

# Turning population viability analysis on its head: using stochastic models to evaluate invasive species control strategies

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**Abstract** Control or eradication of invasive species is costly in terms of finances, labour and ecological and economic impact; the decision of how best to affect eradication or control may have long-term implications and costs. We suggest using population viability analysis (PVA) as a tool to evaluate relative efficacy of different control options for invasive species. PVA explicitly accounts for stochastic events impacting survival of populations at low abundance, which is critically important for representing founder effects of invasive species and appropriately

calculating relative eradication probabilities. We demonstrate how PVA may be used to compare control options for hypothetical invasive populations of smallmouth bass, zebra mussels and northern pike. The model is parameterized using readily available parameters from the literature and provides a time series of population projections with uncertainty, as well as outcomes such as total control cost, probability of eradication and final abundance. Sensitivity analysis demonstrates that the ranking of various control options may change with parameter misspecification, demonstrating the importance of evaluate sensitivity prior to a final decision. When considering the appropriate response to invasive species, there is a trade-off between acting quickly and carefully considering all options using best available knowledge. PVA provides a balance between these two choices by providing a means to compare all control options and perspective values collaboratively with agencies and stakeholders in a way that quickly builds consensus for the most appropriate option(s) and facilitates action.

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Article Impact Statement: We present population viability analysis to accurately compare control options for invasive species in a decision-friendly framework.

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## Introduction

Invasive species extol massive costs to ecological and economic systems worldwide (Mack et al. 2000; Pimentel et al. 2005) demonstrating the need to both contain the spread of these populations and control or

eradicate existing invasive populations. Risk analyses have repeatedly shown the ecological and economic benefits of control or eradication often outweigh costs (Leung et al. 2002; Vander Zanden et al. 2010; though see caution in Manchester and Bullock 2000). The choice of how to control or eradicate an invasive species is a difficult decision that includes factors such as the efficacy versus cost of different methods (Maguire 2004; Buhle et al. 2005) and the potential ecological, economic and social impacts of invasive population growth (Stohlgren and Schnase 2006).

A further consideration is when to begin implementing removal. It may be difficult to communicate the urgency of recently established invasive populations because adverse effects may be largely undetected and difficult to predict, particularly in a novel ecosystem. It is also hard to forecast the potential magnitude of the problem soon after invasion because the carrying capacity is largely unknown, thereby making the potential abundance difficult to communicate (akin to invasion risk; Stohlgren and Schnase 2006). Delaying action will increase time to eradication, and therefore overall program costs, or may mean the difference between eradication and mere population control (Simberloff 2003; Buhle et al. 2005; Strayer 2009). Several authors have shown delaying action against invasive species results in higher abundance and costs associated with control and a diminishing probability of eradication (Simberloff 2003).

Population viability analyses (PVA) are commonly used in evaluating recovery of species at risk of extirpation (Beissinger 2002). These models explicitly consider stochastic events impacting survival of various life stages for populations at low numbers (the “small population paradigm; Caughley 1994). PVA models are often used to predict future population size and structure, extinction probability and response to management actions (Coulson et al. 2001). While PVA models have come under scrutiny in recent years (reviewed in Beissinger 2002; Reed et al. 2002), it is generally accepted that they are useful in evaluating the relative strength of support for various management actions (Reed et al. 2002). These same considerations are important when considering invasive species control options: stochastic processes affect the probability of invasive species establishment and eradication, especially if early detection is possible (Mack et al. 2000); and predicting the exact

fate of the population is less important than the action that is most likely to produce desired results. PVA may have utility as a mechanistic driver for decision support tools around strategies for controlling invasive species. Specifically, PVA models may be useful in determining which management actions or level of removal effort will improve probability of eradication.

Our objective is to demonstrate how a PVA model might be used to evaluate a variety of control strategies for invasive species and how it can be embedded at the core of any multicriteria decision analysis. We adapt a previously published age-structured PVA (Pine et al. 2013) and adapt it to evaluate control methods for both recent and established populations of invasive species. We show how such a model can be used to evaluate a number of important performance criteria and how this can be communicated to decision makers. Finally, we demonstrate application on three case studies: smallmouth bass (*Micropterus dolomieu*), zebra mussel (*Dreissena polymorpha*) and northern pike (*Esox lucius*).

## Methods

### Population viability analysis model

The adopted population viability analysis model is based on the individual-based age-structured model described in Pine et al. (2013), which assumes density dependent survival in early (pre-recruit) stages, followed by density-independent, length-based survival thereafter. The pre-recruit phase is divided into  $n_s$  stanzas, each with its own functional response (i.e. used to define various ontogenetic stages such as eggs or settling larvae). Animals in each stanza may be affected by targeted removals (e.g. targeting eggs, larvae). Recruited animals are age-structured and may be affected by any number of general capture methods such as traps, hunting or fishing. The selectivity of each gear used on recruited animals may be size-structured and defined using parametric equations. Survival of all individuals results from a Bernoulli process (i.e. an individual lives or dies in the next time step) where expected probability of survival is based on natural mortality and mortality due to any removal process on that stanza or age-class. The model is repeated  $n_{sim}$  times and the proportion of simulations with no animals remaining at the end of  $T$  years defines

the eradication probability. All indices, controls, parameters and derived variables are listed in Table 1. We implement the model in R (R Core Development Team 2016) with parameters called from *csv* files. For convenience, we provide the code and parameters as an example of how to implement this model (<https://a100.gov.bc.ca/pub/acat/public/viewReport.do?reportId=53038>).

The model begins by establishing stock-recruitment parameters from calculations of equilibrium population structure at carrying capacity. Length- (T2.1), weight- (T2.2) and fecundity-at-age (T2.3) are first calculated. Instantaneous mortality of recruited animals is assumed to be inversely related to length, following the Lorenzen (2000) model. Asymptotic mortality (the minimum adult mortality rate) rate is calculated from *A*, the age at which survivorship is 1%. Back-calculation of asymptotic mortality ( $M_\infty$ ) from *A* proceeds similar to the method of Hoenig (1983; T2.4). Survival in each time-step follows Lorenzen (2000; T2.5), which is used to calculate survivorship (T2.6) to each age. The product of survivorship and fecundity-at-age for females provides equilibrium spawners per recruit (T2.7), which is used to calculate Beverton–Holt recruitment parameters (i.e. density dependent juvenile survival; Walters and Martell 2004; T2.8–T2.9).

Beverton–Holt parameters are modified by relative mortality and habitat capacity for each pre-recruit stanza (T2.10–T2.11) to give stanza-specific Beverton–Holt recruitment parameters (which scale mortality by density of competitors within a cohort; Pine et al. 2013). If cannibalism is thought to occur in pre-recruit stanzas (i.e.  $p_{cann} > 0$ ), the maximum survival of each stanza can be modified as a log-linear relationship with cannibal abundance (where cannibalistic ages are specified by the user; T2.12–13). This formulation is based on the reformulation of the Beverton–Holt model of the form (Walters and Korman 1999)

$$R = \frac{N_0 e^{-M_0}}{1 + \frac{M_1}{M_0} (1 - e^{-M_0}) N_0} \tag{1}$$

where  $e^{-M_0}$  is maximum survival at low spawning stock and  $\frac{M_1}{M_0} (1 - e^{-M_0})$  is the carrying capacity parameter. In the case of cannibalism,  $M_0$  is modified as a function of likely cannibalistic age-classes:

$$M_0 = \rho + \tau C \tag{2}$$

where  $\rho$  is mortality independent of cannibalism,  $\tau$  is the cannibalism-dependent parameter and  $C$  is the sum of animals in age-classes where cannibalism may occur. This altered formulation results in approximately Ricker-type recruitment (e.g. overcompensation at high spawner abundance; Walters and Martell 2004). In the case of multiple pre-recruit stanzas, this linear model proceeds in the same way with intercept and slope calculated in T2.14–T2.15 (Table 2).

Abundance of recruited animals in the first year is determined in one of two ways. If initial population abundance is close to carrying capacity (i.e.  $V_1 \geq 0.9R_0 \sum l x_a$ ), abundance is randomly allocated among age-classes assuming a multinomial distribution

$$N_{t=1,a} \sim MN(V_1, l x_a e^{\varepsilon_a}); \quad \varepsilon_a \sim N(0, \sigma_R) \tag{3}$$

where random year-class strength is given by  $\varepsilon_a$ . Early simulations identified the 90% carrying capacity as an appropriate threshold above which population structure is relatively unaffected by this approximation. This approximation will under-represent early year-classes if the population is still growing because of the steady-state assumption. Therefore, if initial abundance is below 90% of carrying capacity, initial age-structure is established by deterministically simulating the population from a low abundance (starting with  $R^* = 10^{-15}$  recruits) until the population reaches the current specified abundance ( $V_1$ ). This initialization proceeds by first calculating the abundance of each age-class

$$N_{t,a}^* = N_{t-1,a-1}^* S_{a-1} \tag{4}$$

where  $N^*$  refers to numbers in the initialization. Eggs ( $E_{t,a}^*$ ) in each initial time-step are calculated as the product of female numbers-at-age (assuming equal sex ratio) and fecundity-at-age (T2.3) and recruitment is calculated using the stage-independent Beverton–Holt function

$$N_{t,a=1}^* = \frac{E_{t-1}^* e^{-(\rho+\tau C_t)}}{1 + \frac{e^{-(\rho+\tau C_t)}}{M_1} (1 - e^{-(\rho+\tau C_t)})}, \tag{5}$$

where

**Table 1** Model controls, indices, parameters and derived variables used in PVA\_invas

Symbol	Value			Description
<i>Indices</i>				
$t$	{1, 2, ..., $n_T/dt$ }			Time-step (can be sub-annual if $dt < 1$ )
$a$	{ $A_R/dt, \dots, A/dt$ }			Age from age at recruitment to oldest age-class in $dt$ steps
$i$	{1, 2, ..., $E_i$ }			Individual number
$s$	{1, 2, ..., $n_s$ }			Recruitment stanza
$g$	{1, 2, ..., $n_g$ }			Capture gear for recruited animals
<i>Controls</i>				
	Smallmouth bass	Zebra mussel	Northern pike	
$dt$	0.25	0.10	0.25	Length of time-step (years)
$n_T$	50	20	50	Number of time-steps
$n_s$	2	2	1	Number of stanzas
$A_R$	1	0.1	1	Age-at-recruitment
$n_g$	2	3	3	Number of capture gears for recruited animals
$n_{sim}$	1000	1000	1000	Number of population simulations
$samp_t$	1	0.1; 0.1; 0.1	0.3; 0.3; 0.3	Time-step when each control gear for recruited animals is used
$q_R$	Table 4	Table 5	Table 6	Maximum catchability of each pre-recruit gear (proportion of stanza captured per unit sampling effort at low abundance)
$q_A$	Table 4	Table 5	Table 6	Maximum catchability of each size-selective gear for recruited animals
$t_{start}$	{1; 5}	{1; 5}	1	Time-step when sampling begins (allows for delayed start time)
$E_{f_{R,s}}$	See text	Table 5	Table 6	Sampling effort for stanza- $s$ per time-step for pre-recruit stanzas
$E_{f_{A,g}}$	See text	Table 5	Table 6	Sampling effort for gear- $g$ per time-step for recruited animals
$v_{1,g}$	Table 4	Table 5	Table 6	Proportional to rate of increase of ascending limb of dome-shaped selectivity function
$v_{2,g}$	Table 4	Table 5	Table 6	Proportional to length at 50% selectivity on ascending limb of selectivity function
$v_{3,g}$	Table 4	Table 5	Table 6	Proportional to rate of decline on descending limb of selectivity function ( $0 < v_c < 1$ )
$C_{f,R}$	Table 4	Table 5	Table 6	Annual fixed cost of using each pre-recruit removal gear
$C_{f,A}$	Table 4	Table 5	Table 6	Annual fixed cost of using each post-recruit removal gear
$C_{E,R}$	Table 4	Table 5	Table 6	Cost per unit effort for each pre-recruit removal gear
$C_{E,A}$	Table 4	Table 5	Table 6	Cost per unit effort for each post-recruit removal gear
<i>Model parameters</i>				
$R_0$	U(1000, 2000)	U( $10^4$ , $10^5$ )	U(1000, 5000)	Unexploited recruits
$\kappa$	9.24 <sup>a</sup>	52.78 <sup>b</sup>	6.1 <sup>n</sup>	Compensation ratio in recruitment
$p_{cann}$	0.20 <sup>b</sup>	0.25 <sup>i</sup>	0.5 <sup>o</sup>	proportion of pre-recruit mortality at equilibrium due to cannibalism
$K$	0.15 <sup>c</sup>	0.56 <sup>j</sup>	0.34 <sup>p</sup>	Metabolic rate parameter of von Bertalanffy function
$A$	15 <sup>d</sup>	3 <sup>k</sup>	13 <sup>q</sup>	Maximum age (e.g. probability of survival to age $A = 1\%$ )
$a_f$	6000 <sup>e</sup>	40,000 <sup>l</sup>	6,000 <sup>f</sup>	Fecundity multiplier on weight
$w_m$	0.4 <sup>e</sup>	0.12	0.15	Weight at maturity relative to asymptotic weight
$t_{spn}$	0.75–1.0	0.0–1.0	0.75–1.0	Start and end of spawning time as proportion of year
$M_s^*$	0.05; 0.08	0.8, 0.5	1	Maximum survival for each pre-recruit stage (relative values)
$B_s^*$	10; 9	10, 3	1	Available habitat for each pre-recruit stage (relative values)
$V_1$	2000	1000	107	Initial number of vulnerable animals
$cann_a$	5 <sup>f</sup>	1 <sup>m</sup>	1 <sup>s</sup>	Age at which animals become cannibalistic on pre-recruits (if $p_{cann} > 0$ )
$\beta$	0.5 <sup>g</sup>	0.7	0.253 <sup>t</sup>	Rate at which population area expands (hyperstability parameter)
$\sigma_R$	0.25	0.6	0.4	Standard deviation in recruitment
<i>Derived variables</i>				
$l_a$				Length
$w_a$				Weight
$M_\infty$				Minimum instantaneous mortality
$f_a$				Fecundity

**Table 1** continued

	Smallmouth bass	Zebra mussel	Northern pike
$spn_t$			Time-steps when spawning occurs (0/1 flag)
$spn_a$			Ages when spawning occurs (0/1 flag)
$S_a$			Survival
$v_{a,g}$			Selectivity of gear- $g$
$lx_a$			Survivorship
$\varphi_0$			Unexploited eggs-per-recruit
$\alpha^*$			Maximum survival of Beverton–Holt recruitment function
$\beta^*$			Carrying capacity parameter of Beverton–Holt recruitment function for each stanza- $s$
$\alpha_s^*$			Maximum survival of Beverton–Holt recruitment function
$\beta_s^*$			Carrying capacity parameter of Beverton–Holt recruitment function for each stanza- $s$
$R_t$			Annual recruitment to age- $A_R$
$N_{t,s}$			Population abundance for pre-recruited animals in year- $t$ and stanza- $s$
$N_{t,a}$			Population abundance for recruited animals in year- $t$ and age- $a$
$E_t$			Annual egg production
$C_{t,g}$			Annual catch by gear
$q_N$			Density-dependent catchability
$F_{t,a}$			Instantaneous sampling mortality rate by age-class

Parameter values shown are biological parameters used for the smallmouth bass example

<sup>a</sup>Back-calculated from Ricker recruitment model parameter estimates calculated in Zipkin et al. (2008) using their estimate of constant adult natural mortality of 0.3

<sup>b</sup>Estimated (Schoenebeck and Hansen 2005)

<sup>c</sup>Estimated (Shuter et al. 1987); near median of estimated values in meta-analysis (Beamesderfer and North 1995)

<sup>d</sup>Based on observed catch-at-age distribution (Shuter et al. 1987)

<sup>e</sup>Based on fecundity measurements (Chu 2001)

<sup>f</sup>Based on Clady (1974)

<sup>g</sup>Based on Schoenebeck and Hansen (2005)

<sup>h</sup>Estimated using Beverton–Holt model applied to data presented in Strayer and Malcolm (2006)

<sup>i</sup>Assumed based on Miller and Haynes (1997)

<sup>j</sup>Estimated using Ford-Walford model applied to data presented in Strayer and Malcolm (2006)

<sup>k</sup>Based on Mackie (1993) and Conides et al. (1995)

<sup>l</sup>Based on observed egg mass (Conides et al. 1995)

<sup>m</sup>Based on suggestion by Miller and Haynes (1997) that adults suppress veligers

<sup>n</sup>Estimated (Myers et al. 1999)

<sup>o</sup>Based on observation (Giles et al. 1986)

<sup>p</sup>Estimated (Pierce et al. 2003)

<sup>q</sup>Based on age composition (Millar and Kennedy 1948)

<sup>r</sup>Estimated (Jones 1990)

<sup>s</sup>Based on Giles et al. (1986)

<sup>t</sup>Estimated (Schoenebeck and Hansen 2005)

$$\rho = -\ln(\alpha)(1 - p_{cann}),$$

$$\tau = -\ln(\alpha) \frac{p_{cann}}{R_0 \sum_{a=\{cann_a\}} (lx_a spn_a)}$$

and

$$M^1 = \frac{\beta \ln(\alpha)}{\alpha - 1}.$$

Regardless of how the population is initiated (steady-state approximation or deterministic simulation), egg production in the first year will be given by T2.16.

**Table 2** Functions used to initialize size structure and time-independent variables of the model

T2.1	$l_a = 1 - e^{-Ka}$
T2.2	$w_a = l_a^3$
T2.3	$f_a = a_f(w_a - w_m)$
T2.4	$M_\infty = \frac{\ln(0.01)K}{\ln(l_{a=A_R}) - \ln\left[l_{a=A_R} + e^{K\frac{(A-A_R)}{dt}} - 1\right]}$
T2.5	$S_a = \left(\frac{l_a}{l_a + e^{K\frac{a}{dt}} - 1}\right)^{\frac{M_\infty}{K}}$
T2.6	$lx_a = \begin{cases} 1 & a = A_R \\ \prod_{d=A_R}^{a-1} S_d & a > A_R \end{cases}$
T2.7	$\varphi_0 = \sum_{a=1}^A \frac{lx_a f_a s p n_a}{2}$
T2.8	$\alpha = \frac{K}{\varphi_0}$
T2.9	$\beta = \frac{K-1}{R_0 \varphi_0}$
T2.10	$\alpha_s = \alpha e^{\left(\sum_{s'} M_{s'}\right)}$
T2.11	$\beta_s = \frac{B_s B}{\sum_{s'} (\beta_{s'} \prod_{s''=s'-1}^{s''=s'} \alpha_{s''})}$
T2.12	$M_s^0 = -\ln(\alpha_s) = \rho_s + \tau_s \left[ R_0 \sum_{a=cann_a} (lx_a s p n_a) \right]$
T2.13	$M_s^1 = \frac{\beta_s M_s^0}{1 - \alpha_s}$
T2.14	$\rho_s = M_s^0 (1 - p_{cann})$
T2.15	$\tau_s = M_s^0 \frac{p_{cann}}{R_0 \sum_{a=\{cann_a\}} (lx_a s p n_a)}$
T2.16	$E_{t=1} = \sum_{i=1}^{N_{t=1}} f_a$

Recruitment in subsequent years is based on survival through each pre-recruit stanza. Survival from one stanza to the next is given by the product of focused removals (T3.3) and the stanza-specific stock-recruitment function (T3.1). Survivors from the last pre-recruit stanza become recruited fish ( $N_{t+AR-1,a=AR}$ ).

Survival of each recruited age-class each time-step is given by T3.4.  $E_{t,g}$ , the capture effort applied each time-step by gear- $g$ , is set to zero except for time-steps corresponding with time of year that gear is used, which is specified by the user. Selectivity,  $v_{a,g}$  is given by the three-parameter Thompson (1994) model, which can produce logistic or peaked selectivity with length (T3.7) (Table 3).

Each control gear is described by a density-dependent constant of proportionality (termed

catchability in fisheries literature) that relates catch-per-unit effort to abundance, or equivalently, removal effort to instantaneous removal mortality (Walters and Martell 2004). Catchability may be density dependent for a number of reasons, but a likely mechanism in aquatic invasive species is due to individuals concentrated in high quality habitat as abundance declines, which are then targeted for removal. In this example, the invaded area will increase much slower rate than abundance. Instances where catch rates remain high as abundance drops are referred to as hyperstable; alternatively, hyperstability occurs when catch rates drop faster than abundance. The area occupied by the population is determined by

$$A_N = \gamma N^\beta, \tag{6}$$

where  $\gamma$  is the density-independent rate of increase in the area occupied by the population as the population grows and  $\beta$  is the rate at which population density changes. Catchability is the proportion of area affected by the removal gear

$$q_{N,g} = \frac{\delta_g}{A_N}, \tag{7}$$

where  $\delta_g$  is the area swept by one unit of removal gear- $g$ . These two equations can be combined into the standard equation for hyperstability:

$$q_{N,g} = q_g N^{-\beta}. \tag{8}$$

Equations 6–8 imply that as  $\beta$  increases, invaded area grows more steadily with abundance (Fig. 1). As

**Table 3** Functions used to simulate population dynamics through time

T3.1	$N_{t,s+1} \sim \text{BIN} \left( N_{t,s} + \frac{e^{-F_s - M_{s,t}^0 + \psi_{t,s}}}{1 + \frac{M_{s,t}^0}{M_{s,t}^0} (1 - e^{-M_{s,t}^0})} \right); \quad \psi_{t,s} = N(0, \sigma_R)$
T3.2	$M_{s,t}^0 = \rho_s + \tau_s \sum_{a=\{cann_a\}} (N_{t,a})$
T3.3	$F_s = q_s E f_{R,s}$
T3.4	$N_{t+1,a+1} \sim \text{BIN}(N_{t,a}, e^{-Z_{t,a}})$
T3.5	$Z_{t,a} = M_a + F_{t,a}$
T3.6	$F_{t,a} = \sum_{g=1}^{n_g} q_{N,g} E f_{A,t,g} v_{a,g}$
T3.7	$v_{a,g} = \frac{1}{1 - \gamma_{3,g}} \left( \frac{1 - \gamma_{3,g}}{\gamma_{3,g}} \right)^{\gamma_{3,g}} \frac{\exp(\gamma_{3,g} \gamma_{1,g} [l_a - \gamma_{2,g}])}{1 + \exp(\gamma_{1,g} [l_a - \gamma_{2,g}])}$

invaded area increases, the gear sweeps a progressively smaller proportion of the invaded area, implying catchability declines with abundance.

The  $q_g$  parameter is probability of capture at low abundance. To determine the two unknown parameters  $q_g$  and  $\beta$ , it is best to think about how catch per unit effort would change as the population grows. For example if controlling the population with a single unit of gear- $g$  at population abundances  $N_1 = 50$  and  $N_2 = 200$  were to yield catch rates of  $CPUE_1 = 5$  and  $CPUE_2 = 15$ ,  $\beta$  could be calculated as

$$\beta = 1 - \frac{\ln(5) - \ln(15)}{\ln(50) - \ln(200)} = 0.207. \tag{9}$$

Noting that  $q_{N,g} = \frac{CPUE_g}{N}$ , Eq. 9 can be substituted into Eq. 8 to give  $q_N = 0.225$ .

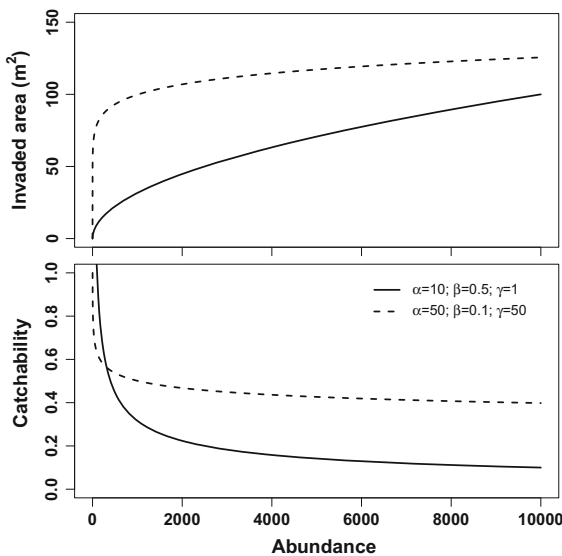
### Multicriteria decision analysis

Multicriteria decision analysis involves combining a series of uncertain information such as projected abundance, costs and risk assessment and evaluating against preferences of several agencies and/or stakeholders in a way that will promote understanding and rational, repeatable decisions. There are a number of methods to quantitatively or qualitatively presenting and comparing multiple criteria for making a decision

(reviewed in Kiker et al. 2005), but each of these requires accurate and reproducible expected outcomes of different management actions. Results from the PVA model form the biological component of a multicriteria decision analysis (Maguire 2004; Kiker et al. 2005). Other objectives leading to a decision on how to react to an invasive species may include cultural, economic, social and ecosystem costs of the removal strategy and/or persistence of the invasive species. The objectives used to make a decision are case-specific and will be developed by stakeholders and experts in each respective field depending on site-specific concerns. We do not include those criteria here; however most or all of these additional multi-disciplinary costs will be based on the control costs, the probability of eradication and the abundance at the end of the control timeframe evaluated for each control option evaluated. We present a matrix of information for consideration by decision makers, which includes annual control costs, expected cost of control from the current day to either 100% eradication or the end of the timeframe considered, probability of eradication, time to 100% eradication as well as final abundance (with 95% quantiles) at the end of control.

### Case study 1: smallmouth bass

Smallmouth bass is a popular pelagic recreationally-fished species, native to east-central North America (Scott and Crossman 1998). Its popularity has led to government sanctioned stocking and unsanctioned transfers (e.g. bait-bucket transfers; Litvak and Mandrak 1993) into much of temperate North America and at least nine other countries around the world (Carey et al. 2011; Loppnow et al. 2013). However, its effect on native fish and invertebrates often outweighs the social benefits. Most attempts to control invasive smallmouth bass have failed either due to difficulty, expense, adverse environmental effects of control measures (e.g. piscicides; Davis et al. 2017) or resistance by local anglers (Tyus and Saunders 2000; Carey et al. 2011; Loppnow et al. 2013). Moreover, population control may also be difficult because populations are purposely established by anglers who ‘hide’ their existence from managers or because decisions are made to remove long-established populations.



**Fig. 1** Invaded area (top panel) and resultant changes in catchability (bottom panel) as abundance of an invading species increases under different assumptions of how invaded area changes with abundance

The PVA model was first determined based on the structure of the pre-recruit stanzas. Relative maximum mortality for eggs (stanza 1) and guarded juveniles (stanza 2) were set to 0.05 and 0.08 and relative available habitat declined from 10 to 9. Density-dependent mortality was limited to the first year of growth. Initial abundance of vulnerable fish was set at 2000 and therefore very close to carrying capacity. Justification for all other parameters is described in Table 1.

Removal options for smallmouth bass evaluated include: nest destruction, targeted at either eggs or young-of-the-year being guarded by male parents; electrofishing juveniles and adults; or angling targeting older juveniles and adults (although several other options have been proposed in Lopppnow et al. 2013). Destroying eggs in nests is assumed to be very effective, with a maximum catchability of 0.6; destroying nests with free-swimming juveniles is somewhat less effective with maximum catchability of 0.5. Angling is assumed to have a maximum catchability of 0.1 and electrofishing is assumed to have a maximum catchability of 0.05. These relative values are consistent with the meta-analysis conducted by Lopppnow et al. (2013). Note that actual catchability values are only important if exact prescriptions for removal effort are important. In our decision matrix, we consider every combination of these removal options. It was assumed that each removal option was equally time-consuming, so in each scenario, 12 units of effort were available and divided equally among the options being evaluated (e.g. if nest destruction at egg stage, electrofishing and angling were being used together, each would get four units of effort). We further evaluate how final abundance after 50 years of removal and time to eradication will change if removal is immediately initiated (assuming an initial abundance of 2000 fish) or if removal is delayed by 5 years. Catchability and selectivity parameters, as well as fixed and effort-based costs for each option are shown in Table 4.

#### Case study 2: zebra mussel

Zebra mussels were initially introduced to North America in 1986 from ballast water released into St. Clair River in the mid-1980s (Hebert et al. 1989; Roberts 1990), whereupon the species quickly invaded most of the Laurentian Great Lakes (Griffiths et al.

1991). It has since invaded much of eastern North America, with additional isolated invasions in several watersheds in western states and provinces (United States Geological Survey 2017). Zebra mussels rapidly disperse within watersheds as free-swimming veligers are carried downstream (Bodamer and Bossenbroek 2008) or can disperse upstream when settled juveniles and adults are attached to boats (Johnson and Padilla 1996). Zebra mussels experience rapid population growth and are very difficult to eradicate once established. Their establishment often results in extensive economic impacts as they clog intake pipes of industrial facilities (Leung et al. 2002). Their high filtration rate and transference of nutrients from pelagic to benthic pathways results in a reorganization of freshwater communities and food webs (Miehls et al. 2009).

We evaluated a hypothetical invasion scenario for zebra mussels. Equilibrium number of zebra mussel recruits was assumed uniformly distributed between 10,000 and 100,000 mussels. Weight at maturity was assumed to be 12% of asymptotic weight and cannibalism was assumed to start at age-1. The hyperstability parameter was presumed to be 0.7 by suggesting manual catch rates would increase from 100 to 200 mussels if total abundance increased from 150 to 1500. Finally, to parameterize the multi-stanza recruitment function, it was assumed that relative maximum mortality for veligers (stanza 1) and recently settled juveniles declined from 0.8 to 0.5, whereas available habitat for the two stanzas decreased from 1000 to 300 based on potential limitations in settling habitat. These parameters represent hypotheses that might be proposed by experts; all other parameter justification is provided in Table 1.

Removal options for zebra mussels are generally classed as manual removal, oxygen deprivation, physical removal or chemical treatment. Manual removal involves physical removal using hand tools and can be augmented using suction or hydroblasting. These options involve divers coming into physical contact with mussels to effectively control the population. Oxygen deprivation is accomplished by laying tarps over attached mussel beds; also accomplished using divers. Physical methods can include thermal shock, freezing or desiccation and are limited to situations where these methods may be employed (e.g. artificial ponds, reservoirs or water and power facilities). Chemical options involve application of one of a



**Table 4** Catchability, selectivity and costs associated with smallmouth bass control scenarios. Costs are hypothetical

	Catchability			Selectivity parameters			Fixed costs (\$)		Variable costs (\$)	
	Eggs	Juveniles	Recruited fish	$v_a$	$v_b$	$v_c$	Pre-recruits	Recruited fish	Pre-recruits	Recruited fish
Nest destruction (eggs)	0.60	0.00	0.00				2000	0	1000	0
Nest destruction (juveniles)	0.00	0.50	0.00				2000	0	1000	0
Electrofishing	0.00	0.00	0.10	15	0.5	0.5	0	2000	0	1000
Angling	0.00	0.00	0.05	25	0.7	0	0	2000	0	1000

suite of chemicals to affect the biology of veligers and/or attached subadults and adults. Some chemicals are used only in facilities because of their known effects on other ecosystem components, but others are considered for natural systems.

In our decision analysis of how to control or eradicate zebra mussels, we consider various combinations of manual removal, tarping to induce oxygen deprivation and a chemical removal option. We assume zebra mussels have been detected at an early stage of invasion, i.e. initial abundance of 1000 individuals. This reflects extremely early detection (e.g. Nalepa et al. 1995), but this is increasingly realistic with monitoring programs and increasingly sensitive water testing techniques (e.g. Egan et al. 2013). We explore the following removal options: chemical removal which equally targets veligers, recently settled juveniles and older mussels; manual removal which targets settled juveniles and older mussels, where selectivity increases with size; tarping, which targets settled juveniles and older mussels equally; and a combination of manual removal and tarping. Each removal strategy is also evaluated assuming removal is initiated or after a 5-year delay, which may help communicate the importance of action or even regular monitoring to detect invasions. All options are repeated 10 times per year (once per time-step). Catchability and selectivity parameters, as well as effort, fixed and effort-based costs for each removal option are listed in Table 5.

### Case study 3: northern pike

Northern pike are a large-bodied piscivores often found in shallow habitats with ample vegetative cover

(Scott and Crossman 1998). Their distribution is circumpolar around the northern hemisphere and occur across North America, but are absent from the Fraser and Columbia watersheds (Scott and Crossman 1998; McPhail 2007). Due to their popularity among anglers, northern pike have been intentionally introduced beyond their native range by management agencies, including into the upper Columbia River drainage at Coeur d'Alene Lake (Rich 1993; McMahon and Bennett 1996). Illegal stocking has also occurred in other areas, such as the Flathead River, Montana (Muhlfeld et al. 2008). Within the upper Columbia River, northern pike have now extended their range to the transboundary reach, near the confluence of the Columbia and Pend d'Oreille rivers. Northern pike can reach > 25 cm by their first year and can consume prey as large as 75% their length (McPhail 2007); as such, they are targeted for removal by government agencies in both Canada and the United States, as they pose a risk to federally listed fish species (including many salmon species, *Oncorhynchus* spp. and white sturgeon, *Acipenser transmontanus*).

Northern pike removal strategies were evaluated using the PVA model. The model assumes a single pre-recruit stanza which lasts to age-1, so relative maximum mortality and available habitat were both set to 1.0 (Table 1). The model was run for 50 years with four time-steps per year.

Pike suppression in the Columbia River system began in 2014 in Canada (Baxter and Doutaz 2017) and in Washington State in 2015 (Lee and King 2015). Various methods have been used in recent years to capture and contain northern pike in both federal jurisdictions (reviewed in Amec Foster Wheeler

**Table 5** Catchability, selectivity, removal effort and costs associated with zebra mussel control scenarios. Costs are hypothetical

	Catchability			Selectivity parameters			Removal effort		Fixed costs (\$)		Variable costs (\$)	
	Veligers	Juveniles	Recruited mussels	$v_a$	$v_b$	$v_c$	Pre-recruits	Recruited mussels	Pre-recruits	Recruited mussels	Pre-recruits	Recruited mussels
Chemical	0.95	0.95	0.95	10	-1	0.01	1	1	0	20,000	0	10,000
Manual	0.00	0.25	0.50	15	0.01	0	1	1	0	5000	0	2000
Tarping	0.00	0.95	0.50	10	-2	0	1	1	0	5000	0	5000

Environment and Infrastructure 2017), including gill net suppression, capture in index electrofishing and angling reward programs. These efforts have included mark-recapture estimates from 2015 to 2017 and provided relative catch rates for the different methods within the Canadian reach. For simplicity, we use these estimates of catch rates and abundance reported in Baxter and Doutaz (2017) and Amec Foster Wheeler Environment and Infrastructure (2017; Table 6) to calculate catchability for the three gears. Annual gill netting currently involves approximately 10 days of netting with each day of netting representing 14 nets set per day. Electrofishing effort was assumed to be the same as currently, so relative effort was set to 1.0. Angling removal in the Columbia system is actually a public removal program where anglers who return pike heads are entered into a draw for \$2000 CAD in prizes. Angling was assumed to proceed with an effort of 1.0 relative to current rates. We consider every combination of these removal options, starting immediately. Additionally, we evaluate an enhanced suite of removal options where the effort for each gear is three times the current rate (Table 6).

### Sensitivity analysis

Decisions on how to control invasive species are partially dependent on rankings of relative cost, probability of eradication and final abundance of each control option. To explore sensitivity of control option decisions to parameter uncertainty, the relative rank all control options within each metric (e.g. cost, eradication probability) was explored when each biological parameter was increased by 10%. If the relative rank of each metric does not change with a

change in parameters, especially for top-ranked control options, the decision process is relatively insensitive to misspecification of that parameter (Peterman and Anderson 1999).

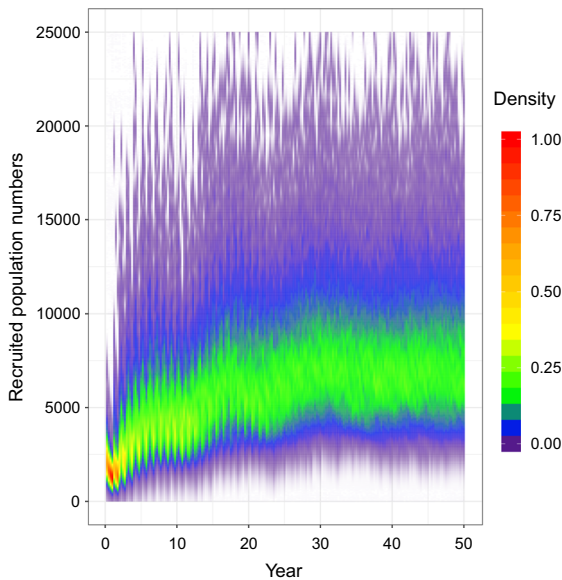
### Results

The smallmouth bass population was near carrying capacity, so only increased over the first 6 years if no removal strategies were in place and then demonstrated boom and bust population growth with a periodicity of approximately 11 years due to a progressive increase in cannibalism as abundance increased (Fig. 2). Of the 1000 simulations performed, none were randomly extirpated due to stochastic variation.

Smallmouth bass eradication was possible with some removal strategies, partially because of the high effort put into removal each year (Fig. 3). However, different strategies required different amounts of time before eradication was guaranteed. Destroying nests with eggs or juveniles was generally the best method for control and eradication and led to lower overall cost because these methods and their costs stopped once the population was eradicated. Any strategy involving egg removal as an option led to high probability of eradication, but sole use of either method involving nest destruction (e.g. targeted egg removal or juvenile removal) was the best means to achieve eradication in less than 50 years. Delaying initiation of smallmouth bass control by 5 years usually resulted in an increase in the time necessary to eradicate the population. Since the initial population was already near the carrying capacity, delaying control for 5 years usually meant a 5-year extension

**Table 6** Catchability, selectivity, removal effort and costs associated with northern pike control scenarios. Costs are hypothetical

	Catchability	Selectivity parameters			Removal effort	Fixed costs (\$)	Variable costs (\$)
		$v_a$	$v_b$	$v_c$			
Gill netting	0.165	15	0.3	0	{10, 30}	2000	1000
Electrofishing	0.02	15	0.2	0.3	{20, 60}	2000	2000
Angling	0.05	25	0.5	0	{1, 3}	2000	0



**Fig. 2** Distribution of population trajectories for an invasive smallmouth bass population increasing from 2000 individuals over 50 years. Hotter colours indicate a higher density of simulations coincided with a particular population abundance at a particular time. Distribution is the result of 1000 simulations run with no removal strategies being implemented

until the time to eradication. For control measures that did not lead to eradication, delay resulted in no real difference in final abundance (Fig. 3).

The zebra mussel population also increased slowly over the first 2 years for most trajectories even when no removal strategies were in place (Fig. 4). However, the population quickly increased thereafter, showing boom-bust population cycles as in the smallmouth bass due to cannibalism at high population densities. The population reached carrying capacity within the first 4 years, though the exact magnitude of population abundance was uncertain from the simulation because  $R_0$  was set with such a wide range, reflecting uncertainty in the magnitude of the zebra mussel

impact. Of the 1000 simulations performed, 0.2% resulted in eradication within the first 5 years due to random stochastic events when the population was at low abundance, though no more simulations declined to zero thereafter.

No removal strategies could guarantee eradication of zebra mussels (Fig. 5); however all had some effect on the final abundance. Immediate chemical treatment had the high impact on final abundance and had the lowest cost; eight percent of simulations resulted in eradication after 20 years. Manual removal paired with tarping had a similar impact on final abundance, also with an eight percent probability of eradication, but the cost was nearly five times that of chemical removal. Delay by 5 years generally did not improve the likelihood of eradication over doing nothing, but as equally effective at controlling abundance.

The northern pike remained relatively stable for the first 2 years, but increased quickly thereafter (Fig. 6). The population reached carrying capacity after approximately 10 years, but predicted annual abundance varied from approximately 2000 to more than 20,000. None of the pike scenarios randomly declined to extinction in the absence of control efforts.

None of the ongoing efforts aimed at controlling northern pike are likely to lead to eradication of the species from the upper Columbia River and differences in abundance after 50 years were minor (Fig. 7). Increasing the amount of control to three times the current level led to a probability of eradication of approximately 30% in scenarios where gill netting and electrofishing were used together as a control strategy. The most inexpensive strategy among relatively successful enhanced options was to use all methods simultaneously, primarily because it had the lowest expected time to eradication.

Metrics of success for different control options could be sensitive to parameter inputs in certain cases.

	Annual cost (\$)	Expected cost (\$)	Probability of eradication	Expected time to eradication	Median abundance (95% quantiles)
<i>No action</i>	0	0	0.00	50 (50, 50+)	7345.5 (3968.2, 14361.6)
<i>Immediate egg removal</i>	14,000	319,841.5	1.00	23 (15, 38)	0 (0, 0)
<i>Immediate juvenile removal</i>	14,000	359,122.8	1.00	26 (17, 40)	0 (0, 0)
<i>Immediate angling</i>	14,000	700,700	0.00	50 (50, 50+)	7288 (4050, 14374.4)
<i>Immediate electrofishing</i>	14,000	700,700	0.00	50 (50, 50+)	7318 (3940.3, 14372.4)
<i>Immediate egg and juvenile removal</i>	16,000	396,748.4	1.00	25 (16, 42)	0 (0, 0)
<i>Immediate egg removal and angling</i>	16,000	669,260.6	0.90	42 (25, 50+)	0 (0, 6)
<i>Immediate egg removal and electrofishing</i>	16,000	709,781.1	0.76	44 (29, 50+)	0 (0, 22)
<i>Immediate juvenile removal and angling</i>	16,000	769,136.4	0.40	48 (30, 50+)	2 (0, 101)
<i>Immediate juvenile removal and electrofishing</i>	16,000	786,898.1	0.21	49 (34, 50+)	10 (0, 133.1)
<i>Immediate angling and electrofishing</i>	16,000	800,800	0.00	50 (50, 50+)	7330.5 (4041.8, 14324.6)
<i>Immediate all options</i>	20,000	939,138.2	0.51	47 (29, 50+)	0 (0, 67)
<i>Delay egg removal</i>	14,000	338,255.9	1.00	29 (20, 45)	0 (0, 0)
<i>Delay juvenile removal</i>	14,000	374,454.1	1.00	32 (23, 50+)	0 (0, 0)
<i>Delay angling</i>	14,000	630,630	0.00	50 (50, 50+)	7327.5 (3793.2, 14230.3)
<i>Delay electrofishing</i>	14,000	630,630	0.00	50 (50, 50+)	7334 (4012.9, 14453.2)
<i>Delay egg and juvenile removal</i>	16,000	419,154.7	1.00	31 (22, 48)	0 (0, 0)
<i>Delay egg removal and angling</i>	16,000	684,684	0.50	48 (33, 50+)	1 (0, 28)
<i>Delay egg removal and electrofishing</i>	16,000	699,146.4	0.34	49 (35, 50+)	2 (0, 36)
<i>Delay juvenile removal and angling</i>	16,000	716,171.5	0.10	50 (40, 50+)	22 (0, 154.2)
<i>Delay juvenile removal and electrofishing</i>	16,000	718,702	0.04	50 (41, 50+)	32.5 (0, 176)
<i>Delay angling and electrofishing</i>	16,000	720,720	0.00	50 (50, 50+)	7275 (4054.7, 14247.9)
<i>Delay all options</i>	20,000	891,210.3	0.16	50 (39, 50+)	12 (0, 98)

**Fig. 3** Model output across control options for smallmouth bass. Decisions considered are whether to initiate removal, which (of 10 combinations) removal options to conduct and whether to begin removal immediately or delay for 5 years.

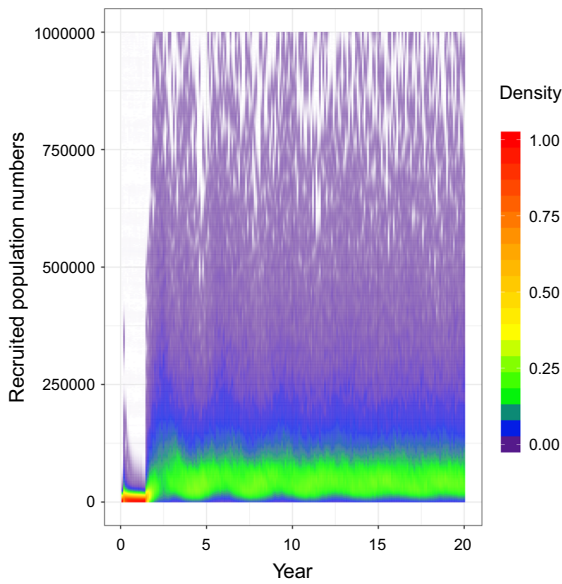
For example, the top-ranked control option for zebra mussels when considering probability of eradication and abundance was only sensitive to natural mortality (as indicated by maximum age), weight at maturity and initial abundance (Figures S1, S2). Conversely, the most inexpensive control option, immediate chemical removal, had a considerable decline in rank with a 10% increase in any population parameter (Figure S3). Sensitivity of rankings among smallmouth bass control options was different because many options led to eradication. Increasing parameters by 10% had little effect on most top-ranked options when considering median final abundance because most still resulted in at least 50% eradication probability (Figure S4). Similarly, most of the most highly ranked control options with respect to cost and probability of eradication were insensitive to parameter uncertainty (Figures S5, S6). Control options that

Each scenario output is the result of 1000 simulations. Expected cost is calculated as mean control cost until eradication; expected time to eradication is the mean years to eradication across all simulations, with range in brackets

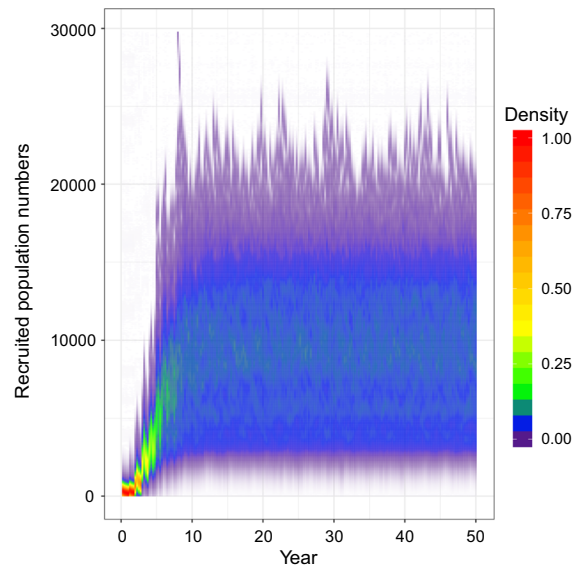
led to the lowest final abundance for northern pike were relatively stable, although parameters linked to productivity ( $\kappa, p_{cann}$ , von Bertalanffy  $K, A, a_f$ ) did cause rank to change for some control options (Figure S7). Probability of eradication was also sensitive to many of these parameters (Figure S8), though the best option (enhanced sampling using all gears) was only affected by  $K$ . The least expensive control options for northern pike were again sensitive to uncertainty in all parameters (Figure S9).

## Discussion

Soon after colonization, invasive species populations are at low abundance and particularly sensitive to stochastic events, which dictate whether each individual survives or does not. This partially explains why



**Fig. 4** Distribution of population trajectories for an invasive zebra mussel population increasing from 1000 individuals over 20 years. Hotter colours indicate a higher density of simulations coincided with a particular population abundance at a particular time. Distribution is the result of 1000 simulations run with no removal strategies being implemented



**Fig. 6** Distribution of population trajectories for an invasive northern pike population increasing from 107 individuals over 50 years. Hotter colours indicate a higher density of simulations coincided with a particular population abundance at a particular time. Distribution is the result of 1000 simulations run with no removal strategies being implemented

many intentional and unintentional introductions fail to establish (Kowarik 1995; Kolar and Lodge 2002). Our use of population viability analysis to evaluate invasive species control options supports the assertion by many authors that early action is imperative to rapid eradication because populations at low levels already have a high likelihood of dying out

(Simberloff 2003). For example, when zebra mussels were initially detected with 1000 individuals, 0.3% of simulations went extinct with no intervention due simply to demographic stochasticity. Detecting zebra mussels when abundance is only 100 individuals leads to a 98% probability of naturally dying out (results not shown); however detection at such a low abundance is

	Annual cost (\$)	Expected cost (\$)	Probability of eradication	Expected time to eradication	Median abundance (95% quantiles)
<i>No action</i>	0	0	0.00	20 (1, 20+)	72047.5 (12884.5, 448136)
<i>Immediate chemical removal</i>	70,000	1,305,895	0.08	19 (1, 20+)	28923.5 (0, 123380.6)
<i>Immediate manual removal</i>	1e+05	1,998,296	0.00	20 (1, 20+)	63385.5 (10842.7, 319965.8)
<i>Immediate tarping</i>	150,000	2,981,979	0.01	20 (1, 20+)	48714 (9087.4, 233741)
<i>Immediate manual and tarping</i>	340,000	6,339,513	0.08	19 (1, 20+)	29421 (0, 119028.8)
<i>Delay chemical removal</i>	70,000	1,050,349	0.00	20 (2, 20+)	29701.5 (6623.3, 129088.9)
<i>Delay manual removal</i>	1e+05	1,500,499	0.00	20 (2, 20+)	65707 (11617, 312646.7)
<i>Delay tarping</i>	150,000	2,250,899	0.00	20 (1, 20+)	49092 (10717.5, 210835.6)
<i>Delay manual and tarping</i>	340,000	5,102,037	0.00	20 (1, 20+)	29546.5 (5792.2, 120865.1)

**Fig. 5** Model output across control options for zebra mussel. Decisions considered are whether to initiate removal, which (of four combinations) removal options to conduct and whether to begin removal immediately or delay for 5 years. Each scenario

output is the result of 1000 simulations. Expected cost is calculated as mean control costs until eradication; expected time to eradication is the mean years to eradication across all simulations, with range in brackets

	Annual cost (\$)	Expected cost (\$)	Probability of eradication	Expected time to eradication	Median abundance (95% quantiles)
<i>No action</i>	0	0	0.00	50 (50, 50+)	9041 (3212.8, 16508.3)
<i>Ongoing gill net</i>	12,000	600,600	0.00	50 (50, 50+)	7751 (2733.8, 16275.6)
<i>Ongoing electrofishing</i>	42,000	2,102,100	0.00	50 (50, 50+)	8957.5 (3330.1, 16265.8)
<i>Ongoing angling</i>	2,000	100,100	0.00	50 (50, 50+)	9053.5 (3218, 15927.8)
<i>Ongoing gill netting and electrofishing</i>	54,000	2,702,700	0.00	50 (50, 50+)	7930 (2594.1, 16208.5)
<i>Ongoing gill netting and angling</i>	14,000	700,700	0.00	50 (50, 50+)	7981.5 (2670.9, 16727.7)
<i>Ongoing electrofishing and angling</i>	44,000	2,202,200	0.00	50 (50, 50+)	8999.5 (3213.5, 16447.9)
<i>Ongoing all</i>	56,000	2,802,800	0.00	50 (50, 50+)	7926.5 (2540.8, 16899.8)
<i>Enhanced gill net</i>	32,000	1,585,264	0.02	49 (9, 50+)	5886.5 (1148.5, 17371.7)
<i>Enhanced electrofishing</i>	122,000	6,106,100	0.00	50 (50, 50+)	8691.5 (3127.7, 16508)
<i>Enhanced angling</i>	2,000	100,100	0.00	50 (50, 50+)	8949.5 (3191.7, 16239.8)
<i>Enhanced gill netting and electrofishing</i>	154,000	6,241,695	0.30	40 (7, 50+)	4149.5 (0, 16494.8)
<i>Enhanced gill netting and angling</i>	34,000	1,681,484	0.02	49 (10, 50+)	5773 (1096.2, 17501.9)
<i>Enhanced electrofishing and angling</i>	124,000	6,206,200	0.00	50 (50, 50+)	8800.5 (3085.5, 16411.3)
<i>Enhanced all</i>	156,000	6,029,808	0.34	39 (7, 50+)	3453.5 (0, 16538.8)

**Fig. 7** Model output across control options for northern pike. Decisions considered are whether to initiate removal, which (of seven combinations) removal options to conduct and whether to begin removal immediately or delay for 5 years. Each scenario

unlikely without frequent monitoring. While our demographic model is a simple representation of how propagule pressure (the joint effect of the number of individuals in an invasion, quality of the individuals and the number of invasion events) will influence probability of successful invasion (Allendorf and Lundquist 2003), it likely represents the critical early stages of invasion better than most deterministic models.

It is important to recognize that several species-specific parameters will not accurately represent any particular invasive population. One of the reasons that the impact of invasive species is unknown is due to the myriad ways in which a species may interact with a novel environment (Parker et al. 2013). While population viability analysis may be used to show how to quickly evaluate and compare various management responses to non-native species with little biological knowledge, the recommended action will only be as good as the parameters provided. As controls and monitoring are initiated, knowledge regarding the invasive population and its response to control will accumulate. Models such as that presented here should be continuously used as information accumulates with updated parameters and controls to verify the most

output is the result of 1000 simulations. Expected cost is calculated as mean control cost until eradication; expected time to eradication is the mean years to eradication across all simulations, with range in brackets

appropriate course of action, as we have shown with northern pike in the transboundary reach of the Columbia River. This ‘learning by doing’ approach harkens to the original intent of passive adaptive management (Walters 1986) and will improve success of invasive species control (Simberloff 2003).

It is important to note that the model and framework we outline here is not only useful for rapid response to new invasions. Some populations may be too large or habitat too degraded for any meaningful expectation of eradication and therefore, it will be unnecessary to use a PVA because the stochastic eradication probability at low abundance is irrelevant. Moreover, many invasions, especially for small or cryptic species are not detected until they are relatively well established (Crooks and Soule 1999), and the likelihood of stochastic events leading to failure is low. If the decision being addressed is only to evaluate different methods of control, a simpler demographic model may be sufficient (e.g. Govindarajulu et al. 2005). However, although a PVA may not be necessary in this situation, using the model presented here is perfectly reasonable to address already established invasive populations, especially if it is embedded within a decision analysis framework (Maguire 2004). There

are certainly situations where values change over time and it becomes politically or socially preferable to consider control of a well-established population. Alternatively, there may be populations that have undergone control measures for years and decision makers would like to consider other control options. As we demonstrate with our smallmouth bass case study, it is possible to make meaningful decisions regarding control or eradication measures for established populations. Using a framework like that recommended here will provide information on impacts of various control measures on biological and economic outcomes of importance, which are useful in making a decision on control (Benke et al. 2011). The strength in a process such as that described here is the use of a decision analysis to use model predictions to drive informed decisions.

The single largest limitation of our method is it simulates a closed population, which may not be true in any particular situation. For example, the northern pike population in the Canadian transboundary stretch of the Columbia River is likely to continuously receive immigrants from either the Coeur d'Alene River or downstream sections of the Columbia River. Separation of local recruitment and immigration will obviously influence success of control options (Norman and Whitlege 2015). However, this could easily be accommodated by either considering the entire invaded area or by modifying the model to simulate continuous immigration into the habitat. Conversely, in situations where movement within an open system are relatively restricted (e.g. Coggins et al. 2011; Bair et al. 2018), a framework such as that presented here would still be effective at evaluating various control options.

The decision on how to address establishment of an invasive species will involve many criteria such as the net environmental and economic benefits, regulatory hurdles associated with some treatment methods (e.g. pesticides), and stakeholder input (Benke et al. 2011). As such, measuring the impact of different decisions on these various criteria will be based on other disciplines. We chose to not present a complete decision analysis incorporating all possible objectives because we strongly feel the choice of objectives and measures will be case-specific and determined by stakeholders invested in the decision (Maguire 2004). The process of building a common understanding of the necessary objectives across all stakeholders and

agencies is arguably one of the most important elements of successful invasive species management (Estevez et al. 2014). The abundance, cost of control and probability of eradication are some of the objectives to consider in this context, but ecological, social and ecosystem-level objectives will be (at least partially) based on these elements. Once all objectives and measures are in place, it will be important to use a carefully considered multicriteria decision analysis to determine how to proceed (Kiker et al. 2005).

Simberloff (2003) stressed the importance of rapid action following detection of invasive species. He points out that the precautionary principal should apply, meaning you should not wait for good population biology before attempting eradication measures. Simberloff instead advocates a “learn while you go” approach: try to eradicate the focal species and learn about the biology as you do so. Others point to the associated problems with potentially ill-advised removal strategies, such as biological control (Messing and Wright 2006) or damage to co-occurring species (Manchester and Bullock 2000; Rinella et al. 2009). While we have shown the impacts of delayed action on final abundance and potential time to eradication, the improved information and parameter estimates that may be obtained if action is delayed were not considered. In that way, we agree with Simberloff (2003) that somewhat inaccurate parameter estimates are not sufficient justification for delaying removals. The approach advocated here represents a middle-ground: basic population parameters obtained from existing literature or ongoing monitoring can be used to quickly evaluate various removal strategies to determine the best strategy. As removal proceeds, outcomes can be revisited in light of improved parameter estimates, as advocated by Simberloff (2003). This is relevant both for recent invasions and for well-established populations. Our results have shown the decision on how to act is relatively insensitive to parameter misspecification, because relative differences in final abundance are consistent, even when absolute values are stochastic. We further emphasize evaluating removal strategies with relevant stakeholders in a setting that allows all viewpoints and values to be heard and considered. Careful communication in a structured decision-making workshop has been shown the most effective means of reaching consensus and avoiding short- and long-term conflict (Estevez et al. 2014).

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