**Title**: The translocation trade-off for eastern sand darter (*Ammocrypta pellucida*): balancing harm to source populations with the goal of re-establishment

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**Abstract:** Using translocations to recover populations requires a sufficiently large number of individuals from source populations, but removing too many individuals could lead to source population collapse. To understand the trade-off between the probabilities of source population extirpation and translocation success, matrix population models that incorporate Allee effects, density-dependence, and demographic and environmental stochasticity were combined with a model that simulates removals from source populations. We apply these models to eastern sand darter (*Ammocrypta pellucida*; Threatened) translocation scenarios in Canada. Results suggest that translocations most often require source populations >20,000 individuals, as source population extirpation probability increased with the number and frequency of removals. Transport mortality or losses immediately following introduction further affected translocation success. Uncertainty around life-history parameters and the strength of Allee effects led to additional uncertainty about the required source population size. Although stochastic processes affected the probability of translocation success, factors such as stocking density and frequency can be controlled, and therefore, translocation may be a viable strategy for eastern sand darter recovery, even when applying cautious thresholds to guard against uncertainty.

**Keywords:** Allee effects, density dependence, eastern sand darter, population modelling, reintroduction

## Introduction

The number of species at heightened risk of extinction continues to rise (Chapin III et al. 2000; Rockström et al. 2009). Reversing this trend requires rigorous evaluation and implementation of a variety of conservation strategies (Rands et al. 2010). For most imperilled species, habitat restoration represents the first step toward recovery (Dobson et al. 1997), but due to dispersal constraints, habitat restoration alone may be insufficient. In these cases, species reintroduction may be considered, which involves the intentional release of individuals into part of the species' native range from which it has been extirpated (Armstrong and Seddon 2010). Species reintroductions involve moving individuals from one location to another, often from a source population to a restored site (i.e., translocation; Seddon 2010; Spurgeon et al. 2015). Individuals may also be bred in captivity and subsequently released (i.e., captive rearing and release; Roques et al. 2018). Captive rearing programs often bring increased costs due to the operation of breeding facilities and challenges with maintaining genetic diversity in captive environments. As a result, translocations of wild individuals are more often considered to meet management goals (Swan et al. 2018; Lamothe and Drake 2019).

Populations of imperilled species are inherently small and the removal of individuals from those populations can bring considerable risks. Removing too many individuals from the source population can lead to the loss of valuable breeding individuals and genetic diversity (George et al. 2009; Pine et al. 2013), potentially causing the source population to collapse. Alternatively, translocating insufficient numbers from the source population can lead to establishment failure due to Allee effects (Daredec and Courchamp 2007; Armstrong and Wittmer 2011) and (or) issues with inbreeding for captive breeding programs (Jamieson 2011).

As well, removals from source populations can impose unnecessary harm and increase the susceptibility of populations to stochastic events.

To achieve conservation goals, re-establishing populations through translocation should never lead to the loss of a source population; rather, translocations must be considered in terms of achieving maximum benefit for the species as a whole. Determining which individuals and how many to remove from the source population is, therefore, a critically important decision when planning translocation efforts and one of the top questions in reintroduction biology (Armstrong and Seddon 2008). If wild populations are being considered as a source for translocations, the probability of re-establishing a self-sustaining population must be assessed against the likelihood of compromising source population viability (Pine et al. 2013), and optimized by determining how many individuals can be removed while ensuring a reasonable probability of success (Vincenzi et al. 2012).

Models can be useful for evaluating the outcome of translocation strategies, particularly when testing the success of alternative management strategies through quantitative predictions and expectations (Schaub et al. 2009; Chauvenet et al. 2012; Pérez et al. 2012). As well, multiple forms of uncertainty (e.g., environmental and demographic stochasticity, Allee effects, catastrophic events) can be incorporated into models to generate realistic bounds for predictions that can be used for management decisions. However, rarely have models been used to simultaneously evaluate the cost-benefit trade-off of removals from source populations and additions to recipient populations (e.g., Hearne and Swart 1991; Dimond and Armstrong 2007; Todd and Lintermans 2015), particularly for imperilled fishes (Armstrong and Reynolds 2012). Here, models are developed to answer three primary questions for species translocation using a cost-benefit framework:

1) How is the establishment probability of translocated populations affected by life-history characteristics and the number of individuals released?
2) What is the consequence of removing individuals from source populations given different numbers removed and life-history characteristics?
3) What is the optimal trade-off between removals from source populations and the probability of successful re-establishment?

Using eastern sand darter (*Ammocrypta pellucida*) as a case study to address these questions, matrix population models were developed to mimic the effects of removal on source populations while evaluating the probability of translocation success. Eastern sand darter (Ontario designatable unit) was chosen because translocation is identified as a potential recovery strategy in Canada (COSEWIC 2009; Fisheries and Oceans Canada 2012), but has yet to occur in-part due to concerns that translocations could harm local source populations without evidence of potential success. As such, the results from these models are placed in a cost-benefit framework to inform species managers on the trade-offs and risks of various translocation strategies. Although eastern sand darter is used here as a case study and the results are relevant to future management of this species, the model is designed to answer general questions about factors that influence extirpation and establishment probabilities across species and life-history strategies.

## Materials and methods

### *Study species*

Eastern sand darter is a relatively small (<90 mm), benthic freshwater fish that has experienced declines in abundance and distribution across its Canadian range since the 1970s, including population extirpations (COSEWIC 2009; Fisheries and Oceans Canada 2012). Agricultural land-use practices and urbanization leading to increased siltation (Drake et al. 2008) are the primary factors implicated in eastern sand darter declines (Fisheries and Oceans Canada 2012). Increased siltation alters benthic food webs, reduces the ability of eastern sand darter to burrow, and likely impairs physiological function (Kemp et al. 2011). Extant populations in Canada remain at risk of siltation and upstream expansion of the invasive round goby (*Neogobius melanostomus*; Poos et al. 2010); however, improvements in habitat conditions at sites free of invasive species could allow for future translocations (Lamothe et al. 2019a).

***Population model structure***

The life cycle of eastern sand darter was modelled using a density-dependent, age-structured, birth-pulse, pre-breeding matrix model with annual projection intervals (Caswell 2001). Age-structured matrix population models use population vital rates to project age-specific population sizes over time and are a common tool for modelling extinction and recovery of imperilled species when developing conservation plans (Fagan et al. 2001; Fieberg and Ellner 2001). Population growth rate ($\lambda$; see Table 1 for definitions of symbols) represents the long-term projection of population status based on current or simulated conditions. When $\lambda = 1$ the population is stable, when $\lambda > 1$ the population is growing exponentially, and when $\lambda < 1$ the population is declining.

As is common for imperilled freshwater fishes (Winemiller 2005), eastern sand darter follows an opportunistic life-history, with a relatively short generation time, high reproductive effort, small body size, low batch fecundity, and low investment per offspring (Finch et al. 2018). However, like most species, there is variation and uncertainty around eastern sand darter vital rates (Finch et al. 2013). For example, differences in the number of clutches, age at maturity, and total clutch size have been reported for eastern sand darter across the species distribution (Finch et al. 2018). Therefore, two divergent life-history strategies ($\mathbf{A_1}$ and $\mathbf{A_2}$) were modelled here to bound the range of possible translocation outcomes. Life-history scenario $\mathbf{A_1}$ was considered to represent a long-lived, fecund population where eastern sand darter was assumed to mature at age 1 ($t_{mat}$), with a longevity of 4 years ($t_{max}$), and produce 3 clutches per year ($C$: Table 2):

$$\mathbf{A_1} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ \sigma_1 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 \end{bmatrix}. \ (1)$$

Alternatively, the second life-history model, $\mathbf{A_2}$, represented a more conservative scenario where $t_{mat} = 2$ years, $t_{max} = 3$ years, and $C = 2$ clutches per year (Table 2):

$$\mathbf{A_2} = \begin{bmatrix} 0 & F_2 & F_3 \\ \sigma_1 & 0 & 0 \\ 0 & \sigma_2 & 0 \end{bmatrix}. \ (2)$$

Elements within $\mathbf{A_1}$ and $\mathbf{A_2}$ included age-specific fertility rates ($F_t$) and annual survival ($\sigma_t$). Fertility rates describe the contribution of offspring from an adult in age-class $t$ to the next census of age-1 individuals. Fertility ($F_t$) was calculated as a function of the proportion of females in the population ($\varphi = 0.5$), the proportion of the population mature at age $t$ ($\rho_t$), mean age-specific fecundity ($f_t$), or the mean number of eggs produced per clutch per individual in age-class $t$, the number of clutches per year ($C$), density-dependent young-of year (YOY) survival ($\sigma_{0,Et}$), and an Allee effect ($a_f$):

$$F_t = \varphi \rho_t f_t C \sigma_{0,Et} a_f. \ (3)$$

Based on observed egg counts and size distributions of eastern sand darter in Ontario, mean fecundity ($f_t$) was assumed to be constant across age classes at 71.5 eggs·clutch$^{-1}$ and mean age 1+ survival was assumed to be constant across age classes at 38.6% (Finch et al. 2018). Because a pre-breeding matrix structure was used, YOY survival was incorporated to account for persistence to the next census.

Density-dependence was incorporated as a Beverton-Holt function applied to YOY annual survival ($\sigma_{0,Et}$) as a function of the number of eggs produced ($E_t$):

$$\sigma_{0,\,Et} = \frac{\sigma_{0,max}}{1 + {}^{bE_t}\!/_{K}}, \; (4)$$

where $\sigma_{0,max}$ is maximum survival achieved at a population of zero individuals, $K$ is carrying capacity (age-1+ eastern sand darter) when $\bar{\lambda} = 1$, and $b$ is the density-dependence coefficient (e.g., Fig. S1). Maximum population growth rate ($\lambda_{max}$) was estimated from an allometric relationship to weight at maturity ($W_{mat}$; g; Randall and Minns 2000), where:

$$\lambda_{max} = e^{2.64 W_{mat}^{-0.35}}. \; (5)$$

To provide a precautionary estimate, the lower prediction interval from the regression model of Randall et al. (1995) was used to define $\lambda_{max}$ for eastern sand darter, which was equal to 2.69. Like most imperilled species, $\lambda_{max}$ for eastern sand darter is uncertain. Therefore, three potential $\lambda_{max}$ values were used to simulate different maximum recovery rates: 1.56, 2.13, and 2.69. The density-dependence parameter, $b$, was solved for to give a stable, mean population size at $K$ under each $\lambda_{max}$ (1.56, 2.13, and 2.69) and life-history model ($\mathbf{A_1}$ and $\mathbf{A_2}$).

Weight at age $t$ ($W_t$; g) was predicted from eastern sand darter length data (Drake et al. 2008) using:

$$W_t = 1.009 \times 10^{-5} L_t^{2.84}. \; (6)$$

Length ($L_t$) was assumed to follow a von Bertalanffy growth function:

$$L_t = L_\infty\left(1 - e^{-k(t + t_0)}\right), \; (7)$$

where $L_t$ is total length (TL; mm) at age $t$, $t_0$ is the hypothetical age at which the fish would have a length of zero (-0.47), $L_\infty$ is the asymptotic length (55.52 mm), and $k$ is a growth parameter (1.59; Finch et al. 2013).

Allee effects ($a_f$) represent a reduction in population growth rate when populations are small and were modelled as a proportional reduction in fertility rates structured as a Holling type III function:

$$a_{f,N_A} = \frac{{N_{A,t}}^2}{a^2 + {N_{A,t}}^2}, \quad (8)$$

where $N_{A,t}$ is adult abundance at time $t$ and $a$ is the Allee effect coefficient representing the population size at 50% reproductive success (i.e., fertility). A type III function was chosen as the magnitude of Allee effects are expected to be relatively high at small population sizes and tail off as the population grows. Given that the true magnitude of Allee effects in nature is uncertain, simulations were run with two levels of Allee effects by setting $a$ to 50 and 100 adults (Fig. S2).

Demographic stochasticity represents the variation in vital rates that results from small population sizes (Lande 1993; Morris and Doak 2002). Demographic stochasticity of age-specific survival ($\sigma_t$) was incorporated by summing $N$ draws from a binomial distribution with mean of $\sigma_t$ and dividing by $N_t$ to give the annual average (Morris and Doak 2002). Demographic stochasticity of age-specific fecundity ($f_t$) was incorporated by taking the mean of $N_a/2$ draws (to represent females only) from a Poisson distribution with mean $f_t$ to give the annual average. As $N$ increases, the impact of demographic stochasticity lessens, with an increased likelihood that the annual vital rates approach the species' mean. Demographic stochasticity was only applied when population sizes were $\leq$ 500 individuals.

Environmental stochasticity represents population-level variation in vital rates due to inter-annual changes in environmental factors leading to variation in fertility and mortality

(Lande 1993). Information relating vital rates to environmental factors for imperilled small-bodied fishes, including eastern sand darter, is lacking, and was therefore estimated using data from across species and life stages (Bradford 1992). Annual instantaneous mortality, $M_t$ = -log($\sigma$), was allowed to vary as a normal distribution with a coefficient of variation (CV) of 0.2 (Fig. S3). Across species and life stages, variance in mortality increases as a function of $M$, where sd($M$) = $0.39M^{1.12}$ (Bradford 1992). Rearranging this relationship leads to a CV($M$)~0.4; however, Mertz and Myers (1995) suggest that an estimated CV($M$)~0.4 is likely inflated from measurement effort in field estimates of $M$. Therefore the inter-annual variability in $M$ is better represented by a constant CV of 0.2 for age 1+ fish (Mertz and Meyers 1995). Variability in YOY survival assuming a CV of 0.2 was too great and was therefore set to 0.1 to limit variation in population growth rate to a reasonable level. Annual fecundity was varied as a log-normal distribution with a log-standard deviation of 0.05, which generated a reasonable range of population-level fecundity values (Fig. S4).

**Minimum viable population size**

Minimum viable population (MVP) describes the absolute minimum population size of age 1+ individuals that has a certain probability of remaining extant over some period of time despite the continuous effects of stochasticity and catastrophic events (Shaffer 1981). Here, that time was set to 100 years (52 eastern sand darter generations) with a desired persistence probability of 95% ($MVP_{95\%}$). $MVP_{99\%}$ values were used as our translocated population carrying capacities ($K$) because populations size has not been estimated for eastern sand darter populations in Ontario. Furthermore, as $K$ is unknown for new populations, it was assumed that translocation efforts would only occur at previously occupied locations with enough habitat to sustain $MVP_{99\%}$.

However, note that the capacity of a translocated population to surpass the $MVP_{99\%}$ would be ideal when attempting to relocate individuals into formerly occupied habitats. Nevertheless, $MVP_{99\%}$ is likely a highly conservative estimate of the number of individuals needed to support a self-sustaining eastern sand darter population given the opportunistic life-history strategy (Winemiller 2005).

The rate of catastrophic events, defined as a reduction in population abundance of greater than 50% (Reed et al. 2003b), can strongly affect calculations of MVP for small-bodied fishes (Reed et al. 2003a; Vélez-Espino & Koops 2012). Here, the rate of catastrophes was set to 10% per generation or, on average, one catastrophe every 19-20 years. The rate of die-off was sampled from a beta distribution with shape parameters of 0.762 and 1.500, scaled between 0.5 and 1.0 (i.e., 50% to 100% of the population; Fig. S5), and fitted to data from Reed et al. (2003b). Reid et al. (2003b) collected data on the frequency and magnitude of catastrophic events from 308 studies on 88 vertebrates and found an inverse relationship between the frequency and magnitude of catastrophes. Allee effects, demographic and environmental stochasticity, and density-dependence were all similarly incorporated into MVP calculations as described above.

Simulations were run for differing values of $K$ ranging from 1,000 to 100,000 individuals for each combination of life-history strategy ($\mathbf{A_1}$ and $\mathbf{A_2}$) and for three different maximum population growth rates ($\lambda_{max}$ = 1.56, 2.13, and 2.69). Simulations were run for 100 years with 10,000 replicates. Populations were considered extirpated if less than two age 1+ fish remained in the population. Binomial outputs (1: extirpation, 0: extant) were fit using a logistic regression with log($K$). Model predictions for a 1% and 5% probability of extirpation represent MVP values.

**Translocation simulation**

The effects of density-dependence, environmental and demographic stochasticity, and Allee effects, with a rate of catastrophic mortality events of 10% per generation, were also incorporated into the translocation simulations. Initial population size of the translocated populations was set to zero and $K$ was set to $MVP_{99\%}$. To simulate stocking efforts, 50 to 2,000 individuals were introduced annually for one, five, or 10 years. The age-structure of the translocated individuals was set to equal the stable stage distribution of the source populations (age-1 to $t_{max}$). Stocked fish followed the same life-history strategy ($\mathbf{A_1}$ or $\mathbf{A_2}$) as the source population. This assumption may be a simplification of nature, as the translocated population may show changes in fertility or survival in response to the change in habitat (e.g., Vincenzi et al. 2012; Healy et al. 2020); nevertheless, life history strategies are likely to be similar owing to the habitat specificity of the species. A range of translocation mortality rates ($m$; 10-90%) were simulated, which might occur from the stress of capture, transport conditions, the impact of actual stocking mechanisms (e.g., using pressurized hoses from transport trucks), or post-release factors due to the translocation event (e.g., immediate predation, emigration, inability to find suitable habitat).

Within the simulations, eastern sand darter was removed pre-spawn and allowed to spawn in the translocated site in the same year with no additional mortality occurring before spawning beyond $m$ (i.e., best-case scenario); however, further simulations were performed to simulate the potential effect of delayed reproduction post translocation, where translocated eastern sand darter were required to survive a full year prior to reproduction (Supporting Information). Simulations were run for two levels of Allee effects, with the Allee effect parameter, *a*, set to 50 or 100 (Fig. S2) for 50 years with 5,000 replicates. A translocation was considered successful if the population remained extant post-stocking and if the geometric mean population abundance was greater than $MVP_{95\%}$ over the last 15 years of the simulation (years 36 to 50). Logistic regressions were then fit between success/failure and the number of individuals introduced, log($N$), years stocked, log($\lambda$), and $m$. Finally, scenarios were considered where translocations resulted in at least a 90% chance of success with a 1% probability of extirpation or less.

**Removals from source populations**

A population viability analysis was run to determine the impact of removing individuals from a source population for seeding translocation efforts. Population viability analysis is closely related to MVP simulations, but seeks to inform the likelihood that a population will persist into the future without attempting to estimate the absolute minimum population (Boyce 1992). Simulations were run for 50 years, using 5,000 repetitions, with a 10% probability of catastrophe per generation. Source population carrying capacity ($K$) was set to values ranging from $MVP_{95\%}$ and 10 times $MVP_{95\%}$. By setting $K$ high, the source population is assumed to be stable, self-sustaining, and abundant (an important consideration for selecting a source population). Similar to the MVP analysis, removal simulations incorporated Allee effects, demographic and environmental stochasticity, and density-dependence. For each simulation, $n$ age-1 to $t_{max}$ eastern sand darter were removed from one population (pre- or post-spawn), where $n$ ranged from 0 to 2,000. For the purposes of clarity, post-spawn removal simulations are presented in the Supporting Information. To align with translocation simulations, annual removals occurred for one, five, or 10 years, and extirpation occurred when less than two age 1+ fish remained.

Although the translocation of individuals from multiple populations has been identified as useful to improve the probability of successful reintroduction efforts (e.g., greater opportunity for adaptive genetic diversity; Houde et al. 2015), a single population was used here to simplify the modelling process and consider the situation where a single population may be the only remaining source of individuals.

**Balancing the impact of removals with successful establishment**

To inform translocation decisions, we present model results in a cost-benefit framework. The probability of extirpation over 50 years was calculated for the translocated population as the potential cost of translocation. The potential benefit was calculated as the probability of successfully establishing the translocated population. When these probabilities are plotted together, the state-space can be divided into four quadrants that represent the cost-benefit trade-off (Fig. 1). Quadrant 1 represents the unacceptable outcome associated with a low probability of success (< 90%) and a high risk of extirpation (> 1%). Quadrant 2 represents the risky outcome with a high probability of success (≥ 90%) but a high risk of extirpation (> 1%). Quadrant 3 represents the undesirable outcome of a low probability of success (< 90%) despite a low risk of extirpation (≤ 1%). Finally, quadrant 4 represents the optimal outcome where a high probability of success (≥ 90%) is paired with a low risk of extirpation (≤ 1%). Due to the importance of preserving source populations, translocation decisions may warrant alternative weighted interpretations of costs and benefits. We present model results in the cost-benefit framework with the optimal outcome defined by at least a 90% probability of success for the translocated population while limiting the probability of extirpation for the source population to no more than 1%.

All models were run in R Version 3.5.0 using base R functions (R Core Team 2018) and the 'popbio' (Stubben and Milligan 2007) package with plots generated using 'ggplot2' (Wickham 2009).

## Results

### Minimum viable population size

The minimum viable population size for eastern sand darter needed to achieve 99% ($MVP_{99\%}$) probability of persistence given a 10% chance of catastrophic decline per generation varied over a five-fold range (8,403 to 44,018 adults) depending on life-history strategy (i.e., $\mathbf{A_1}$ or $\mathbf{A_2}$), maximum population growth rate ($\lambda_{max}$), and level of Allee effect (Fig. 2). MVP estimates were greatest for populations demonstrating low $\lambda_{max}$, experiencing strong Allee effects ($a$ = 100), and following the $\mathbf{A_2}$ life-history strategy (Fig. 2). Fewer individuals were needed to achieve 95% probability of persistence ($MVP_{95\%}$ = 2,451-14,927 adults; Fig. 2).

### Translocation scenarios

The number of eastern sand darter released, number of consecutive years of release, $\lambda_{max}$, and translocation mortality rates were important predictors of translocation success (Table 3), where success was defined as an extant translocated population with a geometric mean abundance greater than $MVP_{95\%}$ over the last 15 years of the simulation. As expected, the probability of a successful translocation increased with greater numbers of released individuals, more frequent stocking events, and with populations that had higher maximum population growth rates (Fig. 3; Table 3). Furthermore, more individuals were needed to achieve translocation success with higher rates of translocation mortality (Fig. 3). For example, the number of eastern sand darter

(**$A_1$** life-history) needed for a successful pre-spawn stocking translocation was 7.50 to 8.28 times higher when *m* = 90% compared to when *m* = 10%, dependent on the degree of Allee effect (Tables S1-S4). Overall, post-spawn stocking required more individuals to achieve the equivalent probability of translocation success compared to pre-spawn stocking (Figs. S6–S16).

**Removals from source populations**

Single-event removals of eastern sand darter from a stable, self-sustaining, and abundant source population resulted in no measurable probability of extirpation; however, the probability of extirpation increased with larger and more frequent removal events (Fig. 4). For example, removing 1,000 **$A_1$** eastern sand darter annually for 10 years from a source population with $K$ = 25,000 individuals results in an approximately 25 times higher probability of extirpation (5.18%) than if 1,000 individuals were removed in a single event (0.21%). Furthermore, the probability of extirpation resulting from removals of 1,000 **$A_1$** eastern sand darter annually for 10 years from a source population with $K$ = 25,000 was 3.29 times higher for populations with $\lambda_{max}$ = 1.56 versus $\lambda_{max}$ = 2.69 (Fig. 4; Table S5). Generally, the probability of extirpation of eastern sand darter populations was similar across life-history strategies (Figs. 4, S17-S23).

**Balancing the impact of removals with successful establishment**

Balancing the probability of source population extirpation with the potential success of translocation was dependent on the strength of Allee effects in the translocated population, $\lambda_{max}$, $K$, and the removal/stocking frequency and numbers of individuals removed (Fig. 5). Again, consider the scenario where **$A_1$** eastern sand darter is removed annually for a decade and translocated to a historically occupied habitat with a 50% translocation mortality rate and strong

Allee effects ($a$ = 100). For this scenario, approximately 105 individuals need to be translocated from a population of at least 10,759 individuals for a decade to achieve the optimal outcome if $\lambda_{max}$ = 2.69 where the probability of success is ≥ 90% and risk of source population extirpation is ≤ 1% (Fig. 5); however, if $\lambda_{max}$ = 1.56, a source population of approximately 46,817 individuals is needed with more than double the number of individuals ($n$ = 235) removed for a decade to achieve a ≥ 90% probability of successful establishment with a low probability of extirpation (i.e., ≤ 1%; Fig. 5).

In the case where only one translocation event occurs, more individuals need to be removed to achieve the optimal outcome and ensure success (Quadrat 1; probability of success is ≥ 90% and risk of source population extirpation is ≤ 1%); for example, if $\lambda_{max}$ = 2.13, $a$ = 100, and $m$ = 50%, 622 individuals need to be removed from a source of at least 13,038 adults (~5% of the population; Fig. 5). Alternatively, if a five-year removal program was initiated, over 20,000 $\mathbf{A_1}$ individuals are needed as a source population if $\lambda_{max}$ = 2.13, $a$ = 100, and $m$ = 50% (Fig. 5). A longer-term approach where annual translocation programs remove 500 $\mathbf{A_1}$ individuals for 10 years from a source population with a $\lambda_{max}$ = 2.13, a source population size of approximately 39,421 individuals would be needed to achieve the optimal outcome (Fig. 5). The best-case scenarios occurred when $\mathbf{A_1}$ individuals were removed pre-spawn and stocked immediately because reproduction was assumed to occur shortly thereafter in the reintroduced population; removing individuals post-spawn was less successful, requiring more individuals to be removed and risking greater harm on the source population (Figs. S24, S25).

## Discussion

Like many management scenarios, predicting the success of translocations is challenging and depends on a variety of interacting abiotic, biotic, and stochastic processes that can differ across spatial and temporal scales. Assuming that suitable habitat and large source populations are available, our models demonstrate that translocation of eastern sand darter can be successful while imposing minimal effects to source populations, even in the face of Allee effects, catastrophic events, demographic and environmental stochasticity, and density-dependent population growth. However, this conclusion is contingent on the availability of an abundant, stable source population, since the probability of source population extirpation increases when population sizes are small. Therefore, initiation of translocation efforts while source populations remain large will maximize success while minimizing the risk of extirpation.

Despite the cautious threshold used for the trade-off between removals from a source population and the probability of translocation success (i.e., 1% extirpation, 90% success), a variety of scenarios were supported for achieving successful eastern sand darter translocations. Nevertheless, variation among these scenarios was dependent on variables with considerable uncertainty and it is unlikely that variables such as local population growth rate or the magnitude of Allee effects will be quantified for most species in need of reintroduction (Daredec and Courchamp 2007). Using a variety of parameterizations and scenarios provides one approach for considering the consequences of model uncertainty; for example, our models demonstrated that underestimating the source population size can unknowingly lead to situations with high risk of extirpation and a low probability of success, especially given the nonlinearities (e.g., Fig. 5).

Two factors in our models that can be actively manipulated by managers to achieve success included the total number of individuals introduced and translocation mortality. Maximizing the number of propagules released during translocation is an obvious approach to avoid the influence of stochastic events and maximize the likelihood of success (Daredec and Courchamp 2007). For imperilled species with few populations remaining, however, removal of large numbers of individuals could be catastrophic when source populations are small. As such, it is critical that translocation mortality, defined here to include mortality related to handling, the translocation process (i.e., transport and release), and post-release factors, is reduced. Approaches to minimize mortality during the transport process are well-documented, including the use of live-hatchery vehicles with controlled environments for transport and fasting organisms prior to transport to minimize stress, oxygen demand, and fouling of the transport environment (Cowx 1994). Simple experiments with surrogate species could improve knowledge on optimal transport conditions for imperilled fishes, thus reducing translocation mortality and reducing the number of propagules needed for translocation.

Further experimentation is needed to understand how the immediate loss of propagules after introduction can be reduced. For example, following its introduction to a lake in Nova Scotia, captive-bred Atlantic whitefish (*Coregonus huntsmani*; Endangered) remained close to the release site and were observed foraging during the day, leaving individuals susceptible to piscivory by aerial visual predators (e.g., common loon *Gavia immer*; Cook et al. 2014). Alternatively, reintroduction experiments of razorback sucker (*Xyrauchen texanus*) to the Colorado River indicated that post-stocking dispersal was rapid, most often characterized as downstream drift; however, razorback sucker that were preconditioned to the flow conditions were significantly less likely to disperse downstream than individuals reared in ponds (Mueller et al. 2003). Given the differences in life-history and ecology of eastern sand darter to other reintroduced species, experiments are needed to understand post-release dispersal patterns and the magnitude of immediate mortality while testing management strategies to reduce both factors.

Our models contained several assumptions that may or may not be reflected in nature including that translocated populations would demonstrate maximum population growth rates, catastrophes would be relatively infrequent compared to the lifespan of the species, and that translocated populations would demonstrate identical life-history characteristics to the source population. Furthermore, the models presented here did not incorporate potential genetic consequences of small founding populations, which can reduce the probability of persistence of translocated individuals and therefore increase potential harm to the species (e.g., Ahlroth et al. 2003; Jamieson 2011). Nevertheless, incorporating many parameterizations of influential variables with considerable uncertainty and modelling the most divergent life-histories provides a general understanding of the risks of source population extirpation and potential benefits to the species when undergoing translocation.

**Management implications**

Eastern sand darter is presumed extirpated in Big Otter Creek, Catfish Creek, and the Ausable River in southwestern Ontario (Fisheries and Oceans Canada 2012). Due to the small body size of the species, the likelihood of natural dispersal from disjunct source populations (Thames River, Grand River, Sydenham River, certain nearshore areas of Lake St. Clair and Lake Erie) to historically extirpated sites is unlikely. Reintroduction through captive breeding or translocation has yet to occur for this species in Canada (Lamothe et al. 2019b). The models presented here demonstrate that an understanding of source population size, combined with the evaluation of uncertainty for variables with little management control (e.g., Allee effects, catastrophe rates, environmental and demographic stochasticity) can provide a set of quantitative scenarios where the probability of translocation success is high for eastern sand darter, despite considering the demographic effects that could restrict population persistence. However, like many species under consideration for translocation, knowledge gaps and uncertainties exist for eastern sand darter that raise questions about the success of translocations in the wild.

First, uncertainties exist as to whether habitat conditions at extirpated sites have recovered sufficiently to allow the persistence of eastern sand darter. The first step in deciding if reintroduction is an appropriate management strategy is determining whether suitable habitat exists at historically occupied sites (Lamothe and Drake 2019). Research is ongoing to determine if present-day fish community and habitat conditions in Big Otter Creek are capable of supporting translocated individuals (e.g., evaluation of fish community including known competitors - Barnucz et al. 2020); quantifying substrate characteristics at extirpated sites). Second, there are few estimates of population size for many imperilled freshwater fishes in North America, including eastern sand darter (COSEWIC 2009; Fisheries and Oceans Canada 2012), which hinders the ability to estimate source population stability and the potential harm of removals. Moreover, formal captive breeding efforts of eastern sand darter for supplementing or fully supporting reintroduction efforts have yet to be initiated in Ontario. Although development of standardized sampling protocols to quantify the abundance of a species is costly and time-intensive, such approaches are warranted for imperilled species, including eastern sand darter, to better understand and resolve the translocation trade-offs described here (Pope et al. 2010).

## Acknowledgements

Funding was provided by Fisheries and Oceans Canada's Species at Risk Program and a Natural Sciences and Engineering Research Council Visiting Fellowship to KAL. The authors thank E. Quider for insightful questions and comments during the development of this study.

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**Table 1** Description of variables used to model the life-cycle and translocation of eastern sand darter.

| *Symbol* | *Variable* | *Description* |
|---|---|---|
| $\lambda$ | Population growth rate | The long-term change in population size based on current conditions |
| $\mathbf{A_1}$; $\mathbf{A_2}$ | Life-history scenarios | Two distinct life-cycle models for eastern sand darter |
| $F_t$ | Fertility rate | Contribution of offspring from an adult in age class *t* to the next-census of age-1 individuals |
| $\sigma_t$ | Survival rate | Rate of survival for individuals of age class *t* to the next census |
| $\varphi$ | Female proportion | Proportion of females in the population |
| $\rho_t$ | Mature proportion | Proportion of mature individuals in the population at age *t* |
| $f_t$ | Fecundity | Mean number of eggs produced per clutch per individual in age-class *t* |
| $C$ | Number of clutches | Number of clutches per year |
| $\sigma_{0,Et}$ | YOY survival rate; Density dependence | A Beverton-Holt function applied to young-of-year annual survival |
| $a_f$ | Allee effect | A Holling type III function applied as a proportional reduction in breeding success |
| $t_{mat}$ | Age-at-first-maturity | Age in years at which eastern sand darter become mature and contribute offspring to the population |
| $t_{max}$ | Longevity | Maximum life-span in years |
| $W_t$ | Weight | Weight at age *t* |
| $L_t$ | Length | Length at age *t* |
| $t_0$ | Age zero | Hypothetical age at which fish would have had a length of 0 |
| $L_\infty$ | Asymptotic length | A von Bertalanffy growth function parameter indicating the average length of eastern sand darter if it grew for an infinitely long timeframe |
| $k$ | Curvature | A von Bertalanffy growth function parameter that determines how quickly eastern sand darter reaches $L_\infty$ |
| $E_t$ | Egg density | Number of annual eggs produced |
| $b$ | Density-dependence coefficient | Beverton-Holt function parameter that determines strength of density dependence |
| $K$ | Carrying capacity | Maximum population size that can be sustained indefinitely |
| $MVP_{\%}$ | Minimum viable population size | Minimum viable population size with some level of confidence |
| $M_t$ | Mortality | Annual instantaneous mortality |
| $m$ | Translocation mortality | Mortality resulting from transport or immediately post-stocking |

**Table 2** Values for variables used to model two life-history scenarios (**$A_1$** and **$A_2$**) of eastern sand darter.

| | *Life-history scenario* | |
|---|---|---|
| *Variable* | **$A_1$** | **$A_2$** |
| $t_{max}$ | 4 | 3 |
| $t_{mat}$ | 1 | 2 |
| $C$ | 3 | 2 |
| Generation time | 1.92 | 1.92 |
| $\sigma_{0,\lambda=1}$ | 0.00609 | 0.02593 |
| $\sigma_{0,\max,\lambda=1.56}$ | 0.01176 | 0.07131 |
| $\sigma_{0,\max,\lambda=2.13}$ | 0.01766 | 0.14150 |
| $\sigma_{0,\max,\lambda=2.69}$ | 0.02350 | 0.23410 |
| $b_{,\lambda=1.56}$ | 0.00883 | 0.06896 |
| $b_{,\lambda=2.13}$ | 0.01865 | 0.17890 |
| $b_{,\lambda=2.69}$ | 0.02842 | 0.32437 |

**Table 3**. Logistic regressions of translocation success versus failure when translocation occurs pre- and post-spawn for the two life-history scenarios (**$A_1$** and **$A_2$**) and two levels of Allee effects ($a$ = 50 or 100). All estimates are significant with $p < 0.001$.

| | *Pre-spawn stocking* | | | *Post-spawn stocking* | | |
|---|---|---|---|---|---|---|
| *Variable* | *Estimate* | *SE* | *z* | *Estimate* | *SE* | *z* |
| **$A_1$**; $a = 50$ | | | | | | |
| Intercept | -9.55 | 0.02 | -505.71 | -13.61 | 0.03 | -538.73 |
| log($N$) | 2.01 | 0.00 | 619.44 | 2.43 | 0.00 | 606.46 |
| log($\lambda$) | 3.05 | 0.01 | 238.10 | 3.27 | 0.01 | 235.13 |
| Years stocked | 0.34 | 0.00 | 380.94 | 0.39 | 0.00 | 390.98 |
| $m$ | -5.31 | 0.01 | -431.44 | -6.18 | 0.01 | -435.23 |
| **$A_1$**; $a = 100$ | | | | | | |
| Intercept | -12.06 | 0.02 | -542.26 | -16.62 | 0.03 | -531.82 |
| log($N$) | 2.21 | 0.00 | 626.01 | 2.65 | 0.00 | 573.69 |
| log($\lambda$) | 3.26 | 0.01 | 245.23 | 3.52 | 0.01 | 238.19 |
| Years stocked | 0.35 | 0.00 | 381.72 | 0.42 | 0.00 | 388.01 |
| $m$ | -5.58 | 0.01 | -430.20 | -6.62 | 0.02 | -429.97 |
| **$A_2$**; $a = 50$ | | | | | | |
| Intercept | -13.03 | 0.03 | -518.47 | -17.25 | 0.03 | -525.75 |
| log($N$) | 2.49 | 0.00 | 587.73 | 2.82 | 0.00 | 566.85 |
| log($\lambda$) | 4.05 | 0.01 | 275.80 | 4.38 | 0.02 | 277.41 |
| Years stocked | 0.46 | 0.00 | 420.70 | 0.51 | 0.00 | 419.85 |
| $m$ | -6.50 | 0.01 | -438.18 | -7.21 | 0.02 | -435.02 |
| **$A_2$**; $a = 100$ | | | | | | |
| Intercept | -15.90 | 0.03 | -531.67 | -20.53 | 0.04 | -508.17 |
| log($N$) | 2.68 | 0.00 | 581.19 | 3.04 | 0.01 | 531.96 |
| log($\lambda$) | 4.32 | 0.02 | 281.53 | 4.58 | 0.02 | 272.83 |
| Years stocked | 0.48 | 0.00 | 418.28 | 0.53 | 0.00 | 409.05 |
| $m$ | -6.79 | 0.02 | -434.45 | -7.54 | 0.02 | -423.59 |

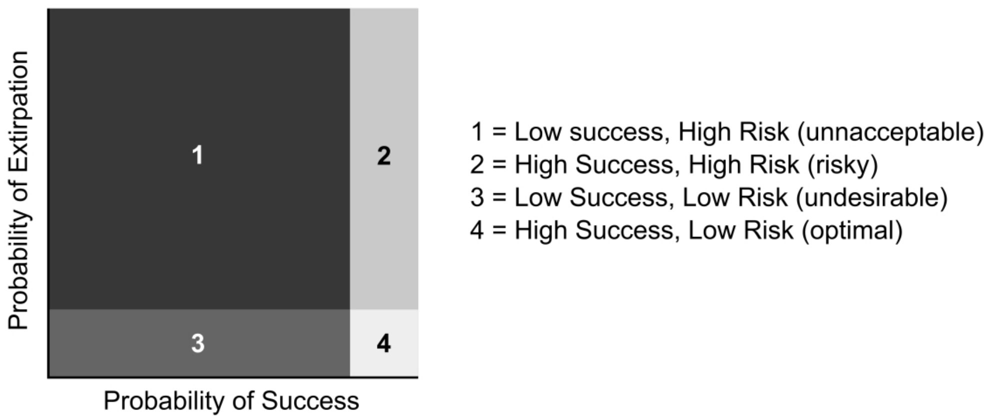


Figure 1 A cost-benefit framework where 1 = unacceptable outcome (low chance of success; high risk of extirpation), 2 = risky outcome (high chance of success; high risk of extirpation), 3 = undesirable outcome (low chance of success; low risk of extirpation), and 4 = optimal outcome (high chance of success; low risk of extirpation). The asymmetrical quadrants represent weighted costs and benefits, where an optimal outcome is defined by a much higher probability of success than extirpation.

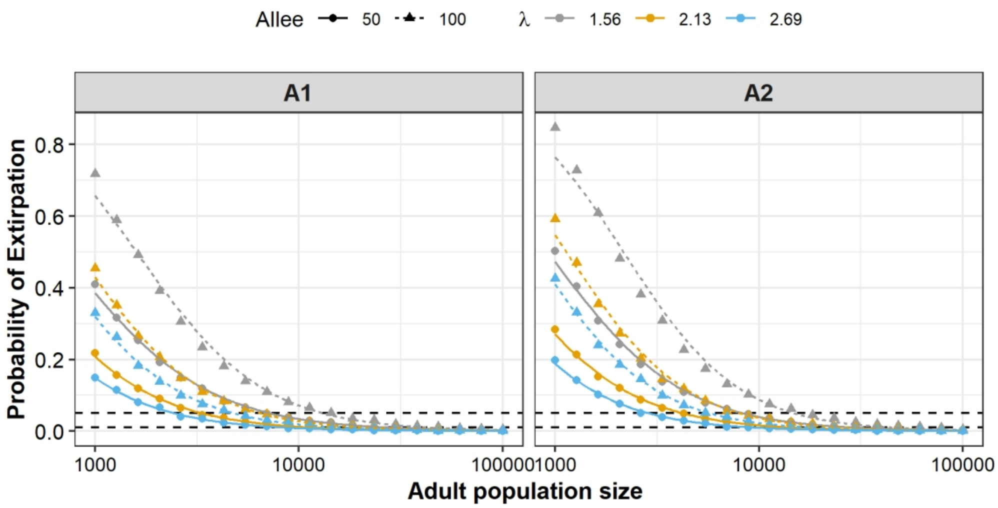


Figure 2 Identification of the minimum viable population (MVP) at 95% and 99% probabilities of persistence (5% and 1% probability of extirpation, respectively; dashed lines) for three maximum population growth rates (λmax = 1.56, 2.13, 2.69), two levels of Allee effect (a = 50, 100), and two life-history strategies A1 and A2.

165x88mm (300 x 300 DPI)

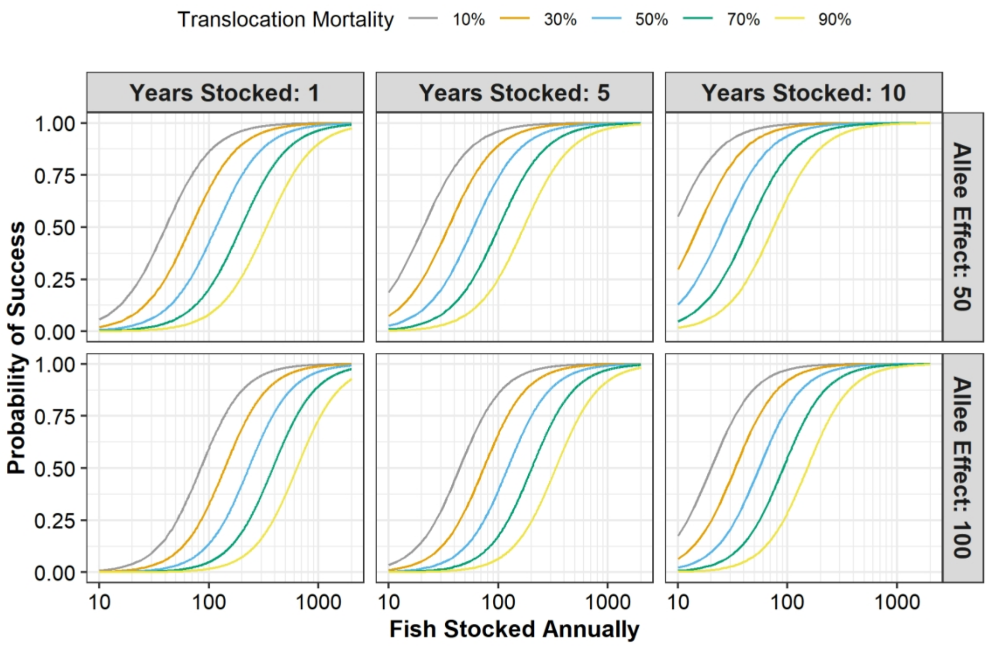


Figure 3 Probability of translocation success as a function of fish stocked annually (log-scale) for two different strengths of Allee effects (rows), across one, five, or 10 years of stocking (columns), and various degrees of translocation mortality (10-90%; colours). Success is defined as an adult population maintained after stocking stopped with a geometric mean population size greater than 5% extinction probability (MVP95%) over the last 15 years of the simulation. Shown is life history strategy A1, where introductions were performed pre-spawn and population growth rate was 2.13. Results of additional simulation scenarios are presented in Supplemental Material.

165x111mm (300 x 300 DPI)

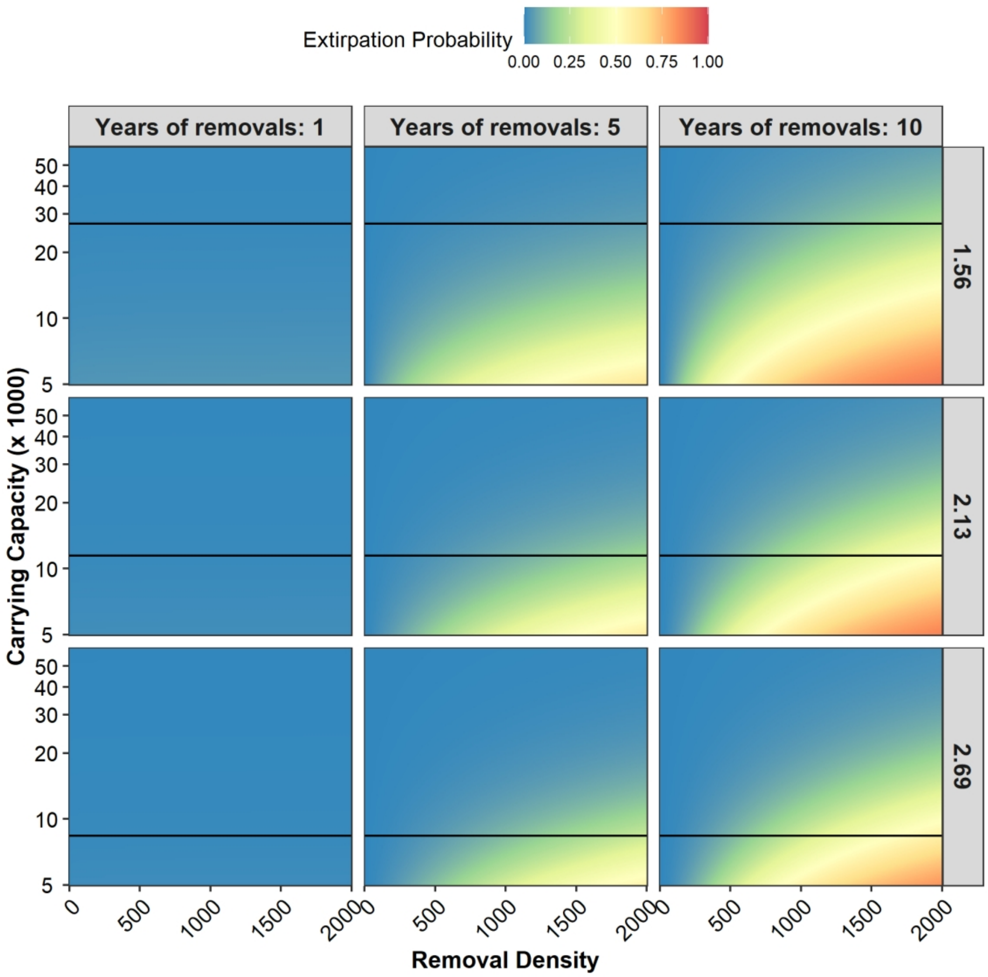


Figure 4 Extirpation probability of source populations after 50 years as a function of the number of fish removed and carrying capacity. Plots separated by years of removals (columns: one, five, or 10 years) and maximum population growth rate (rows: 1.56, 2.13, or 2.69). Shown is life-history strategy A1, with a low Allee effect (a = 50), and where removals were performed pre-spawn. Black lines indicate simulated MVP99% for each population growth rate (Fig. 2).

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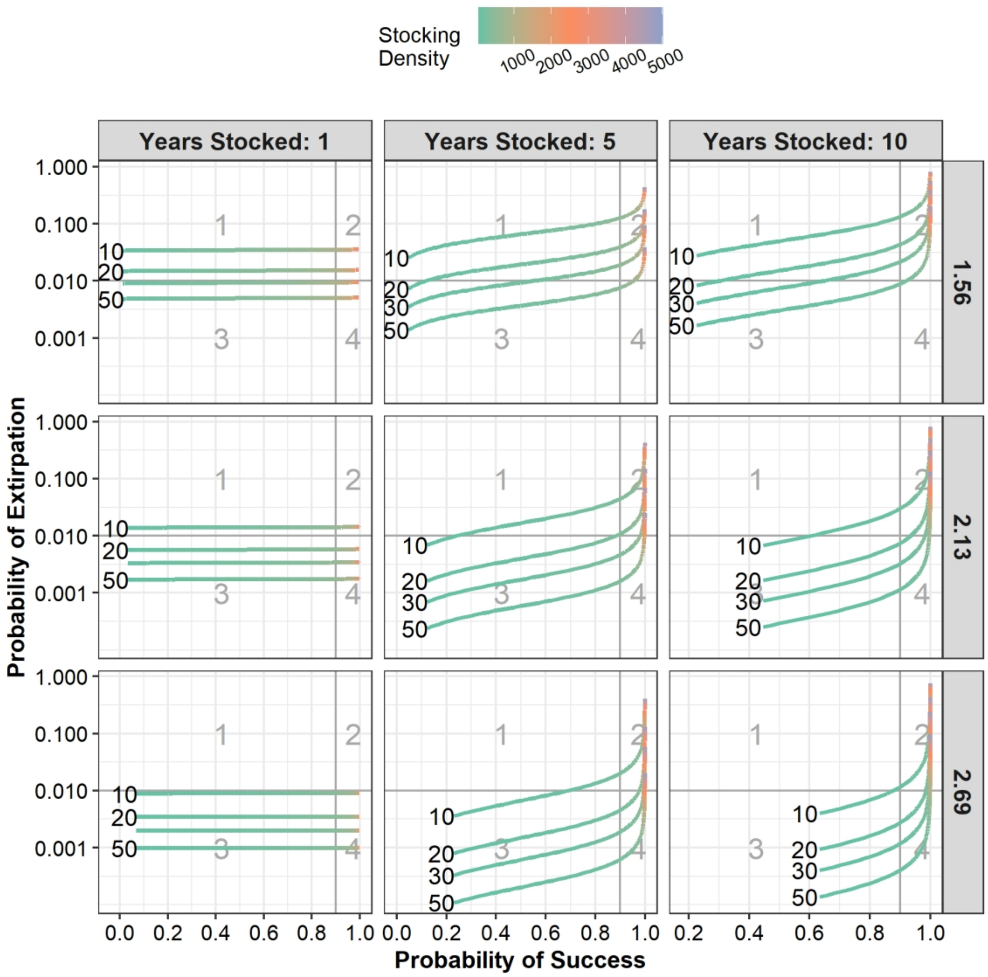


Figure 5 Probability of extirpation (log-scale) of source stocks of various carrying capacities (10 = 10,000, 20 = 20,000, 30 = 30,000, 50 = 50,000 individuals) versus the probability of successful translocation. Presented are the results when removing individuals for one, five, or 10 consecutive years pre-spawn from a source population and releasing them immediately. In this scenario, the source and stocked populations are composed of A1 individuals with a 50% translocation mortality across population growth rates (λ = 1.56, 2.13, 2.69) and high Allee effect (a = 100). Probability of success is defined as maintaining a post-stocking adult population with a geometric mean population size greater than MVP95% over the last 15 years of the simulation. The black lines represent the boundaries of the cost-benefit outcomes with an optimal outcome of ≤ 1% probability of extirpation for a ≥ 90% probability of success (c.f., Fig. 1).

165x165mm (300 x 300 DPI)