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REGULAR ARTICLE

EVALUATING THE STATUS AND POPULATION BIOLOGY OF AN IMPERILED FRESHWATER MUSSEL, PURPLE WARTYBACK (*CYCLONAIAS TUBERCULATA*), IN SOUTHERN ONTARIO, CANADA

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ABSTRACT

The Purple Wartyback (PWB; *Cyclonaias tuberculata*) is considered threatened in Canada due to the loss of populations in the Detroit River and Lake Erie and possible declines in remaining populations (Ausable, Sydenham, and Thames rivers). Many aspects of PWB life history and population ecology have not been investigated for Canadian populations. We used data from the Fisheries and Oceans Canada Unionid Monitoring and Biodiversity Observation network to estimate PWB population and life-history parameters in the Sydenham and Thames rivers. This mussel occurred at high density in the Sydenham River, but at low density in the Thames River; however, both populations exhibited positive population growth and strong recruitment. Population growth rate in the Sydenham River was 1.047 (credible interval [CI]: 1.037–1.058) from 1999 to 2015, and population growth rate in the Thames River was 1.157 (CI: 1.100–1.221) from 2004 to 2017. Estimated annual adult survival rate (mean ± SE) from catch-curve analysis of empty shells, with measured ages, across both populations was 0.950 ± 0.007. Estimated survival from catch-curve analysis of live individuals, with estimated ages, was 0.966 ± 0.001 and 0.884 ± 0.009 for the Sydenham and Thames rivers, respectively. Our results show that populations of PWB are robust in the Sydenham River and small but growing rapidly in the Thames River.

KEY WORDS: unionid, freshwater mussels, Purple Wartyback, species at risk, integrated nested laplace approximation, population ecology

INTRODUCTION

Ontario is the center of freshwater mussel biodiversity in Canada, but almost a third of Ontario's species are considered at risk (endangered, threatened, or special concern; Reid and Morris 2017). A better understanding of mussel population ecology is needed to aid recovery planning for at-risk species. Quantifying life-history traits and estimating population size and trajectories are recommended in the recovery strategies for all at-risk mussel species in the Great Lakes basin in Canada (Drake et al. 2021), but addressing gaps in our knowledge of population ecology requires prioritizing nonlethal sampling methods to reduce the impacts of research on at-risk species (Castañeda et al. 2021).

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The Purple Wartyback (PWB; *Cyclonaias tuberculata*) is considered threatened in Canada (COSEWIC 2022). This mussel is widespread in the Mississippi River basin, but in Canada it is restricted to the Lake St. Clair and Lake Huron drainages of the Great Lakes basin in southern Ontario. Populations in the Detroit River and Lake Erie appear to be extirpated after the invasion of dreissenid mussels, and remaining Canadian populations may be declining (Ausable, Sydenham, and Thames rivers; COSEWIC 2022).

The population biology of PWB in Canada is poorly known. Information about population growth rate, survivorship, and recruitment is critical for accurately assessing and monitoring population status (Haag and Williams 2014). Fisheries and Oceans Canada (DFO) conducts regular quadrat-based monitoring (Unionid Monitoring and Biodiversity

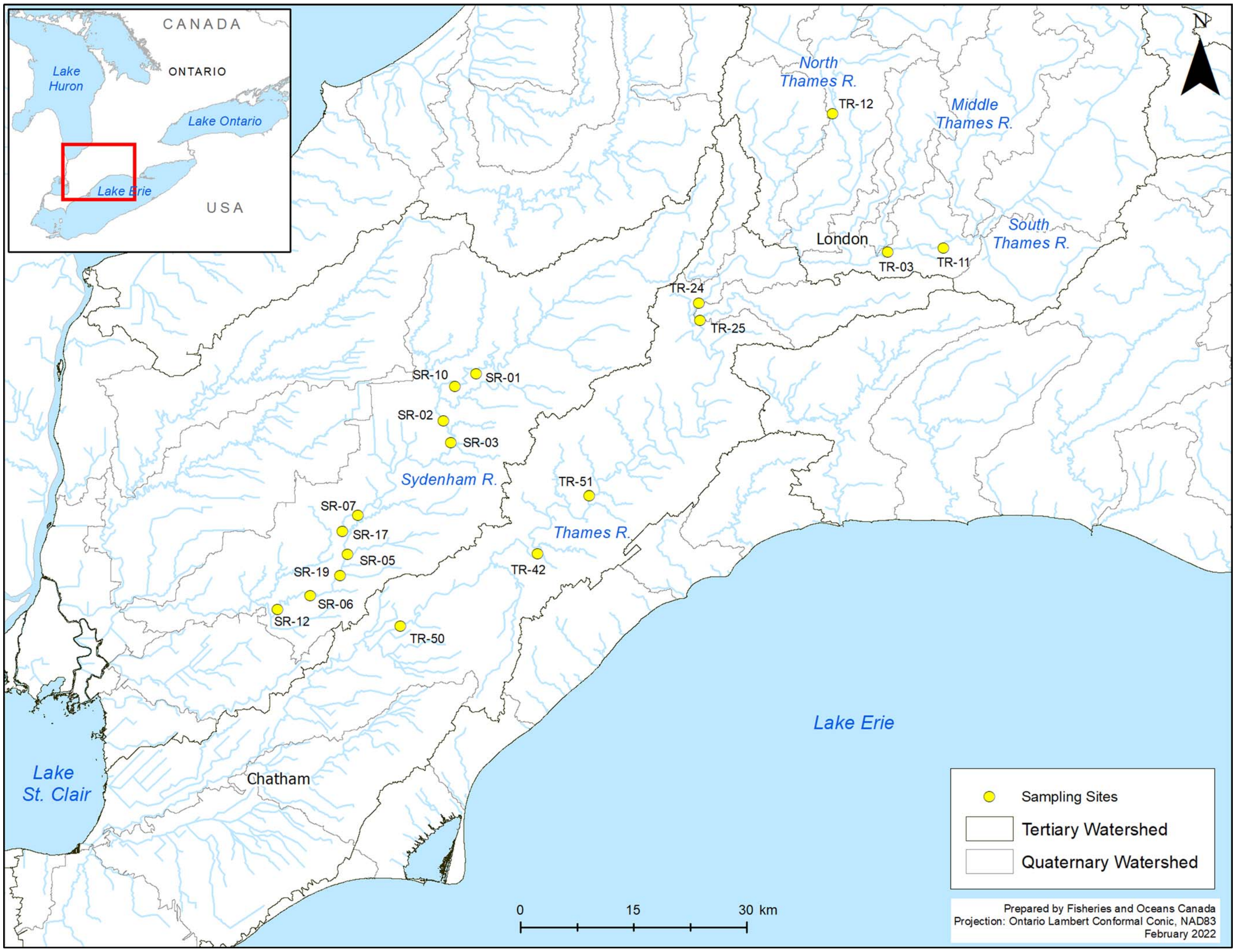

Figure 1. Location of Unionid Monitoring and Biodiversity Observation network sites sampled in the Sydenham (SR) and Thames (TR) rivers. Inset map shows the location of the study area in southern Ontario, Canada.

Observation [UMBO] network) of mussel populations in southern Ontario that includes sampling in the Sydenham and Thames rivers (Metcalfe-Smith et al. 2007; Sheldon et al. 2020; Fig. 1). We used UMBO data to estimate PWB population and life-history parameters in the Sydenham and Thames rivers to improve current understanding of PWB population ecology in southern Ontario.

METHODS

Study Area

The Sydenham and Thames rivers are tributaries of Lake St. Clair that drain approximately 2,700 and 5,800 km^2, respectively (Fig. 1; DFO 2018; SCRCA 2022). Both rivers run through the Carolinian Life Zone, making them among the most biologically diverse areas in Canada (Clarke 1992; Quinlan 2013; Carolinian Canada 2022). Land use in both watersheds is predominantly agricultural, comprising 80–85% of the watershed area (Nürnberg and Lazerte 2015; DFO 2018). Together, the watersheds supported 35 mussel species historically, and >30 species remain in each (Staton et al. 2003; McNichols-O'Rourke et al. 2012; Quinlan 2013). The Sydenham and Thames river watersheds support 14 and 11 mussel species, respectively, that are considered at risk in Canada (Cudmore et al. 2004; Goguen et al. 2022; DFO, unpublished data).

Sampling

We selected, from the UMBO network, 10 sites in the Sydenham River and 8 sites in the Thames River that encompass the distribution of PWB within these watersheds (Fig. 1). We sampled each site twice: we sampled the Sydenham River sites initially between 1999 and 2003 and resampled them between 2012 and 2015; we sampled the Thames River sites initially between 2004 and 2010 and resampled them between 2015 and 2017.

Methods for all sampling events were based on Metcalfe-Smith et al. (2007) and Sheldon et al. (2020). We surveyed sites by using a systematic sampling design with three random starts (Strayer and Smith 2003). With one exception (see subsequent), we divided each site into approximately 25–3×5 m blocks. Within each block, we randomly selected three 1-m^2 quadrats and hand excavated the substrate to a depth of approximately 10 cm. We identified all mussels detected and measured shell length (maximum anterior-to-posterior distance, nearest 0.1 mm) by using Vernier calipers. We returned substrate and mussels to each quadrat and replaced the mussels in a natural position.

In 2012, we surveyed one site in the Sydenham River (SR-06) following the methods described previously, but we then sampled all remaining quadrats so that the entire 375-m^2 area was excavated (Reid and Morris 2017). We used results of the full excavation at this site as an out-of-sample test of model performance (see Data Analysis).

Empty shells were collected at UMBO sites during targeted surveys in 2018 and 2019 for use in developing a length-at-age relationship. We identified, counted, and collected empty fresh shells (i.e., tissue present, intact ligament, intact periostracum). We measured the shell length of each individual and estimated its age (in years) by interpreting radial thin sections cut from one valve. We prepared thin sections following standard methods for bivalves (Neves and Moyer 1988; Haag and Staton 2003; Haag and Commens-Carson 2008; Haag and Rypel 2011), described herein as follows. We used a Buehler IsoMet 4000 precision saw (Buehler Ltd., Whitby, ON, Canada) with a 1-μm specimen positioning system to cross section each valve from the umbo to the outer margin, intersecting the annual rings at right angles. We set blade speed and feed rate to 1,900 rpm and 16.0 mm/min, respectively, and we programmed cut length to match the shell length. We made a second cut, perpendicular to the first, if the first section was too large to fit on a standard glass slide (7.62 cm × 2.54 cm). We polished the cut surface with a series of successively finer grit wet sandpapers (e.g., 600, 1200, 2000) and then affixed the cut surface to a glass slide with epoxy, with curing allowed for 48 h. We made a second cut to remove excess shell, leaving a 600-μm thin section epoxied to the slide and polished the thin section as described previously.

We viewed thin sections using either a SMZ800 stereo microscope or an eclipse Ci compound light microscope (Nikon, Mississauga, ON, Canada) at various magnifications. We identified annuli as shell rings that were continuous from the umbo to the shell margin, and they typically included dark and light areas between annuli, which potentially represented variation in growth rate or environmental conditions during the growing season (Haag and Commens-Carson 2008). Three qualified readers independently assessed each thin section. If there were discrepancies between age counts that could not be resolved, we did not include that thin section in the analysis.

Data Analysis

We conducted all analyses using R 4.1.2 (R Core Team 2021). We described growth of PWB by fitting length-at-age data to a von Bertalanffy growth function (VBGF):

$$L_t = L_\infty\left(1 - e^{-kt}\right), \tag{1}$$

where L_t is length at age t, L_∞ is asymptotic length, and k is the growth coefficient. We estimated parameters with Bayesian methods by using NIMBLE (de Valpine et al. 2017, 2022). We assumed a log-normal error structure to prevent negative credible intervals (CIs; Ogle 2016), and we used noninformative priors. We collected 61 empty shells across both waterbodies for aging, 31 from the Sydenham River and 29 from the Thames River; for one shell, the river of origin was uncertain. We reached a consensus age for all collected PWB shells.

We generated length–frequency distributions for pooled sites across years for both the Sydenham and Thames rivers by using ridgeline plots (Wilke 2022). We identified putative juveniles based on estimated age at maturity (T_{mat}) and length at maturity (L_{mat}). Neither parameter is known for Ontario populations of PWB. We estimated T_{mat} using the following equation:

$$T_{\mathrm{mat}} = 0.69k^{-1.031} - 1, \tag{2}$$

where k is the VBGF growth coefficient (Haag 2012). We then used equation (1) to estimate L_{mat}. We investigated the change in the proportion of juveniles through time with logistic regressions where individuals were represented as a Boolean, 1: juvenile; 0: adult. Site was included as a random effect if there were improvements in deviance information criterion (DIC).

We estimated annual survival of adult PWB by using the Chapman–Robson method for catch-curve analysis (Chapman and Robson 1960; Smith et al. 2012) based on empty shells collected in 2018 and 2019 and live shells from all sample years where age was estimated based on the VBGF. We estimated survival ($\hat{S}$) by using the following equation:

$$\hat{S} = \frac{\bar{T}}{1 + \bar{T} - \frac{1}{n}}, \tag{3}$$

where n is the total number of fully recruited mussels observed and $\bar{T}$ is the mean age of mussels fully recruited to sampling. We calculated the SE of survival rate using the following equation:

$$\mathrm{SE}_{\hat{S}} = \sqrt{\hat{S}\left(\hat{S} - \frac{\bar{T} - 1}{n + \bar{T} - 2}\right)}. \tag{4}$$

We performed catch-curve analysis on the aged empty shells pooled from both rivers: that analysis assumes that mortality and recruitment are constant, all individuals are equally available to sampling, and there is no error in age estimation (Ogle 2016). If the smaller shells of younger PWB degraded faster or were more likely to be removed from the system (e.g., via predation or water currents) than larger shells of older PWB, the assumption of equal availability to sampling will be violated and the estimates biased, likely toward estimating greater survival. In addition, if shells persist in the system for a long period of time, the survival estimate may not represent contemporary conditions. As a comparison, we performed an additional catch-curve analysis by assigning ages to the live PWB sampled during the study. We used the Bayesian VBGF fit to generate predicted length distributions for each age-class (Age-0 to the maximum observed age in each river), incorporating parameter uncertainty and residual variance. We used these posterior predictive distributions to generate an age-length key representing the probability that lengths, binned into 10-mm groups, belonged to each age-class. We assigned ages to sampled PWB based on their measured length by using the Iserman and Knight method (Iserman and Knight 2005; Ogle 2016). We assigned live-shell ages based on the river-specific age-length key generated from the VBGF (Figs. A1 and A2). We performed the catch-curve and age-length key analyses using the FSA package (Ogle et al. 2022).

We estimated population density and trajectory by fitting the UMBO data with separate models for the Sydenham and Thames rivers. We used a hierarchical Bayesian approach with integrated nested laplace approximation (INLA; Rue et al. 2009), which uses deterministic methods to make Bayesian inferences allowing for faster computations than Markov Chain Monte Carlo methods. We modelled density (mussels/m^2) as a function of sample year with sample site included as a random effect. We modelled the data using the negative binomial (NB) distribution as preliminary analysis demonstrated using the Poisson distribution resulted in a model that was overdispersed. The model was represented by

$$y_{is} \sim \mathrm{NB}(\mu_{is}, \theta), \tag{5}$$

$$E(y_{is}) = \mu_{is}, \tag{6}$$

$$\mathrm{var}(y_{is}) = \mu_{is} + \frac{{\mu_{is}}^2}{\theta}, \tag{7}$$

$$\log(\mu_{is}) = \alpha + \beta \cdot \mathrm{year}_i + \mathrm{site}_s, \tag{8}$$

where y_{is} represents PWB count from quadrat i and site s, μ_{is} is the expected mean density, and θ is the size parameter of the negative binomial distribution indicating the extent of overdispersion; α is the intercept representing the initial mean density; the covariate year is the year sampled beginning at 0 (survey year subtracted from the first survey year); β is the slope of the year effect representing the instantaneous rate of population growth where population growth rate is $\lambda = e^{\beta}$; *site* represents the site random effect, which was assumed to be independent and identically distributed with a mean of 0 and SD σ_{site}. To determine the importance of including site as a random effect we compared DIC values to the models omitting the random effect. We used the log-gamma prior with shape and rate parameters of 1 and 0.05 for the site hyperparameter (Carroll et al. 2015). We used the default uninformative prior for fixed effects, a normal distribution with a mean of 0 and precision of 0.001.

We used the full excavation of site SR-06 in 2012 as an out-of-sample test of model performance. We compared observed density and the total number of PWB collected to predictions from the fitted model.

RESULTS

In total, 3,275 live PWB were sampled: 3,085 in the Sydenham River and 190 in the Thames River. Density in the Sydenham River was 2.06 mussels/m^2, compared with 0.17 mussels/m^2 in the Thames River. In the Sydenham River, 1,190 PWB were collected in the first sampling period and 1,895 were collected in the second sampling period. An increase in density between sample periods was observed at 8 of the 10 sites in the Sydenham River (Table A1). In the Thames River, 26 and 164 PWB were collected in the first and second sampling periods, respectively, and six of the eight sample sites showed an increase in mean density (Table A1).

Individuals ranged in size from 9.0 to 198.9 mm across both rivers, with a mean length of 80.4 mm in the Sydenham River and 59.8 mm in the Thames River. Mean length in the Sydenham River was significantly greater than that of mussels in the Thames River ($t = 11.9$, $P < 0.001$). The lengths of aged shells ranged from 12.6 to 128.0 mm (mean: 76.3 mm) in the Sydenham River and from 24.4 to 110.6 (mean: 82.3) in the Thames River. The ages ranged from 1 to 92 yr (mean: 26.1 yr) in the Sydenham River and from 2 to 32 yr (mean: 17.6 yr) in the Thames River. There was overlap in the length-at-age data between rivers and no apparent difference in growth; river did not have an important effect on the L_∞ or k parameters when included in the model fit. Consequently, the data were pooled to produce one growth curve common to both rivers, thereby allowing us to retain the "uncertain" shell in the analysis. The VBGF (Fig. 2) coefficient estimates were $L_\infty = 110.9 \pm 3.63$ mm (SE) and $k = 0.091 \pm 0.006$ (SE).

The number of empty shells was highest for age 7 individuals, allowing survival rate to be estimated over ages 7–92. The Chapman–Robson catch-curve survival rate estimate was 0.950 ± 0.007 (SE) or an instantaneous mortality rate of 0.051 ± 0.008 (SE). Length frequency distributions of empty shells and live individuals were similar (Fig. 3). There was a slight bias towards larger size-classes (greater mode) in the empty shell sample, but it appears to be a reasonable approximation of the live individuals sample. The number of live individuals was highest for age 8, allowing survival to be estimated over ages 8–92. The Chapman–Robson catch-curve survival rate estimate was 0.965 ± 0.001 (SE) for rivers combined; the survival rate estimate for the Sydenham River was 0.966 ± 0.001 (SE) for ages 8–92; and the survival rate estimate for the Thames River was 0.883 ± 0.009 (SE) for ages 6–32.

Age at maturity for PWB was estimated to be 7.2 yr, representing a length at maturity of 53.1 mm. Length frequency distributions and mean length of PWB were relatively stable

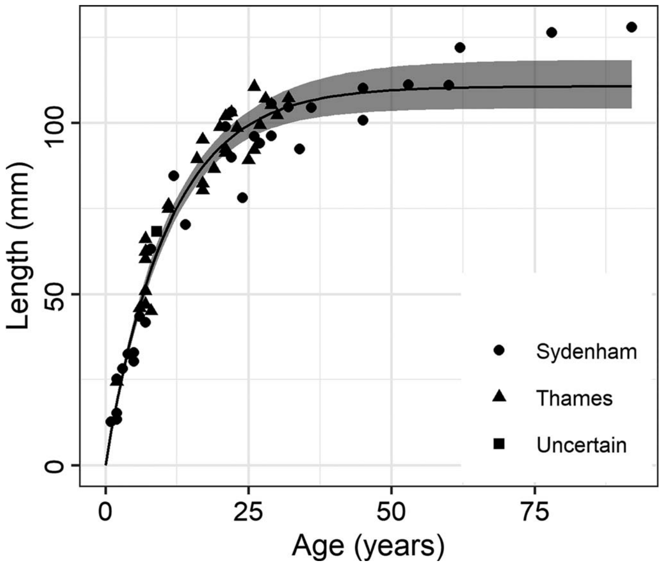

Figure 2. Length-at-age relationship for Purple Wartyback (*Cyclonaias tuberculata*) in the Sydenham and Thames rivers. The solid line represents the fitted von Bertalanffy growth function ($L_t = 110.9(1 - e^{-0.091t})$) and the gray region represents the 95% credible interval.

across years in the Sydenham River (Fig. 4). Juveniles (<53.1 mm) were present in all years and made up 11–18% of the population (mean across years: 13.3%). Logistic regression of juveniles included site as a random effect and indicated a slight decrease in the proportion of juveniles ($P_{\text{juv.}}$) over time [$\text{logit}(P_{\text{juv.}}) = -0.032\text{year} - 1.57$; $P < 0.001$; $\Delta\text{DIC} = 20.6$]. In the Thames River, length frequency distributions appeared to be bimodal in some years and mean length varied among years. Juveniles were present in all years and made up 14–58% of the population (mean across years: 46.8%). Logistic regression omitted site as a random effect and indicated an increase in the proportion of juveniles [$\text{logit}(P_{\text{juv.}}) = 0.13\text{year} - 1.47$; $P = 0.01$; $\Delta\text{DIC} = 0.02$].

The negative binomial model described the quadrat data well with no apparent violations of model assumptions, no overdispersion, and an appropriate number of 0's in model predictions (i.e., no zero-inflation; Table 1). The random site effect was important for both rivers; ΔDIC values of comparisons with models without the site effect were 753 and 139, respectively, for the Sydenham and Thames rivers. The slope of density over time was positive in both rivers (Fig. 5; Table 1). Population growth rate (λ) in the Sydenham River between 1999 and 2015 was 1.047 (95% CI: 1.037–1.058), and λ in the Thames River between 2004 and 2017 was 1.157 (95% CI: 1.100–1.221; Table 2). The expected mean-density estimate for the Sydenham River in 2015 was 1.82 mussels/m^2; for the Thames River in 2017, it was 0.12 mussels/m^2. The estimated population size in the sampled area of the Sydenham River in 2015 was 10,504 (95% CI: 9,563–11,505); for the Thames River in 2017, it was 872 (95% CI: 696–1,091).

During the full excavation of site SR-06, the number of PWB collected ranged from 1 to 36 mussels per quadrat with a mean density of 6.98 mussels/m^2 and the total number of PWB collected was 2,616. The model predicts the expected mean density at site SR-06 in 2012 to be 6.07 mussel/m^2 (95% CI: 5.23–7.04) and the whole-site PWB abundance to be 2,277 mussels (95% CI: 1,960–2,641). The density and total number of PWB collected were within 95% CIs of the model estimates.

DISCUSSION

Populations of PWB in both the Sydenham and Thames rivers experienced positive population growth over the survey time frame. However, these two populations differed in several aspects. The Thames River population had lower abundance and density, but it had a higher population growth rate, than the Sydenham River. The high proportion of juveniles and smaller mean size in the Thames River population support a rapidly growing population. The Sydenham River population had higher abundance and density, lower population growth rate, larger mean size, and more stable length–frequency distributions, all of which suggest a population nearer carrying capacity. In contrast to the Thames and Sydenham populations, the only other remaining population in Canada, in the Ausable River, occurs at low density and shows no evidence of population growth (K. Jean, Ausable Bayfield Conservation Authority, personal communication). It is unknown

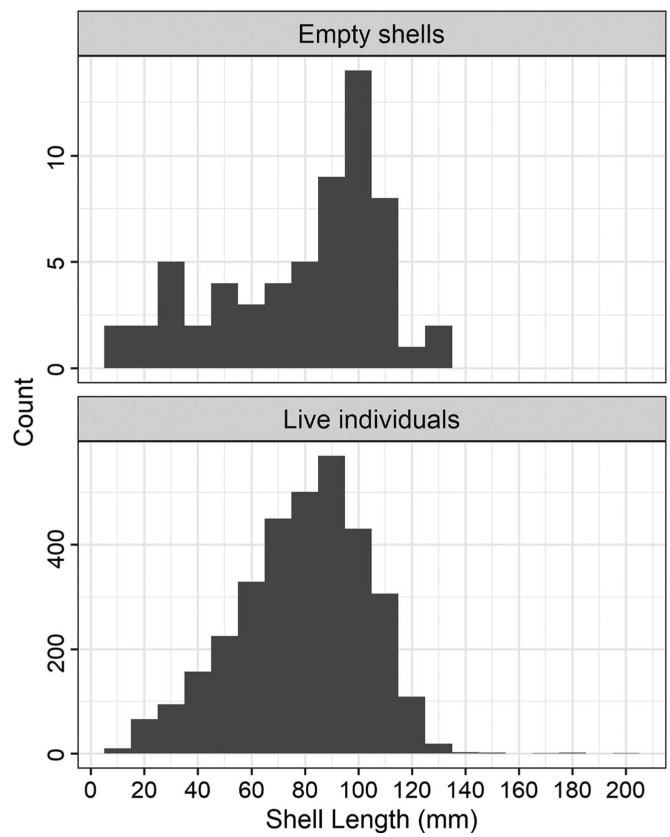

Figure 3. Length frequency distributions of empty shells and live individuals of Purple Wartyback (*Cyclonaias tuberculata*) from the Sydenham and Thames rivers.

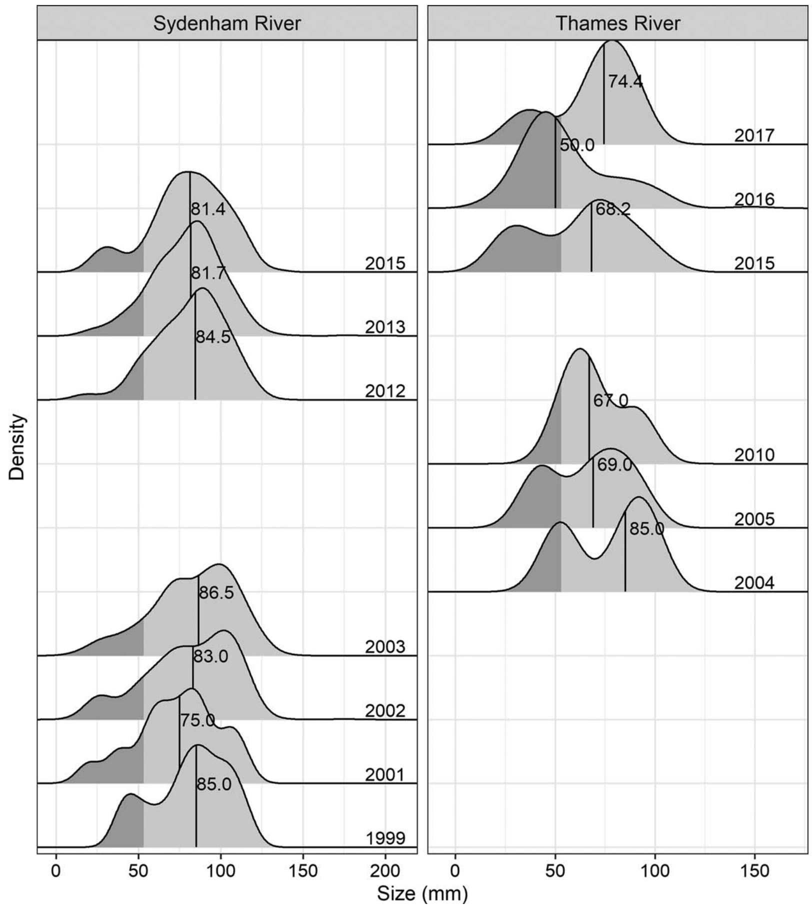

Figure 4. Length distributions of Purple Wartyback (*Cyclonaias tuberculata*) in the Sydenham and Thames rivers over time. Dark gray indicates putative juveniles based on length (<53.1 mm), and light gray indicates adults. Median annual lengths are reported and represented with vertical lines.

why the three Canadian populations of PWB exhibit such different population dynamics.

Density estimates for sparse populations, such as those in the Thames River, can have low precision (Strayer et al. 1997; Lane et al. 2021), which could have influenced our population growth rate estimates. However, our large sample size resulted in a growth rate estimate with a low SE, providing confidence in our estimate. Our conclusion of high population growth rate is supported by the large percentage of juveniles in the population and its low mean mussel size. A population growth rate of >15% is high for most unionids, particularly a long-lived species such as PWB, but growth rates >20% are reported for some species (Patterson 1985; Jones and Neves 2011). Nevertheless, the high population growth rate of PWB in the Thames River is unlikely to be maintained indefinitely as the population approaches carrying capacity.

Purple Wartyback co-occur with many other species at risk (SAR) in the Sydenham and Thames rivers, all of which

Table 1. Parameter estimates for models to estimate density of Purple Wartyback (*Cyclonaias tuberculata*) over time in the Sydenham and Thames rivers. LCI and UCI is the lower and upper 95% credible interval, respectively. θ is the size parameter of the negative binomial distribution, and σ_{site} is the standard deviation of the site random effect.

	Sydenham River				Thames River			
	Median	LCI	UCI	SD	Median	LCI	UCI	SD
Fixed effect								
Intercept	−0.161	−0.863	0.535	0.351	−3.998	−5.575	−2.663	0.730
Year	0.046	0.036	0.057	0.005	0.146	0.096	0.200	0.027
Hyperparameter								
θ	1.864	1.581	2.207	0.160	1.223	0.662	2.535	0.486
σ_{site}	0.942	0.375	2.065	0.440	0.373	0.105	1.127	0.272

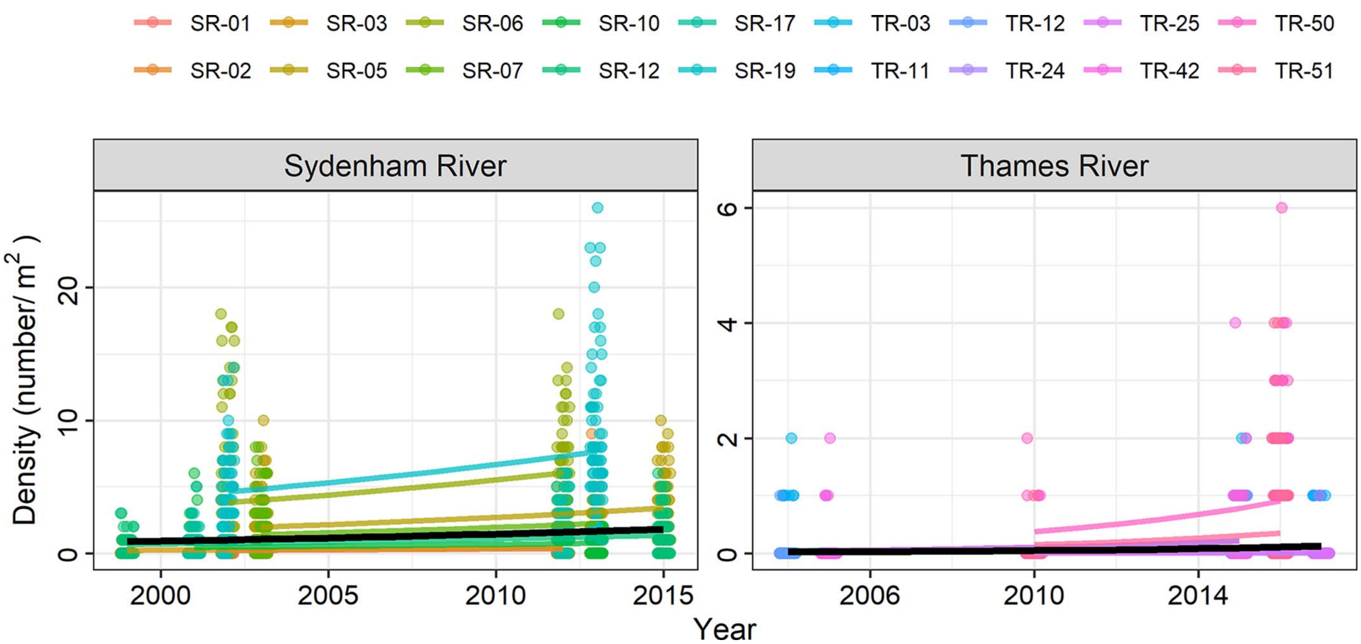

Figure 5. Density of Purple Wartyback (*Cyclonaias tuberculata*) in the Sydenham and Thames rivers (SR and TR, respectively) over time. Colored lines represent fitted relationships for each site, and the black line shows the mean trend for each river across sites.

may have benefitted from conservation actions such as identification and protection of critical habitat and the implementation of mitigation measures to reduce threats within these watersheds (DFO 2018). These actions may have been factors in overall improvement in water quality in both systems, which likely further contributed to increasing populations of PWB. Another at-risk species, the Wavy-Rayed Lampmussel (*Lampsilis fasciola*), showed high population growth and range expansion in the Thames River, leading to a downgrading of its conservation status (COSEWIC 2010).

Our estimates of PWB survival rate from catch-curve analysis of empty shells could be biased to a varying extent based on the shell decay rate. If shells decay slowly and persist in the environment for a long time, our annual survival rate estimates may be underestimated because of the accumulation of individuals that died over several years. Furthermore, if shell decay rates differ across ages, our estimates may be inflated. Unionid shell decay rate relates to both extrinsic factors, such as water chemistry and current, and intrinsic factors, such as shell size and robustness (Strayer and Malcom 2007; Ilarri et al. 2019); however, we have no information about decay rates in our study rivers. Despite the potential for bias, the similarity of our survival estimates from empty shells to survival calculated from live individuals, as well as the similarity of length–frequency distributions for empty shells and live individuals, support the accuracy of our estimates. In the Thames River, our survival estimate from live individuals (0.884) was lower than that from empty shells (0.950). This discrepancy could have been caused by the lower maximum observed age (32 yr), smaller mean size and smaller sample size in the Thames River, resulting in a less precise estimate from live individuals.

No other estimates of PWB survival rate are available, but our estimates are similar to predicted and observed values for other long-lived unionids. Based on a relationship between

Table 2. Summary of population parameters (95% credible intervals) for Purple Wartyback (*Cyclonaias tuberculata*) in the Sydenham and Thames rivers.

Parameter	Sydenham River	Thames River
Abundance at sample sites	10,504 (9,563–11,505)	872 (696–1091)
Density (mussels/m^2)	1.82 (0.94–3.87)	0.12 (0.03–0.42)
Population growth rate (λ; y^{-1})	1.047 (1.037–1.058)	1.157 (1.10–1.221)
% juveniles	14	49
Juvenile trend	↘	↗
Mean length (mm)	80.4	59.8
Length end	→	↘
Survival rate (dead shells)	0.950 (±0.007 SE)	
Survival rate (live individuals)	0.966 (±0.001 SE)	0.884 (±0.009 SE)

instantaneous mortality rate (M) and life span (T_{max}) for 14 species from 15 populations ($M = 4.171 T_{max}^{-1.070}$; Haag 2012), our maximum observed age of 92 for PWB gives a predicted instantaneous mortality rate of 0.033, or a survival rate of 0.968, which is similar to our estimates for empty shells and live individuals from the Sydenham River. Annual survival rates of the long-lived *Amblema plicata* and *Popenaias popeii*, estimated by mark–recapture methods, were 0.97 and 0.98, respectively (Hart et al. 2001; Inoue et al. 2014). Similarly, annual survival was >0.90 for three unionid species in a 4-yr mark–recapture study (Villella et al. 2004). Mark–recapture studies are needed to corroborate the survival estimates we obtained from catch-curve analysis.

The VBGF parameters provide insight into important life-history characteristics such as growth rate, maximum size, life span, age at maturity, and relative shell mass (Haag and Rypel 2011; Haag 2012). The only other published values for PWB growth coefficients are from West Virginia, USA, where L_∞ was 87.0–113.9 mm and k was 0.110–0.164 in the New River and L_∞ was 90.6 mm and k was 0.094 in the Greenbrier River; the maximum age observed in these populations was 91, and length at maturity was 58.6 mm (Jirka 1986). Our estimates of a long life span (92 yr), delayed maturity (7.2 yr), and slow growth ($k = 0.091$) for PWB in Ontario are consistent with the expectation of an equilibrium species adapted to stable habitats (Haag 2012).

The UMBO survey design was not based on randomized site selection; instead, it used prior knowledge to select sites with high mussel density and SAR occurrence. As a result, extrapolation of our density estimates outside of the survey sites is inappropriate (Reid and Morris 2017), and we were unable to make system-wide estimates of density or population size. However, the wide distribution of survey sites within each system means that our estimates of population growth and recruitment may reflect the entire river. In addition, the survey protocol provides accurate and precise estimates of mussel density for common species, such as PWB in the Sydenham River, and it provides reliable detection of large changes in density, even when density is <0.1 mussels/m^2 (Reid and Morris 2017). Although PWB populations in the Detroit River and Lake Erie may be extirpated, populations in the Sydenham and Thames rivers appear to be large and robust or increasing in recent years.

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Appendix

Table A1. Summary of sample data for Purple Wartyback (PWB; *Cyclonaias tuberculata*).

River	Site	Latitude	Longitude	Year	No. of Blocks	No. of Quadrats	No. of PWB	Density (no./m^2)	SE
Sydenham River	SR-01	42.86	−81.79	2002	24	72	14	0.19	0.006
				2012	24	72	23	0.32	0.008
	SR-02	42.806	−81.847	2003	26	78	80	1.03	0.016
				2013	25	75	125	1.67	0.023
	SR-03	42.779	−81.835	1999	23	69	11	0.16	0.005
				2012	23	69	30	0.43	0.012
	SR-05	42.651	−82.01	2003	23	69	139	2.01	0.032
				2015	25	75	251	3.35	0.035
	SR-06	42.604	−82.072	2002	26	78	341	4.37	0.065
				2012	25	75	395	5.27	0.051
	SR-07	42.697	−81.99	2003	27	81	173	2.14	0.025
				2013	25	75	95	1.27	0.021
	SR-10	42.846	−81.825	2001	25	75	47	0.63	0.015
				2013	25	75	41	0.55	0.011
	SR-12	42.589	−82.126	1999	26	78	33	0.42	0.009
				2015	25	75	123	1.64	0.019
	SR-17	42.679	−82.017	2001	27	81	48	0.59	0.011
				2012	25	75	166	2.21	0.023
	SR-19	42.626	−82.023	2002	25	75	304	4.05	0.043
				2013	25	75	646	8.61	0.073
Thames River	TR-03	42.982	−81.114	2004	22	66	9	0.14	0.006
				2015	25	75	10	0.13	0.005
	TR-11	42.983	−81.024	2004	22	66	3	0.05	0.003
				2017	25	75	8	0.11	0.04
	TR-12	43.15	−81.192	2004	21	63	1	0.02	0.002
				2015	25	75	6	0.08	0.004
	TR-24	42.932	−81.424	2010	25	75	0	0	0
				2017	25	75	0	0	0
	TR-25	42.912	−81.424	2010	25	75	0	0	0
				2017	25	75	1	0.01	0.002
	TR-42	42.643	−81.703	2005	23	69	6	0.09	0.005
				2015	25	75	14	0.19	0.008
	TR-50	42.564	−81.93	2010	15	45	6	0.13	0.009
				2016	25	75	85	1.13	0.017
	TR-51	42.709	−81.616	2010	25	75	1	0.01	0.002
				2016	25	75	40	0.53	0.012

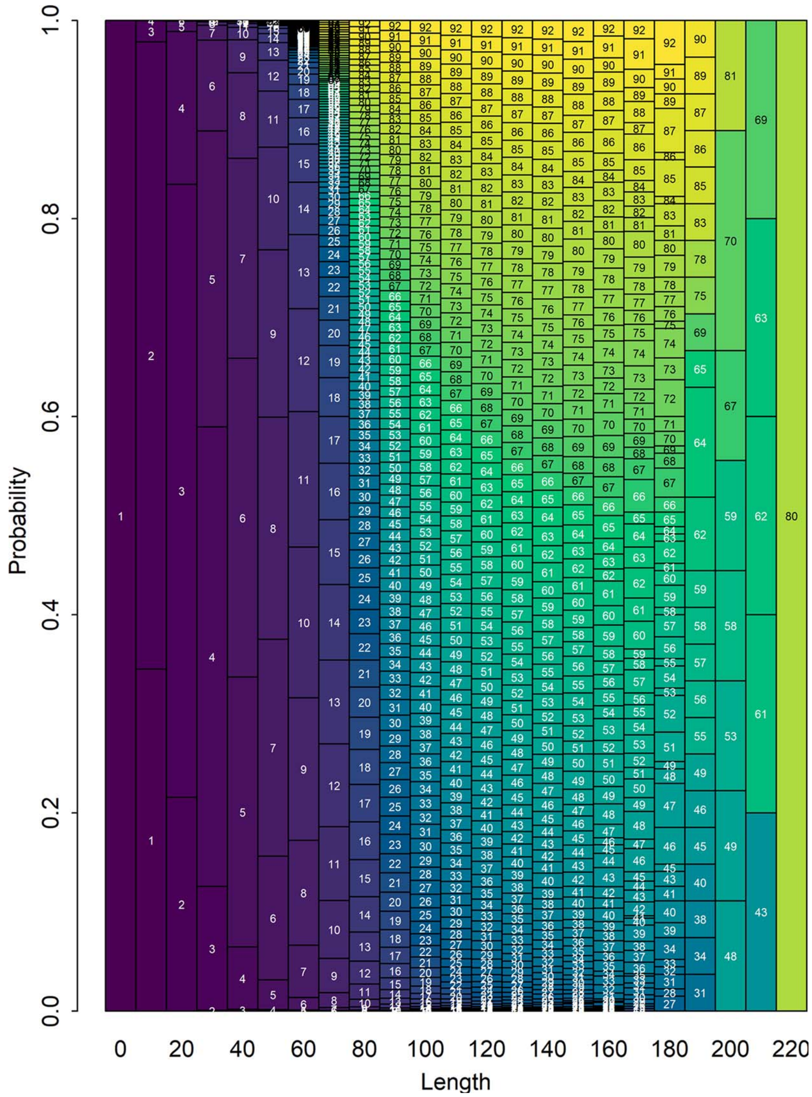

Figure A1. Age-at-length key for Purple Wartyback (*Cyclonaias tuberculata*) from the Sydenham River developed from von Bertalanffy growth function length-at-age predictions. The x axis represents 10-mm length bins, the y axis represents age probabilities, and the tiles represent ages (1–92).

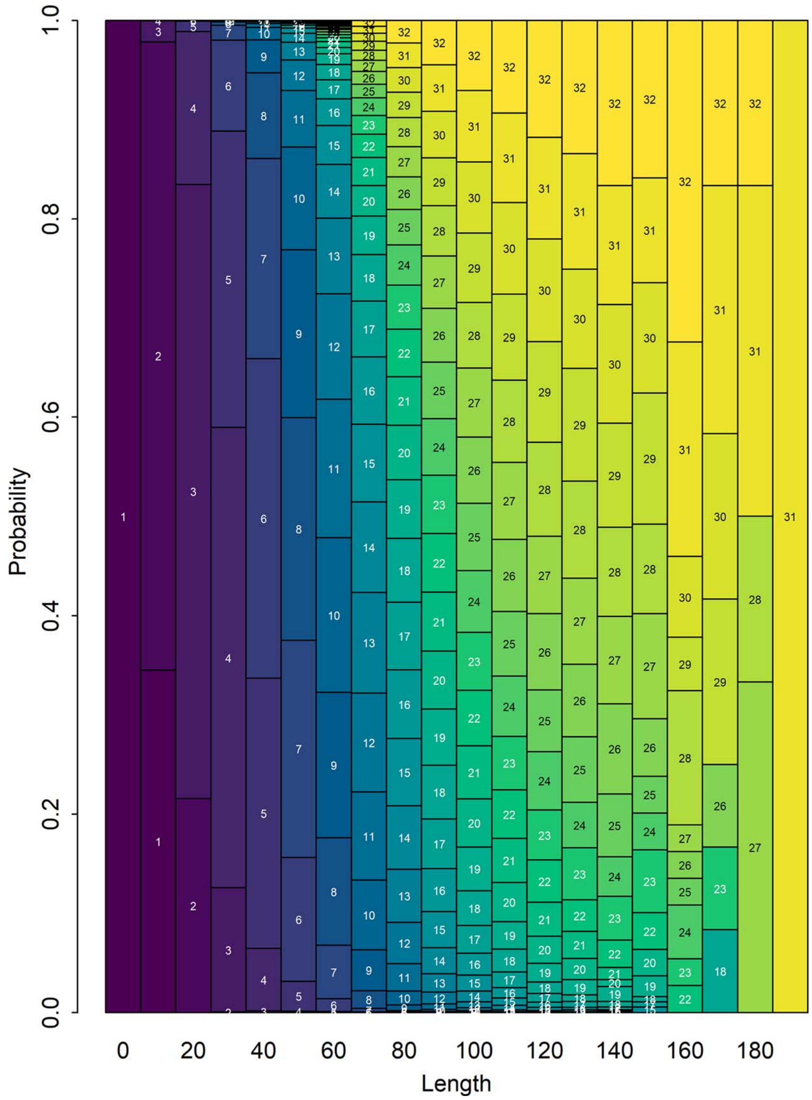

Figure A2. Age-at-length key for Purple Wartyback (*Cyclonaias tuberculata*) from the Thames River developed from von Bertalanffy growth function length-at-age predictions. The x axis represents 10-mm length bins, the y-axis represents age probabilities, and the tiles represent ages (1–32).