1}{n}}. \qquad (12)$$

Where $\bar{T}$ is the mean age of mussels fully recruited to sampling and n is the total number of mussels. The use of spent shells to estimate mortality may violate the assumptions of catch curve analysis if shells decay at significantly different rates across sizes or if large shells persist in the environment for an exceedingly long period of time. The decay rate of unionid shells is related to both extrinsic factors, such as water chemistry and currents, and intrinsic factors, such as shell size and robustness (Strayer and Malcom 2007, Ilarri et al. 2019). Decay rates in lotic habitats of a species with a robust shell ranged from approximately 2–4% per month (Ilarri et al. 2019). If we assume exponential decay, shells would be 99% eroded after 9.6–19.2 years. Since spent shells used for ageing were relatively intact (i.e., complete margins, intact periostracum, bright nacre), we assume that less than a decade had passed since the individual died.

Survival rate was estimated over age 7 (peak frequency) to 33. Mean survival rate was 0.883 (se: 0.0135) or an instantaneous mortality of 0.124 (se: 0.015).

This estimate of mean adult survival was held constant for both young and old adult stages. No data, however, were available to inform survival rate for Kidneyshell age-1+ juveniles. To estimate age-1+ juvenile survival, a beta regression relationship was fitted between adult (σ_a) and juvenile (σ_j) survival rates based on data from 11 species reported by Haag (2012). The fitted relationship was (Figure 7, left panel):

$$logit(\sigma_j) = 4.38\sigma_a - 2.52 \quad (\varphi = 8.51; p < 0.01;\ pseudo\ r^2 = 0.493). \qquad (13)$$

Equation 13 gives a mean estimate of age-1+ juvenile survival for Kidneyshell of 0.794 (variance = 0.0172). Because σ_j is an unknown parameter for Kidneyshell it was included in the population model as a stochastic parameter. Therefore, for each model run, σ_j was drawn from a probability distribution to give a random value for that simulation. The distribution used to generate stochastic juvenile survival rates was $Beta(6.76, 1.75)$ (Figure 7, right panel) based on the mean and variance produced from Equation 13.

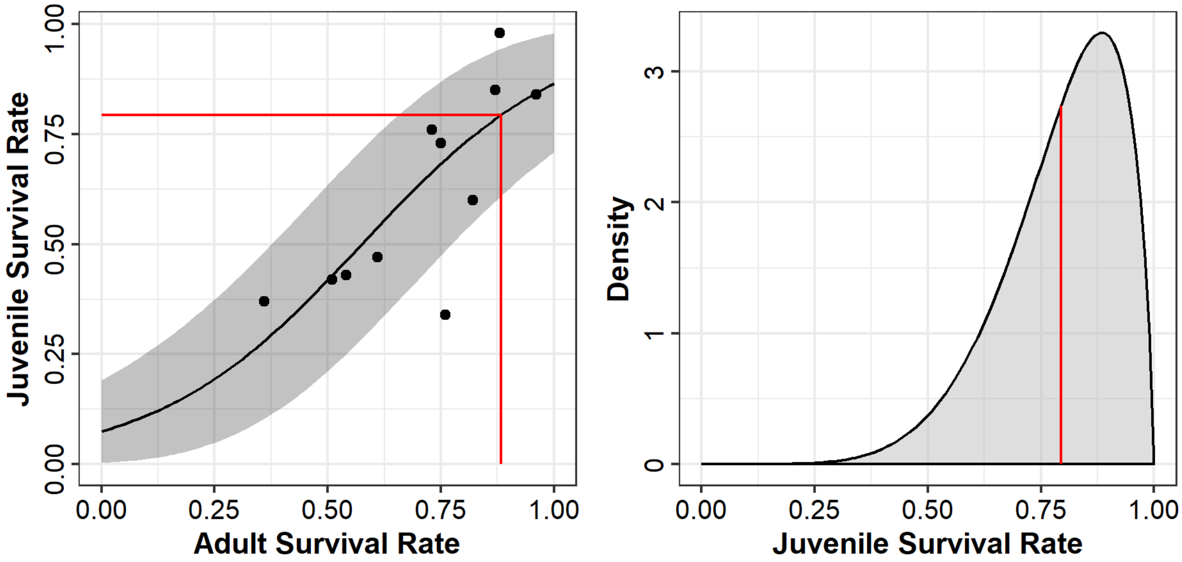

Figure 7. Age-1+ Juvenile survival rate estimates used in the Kidneyshell population model. The left panel is the beta regression model fit predicting juvenile survival from adult survival with data from Haag (2012); the black line is the mean trend and the grey area are the 80% CIs. The right panel is the beta distribution used to randomly draw juvenile survival estimates in model runs ($Beta(6.76, 1.75)$). The red lines indicate the mean survival estimates for Kidneyshell.

Reproduction

There were insufficient sampling data from small immature Kidneyshell individuals to generate a maturity ogive for determining age-at-maturity. Haag (2012) provides a relationship to estimate age-at-first-maturity from the VBGF growth coefficient (*k*) based on a regression analysis of 16 unionid species. The fitted relationship was $T_{mat} = 0.69k^{-1.031} - 1$ $(r^2 = 0.94)$. This gives an estimate for Kidneyshell, where *k* was 0.23, of 2.12 years. These estimates represent the age-of-first-maturity, while the model requires the value of age-of-50%-maturity. Based on the maturity ogives of other unionid species (Haag and Staton 2003) it is likely to take at least 2 years to reach 50% maturity. To account for this uncertainty, age-at-maturity was included in the population model as a stochastic parameter that varied between model runs. Uncertainty in T_{mat} was represented using a discrete uniform distribution with limits of ages 3 and 5 ($Unif(3, 5)$). This allowed for an equal probability for T_{mat} to be 3, 4 or 5 across model runs.

Kidneyshell reproduction is generally similar to other members of the Unionidae family (COSEWIC 2003). Breeding season begins in August with males releasing sperm into the water and females filtering it out of the water. Kidneyshell are long-term brooders and release their glochidia (larvae mussels) between June and August of the next year. Kidneyshell are obligate parasites of fish hosts. Glochidia must attach to a specific host species to complete their development. White et al. (1996) found four darter species to harbour Kidneyshell glochidia. McNichols (2007) found successful metamorphosis of Kidneyshell glochidia in the laboratory on: Blackside Darter (*Percina maculata*), Fantail Darter (*Etheostoma flabellare*), Johnny Darter (*E.*

nigrum), Iowa Darter (*E. exile*), and Brook Stickleback (*Culaea inconstans*). All five of these species have been observed in the Ausable River and all but Iowa Darter are present in the Sydenham River (McNichols 2007).

Kidneyshell produce conglutinates which mimic prey to attract hosts to increase the likelihood of host infestation. Mortality during the parasitic phase is expected to be high with survival from the glochidial stage to settlement for most unionids in the order of 10^{-5} to 10^{-6} (Haag 2012). After the parasitic phase the juvenile mussels release from the host and settle on the river bottom.

The matrix model requires an estimate of annual recruitment per female. Recruitment represents the number of female offspring surviving to age-1 and includes all aspects of reproduction and subsequent survival including: fecundity, spawning periodicity, sex ratio at birth, probability of glochidia encountering and infesting a host, successful completion of metamorphosis, and survival after detachment from host up to age-1. The sex ratio was estimated to be 1 female per 1.5 male (DFO unpublished). The other aspects are not known for Kidneyshell. Instead, the recruitment value, under a given combination of life-history parameters, was solved for to produce a stable population growth rate (i.e., $\lambda = 1$). This provides an estimate of the average number of newly spawned females that need to survive to age-1 each year for the population to be stable (Figure 8); however, the value of each of the components of recruitment remain unknown.

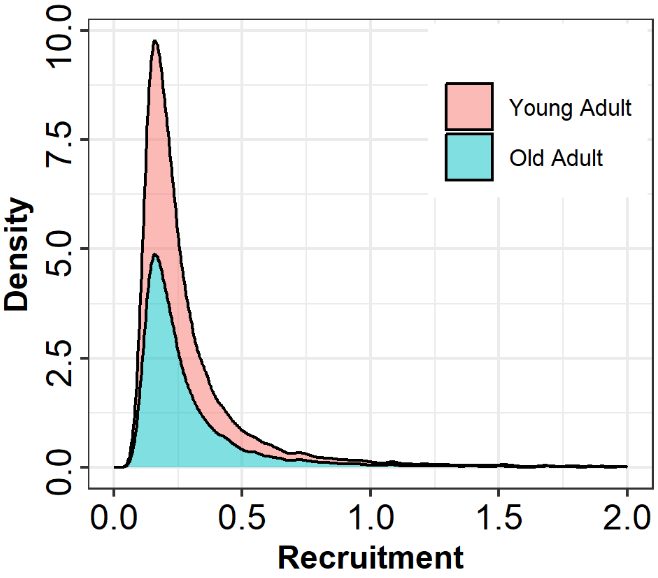

Figure 8. Distribution of estimated recruitment values (the number of female offspring surviving to age-1 produced annually per adult female) from young and old adult Kidneyshell that gave population growth rates of 1.

Kidneyshell, like most freshwater mussels, is primarily dioecious (COSEWIC 2003). Spawning periodicity has not been measured for Kidneyshell; however, evidence from other unionid species suggests spawning may occur annually, as a high percentage (> 90%) of mature females were gravid across six unionid species (Haag and Staton 2003). Fecundity has not been measured for Kidneyshell. Haag (2012) provides a relationship to estimate fecundity from adult length where $Fecundity = 0.213{L_a}^{3.146}$ $(r^2 = 0.751, n = 71)$; however, five outlying species were excluded from the analysis. Using an average adult size of 61 mm estimated from the geometric mean of L_{mat} and L_{max}, calculated from the VBGF (Equation 4), the relationship predicts annual fecundity for Kidneyshell of ~ 88,000 eggs. McNichols (2007) found female Kidneyshell produced a mean of 88,641 (n = 3) glochidia.

Across individuals within a species, fecundity generally increases with mussel length, but there is some evidence to suggest it may plateau or even decrease at older ages, potentially indicative of reproductive senescence (Haag and Staton 2003). Therefore, it is unclear how recruitment will differ between young and old adults in the population matrix model. To allow for potential differences between the two stages an additional parameter, α, was included to represent relative recruitment between young and old adults. Relative recruitment was incorporated as a stochastic parameter (Table 7). To determine relative recruitment, α was first randomly assigned to be either greater or less than 1 with equal probability. If α is greater than 1, the value is drawn from a uniform distribution with limits of 1 and 2 ($Unif(1.0, 2.0)$); if α is less than 1, the value is drawn from a uniform distribution with limits of 0.5 and 1 ($Unif(0.5, 1.0)$). A value of 1 for α means recruitment is constant throughout the adult stage. A value of $\alpha > 1$ means that recruitment of old adults is greater than young adults; possibly from greater fecundity due to increase body size or greater survival of glochidia from older individuals. A value of $\alpha < 1$ means recruitment decreases with age due to some degree of reproductive senescence. The range of α values included in the analyses allows the recruitment of old adults to vary between half that of young adults ($\alpha = 0.5$) up to double that of young adults ($\alpha = 2$). First year survival rate is unknown.

By solving for recruitment, the uncertainty in the various reproductive parameters is reduced to a single value for each matrix. Across replicates with different stochastic life-history parameters the median recruitment value from young adults was 0.21 (95% CI: 0.12–1.23) and from old adults was 0.23 (95% CI: 0.10–1.36). These values represent the number of female offspring per female that need to survive to age-1 to sustain a stable population size. If fecundity is ~ 88,000, the sex ratio of females to males is 1:1.5, and 95% of females spawn annually this gives an approximate survival rate from egg to age-1 of 6.6×10^{-6}. A typical unionid species produces between 0.1–1.3 juveniles per year or 0.05–0.65 juvenile females per year (Haag 2012), which is in line with these recruitment estimates for Kidneyshell.

Density-dependence

Density-dependence was assumed to act during the first year of life. As a largely sedentary species, density-dependence is less likely to impact later life stages. For unionids, density-dependence has the potential to act at two stages during the first year of life: host infestation and settlement. Two possible host species for Kidneyshell (Johnny and Greenside darters) are abundant in the Sydenham system (COSEWIC 2003). It is therefore assumed that Kidneyshell are not limited by host availability in the model. Density-dependence is assumed to act due to habitat availability during settlement following the parasitic phase. Density-dependence was implemented using a Beverton-Holt function with recruitment a function of adult density:

$$d = \frac{R_{max}/R_1}{1 + bN_a/K} \tag{14}$$

Where N_a is adult density, K is carrying capacity, b is the density-dependence coefficient, R_1 is the recruitment when the population is stable and R_{max} is the recruitment when the population is at maximum population growth rate (λ_{max}). Maximum population growth rate was unknown and included as a stochastic parameter (Table 1). λ_{max} was drawn from a uniform distribution with a minimum value of 1.1 and maximum value of 1.4 ($Unif(1.1, 1.4)$). The maximum value was based on the greatest observed P/B ratio reported for a unionid species (Patterson 1985). R_{max} was then solved for in the same manner as recruitment to find the value that results in a population at its maximum growth. The value b was calculated by rearranging Equation 14, as: $b = R_{max}/R_1 - 1$.

The density-dependence matrix **D** was structured as:

$$\mathbf{D} = \begin{bmatrix} 1 & d & d \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{bmatrix}, \qquad (15)$$

And incorporated into Equation 6. The overall impact of population size on the population growth rate (λ) is shown on Figure 9. The population size is depicted as a proportion of the carrying capacity (K), ranging from 1% of K up to 5 times K. The shaded area consists of multiple curves each of which represents a specific combination of randomized parameters.

Figure 9. Distribution of population growth rates (λ) as a function of population size. If population is at carrying capacity (K), the population growth rate is exactly 1. When population is less than K, λ is greater than 1 and when population is greater than K, λ is less than 1.

Stochasticity

Stochasticity was incorporated into simulations at two levels: to account for parameter uncertainty between model runs and to account for annual environmental variability within model runs. Parameter uncertainty was implemented by drawing uncertain parameters from defined probability distributions prior to each model run (Table 7). Uncertain parameters included: age-1+ juvenile survival rate, age-at-maturity, relative recruitment, maximum population growth rate, and the inter-annual variance in recruitment.

Annual environmental stochasticity was incorporated into the model by allowing certain parameters to vary between years within a model run to simulate the changes in vital rates that occur naturally due to variation in environmental conditions. Environmental stochasticity was applied to annual survival rate and recruitment. Juvenile and adult mortality were allowed to vary following a log-normal distribution with a CV of 0.15, which was the approximate amount of error in annual survival rate estimated from the Chapman-Robson catch curve analysis. To account for similarities in mortality experienced by adults and juveniles, mortality was assumed to correlate between the two age classes with a correlation value of 0.8. The variability in recruitment was unknown. Therefore, the amount of variability in recruitment incorporated into simulations was included as an independent stochastic variable (Table 7). Recruitment was varied using a log-normal distribution with a CV drawn from a uniform distribution with limits of

0.15 and 0.5 ($Unif(0.15, 0.5)$). The minimum value, 0.15 was chosen to mirror the variability in survival rate as first year survival as an element of recruitment. The upper limit was chosen arbitrarily but is set to allow greater variation in recruitment success between years. At the upper 95% confidence limit of old adult recruitment, 1.23, a CV of 0.5 allows for an upper 95% confidence limit value for recruitment of 3.05 meaning that under exceptional environmental conditions 3.05 female offspring could survive to age-1 per adult female.

IMPACT OF HARM

The impact of anthropogenic harm to a Kidneyshell population was assessed with deterministic elasticity analyses of the projection matrix and stochastic simulations.

Elasticity analysis of matrix elements is a method to quantify the impact of changes to vital rates on a population. The elasticity of λ value represents the proportional change to the population growth rate (λ) from a proportional change in a vital rate. For example, an elasticity of λ value of 0.1 for recruitment would indicate that the population growth rate would increase by 1% if recruitment increased by 10%.

Elasticities are useful as they allow for assessment of how impactful any changes to vital rates and other model parameters may be to a population. Because they represent proportional changes, their values are directly comparable. They are preferable to simulation analyses because of the speed with which they can be estimated, allowing for many more perturbations to be examined than simulations. Elasticities are limited, however, as they represent permanent changes, accurately represent only small perturbations (i.e., < 30% changes) and assume all other model parameters remain unchanged. As a result, simulation analysis was used to examine the effects of transient or periodic harm to a population.

Elasticity of λ

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

$$\varepsilon_\lambda = \frac{\nu}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial\nu}, \qquad (16)$$

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

A range of potential vital rate elasticities were estimated by allowing uncertain parameters (Table 7) to vary. As well, population growth rate was allowed to vary by incorporating the effect of density on recruitment (Equations 14 and 15). This was accomplished by randomly generating adult density as a proportion of carrying capacity, ranging from 1% of *K* up to 10 times *K* (1–1000%), using a draw from a uniform distribution on a log scale ($e^{Unif(\ln(0.01), \ln(10))}$). $\lambda = 1$ when $N_a = K$, $\lambda < 1$ when $N_a > K$ and $\lambda > 1$ when $N_a < K$ up to a maximum λ of 1.4. The elasticity analysis was replicated 5,000 times.

Simulation

Simulation analysis was used to investigate the impacts of stage-specific harm on adult population density. Stage-specific survival rates were reduced by some level of harm, ranging from 0 to 99%. This harm was applied at different frequencies (once every 1, 2, 5 and 10 years) over a 100 year simulation period. A frequency of 1 indicates that harm is constant and applied every year, whereas a frequency of 10 indicates that harm is periodic and applied once every 10 years. As a density-dependent model, for simulations where harm intervals are greater than one year, the population has the potential to recover between applications of harm as conditions are returned to the initial state. One thousand replicates were simulated for each combination of harm frequency, harm level and targeted life-stage. Simulations were initialized at carry capacity, which was chosen to be 10,000. To measure the impact of harm, the mean population size over the last 15 years of simulation was divided by the initial carrying capacity, resulting in a proportion of *K*.

POPULATION VIABILITY

Abundance: Minimum Viable Population (MVP)

The concept of demographic sustainability was used to identify abundance requirements for Kidneyshell population viability. Demographic sustainability is related to the concept of a minimum viable population (MVP, Shaffer 1981), and is here defined as the minimum adult population size, where 'adult' corresponds to mature females, that results in a desired probability of persistence over 100 years or ~ 10 Kidneyshell generations. Generation time (ζ) was estimated from stochastic projection matrices (Caswell 2001) with $\lambda = 1$ producing $\zeta = 10.7$ (CI: 9.3–12.4). MVP was estimated using simulation analysis which incorporated environmental stochasticity and density-dependence.

Important elements incorporated in population viability analysis include: the 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 time frame should be sufficient to represent long-term population viability; 100 years was selected as it equates to approximately 10 Kidneyshell generations and is likely reasonable for informing management decisions.

Catastrophes are defined as a greater than 50% decrease in population size and may be from natural or anthropogenic causes. The rate and severity of catastrophic events within Kidneyshell populations is not known. Based on a meta-analysis, Reed et al. (2003) concluded that, among vertebrate populations, catastrophic die-offs that resulted in a one-year decrease in population size >50% occurred at a rate of 14% per generation on average. The rate of catastrophic die-offs among invertebrate populations is unknown and was included in simulations as a stochastic parameter by drawing from a uniform distribution with limits of 0.05 and 0.2 ($Unif(0.05, 0.2)$) to allow for catastrophe rates of 5% to 20% per generation. These rates correspond to an annual catastrophe probability limits of 0.48% and 2.07%, respectively. A catastrophe was included as an impact on all life-stages simultaneously, 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), $Beta(0.762, 1.5) \times (1 - 0.5) + 0.5$), representing the probability of a 50% to 100% decline in population size.

Quasi-extinction accounts for the compounding of Allee effects, demographic stochasticity and inbreeding depression (Lande 1988) leading a population to extinction once the quasi-extinction threshold is crossed. The value of the quasi-extinction threshold cannot be empirically measured; therefore, 25 adult females was used as a reasonable approximation (Morris and Doak 2002).

Density-dependent stochastic simulations were conducted for populations with various initial female abundances ranging from 100 to 10,000 (initial density represented adult female carrying capacity, K_a, where $\lambda = 1$). These K_a values were chosen to provide a sufficiently broad range for estimating a probability of extinction curve. Simulations were run for 100 years. Independent simulations incorporated annual catastrophe rates drawn from a uniform distribution between 0.48% and 2.07%. Each simulation was replicated 10,000 times and quasi-extinctions were tracked across all the simulations. The probability of extinction (P_{ext}) was modelled as a logistic regression that was a function of $\log_{10}$ transformed initial female density ($\log_{10}(K_a)$), catastrophe rate per generation (P_{cat}), and all uncertain population model parameters (Table 7) where:

$$P_{ext} = \frac{1}{1+e^{-(X\beta)}}, \tag{17}$$

Where $\boldsymbol{X}$ is a matrix of all covariates and $\boldsymbol{\beta}$ a vector of coefficients including the intercept. 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) represents the quantity of habitat required to support a population of MVP size (Velez-Espino et al. 2010). MAPV is estimated simply as MVP divided by population density. Density estimates were available for Kidneyshell populations in the Sydenham and Ausable Rivers from a hierarchical Bayesian model fit to quadrat survey data. Median density, estimated from the model fit, was 0.98 mussels/m^2 (95% CI: 0.78–1.23) in the Sydenham River and 0.19 mussels/m^2 (95% CI: 0.12–0.28) in the Ausable River. These data represent whole population densities, whereas MVP is specific to adult females. A 1:1.5 female-to-male sex ratio can be assumed and based on the length frequency distribution, sampled mussels were approximately 92% adult in the Sydenham River and 90% adult in the Ausable River. Based on these assumptions, the density of female adults can be derived.

In addition, both these populations have a positive population trajectory with population growth rate estimates of 1.13 (95% CI: 1.11–1.15) in the Sydenham River and 1.069 (95% CI: 1.02–1.126) in the Ausable River. Therefore, the current densities may not represent carrying capacity for the habitat and could therefore produce over-estimates of the quantity of habitat required to house a MVP sized population, which assumes population stability. The matrix population model can be used to extrapolate an estimate of the density given a stable population size based on the current density and population growth rate.

Given these considerations, MAPV was estimated using two approaches. The first approach assumed the current population densities are representative of the density at population stability (i.e., the population will occupy more habitat as the population grows) and uses the current densities to estimate MAPV. The second method was to assume the population will become more dense as it reaches population stability and uses the extrapolated densities to calculate MAPV.

POPULATION PROJECTIONS

Projections of the time to reach MVP was estimated for Kidneyshell populations using simulation analysis similar to MVP simulations and incorporated uncertain parameters, environmental stochasticity, density-dependence, and catastrophes in the same manner. Initial population size was randomly chosen from between 1% and 99% of the MVP value. The time taken for the population to exceed MVP for a given catastrophe rate, maximum λ and initial population was recorded.

To examine the effects of carrying capacity (K) on the time to reach MVP, four carrying capacity values were used for the simulations: 1x, 1.5x, 2x or 5x of the MVP value. Simulations were repeated 10,000 times at each carrying capacity. Setting K at MVP can be viewed as assuming the minimum population size necessary for population persistence. This assumption would also result in the longest projected times to reach a viable population. Higher K would result in shorter times to reach MVP.

RESULTS

IMPACT OF HARM

The impact of harm to Kidneyshell populations was analyzed with deterministic elasticity analysis on the population growth rate (Figures 10 and 11) and through the use of population simulations (Figure 12).

Elasticity of λ

The elasticity of λ to perturbations of vital rates gives an indication of how the population may respond to small (< 30%) changes in vital rates. The results of this elasticity analysis may not hold for large vital rate changes. Positive elasticity values indicate that population growth rate will increase if the vital rate is increased and negative values indicate the population growth rate will decrease if that vital rate increases.

Figure 10 presents elasticity estimates for recruitment (*R*), survival rates for age-1+ juveniles (σ_j) and adults (σ_a), and age-at-maturity (T_{mat}). Elasticities demonstrate which vital rates, if changed, have the greatest impact on population growth rate. In most instances, Kidneyshell populations were most sensitive to changes to adult survival rate. Juvenile survival rate had the next greatest elasticities and under some conditions had a greater elasticity value than adult survival. Age-at-maturity produced negative elasticities indicating that increases to T_{mat} would cause a decrease in λ. Recruitment encompasses all aspects of reproduction, including egg production and first year survival rate, and the elasticity value for recruitment can apply to any of these aspects independently. Under most conditions, however, recruitment had small elasticities relative to adult survival. As well, the elasticity of recruitment from old adults was small and less than that of young adults.

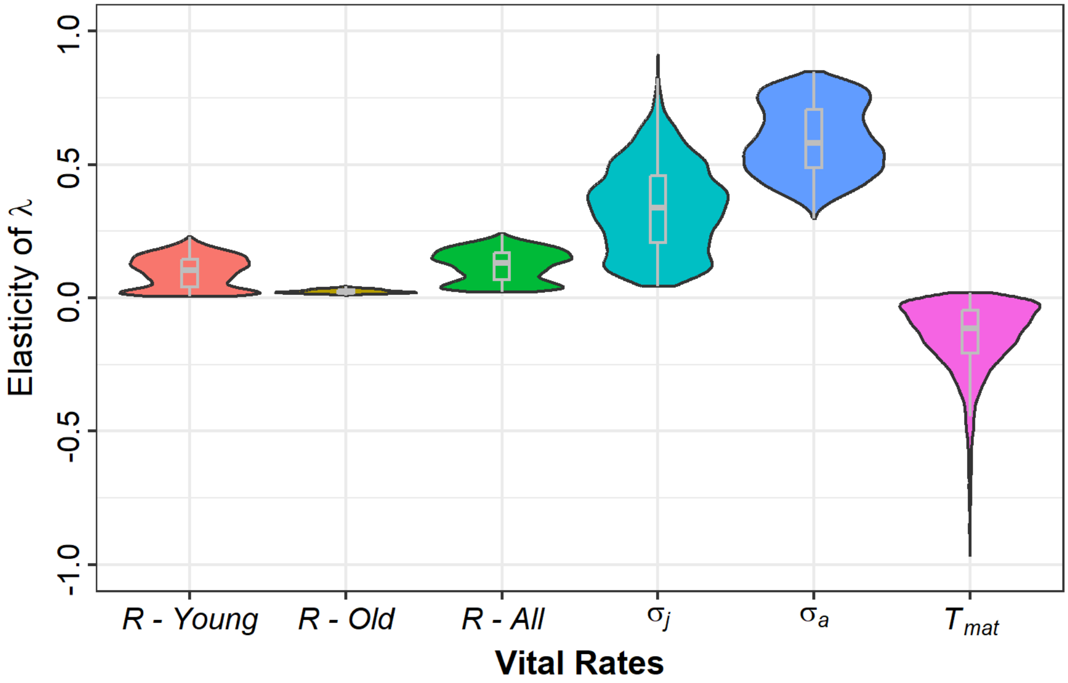

Figure 10. Elasticity of λ analysis results for Kidneyshell population represented using violin and box plots. Results reflect different values of population growth rate. R represents total recruitment across all stages and σ represents survival rate for the age-1+ juvenile (j) and adult (a) stages and T_{mat} represents age-at-maturity.

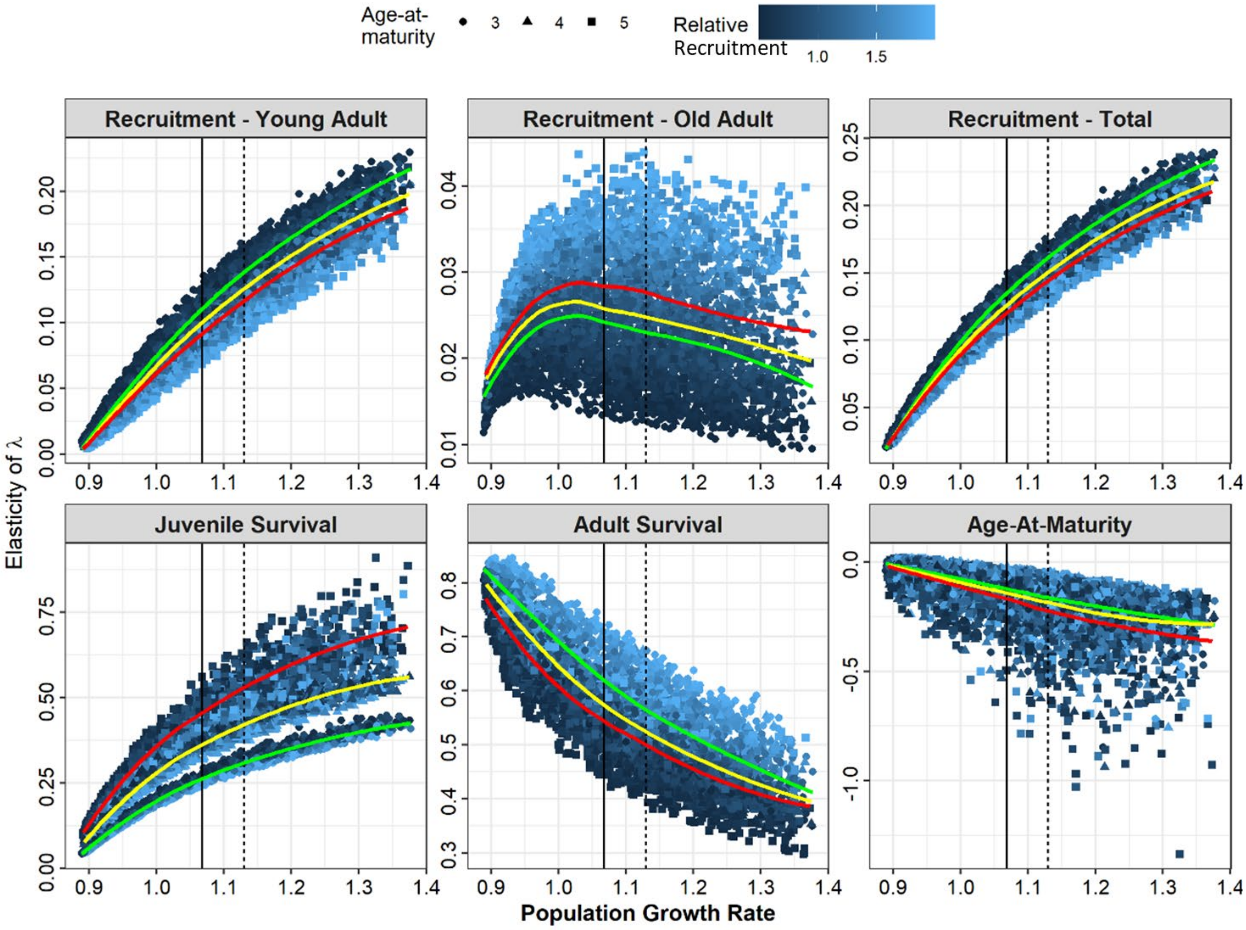

Figure 11. Elasticity of λ analysis results for Kidneyshell populations plotted against population growth rate. Panels represent the vital rate elasticities. Point colour indicates the relative recruitment parameter, α, and plot symbol represents age-at-maturity. The coloured curves represent the smoothed loess curve for the three ages-at-maturity with green, yellow and red representing T_{mat} at 3, 4 and 5 respectively. The vertical lines represent median estimate of population growth rate for Ausable River (1.07, solid) and Sydenham River (1.13, dashed) populations. NOTE: different y-axis scales.

The elasticity values for vital rates were influenced by population state (λ) and other life-history parameter values (Figure 11). Correlations between elasticity estimates and life-history parameter values indicated how influential the life-history parameter values are on the elasticity estimates (Table 8). Absolute correlation values > 0.1 indicate that the elasticity estimate was sensitive to the value of a particular life-history parameter. The most influential parameters were population growth rate, age-at-maturity, and relative recruitment (Table 8). The elasticity values of young adult recruitment and age-1+ juvenile survival increased significantly with λ while that of adult survival and age-at-maturity decreased; absolute correlation values were > 0.8 indicated a strong dependency. When λ < ~ 1.05, the elasticity values of adult survival are always greater than that of juvenile survival. When λ ≥ ~ 1.05 the elasticity of juvenile survival can be greater than adult survival depending on the values of other life-history parameters (especially age-at-maturity and relative recruitment). There are no λ values where juvenile survival elasticity is always greater than adult survival. The elasticity of juvenile survival was also influenced by age-at-maturity. When maturity occurred later, elasticity of juvenile survival becomes greater and at greater λ values the importance of T_{mat} increased. The elasticity value of adult survival was influenced by relative recruitment. With increased relative recruitment, a greater proportion of reproduction occurs later in life and this caused an increase in population sensitivity to adult survival. Relative recruitment influenced the elasticity value of old adult recruitment as well; however, the magnitude of the difference was small (≤ 0.04). The value of juvenile survival also has an influence on the elasticity values of age-at-maturity.

Table 8. Pearson correlations between uncertain life-history parameters and elasticity estimates. Absolute values > 0.1 indicate when elasticity estimates were sensitive to the value of a life-history parameter.

	Life-History Parameters			
Vital Rate Elasticity	**Lambda**	**Age-at-maturity**	**Relative Recruitment**	**Age-1+ Juvenile Survival**
Age-1+ Juvenile Survival	0.84	0.45	-0.10	-0.11
Adult Survival	-0.87	-0.20	0.39	-0.11
Recruitment – Young Adult	0.96	-0.13	-0.21	-0.07
Recruitment – Old adult	0.03	0.23	0.85	-0.09
Recruitment – Total	0.98	-0.10	-0.11	-0.08
Age-at-maturity	-0.64	-0.13	0.10	0.68

The range of elasticity estimates for the Ausable and Sydenham Kidneyshell populations was calculated based on their respective current population growth rates (Table 9). Since the Ausable River population has a lower current rate of growth, it is more sensitive to adult survival perturbations and less sensitive to age-1+ juvenile survival and recruitment perturbations compared to the Sydenham River population.

Table 9. Elasticity of λ estimates for Ausable River and Sydenham River populations of Kidneyshell. Positive values represent a positive relationship between the vital rate and λ while negative values indicate a negative relationship. LCI and UCI are the lower and upper 95% confidence intervals respectively.

	Elasticity Values		
Vital Rate	**Median**	**LCI**	**UCI**
Ausable River			
Age-1+ Juvenile Survival	0.365	0.204	0.574
Adult Survival	0.564	0.423	0.725
Recruitment – Young Adult	0.110	0.054	0.159
Recruitment – Old adult	0.025	0.014	0.039
Recruitment – Total	0.136	0.087	0.176
Age-at-maturity	-0.136	-0.341	-0.040
Sydenham River			
Age-1+ Juvenile Survival	0.420	0.282	0.620
Adult Survival	0.527	0.413	0.665
Recruitment – Young Adult	0.127	0.091	0.163
Recruitment – Old adult	0.024	0.014	0.040
Recruitment – Total	0.152	0.127	0.180
Age-at-maturity	-0.156	-0.558	-0.058

Simulation

Simulation analysis was used to investigate the impact of anthropogenic harm to stable population size and investigate the effects of periodic perturbations occurring annually (for comparison to elasticity analysis), every second year, fifth year, and tenth year. Harm was applied at regular intervals to either the recruitment stage, the juvenile stage, the adult stage or to all three stages.

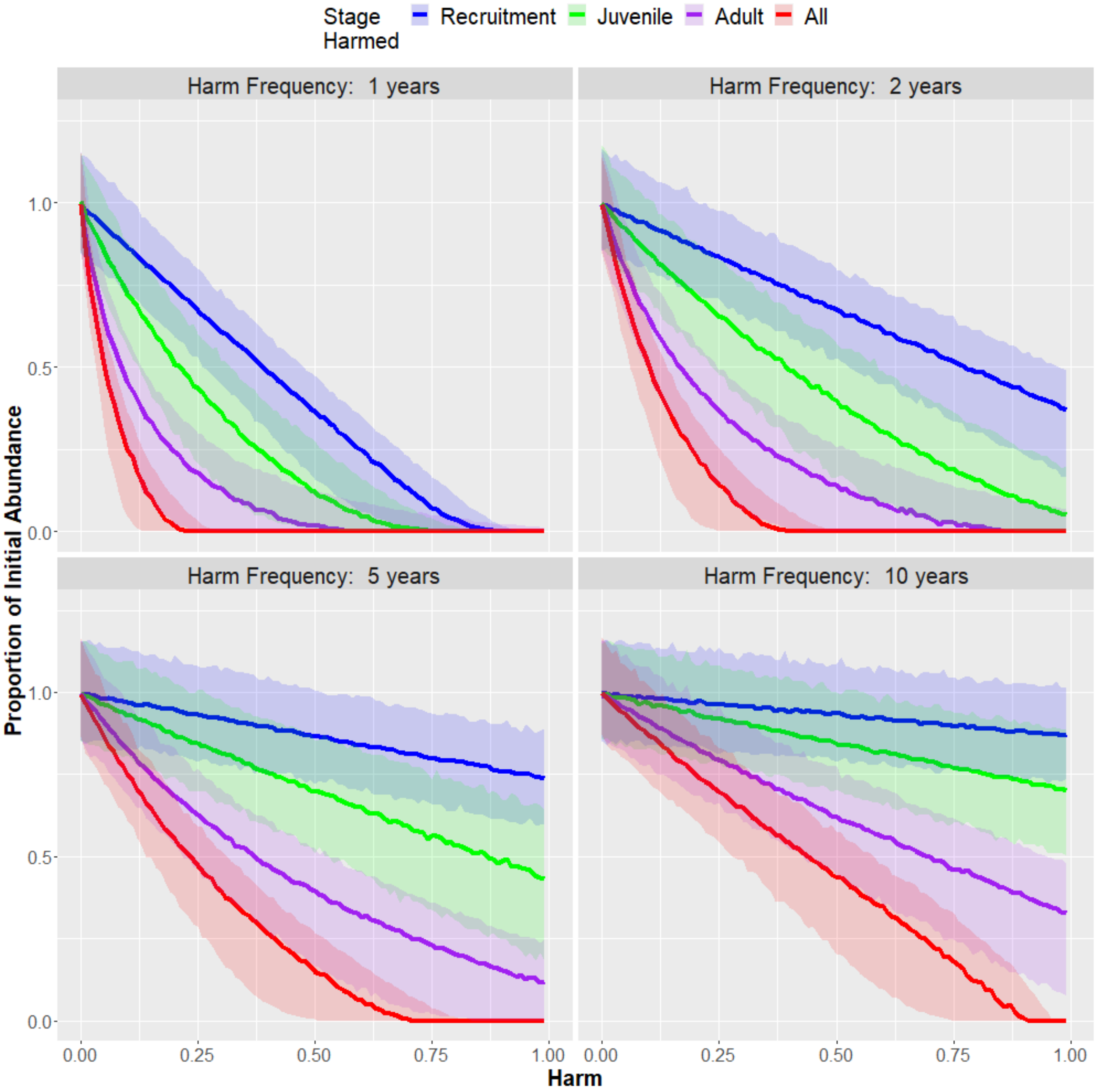

Figure 12. Results from harm simulation analysis where harm is applied at different frequencies to a Kidneyshell population. The colours represent the life-stage(s) harmed: recruitment (blue), age-1+ juvenile (green), adult (purple), and total population (red). The x-axis represent the proportional harm (e.g., annual mortality) applied to the life-stage and the y-axis represents the proportional decrease in adult abundance in the final 15 years of a 100 year simulation. The solid lines represent the median impact and the surrounding polygons represent 95% confidence intervals.

Figure 12 depicts the impact of harm to an adult female Kidneyshell population. Harm has the strongest impact when applied to all life-stages. When harm is applied to only a single life-stage, perturbations to the adult stage produce the strongest impact on density. Annual mortality rates of only ~ 3% applied to the adult stage resulted in a 25% reduction in population size. With biennial harm this became ~ 6%, ~ 15% with harm occurring every 5 years, and ~ 30% every 10 years. Harm applied to the age-1+ juvenile life-stage has a weaker impact where 25% population reduction occurs at ~ 10% annual mortality. Kidneyshell populations were least impacted by harm to recruitment, representing interruptions to reproduction or harm to glochidia/post-settlement age-0 mussels. These results are consistent with the results from the elasticity of λ analysis.

POPULATION VIABILITY

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was assessed using population simulations which incorporated parameter uncertainty, environmental stochasticity and density-dependence. Simulation outputs of binomial quasi-extinction (1: extinct, 0: extant) were fitted using a logistic regression as a function of adult female abundance, generational catastrophe rate and all uncertain parameters. Models were compared using the Akaike information criterion (AIC) method and the best model included population size, catastrophe rate and maximum population growth rate (λ_{max}) as covariates (Table 10; Figure 13).

Table 10. Logistic regression model results for Kidneyshell extinction probability. K_a represents adult female population size, P_{cat} represents catastrophe rate per generation and (λ_{max}) represents maximum population growth rate.

Parameter	Value	Standard error	p-value
Intercept	4.97	0.17	<0.001
$\log_{10}(K_a)$	-3.13	0.03	<0.001
P_{cat}	13.84	0.26	<0.001
λ_{max}	-0.86	0.12	<0.001

The minimum viable population (MVP) size was estimated from the logistic regression model using randomly selected generational catastrophe rates between 5% and 20% and maximum population growth rates between 1.1 and 1.4. The mean MVP estimate of adult females, which corresponds to a 5% extinction risk over 100 years, was ~ 600 (95% CI: 260–1,150) and to a 1% extinction risk over 100 years was ~ 2,100 (95% CI: 900–3,900). If a 1:1.5 female-to-male sex ratio was assumed, then the MVP values for all adult Kidneyshell would be ~ 1,500 (95% CI: 650–2,875) and ~ 5,250 (95% CI: 2,250–9,750) for 5% and 1% extinction risks over 100 years respectively. Extinction probability over 100 years for any adult female population size can be estimated from the fitted logistic relationship with a given catastrophe rate and maximum population growth as:

$$P_{ext} = \frac{1}{1+e^{-(4.97-3.13\,log_{10}(\mathrm{K}_a)+13.84\mathrm{P}_{cat}-0.86\,\lambda_{max})}}. \tag{18}$$

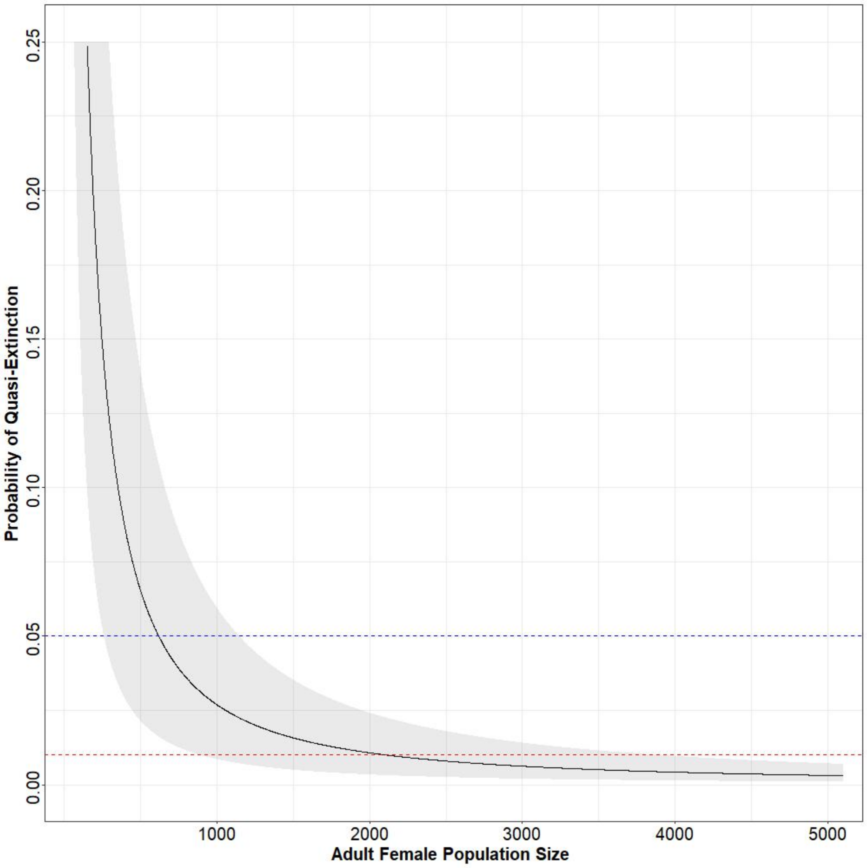

Figure 13. The probability of quasi-extinction within 100 years as a function of adult female population size. The solid black line represents the logistic regression trend with the grey region representing the 95% confidence intervals (for P_{cat} ranging from 5% to 20% per generation and λ_{max} ranging from 1.1 to 1.4). The blue and red horizontal dashed lines represent the 5% and 1% threshold for quasi-extinction respectively.

Habitat: Minimum Area for Population Viability (MAPV)

The habitat quantity required to support an MVP sized population of Kidneyshell was estimated using two methods based on either the current densities or the extrapolated densities in a stable population.

The current density of adult females in the sampled sites of the Ausable River was 0.072 mussels/m^2 (95% CI: 0.044–0.099) and for the Sydenham River was 0.369 mussels/m^2 (95% CI: 0.291–0.449). This corresponds to median MAPV estimates of ~ 260 ha (95% CI: 105–680) for the Ausable River and ~ 50 ha (95% CI: 22–113) for the Sydenham River (Figure 14, left panel).

The extrapolated adult female densities in a stable population was based on the estimate of current population density, population growth rate, and the projection matrix with the assumed density-dependence relationship. Expected density of adult females in the Ausable River that gave a $\lambda = 1$ was 0.17 mussels/m^2 (95% CI: 0.004–3.1) and for the Sydenham River was 1.71 mussels/m^2 (95% CI: 0.19–24.7). This corresponds to median MAPV estimates of ~ 108 ha (95% CI: 4.7–5,100) for the Ausable River and ~ 10 ha (95% CI: 0.62–109) for the Sydenham River (Figure 14, right panel).

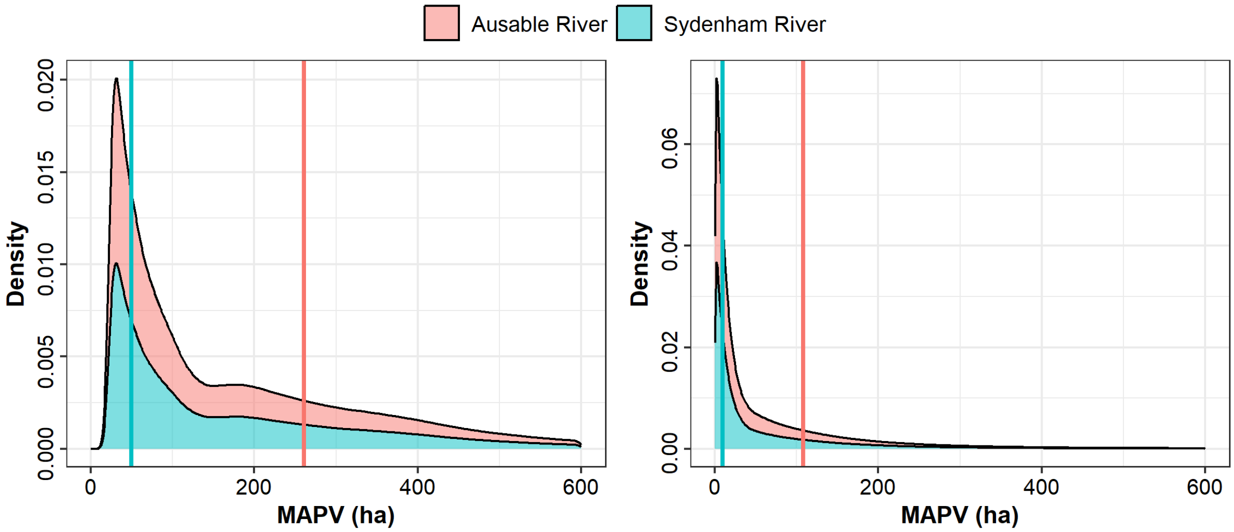

Figure 14. Density plot of the estimated minimum area for population viability (MAPV) for Kidneyshell populations based on current densities (left panel) or expected densities at stable population (right panel). The colours represent the population in the Ausable River (red) and Sydenham River (blue). The vertical lines indicate the median estimates.

POPULATION PROJECTIONS

Projected time for Kidneyshell populations to reach MVP was estimated through model simulations (Figure 15). Time to reach MVP decreases as *K* increases relative to MVP. Of the carrying capacities examined, the largest reduction in time to reach MVP is when *K* is increased from 1x to 1.5x of MVP. Subsequent increases in *K* had less impact in reducing the time to reach MVP. This is due to the decrease in population growth rate when populations are near carrying capacity. If *K* is exactly at MVP, this slowdown in population growth occurs just as the population is near MVP; whereas if *K* is even slightly above MVP, this slowdown does not occur.

For simulated populations with initial population sizes within the credible range of projected abundances in the sampled portion of the Ausable River in 2019 (1,129, 95% CI: 933–1,360), 87% of the simulated populations reach MVP within 100 years and the median time to reach MVP was 52 years (95% CI: 22–167) if *K* was the same as the MVP. If *K* was twice the MVP value, the median time is reduced to 16 years (95% CI: 11–42). The Kidneyshell population within the sampled portion of the Sydenham River currently exceeds the estimated MVP.

These population projections assume there is sufficient habitat for Kidneyshell and that the environmental conditions and the fish and mussel communities are similar to current conditions. Population projections also assume the sites in the Ausable River are connected and can be treated as a single population.

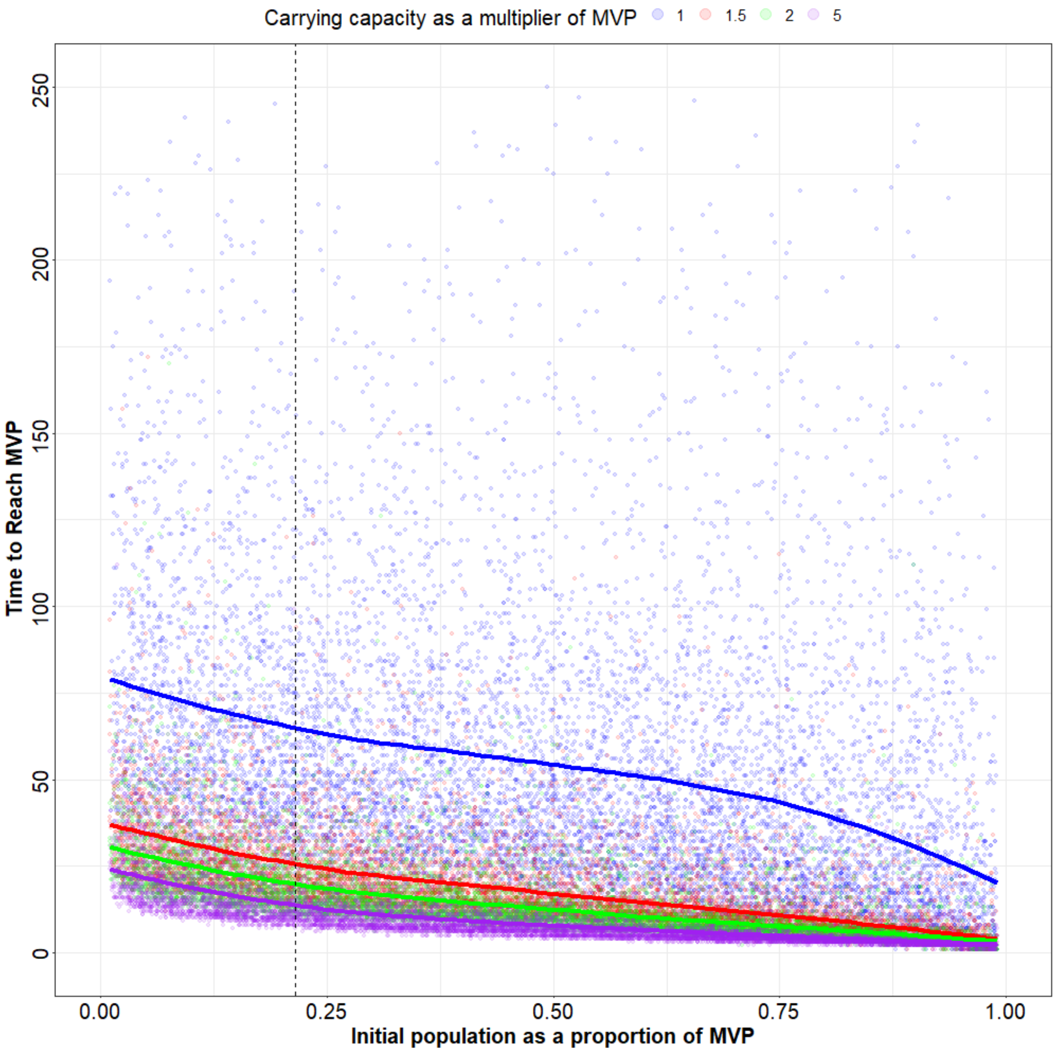

Figure 15. Scatterplot of projected times for simulated Kidneyshell populations to reach minimum viable population size (MVP) based on their initial population as a proportion of MVP. The colours represent the carrying capacity as a multiple of MVP: 1x, 1.5x, 2x and 5x. The curves represent the smoothed loess curve for each of the four carrying capacities. The vertical dashed line represents the median estimated abundance (as a proportion of the MVP) within Ausable River sample sites in 2019.

DISCUSSION

Kidneyshell data gathered from the UMBO network in the Sydenham and Ausable Rivers were analyzed to estimate density, population trajectory, and various life-history parameters. Based on these estimates, with literature values filling data gaps, a population model for Kidneyshell was developed to make predictions on how the population may respond to anthropogenic harm, to estimate abundance and habitat requirements for population viability, and to project the time needed for populations to reach a minimum abundance for population viability (i.e., MVP). The model accounted for parameter uncertainty, environmental stochasticity and density-dependent effects. The results of these model analyses can be used to inform management decisions about population status, allowable harm, recovery targets, and time to recovery.

Although Kidneyshell can be found outside of the UMBO sample sites in both rivers, projections of abundance and population trajectory were based only on the sampled sites. This method provides conservative, minimum estimates of the Kidneyshell population in both rivers but avoids the uncertainties associated with trying to extrapolate outside of the sample sites. Populations of Kidneyshell within the sample sites in both the Ausable and Sydenham Rivers exhibited positive population growth over the survey period but the two populations differ when examined in detail. The Ausable River population exhibited positive growth in 3 of its 5 sites with an overall median λ of 1.07 (95% CI: 1.02–1.126). The projected abundance for the sample sites in the Ausable River in 2019 was 1,129 (95% CI: 933–1,360), but ~ 74% of the population was located in site AR-24. These results indicate a population where growth is mostly limited to one site while other sites either maintained a stable population or experienced a decline. In contrast, the Sydenham River population exhibited growth in all 10 of its sampling sites with an overall median λ of 1.13 (95% CI: 1.11–1.15). The projected abundance for the Sydenham sample sites in 2022 was 6,949 (95% CI: 5,371–9,059) and the population is more evenly spread out among its sites. The most populous site (SR-19) contained ~ 37% of the projected total abundance. These results would indicate a comparatively healthier Kidneyshell population which is experiencing growth at multiple locations. The λ estimate for both rivers are in line with population growth rates of other long-lived, slow-growing unionid species which tends to be close to 1 even for growing populations (Villella et al. 2004, Haag 2012).

Multiple methods were used to assess the impacts of harm to a Kidneyshell population. Most results indicate that Kidneyshell are most sensitive to changes in adult survival. Harm simulations show the greatest impact on stable population size was adult survival, followed by juvenile survival, and recruitment had the least impact. An ~ 3% annual mortality applied to Kidneyshell adults reduced the population by 25%. Such a large reduction resulting from a minor level of applied mortality indicates a high sensitivity to potential harm to adults.

Under the elasticity of λ analysis, the sensitivity of the population to survival rates for various life-stages exhibit the same trend (i.e., adult survival > juvenile survival > recruitment). This is generally the case when the population is decreasing or is stable (i.e., when λ ≤ ~ 1.05); however, as the population grows, it becomes less sensitive to adult survival and more sensitive to juvenile survival and when λ > ~ 1.05, the elasticity value for juvenile survival can overlap or surpass that of adult survival depending on other life-history parameters. Population growth for Kidneyshell in the Sydenham River was 1.13 (95% CI: 1.11–1.15), therefore, harm applied to juveniles may have an equal or greater effect on the population as harm applied to adults. The situation is more variable for the Ausable River population, which has a median λ of 1.07 (95% CI: 1.02–1.126). The median and lower estimates of λ would be in the range where adult survival is of greater importance but higher λ estimates would be in the range where the elasticities of adult and juvenile survival overlap. Finally, changes in recruitment did not have as large an impact on population growth rate or stable adult abundance as changes to juvenile or adult survival. The pattern of increased sensitivity to the adult stage and low sensitivity to recruitment has been identified in other long-lived unionids (Haag 2012).

Elasticity estimates were affected by uncertain life-history parameters. For example, age-at-maturity influenced the elasticity estimate for juvenile survival. As T_{mat} increased, the population generally became more sensitive to the juvenile stage. At $T_{mat} = 3$, the mean elasticity estimate for juvenile survival across population growth rates was ~ 0.25 while at $T_{mat} = 5$ it was ~ 0.43. Also, the elasticity for adult survival generally increased with relative recruitment (α). As a greater proportion of reproduction occurred later in life, the adult life-stage became more important for population growth.

Estimates of requirements for population viability were based on simulation analysis to determine the population sizes required for demographic sustainability through estimates of minimum viable population size (MVP). Persistence probability depends on population size, catastrophe rate and maximum population growth. For a 99% persistence probability over 100 years, Kidneyshell requires ~ 2,100 (95% CI: 900–3,900) adult females, which translates to ~ 5,250 (95% CI: 2,250–9,750) adults of both sexes assuming a 1:1.5 female-to-male sex ratio. The upper confidence interval is associated with higher catastrophe rates and lower maximum population growth while the lower confidence interval is associated with lower catastrophe rates and higher maximum population growth.

The MVP was compared with the projected current abundances of Kidneyshell population within the sample sites of both rivers. The Kidneyshell abundance in Sydenham River sample sites is above MVP while the abundance in Asuable River sample sites is approximately 20% of MVP. Kidneyshell can be found outside of the UMBO sample sites in the Ausable River therefore the river-wide total population should be closer to or possibly above MVP; however, a population projection was conducted to examine how long it would take for the Ausable population to reach MVP assuming the UMBO sites contained the entirety of the Kidneyshell population. This was done to provide a conservative timeframe for managing population recovery in the Ausable River. Under this assumption, the median projected time for the Ausable population to reach MVP is 52 years (95% CI: 22–167) if MVP was set as the carrying capacity (*K*). Time to reach MVP would be reduced if the initial population is higher or if *K* is greater than MVP. If *K* was twice the MVP value, the median time to reach MVP would be reduced to 16 years (95% CI: 11–42).

Estimates of MVP were converted to habitat requirements by dividing the MVP by either the current population density estimates or by the extrapolated stable population density estimates for the two river systems. Habitat requirement based on current densities corresponds to ~ 260 ha (95% CI: 105–680) for the Ausable River and ~ 50 ha (95% CI: 22–113) for the Sydenham River. The extrapolation method gives MAPV estimates of ~ 108 ha (95% CI: 4.7–5,100) for the Ausable River and ~ 10 ha (95% CI: 0.62–109) for the Sydenham River. Upper confidence interval estimates correspond to lower estimates of current density, lower population growth rate and higher catastrophe rates. MAPV estimates calculated with current densities have a higher median value but tighter confidence interval range compared to the estimates made with extrapolated stable population densities. MAPV estimates are highly sensitive to the population density used in its calculation. The process for estimating stable population density is sensitive to the current abundance and population growth rate (λ), which were randomly drawn from a range of values, and to the density-dependence function. The relationship between stable population density and current λ is non-linear. Small differences in λ, especially near the upper range of values, can lead to vastly different density estimates.

Projections of population viability and trajectory assume the habitat and the biological community in the Ausable and Sydenham Rivers are maintained at current conditions. Deteriorating conditions would likely lead to higher requirements for population viability (both abundance and habitat) and more time needed for Kidneyshell populations to reach MVP.

UNCERTAINTIES

There are numerous uncertainties in the parameterization of the population model for Kidneyshell. Uncertain parameters included: nearly all aspects of recruitment, juvenile survival, age-at-maturity, and maximum population growth rate. For example, the age-at-maturity could not be determined from field data due to a lack of small-sized, immature individuals and an allometric relationship was used to fill in the data gap. To address this issue, a range of potential values were used for these parameters, based on probability distributions. This allows the potential life-history dynamics to be represented in the simulations and gave a range of results. Inclusion of parametric uncertainty is important and can have significant influence on the conclusions drawn from population viability analysis (McGowan et al. 2011).

Current population estimates are based only on the sample sites in both rivers. There was insufficient information to extrapolate abundance outside those sites. Since Kidneyshell can be found outside the sample sites, these estimates are underestimates of the true population abundance. This contributes to uncertainties regarding the status of the Ausable River population in relations to whether it is below MVP and, if below, how much time it would take for the population to reach MVP.

The frequency of catastrophic events for Kidneyshell were unknown but significantly affect estimates of MVP. It is not known whether the chosen catastrophe probability interval between 5% and 20% per generation accurately reflects realistic conditions. However, since Kidneyshell is a long-lived species which buries itself in the sediment, the probability of catastrophe may tend to be lower. The severity of these events was modelled with a beta distribution using data from the Reed et al. (2003) meta-analysis but these findings were based on vertebrate populations; its applicability may be limited when used to describe sessile mussel populations which are less capable of using movement to mitigate the impact of catastrophic events.

Interactions between Kidneyshell and their host species were not explicitly included in the population model even though the health of the host population(s) will have a significant impact on the Kidneyshell populations. The host species for Kidneyshell has not been empirically determined in Canada, although likely hosts inferred from US findings are also native to Canada. Therefore, it is not known whether Kidneyshell populations are limited by host availability. The abundance of unionid species in a river system tends to be correlated with the abundance of their host species (Haag 2012). As well, previous simulation analysis of Hickorynut (*Obovaria olivaria*) populations demonstrated that host abundance and trajectory was a strong determinate of mussel abundance (Young and Koops 2013). For this model, the host population was assumed to be maintained at current levels and sufficiently abundant that it has no impact on Kidneyshell reproduction. Violation of this assumption may suggest Kidneyshell abundance is related to the population dynamics of those host species in the Ausable and Sydenham Rivers. For instance, if the population of those host species were subjected to catastrophic events, the population of Kidneyshell may be indirectly impacted even if the events applied no direct mortality on the mussel species. These considerations could result in greater requirements for population viability. If host population(s) become extirpated from the two rivers, it is likely Kidneyshell will become extirpated as well.

The effects of community interactions on Kidneyshell are also poorly known. Predation on the mussel or their host species could pose a risk to Kidneyshell population. Low water levels, exacerbated by climate change, could potentially expose Kidneyshell to increased predation by opportunistic terrestrial predators, although Owen et al. (2011) found that Kidneyshell are generally at lower risk of predation by muskrats compared to mussel species with thinner shells. Invasive species (e.g., Round Goby, Zebra Mussel) may impact Kidneyshell directly through predation or competition or indirectly via negative impacts on their host fishes.

The impact of environmental factors on Kidneyshell vital rates are not well understood. Unionid mussels are sensitive to water quality which can have a large effect on their growth and survival. Land usage around the Ausable and Sydenham Rivers can have a major influence on the runoffs which enters into them. Contaminants such as ammonia and metals have been shown to increase unionid mortality in lab studies, particularly for individuals in early life-stages (Augspurger et al. 2004, Wang et al. 2007, Gillis et al. 2008), and significant differences has been found in mussel abundances between the upstream and downstream area of a water treatment plant (Gillis et al. 2017). Cumulative effects of multiple contaminants or of contaminants with other environmental stressors may also be important. However, studies detailing the quantitative relationship between Kidneyshell vital rates and environmental contaminants remain unavailable. Under conditions where environmental factors are reducing

Kidneyshell survival rates, population viability requirements (i.e., MVP and MAPV) will need to be higher to compensate for the reduced population growth rate. Elasticity analysis and harm simulations may also be useful as a guide to estimate the negative effects of these environmental factors on Kidneyshell population. Fully incorporating environmental effects into the population model to analyze negative environmental impacts or potential mitigation measures will require more information on the relationship between those factors and Kidneyshell vital rates.

Kidneyshell in each of the Ausable and Sydenham Rivers were treated as a single independent population, with reproduction and survival subjected to the same environmental conditions. More complex population structure is possible which may affect how abundance is estimated and the persistence probability of the population as a whole. Meta-population structure, with migration or inter-breeding among sub-populations, can drastically increase population persistence but this decreases when stochastic environmental conditions among sub-populations are correlated (Palmqvist and Lundberg 1998, Reed 2004). If there is a degree of independence among Kidneyshell sub-populations within the Ausable or Sydenham Rivers persistence probability may be greater than estimated here.

ELEMENTS

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

Life-history parameters for Kidneyshell were estimated for populations in the Ausable and Sydenham Rivers. The value for each life-history parameter used in the modelling is presented in Table 7. Many life-history characteristics of Kidneyshell remain unknown. Uncertainties were represented with probability distributions to capture the range of values possible for the species (Table 7). The Methods section provides explanation of the parameter selections.

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

Potential abundance targets were estimated using population viability analysis and estimates of minimum viable population (MVP). Simulations incorporated density-dependence, environmental stochasticity, parameter uncertainty and random catastrophes. Persistence probability is influenced by population size, maximum population growth and catastrophe rates. Under a 99% probability of persistence over 100 years, the MVP is ~ 5,250 (95% CI: 2,250–9,750) adults of both sexes. With a 95% chance of persistence over 100 years, the MVP is ~ 1,500 (95% CI: 650–2,875) adults of both sexes. The upper confidence interval of MVP estimates correspond to simulations with more frequent catastrophes and lower maximum population growth.

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 Kidneyshell population dynamics parameters

Population growth rates of Kidneyshell populations in the Ausable and Sydenham Rivers were estimated from quadrat survey data collected between 2006–2019 and 1999–2022 respectively. Population growth rates (λ) were estimated to be 1.07 (95% CI: 1.02–1.13) in the Ausable River and 1.13 (95% CI: 1.11–1.15) in the Sydenham River.

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

The quantity of habitat required to support an MVP sized population of Kidneyshell was estimated by determining the density of a stable population given the population's current density, growth rate and the modelled form of density-dependence. Estimated adult female densities of a stable population were: 0.17 mussels/m^2 (95% CI: 0.004–3.1) in the Ausable River and 1.71 mussels/m^2 (95% CI: 0.19–24.7) in the Sydenham River. This corresponds to median MAPV estimates of ~ 108 ha (95% CI: 4.7–5,100) and ~ 10 ha (95% CI: 0.62–109) for the Ausable and Sydenham Rivers respectively. Upper confidence interval estimates correspond to lower estimates of current density, lower population growth rate and greater catastrophe rates.

If the modelled density-dependence was removed from the calculation of MAPV and the current female adult densities were used, the median MAPV estimates for the Ausable River would be ~ 260 ha (95% CI: 105–680) and the estimates for the Sydenham River would be ~ 50 ha (95% CI: 22–113).

The MAPV estimate only identifies the amount of habitat required to house an MVP sized population and does not account for other considerations such as habitat to support host populations or the spatial configuration of populations. For example, unionid mussels reproduce by spermcasting where males release sperm which is siphoned from the water by females during filter feeding (Haag 2012). In a lotic environment, successful fertilization can only be achieved when males exist upstream of females and only habitat where successful fertilization is possible can contribute to MAPV.

Based on estimates of the current geographical range occupied by Kidneyshell in the Ausable and Sydenham Rivers (Colm and Morris 2025) and an estimated 91.3% of that geographical range being suitable habitat for Kidneyshell (Daniel et al. 2018), the quantity of available suitable habitat is ~ 100 ha and ~ 220 ha in the Ausable and Sydenham Rivers, respectively. These results suggest that the Sydenham River has sufficient habitat to sustain a population at MVP but the Ausable River may not have sufficient habitat.

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

Population count was estimated from the quadrat data model for the Ausable and Sydenham Rivers but was restricted to the survey area. The estimated number of Kidneyshell in the sampled region of the Ausable River was 1,129 (95% CI: 933–1,360) in 2019 and in the Sydenham River was 6,949 (95% CI: 5,371–9,059) for 2022.

The estimate for the Sydenham River was greater than MVP. The estimate for the Ausable River was less than MVP. Simulations were conducted to determine how long it would take for the Ausable River population (survey sites only) to reach MVP size given its current trajectory. Under ideal conditions, the Ausable River population is projected to reach MVP ~ 87% of the time in 100 years or less.

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 mitigation measures and Kidneyshell mortality rates or productivity. Therefore, it is difficult to provide guidance about the effect of mitigation measures on 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

Population growth rates of Kidneyshell populations in the Ausable and Sydenham Rivers were estimated from quadrat survey data collected between 2006–2019 and 1999–2022 respectively. Population growth rates (λ) were estimated to be 1.07 (95% CI: 1.02–1.13) in the Ausable River and 1.13 (95% CI: 1.11–1.15) in the Sydenham River.

The abundance estimate at sample sites in the Sydenham River was greater than MVP. The abundance estimate at sample sites in the Ausable River was less than MVP. Simulation results indicated that the Ausable River population would require 52 years (95% CI: 22–167) to reach MVP in the survey locations.

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 Table 7 are based on the best available data for these populations and should be used for future population modelling until better data are available. Details regarding how the parameters were estimated and source data used are outlined in the Methods section of this report.

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

Maximum allowable harm can be estimated from elasticities (Table 9) by calculating the change in a vital rate that maintains a population growth rate ≥ 1. As there is a high degree of uncertainty in the model it is precautionary to use the upper confidence interval of the elasticity in the harm assessment (represented by the lower confidence interval if the maximum allowable harm estimates presented in Table 11). Allowable harm applies when a population has an initial λ > 1. Maximum allowable harm is estimated as (Vélez-Espino and Koops 2009):

$$Maximum\ allowable\ harm = \left(\frac{1}{\varepsilon_\lambda}\right)\left(\frac{1-\lambda}{\lambda}\right). \qquad (19)$$

Where λ is the current population growth rate and ε_λ, is the elasticity estimate for the perturbed vital rate. Maximum allowable harm is estimated for the Sydenham and Ausable Rivers based on the full range of estimates of their population growth rate; Sydenham River: 1.11–1.15, Ausable River: 1.02–1.126.

The maximum amount of harm consistent with the objective to maintain stable or growing populations (i.e., population growth rate at or above 1) was estimated for the Ausable and Sydenham River based on their current states (Table 11). The Kidneyshell populations in the two rivers differ in their current rates of population growth and, therefore, the estimates of maximum allowable harm differ. The pattern in stage-specific maximum allowable harm is similar between the two rivers with adult survival having the lowest allowable harm estimates, followed by juvenile survival and with recruitment having the highest. The Ausable River population consistently has lower maximum allowable harm estimates for each vital rate as well as a wider confidence interval for those estimates compared to the Sydenham River population. This reflects the wider range and a lower minimum for the Ausable River population growth rate estimate. Maximum allowable harm if both juvenile and adult stages were impacted was also estimated (Table 11).

Table 11. Maximum allowable harm estimates for Ausable River and Sydenham River populations of Kidneyshell. The values represent the maximum proportional decrease in vital rates that allow the population to maintain a population growth rate ≥ 1. Allowable harm estimates are made based on estimated population growth rates for each river; Ausable River: 1.02–1.126, Sydenham River: 1.11–1.15. LCI and UCI are the lower and upper 95% confidence intervals respectively.

	Max. Allowable Harm		
Vital Rate	**Median**	**LCI**	**UCI**
Ausable River			
Juvenile Survival	0.21	0.03	0.42
Adult Survival	0.15	0.01	0.31
Juvenile & Adult Survival	0.09	0.009	0.16
Recruitment	0.62	0.09	0.92
Sydenham River			
Juvenile Survival	0.28	0.18	0.43
Adult Survival	0.22	0.14	0.33
Juvenile & Adult Survival	0.12	0.09	0.17
Recruitment	0.76	0.60	0.93

Estimates of maximum allowable harm for Kidneyshell population in the Ausable and Sydenham Rivers were based on estimates of the current population growth rate in both rivers and the elasticity of λ analysis while accounting for uncertainty in life-history parameters. These allowable harm estimates represent the level of mortality which would cause population growth rate to decrease to 1. Due to the uncertainty in the estimates for life-history parameters and population growth rate, it would be more prudent to use the estimate at the lower confidence interval as the benchmark for maximum allowable harm instead of the median. Under these criteria, the Ausable River population has no scope for harm while the Sydenham River population can tolerate minor increases in mortality (up to ~ 10%). Imposition of maximum allowable harm would stop any population growth and prevent a population from reaching its recovery target if the population is below that threshold.

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