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Recovery target and long-term projections for the Black Redhorse (*Moxostoma duquesnei*)

Cible de rétablissement et projections à long terme pour le chevalier noir (*Moxostoma duquesnei*)

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ABSTRACT

In 2005, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed the Black Redhorse (*Moxostoma duquesnei*) as Threatened in Canada. Here we build on previous population modelling aimed at assessing allowable harm to present abundance recovery targets and long-term projections in support of a recovery potential assessment (RPA). Based on a demographic sustainability objective (i.e., the population is self-sustaining over the long term), we propose abundance recovery targets of 8 049 adult Black Redhorse per population, which will require up to 621 544 m^2 of adult habitat per population. Current population abundances are unknown, so long-term projections were generated from an initial population size 10% of the target. These projections show that 8 049 adults is an attainable target and that adult population structure is expected to have a low influence in the recovery timeframes. Our analyses indicate that the best way to reduce the uncertainty in population responses to recovery is to aim for a proactive recovery strategy, targeting several vital rates simultaneously.

RÉSUMÉ

En 2005, le Comité sur la situation des espèces en péril au Canada (COSEPAC) a désigné le chevalier noir (*Moxostoma duquesnei*) en tant qu'espèce menacée au Canada. Dans le présent document, nous nous inspirons de la modélisation de la population antérieure qui était destinée à évaluer les dommages admissibles pour établir des cibles de rétablissement de l'abondance de l'espèce et des projections à long terme à l'appui d'une évaluation du potentiel de rétablissement (EPR). D'après un objectif de durabilité démographique (c.-à-d. une population autonome à long terme), nous proposons des cibles d'abondance de 8049 adultes par population de chevalier noir, lesquelles auront chacune besoin d'une superficie d'habitat atteignant 621 544 m^2. L'abondance des populations actuelles est inconnue, c'est pourquoi des projections à long terme ont été produites en fonction d'un effectif initial correspondant à 10 % de la cible. Ces projections démontrent que l'objectif de 8049 adultes représente une cible possible et que la structure des populations d'adultes devrait avoir une faible incidence sur l'échéancier du rétablissement. Nos analyses indiquent que la meilleure manière de réduire l'incertitude quant au rétablissement des populations est de mettre l'accent sur un programme de rétablissement proactif axé simultanément sur plusieurs cycles vitaux.

INTRODUCTION

The present study constitutes an extension to the work of Vélez-Espino and Koops (2007a) in which a demographic approach to determine allowable harm in freshwater species at risk was applied to Black Redhorse (*Moxostoma duquesnei*). COSEWIC (2005) has recommended a Threatened status for the Black Redhorse in Canada. Fisheries and Oceans Canada (DFO 2005a; DFO 2005b) uses a recovery potential assessment (RPA) to provide the information and scientific advice in support of its requirements under the *Species At Risk Act* (SARA). This scientific information also serves as advice to the Minister of Fisheries and Oceans Canada regarding listing of the species under SARA. The RPA plays an important role in this process and consists of three fundamental phases: determination of species status, assessment of the scope for human-induced harm (allowable harm), and the identification of mitigation strategies (DFO 2005a; DFO 2005b). The mitigation component of the RPA requires the identification of recovery targets, timeframes for recovery, and the specification of the uncertainty of outcomes associated with management actions (DFO 2005a; DFO 2005b). Herein, we address these mitigation aspects by proposing a population-based recovery target for Black Redhorse and conducting long-term projections of population recovery under a selection of hypothetical management scenarios.

METHODS

Vélez-Espino and Koops (2007a) modelled the Black Redhorse life cycle in 4 stages (Figure 1): young-of-the-year (YOY; stage 1; from egg to the end of the first year of life), juveniles (stage 2; from the end of the first year to the age of first maturity), young adults (stage 3; first half of the adult period, which covers the period from first reproduction to maximum observed age at reproduction) and old adults (stage 4; second half of the adult period). The adult stage was divided into young and old adults to reduce the loss of information caused by averaging vital rate values with high variance in species with long juvenile and/or adult periods. Important information can be lost by pooling all adult individuals into a single stage when modelling long-lived fishes with substantial increments in adult size and associated fertility rates (e.g., Crouse et al. 1987).

Using a stochastic approach, Vélez-Espino and Koops (2007a) determined that allowable harm for survival rates of YOY, juveniles, and young adults should be less than 19%, 14%, and 17%, respectively, based on the lower sensitivity bound for population response (Figure 2). But the application of a precautionary approach revealed that allowable harm for survival rates of young adults should be less than 13%. Further, Black Redhorse population dynamics were predicted to be highly resilient to extreme reductions in survival rates of age-7 and older individuals. Combining these results with information on body length within stages, minimum size limits can be determined to assist fishing regulations (see Figure 3).

Vélez-Espino and Koops (2007a) determined that reductions in habitat used by YOY, age-one and older (except spawning habitat), and spawners should be less than 12%, 37%, and 13%, respectively, for the Black Redhorse population occupying the segment of the Grand River between the Paris and Wilkes dams, Brantford. How these numbers can be transferred to other Black Redhorse populations will depend on the allocation of available habitat among the life stages. These levels of harm through habitat loss were precautionary given the uncertainty in population responses and corresponded to a maximum annual population growth of 8% as inferred for Canadian populations of Black Redhorse (Figure 4; Vélez-Espino and Koops 2007a).

Recovery target

SARA does not define recovery in the Act, but expert groups are expected to reach consensus on the biological characteristics of a population that constitute "recovery" as a core part of science support to recovery planning (DFO 2005c). This has been difficult and it remains a challenge to ensure that recovery targets are scientifically well-based. DFO's framework for developing science advice on recovery targets for aquatic species in the context of the Species at Risk Act (DFO 2005c) identified direct estimates of total population size and total range occupied as the preferred currencies for specifying recovery targets and focusing recovery efforts.

Among the alternative population-based approaches (e.g., evolutionary potential, demographic sustainability, ecological function, social dynamics, historical baseline, maximum, or status quo) that can be used to set abundance recovery targets, seeking demographic sustainability is considered the most conservative and quantitatively feasible (Sanderson 2006). Achieving demographic sustainability is a suitable approach to determine recovery targets not only because demography is more tractable than other aspects of animal ecology such as genetics, behaviour, or ecological function, but demographic data are amenable to the family of population modelling tools known as population viability analysis (PVA: Beissinger and McCullough 2002, Sanderson 2006).

With demographic sustainability (i.e., population is self-sustaining over the long term) as the criterion for setting recovery targets consistent with conditions set out in SARA section 73(3), we used an allometry between maximum population growth rate and minimum viable population size (*MVP*; Shaffer 1981) developed by Reed et al. (2003) to compute the minimum population size for demographic sustainability, defined as the number of adults required for a 99% probability of persistence over 40 generations. Using this predictive equation ($\log_e MVP = 9.36 - 1.55 \log_e \lambda_{max}$; $R^2 = 0.32$; $p < 0.0001$; λ_{max} = maximum population growth rate), *MVP* was computed for each λ_{max} value generated from life tables with alternative mean ages at maturity as $e^{2.64\ W\wedge\ -0.35}$ (Randall and Minns 2000), where W is adult weight at maturity in grams. Given that age at maturity is variable among populations (Bowman 1970; Howlett 1999; Reid and Mandrak 2002) and that mean age at maturity of females in Canadian populations has been estimated as 6.3 for the Muskegon River and 8.8 for the Grand River (Reid 2006), *MVP* was computed at maturation ages of 6, 7, 8, and 9.

Minimum area for population viability

Although Black Redhorse are found throughout much of the Mississippi River and lower Laurentian Great Lakes basin, remnant Canadian populations are confined to small areas in the Grand, Thames, Ausable, Bayfield and Maitland river watersheds (Mandrak and Casselman 2004). Using a predictive equation of area per individual (*API*) based on body size, $API = e^{-13.28} L^{2.904}$ (Randall et al. 1995, Minns 2003), the minimum area for population viability (*MAVP*) was calculated separately for young adults (less than seven years old) and old adults (seven years old and older) as the product of *MVP* and the *API* corresponding to these life stages. Area per individual per stage (API_j) was computed as the geometric mean of area per individual (m^2) at points in the life cycle delimiting each stage (see Mandrak and Casselman 2004): age of first maturity and age 7 for $API_{Young\ adult}$, and age 7 and maximum reproductive age (age 11) for $API_{Old\ adult}$.

Recovery timeframes

A logistic model of population growth was used to determine recovery timeframes under a variety of hypothetical management scenarios to characterize patterns of population response to recovery strategies. To apply the logistic growth model, it is necessary to know the carrying capacity of the system (*K*), the population size prior to any recovery action (N_0), and the intrinsic rate of increase generated by the management scenario (*r*). The recovery timeframe for a specific management scenario is determined as the number of years (t) necessary to reach the recovery target (N_t).

(1) $$N_t = \frac{K\,N_0}{\left(K - N_0\right)e^{-r\,t} + N_0}$$

Estimates of habitat supply per life stage (see Vélez-Espino and Koops 2007a) corresponding to the Black Redhorse population in the Grand River between the Paris and Wilkes dams, Brantford, produced carrying capacities of 25 000 adults. Although current adult population size may exceed the recovery target in this population (personal communication; Scott Reid, Ontario Ministry of Natural Resources) we conducted long-term projections using this carrying capacity and initial population sizes equivalent to 10% of the recovery target, and an intrinsic rate of increase prior to recovery actions of -0.073 as determined by Vélez-Espino and Koops (2007a) on the basis of the COSEWIC designation status. This combination of population parameters represents a hypothetical population. Knowledge of the carrying capacity and initial population size for other locations will enable site-specific applications of this methodology.

Changes in population growth affected by alternative management scenarios was calculated via stochastic perturbation analysis (equations 2 and 3) representing the lowest and highest population responses to recovery as determined by the demographic sensitivity indices (elasticities; ε_v) of individual vital rates (Vélez-Espino and Koops 2007a):

(2) $$\lambda_{New} = \lambda_0\left(1 + \sum_{v=1}^{n} \varepsilon_v \delta_v\right)$$

(3) $$r = \log_e\left(\lambda_{New}\right)$$

where λ_0 is the finite population growth rate before recovery actions, δ_v is the proportional increase in vital rate *v*, and *n* is the number of vital rates simultaneously perturbed by a specific recovery strategy.

Many alternative management scenarios targeting any combination of vital rates can be simulated. Here we conduct long-term projections for five hypothetical recovery strategies emulating positive and increasing impacts on the vital rates derived from habitat rehabilitation, habitat enhancement, stocking, and fishing regulations. The proactive nature of the recovery strategy increases from strategy 1 to strategy 5. Strategy 1 simulates a 20% increase in YOY survival (e.g., through habitat rehabilitation) while allowing a 20% fishing mortality in old adults. Strategy 2 adds to the actions implemented in Strategy 1 a 20% increase in juvenile survival (e.g., through habitat rehabilitation and stocking). Strategy 3 adds a 20% increase in young adult survival (e.g., through fishing regulations for young adults). Strategy 4 adds a 20% increase in fecundity rates of the two adult stages (e.g., through improvement and enhancement of spawning habitat). Lastly, Strategy 5 adds to the actions implemented in Strategy 4 the removal of harm in old adults (e.g., through the total closure of the fishery for adults).

Finally, although recent syntheses of life history traits in North American freshwater fishes (e.g., Winemiller and Rose 1992) indicate that all species in the genus *Moxostoma* are annual univoltine spawners, we repeated the above projections of recovery timeframes for semi-annual conditions. This analysis was considered potentially relevant given the large reproductive investment in the form of gonadal mass observed in redhorse species in Canada (Scot Reid, Ontario Ministry of Natural Resources, *personal communication*) and the biological challenge posed by annual allocation of energy to gonadal development. This alternative projection of recovery timeframes required a 50% reduction in fertility, representing a halving of the reproductive effort caused by semi-annual spawning, prior to the implementation of recovery strategies.

RESULTS

The recovery target ranged from 7671 adult fish when average age at maturity is 6 years to 8 049 adult fish when average age at maturity is 9 years (Table 1). These abundances translated into minimum areas for population viability ranging from 150 582 m^2 to 158 002 m^2 for a population comprised entirely by young adults and from 592 355 m^2 to 621 544 m^2 for a population entirely consisting of old adults (Table 1). A precautionary recovery target of 8 049 adults is recommended for Black Redhorse. We used this number for the long-term projections and to determine recovery timeframes.

Long-term population projections under the five hypothetical recovery strategies indicated that a 20% increase in YOY survival while allowing a 20% mortality on old adults (Strategy 1) cannot produce recovery regardless of whether the lower or upper bound of population response is used in the projections (Figure 5). By simultaneously increasing YOY and juvenile survival by 20% each (Strategy 2), rapid population growth is produced and the recovery target is projected to be reached after 119 years when using the lower bound of population response and after 29-30 years when using the upper bound. This large uncertainty in recovery timeframes is substantially reduced under a more proactive recovery strategy that also increases young adult survival by 20% (Strategy 3). In this case, the recovery target can be reached after 17-48 years (upper-lower bound). Adding a 20% increase in fecundity rates to the recovery strategy (Strategy 4) reduces recovery timeframes to 11-37 years. Removing the 20% allowable fishing mortality on old adults produced negligible changes to long-term projections, as expected from the low sensitivity of population growth to perturbations in the survival of this stage (Vélez-Espino and Koops 2007a).

Most of the uncertainty in the projections of recovery timeframes is related to stochastic variation in vital rates and therefore population responses to recovery strategies. By increasing the proactive nature of the recovery strategy this uncertainty decreases, particularly for recovery strategies targeting vital rates that produce the largest relative responses in population fitness. As a corollary to this result, improving the survival of old adults contributes so little to recovery that regulating mortality rates on this stage produces little benefits to population performance.

Finally, the repetition of the projection of recovery timeframes for semi-annual spawning periodicity demonstrated that the sensitivity of recovery timeframes to spawning periodicity is particularly large when the lower bounds of sensitivity to recovery are used and when recovery efforts are relatively low. On the other hand, when the upper bounds of sensitivity to recovery are used (i.e., population responds strongly to recovery actions) and when the management strategy is characterized by high recovery efforts in a proactive scenario, the influence of semi-annual spawning periodicity on recovery timeframes is extremely low (Table 3). This is particularly obvious for recovery strategies 3, 4, and 5. Nevertheless, the difference in projected recovery timeframes between lower and upper bounds of sensitivity to recovery increased substantially when spawning periodicity changed from annual to semi-annual.

DISCUSSION

These analyses have shown that a recovery target of 8 049 adult fish could be managed, with flexibility, under the modelled conditions of populations selected for recovery. This flexibility is the result of the poor sensitivity of projections of recovery timeframes to the stage structure of the adult population. More specifically, three particular scenarios can be considered. First, for populations where habitat constraints indicate that the minimum area for population viability in terms of old adults (i.e., 621 544 m^2) is not available, but the minimum area for population viability in terms of young adults (i.e., 158 002 m^2) is available, then a recovery target of 8 049 young adults might be considered. This option is supported by the small demographic contributions of old adults. Second, if there are no habitat constraints, 8 049 old adults can be accommodated, and the current population size is far below the recovery target, then 8 049 adult fish, regardless of age, would constitute an appropriate recovery target. Finally, if the adult population size is estimated to be close to or above the recovery target, then choosing 8 049 old adults as the recovery target would constitute an appropriate target and counterbalance the perception that fishing mortality on this stage can be absolute without causing important reductions to population fitness. Furthermore, keeping at least 8 049 old adults in a highly productive stream would provide additional protection to those populations for which recovery actions are apparently unnecessary and provide for potentially beneficial maternal effects from older, larger females (e.g., Johnston 1997) that were not included in the population model.

Our metric of required habitat (*MAPV*) is based on the concept of demographic sustainability and pertain exclusively to the area requirements of a minimum viable number of adults using good quality habitat. *MAPV* does not specify the amount of required habitat needed for juvenile fish. Therefore, a complete description of required habitat, derived from our approach, still needs basic demographic data (i.e., age or stage structure) and knowledge of stage-specific habitat preferences to specify the amount of juvenile habitat necessary to sustain the minimum viable adult population size. Further, our estimates of adult *MAPV* may underestimate habitat requirements for population viability given our use of area per individual (*API*) of adults based on size at maturity; larger individuals require larger *API*s (Randall et al. 1995, Minns 2003).

Our results indicate that the best way to reduce uncertainty in population responses to recovery is to aim for a proactive recovery strategy, targeting several vital rates simultaneously. Although our projections are based on an adult population size prior to recovery at 10% of the recovery target, it is easy to appreciate that simultaneously increasing YOY and juvenile survival by 20% or more through habitat rehabilitation and stocking, for example, might suffice to reach recovery targets, and that recovery timeframes may be substantially reduced if additional increments in the survival of young adult were achieved through fishing regulations, such as increasing the minimum size limit to direct most of the fishing mortality to old adults. Further, as expected from the analysis of allowable harm in Black Redhorse (Vélez-Espino and Koops 2007a), our projections show that any reduction in fishing mortality on old adults, including complete closure of the fishery, produces a meagre demographic benefit and a poor contribution to the protection or recovery of the population.

Proper stochastic projections of recovery timeframes, using the methodology described by Vélez-Espino and Koops (2007b, 2008), were not possible due to data limitations. However, the use of lower and upper bounds of population responses to recovery served as a means to incorporate the influence of environmental stochasticity on recovery timeframes. Given the data limitations, long-term projections conducted herein correspond to hypothetical scenarios. Implementing the present methodology in recovery strategies of Black Redhorse populations will require estimates of current population sizes, particularly of adults, and estimates of habitat availability. The former is necessary to determine N_0 in the logistic model, and the latter to determine carrying capacities and minimum areas for population viability. Finally, field research on spawning periodicity would be beneficial given its influence on the uncertainty in long-term projections of recovery timeframes.

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Table 1. Minimum viable population (*MVP*) and minimum area for population viability (*MAPV*) recommended for Black Redhorse and based on different mean age at maturity. *MVP* estimated as a function of the population growth rate (Reed et al. 2003) and *MAPV* estimated as function of area per individual (Randall et al. 1995, Minns 2003).

Mean age at maturity	Population growth	*MVP*	*MAPV* (m^2) Young adults	*MAPV* (m^2) Old adults
6	1.31	7 671	150 582	592 355
7	1.3	7 763	152 388	599 459
8	1.28	7 951	156 078	613 976
9	1.27	8 049	158 002	621 544

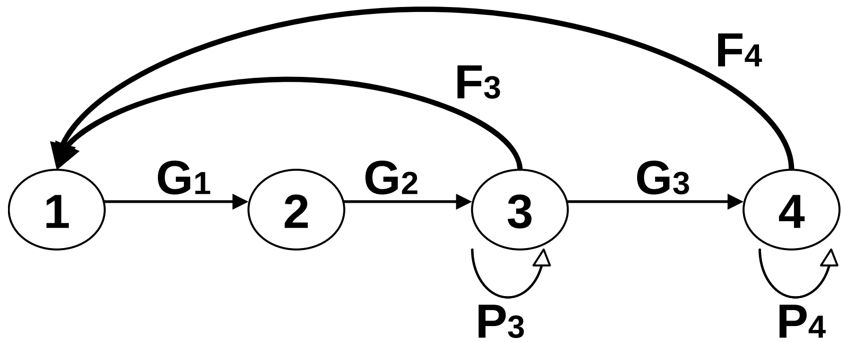
Table 2. Five hypothetical recovery strategies representing positive and increasing impacts on vital rates derived from habitat rehabilitation and enhancement, stocking, and fishing regulations. The proactive forcefulness of the recovery strategy increases from strategy 1 to strategy 5. AH: Allowable harm.

Strategy	Survival				Fecundity	Implementation
	YOY	Juvenile	Young adult	Old adult		
1	20% increase			20% AH		Habitat rehabilitation
						+
2	20% increase	20% increase		20% AH		Habitat rehabilitation + stocking
						+
3	20% increase	20% increase	20% increase	20% AH		Fishing regulations for young adults
						+
4	20% increase	20% increase	20% increase	20% AH	20% increase	Rehabilitation/enhancement of spawning habitat
						+
5	20% increase	20% increase	20% increase	No harm	20% increase	Closing fishery for old adults

Table 3. Projected recovery timeframes for initial population sizes of 10% of the recovery target (8 049 adult fish) corresponding to lower and upper bounds of sensitivity to recovery for individual vital rates and in response to management strategies shown in Table 2. Recovery timeframes are projected for both annual and semi-annual spawning periodicity. The last column shows the difference in years between projections for lower and upper bounds of sensitivity to recovery.

Spawning periodicity	**Recovery Strategy**	**Recovery timeframe (yr)**		**Difference between lower and upper**
		Lower	Upper	
Annual	1	Never	Never	N/A
	2	119.0	29.5	89.5
	3	47.5	16.5	31.0
	4	36.5	11.0	25.5
	5	36.5	11.0	25.5
Semi-annual	1	Never	Never	N/A
	2	Never	69	∞
	3	514.0	24.0	490.0
	4	118.0	14.0	104.0
	5	118.0	14.0	104.0

(*a*)



(*b*)

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ G_1 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Figure 1. Generalized Black Redhorse life cycle (*a*) and corresponding stage-structured projection matrix A (*b*). The life cycle was divided into four stages: young-of-the-year (stage 1), juvenile (stage 2), young adult (stage 3), and old adult (stage 4). F_i represents stage-specific fecundity coefficient, P_i the probability of surviving and remaining in the same stage, and G_i the probability of surviving and moving to the next stage.

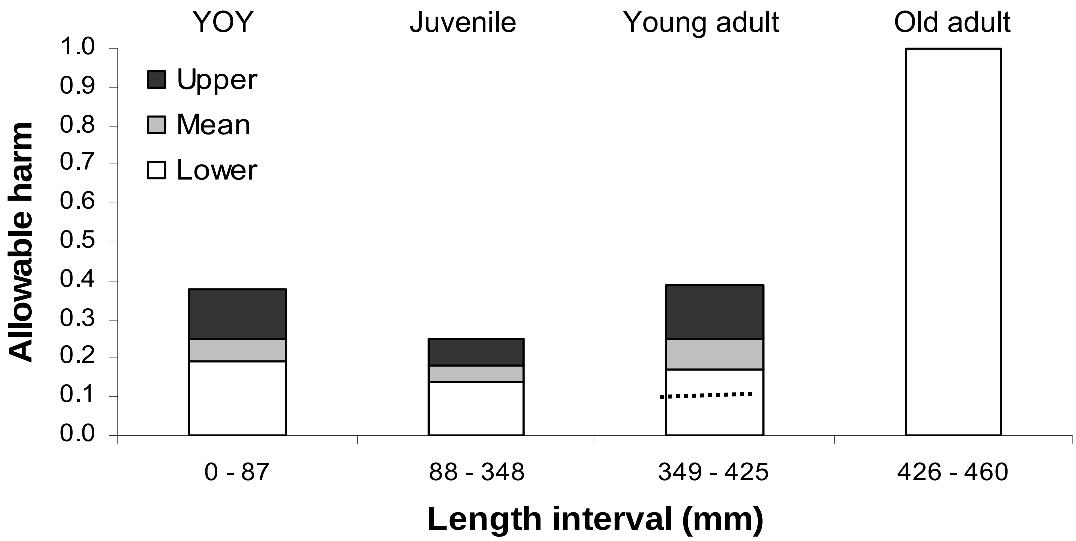


Figure 2. Allowable harm in terms of proportional mortality for Black Redhorse at different life stages and their corresponding size intervals. Lower 95% confidence bound (white); mean value of allowable harm (grey); upper 95% confidence bound (black). The dashed line indicates the most precautionary value for young adults.

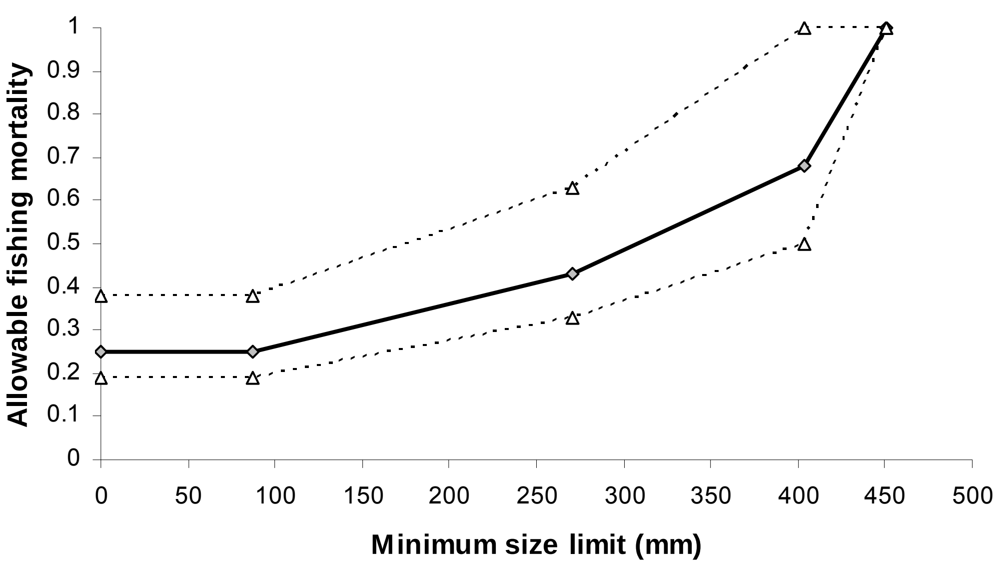


Figure 3. Allowable fishing mortality as a function of minimum size limit. Solid line: mean allowable harm. Dashed lines: 95% confidence bounds.

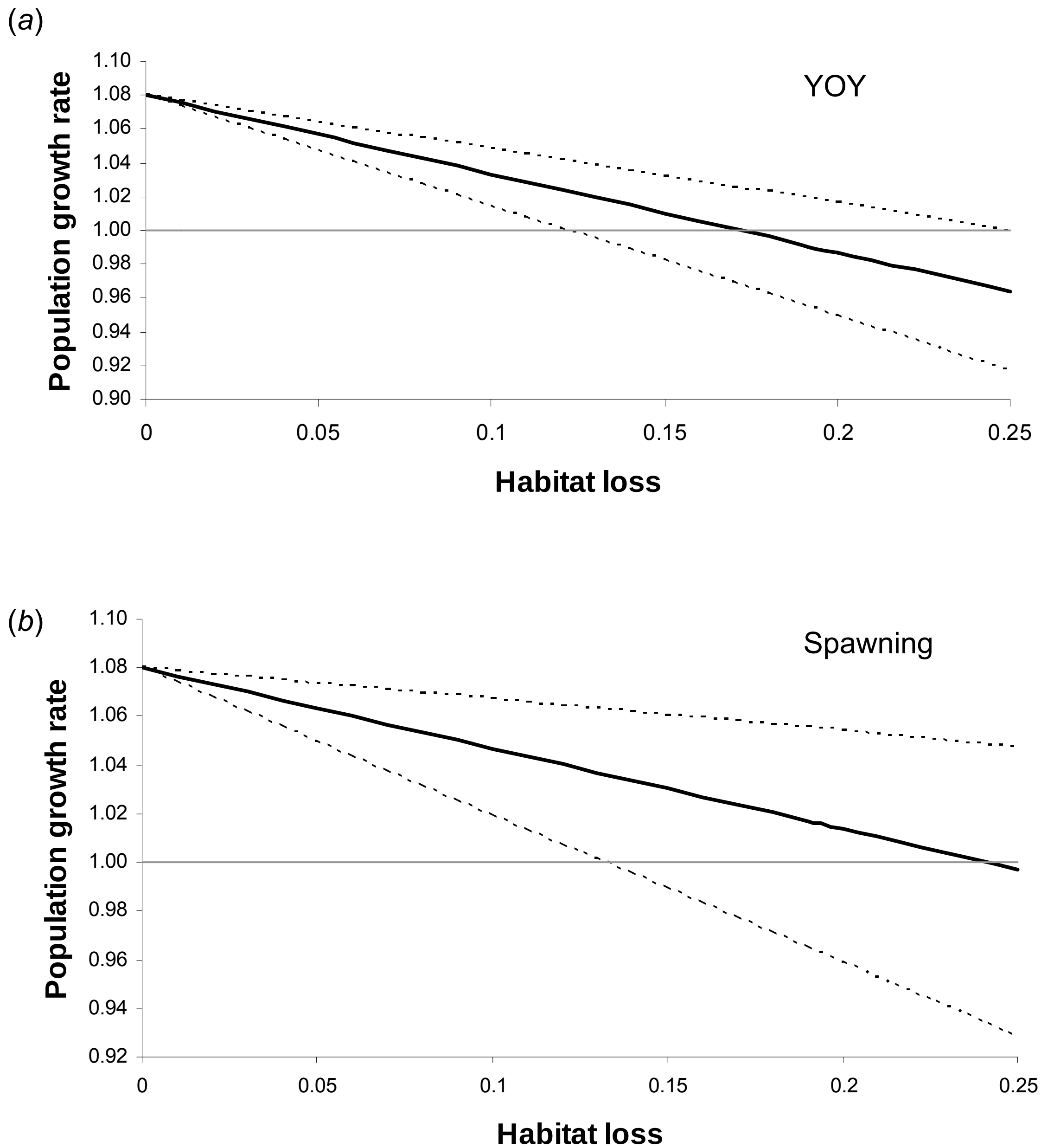


Figure 4. Effect of proportional habitat loss on maximum population growth rate for the Black Redhorse population occupying the segment of the Grand River between the Paris and Wilkes dams, Brantford. Solid line represents mean population response; dashed lines represent 95% confidence limits for population response. (*a*) Essential habitat for young-of-the-year (YOY); (*b*) Essential spawning habitat.

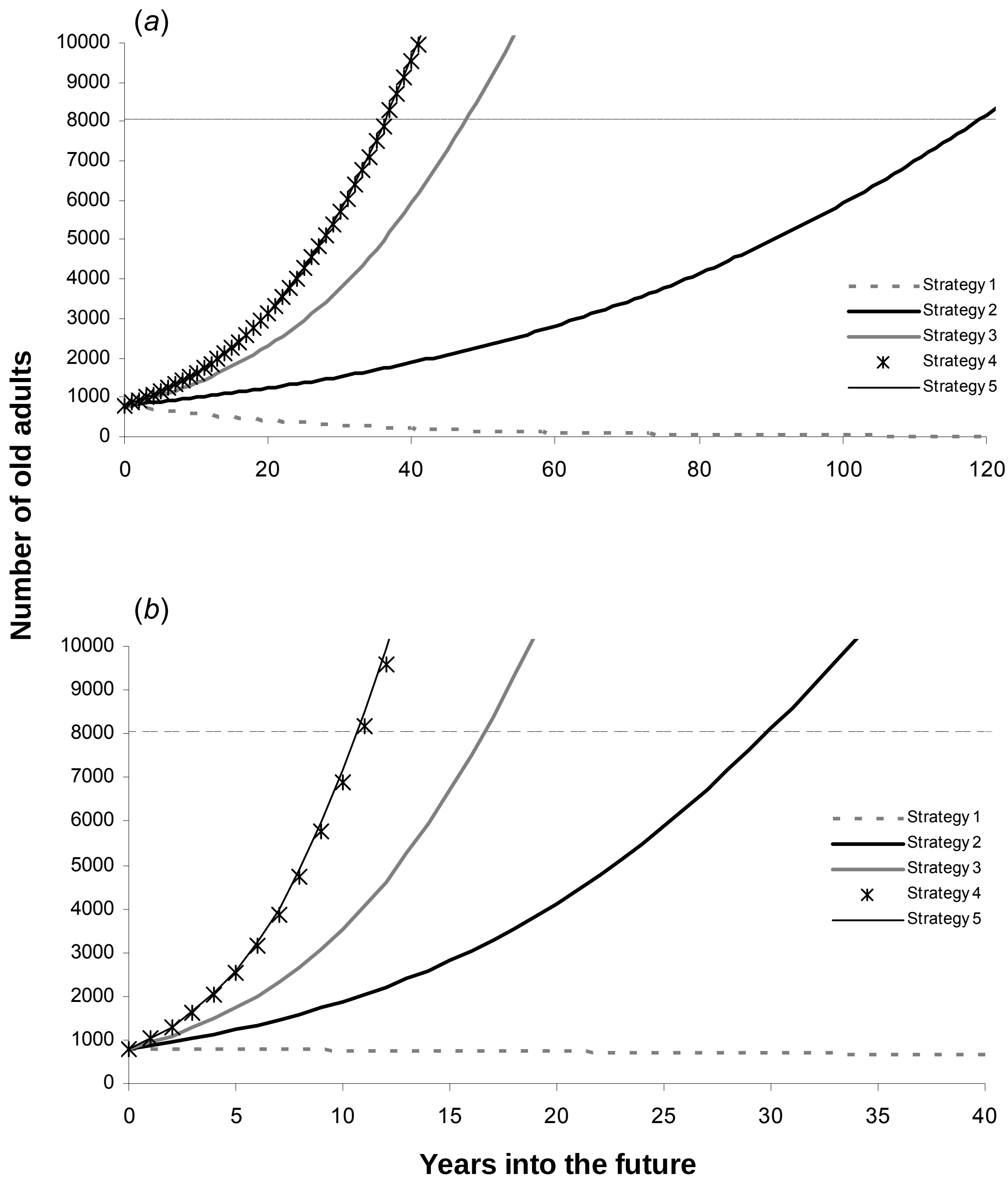


Figure 5. Long-term projections of adult population size generated by the five hypothetical management strategies (Table 2). Projections were generated with a logistic model incorporating (*a*) the lower bound of sensitivity to recovery for individual vital rates and (*b*) their upper bound. The horizontal line represents the recovery target of 8 049 adults.

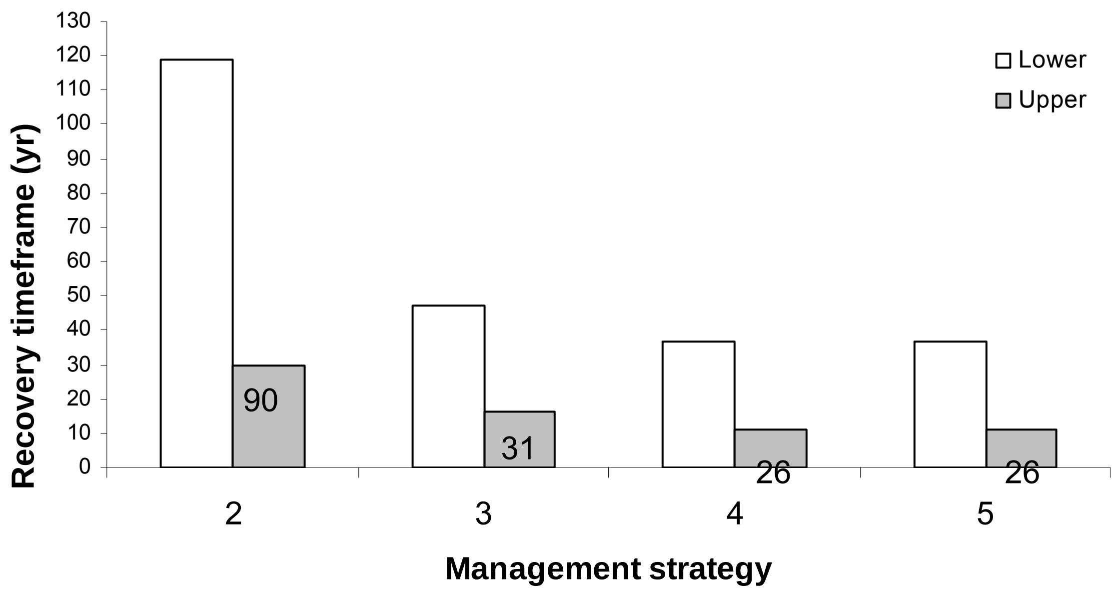


Figure 6. Recovery timeframes predicted with the lower and upper bounds of sensitivity to recovery. The inserted numbers indicate the uncertainty in recovery timeframes.