

On the mechanistic underpinning of discrete-time population models with complex dynamics

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Received 16 June 2003; received in revised form 16 October 2003; accepted 16 January 2004

Abstract

We present a mechanistic underpinning for various discrete-time population models that can produce limit cycles and chaotic dynamics. Specific examples include the discrete-time logistic model and the Hassell model, which for a long time eluded convincing mechanistic interpretations, and also the Ricker- and Beverton–Holt models. We first formulate a continuous-time resource consumption model for the dynamics within a year, and from that we derive a discrete-time model for the between-year dynamics. Without influx of resources from the outside into the system, the resulting between-year dynamics is always overcompensating and hence may produce complex dynamics as well as extinction in finite time. We recover a connection between various standard types of continuous-time models for the resource dynamics within a year on the one hand and various standard types of discrete-time models for the population dynamics between years on the other. The model readily generalizes to several resource and consumer species as well as to more than two trophic levels for the within-year dynamics.

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Keywords: Beverton–Holt model; Continuous-time model; Discrete-time model; Hassell model; Logistic model; Overcompensation; Population dynamics; Resource consumption; Ricker model

1. Introduction

Discrete-time population models have received a great amount of attention for the complex and intriguing dynamics they can produce even in the simplest systems. With few exceptions, however, these models lack a clear mechanistic interpretation in terms of underlying ecological interactions that occur between two population censuses. For example, the discrete logistic model (also called the quadratic map) is usually presented as the literal (but not dynamical) equivalent of the continuous-time logistic model. The Hassell (1975) model was introduced as a descriptive model and was used for statistical data fitting (Hassell et al., 1976). In this paper we present a single ecological underpinning for various discrete-time population models including the discrete logistic model and the Hassell (1975) model, but also the models of Ricker (1954) and of Beverton

and Holt (1957) for which different mechanistic interpretations are well known.

An unstructured discrete-time population model must be overcompensating (i.e. the population density x_{n+1} in the next year must have a local maximum as a function of the current population density x_n ; Gurney and Nisbet, 1998, p. 128) in order to produce cycles or chaos. Undercompensating models (where x_{n+1} increases monotonically with x_n) can produce only monotonous convergence to an equilibrium. The mechanistic underpinning of between-year overcompensation is therefore of interest (see, e.g. Jensen, 1994; Nedorezov and Nedorezova, 1995; Gyllenberg et al., 1997; Sumpter and Broomhead, 2001; Gamarra and Sole, 2002; Johansson and Sumpter, 2004).

Discrete-time models are used when reproduction happens once a year as a discrete event, while deaths may occur continuously during the course of a year. Mere instantaneous density dependence of the death rate, however, does not yield overcompensating between-year dynamics (Nedorezov and Nedorezova, 1995; Gyllenberg et al., 1997). One may assume density dependence in fecundity such that it leads to

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overcompensation, but then overcompensation is incorporated by assumption rather than as the outcome of an underlying ecological mechanism (Nedorezov and Nedorezova, 1995).

In this paper we present a model in which density dependence of fecundity derives from a resource–consumer model for the within-year dynamics. By applying a time-scale argument, we keep the between-year dynamics of the consumer one-dimensional. We demonstrate that within our framework, the between-year dynamics of the consumer is always overcompensating unless there is an influx of resources from the outside into the system. In the second part of this paper, we simplify the model by assuming no adult consumer mortality during the season (all adult consumers die at the end of the season). Using various standard equations for the continuous-time population growth of the resource, we then recover various standard overcompensating discrete-time models for the between-year dynamics of the consumer. In the last sections, we briefly discuss similar models with multiple resource and consumer species and with more trophic levels, and we analyse the between-year dynamics of the consumer with adult mortality during the season.

2. The model

Consider a population of consumers with population density $x_n(t)$ at time t within year $n = 0, 1, 2, \dots$, living off some food source with density $R_n(t)$, and producing eggs at a per capita rate proportional to the rate of food intake. The density of eggs accumulated since the beginning of the year is denoted by $E_n(t)$. Within each year, time t runs from zero to one, and the within-year dynamics is given by

$$\begin{aligned}\dot{R}_n(t) &= \alpha R_n(t) f(R_n(t)) - \beta R_n(t) x_n(t), \\ \dot{E}_n(t) &= \gamma \beta R_n(t) x_n(t) - \delta E_n(t), \\ \dot{x}_n(t) &= -\mu x_n(t).\end{aligned}\quad (1)$$

Here α is a scaling factor for the resource population growth rate, β denotes the consumption rate, γ the conversion of food into eggs, δ the rate of egg mortality during the season and μ the mortality rate among adult consumers (note that in Sections 3–5, we shall assume $\mu = 0$). The function f is assumed to be continuous and monotonically decreasing on $(0, \infty)$ such that $\lim_{R \downarrow 0} Rf(R)$ is finite and such that for some given positive K , $f(R) > 0$ if $R < K$ and $f(R) < 0$ if $R > K$. As a consequence, K is the unique asymptotically stable positive equilibrium density for the resource dynamics if no consumers are present.

At the end of the season ($t = 1$) all adult consumers die, and the next year's population is recruited from the eggs that survive the winter. Eggs that do not hatch at

the beginning of the next year are assumed to be lost. Next year's initial resource density is equal to what remains from the present year multiplied by a factor describing winter survival. The between-year dynamics is thus given by

$$\begin{aligned}R_{n+1}(0) &= \rho R_n(1), \\ E_{n+1}(0) &= 0, \\ x_{n+1}(0) &= \sigma E_n(1),\end{aligned}\quad (2)$$

where σ and ρ denote the winter survival probabilities for the eggs and the resource, respectively.

We simplify the model by assuming that the within-year dynamics of $R_n(t)$ is much faster than the within-year dynamics of $E_n(t)$ and $x_n(t)$, i.e. α and β are large compared to $\gamma\beta$, δ and μ . A two-time-scale analysis of Eq. (1) then shows that the within-year resource dynamics has a unique asymptotically stable quasi-equilibrium

$$\hat{R}_n(t) = \begin{cases} f^{-1}\left(\frac{\beta}{\alpha} x_n(t)\right) & \text{if } x_n(t) \in [0, x^*), \\ 0 & \text{if } x_n(t) \geq x^*, \end{cases}\quad (3)$$

where $x_n(t) = x_n(0)e^{-\mu t}$ and $x^* = (\alpha/\beta) \lim_{R \rightarrow 0} f(R)$, which may be finite or infinite. We assume that during the year the resource density stays on the quasi-equilibrium, i.e. $R_n(t) = \hat{R}_n(t)$ for all t . Note that this implies that we allow for the full recovery of the resource whenever the quasi-equilibrium becomes positive again after the resource density has become zero earlier during the same year or at the end of the previous year. The rationale behind this is that given the assumption of fast resource dynamics, small perturbations in the resource density instantaneously restore the resource at its positive resource equilibrium density. (Alternatively, we might assume that the resource does not recover once it has gone extinct. The implications of such an assumption are discussed in the second half of Section 6.)

Substitution of the resource density $R_n(t)$ in Eq. (1) by the quasi-equilibrium $\hat{R}_n(t)$ from Eq. (3) gives a first-order linear differential equation for the egg density $E_n(t)$, which is readily integrated. Substitution of the egg density $E_n(1)$ at the end of the season into the equation for $x_{n+1}(0)$ in Eq. (2) subsequently gives

$$x_{n+1}(0) = x_n(0) \left[\sigma \gamma \beta e^{-\delta} \int_0^1 \hat{R}_n(t) e^{(\delta-\mu)t} dt \right].\quad (4)$$

Eqs. (3) and (4) together completely describe the between-year dynamics of the consumer species.

2.1. Overcompensation in the between-year consumer dynamics

In the appendix we show that if $\lim_{R \rightarrow 0} Rf(R) = 0$, then the between-year consumer dynamics is necessarily

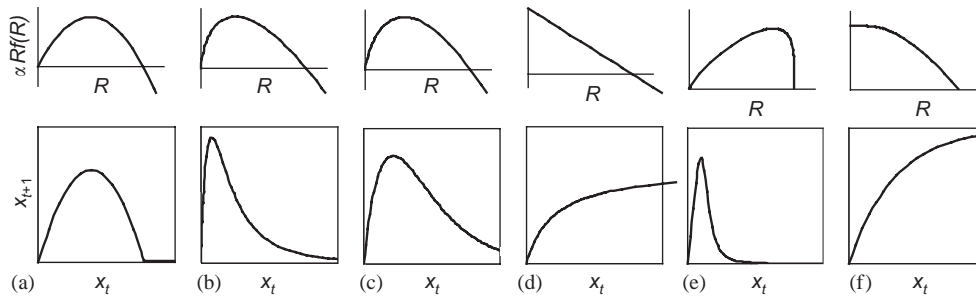


Fig. 1. Within-year resource dynamics (upper panels) and between-year consumer dynamics (lower panels) in the models of Sections 3 and 4. Note that the between-year consumer dynamics is undercompensating only when resource growth ($\alpha Rf(R)$) is positive at zero resource density (in (d) and (f)), which indicates inflow of the resource from outside the system. In all models, R is scaled such that $\lambda \equiv (\sigma\gamma\beta/\delta)(1 - e^{-\delta}) = 1$; by scaling $x, \beta/\alpha$ (and hence b) can be chosen arbitrarily; α is absorbed in scaling the vertical axes of the upper panels. (a) The discrete logistic model (Eqs. (6) and (7) with $K = 3.5$ and hence $a = 3.5$). (b) The Hassell model (Eqs. (8) and (9) with $K = 35$ and $\theta = 0.8$; it follows that $a = 35$ and $c = 5$). (c) The Ricker model (Eqs. (10) and (11) with $K = 10$ and hence $a = 10$). (d) The Beverton–Holt model (Eqs. (12) and (13) with $K = 3.5$ and hence $a = 3.5$). (e) The Maynard–Smith model (Eqs. (16) and (17) with $a = 10$ and $c = 5$; in the reconstructed resource dynamics, $K = 10$). (f) The Skellam model (Eq. (18) with $a = 3$).

overcompensating in the sense that $x_{n+1}(0)$ as a function of $x_n(0)$ has a global maximum and that at large values of $x_n(0)$ either $x_{n+1}(0) = 0$ or $x_{n+1}(0)$ is strictly decreasing. In most ecological settings $\lim_{R \rightarrow 0} Rf(R) = 0$ if and only if there is no influx of the resource from the outside into the system. In other words, undercompensating between-year dynamics requires a continuous influx of the resource, and without such influx, the between-year consumer dynamics is overcompensating and hence liable to exhibit complex dynamics such as cycles or chaos.

To understand this proposition heuristically, note from Eq. (1) that the rate of total egg production at the quasi-equilibrium is proportional to $R_n f(R_n)$, and thus most eggs would be produced if R_n were constant at the optimal harvesting density \hat{R} that maximises $R_n f(R_n)$. Large consumer densities, however, push the resource density below the optimal harvesting level. If R_n is less than \hat{R} throughout the season, then further increasing $x_n(0)$ decreases the total egg production as long as it is positive, i.e. we have overcompensation. Undercompensation in this model is possible only if $\hat{R} = 0$, for which $\lim_{R \rightarrow 0} Rf(R)$ must be positive.

3. The case of zero adult mortality ($\mu = 0$)

If the mortality among adult consumers during the season is negligible, i.e. if $\mu = 0$, then $x_n(t)$ and $\hat{R}_n(t)$ remain constant during the season, and the between-year dynamics of the consumer simplifies to

$$x_{n+1} = \begin{cases} \lambda x_n f^{-1}((\beta/\alpha)x_n) & \text{if } x_n \in [0, x^*), \\ 0 & \text{if } x_n \geq x^*, \end{cases} \quad (5)$$

where $x_n = x_n(0)$, $\lambda = (\sigma\gamma\beta/\delta)(1 - e^{-\delta})$ and $x^* = (\alpha/\beta) \lim_{R \rightarrow 0} f(R)$ as defined as in the first line below Eq. (3). Although the case $\mu = 0$ may be somewhat

special, it reveals a relation between various well-known types of continuous-time dynamics for the resource within a year on the one hand, and other well-known types of discrete-time dynamics for the consumer between years on the other. Here are some examples (Fig. 1 illustrates the various functions $\alpha R_n f(R_n)$ used for resource dynamics in the absence of consumers, and the resulting between-year map of the consumer dynamics, $x_{n+1}(x_n)$).

3.1. The discrete logistic model (Fig. 1a)

Suppose that if no consumers are present, the within-year resource dynamics is given by the continuous logistic equation

$$\dot{R}_n(t) = \alpha R_n(t) \left(1 - \frac{R_n(t)}{K} \right). \quad (6)$$

Then $f(R) = 1 - R/K$ and $x^* = \alpha/\beta$, so that from Eq. (5) we recover a truncated version of the discrete logistic equation

$$x_{n+1} = \begin{cases} \alpha x_n (1 - b x_n) & \text{if } x_n \in [0, x^*), \\ 0 & \text{if } x_n \geq x^*, \end{cases} \quad (7)$$

where $a = \lambda K$ and $b = \beta/\alpha$. The truncation at $x_n = x^*$ arises naturally from the underlying within-year dynamics and prevents next year's population density from becoming negative at values of $x_n \geq x^*$. Depending only on the value of the compound parameter a , the dynamics spans the whole range from a stable equilibrium via periodic orbits to full chaos (see, e.g. Devaney, 1989, for a detailed analysis). For $a > 4$, the consumer population will go extinct in finite time for almost every initial consumer density. Note that the continuous logistic model (Eq. (6)) itself can be given a mechanistic underpinning, e.g. by a continuous-time site-based model with death and recolonization

analogously to the metapopulation model of Levins (1969); see, e.g. (Johansson and Sumpter, 2004).

3.2. The Hassell-model (Fig. 1b)

Suppose that without consumers the within-year resource dynamics is given by the Von Bertalanffy equation

$$\dot{R}_n(t) = \alpha R_n^\theta(t) - \alpha K^{\theta-1} R_n(t) \tag{8}$$

for some $\theta \in (0, 1)$. This equation is best known as describing the growth of individual body size (with $\theta = \frac{2}{3}$; see, e.g. Thieme, 2003, pp. 33–35). With $\theta = \frac{1}{2}$, the Von Bertalanffy equation corresponds to the so-called sub-exponential population growth of replicators with self-inhibition and exponential decay (Szathmáry, 1991). More generally, the equation can be regarded as a crude model of population growth when intra-specific interference leads to self-inhibited reproduction while the *per capita* mortality rate remains constant. From Eq. (8) we have $f(R) = R^{\theta-1} - K^{\theta-1}$ and $x^* = \infty$, so that from Eq. (5) we recover the Hassell (1975) model

$$x_{n+1} = \frac{ax_n}{(1 + bx_n)^c} \tag{9}$$

for all $x_n \geq 0$, where $a = \lambda K$, $b = (\beta/\alpha)K^{1-\theta}$, and $c = 1/(1 - \theta)$. Since $c > 1$, in the present context the model is always overcompensating. The dynamics of Eq. (9) only depends on the parameters a and c and is as rich as that of the discrete logistic model (7), although extinction in finite time cannot occur (Hassell, 1975).

3.3. The Ricker model (Fig. 1c)

Suppose that without consumers, the within-year resource dynamics is given by the Gompertz equation

$$\dot{R}_n(t) = \alpha R_n(t) \left(1 - \frac{\ln R_n(t)}{\ln K} \right) \tag{10}$$

with $K > 1$ (see, e.g. Edelstein-Keshet, 1988). The Gompertz equation describes a population where the *per capita* growth rate declines exponentially with time, e.g. due to a deteriorating environment. An equivalent expression for Eq. (10) is $\dot{R}(t) = \lambda e^{-\nu t} R_n(t)$ for certain positive constants λ and ν . The Gompertz equation has been applied to populations of bacteria (e.g. Lay et al., 1998) and also occasionally to animal populations (Pradhan and Chaudhuri, 1998; Chavarria and de la Torre, 2001). From Eq. (10) we have $f(R) = 1 - \ln R/\ln K$ and $x^* = \infty$, so that from Eq. (5) we recover the Ricker (1954) model

$$x_{n+1} = ax_n e^{-bx_n} \tag{11}$$

for all $x_n \geq 0$, where $a = \lambda K$ and $b = (\beta/\alpha) \ln K$. Note that the present ecological mechanism is totally different from the one proposed by Ricker (1954) himself. The

dynamics only depends on the value of a , and are qualitatively similar to that of Eq. (9).

3.4. The Beverton–Holt model (Fig. 1d)

Suppose that the within-year resource dynamics in absence of the consumer is given by

$$\dot{R}_n(t) = \alpha - \frac{\alpha R_n(t)}{K} \tag{12}$$

In other words, there is a constant influx of the resource into the system at a rate α and an efflux or decay at a *per capita* rate of α/K . Thus, $f(R) = (1/R) - 1/K$ and $x^* = \infty$, so that from Eq. (5) we recover the model of Beverton and Holt (1957)

$$x_{n+1} = \frac{ax_n}{1 + bx_n} \tag{13}$$

for $x_n \geq 0$ and with $a = \lambda K$ and $b = (\beta/\alpha)K$. Thieme (2003, pp. 40–42) used a similar approach to derive *continuous* population dynamics with a birth term of the form $ax/(1 + bx)$. Note that this is our first example with undercompensating between-year dynamics.

4. The inverse problem

Consider the inverse problem: given a specific expression for the between-year consumer dynamics, what would be the underlying within-year resource dynamics? With $\mu = 0$ we can generate any type of between-year consumer dynamics provided it is of the form

$$x_{n+1} = \begin{cases} x_n g(x_n) & \text{if } x_n \in [0, L), \\ 0 & \text{if } x_n \geq L, \end{cases} \tag{14}$$

where $L > 0$ may be finite or infinite and where, for some $K > 0$, the function $g: [0, L) \rightarrow (0, K]$ is continuous, monotonically decreasing and onto. The underlying within-year resource dynamics in absence of consumers is then given by

$$\dot{R} = \beta R g^{-1}(\lambda R) \tag{15}$$

for $R \in (0, K/\lambda]$, which is readily verified by substitution into Eq. (5). Scale R such that λ equals 1. K is then the equilibrium resource density in the absence of the consumer, whereas L is equal to x^* as defined in the line below Eq. (3). The details of the right-hand side of Eq. (15) for $R > K$ are irrelevant, because $R(t)$ cannot pass through the point $R = K$, which is an equilibrium of Eq. (15). However, the resulting within-year resource dynamics may lack a clear ecological interpretation or may not be expressed in terms of known functions. For example, suppose we want to know the resource dynamics underlying the model of Maynard Smith (1974, p. 53) and Maynard

Smith and Slatkin (1973)

$$x_{n+1} = \frac{ax_n}{1 + bx_n^c} \tag{16}$$

for $x_n \geq 0$ and $a > 0$, $b > 0$ and $c > 0$. Since $g(x) = a/(1 + bx^c)$, it follows from Eq. (15) that the within-year resource dynamics is given by

$$\dot{R} = \alpha R \left(\frac{1}{R} - \frac{1}{K} \right)^{1/c} \tag{17}$$

for $R \in (0, K]$ and with $K = a$ and $\alpha = \beta(a/b)^{1/c}$ (see Fig. 1e). It is unclear, however, how Eq. (17) can be interpreted as a difference of a separate growth term and decay term. In other words, the Maynard Smith model does not permit an obvious mechanistic interpretation in terms of resource consumption, except when $c = 1$, in which case the model coincides with that of Beverton and Holt (1957).

As a second example, suppose we want to find the underlying resource dynamics that produces the discrete-time model of Skellam (1951)

$$x_{n+1} = \frac{a}{b}(1 - e^{-bx_n}) \tag{18}$$

for $x_n \geq 0$, and with $a > 0$ and $b > 0$ (written in the above form, b only scales x). Thus,

$$g(x) = \begin{cases} a & \text{if } x = 0, \\ \frac{a}{b}(1 - e^{-bx})/x & \text{if } x > 0. \end{cases} \tag{19}$$

While g is a strictly decreasing function and can be inverted numerically (see Fig. 1f), its inverse cannot be expressed in terms of known functions.

5. Generalizations of the model with zero adult mortality ($\mu = 0$)

In this section, we briefly consider two extensions of the basic model in Eq. (1), still assuming that adult consumer mortality is negligible during the season ($\mu = 0$).

5.1. Multiple resources and consumer species

The basic model in Eq. (1) with $\mu = 0$ readily generalizes to multiple species (k resource species and m consumers, where the dynamics of all resources are fast compared to the dynamics of consumers). Let the within-year dynamics be given by

$$\dot{R}^{(i)}(t) = \alpha_i R^{(i)}(t) f_i(R^{(i)}(t)) - R^{(i)}(t) \sum_{j=1}^m \beta_{ij} x^{(j)}$$

for $i = 1, \dots, k$,

$$\dot{E}^{(j)}(t) = x^{(j)} \sum_{i=1}^k \gamma_{ij} \beta_{ij} R^{(i)}(t) - \delta_j E^{(j)}(t)$$

for $j = 1, \dots, m$,

$$\dot{x}^{(j)} = 0 \quad \text{for } j = 1, \dots, m. \tag{20}$$

Note that in this model, there is no direct competition between resource species; they interact only via shared consumers that prey upon them. In quasi-equilibrium of the resources

$$\hat{R}^{(i)} = \max \left\{ 0, f_i^{-1} \left(\sum_j \frac{\beta_{ij}}{\alpha_i} x^{(j)} \right) \right\},$$

and therefore the between-year dynamics of the consumers is given by

$$x_{n+1}^{(j)} = x_n^{(j)} \sum_i \lambda_{ij} \max \left\{ 0, f_i^{-1} \left(\sum_l \frac{\beta_{il}}{\alpha_i} x_n^{(l)} \right) \right\}, \tag{21}$$

with $\lambda_{ij} = (\sigma_j \gamma_{ij} \beta_{ij} / \delta_j)(1 - e^{-\delta_j})$. If, for example, a single consumer exploits two resources with, respectively, continuous-time logistic and Von Bertalanffy growth, then the resulting between-year dynamics of the consumer is

$$x_{n+1} = x_n \left[\lambda_1 K_1 \left(1 - \frac{\beta_1}{\alpha_1} x_n \right)^+ + \lambda_2 \frac{K_2}{(1 + (\beta_2/\alpha_2)x_n)^c} \right],$$

i.e. the sum of a truncated discrete-time logistic term and a Hassell term. In case of several consumers, their between-year growth rates contain identical terms except for different weighing factors λ_{ij} .

5.2. Three or more trophic levels: ‘‘Echoing’’

Consider a model with three trophic levels, where the bottom species (R) exhibits density-dependent population growth in absence of the others, whereas species C exploits R and is exploited by the top consumer x that has discrete generations

$$\begin{aligned} \dot{R}_n(t) &= \alpha R_n(t) f(R_n(t)) - \beta' R_n(t) C_n(t), \\ \dot{C}_n(t) &= \gamma' \beta' R_n(t) C_n(t) - \beta C_n(t) x_n - \delta' C_n(t), \\ \dot{E}_n(t) &= \gamma \beta C_n(t) x_n - \delta E_n(t), \\ \dot{x}_n(t) &= 0. \end{aligned} \tag{22}$$

Assume that the dynamics of the two bottom species is fast compared to the top consumer such that $R_n(t)$ and $C_n(t)$ attain a quasi-equilibrium (which is always globally attracting; cf. Hofbauer and Sigmund, 1998, Chapter 4.3, pp. 34–37). The between-year dynamics of the top consumer is then

$$x_{n+1} = \lambda x_n \hat{C}_n = \begin{cases} \lambda x_n \frac{\alpha}{\beta'} f \left(\frac{\beta x_n + \delta'}{\gamma' \beta'} \right) & \text{if } x_n \in [0, x^*), \\ 0 & \text{if } x_n \geq x^*, \end{cases} \tag{23}$$

with $x^* = (\gamma'\beta'K - \delta')/\beta$ and with $\lambda = (\sigma\gamma\beta/\delta)(1 - e^{-\delta})$ as before. Note that with three trophic levels, the function f itself is “echoed” in the between-year map of the top consumer, whereas with two trophic levels, the shape of the between-year map is given by the inverse of f (see Eq. (5)). In addition, there is a translation term in the argument of f (which is, however, small if the consumption-independent death rate of the middle species, δ' , is small).

With more than three trophic levels, the stability of the quasi-equilibrium may not be guaranteed. However, if each trophic level has a different time-scale with the bottom species being the fastest and the top consumer being the slowest, then the stability of the quasi-equilibrium is ensured. Depending on whether the number of trophic levels is odd or even, the function f or its inverse, a property of the species at the bottom trophic level, is “echoed” in the between-year dynamics of the top consumer. (Note that with more than three trophic levels, translation terms appear in the between-year growth rate both in the argument of f or f^{-1} and outside of it.)

6. The case of positive adult mortality ($\mu > 0$)

If the mortality among adult consumers during the season is not negligible, i.e. $\mu > 0$, then the integral in Eq. (4) usually cannot be calculated explicitly. Among the examples in Sections 3 and 4, the case of a logistically growing resource is a notable exception. For this case we find $x^* = \alpha/\beta$ and

$$x_{n+1} = \begin{cases} ax_n(1 - bx_n) & \text{if } x_n \in [0, x^*), \\ a'x_n(1 - b'x_n + c'x_n^{(\delta-\mu)/\mu}) & \text{if } x_n \in [x^*, x^*e^\mu), \\ 0 & \text{if } x_n \geq x^*e^\mu, \end{cases} \tag{24}$$

where

$$a = \frac{\sigma\gamma\beta K}{\delta - \mu}(e^{-\mu} - e^{-\delta}), \quad b = \frac{\beta(\delta - \mu)}{\alpha(\delta - 2\mu)} \frac{(e^{-2\mu} - e^{-\delta})}{(e^{-\mu} - e^{-\delta})},$$

$$a' = \frac{\sigma\gamma\beta K}{\delta - \mu}e^{-\mu}, \quad b' = \frac{\beta(\delta - \mu)}{\alpha(\delta - 2\mu)}e^{-\mu}$$

and $c' = \frac{\mu}{\delta - 2\mu}(\beta/\alpha)^{(\delta-\mu)/\mu}e^{\mu-\delta}$.

For $0 \leq x_n < x^*$ and $x_n \geq x^*e^\mu$ we recover the truncated discrete logistic equation in Eq. (7) (albeit with different parameters), but for $x^* \leq x_n < x^*e^\mu$ the two models are different (Fig. 2a).

Whenever $x^* < \infty$, the right-hand side of Eq. (4) consists of three parts like in the example in Eq. (24). The reason for this is the following: (i) If $x_n(0) < x^*$, then $x_n(t) < x^*$ for all t . Hence, from Eq. (3), $\hat{R}_n(t) > 0$ for all t , so that eggs are being produced during the whole season. (ii) If $x^* < x_n(0) < x^*e^\mu$, then $x_n(t) > x^*$ for

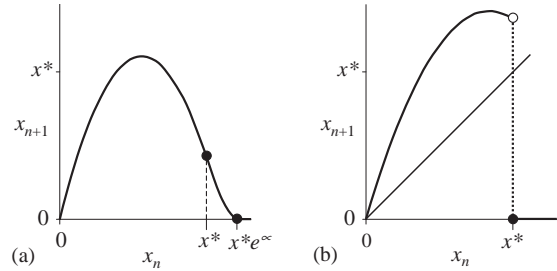


Fig. 2. The between-year consumer dynamics for logistic within-year resource growth and positive adult mortality, with (a) assuming that the resource can recover from extinction (Eq. (24)) and (b) assuming that resource density stays zero once it has reached zero. In (a), the resource is extinct during the first part of the season when $x^* < x_n(0) < x^*e^\mu$, and it goes extinct during the entire season only if $x_n(0) > x^*e^\mu$. In (b), the resource is extinct at the beginning of the season and therefore during the entire season when $x_n(0) > x^*$. Note that in the example shown in (b), no positive equilibrium exists (i.e. there is no positive point intersection with the line $x_{n+1} = x_n$) even though the equilibrium at zero population density is repelling. Parameter values: (a) $\sigma\gamma\beta K = 7$, $\alpha/\beta = 1$, $\delta = 1$ and $\mu = 0.2$, (b) $\sigma\gamma\beta K = 10$, $\alpha/\beta = 1$, $\delta = 1$ and $\mu = 1.2$.

$t < t^*$ and $x_n(t) < x^*$ for $t > t^*$, where $t^* = (1/\mu) \ln x_n(0)/x^* < 1$. Hence, $\hat{R}_n(t) > 0$ only for $t > t^*$, so that eggs are being produced only during the later part of the season. (iii) If $x_n(0) > x^*e^\mu$, then $x_n(t) > x^*$ for all t , so that $R_n(t) = 0$ for all t , and no eggs are being produced anytime. In spite of consisting of three parts, one readily shows that the right-hand side of Eq. (4) as a function of $x_n(0)$ is continuously differentiable at $x_n(0) = x^*$ as well as at $x_n(0) = x^*e^\mu$ (cf. Fig. 2a). Generally, it is not twice differentiable at these points.

Till now we assumed that the resource population can fully recover even after its density has become zero at some earlier time, for example, by an otherwise negligible level of immigration. If instead we assume that the resource density stays zero once it has reached zero, then (i) for $x_n(0) < x^*$, $R_n(t)$ is positive and hence eggs are being produced during the entire season like previously, but (ii) for $x_n(0) \geq x^*$, $R_n(t)$ is initially zero and stays zero during the entire season, and therefore no eggs are being produced anytime during the season, also not after the consumer population has become so small that the quasi-equilibrium of the resource has become positive again. As a consequence, the right-hand side of Eq. (4) as a function of $x_n(0)$ has a discontinuity at the point $x_n(0) = x^*$. Because of this, the between-year dynamics can be dramatically different from that under the assumption of full recovery of the resource. In particular, there may not exist a positive equilibrium for the between-year consumer dynamics even if the zero population density is unstable, in which case the consumer population goes extinct in finite time irrespective of its initial state (cf. Fig. 2b). We would like to emphasize, however, that without the possibility of spontaneous recovery of the resource population, the

results are not robust against small perturbations in the resource density.

7. Discussion

In discrete-time models, the population densities x_n and x_{n+1} in two consecutive years can be seen, respectively, as the input and as the output of processes occurring during the intervening period here referred to as the within-year dynamics. The output of one year is the input of the next year. Suppose that the within-year dynamics is given by a single ordinary differential equation where the input determines only the initial condition of the system (and nothing else), and suppose that the dependence of the initial condition on the input is monotonic. If also the output is a monotonic function of the state of the system at the end of the season, then there is necessarily a monotonous relation between the input and the output, and hence the between-year dynamics is undercompensating (Nedorezov and Nedorezova, 1995; Gyllenberg et al., 1997; the latter authors also show that if fecundity is traded-off with density-dependent offspring survival during the year, then adjustable reproductive strategies may lead to overcompensation, but the evolutionarily *optimal* reproductive strategy again gives undercompensation).

If the within-year dynamics involves structured populations (Gyllenberg et al., 1997) or interacting species (Gamarra and Sole, 2002), then the input–output relation may be non-monotonous and thus gives rise to overcompensation between years, possibly with complex dynamical behaviour such as cycles or chaos. Note that population structure or inter-specific interactions on the level of the between-year dynamics imply time delays across different years, which may further destabilise the between-year dynamics (see Turchin and Taylor, 1992).

In our model, the within-year dynamics involves population structure (eggs and adults) as well as inter-specific interactions (resource and consumers). The eggs, however, interact neither with the adults nor with the resource, but merely accumulate. Moreover, by the assumption of fast resource dynamics, the within-year dynamics is confined to a one-dimensional manifold and can be represented by a single ordinary differential equation for the density of the eggs. How, then, does our model lead to overcompensation between years? The reason for this is that the input (i.e. the density of adults at the beginning of the season) affects the rate of egg production and therefore affects the differential equation itself and not just the initial condition. In fact, the initial condition is independent of the input, because the egg density at the beginning of the season is by assumption always zero. The situation is comparable to that described by Ricker (1954), where the adults affect (through cannibalism) the rate of mortality of the eggs

(or juveniles), so that the input not only affects the initial density of eggs (which are produced in a single burst at the beginning of the season) but also the within-year dynamics itself.

When the within-year dynamics depends on the input in other ways than merely through initial conditions, then overcompensation is possible because of delayed density dependence. What our model contributes is an explicit ecological underpinning for this time delay, and hence for overcompensation. Assuming that the system is closed, the between-year dynamics of the consumer is always overcompensating and hence liable to exhibit complex dynamics such as cycles or chaos. Undercompensating between-year dynamics in our model requires a continuous influx of the resource.

For different types of continuous resource dynamics, we recover different standard discrete-time models including the discrete logistic model, the Hassell (1975) model, the Ricker (1954) model and the Beverton–Holt (1957) model. While different continuous-time models of single populations have qualitatively similar dynamics (i.e. convergence to a fixed point), our model shows that the exact form of the continuous-time dynamics for the resource can be important for the qualitative behaviour of the discrete-time model for the population on the next trophic level. For example, in the discrete logistic model a population can go extinct in finite time, whereas in the Hassell (1975) model and in the Ricker (1954) model extinction in finite time is not possible, even though the underlying continuous-time resource dynamics are very similar (Fig. 1a–c).

Concerning the discrete logistic model, Jensen (1994) offered a derivation where adults produce offspring within a season at a rate linearly dependent on the density of the adults, but they did not give an underlying mechanism for the density dependence of the birth rate. Gyllenberg et al. (1997) obtained the discrete logistic equation as a limiting case in a structured population model with competition for space. Note that the dynamical properties of the discrete and the continuous logistic models are entirely different, and hence the naive discretization of the continuous logistic model is not acceptable as the “derivation” of the discrete logistic model; the discrete-time homologue of the continuous logistic model is the Beverton–Holt model (see, e.g. Yodzis, 1989, pp. 73–74; Thieme, 2003, pp. 83 and 100).

In this paper, we utilized a resource–consumer system with time-scale separation to derive various one-dimensional discrete-time models. An alternative way to give mechanistic underpinnings to several discrete-time models is to start with a site-based model with different types of local interactions between individuals (Johansson and Sumpter, 2004). A site-based model was used by Skellam (1951), and also the Ricker model can be derived in the site-based framework (Sumpter and Broomhead, 2001). Johansson and Sumpter (2004) also

considered the inverse problem in the site-based framework, and found that it cannot reproduce the discrete logistic model in a biologically sensible way. In contrast, the (truncated) discrete logistic and the Ricker models can be obtained in our framework, but the resource dynamics necessary for obtaining the Skellam model could not be expressed with known functions. In a third framework assuming severe cannibalism in a short period after birth, Thieme (2003, Chapter 13.7) showed that a number of standard models can be obtained depending on the distribution of the (stochastic) duration of the larval stage subject to cannibalism: exponential distribution yields the Beverton-Holt model, Gamma distribution (i.e. many larval stages each with exponentially distributed duration) yields the Hassell model, whereas (as well known) a fixed duration yields the Ricker model. Obviously, different frameworks can provide underpinnings to different sets of discrete-time models. Unfortunately the Maynard Smith model, which has been advocated for its flexibility and good fit to empirical data (Bellows, 1981), seems to elude a mechanistic interpretation.

Our model generalizes to multiple resources and consumer species (with different types of resource dynamics leading to different terms in the between-year growth rate of the consumers), and to more trophic levels (with “echoing”). The inclusion of nonlinear functional responses unfortunately makes the equations messy, with no apparent relations between simple models. Overcompensation, however, is preserved also with nonlinear functional responses, whenever the quasi-equilibrium does not bifurcate during the season for all initial consumer densities in some open interval (see the appendix).

Acknowledgements

This research was supported by the Finnish Academy of Sciences (Grants 53980 and 50169) and by the European Research Training Network ModLife funded through the Human Potential Programme of the European Commission (HPRN-CT-2000-00051).

Appendix

Here we show that if $\lim_{R \rightarrow 0} Rf(R) = 0$, then the $x_{n+1}(0)$ in Eq. (4) as a function of $x_n(0)$ has a global maximum, and $x_{n+1}(0) = 0$ or $x_{n+1}(0)$ is strictly decreasing for sufficiently large values of $x_n(0)$.

First, suppose that x^* is finite. Then $x_{n+1}(0) = 0$ if $x_n(0) = 0$ or $x_n(0) \geq x^*e^\mu$, while $x_{n+1}(0) > 0$ if $0 < x_n(0) < x^*e^\mu$. Since the right-hand side of Eq. (4) depends continuously on $x_n(0)$, it follows that $x_{n+1}(0)$ has a global maximum at some $x_n(0) \in (0, x^*e^\mu)$. To see

why $x_{n+1}(0) = 0$ for $x_n(0) \geq x^*e^\mu$, note that if $x_n(0) \geq x^*e^\mu$, then $x_n(t) \geq x^*$ for all t , so that from (3) $\hat{R}_n(t) = 0$ for all t , and hence from Eq. (4) $x_{n+1}(0) = 0$.

Next, suppose that x^* is infinite. We show that there exists a number $\tilde{x} > 0$ such that $x_{n+1}(0)$ as a function of $x_n(0)$ is monotonically decreasing on $(\tilde{x}e^\mu, \infty)$. Since $x_{n+1}(0)$ is increasing for $x_n(0)$ close to zero, it follows that $x_{n+1}(0)$ has a global maximum at some $x_n(0) \in (0, \tilde{x}e^\mu)$. To show that such a number \tilde{x} indeed exists, note from the equation for $R_n(t)$ in Eq. (1) that at the quasi-equilibrium $\alpha \hat{R}_n(t) f(\hat{R}_n(t)) = \beta \hat{R}_n(t) x_n(t)$, so that Eq. (4) can also be written as

$$x_{n+1}(0) = \sigma \gamma \alpha e^{-\delta} \int_0^1 \hat{R}_n(t) f(\hat{R}_n(t)) e^{\delta t} dt. \tag{A.1}$$

If $\lim_{R \rightarrow 0} Rf(R) = 0$, then $Rf(R)$ has at least one local maximum on the open interval $(0, K)$, because $\lim_{R \rightarrow K} Rf(R) = 0$, while $Rf(R) > 0$ for $0 < R < K$. Let \tilde{R} be the smallest value of R at which $Rf(R)$ has a local maximum; then $Rf(R)$ is monotonically increasing on $(0, \tilde{R})$. Let now $\tilde{x} = (\alpha/\beta)f(\tilde{R})$. If $x_n(0) > \tilde{x}e^\mu$, then $x_n(t) > \tilde{x}$ and hence $\hat{R}_n(t) < \tilde{R}$ for all $t \in [0, 1]$ (recall that $\hat{R}_n(t) = f^{-1}((\beta/\alpha)x_n(t))$ and f is monotonically decreasing). Thus, by construction, each step in the composite map $x_n(0) \mapsto x_n(t) \mapsto \hat{R}_n(t) \mapsto \hat{R}_n(t)f(\hat{R}_n(t))$ is monotonous in such a way that the total is a monotonically decreasing function of $x_n(0) > \tilde{x}e^\mu$ for all t . Hence, from Eq. (A.1) it now follows that $x_{n+1}(0)$ as a function of $x_n(0)$ is monotonically decreasing on $(\tilde{x}e^\mu, \infty)$, which completes the proof.

Functional response: Consider the generalized model

$$\begin{aligned} \dot{R}_n(t) &= \alpha R_n(t) f(R_n(t)) - \beta R_n(t) h(R_n(t)) x_n(t), \\ \dot{E}_n(t) &= \gamma \beta R_n(t) h(R_n(t)) x_n(t) - \delta E_n(t), \\ \dot{x}_n(t) &= -\mu x_n(t), \end{aligned} \tag{A.2}$$

where h is a positive function on $(0, \infty)$ and $R_n(t)h(R_n(t))$ is an arbitrary functional response (e.g. $h(R) = 1/(R + H)$ corresponds to the well-known Holling Type II functional response). In quasi-equilibrium, we have $\alpha f(\hat{R}_n(t)) = \beta x_n(t) h(\hat{R}_n(t))$. Note that since both f and h may be nonlinear functions, there may be multiple quasi-equilibria. A quasi-equilibrium $\hat{R}_n(t)$ is stable if $d\hat{R}_n/dR_n < 0$, i.e. if $\alpha f'(\hat{R}_n(t)) < \beta x_n(t) h'(\hat{R}_n(t))$.

Suppose that there exists an open interval (ξ_1, ξ_2) such that if $x_n(0) \in (\xi_1, \xi_2)$, then $0 < \hat{R}_n(t) < \tilde{R}$ and there is no bifurcation of $\hat{R}_n(t)$ for $t \in [0, 1]$. By implicit differentiation of the quasi-equilibrium condition, we obtain

$$\frac{d\hat{R}_n(t)}{dx_n(t)} = \frac{\beta h(\hat{R}_n(t))}{\alpha f'(\hat{R}_n(t)) - \beta x_n(t) h'(\hat{R}_n(t))},$$

which is negative whenever the quasi-equilibrium is stable. Thus, like in the model in Eq. (1), increasing the number of consumers at the beginning of the season (and hence throughout the season since $x_n(t) = x_n(0)e^{-\mu t}$) decreases the stable quasi-equilibrium

resource abundance at all $t \in [0, 1]$. Analogously to Eq. (4), the between-year dynamics of the consumer is given by

$$\begin{aligned} x_{n+1}(0) &= \sigma\gamma\beta e^{-\delta} \int_0^1 \hat{R}_n(t) h(\hat{R}_n(t)) x_n(t) e^{\delta t} dt \\ &= \sigma\gamma\alpha e^{-\delta} \int_0^1 \hat{R}_n(t) f(\hat{R}_n(t)) e^{\delta t} dt, \end{aligned} \quad (\text{A.3})$$

which is the same as Eq. (A.1). Therefore, the proof above also holds for the model with a functional response, from which it follows that $x_{n+1}(0)$ is a decreasing function of $x_n(0) \in (\xi_1, \xi_2)$. Note that bifurcations of the resource quasi-equilibrium may lead to discontinuous between-year maps of the consumer.

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