

Allee Effects and the Risk of Biological Invasion

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The Allee effect is a nonlinear phenomenon exhibited in the population dynamics of sparse populations in which the per capita population growth rate increases with increasing population density. In sufficiently sparse populations, the Allee effect may lead to extinction and is known to generate a threshold in the probability of establishment when presented as a function of introduced population size or density. As introduced populations are generally small, Allee effects are probably common in biological invasions and their consideration is necessary for accurately assessing the risk of invasion by many species, including all sexually reproducing species. *Bythotrephes longimanus*, an invasive, freshwater, cladoceran zooplankton from Europe, is one such species. Here, I review a previously published model of the Allee effect for continuously sexually reproducing species. Then, I develop a new model for seasonally parthenogenetic species such as *Bythotrephes*, and thereby demonstrate the potential consequences of Allee effects. This result underscores the importance of considering nonlinear phenomena, including thresholds, when conducting risk analysis for biological introductions.

KEY WORDS: Allee effect; biological invasion; *Bythotrephes longimanus*; risk analysis; risk assessment

1. INTRODUCTION

Biological invasions are currently the leading threat to the diversity of freshwater lakes worldwide⁽¹⁾ and exceedingly costly to society.⁽²⁾ Because most biological invasions result from the anthropogenic introduction of nonindigenous species, there is an increasing need for techniques for analyzing the risk that introduced species will establish viable populations and become a nuisance. A large body of theoretical literature in ecology has accumulated describing models of stochastic growth and decline of populations and for calculating the probability of extinction.⁽³⁾ It has been proposed that this theory may be employed in risk analysis of biological invasion to predict the probability that introduced populations establish, on the grounds that the probability of persistence (= establishment) equals one minus the probability

of extinction.^(3,4) Models traditionally employed in this context often assume that population growth is roughly exponential, i.e., populations exhibit a constant growth rate.⁽⁵⁾ However, an increasing body of empirical studies suggests that for many species population growth should be modeled with Allee effects.⁽⁶⁾

In general, the Allee effect occurs when the growth rate of sparse populations increases with increasing population density (see Fig. 1). This acceleration results from increased mate finding, forage ability, or defense in species that exhibit cooperation among individuals, including all sexually reproducing species. When severe, deterministic models of the Allee effect generate an unstable equilibrium, above which populations increase to carrying capacity and below which populations diminish until extinct. Among other things, a mechanistic, stochastic model of the Allee effect in mate-limited populations can be used to predict the probability of extinction,⁽⁷⁾ from which the probability of persistence can be calculated.

Although Allee effects are often of negligible importance in large, naturally occurring populations,

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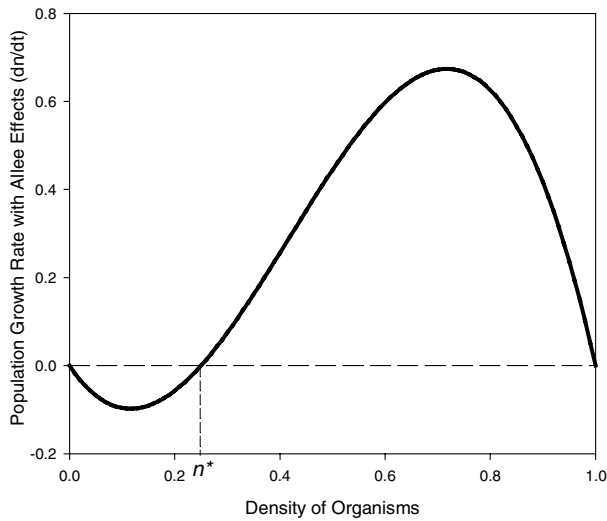


Fig. 1. The Allee effect occurs when population growth rate increases with increasing population size or density. Here, the Allee effect is represented by the equation $dn/dt = rn(1-n)(n-a)$ (after Reference 14). When severe, the Allee effect exhibits an unstable equilibrium (n^*). Here, for simplicity, population density is presented as a fraction of carrying capacity.

they are particularly relevant to the risk assessment and regulation of introduced species (including genetically modified organisms), because such populations generally are initially sparse in the recipient ecosystem. This will be especially true in scenarios where organisms are expected to rapidly disperse after release, such as might occur for passively dispersed propagules. In particular, plankton unintentionally released in ballast water and plants that are primarily dispersed by wind are likely to exhibit Allee effects. In contrast, species whose pathways of dispersal facilitate aggregation (such as in packing materials) are less likely to exhibit Allee effects and thereby exhibit higher probabilities of invasion. Since conclusions that result from exponential models may severely overestimate the risk of invasion for species that exhibit an Allee effect, and because Allee effects may introduce thresholds that do not occur for exponentially growing populations, careful consideration of this phenomenon is critical to accurately assessing the risk of biological invasion.

After reviewing the consequences of Allee effects in a continuously sexually reproducing population, I extend the application of this theory by investigating the Allee effect on an inter-annual scale for a seasonally parthenogenetic species, thereby indicating the broad range of life histories and species to which Allee effects may apply. As a model species

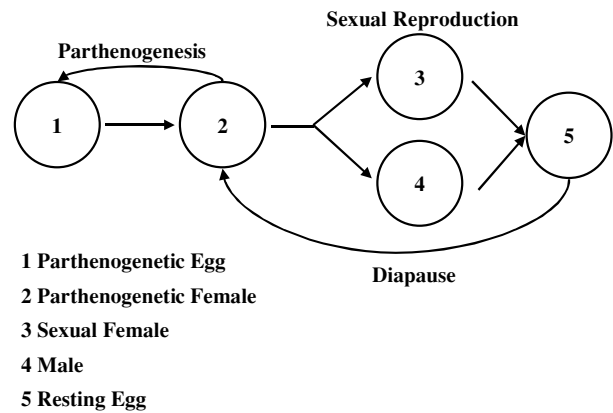


Fig. 2. The periodically parthenogenetic life cycle of *Bythotrephes* results in a short period of sexual reproduction when resting eggs are being produced during the late summer or fall. The duration of sexual reproduction and the density of males jointly determine mate success in theoretical models, potentially inducing an Allee effect.

to demonstrate the consequences of Allee effects in biological invasions, I consider *Bythotrephes longimanus*, a palearctic, freshwater, predatory cladoceran zooplankton that has been invasive in the lakes of the Midwestern United States and neighboring areas of Canada and was likely released into the Great Lakes in ballast water in the early 1980s.^(8,9) Like most cladocera, *Bythotrephes* reproduces parthenogenetically during the summer, after which males are produced and sexual reproduction ensues so that overwintering occurs as sexually produced resting eggs (Fig. 2). Since resting egg production is mostly determined by the density of individuals during sexual reproduction, this intermittently asexual life history produces an interesting opportunity for the Allee effect to occur: introduced populations must achieve a critical density in the first growing season in order to locate mates during the brief period of sexual reproduction. Other species of cladocera are also known to be invasive, including *Eubosmina coregoni*, *Daphnia lumholtzi*, and *Cercopagis pengoi*, indicating that the results presented here have more general application.

2. MODELS

Here, I review the model of Allee effects for continuously sexually reproducing species developed by Dennis.⁽⁷⁾ Then, I develop a difference model for seasonally parthenogenetic species such as *Bythotrephes*. By considering the same factors in each model, mate limitation and demographic stochasticity, I am able

Table I. Parameter Definitions and Values

Parameter	Definition and Source	Value	Equations
<i>n</i>	Number of individuals	N/A	1, 10, 11, 12
<i>n</i> ₀	Initial number of individuals	0–200	2, 3, 10, 12
<i>θ</i>	Allee effect parameter	25	1, 2, 3
<i>μ</i>	Instantaneous death rate	0.4	2, 3, 3
<i>λ</i>	Instantaneous birth rate	0.5	2, 3, 3
<i>μ</i>	Instantaneous death rate ^a	0.075	4, 6, 9–12
<i>λ</i>	Instantaneous birth rate ^a	0.15	4, 6, 9–12
<i>c</i>	Clutch size ^b	4.0	5, 6, 9
<i>e</i>	Probability of emergence ^c	0.65	5, 6, 9
<i>t</i>	Duration of parthenogenetic reproduction ^a	70 d	4, 6, 9
<i>d</i>	Detection radius ^d	9 × 10 ⁻³ m	7, 9
<i>n</i>	Population density	N/A	4–7
<i>n</i> [*]	Allee threshold difference model ^e	1.0 × 10 ⁻³	9
<i>v</i>	Swimming speed ^f	23.3 m h ⁻¹	7, 9
<i>τ</i>	Duration of mating ^a	21 d	8, 9
<i>P_m</i>	Proportion of females that mate	N/A	5, 6, 8
<i>Z</i>	Mate encounter rate	N/A	7, 8

Note: Italics indicate that values were chosen for heuristic purposes. Parameters in bold vary with environmental conditions; values chosen are typical of estimates for Great Lakes *Bythotrephes* populations.

^aJarnagin.⁽¹⁵⁾

^bYan and Pawson.⁽¹⁶⁾

^cHerzig.⁽¹⁷⁾

^dA. Blukacz (personal communication).

^eValue calculated from Equation (9), units are individuals m⁻³.

^fRivier.⁽¹⁸⁾

to compare the resulting probability of establishment for the different life cycles. Parameter values used to evaluate all models are listed in Table I.

2.1. Continuous Growth of Sexually Reproducing Populations

To evaluate the role of Allee effects in sparse populations, Dennis⁽⁷⁾ considers the continuous birth-death process with mating probability represented by the rectangular hyperbola

$$P_m = \frac{n}{n + \theta}, \tag{1}$$

where *n* is the population density and *θ* is the density at which half of the female population mates successfully in one time unit, in this case during the period of sexual reproduction (Fig. 3). The general birth-death process is a standard model for stochastic population

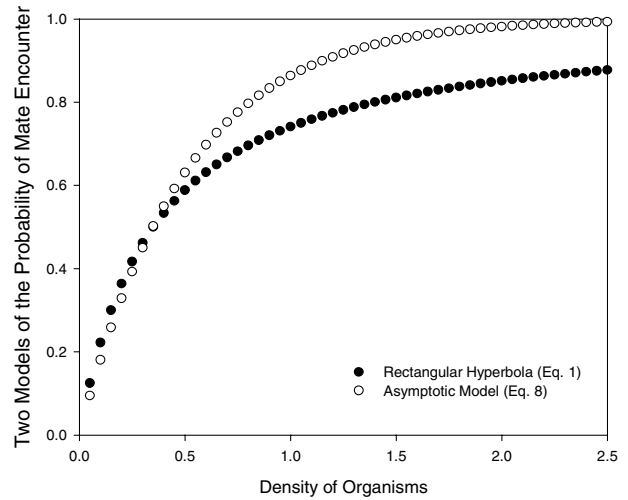


Fig. 3. Two models of mate limitation. The rectangular hyperbola (Equation (1)) was used by Dennis,⁽⁷⁾ while the asymptotic model (Equation (8)) has a mechanistic interpretation given by Gerritsen.⁽¹⁹⁾ The consequences of each for the probability of invasion were determined by Dennis⁽⁷⁾ to be similar in simulations.

growth^(10,11) and assumes that the population grows or declines by one individual in each time step with probabilities dependent on the time-independent death and birth rates *μ* and *λ*. One result of this model is that the probability of extinction is given by⁽⁷⁾

$$P_{\text{ext}} = \sum_{x=n_0}^{\infty} \binom{\theta + x}{x} \left(1 - \frac{\mu}{\lambda}\right)^{\theta+1} \left(\frac{\mu}{\lambda}\right)^x, \tag{2}$$

and that the probability of establishment (1 – *P_{ext}*) exhibits a threshold in the form of a sigmoidal response to increasing the size of the introduced population (Fig. 4). When compared to the result of a nonmate-limited birth-death process, where the probability of extinction is given by^(7,11)

$$P_{\text{ext}} = \begin{cases} (\mu/\lambda)^{n_0} & \lambda > \mu \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

(and the probability of establishment is 1 – *P_{ext}*), the Allee effect clearly reduces the risk of biological invasion at small population densities (Fig. 4). Note that *θ* is the key parameter determining this result. As *θ* approaches 0 the solution to the nonmate-limited model (Equation (3)) is recovered.

This result is important for understanding the significance of the Allee effect to biological invasions generally. First, the Allee effect introduces a threshold into the probability of persistence, which should have consequences for how the risk of invasive species is

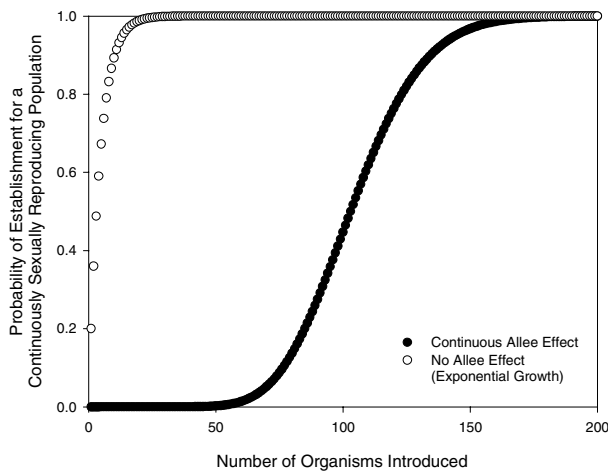


Fig. 4. An Allee effect produced by the rectangular hyperbola mate-limitation model exhibits a threshold in the probability of persistence for a continuously sexually reproducing population. A birth-death process with no Allee effect (exponential model) is presented for comparison.

understood and managed. At introduced population sizes far from the threshold, management efforts will have little effect on the probability of establishment. However, in the vicinity of the threshold the probability of establishment is very sensitive to small perturbations. Inaccuracies that result from sampling error, model misspecification, or variable management effectiveness will have severe and unpredictable consequences for estimated establishment probability. Second, efforts to model the Allee effect in biological invasions should only be undertaken after carefully studying the parameter θ , since it determines the location of the threshold. This result is generally true for continuously sexually reproducing species and should be broadly applicable. However, the assumption of continuous sexual reproduction is violated in the case of *Bythotrephes* because of seasonal parthenogenesis, suggesting that a different modeling framework would be more appropriate.

2.2. Difference Model for Seasonally Parthenogenetic Species

Since the sexual reproduction in *Bythotrephes* occurs at the end of summer growth, populations generally are at their peak density, providing a convenient point for tracking changes in population size across years. Peak density in any given year is given by the

expectation of population size at time t for a simple birth-death process

$$E[n_t] = n_e \exp\{(\lambda - \mu)t\}, \quad (4)$$

where n_e is the initial population size (i.e., emergence from resting eggs in the spring) and t is the duration of summer population growth.⁽¹¹⁾ The density of emerging resting eggs is

$$n_e = ecP_m n_{i-1}, \quad (5)$$

the product of peak density in the previous year (n_{i-1}), the proportion of females that successfully mated (P_m), which may be a constant or a function, average clutch size produced (c), and the proportion of resting eggs that emerge (e). Combining Equations (4) and (5) and substituting the subscript i (denoting years) for t (time) results in a difference model for inter-annual population growth

$$n_i = ecP_m n_{i-1} \exp\{(\lambda - \mu)t\}. \quad (6)$$

This model is the basis for the rest of my analysis.

2.3. Mate-Finding Model

Several models of mate limitation are available from which P_m can be derived.⁽⁷⁾ Given the random movement, Gerritsen and Strickler⁽¹²⁾ developed a model for the zooplankton encounter rates as a function of swimming speed and detection radius. Assuming that the sex ratio is one, the rate of mate encounter equals

$$Z = \frac{2\pi}{3} d^2 n v, \quad (7)$$

where d is the detection radius, n is the population density, and v is average swimming speed (assumed to be the same for both males and females). (Note that this is not exactly correct because *Bythotrephes* probably locates conspecifics by sight (Blukacz, personal communication), thus the detection volume is not spherical as assumed by Gerritsen and Strickler.⁽¹²⁾ To my knowledge, the consequences of this assumption are unknown.) Assuming that encounters are Poisson distributed and occur at rate Z , the probability that a female locates a mate in time τ is the asymptotic function (Fig. 3)

$$P_m = 1 - \exp\{-Z\tau\}. \quad (8)$$

Substituting Equation (8) into Equation (6) and solving for the equilibria obtains

$$n^* = 0, \frac{-3 \ln \left(1 - \frac{1}{ce \exp\{(\lambda - \mu)t\}} \right)}{2\tau\pi d^2 v}. \quad (9)$$

Evaluating the nonzero equilibrium from Equation (9) at independently estimated parameter values (Table I) produces critical density $n^* \approx 1.0 \times 10^{-3}$ individuals m^{-3} . If we make the simplifying assumption that intrinsic population growth rate does not vary between years, estimating the probability of persistence is now reduced to estimating the probability of attaining n^* within the first growing season through parthenogenetic reproduction.

2.4. Probability of Establishment

In keeping with the result obtained above for a continuously sexually reproducing population, I evaluate the probability of attaining the threshold n^* according to a simple nonmate-limited birth-death process. That is, my assumption is that only demographic stochasticity applies. I begin with the initial condition that populations are introduced at the beginning of the growing season ($t = 0$), the consequence of which is that n^* must be attained by time $t = 70$ for establishment to occur. Since the probability density of population size n at time t is given by Richter-Dyn and Goel⁽¹⁰⁾ as

$$P_{n,n_0}(t) = \left(\frac{\lambda}{\mu}\right)^n \sum_{k=0}^{\min(n_0,n)} (-1)^k \binom{n_0+n-k-1}{n-k} \times \binom{n_0}{k} \left(\frac{e^{(\lambda-\mu)t} - 1}{(\lambda/\mu)e^{(\lambda-\mu)t} - 1}\right)^{n_0+n-k} \times \left(\frac{(\mu/\lambda)e^{(\lambda-\mu)t} - 1}{e^{(\lambda-\mu)t} - 1}\right)^k, \quad (10)$$

where n_0 is the population size at $t = 0$, the probability that a population introduced at size n_0 is greater than or equal to n^* at t is

$$P_{n \geq n^*, n_0}(t) = 1 - \sum_{n=0}^{n^*-1} P_{n,n_0}(t). \quad (11)$$

In contrast, for a population that grows without Allee effects, i.e., one that does not need to attain a critical density to mate, the probability of establishment is one minus Equation (3), i.e.,

$$P_{\text{est}} = 1 - \left(\frac{\mu}{\lambda}\right)^{n_0}, \quad (12)$$

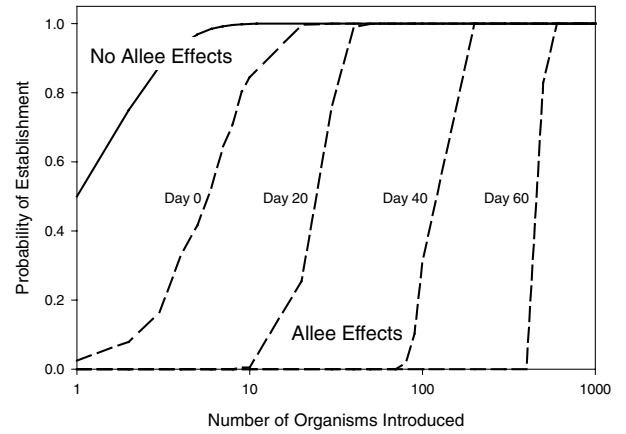


Fig. 5. Model results indicate that seasonal parthenogenesis causes *Bythotrephes* (dashed lines) to require greater initial population sizes for high probabilities of establishment than for species that grow according to an asexual birth-death process (solid line). A model in which the population must obtain a critical density of $n^* = 1.0 \times 10^{-3}$ by day 70 requires increasingly large population sizes as the summer season progresses. The establishment curve is plotted for each of several introduction dates (days 0, 20, 40, and 60). Simulation results were obtained from an algorithm described by Renshaw⁽¹¹⁾ for the simple birth-death process.

where $\lambda > \mu$, and 0 elsewhere. The probability of establishment as a function of introduced population size is different for populations modeled by Equation (11) (seasonally mate-limited populations) than those modeled by Equation (12) (populations that are never mate limited) (Fig. 5). Importantly, the probability of establishment for the inter-annual Allee effect is everywhere less than that for species without an Allee effect, consistent with the general conclusion that failing to account for Allee effects results in overestimating the probability of establishment. Furthermore, a comparison of Figs. 4 and 5 reveals that the threshold that occurs in continuously sexually reproducing species recurs in seasonally parthenogenetic species when the population is introduced at the beginning of the growing season (day 0) and has the entire summer to reproduce, though it occurs at a relatively small number of individuals. To determine the probability of the establishment at later introduction dates, I simulated the birth-death process (Reference 11, p. 38) for populations introduced into a 10 ha lake 10-m deep on days 0, 20, 40, and 60 of a 70-day growing season. If the population succeeded in obtaining the density $n^* \approx 1.0 \times 10^{-3}$ individuals m^{-3} , the population was declared to have established. The results of this simulation indicate that as the season progresses an increasing number of individuals are

required for a high probability of establishment (Fig. 5). Note the logarithmic scale of the x -axis.

2.5. Factors Influencing Invasion Success: Overcoming Allee Effects

To consider how the biological characteristics of *Bythotrephes* influence invasiveness, I conducted a local sensitivity analysis in Equation (9) by plotting n^* over a biologically plausible range for each variable, while holding all other variables constant at the values in Table I. The variables c , $r = \lambda - \mu$, τ , and d are plotted on the primary x -axes in Fig. 6; e , t , and v , each of which are linear with one of the former variables, are plotted on the secondary x -axes. This figure indicates that critical density (Equation (9)) is most sensitive to changes in the parthenogenetic population growth rate (or, equivalently, lengthening the growing season) and is reasonably insensitive to other parameters. These results can be interpreted in

two ways. First, local sensitivity indicates how small changes in the biology of *Bythotrephes* or differences between *Bythotrephes* and similar species would affect the critical density n^* , and hence the probability that the population obtains the critical threshold. Alternatively, the sensitivity of n^* to these variables indicates the effects of error in parameter estimates. Measurement error in variables to which n^* is insensitive is relatively unimportant for computing the probability of establishment; error in variables to which n^* is highly sensitive will be of greater importance.

3. DISCUSSION

The result obtained here demonstrates the likely importance of the Allee effect in the process of establishment and its consequences for the risk of invasion. First, in general, the Allee effect lowers the risk of establishment for sparse, sexually reproducing populations. Second, a comparison of models for continuous

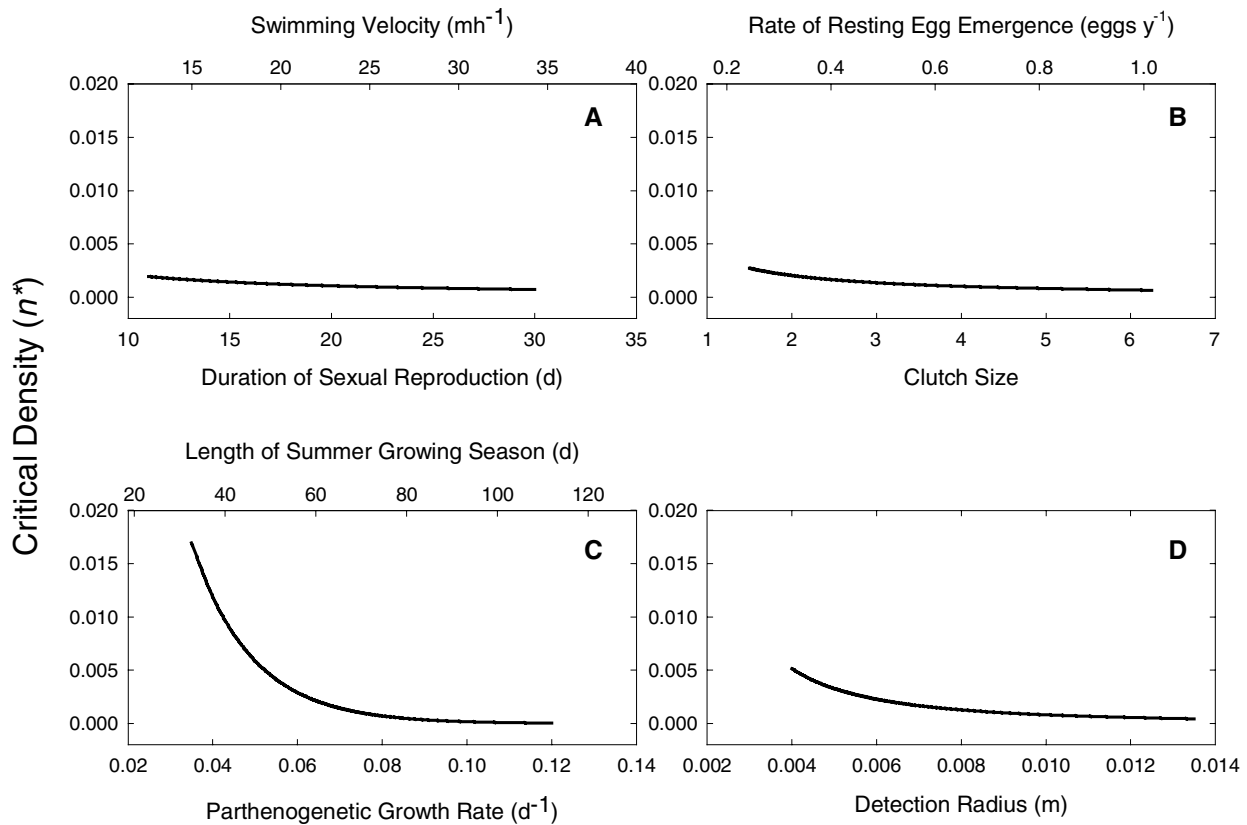


Fig. 6. Sensitivity of Equation (9). The change in critical density (n^*) with changes in (A) the duration of sexual reproduction and swimming speed, (B) clutch size and the rate of resting egg emergence, (C) parthenogenetic population growth rate and the length of the summer growing season, and (D) detection radius.

versus seasonal mate limitation (Fig. 4 vs. Fig. 5) illustrates that the threshold that occurs in continuously mate-limited populations, below which the probability of establishment is negligible, is absent or severely reduced in seasonally mate-limited populations introduced at the beginning of the summer growing season. That is, the parthenogenetic period of reproduction in the seasonal model greatly increases the probability that a species like *Bythotrephes* will establish viable populations when compared to continuously mate-limited populations, such as most copepods. This is because seasonally parthenogenetic species are only mate limited at the end of the summer, following a period of exponential population growth.

In contrast, seasonal parthenogenesis reduces the probability of establishment for *Bythotrephes* compared to species never subject to mate limitation, such as most rotifers. As expected, this effect is more pronounced as the number of days remaining in the growing season declines. At the very end of the growing season quite a large number of individuals are required to guarantee sexual reproduction and establishment. Because of the range of biologically realistic model parameterizations, more precise predictions about how life history and mating system will influence the probability of establishment are not possible without also considering features of the specific system in which species are introduced—including physical and chemical characteristics and spatial extent—and the characteristics of particular species. This implies that strategies to identify “colonizing species” on the basis of just one characteristic such as population growth rate are apt to overlook other factors likely to enhance or diminish the probability of establishment. For example, for *Bythotrephes*, parameters governing mate encounters, including the duration of sexual reproduction, clutch size, mate-detection distance, and lake size (which affects population density) all affect mate-encounter rates and resting egg production. For this reason, risk assessments based on population demography should focus on particular species of concern in specific local contexts.

In this model, increasing population growth rate or the duration of the summer growing season dramatically reduces the critical density required for establishment to occur (Fig. 6C). This result is consistent with the (controversial) idea that high population growth rates cause certain species to be extremely invasive when they might otherwise be more benign. However, because growth rate interacts with other parameters, the more general conclusion that species exhibiting high growth rates will be invasive is un-

warranted. Since the parameters governing mate limitation (θ , or v , d , and c) are usually far more difficult to estimate than growth rate, the conclusion for *Bythotrephes* that critical density is relatively insensitive to small changes in these parameters is fortunate. While a future analysis will investigate these factors in greater detail, the current analysis probably represents a reasonable approximation of the full process.

The models presented here incorporate only demographic stochasticity. Environmental stochasticity (fluctuations in parameter values due to external factors) also reduces the probability of establishment for introduced populations. I obtained a straightforward solution to n^* based on the assumption that λ and μ are constant within a growing season and among years. In general, the additional parameters required to model environmental stochasticity may be difficult to measure (but see Reference 5); however, the qualitative effect is known. Incorporating environmental stochasticity will decrease the probability of establishment at all population sizes, not just populations near the equilibrium values.⁽¹³⁾ A future risk analysis for the invasion of *Bythotrephes* will investigate these factors and additionally relax the assumption that sex ratio equals one.

Allee effects likely influence other aspects of invasion risk as well, including the spatial spread of introduced populations. Where postrelease emigration exceeds population growth, the population density decreases, potentially inducing an Allee effect. For actively dispersing species, dispersal may be a function of density so that introduced population density, the initially occupied area, and the geometry of the advancing wave front are all implicated in the success or failure of establishment for introduced propagules.⁽¹⁴⁾ For passively dispersing species, advection is analogous to increasing mortality. The consequence is to modify the shape of the probability of establishment curves depicted in Figs. 4 and 5, and to decrease the probability of establishment at all introduction sizes. Adequate risk analysis of biological invasion cannot neglect these spatial considerations. Thus, estimates derived from the birth-death process are an upper bound on the probability of establishment.

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