

Temperature-dependent Allee effects in a stage-structured model for *Bythotrephes* establishment

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Abstract Whether the invasive freshwater cladoceran *Bythotrephes longimanus* can establish after introduction into a water body depends on several biotic and abiotic factors. Among these, water temperature is important because both development rates and mode of reproduction (parthenogenetic or sexual) in

Bythotrephes are influenced by temperature. We built a stage-structured model for the population dynamics of *Bythotrephes* based on the temperature-dependency of events in its life cycle and used the density of resting eggs at the end of each year to track changes in population density. The model was parameterized using data from published laboratory experiments and data on the *Bythotrephes* population in Harp Lake, Canada, from 1994 to 2005. The parameterized model was then used to simulate the outcome of invasions with different initial resting egg densities under different temperature regimes. A strong Allee effect emerged from the model, i.e. there is a critical threshold density above which the population can establish and below which it goes extinct. We showed analytically that the existence of an Allee effect arises from the model structure and is therefore robust to the parameter values. An increase in temperature reduces the establishment threshold for introductions in the same year as well as for introductions in the previous years. We therefore hypothesize that climate warming might facilitate *Bythotrephes* invasions. Finally, we study how the establishment threshold is influenced by the timing of the introduction event and thus identify time periods during the year when lakes may be particularly susceptible to *Bythotrephes* invasions.

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Introduction

The spread of *Bythotrephes longimanus* in North America

The spiny water flea, *Bythotrephes longimanus* Leydig, is a freshwater cladoceran native to the Palearctic region that is spreading in North America. *Bythotrephes* is a predatory species whose diet consists of small crustaceans (e.g. *Daphnia*), Bosminidae, and copepods (Lehman and Branstrator 1995; Schulz and Yurista 1995, 1998; Pothoven et al. 2001). As a generalist predator, *Bythotrephes* can have strong effects on the diversity and structure of invaded aquatic communities (Lehman 1991; Lehman and Caceres 1993; Dumitru et al. 2001; Yan et al. 2002). The first North American occurrence of *Bythotrephes* was reported in 1982 for Lake Ontario (Johannsson et al. 1991). Genetic studies suggest that the North American *Bythotrephes* population originated from the Baltic Sea/Lake Ladoga area (Berg et al. 2002). *Bythotrephes* individuals presumably travelled to North America in the ballast water of a cargo ship (Sprules et al. 1990). The current North American distribution of *Bythotrephes* includes all of the Great Lakes as well as many inland lakes and reservoirs in Ontario, Manitoba, Minnesota, Michigan, Ohio and Wisconsin (Therriault et al. 2002; Branstrator et al. 2006). The spread of *Bythotrephes* to new water bodies in the invaded range seems to be largely human-mediated, with boater traffic as an important vector (MacIsaac et al. 2004; Weisz and Yan 2010).

Bythotrephes individuals that have been introduced to a new water body will initially form a sparse population. Although reproduction in *Bythotrephes* is asexual throughout most of the year, the population needs to reproduce sexually to survive as resting eggs to the next year, which requires a sufficient number of encounters between females and males. Thus, we suspect that *Bythotrephes* populations might be subject to a demographic Allee effect, i.e. the per capita growth rate of *Bythotrephes* populations might be positively density-dependent at low population sizes (Stephens et al. 1999). A strong demographic Allee effect exists if there is a critical density above which a population can establish and below which it goes extinct (Taylor and Hastings 2005). In natural populations, there are many possible causes for such

an Allee effect. Apart from the difficulty of encountering mates at low densities, it can be caused by inbreeding depression, stochastic sex-ratio fluctuations at low densities, or predator–prey interactions (Gascoigne et al. 2009; Kramer et al. 2009; McLellan et al. 2010). Allee effects can have a significant impact on whether and how fast a species can spread into a new habitat (Lewis and Kareiva 1993; Taylor and Hastings 2005). The implications of an Allee effect for *Bythotrephes* establishment probability in a stochastic model have been examined by Drake (2004). Quantifying the strength of a potential Allee effect in *Bythotrephes* and its dependence on biotic and abiotic factors might help us to better understand the geographical pattern of the *Bythotrephes* spread in North America and to identify currently uninvaded waterbodies that are at a high risk of being invaded.

Modeling populations exhibiting an Allee effect

Often, models for species that are known to have a critical establishment threshold include an Allee effect that is explicitly built into the model equations (many examples can be found in Boukal and Berec 2002). This phenomenological approach, however, requires a priori knowledge on the magnitude of the Allee threshold. It does not model the biological processes explicitly that lead to a reduction in per capita growth rate at low densities. In contrast to these phenomenological models, there are more mechanistic models, where the existence and magnitude of the Allee effect is allowed to emerge from the biologically motivated model structure (Veit and Lewis 1996; McCarthy 1997; Drake 2004; Molnar et al. 2008; Jerde et al. 2009). In this study, we take this mechanistic approach and demonstrate that an Allee effect emerges from a model based on the life cycle of *Bythotrephes*.

Bythotrephes life cycle (see Fig. 1)

Since adults do not overwinter in North American lakes (Yurista 1997), each year in spring, a new *Bythotrephes* population is initiated when neonate females hatch from resting eggs that were sexually produced in the previous year. To reach maturity, a sexually produced female molts three times, each time adding a segment with a pair of barbs (paired articular spines) to its tail spine (Burkhardt 1994).

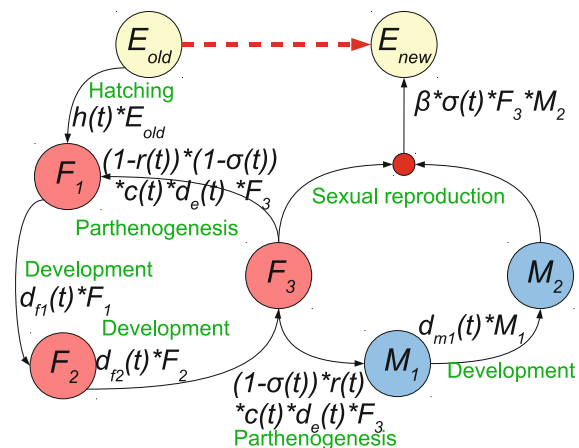


Fig. 1 A graphical representation of our *Bythotrephes* life cycle model. The variables (shown in circles), transitions (arrows and text), and transition rates (formulas) are explained in the text and defined in Tables 1 and 2. The dashed arrow indicates that there is a discrete-time model that links the numbers of resting eggs in subsequent years (see Eq. 9). Mortality is not shown in this graph

The number of pairs of barbs allows one to distinguish between individuals belonging to different life-history stages. Once mature, a female starts to reproduce parthenogenetically. It deposits a clutch of ameiotic eggs without shell into its brood sac. The embryos go through several stages (early embryo, “red-eye” stage, and “black-eye” stage, Yurista 1992) before they are finally released as neonates by the rupture of the softened brood sac. In general, a parthenogenetically produced female reaches maturity in the third instar (Branstrator 2005) whereas adult males carry only two pairs of barbs (Yurista 1992). Throughout most of the season, *Bythotrephes* populations reproduce parthenogenetically. Since the sex in *Bythotrephes* and other cladocerans is determined environmentally and not genetically (Egloff et al. 1997), females can produce male and female clones of themselves. The question how environmental factors like temperature, starvation, crowding and photoperiod act together to determine the sex of cladocerans has mainly been studied in *Daphnia* thus far and is not well understood yet (Hobæk and Larsson 1990; Eads et al. 2008). Some males can be observed in summer, but male production peaks in autumn when water temperatures go down (Straile and Hälbich 2000). At about the same time, mature females start to undergo an anatomical transformation that enables them to produce meiotic resting eggs

after internal fertilization by males (Egloff et al. 1997). However, male and resting egg production might have different environmental cues (Hobæk and Larsson 1990). The resting eggs sink to the sediment, where they stay until the next spring. Some eggs produced early in the season might already hatch in autumn, but in general they need a refractory period during which they are exposed to cold temperatures before they can be activated for hatching by warmer temperatures (Brown and Branstrator 2005).

There are different ways of translating information on an organism’s life cycle into a quantitative model, each with specific applications. We chose to describe the densities of the different life-history stages and the transitions between them as a system of ordinary differential equations because *Bythotrephes* populations have discrete life-history stages while reproduction and development from one stage to the next happen continuously throughout the season. The most important part of a life history model framed in terms of ordinary differential equations are the transition rates between the stages. The rates at which events in the *Bythotrephes* life cycle occur (e.g. development from one stage to the next, production of resting eggs) are influenced by several factors including temperature and food abundance. In this study, we focus on temperature as the driving factor of the *Bythotrephes* life cycle.

Climate change and biological invasions

Global warming is leading to an increase in average water temperature of North American lakes (Hostetler and Small 1999). Since many processes in the life cycle of *Bythotrephes* are temperature-dependent, this will have an impact on population dynamics and spread of the invader. Like the rates of most other biological and biochemical processes, the development rates in the *Bythotrephes* life cycle increase with temperature, allowing for higher per capita growth rates, but only up to an optimum temperature. Furthermore, warmer temperatures in spring may lead to an earlier hatching of resting eggs so that the population has a longer growing season. However, the impacts of climate change on lakes and their communities might not always be easy to predict. Complex models have been developed to understand the dynamics of temperature profiles in lakes (e.g. Gal et al. 2003).

Objectives

In this study, we synthesize current knowledge on the *Bythotrephes* life cycle within a quantitative model and try to obtain realistic estimates for its parameters, from the literature and from information on the *Bythotrephes* population in Harp Lake, Ontario (see “Data on the *Bythotrephes* population of Harp Lake”). We use the model to derive hypotheses on the influence of temperature shifts and introduction scenario on the number of introduced individuals required for successful establishment. While previous studies on *Bythotrephes* population dynamics have mostly focused on parthenogenetic reproduction (e.g. Hall and Yan 1997), we explicitly model the production of males and subsequent sexual reproduction. Since all individuals in a given year are recruited from resting eggs produced sexually in the previous year, these processes are important for the interannual dynamics of *Bythotrephes* populations.

Model

The intra-annual dynamics of a *Bythotrephes* population in year n are formulated as a system of coupled non-autonomous ordinary differential equations that track the volumetric densities of each of the life-history stages (defined in Table 1, see also Fig. 1) as a function of the day of the year, t :

$$\underbrace{\frac{dE_{old}^{(n)}}{dt}}_{\text{rate of change of old resting eggs}} = - \underbrace{h(t) \cdot E_{old}^{(n)}}_{\text{hatching of resting eggs}}, \tag{1}$$

$$\begin{aligned} \underbrace{\frac{dF_1^{(n)}}{dt}}_{\text{rate of change of 1st instar females}} &= \underbrace{h(t) \cdot E_{old}^{(n)}}_{\text{hatching of resting eggs}} \\ &+ \underbrace{(1 - \sigma(t)) \cdot (1 - r(t)) \cdot c(t) \cdot d_e(t) \cdot F_3^{(n)}}_{\text{parthenogenetic reproduction}} \\ &- \underbrace{d_{f1}(t) \cdot F_1^{(n)}}_{\text{development from 1st to 2nd instar}} - \underbrace{\mu \cdot F_1^{(n)}}_{\text{mortality}}, \end{aligned} \tag{2}$$

$$\begin{aligned} \underbrace{\frac{dF_2^{(n)}}{dt}}_{\text{rate of change of 2nd instar females}} &= \underbrace{d_{f1}(t) \cdot F_1^{(n)}}_{\text{development from 1st to 2nd instar}} \\ &- \underbrace{d_{f2}(t) \cdot F_2^{(n)}}_{\text{development from 2nd to 3rd instar}} - \underbrace{\mu \cdot F_2^{(n)}}_{\text{mortality}}, \end{aligned} \tag{3}$$

$$\underbrace{\frac{dF_3^{(n)}}{dt}}_{\text{rate of change of 3rd instar females}} = \underbrace{d_{f2}(t) \cdot F_2^{(n)}}_{\text{development from 2nd to 3rd instar}} - \underbrace{\mu \cdot F_3^{(n)}}_{\text{mortality}}, \tag{4}$$

$$\begin{aligned} \underbrace{\frac{dM_1^{(n)}}{dt}}_{\text{rate of change of 1st instar males}} &= \underbrace{(1 - \sigma(t)) \cdot r(t) \cdot c(t) \cdot d_e(t) \cdot F_3^{(n)}}_{\text{parthenogenetic reproduction}} \\ &- \underbrace{d_{m1}(t) \cdot M_1^{(n)}}_{\text{development from 1st to 2nd instar}} - \underbrace{\mu \cdot M_1^{(n)}}_{\text{mortality}} \end{aligned} \tag{5}$$

$$\underbrace{\frac{dM_2^{(n)}}{dt}}_{\text{rate of change of 2nd instar males}} = \underbrace{d_{m1}(t) \cdot M_1^{(n)}}_{\text{development from 1st to 2nd instar}} - \underbrace{\mu \cdot M_2^{(n)}}_{\text{mortality}}, \text{ and} \tag{6}$$

$$\underbrace{\frac{dE_{new}^{(n)}}{dt}}_{\text{rate of change of new resting eggs}} = \underbrace{\sigma(t) \cdot \beta \cdot F_3^{(n)} \cdot M_2^{(n)}}_{\text{resting egg production}}. \tag{7}$$

Model structure

Our model with its seven state variables is one of potentially many possible simplified representations of the complex *Bythotrephes* life cycle. The state variables correspond to classes of individuals that can be distinguished in lake samples (see “Data on the *Bythotrephes* population of Harp Lake”) and for which knowledge on development rates is available.

Table 1 The model variables

Name	Explanation	Unit
E_{old}	Density of resting eggs produced in the previous year that will hatch in the current year (number of eggs in the sediment / volume of the corresponding water body)	m^{-3}
F_1	Density of first instar females	m^{-3}
F_2	Density of second instar females	m^{-3}
F_3	Density of mature females (3rd or 4th instar)	m^{-3}
M_1	Density of first instar males	m^{-3}
M_2	Density of second instar males	m^{-3}
E_{new}	Density of resting eggs produced in the current year that will hatch in the following year (number of eggs in the sediment / volume of the corresponding water body)	m^{-3}

It would be possible to further simplify the model by collapsing several developmental stages and summarizing their development rates within one rate constant. In this case, however, the model would lose its ability to mechanistically explain how perturbations acting on different life-history stages would affect the overall population dynamics.

In this simplified model, fourth instar sexually produced and third instar asexually produced females were combined into one stage, F_3 , as it is assumed that neonates and resting eggs are released only in these two stages. In nature, however, when the abundance of third instar females is very low, second instar females are often similar in size to third instar females and have also been observed to reproduce (Pothoven et al. 2001). We do not take this phenomenon into account as high densities of third instar females have been

observed for all years in Harp Lake, Ontario, the lake used for model parameterization.

Since this model attempts to describe *Bythotrephes* population dynamics at very low densities initially after the introduction event, we can assume that resting egg production is limited by and thus proportional to the number of encounters between males and females. At low densities, the encounter rate of an individual female with males is proportional to the density of males. The encounter rates of all females taken together is thus proportional to both the density of sexually reproducing females and males Eq. 7, thereby adding a nonlinearity to the otherwise linear model.

Model coefficients

Most of the coefficients in this model (Table 2) are time-dependent and can be understood as the average rates of the respective processes in the population on a certain day of the year. Since the rates of life-history processes in individual *Bythotrephes* depend on the temperature they experience, we obtained the model coefficients by calculating a weighted average of the corresponding rates in individual *Bythotrephes* located in different vertical temperature zones (see “Accounting for the vertical distribution of *Bythotrephes* in the water column”). The temperature-dependency of development rates and resting egg hatching rate were assumed to be linear and their parameters were extracted from Lehman et al. (1997) and Yurista (1992), respectively (see “Development rates, $d_e(t)$, $d_{f1}(t)$, $d_{f2}(t)$, $d_{m1}(t)$ ” and “Population hatching rate of resting eggs, $h(t)$ ”). The clutch size, $c(t)$, and the

Table 2 The model coefficients.

Name	Explanation	Unit	Parameterization
$h(t)$	Hatching rate of resting eggs	day ⁻¹	Yurista (1992)
$d_{f1}(t)$	Development rate from female instar 1 to instar 2	day ⁻¹	Lehman et al. (1997)
$d_{f2}(t)$	Development rate from female instar 2 to instar 3	day ⁻¹	Lehman et al. (1997)
$d_{m1}(t)$	Development rate from male instar 1 to male instar 2	day ⁻¹	Lehman et al. (1997)
$d_e(t)$	Embryonic development rate	day ⁻¹	Lehman et al. (1997)
$\sigma(t)$	Proportion of females that are reproducing sexually	1	Harp Lake data (generalized linear model)
$r(t)$	Proportion of males in parthenogenetic offspring	1	Harp Lake data (nonlinear least squares)
$c(t)$	Clutch size of parthenogenetic broods	1	Harp Lake data (generalized linear model)
μ	Density-independent death rate (e.g. predation)	day ⁻¹	Harp Lake data (nonlinear least squares)
β	Rate constant of resting egg production (corrected for resting egg mortality)	day ⁻¹ m ³	Harp Lake data (nonlinear least squares)

The parameterization is explained in the text and in the “Appendix”

proportion of females that are reproducing sexually, $\sigma(t)$, were parameterized by fitting generalized linear models with temperature and day of the year as explanatory variables to data from Harp Lake, Ontario ($n = 1,047$ and $n = 5,064$, respectively, see “Clutch size, $c(t)$ ” and “Proportion of females that are reproducing sexually, $\sigma(t)$ ”). Day of the year was used as a surrogate for factors other than temperature that varied seasonally and influenced the model coefficients.

Since males have been observed mainly at the end of the season, even although similarly low temperatures also occur at the beginning of the season, we hypothesized that the proportion of females in parthenogenetic broods, $r(t)$, is not temperature- but time-dependent. We assumed that early in the year, parthenogenetic females produce only female offspring and that there is a critical time t_0 after when females switch to also producing a proportion p of males. This behavior can be modeled as:

$$r(t) = \begin{cases} 0 & t \leq t_0 \\ p & t > t_0 \end{cases} \approx p \cdot \frac{(1 + \tanh(t - t_0))}{2}, \quad (8)$$

with t measured in days.

The mortality, μ , was assumed to be constant for all times and all stages (except resting eggs). It summarizes density-independent mortality that may come from different sources such as predation or starvation due to interspecific competition for food. Since our model describes population dynamics at low densities, intraspecific competition for resources is not included. We also assumed β to be constant, so that the resting egg production is determined only by the densities of both third instar sexually reproducing females and second instar males. The parameters μ , p , t_0 , and β were unknown, and had to be estimated from time series data on the *Bythotrephes* population in Harp Lake.

Solving the model

To solve this system of ordinary differential Eqs. 1–7 for multiple years, we solve it for 1 year over a time interval from the beginning of the growing season in spring, indicated by t_s , to its end in fall, indicated by t_f , and use the density of new resting eggs at the end of the season $E_{new}^{(n)}(t_f)$ as initial condition for $E_{old}^{(n+1)}(t_s)$ in the subsequent year. We thereby assume that resting eggs cannot stay in the sediment for more than one winter, which is supported by evidence that

Bythotrephes diapausing eggs last only 3/4 of a year (Andrew and Herzig 1984) and are thus short-lived in comparison to the diapausing eggs of other cladocerans (Yurista 1997).

Since resting eggs in the model are not available for hatching until the next year, there is no feedback of the density of new resting eggs on the other variables within the same year. We can thus split the model (Eqs. 1–7) into a linear (Eqs. 1–6) and a nonlinear part (Eq. 7), which is convenient for analytical purposes. The linear continuous time part (Eqs. 1–6) describes all processes in the life cycle of *Bythotrephes*, except for the production of resting eggs. The nonlinear part models the production of resting eggs, a key process for the year-to-year dynamics of *Bythotrephes* populations. Instead of solving Eq. 7 simultaneously with the linear differential equations, we can first solve the linear system (Eqs. 1–6) and then integrate the rate of resting egg production over the course of a year n (from t_s to t_f) and take the value of this integral as the initial condition for the continuous-time model in the following year $n + 1$:

$$\underbrace{E_{n+1}}_{\text{new resting eggs after year } n+1} = f \underbrace{(E_n)}_{\text{new resting eggs after year } n} = \int_{t_s}^{t_f} \beta \cdot \underbrace{\sigma(t) \cdot F_3^{(n+1)}(t, E_n)}_{\text{sexually reproducing 3rd instar females}} \cdot \underbrace{M_2^{(n+1)}(t, E_n)}_{\text{2nd instar males}} dt, \quad (9)$$

where $E_n = E_{new}^{(n)}(t_f)$ and $F_3^{(n+1)}(t, E_n)$ and $M_2^{(n+1)}(t, E_n)$ are the densities at time t of third instar females and second instar males in year $n + 1$, respectively, if the resting egg density at the beginning of the year was E_n . Equation 9 is a discrete-time model that links the densities of resting eggs in subsequent years. The continuous-time model described above (Eqs. 1–6) is nested inside this discrete-time model, because the solution to the continuous-time model is needed to obtain $F_3(t, E_n)$ and $M_2(t, E_n)$. As a whole, our model can be classified as a semi-discrete model (Mailleret and Lemesle 2009).

We have derived a model that links *Bythotrephes* resting egg densities in subsequent years via a mechanistic model for the life cycle. This is the first time a model for the population dynamics of *Bythotrephes* is based on its full life cycle, including key processes such as the production of males and sexual

reproduction. This allows us to explore the dynamics of *Bythotrephes* populations spanning multiple years, whereas previous models have focused on population growth within one season.

Model analysis for an Allee effect

We will now analyze the interannual dynamics of the model and demonstrate that a population described by Eqs. 1–6 and 9 inherently exhibits a strong demographic Allee effect, and identify the source of this phenomenon. A strong demographic Allee effect exists if there is a critical establishment threshold such that the population can only establish if its initial size is above this threshold. To demonstrate this for our model, we need to show that it has a stable equilibrium at 0 and that there is at least one more equilibrium at a positive density, such that the smallest non-zero equilibrium is unstable.

As the continuous-time model describing the densities of the different stages (except resting eggs) over one season (Eqs. 1–6) is linear and homogeneous, the density of a certain stage at a certain point in time in year $n + 1$ is proportional to the number of resting eggs, E_n , at the beginning of the year. We can imagine each resting egg going through its life stages and eventually producing a clonal offspring population independently of all other resting eggs that were present at the beginning of the year. If there are no resting eggs at the beginning of the year, there will be none at the end of the year either. We can thus decompose $F_3^{(n+1)}(t, E_n)$ and $M_2^{(n+1)}(t, E_n)$:

$$F_3^{(n+1)}(t, E_n) = E_n \cdot f_3^{(n+1)}(t) \geq 0, \quad \text{and} \quad (10)$$

$$M_2^{(n+1)}(t, E_n) = E_n \cdot m_2^{(n+1)}(t) \geq 0, \quad (11)$$

where the functions $f_3^{(n+1)}(t) > 0$ and $m_2^{(n+1)}(t) > 0$ describe the densities of third instar females and second instar males in year $n + 1$, respectively, resulting from one unit of resting eggs. Then Eq. 9 becomes:

$$\begin{aligned} E_{n+1} &= f(E_n) \\ &= E_n^2 \cdot \beta \cdot \int_{t_s}^{t_f} \sigma(t) \cdot f_3^{(n+1)}(t) \cdot m_2^{(n+1)}(t) dt \\ &= k \cdot E_n^2, \end{aligned} \quad (12)$$

where $k = \beta \cdot \int_{t_s}^{t_f} \sigma(t) \cdot f_3^{(n+1)}(t) \cdot m_2^{(n+1)}(t) dt > 0$ is a constant with respect to E_n that summarizes the effect

of all parameter values of the stage-structured model and the temperature regime. $f(E_n)$ has thus the form of a parabola. Solving $E^* = k \cdot E^{*2}$ for E^* yields the two equilibria $E_1^* = 0$ and $E_2^* = \frac{1}{k}$. Stability is assessed by evaluating the first derivative of Eq. 12, $f'(E_n) = 2 \cdot k \cdot E_n$, at the equilibria. An equilibrium E^* is stable if $|f'(E^*)| < 1$ and unstable if $|f'(E^*)| > 1$. Since $f'(0) = 0$ and $f'(\frac{1}{k}) = 2$, our model has a stable equilibrium at 0 and an unstable equilibrium at the positive density $\frac{1}{k}$. Thus, there is always a strong demographic Allee effect for models such as ours that rely on sexual reproduction.

We compared the model specification given in Eq. 9 with an alternative model that assumes that there are always enough males so that the resting egg production is proportional to the density of third instar females (which could be realistic at high population densities, where the number of encounters between males and females is no longer limiting for sexual reproduction):

$$E_{n+1} = f(E_n) = \int_{t_s}^{t_f} \beta \cdot \sigma(t) \cdot F_3^{(n+1)}(t, E_n) dt, \quad (13)$$

which can be written as:

$$E_{n+1} = f(E_n) = \beta \cdot E_n \int_{t_s}^{t_f} \sigma(t) \cdot f_3^{(n+1)}(t) dt = l \cdot E_n, \quad (14)$$

where the constant $l = \beta \cdot \int_{t_s}^{t_f} \sigma(t) \cdot f_3(t) dt$ is the slope of the linear discrete model function. This slope is independent of E_n and depends only on the parameter combination and temperature curve. Therefore, 0 is the only equilibrium of the model (neglecting the special case where the slope is exactly 1). If the slope is smaller than 1, the population goes extinct for all initial egg densities. If the slope is greater than 1, the population can establish, even with a very small density of resting eggs, i.e. there is no Allee effect. We have thus shown that the Allee effect in our model is a consequence of the nonlinear interaction of males and females required for the production of resting eggs. Although the presence of an Allee effect does not depend on the values of the coefficients in Eqs. 1–6, the magnitude of the establishment threshold, $1/k$, does. It is influenced by processes acting at

different life-history stages and by changes in temperature, both if the mean temperature or only the distribution of temperatures over the season is changed.

Numerical methods

Simulations

It is not feasible to analytically calculate the magnitude of the establishment threshold because this would require solving the non-autonomous system of ordinary differential Eqs. 1–6. Thus, we used simulations to determine the critical establishment threshold under different temperature regimes and introduction scenarios. Simulations were also needed to estimate the unknown parameters. The simulations were performed in Matlab R2009b. The system of differential Eqs. 1–7 was solved for 1 year from day $t_s = 132$ (beginning of the growing season in middle May) to day $t_f = 312$ (end of the season in early November) using the differential equation solver `ode45`, which is based on a 4th/5th order Runge–Kutta scheme (Dormand and Prince 1980). The resulting $E_{new}(t_f)$ served as initial condition for $E_{old}(t_s)$ in the following year. The initial densities of all other stages were zero. A function specifying how the temperature depends on time and water depth is needed as input. We used temperature data from Harp Lake, Ontario (see “Data on the *Bythotrephes* population of Harp Lake”).

Nonlinear least squares parameter estimation

In order to estimate the unknown parameters μ , p , t_0 , and β that are part of the parameterized model coefficients, we fit the numerical solution of the model to time series data on the densities of the stages F_1 , F_2 , F_3 , M_1 , and M_2 in Harp Lake in the years 2002–2004 (see “Data on the *Bythotrephes* population of Harp Lake”). The data of these years were selected for parameter estimation because they have a comparatively high number (43) of sampling dates and contain information on the sex of individuals in the sample. To fit the model, we used a

nonlinear least squares method (`lsqcurvefit` in the Matlab optimization toolbox). If errors are independent and normally distributed, the nonlinear least squares parameter estimates correspond to the maximum likelihood estimates. The densities of resting eggs E_{new} and E_{old} were unobserved and did not contribute to the residuals of the model fit. To generate the numerical solution of the model for a given combination of parameters, we used the simulation procedure described above. For each simulation, we needed an initial condition on the number of resting eggs at the beginning of the year to be simulated, $E_{old}(t_s)$. Since we did not have a priori information on the number of resting eggs produced in any year, we estimated the initial condition for the first year of data as an additional parameter. The nonlinear least squares algorithm requires the specification of initial guesses for the parameters and gives the option of putting constraints on them. By constraining the parameter space, we ensured that parameter estimates are biologically reasonable (Table 3). We also had to provide an initial guess for the initial resting egg density, $E_{old}(t_s)$, and we constrained it to the positive real numbers. The ability of the algorithm to identify model parameters was checked using simulated data. Starting with different initial guesses for the parameters, we eventually arrived at the same fit of the model to the data (Fig. 2). The parameter estimates and their 95% confidence intervals are given in Table 3. These estimates were used as default parameter values in all of the following methods.

Determination of the establishment threshold

The establishment threshold, E_C , is the non-zero equilibrium of the model Eq. 9. We used simulations to determine the magnitude of this threshold for a given combination of parameter values and a given temperature profile (assumed to be the same for every year). We interpreted this task as a boundary value problem with the initial condition for resting eggs, $E_{old}(t_s)$, as unknown parameter and used `bvp4c`, Matlab’s boundary value solver for ordinary differential equations, which implements a collocation method (Shampine et al. 2000). The condition to be fulfilled was that the density of resting eggs produced

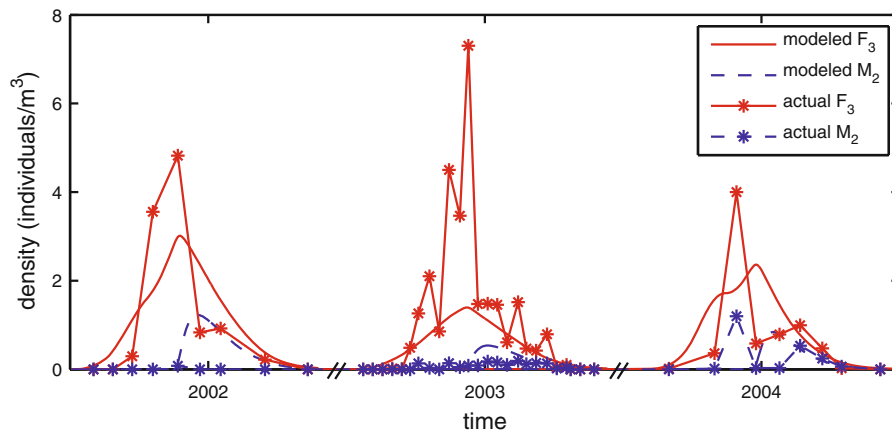


Fig. 2 Model fit to the 2002–2004 Harp Lake data for third instar females (F_3) and second instar males (M_2)

Table 3 Estimation of unknown model parameters

Parameter	Meaning	Unit	Lower constraint	Upper constraint	Estimate	95% confidence interval
μ	Mortality	day ⁻¹	0	∞	0.186	(0.174,0.199)
p	Proportion of males in parthenogenetic broods late in the season	1	0	1	0.300	(0.173,0.427)
t_0	Time of the year at which male production starts	day	120	330	208	(204,213)
β	Rate constant of resting egg production	m ³ day ⁻¹	0	∞	4.83	(0.002,9.69)

at the end of a year equals the unknown starting density of resting eggs:

$$\begin{aligned}
 E_{old}(t_s) &= E_C, F_1(t_s) = F_2(t_s) = \\
 F_3(t_s) &= M_1(t_s) = M_2(t_s) = E_{new}(t_s) = 0, \quad \text{and} \\
 E_{new}(t_f) &= E_C. \tag{15}
 \end{aligned}$$

To study how the critical introduction density of both resting eggs and third instar females depends on the timing of the introduction event, t_i , we solved the boundary value problem again, this time searching for the density of resting eggs or third instar females at time t_i that lets the population reach the critical establishment threshold, E_C , by the end of the season, given that there were no individuals of the other stages at the time of introduction. If the critical density obtained from the model is multiplied by the volume of a given body of water, we obtain the critical propagule size for a single introduction to result in establishment.

Sensitivity analysis

A local sensitivity analysis was performed for each of the model coefficients. The sensitivity to a change in the proportion of males in parthenogenetic offspring, $r(t)$, was studied by separately determining the sensitivity with respect to the parameters p and T_0 in Eq. 8. The local sensitivity of the establishment threshold, E_C with respect to a perturbation of the parameter π away from its estimated value π^{est} is:

$$\frac{\pi}{E_C} \cdot \frac{dE_C}{d\pi} \approx \frac{\frac{E_C^{per} - E_C^{est}}{E_C^{est}}}{\frac{\pi^{per} - \pi^{est}}{\pi^{est}}}, \tag{16}$$

where E_C^{est} is the establishment threshold for the estimated parameters, $\pi^{per} = \pi^{est} + 0.001 \cdot |\pi^{est}|$ is the perturbed parameter value, and E_C^{per} is the establishment threshold for the perturbed parameter combination. For each parameter combination, the magnitude of the establishment threshold was

determined using the boundary value approach outlined above.

In the case of the proportion of females that are reproducing sexually, $\sigma(t)$, the sensitivity was assessed with respect to the logit of the proportion to avoid proportions greater than one.

Temperature-dependency of the establishment threshold

To study how the establishment threshold depends on temperature, we chose the 2002 temperature curve as an example and transformed it by adding the same constant τ to the temperature throughout the whole year for each depth. The magnitude of the establishment threshold was determined over a range of values for τ .

Analysis of multi-year dynamics with different temperature regimes

It is possible to simulate subsequent years with different temperature regimes but also to plot the model curves (Eq. 9) and analyze them graphically using a variant of the cobwebbing method (for an introduction see Otto and Day 2007). We explored two scenarios: a series of years, each of which is warmer than the previous year, and the case of alternating warm and cold years.

Numerical results

Plotting the graph of the discrete-time model (Eq. 9) using the estimated parameters (see Table 3) and the 2002 temperature data, we see that there is an unstable equilibrium at a positive resting egg density (Fig. 3), as expected from the analytical proof for the existence of an Allee effect. The simulations predict the establishment threshold to be at 26.6 resting eggs per m^3 . In Harp Lake, which has a total volume of approximately $9.5 \times 10^6 \text{m}^3$, this would correspond to 2.5×10^8 resting eggs.

Our analytical considerations above tell us that independently of the parameter choice, there will always be an unstable equilibrium at a positive density of resting eggs. However, the magnitude of the establishment threshold may vary strongly

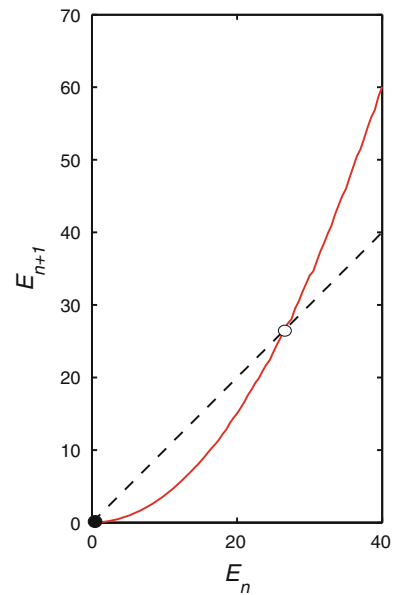


Fig. 3 Graph of the discrete-time model (Eq. 9) that links resting egg densities (E_n) from year to year (solid line), based on the estimated parameters and the 2002 temperature curve. The equilibria are the intersections with the 45°-line (dashed line). There is a stable equilibrium (filled circle) at 0 and an unstable equilibrium (open circle) at $\frac{1}{k} = 26.6$

between different parameter combinations. The local sensitivity analysis shows that it is especially sensitive to the parameters μ and t_0 (Fig. 4). The establishment threshold increases if μ , $\sigma(t)$, or p are perturbed in positive direction from the estimated values. It decreases with increasing hatching and development rates, clutch size, t_0 , or β . Since the magnitude of the establishment threshold is $\frac{1}{k}$ and k is proportional to β , the establishment threshold is proportional to the inverse of β .

If we shift the 2002 temperature curve by a constant over the whole year and over all depths of the lake, we observe that the establishment threshold decreases in a nonlinear way with the increasing temperature, approaching zero for high temperatures (Fig. 5).

The density of introduced individuals required to establish a population depends strongly on the time of the introduction event (Fig. 6). If resting eggs are introduced (Fig. 6a, b), the critical introduction density stays approximately constant throughout spring and summer with a minimum in late May (Fig. 6b). It increases sharply toward the end of the

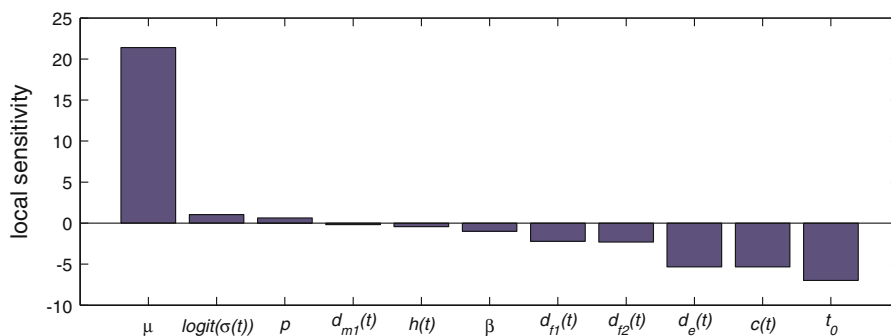


Fig. 4 Local sensitivity of the establishment threshold to perturbations away from the estimated parameters (Table 2)

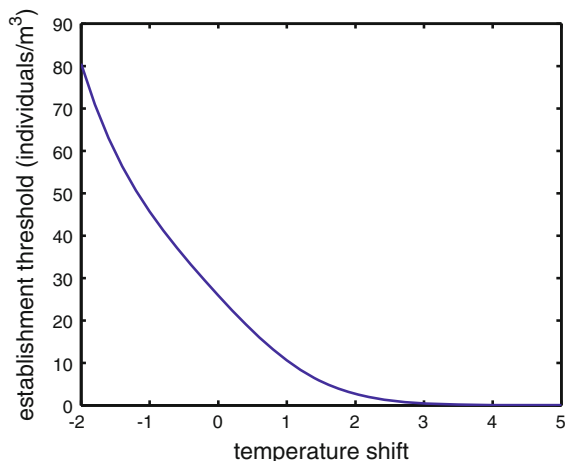


Fig. 5 Influence of a temperature shift in °C on the establishment threshold. The simulations are based on the parameter estimates in Table 3 and the 2002 temperature data

season (Fig. 6a). The critical introduction density for third instar females displays a more complex behavior (Fig. 6c). It is high at the beginning and end of the season and exhibits two minima and a maximum in between.

If there is variation in temperature between years, the number of individuals required for successful establishment depends on the year of introduction and is also influenced by the temperatures in the following years. If *Bythotrephes* individuals are introduced at a density below the establishment threshold for the year of introduction but above the threshold of one of the following warmer years under a climate warming scenario (Fig. 7a), establishment can still be possible (Fig. 7b). In the case of fluctuating temperatures (Fig. 8a), more individuals are required for successful establishment in cold years than in warm years. However, the required densities are both intermediate

between the establishment thresholds for scenarios with only warm years or only cold years (Fig. 8b).

Discussion

Overview

A strong demographic Allee effect emerged from the structure of our *Bythotrephes* life cycle model. It results from the nonlinearity caused by the necessity of interaction between males and females for sexual reproduction. We saw that an increase in temperature over the whole year can lead to a strong decline in the establishment threshold due to the additive effects of temperature on different life-history processes. An increase in temperature makes the growing season longer and speeds up developmental processes. Furthermore, introductions in cold years are more successful if the following years are warmer. All other things being equal, we would expect climate warming to facilitate *Bythotrephes* invasions.

We found that the density of introduced individuals required for establishment depends on the timing of introduction as well as on the life-history stage being introduced. Throughout most of the season, the density of third instar females required for establishment is lower than the critical density of resting eggs, the reason being that a high proportion of resting eggs die before becoming mature *Bythotrephes*. For resting eggs, we predict that the critical density remains in the same order of magnitude from May to August but increases sharply in September, indicating that, for such a late introduction, there is not enough time remaining to go through all life-history stages, reproduce parthenogenetically, and reach a sufficient

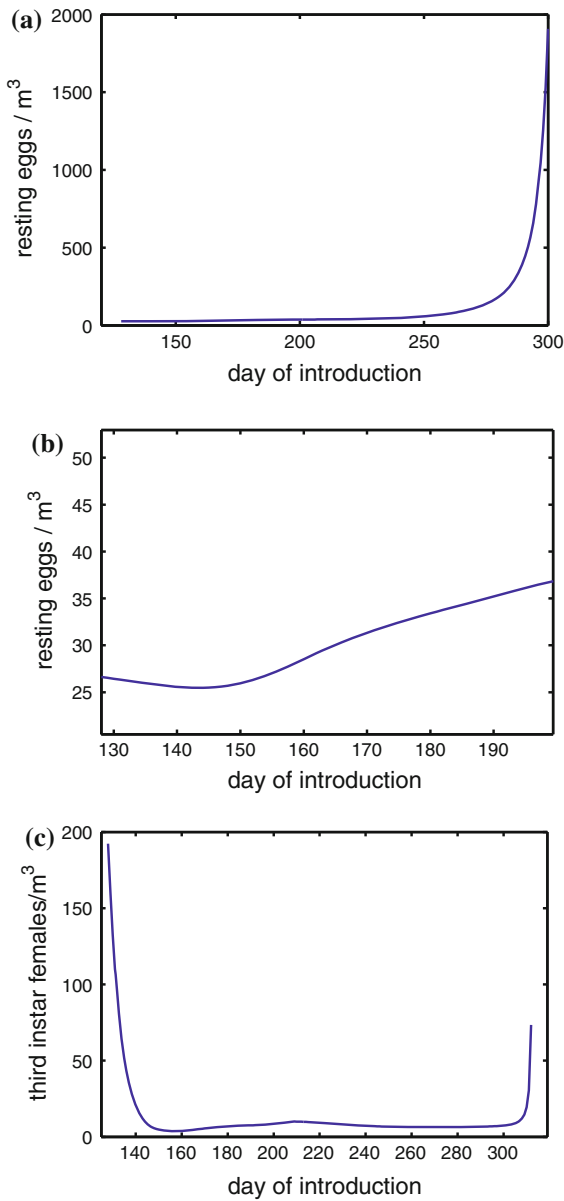


Fig. 6 The critical introduction density of resting eggs **a**, **b** and third instar females **c** as a function of time. The magnification in **b** shows that the critical resting egg density has a minimum of 25.47 individuals/m³ at day 144. The critical density of third instar females has a global minimum of 3.741 at day 157, a local maximum of 10.03 at day 209 and a local minimum 6.358 at day 270. Simulations were based on the parameter estimates in Table 3 and the 2002 temperature data

density for overwintering by the end of the season. Using estimated parameters and the 2002 temperature curve, the minimum critical density occurs at the end of May. At this time of the year, resting egg

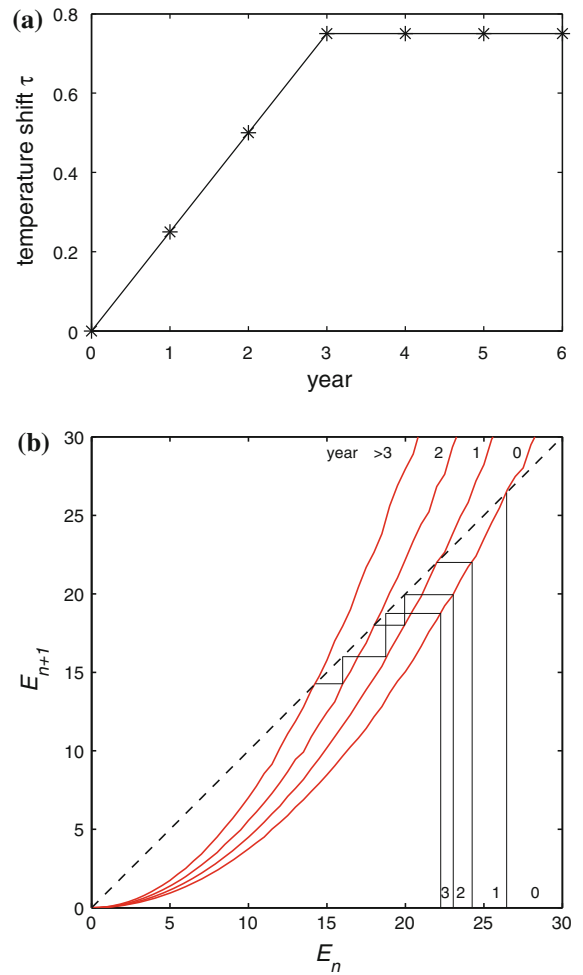


Fig. 7 A climate warming scenario. The temperature shift parameter τ in $^{\circ}\text{C}$ is added to the 2002 temperature data **(a)**. The corresponding model curves that map the numbers of resting eggs in year n , E_n , to the number of resting eggs in the following year, E_{n+1} , are given in **(b)**. The numbers above the x-axis indicate how long it takes for a population of this size introduced in year 0 to reach positive growth rates. The intervals can be constructed by following the straight lines backwards from the equilibria (intersection points with the dashed 45° -line) of the different model curves

introductions would be most likely to result in establishment, while earlier introductions might have a higher mortality relative to development rates. These predictions assume that the introduced resting eggs will all hatch in the year of introduction and do not overwinter until the next year. Introductions of third instar females at the beginning of the season do not seem to have a very high establishment probability. This is because, unlike resting eggs, they

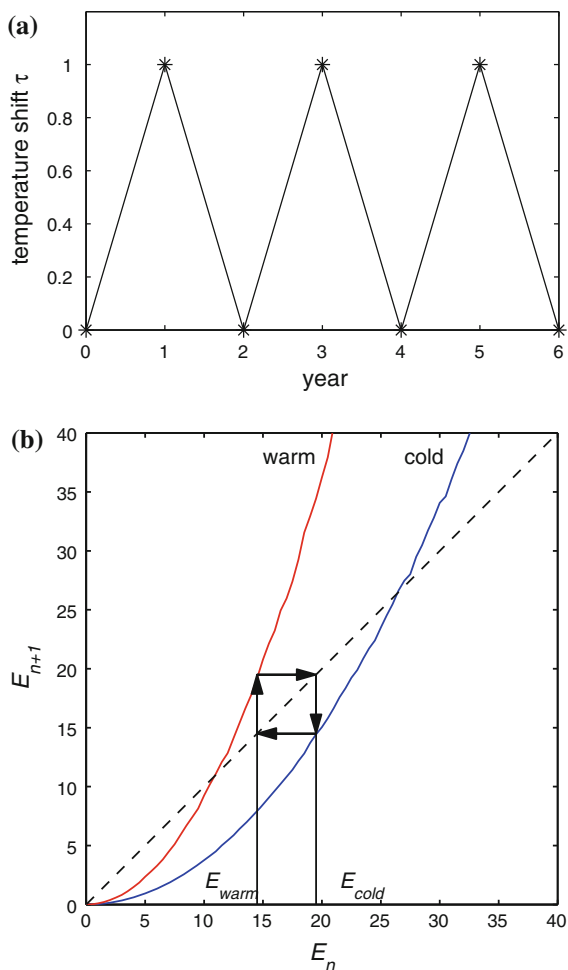


Fig. 8 A scenario with fluctuating temperature. Even years correspond to the 2002 temperature data. Uneven years are 1°C warmer (a). The corresponding model curves for cold years and warm years that map the numbers of resting eggs in year n , E_n , to the number of resting eggs in the following year, E_{n+1} , are given in (b). E_{warm} and E_{cold} are the densities required for successful establishment for introductions in warm and cold years, respectively. The black arrows indicate an unstable equilibrium trajectory, which corresponds to oscillations in population densities

cannot remain in the sediment until conditions become favorable, and, because of low temperatures, reproduction is slow while mortality is relatively high. The critical introduction threshold for third instar females goes down in late May, when invasions become possible. The different minima and the maximum of the establishment threshold during summer indicate that there is a trade-off between the time remaining for population growth, which is decreasing with time, and the availability of males,

which is increasing with time. At the very end of the season, invasions caused by third instar females become less likely again. This happens much later than for resting eggs because third instar females do not have to go through a whole life cycle before they can start producing resting eggs that will survive to the next year. Similarly to these results, Drake et al. (2006) described an invasion window for *Bythotrephes* based on a stochastic model that opens in late May. However, their invasion window does not really close until the end of the season. For the production of resting eggs, they take into account only the individuals present at the end of the season whereas we integrate the rate of resting egg production over the whole year.

The model parameterization provides additional information on *Bythotrephes* biology: The results of the model selection for clutch size and the proportion of sexually reproducing females indicate that temperature, other time-dependent factors, as well as interactions between temperature and time play an important role for these life-history processes. According to the results of the nonlinear least squares parameter estimation (Table 3), the Harp Lake *Bythotrephes* population is suffering a mortality of around 0.19 per day. In late July, females are starting to produce about 30% male offspring. The mortality and the onset of male production have narrow confidence intervals. The highest uncertainty is associated with the rate of resting egg production, β . Its confidence interval spans several orders of magnitude.

Model limitations

As with other similar nonlinear least squares problems, there is no guarantee of exactly finding the parameter combination that yields a global minimum for the residuals. However, in our analyses the results were robust to different initial guesses for parameters fed into the optimization algorithm. Nonetheless we believe that broad confidence intervals for β and p are reflective of rather flat likelihood surfaces. These are the parameters for which the establishment threshold has a relatively low sensitivity. Examination of the model showed that the establishment threshold is proportional to $1/\beta$. It is much more sensitive to the mortality μ , the onset of male production t_0 , the embryonic development rate, and the clutch size.

These parameters are essential for the rate of asexual reproduction and thus our study broadly agrees with Drake (2004) who found that the critical density for his stochastic model for *Bythotrephes* population growth was most sensitive to the length of the summer growing season and the parthenogenetic growth rate.

We attempted to find a combination of parameters that fits the population dynamics of *Bythotrephes* in Harp Lake from 2002 to 2004. Thus, our estimates of some parameters (e.g. the mortality) might reflect local conditions (e.g. the abundance of predators in Harp Lake). Therefore, we have to be careful when applying our parameterized model to lakes with different local conditions and consider reestimating those parameters that are most affected by external conditions, such as the mortality.

If our assumption that resting eggs cannot remain in the sediment for more than one winter is relaxed such that every spring only a proportion α of all resting eggs is hatching, the critical introduction density would be $1/\alpha$ times (i.e. higher than) the establishment threshold without multiple-year egg survival. This is interesting for a potential application of our model to other cyclically parthenogenetic species that form egg banks to a greater extent than *Bythotrephes* does. If, in contrast to literature information (Andrew and Herzig 1984; Yurista 1997), there is considerable impact from an egg bank to the Harp Lake *Bythotrephes* population this could have influenced our estimate of the rate constant of resting egg production, β .

Since it would be difficult to study the temperature-dependency of the establishment threshold for *Bythotrephes* empirically, we might need to use data on changes in the phenology of already established populations in response to changes in temperature (Manca et al. 2007), which can give indirect information on the establishment threshold. However, climate change may have unpredictable effects on thermal stratification, chemical conditions, and on other species in the lake community, so that it will be difficult to make quantitative predictions on how establishment thresholds for *Bythotrephes* populations will change over the next decades. However, we could make our predictions more realistic by incorporating a model of how the temperature in different depths of a lake changes in response to a change in air temperature.

Allee effects

The strong demographic Allee effect detected in our model poses the question as to the biological relevance and the implications of this model phenomenon in natural populations on different scales. An Allee effect on the population level might also lead to an Allee-like effect on the spatial scale of all the lakes available to colonization by *Bythotrephes*. Lewis and Kareiva (1993) have shown in a spatially continuous models that if the local population dynamics exhibit an Allee effect, the species can spread only if a critical area is occupied initially. Analogous predictions result from spatially discrete models. Populations in different lakes can be seen as a metapopulation that might experience a metapopulation Allee effect, i.e. there is a critical number of lakes inhabited by *Bythotrephes*, in order for them to establish on the whole landscape (Zhou and Wang 2004). It could be a fruitful approach to identify regions that might be more or less vulnerable to *Bythotrephes* establishment given their spatial habitat structure.

At low population densities, where the Allee effect plays a role, population dynamics might not be adequately described by a deterministic model because environmental and demographic stochasticity play an important role. With stochasticity, populations can establish even though they start out below the Allee threshold, and populations above the threshold can go extinct (Taylor and Hastings 2005). However, if one includes stochasticity into a deterministic ordinary differential equation model, thus turning it into a diffusion process, the Allee threshold from the deterministic model remains an important quantity. It marks now the inflection point of the extinction probability as a function of the starting population size (Dennis 2002).

In our model, the lower probability of encountering a mate for sexual reproduction at low densities directly translates into an Allee effect on the population level because our model does not include mechanisms for negative density dependence. Certainly, *Bythotrephes* populations will experience negative density dependence at high densities, but we are interested in the establishment process of *Bythotrephes* and therefore in population dynamics at low densities where negative density dependence

should not play a major role. However, for parameter combinations and temperature regimes where positive density dependence is very weak, i.e. the establishment threshold is very small, a small amount of negative density dependence might be enough to compensate the positive density dependence and remove the demographic Allee effect.

Another reason why Allee effects in natural *Bythotrephes* populations might be weaker than predicted by our model or even absent are evolutionary adaptations to life at low densities (Kanarek and Webb 2010), such as aggregations of males and females for mating as they have been observed in other cladocerans (Young 1978), sperm storage, or specialized chemical or mechanic sensing abilities that help males and females to detect each other (Gerritsen 1980). At low densities, such adaptations would not change the structure of the mating function in the model but lead to a modification of the rate constant of resting egg production, β .

The Allee effect we observed resulted from the structure of our model. A similar model, parameterized for another cyclically parthenogenetic invader (i.e. a species that reproduces asexually most of the time, but requires sexual reproduction regularly), would also exhibit an Allee effect. Whenever processes in the life cycle are influenced by temperature, the magnitude of the establishment threshold would also be temperature-dependent. In general, an increase in temperature in the course of climate change would speed up developmental processes, reduce establishment thresholds, and thus facilitate invasions of cyclical parthenogens. If such an Allee effect is not only a model property but also present in natural populations there will be important implications for risk assessment and management. Without an Allee effect, the introduction of a single asexually reproducing individual can be sufficient to start an invasion if the abiotic and biotic conditions are favourable. Models for risk assessment for a cyclically parthenogenetic invader that do not take into account the Allee effect might overestimate establishment probabilities. If an Allee effect exists, invasions would be no longer inevitable despite occasional accidental introduction events, but reducing propagule pressure below the critical threshold could prevent invasions to as yet uninvaded sites.

Propagule pressure

Propagule pressure is one of the few consistent predictors of invasion success (Williamson and Fitter 1996; Colautti et al. 2006; Jeschke and Strayer 2006). It can be partitioned into propagule size (the number of individuals released per introduction event) and propagule number (the number of introduction events, Lockwood et al. 2005). Our model considers the local dynamics of a *Bythotrephes* population after a single introduction event. The critical densities obtained from our model lead to high estimated critical propagule sizes for establishment in any given lake if a homogeneous distribution of *Bythotrephes* individuals in the lake is assumed. The order of magnitude of critical density and propagule sizes agrees with the numbers reported by Kramer et al. (2008) for copepod introductions. However, *Bythotrephes* may stay close to the site of introduction or aggregate in some parts of the lake, such that successful establishment does not necessarily require that the critical density is reached everywhere in the lake. If there are multiple introduction events the spatial distribution of releases strongly influences establishment success. The closer together in space and time and the closer to reflecting boundaries like shores or harbors multiple introduction events are, the higher the invasion success (Drury et al. 2007).

Possible future work

Since the interaction of males and females for sexual production of diapausing eggs is a key process in the life cycle of *Bythotrephes* that determines whether a population can establish at a certain location or not, it is important to study this process and factors that influence it in detail. Most studies on the population dynamics of *Bythotrephes* so far have concentrated on parthenogenetic reproduction and the development rates of females. These processes are certainly very important because they determine whether the population can increase in numbers throughout the year. But ultimately, males and sexual reproduction are necessary for successful establishment of a population in a North American lake on the interannual time scale. This is the first study that calculates establishment thresholds for *Bythotrephes* under consideration of the whole complex life cycle. However, there is a lot of uncertainty associated with the corresponding

parameters and their dependence on temperature. Sex ratio, development rates of males, and rates of resting egg production have hardly been studied in the lab, in contrast to development times of parthenogenetic females. It should be an objective of future *Bythotrephes* to close these gaps of knowledge.

If we want to validate the model presented here, we need three kinds of data for a set of water bodies: temperature curves, presence-absence data, and measures of typical propagule sizes. Thus far, there have been the so-called gravity models which describe propagule pressure as a function of lake characteristics, such as area or diameter, and geographical properties, such as proximity to invaded lakes or big cities (MacIsaac et al. 2004). To be able to make a fruitful link between our mechanistic model for the establishment of *Bythotrephes* and a gravity model, we need to develop a better understanding for the interplay of propagule size and propagule number. For example, the establishment risk would be higher if there is a small number of large releases of *Bythotrephes* than if there is a large number of small releases, possibly distributed over several years. An extension of our model that includes the possibility of multiple introductions combined with a gravity model that predicts propagule sizes and numbers could give a more complete picture of the *Bythotrephes* invasion to North America and allow for a more realistic risk assessment.

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Appendix: Model parameterization details

Data on the *Bythotrephes* population of Harp Lake

Harp Lake, Ontario, (45°23'N, 79°07'W) is an inland lake on the Canadian Shield and has an area of 71.4 ha and a maximum depth of 37.5 m (Hall and Yan 1997). *Bythotrephes* was first detected in 1993 during routine

monitoring by the Ontario Ministry of the Environment (Yan and Pawson 1997), but could have been present at low densities in the previous 1 or 2 years. The data we used for parameter estimation span the years 1994 to 2005. In the years 1994, 1995, and 1997 to 2004, following a stratified random sampling regime, on each sampling date, one randomly chosen location in each of three depth zones in each of three lake regions was sampled. Additionally, a sample was always taken at the deepest position of the lake, resulting in a total of 10 sample locations per sampling date (Hall and Yan 1997). Samples were taken as vertical hauls of a closing tow net with a diameter of 0.75 m, a length of 2.5 m and a 285- μm mesh (Yan and Pawson 1997). For each *Bythotrephes* individual found, instar number, gender, shape of the tail spine, state of the brood and clutch size were determined and stored in a database, with some exceptions: In 1994 and 1997 gender was not determined, so that the variables F_1 and F_2 also include first and second instar males, respectively. For these years, we only use the brood size data, not the densities of each stage. In general, it is difficult to distinguish first instar males from females, which might be a reason for the low observed densities of first instar males.

These data were used to create time series of the densities of the model variables F_1 , F_2 , F_3 , M_1 , and M_2 . We calculated densities for each station separately as number of individuals within a stage divided by the sample volume (corrected for filtration efficiency) in m^3 . The model variables F_1 and F_2 consist of sexually or parthenogenetically produced females of instars one and two, respectively. F_3 is a combination of third instar sexually produced females, which need to molt once more to reproduce, mature fourth instar sexually produced females, and mature third instar parthenogenetically produced females. The density of resting eggs cannot be assessed by sampling the water column. There have been attempts to monitor the number of resting eggs in the sediment (Yurista 1997), but this was not done for Harp Lake during the time period of interest. We averaged the densities of the other stages at all 10 sampling sites to get the average density for each sampling date. The number of sampling dates throughout the growing season differed from year to year, ranging from only 4 in 1999 and 2000 to 25 in 2003. We also extracted information on clutch sizes and mode of reproduction from the Harp Lake

Bythotrephes database. In 2003, there were additional horizontal tows at different depths that can be used to characterize the vertical distribution of the *Bythotrephes* population (Young and Yan 2008).

Temperature profiles from the lake surface to the bottom were measured at the deepest station in Harp Lake by the Ontario Ministry of the Environment on each visit. To obtain the temperature values for depth ϕ on a certain day of the year t , $T(t, \phi)$, we linearly interpolated between the measured time points and depths.

Accounting for the vertical distribution of *Bythotrephes* in the water column

At any moment in time, the individuals of a *Bythotrephes* population are distributed over a range of water depths and thus experience different temperatures, which leads to differences in the rates of temperature-dependent life-history processes. Therefore, we weighted all functions in our model that vary with temperature (e.g., development rates) by the probability of experiencing a certain temperature, which can be constructed from the vertical distribution and the temperature profile. The vertical distribution differs between the life-history stages and varies both seasonally and from day to night (Young and Yan 2008). For any time point and life-history stage, the cumulative *Bythotrephes* proportion $Pr(\phi \leq x)$, i.e. the probability of the depth ϕ of an individual to be smaller or equal to x , can be well described by a function of the form:

$$Pr(\phi \leq x) = \frac{k}{1 + \exp(-a(x - x_c))}, \tag{17}$$

where k , a , and x_c are fitted parameters. By differentiating and normalizing the cumulative density

function, we obtained the corresponding density function that gives the probability density of an individual to be located at depth x :

$$\psi(x) = \frac{ka \cdot \exp(-a(x - x_c))}{1 + \exp(-a(x - x_c)) \cdot K}, \tag{18}$$

where $K = \int_0^{\phi_{max}} \frac{ka \cdot \exp(-a(x - x_c))}{1 + \exp(-a(x - x_c))} dx$ is a normalization constant that ensures that the probability of an individual to be located somewhere between the lake surface and its maximum depth is 1.

Young and Yan (2008) obtained cumulative density functions by fitting Eq. 17 to the distributions measured in Harp Lake in 2003. From their fitted parameters, we constructed probability distributions for day and night for first instar females ($Pr_{day/night}^{(1)}$), second instar females ($Pr_{day/night}^{(2)}$), third instar females ($Pr_{day/night}^{(3)}$), and males ($Pr_{day/night}^{(m)}$). Young and Yan (2008) also modeled the distribution of females that are carrying brood, but since their vertical distribution did not differ from other third instar females, we will use $Pr_{day/night}^{(3)}$ for all processes involving third instar females. To evaluate the time-dependent population mean, $f(t)$, for a given function of temperature, $g(T)$ (e.g. the development rates), we weighted the value of the temperature-dependent function at a given depth and its specific temperature with the probability density of a *Bythotrephes* individual of the stage of interest to be at this depth and integrated this expression over all relevant depths. Additionally, we weighted the values of the integral for day and night by the proportions of day and night, p_{day} and $1 - p_{day}$, respectively, which are functions of the time of the year (analogous to equation B2 in Young et al. 2009):

$$\begin{aligned}
 \underbrace{f(t)}_{\text{population function value}} &= \underbrace{p_{day}(t)}_{\text{proportion day}} \cdot \underbrace{\int_0^{\phi_{max}} g(T(t, x)) \cdot \psi_{day}(x) dx}_{\text{value of the depth-weighted function during the day}} \\
 &+ \underbrace{(1 - p_{day}(t))}_{\text{proportion night}} \cdot \underbrace{\int_0^{\phi_{max}} g(T(t, x)) \cdot \psi_{night}(x) dx}_{\text{value of the depth-weighted function during the night}} \\
 &\quad \text{function value at depth } x \quad \text{daytime } \textit{Bythotrephes} \text{ probability density at depth } x \\
 &\quad \text{function value at depth } x \quad \text{nighttime } \textit{Bythotrephes} \text{ probability density at depth } x
 \end{aligned} \tag{19}$$

Since the probability distributions have been parameterized only for a number of sampling dates, we linearly interpolated $f(t)$ between these sampling dates. The vertical distribution of *Bythotrephes* has been studied in Harp Lake only for 2003. We assumed that the vertical distribution as a function of the day of the year will be similar in other years.

Development rates, $d_e(t)$, $d_{f1}(t)$, $d_{f2}(t)$, $d_{m1}(t)$

Lehman et al. (1997) found that the relationship between temperature and the embryonic development rate can be described by three models that perform equally well over an ecologically relevant range of temperatures. Therefore, we chose their first and most simple model

$$\frac{1}{D} = a \cdot T + b \tag{20}$$

to parameterize the development rates in our dynamical system. It describes the inverse of the development time D , i.e. the development rate, as a linear function of the temperature, T . For the development time from the embryonic red-eye stage, when the eye pigment first becomes visible, to the release as neonate, a and b are 0.0024 and 0.01151, respectively (Lehman et al. 1997). We assumed with Lehman et al. (1997) that all other development times scale linearly with the embryonic development time and used their scaling factors. Restricting the development rates to positive values, we obtained for the development rate between male and female instars 1 and 2:

$$\delta_1(T) = \max(0.022879(\text{°C day})^{-1} \cdot T - 0.12908\text{day}^{-1}, 0). \tag{21}$$

The development rate between female instar 2 and 3 is:

$$\delta_2(T) = \max(0.02464(\text{°C day})^{-1} \cdot T - 0.13902\text{day}^{-1}, 0). \tag{22}$$

The time from beginning of instar 3 to primiparity that Lehman et al. (1997) measured served as approximation for the total embryonic development time in our model, from the deposition of eggs in the brood pouch to their release. Using the appropriate scaling factor, we obtain:

$$\delta_e(T) = \max(0.018991(\text{°C day})^{-1} \cdot T - 0.10715\text{day}^{-1}, 0). \tag{23}$$

All three development rates are for an individual *Bythotrephes* that is experiencing temperature T ; so we used Eq. 19 with $g(T) = \delta_i(T)$ and the corresponding stage-specific vertical distributions $Pr_{day/night}^{(3)}$, $Pr_{day/night}^{(1)}$, $Pr_{day/night}^{(2)}$, and $Pr_{day/night}^{(m)}$ to obtain $d_e(t)$, $d_{f1}(t)$, $d_{f2}(t)$, and $d_{m1}(t)$, respectively.

Population hatching rate of resting eggs, $h(t)$

We developed an individual resting egg hatching rate function dependent on the temperature, T , by taking Yurista’s (1992) hatching rate of 0.014 per day at 10.6°C, a critical temperature of 4°C for hatching to initiate, and the temperature dependency of Eq. 20:

$$H(T) = \max(0.00214(\text{°C day})^{-1} \cdot T - 0.00858\text{day}^{-1}, 0). \tag{24}$$

To calculate the population hatching rate at time t , $h(t)$, we incorporated the temperature the resting eggs were exposed to at the lake bottom, assuming that they were evenly distributed across the lake. With $q(\phi)$ as the density of Harp Lake’s surface area that has depth ϕ , we can write:

$$\underbrace{h(t)}_{\text{population hatching rate}} = \int_0^{\phi_{\max}} \underbrace{H(T(t, \phi))}_{\text{individual hatching rate at depth } \phi} \cdot q(\phi) d\phi. \tag{25}$$

We approximated the integral by summing over a range of depth classes (Fig. 9), with temperatures corresponding to the temperature at the midpoint of each depth class.

Clutch size, $c(t)$

Parthenogenetic clutch size, $c(t)$, the number of asexual embryos per brood, has been observed to change over the course of a year (Pothoven et al. 2001; Yan et al. 2001; Young 2008). Where data were available for the early season, a rapid decline has been observed from clutch sizes as high as 9 to averages between 2 and 4 later in summer (Young 2008). Since we do not know of any functional form that has been suggested to describe the clutch size as a function of time or temperature, we fit a generalized

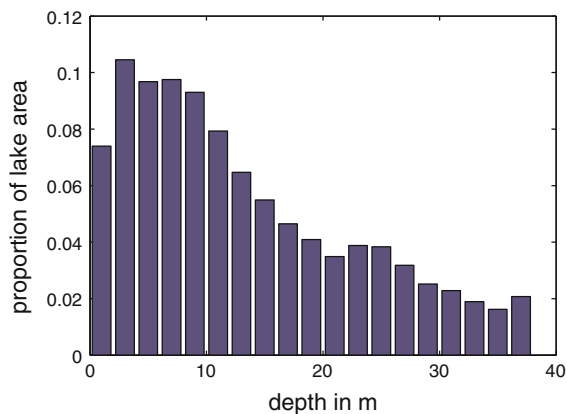


Fig. 9 Bathymetric information for Harp Lake, Ontario, used to calculate the hatching rate of resting eggs $h(t)$. The proportion of each depth class is plotted against the midpoint depth of the class

linear model to relate clutch size data to time and effective temperature experienced by third instar females, $T_e^{(3)}(t)$. To calculate $T_e^{(3)}(t)$, we evaluated Eq. 19 with $g(T(t, x)) = T(t, x)$ and the vertical distribution for third instar females ($Pr_{day/night}^{(1)}$).

We pooled parthenogenetically reproducing females from all years whose clutch size had been scored ($n = 1,047$) and fit a zero-truncated Poisson generalized linear model with a log link (as described in Zuur et al. 2009) using the VGAM package (Yee 2008) in R version 2.10.1 (R Development Core Team 2009) with day of the year and effective temperature experienced by third instar females as factors. Based on Akaike's information criterion (AIC), we chose the model that includes both temperature and day, as well as their interaction:

$$c(t) = \exp(-7.83 + 0.581 \cdot T_e^{(3)}(t) + 0.0468 \cdot t - 0.00308 \cdot T_e^{(3)}(t) \cdot t). \quad (26)$$

Proportion of females that are reproducing sexually, $\sigma(t)$

To obtain a relationship between the proportion of females that are reproducing sexually and the predictors time and effective temperature, we fit a binomial generalized linear model with a logit link (Zuur et al. 2009) to data on the reproduction mode extracted from the Harp Lake database for the years 1994–2004 ($n=5,064$). The best model according to AIC contains temperature, time, and their interaction as factors and is given by:

$$\sigma(t) = \frac{1}{1 + \exp(-60.9 + 0.200 \cdot t + 4.43 \cdot T_e^{(3)}(t) - 0.0146 \cdot t \cdot T_e^{(3)}(t))}$$

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