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Discrete-time travelling waves: Ecological examples

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Abstract. Integrodifference equations are discrete-time models that possess many of the attributes of continuous-time reaction-diffusion equations. They arise naturally in population biology as models for organisms with discrete nonoverlapping generations and well-defined growth and dispersal stages. I examined the varied travelling waves that arise in some simple ecologically-interesting integrodifference equations. For a scalar equation with compensatory growth, I observed only simple travelling waves. For carefully chosen redistribution kernels, one may derive the speed and approximate the shape of the observed waveforms. A model with overcompensation exhibited flip bifurcations and travelling cycles in addition to simple travelling waves. Finally, a simple predator-prey system possessed periodic wave trains and a variety of travelling waves.

Key words: Travelling waves – Integrodifference equations – Bifurcations – Diffusion – Ecology

1 Introduction

Invading species frequently alter the structure and function of entire communities (Crosby 1986). Early ecologists exhibited a profound interest in the biology of these invasions (Elton 1958). A spate of recent volumes (Mooney and Drake 1986; Groves 1986; Drake 1989; Hengeveld 1990) suggests that modern-day ecologists are just as interested: there is ever greater appreciation for the ecological and evolutionary significance of biological invasions.

There is a cogent body of theory that attempts to predict the rates of spread of invading species (Roughgarden 1986). The theory employs reaction-diffusion equations, such as the Fisher equation, to describe populations that simultaneously grow and diffuse. The Fisher equation,

$$\frac{\partial u}{\partial t} = ru(1-u) + D\frac{\partial^2 u}{\partial x^2}, \tag{1}$$

was originally introduced as a model for the spread of an advantageous allele (Fisher 1937); it was then adopted by Skellam (1951) and by Kierstead and Slobodkin (1953) for problems in population ecology. It has, among its solutions, travelling waves $u(x-ct)$ of all velocities $c \geqslant 2\sqrt{rD}$ (Fisher 1937; Kolmogorov et al. 1937). Initial conditions with compact support converge to travelling waves of *minimum* speed $c^* = 2\sqrt{rD}$ (Kolmogorov et al. 1937; Aronson and Weinberger 1975). Initial conditions with "fat tails" evolve into travelling waves with speeds in excess of c^* (McKean 1975; Larson 1978; Murray 1989). A wide variety of reaction-diffusion models exhibit travelling waves (Okubo 1980; Britton 1986; Murray 1989).

How else might one model dispersal? Mollison (1977) has argued for spatial contact models built around *contact distributions* – probability distributions for the distance that an individual moves. Spatial contact models incorporate a variety of contact distributions, including the leptokurtic distributions that are typical of biological populations (Wolfenbarger 1946, 1959, 1979; Okubo 1980). Diffusion is viewed as a mere approximation in which all moments of the contact distribution, other than the second, equal zero.

The earliest contact models were continuous-time models for epidemics (Kendall 1965; Mollison 1972a, 1972b; Atkinson and Reuter 1976; Brown and Carr 1977; Aronson 1977). An important example is Mollison's (1972a) equation for the rate of change of infectious individuals during a simple epidemic:

$$\frac{\partial u}{\partial t} = r\bar{u}(1-u). \tag{2}$$

$u(x, t)$ is the density of infectious individuals as a function of position and time, whereas

$$\bar{u}(x, t) = \int_{\Omega} k(x-y)u(y, t)\, dy \tag{3}$$

is a weighted spatial average of the number of infectives over the domain Ω. The weights are prescribed by the nonnegative contact distribution k,

$$\int_{\Omega} k(y)\, dy = 1. \tag{4}$$

If k lacks an exponentially bounded forward tail, the velocity of propagation is asymptotically infinite (Mollison 1972b). With an exponentially bounded tail, there is a minimum wave speed c^* that dominates the model. Travelling waves exist only for $c \geqslant c^*$ (Atkinson and Reuter 1976; Brown and Carr 1977), as for the Fisher equation.

There are also a growing number of discrete-time spatial contact models. Slatkin (1973), Weinberger (1978, 1984), and Lui (1982a, 1982b, 1983, 1985, 1986, 1989a, 1989b) have carefully analyzed models for changes in gene frequency. Weinberger and Lui, in particular, have concentrated on developing necessary and sufficient conditions on the contact distribution, on nondecreasing growth functions, and on the initial conditions that guarantee convergence to a travelling wave. Recently, discrete-time contact models appeared *de novo*, in population ecology, as integrodifference equations (Kot and Schaffer 1986; Hardin et al. 1988a, 1988b, 1990; Kot 1989; Andersen 1990). Integrodifference equations are functional maps; they describe populations with discrete, nonoverlapping generations and well-defined growth and dispersal stages. Analyses of these ecological models have emphasized steady states, bifurcations, diffusive instability, and chaos. These analyses have neglected travelling waves.

This paper is an attempt to redress this deficiency. In Sect. 2, I review the formulation of integrodifference equations. In Sect. 3, I discuss travelling waves.

I examine the simple travelling waves that arise in the presence of a monotonically increasing growth function in Sect. 4. In Sect. 5, I turn to a model built around the overcompensatory logistic difference equation. For this model, travelling cycles that arise via period-doubling bifurcations supplant a simple travelling wave. Section 6 illustrates the waves of a simple two-species predator-prey system. Concluding comments are relegated to Sect. 7. The writing in this paper is heuristic rather than rigorous: I barely scratch the surface on a number of interesting topics. Sections 5 and 6 are especially short and almost entirely preliminary. The reader is strongly encouraged to develop these topics in far greater detail.

2 Integrodifference equations

Consider an organism with synchronous, nonoverlapping generations. I assume that there are two distinct stages that define the life cycle of this organism: a sedentary stage and a dispersal stage. All growth occurs during the sedentary stage and all movement occurs during the dispersal stage. I further posit density-dependence in growth, but not in dispersal. These assumptions allow me to take the composition of a linear operator (for the dispersal stage) and a nonlinear operator (for the sedentary stage) as my descriptor of growth (Kot and Schaffer 1986).

For the sedentary stage I begin with a nonlinear map

$$N_{t+1} = f(N_t) \tag{5}$$

such as the Beverton–Holt stock-recruitment curve (Beverton and Holt 1957; Pielou 1977)

$$N_{t+1} = \frac{\lambda N_t}{1 + [(\lambda - 1)N_t/K]}, \tag{6}$$

the logistic difference equations (Maynard Smith 1968; May 1972)

$$N_{t+1} = (1 + r)N_t - \frac{r}{K} N_t^2, \tag{7}$$

or the Ricker (1952) curve

$$N_{t+1} = N_t \exp\left[r\left(1 - \frac{N_t}{K}\right)\right]. \tag{8}$$

N_t is the population level at time t. K represents the carrying capacity of the environment. $\lambda = e^r$ and r are the geometric and intrinsic rates of increase.

Equations (6), (7), and (8) appear extensively in the literature. All three maps exhibit density dependence. The Beverton–Holt curve is a model of compensatory growth (Clark 1976): recruitment is a monotonically-increasing, concave function of density. This map has a single nontrivial equilibrium ($N^* = K$) that is asymptotically stable for all $r > 0$. In contrast, the logistic difference equation and Ricker curve exemplify overcompensation. They possess a wide range of dynamical states that includes equilibria, cycles, and chaos (May 1975; May and Oster 1976).

Equation (5) makes no allowance for the dispersion of the population. If we let $N_t(x)$ represent the population density as a function of space at the start of the tth generation's sedentary stage, change occurs in two alternating steps: (1) During the sedentary stage, $N_t(x)$ is mapped into $f(x, N_t(x))$. Explicit spatial dependence (from here on dropped) reflects clinal (spatially varying, time-independent) variation in the parameters. (2) During the dispersal stage, individuals are shuffled about. This shuffling may be modelled with an integral operator. Together these steps yield an integrodifference equation of the form

$$N_{t+1}(x) = \int_\Omega k(x, y) f(N_t(y))\, dy \tag{9}$$

for the growth and dispersal of the population.

The kernel $k(x, y)$ is the cynosure of this formulation. It describes the dispersal of N from y about y. In particular, $k(x, y)\, dy$ is the probability of an individual's dispersing from an interval of length dy about y to an equally small interval about x. As a probability, $k(x, y)\, dy$ must be nonnegative. The kernel may depend on absolute location or on relative distance. In the latter instance, it is truly a contact distribution and Eq. (9) is built around a convolution integral,

$$N_{t+1}(x) = \int_\Omega k(x-y) f(N_t(y))\, dy. \tag{10}$$

There are a number of methods for estimating the kernel from observed data (Silverman 1986). Throughout this paper, I will take the domain to be infinite and the redistribution kernel to be a contact distribution. I will further assume that the contact distribution has exponentially-bounded tails. In particular, there must exist a positive real number μ_0 with the property that the moment generating function satisfies

$$\int_{-\infty}^{+\infty} e^{\mu y} k(y)\, dy < +\infty \tag{11}$$

for all $|\mu| \leqslant \mu_0$. Mollison (1972b) has shown that (11) is necessary in order that continuous-time spatial contact models have a finite speed of propagation; the same appears to be true for discrete-time integrodifference equations. I will concentrate on the exponential distribution

$$k_1(x-y) = \begin{cases} \alpha\, e^{\alpha(x-y)} & x < y \\ 0 & x > y \end{cases} \tag{12}$$

and on the bilateral exponential distribution

$$k_2(x-y) = \tfrac{1}{2}\alpha \exp(-\alpha|x-y|). \tag{13}$$

These two distributions satisfy condition (11). Moreover, they emphasize the degree to which contact distributions may deviate from normality: the exponential distribution is highly skewed while the bilateral exponential distribution is leptokurtic.

3 Simple travelling waves

The simplest interesting behavior arises for integrodifference equations of the form

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y) f(N_t(y))\, dy, \tag{14}$$

with $f(N_t)$ a monotonically-increasing growth function that satisfies

$$f(N) \leqslant f'(0)N. \tag{15}$$

The methods of Weinberger (1978) may then be used to prove the existence of a travelling wave of invasion for a population confronting fresh habitat. Far less is known regarding the behavior of (14) for nonmonotone growth functions.

Simple travelling waves are solutions that satisfy

$$N_{t+1}(x) = N_t(x+c) \tag{16}$$

for some constant c. In effect, each iterate yields a lateral translation c with no other change in the shape of the solution; c is the wave speed of the solution. Substituting (16) into (14), we see that simple travelling waves satisfy the integral equation

$$N(x+c) = \int_{-\infty}^{+\infty} k(x-y) f(N(y))\, dy. \tag{17}$$

$N^* = 0$ and $N^* = K$ will typically appear as constant solutions of Eq. (17). Our concern is with the nonnegative integral curves that connect these fixed points: Solutions that tend to $N^* = 0$ in the limit as $x \to -\infty$ and that tend to $N^* = K$ in the limit as $x \to +\infty$ yield leftward moving waves. We use Eq. (17) to calculate both the speed and the shape of these travelling waves.

Speed

The minimum wave speed is determined by the local behavior of (17) in the neighborhood of $N^* = 0$. For small c, solutions near $N^* = 0$ oscillate; finding a *nonnegative* integral curve to connect the two fixed points is thus impossible. The critical or minimum wave speed c^* is the lowest value of c for which one can find a positive solution curve that decussates $N^* = 0$. The appearance of this solution curve coincides with the first appearance of a positive real eigenvalue for the linearization of (17) in the neighborhood of $N^* = 0$. This eigenvalue is a double root of the correspondent characteristic equation.

The linearization of Eq. (17) in the neighborhood of $N^* = 0$ is just

$$N(x+c) = f'(0) \int_{-\infty}^{+\infty} k(x-y) N(y)\, dy. \tag{18}$$

For a leftward moving wave, one may attempt a solution of the form

$$N(x) = A\, e^{\mu x} \tag{19}$$

for μ positive. After some manipulation, this yields the characteristic equation

$$e^{\mu c} = f'(0) \int_{-\infty}^{+\infty} k(s)\, e^{-\mu s}\, ds. \tag{20}$$

For μ to be a double root, we require that

$$c\, e^{\mu c} = -f'(0) \int_{-\infty}^{+\infty} k(s) s\, e^{-\mu s}\, ds. \tag{21}$$

Equations (20) and (21) together provide us with the minimum wave speed c^*.

Weinberger (1978) proved that the critical wave speed c^* is

$$c^* = \min_{\mu > 0} \left\{ \frac{1}{\mu} \ln \left[f'(0) \int_{-\infty}^{+\infty} k(s)\, e^{-\mu s}\, ds \right] \right\} \tag{22}$$

and that this minimum exists for $f'(0) > 1$.

Shape

We must also extract the shape of the travelling waves from Eq. (17). In general, this is rather difficult. However, for contact distributions (12) and (13), Eq. (17) simplifies and we can make some progress. In particular, by adapting the method of Canosa (1973) and Murray (1989) to integrodifference equations, we are able to expand the solution as a perturbation series.

Example 1 For the exponential distribution

$$k_1(x-y) = \begin{cases} \alpha\, e^{\alpha(x-y)} & x < y \\ 0 & x > y \end{cases} \tag{23}$$

Eq. (17) appears as

$$N(x+c) = \alpha \int_x^{\infty} e^{\alpha(x-y)} f(N(y))\, dy. \tag{24}$$

Differentiating Eq. (24), we obtain the first order delay-differential equation

$$N'(x+c) + \alpha[f(N(x)) - N(x+c)] = 0. \tag{25}$$

With the new unit of length

$$z \equiv \frac{x}{c} \tag{26}$$

Eq. (25) simplifies further, yielding

$$\varepsilon N'(z+1) + [f(N(z)) - N(z+1)] = 0 \tag{27}$$

with

$$\varepsilon \equiv \frac{1}{\alpha c}. \tag{28}$$

We will concentrate on simple, leftward-moving waves that satisfy

$$\lim_{z \to -\infty} N(z) = 0, \qquad \lim_{z \to +\infty} N(z) = K. \tag{29}$$

Our analysis is greatly facilitated by a choice of origin that guarantees

$$N(0) = \frac{K}{2}. \tag{30}$$

It would appear that we have traded an unsavory integral equation (Eq. (17)) for an equally unsavory delay-differential equation (Eq. (27)). However, in the limit of infinitely fast propagation speeds ($c \to \infty$, $\varepsilon \to 0$), Eq. (27) reduces to a difference equation; Eq. (27) may be thought of as a perturbation problem. Since ε multiplies the highest derivative, Eq. (27) would appear to be a singular perturbation problem. However, if the equation has a uniform limit as $\varepsilon \to 0$, a valid solution may be obtained with the regular perturbation series

$$N(z; \varepsilon) = N_0(z) + \varepsilon N_1(z) + \cdots. \tag{31}$$

After substituting Eq. (31) into Eq. (27) and equating like powers of ε, we obtain

$$O(1): \qquad N_0(z+1) = f(N_0(z)) \tag{32a}$$

$$O(\varepsilon): \qquad N_1(z+1) = f'(N_0(z))N_1(z) + N_0'(z+1) \tag{32b}$$

and so on for higher powers of epsilon. Equations (29) and (30), taken with Eq. (31), further dictate that

$$N_0(-\infty) = 0, \qquad N_0(+\infty) = K, \qquad N_0(0) = \frac{K}{2}, \tag{33a}$$

$$N_i(-\infty) = 0, \qquad N_i(+\infty) = 0, \qquad N_i(0) = 0, \tag{33b}$$

for $i = 1, 2, \ldots$. Equations (32a) and (32b) are to be solved successively. Together with Eqs. (33), they yield the shape of the travelling wave.

Example 2 For the bilateral exponential distribution

$$k_2(x - y) = \tfrac{1}{2}\alpha \exp(-\alpha|x - y|). \tag{34}$$

(17) takes on the form

$$N(x + c) = \tfrac{1}{2}\alpha \int_{-\infty}^{+\infty} \exp(-\alpha|x - y|) f(N(y))\, dy \tag{35}$$

which may be written

$$N(x + c) = \tfrac{1}{2}\alpha \int_{x}^{+\infty} \exp[\alpha(x - y)]\, f(N(y))\, dy$$

$$+ \tfrac{1}{2}\alpha \int_{-\infty}^{x} \exp[-\alpha(x - y)]\, f(N(y))\, dy. \tag{36}$$

Differentiating (36) twice yields the second order delay-differential equation

$$N''(x + c) + \alpha^2[f(N(x)) - N(x + c)] = 0. \tag{37}$$

With the new unit of length

$$z \equiv \frac{x}{c}, \tag{38}$$

Eq. (37) yields

$$\varepsilon N''(z + 1) + [f(N(z)) - N(z + 1)] = 0 \tag{39}$$

with

$$\varepsilon \equiv \frac{1}{\alpha^2 c^2}. \tag{40}$$

Equations (29) for the boundary conditions and Eq. (30) for the choice of origin are still appropriate.

We again employ a regular perturbation series

$$N(z; \varepsilon) = N_0(z) + \varepsilon N_1(z) + \cdots \tag{41}$$

and obtain

$O(1)$: $$N_0(z+1) = f(N_0(z)) \tag{42a}$$

$O(\varepsilon)$: $$N_1(z+1) = f'(N_0(z))N_1(z) + N_0''(z+1) \tag{42b}$$

to first order in epilson. The boundary conditions are as before (Eqs. (33)).

4 Compensatory growth

For the Beverton–Holt stock recruitment curve (Eq. (6)), the integrodifference Eq. (14) appears as

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y) \frac{\lambda N_t(y)}{1 + [(\lambda - 1)N_t(y)/K]} \, dy. \tag{43}$$

Given the change of variables

$$u_t(x) \equiv \frac{N_t(x)}{K}, \tag{44}$$

Eq. (43) simplifies to

$$u_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y) \frac{\lambda u_t(y)}{1 + (\lambda - 1)u_t(y)} \, dy. \tag{45}$$

Thus, for simple travelling waves, we wish to satisfy the integral equation (Eq. (17))

$$u(x+c) = \int_{-\infty}^{+\infty} k(x-y) \frac{\lambda u(y)}{1 + (\lambda - 1)u(y)} \, dy \tag{46}$$

subject to

$$\lim_{x \to -\infty} u(x) = 0, \qquad \lim_{x \to +\infty} u(x) = 1 \tag{47}$$

and

$$u(0) = \tfrac{1}{2}. \tag{48}$$

Example 1 For the exponential distribution we have

$$u(x+c) = \alpha \int_{x}^{\infty} e^{\alpha(x-y)} \frac{\lambda u(y)}{1 + (\lambda - 1)u(y)} \, dy. \tag{49}$$

Differentiating Eq. (49), we obtain the first order delay-differential equation

$$u'(x+c) + \alpha \left[\frac{\lambda u(x)}{1 + (\lambda - 1)u(x)} - u(x+c) \right] = 0. \tag{50}$$

Equations (49) and (50) may be studied directly. Even at this stage, however, it is useful to rescale length. Thus, we introduce

$$z \equiv \frac{x}{c}. \tag{51}$$

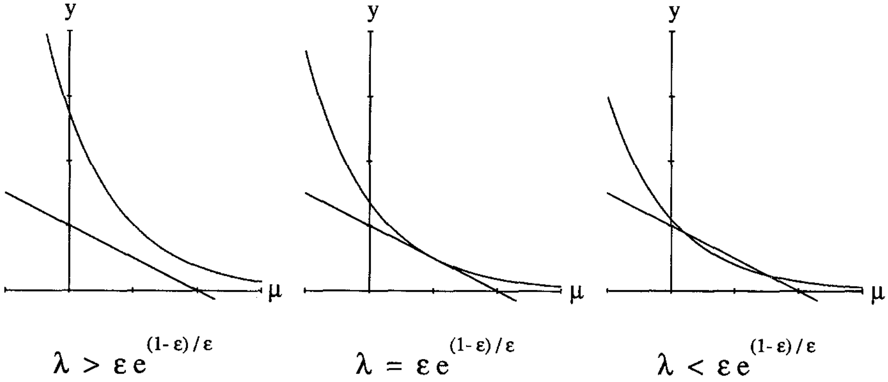


Fig. 1. Real roots of the characteristic equation $\lambda e^{-\mu} = 1 - \varepsilon\mu$. The roots occur at the intersection of the exponential $y = e^{-\mu}$ and the straight line $y = 1 - \varepsilon\mu$. Depending on one's choice of λ and ε, there are 0, 1, or 2 real roots

Equation (50) reduces to

$$\varepsilon u'(z+1) + \left[\frac{\lambda u(z)}{1 + (\lambda - 1)u(z)} - u(z+1)\right] = 0 \tag{52}$$

with

$$\varepsilon \equiv \frac{1}{\alpha c}. \tag{53}$$

Speed

The relevant characteristic equation now appears as the transcendental quasipolynomial (El'sgol'ts and Norkin 1973)

$$\lambda e^{-\mu} = 1 - \varepsilon\mu. \tag{54}$$

Equation (54) has an infinite number of complex roots, contained in some left half of the complex plane. At the same time, it has at most two real roots. Indeed, if we examine the intersections that arise as we plot each side of Eq. (54) as a function of μ (see Fig. 1), we see that there are either 0, 1, or 2 real roots. Real roots emerge at the double root characterized by

$$\lambda e^{-\mu} = \varepsilon. \tag{55}$$

Equations (53), (54), and (55), together, yield the parametric representation

$$\alpha c = 1 + \mu \tag{56a}$$

$$\lambda = \frac{e^{\mu}}{1 + \mu}. \tag{56b}$$

The graph of this function for $\mu \geqslant 0$ (see Fig. 2) relates the critical wave speed c^* to the growth rate λ and the dispersal constant α.

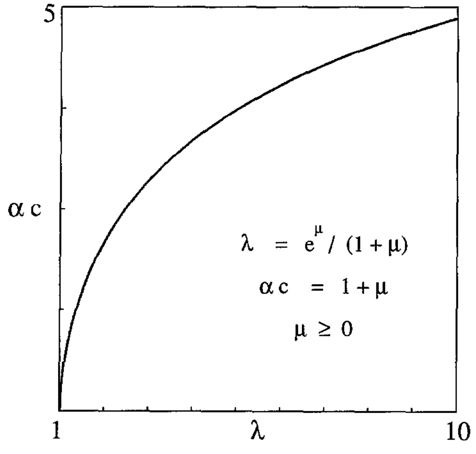


Fig. 2. Minimum speed of advance for the travelling waves of a simple compensatory integrodifference equation. The model is a scalar integrodifference equation with Beverton–Holt growth and an exponential contact distribution. The minimum wave speed c is an increasing function of the geometric growth rate λ and a decreasing function of the dispersal parameter α

Shape

The perturbation scheme (32) reduces to

$$O(1): \qquad u_0(z+1) = \frac{\lambda u_0(z)}{1+(\lambda-1)u_0(z)} \tag{57a}$$

$$O(\varepsilon): \qquad u_1(z+1) = \frac{\lambda}{[1+(\lambda-1)u_0(z)]^2} u_1(z) + u_0'(z+1) \tag{57b}$$

with

$$u_0(-\infty) = 0, \qquad u_0(+\infty) = 1, \qquad u_0(0) = \tfrac{1}{2}, \tag{58a}$$

$$u_i(-\infty) = 0, \qquad u_i(+\infty) = 0, \qquad u_i(0) = 0, \tag{58b}$$

for $i = 1, 2, \ldots$.

Equation (57a) has a closed-form solution that satisfies (58a):

$$u_0(z) = \frac{\lambda^z}{1+\lambda^z}. \tag{59}$$

As a result, Eq. (57b) reduces to

$$u_1(z+1) = \frac{\lambda(1+\lambda^z)^2}{(1+\lambda^{z+1})^2} u_1(z) + \ln\lambda \frac{\lambda^{z+1}}{(1+\lambda^{z+1})^2}. \tag{60}$$

This looks gruesome, but the substitution

$$u_1(z) = \ln\lambda \frac{\lambda^z}{(1+\lambda^z)^2} v_1(z) \tag{61}$$

simplifies Eq. (60) to

$$v_1(z+1) = v_1(z) + 1 \tag{62}$$

which has the solution

$$v_1(z) = z. \tag{63}$$

The solution of Eq. (60) is, therefore,

$$u_1(z) = \ln \lambda \frac{z\lambda^z}{(1+\lambda^z)^2}. \tag{64}$$

Combining Eqs. (59) and (64), we may write

$$u(z) = \frac{\lambda^z}{1+\lambda^z} + \varepsilon \ln \lambda \frac{z\lambda^z}{(1+\lambda^z)^2} + O(\varepsilon^2). \tag{65}$$

In terms of the original variables N and x, the uniformly valid asymptotic solution for all x is thus

$$N(x) = K\left[\frac{e^{rx/c}}{1+e^{rx/c}} + \frac{1}{\alpha c}\frac{(rx/c)\, e^{rx/c}}{(1+e^{rx/c})^2}\right] + O(\varepsilon^2) \tag{66}$$

with

$$r \equiv \ln \lambda. \tag{67}$$

Figure 3 shows a numerically integrated simulation of Eq. (43). A leftward-moving travelling wave is clearly evident. The series (66) for the shape of the travelling wave is asymptotically accurate only in the limit of infinitely large speeds. However, even for small speeds it does passably well. This is readily seen in Fig. 4 wherein we compare a numerically computed wave profile with $O(1)$ and $O(\varepsilon)$ approximations.

Example 2 For the bilateral exponential distribution, Eq. (46) is just

$$u(x+c) = \tfrac{1}{2}\alpha \int_{-\infty}^{+\infty} \exp(-\alpha|x-y|)\frac{\lambda u(y)}{1+(\lambda-1)u(y)}\,dy. \tag{68}$$

Equation (37) is the second order delay-differential equation

$$u''(x+c) + \alpha^2\left[\frac{\lambda u(x)}{1+(\lambda-1)u(x)} - u(x+c)\right] = 0. \tag{69}$$

By rescaling length,

$$z \equiv \frac{x}{c}, \tag{70}$$

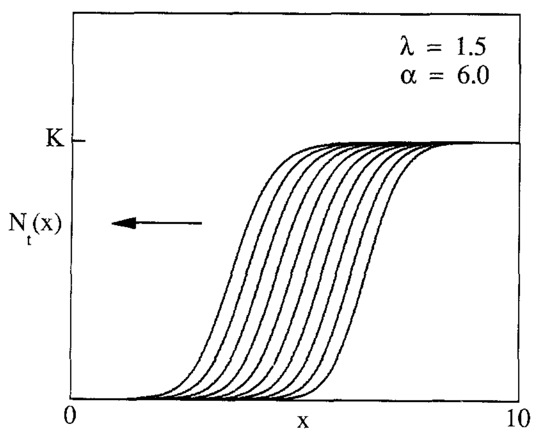


Fig. 3. Travelling wave for a compensatory integrodifference equation. A scalar integrodifference equation with Beverton–Holt growth and an exponential contact distribution readily exhibits a simple, monotonically-increasing travelling wave. This simulation was obtained by numerically integrating the integrodifference equation (using the extended trapezoidal rule) through a transient of twenty iterates and by then integrating and plotting the next ten iterates. The wave maintains its simple shape while moving to the left

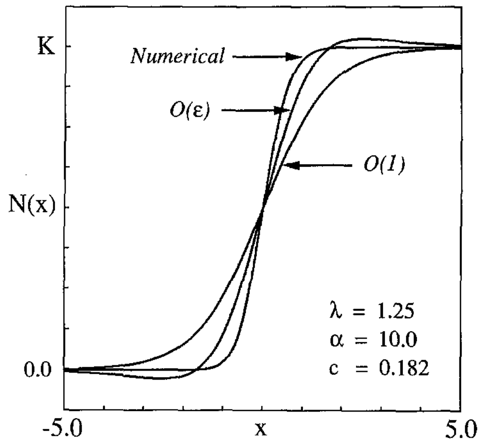


Fig. 4. A comparison of the numerical and perturbation-scheme approximations to a small-speed travelling wave of an integrodifference equation with Beverton–Holt growth and an exponential contact distribution. The numerical solution was obtained by numerically integrating through a large number of iterations so as to allow for convergence to the travelling wave. The $O(1)$ and $O(\varepsilon)$ perturbation-scheme approximations are those contained in Eq. (66)

we may reduce Eq. (69) to

$$\varepsilon u''(z+1) + \left[\frac{\lambda u(z)}{1+(\lambda-1)u(z)} - u(z+1)\right] = 0 \tag{71}$$

with

$$\varepsilon \equiv \frac{1}{\alpha^2 c^2}. \tag{72}$$

Speed

The proper characteristic equation is

$$\lambda e^{-\mu} = 1 - \varepsilon\mu^2. \tag{73}$$

Equation (73) has an infinite number of complex roots, contained in some left half of the complex plane. However, a concave parabola may intersect a convex exponential at most twice; Eq. (73) has either 0, 1, or 2 real roots. Real roots emerge at the double root characterized by

$$\lambda e^{-\mu} = 2\varepsilon\mu. \tag{74}$$

Equations (72), (73), and (74), together, engender the parametric equations

$$\alpha c = \sqrt{\mu^2 + 2\mu} \tag{75a}$$

$$\lambda = \frac{2e^{\mu}}{2+\mu}. \tag{75b}$$

The graph of (75) for $\mu \geqslant 0$ determines the minimum wave speed c^* (see Fig. 5).

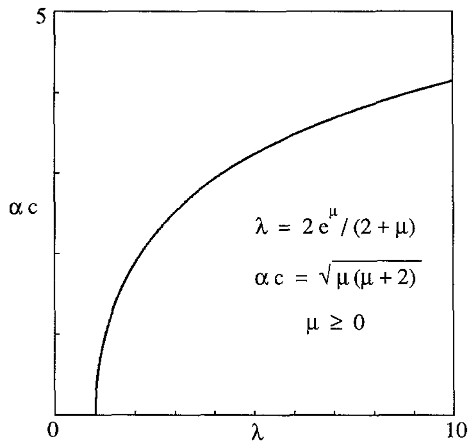


Fig. 5. Minimum speed of advance for the travelling waves of a second compensatory integrodifference equation. The model is a scalar integrodifference equation with Beverton–Holt growth and a bilateral-exponential contact distribution. The minimum wave speed c is an increasing function of the geometric growth rate λ and a decreasing function of the dispersal parameter α

Shape

The perturbation scheme (42) reduces to

$$O(1): \qquad u_0(z+1) = \frac{\lambda u_0(z)}{1 + (\lambda - 1)u_0(z)} \tag{76a}$$

$$O(\varepsilon): \qquad u_1(z+1) = \frac{\lambda}{[1 + (\lambda - 1)u_0(z)]^2}\, u_1(z) + u_0''(z+1) \tag{76b}$$

with

$$u_0(-\infty) = 0, \qquad u_0(+\infty) = 1, \qquad u_0(0) = \tfrac{1}{2}, \tag{77a}$$

$$u_i(-\infty) = 0, \qquad u_i(+\infty) = 0, \qquad u_i(0) = 0, \tag{77b}$$

for $i = 1, 2, \ldots$.

Equation (76a) also has the closed-form solution

$$u_0(z) = \frac{\lambda^z}{1 + \lambda^z}. \tag{78}$$

As a result, Eq. (76b) may be rewritten

$$u_1(z+1) = \frac{\lambda(1+\lambda^z)^2}{(1+\lambda^{z+1})^2}\, u_1(z) + (\ln^2 \lambda)\lambda^{z+1}\, \frac{(1-\lambda^{z+1})}{(1+\lambda^{z+1})^3}. \tag{79}$$

The substitution

$$u_1(z) = \ln^2 \lambda \, \frac{\lambda^z}{(1+\lambda^z)^2}\, v_1(z) \tag{80}$$

reduces Eq. (79) to

$$v_1(z+1) = v_1(z) + \frac{(1-\lambda^{z+1})}{(1+\lambda^{z+1})} \tag{81}$$

so that

$$v_1(z) = v_1(0) + \sum_{i=1}^{z} \frac{(1-\lambda^i)}{(1+\lambda^i)} \tag{82}$$

or

$$v_1(z) = -\sum_{i=0}^{z} \tanh[(\tfrac{1}{2}\ln\lambda)i]. \tag{83}$$

Equation (83) is awkward to the extent that the spatial variable z appears as the upper limit of the summation. For large z, one may approximate Eq. (83) with the Euler–MacLaurin summation formula. For small z, one may expand the hyperbolic tangent in a Taylor series and, switching the order of summation, sum to z term by term. This yields

$$v_1(z) = -\frac{1}{4}(\ln\lambda)z(z+1) + \frac{1}{96}(\ln^3\lambda)z^2(z+1)^2 + \cdots \tag{84}$$

so that

$$u_1(z) = -\frac{1}{4}\ln^3\lambda\,\frac{z(z+1)\lambda^z}{(1+\lambda^z)^2}\left[1 - \frac{1}{24}(\ln^2\lambda)z(z+1) + \cdots\right]. \tag{85}$$

Combining Eqs. (78) and (85), we may write

$$u(z) = \frac{\lambda^z}{1+\lambda^z} - \frac{\varepsilon}{4}\ln^3\lambda\,\frac{z(z+1)\lambda^z}{(1+\lambda^z)^2}\left[1 - \frac{1}{24}(\ln^2\lambda)z(z+1) + \cdots\right] + O(\varepsilon^2). \tag{86}$$

In terms of the original variables N and x, the uniformly valid asymptotic solution for all x is thus

$$N(x) = K\left\{\frac{e^{rx/c}}{1+e^{rx/c}} - \frac{r^3x}{4\alpha^2c^3}\left(1+\frac{x}{c}\right)\frac{e^{rx/c}}{(1+e^{rx/c})^2}\right.$$
$$\left.\times\left[1 - \frac{r^2}{24}\frac{x}{c}\left(1+\frac{x}{c}\right) + \cdots\right]\right\} + O(\varepsilon^2) \tag{87}$$

where

$$r = \ln\lambda. \tag{88}$$

The series (87) is, as before, asymptotically accurate only in the limit of infinitely large speeds. However, for small speeds it now does exceedingly well, as may be seen in Fig. 6.

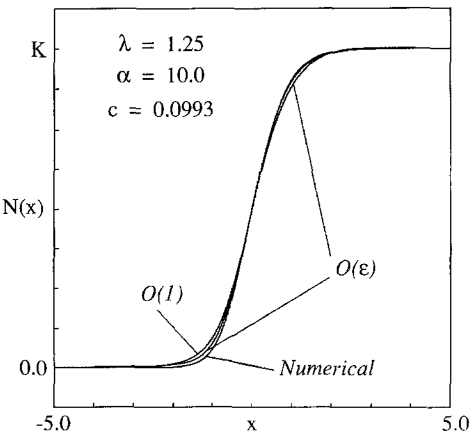


Fig. 6. A comparison of numerical and perturbation-scheme approximations for an integrodifference equation with compensatory Beverton–Holt growth and a bilateral-exponential contact distribution. The perturbation scheme does a superb job of approximating the numerically-observed travelling wave even at small speed

5 Overcompensation

The examples of Sect. 4 possessed simple, monotonically-increasing travelling waves. There was, moreover, little else to be seen with these models. This austerity of form follows from the simplicity of the Beverton–Holt stock recruitment curve: for all $r > 0$, the curve has sigmoidal solutions that are monotonically-increasing functions of time. In our two examples, the tie-in between the monotonicity of the travelling waves and the monotonicity of the underlying time series was quite explicit: the Beverton–Holt equation reappeared as the $O(1)$ equation for the shape of the travelling wave.

Behavior of far greater complexity may arise for models that permit overcompensation. Consider, for example, an integrodifference equation built around the logistic difference equation,

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y)\left[(1+r)N_t(y) - \frac{r}{K}N_t^2(y)\right] dy. \tag{89}$$

Given the change of variables

$$u_t(x) \equiv \frac{N_t(x)}{K}, \tag{90}$$

this simplifies to

$$u_{t+1}(x) = \int_{-\infty}^{+\infty} k(x-y)[(1+r)u_t(y) - ru_t^2(y)]\, dy. \tag{91}$$

For the bilateral exponential redistribution kernel,

$$k(x-y) = \tfrac{1}{2}\alpha \exp(-\alpha|x-y|), \tag{92}$$

we may, in analogy with our second example, consider the perturbation scheme

$$O(1): \qquad u_0(z+1) = (1+r)u_0(z) - ru_0^2(z) \tag{93a}$$

$$O(\varepsilon): \qquad u_1(z+1) = [(1+r) - 2ru_0(z)]u_1(z) + u_0''(z+1) \tag{93b}$$

for the shape of the travelling wave.

There are immediate differences between Eqs. (76a) and (93a). First of all, we can no longer write out a simple closed-form solution for $u_0(z)$. More importantly, since Eq. (93a) is just a rescaled version of the logistic difference equation, it exhibits a variety of solutions (May 1975; May and Oster 1976). For small r, it has solutions that rise from 0 and that tend, monotonically, towards 1. In this instance we expect, once again, simple, monotonically-increasing travelling waves. Figure 7 illustrates a simulation of integrodifference Eq. (89) with kernel (92) in which we observe just such waves. As we increase r, solutions of (93a) still tend towards 1, but with damped oscillations in the neighborhood of 1. These solutions still satisfy all of the relevant boundary conditions (Eqs. (77)) and so we expect the perturbation scheme (93) to go through and the oscillations to manifest themselves in the shape of the travelling wave. Figure 8 demonstrates that this is indeed the case. In particular, Fig. 8 illustrates the travelling wave profile, a damped oscillation, that appeared in a simulation of Eq. (89) for larger r. For still larger r, $u = 1$ becomes unstable. In particular, the underlying difference equation undergoes a period-doubling flip bifurcation: trajectories tend towards a periodic two-cycle rather than the equilibrium. As a result, we

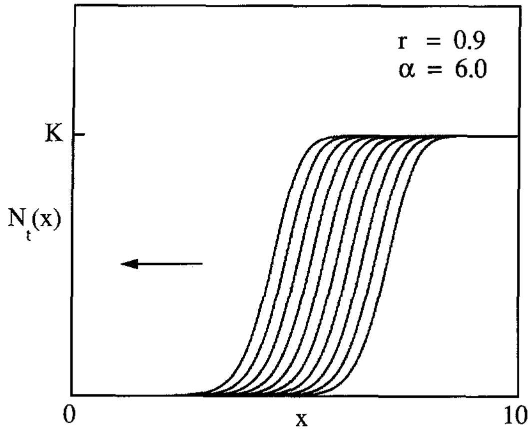


Fig. 7. A simple travelling wave for an overcompensatory integrodifference equation. An integrodifference equation with logistic growth and a bilateral-exponential contact distribution exhibits a simple, monotonically-increasing travelling wave for small r. The simulation was obtained by numerically integrating the integrodifference equation (using the extended trapezoidal rule) through a transient of twenty iterates and by then integrating and plotting the next ten iterates. The wave preserves its shape while moving to the left

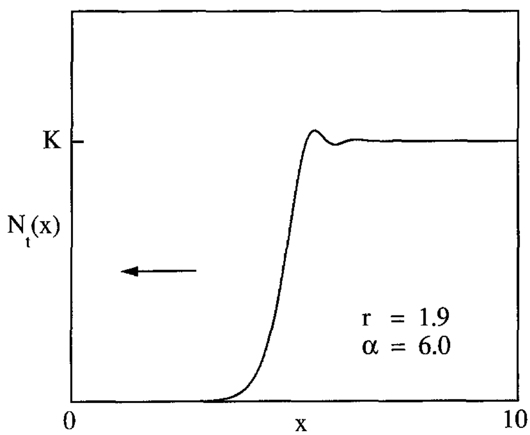
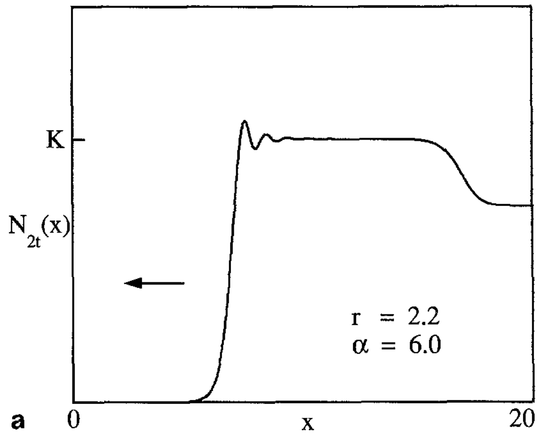


Fig. 8. A travelling wave with damped spatial oscillations. The equation gave rise to the simple travelling wave of Fig. 7 yields a travelling wave with damped spatial oscillations for larger r

can no longer expect the travelling wave profile $u(z)$ to tend to 1 in the limit as $z \to \infty$. Amazingly (see Fig. 9), simulations at higher r now show the existence of a travelling two-cycle. If we sampled the system at every second iterate, we would see a travelling wave. As is, the wave alternates between two profiles, all the while moving to the left. There is, in fact, an entire cascade of period-doubling bifurcations (leading to chaos), both for the logistic difference equation and for integrodifference Eq. (89). Figure 10, for example, shows the travelling four-cycle that appears at the loss of stability of the travelling two-cycle; the wave now alternates between four profiles as it moves to the left.

There are a number of interesting and unanswered mathematical and biological questions that follow from the above observations: Are the critical wave speeds of the travelling cycles truly the same as those predicted for the simple travelling wave? Do these new waves exhibit the same sort of structural universality (Metropolis et al. 1973) found in the logistic difference equation? Can one find, for example, a travelling three-cycle and another travelling four-cycle for larger r? Can one find the same sort of global universality made famous by Feigenbaum (1978, 1979, 1983)? Is there evidence of travelling cycles in nature?



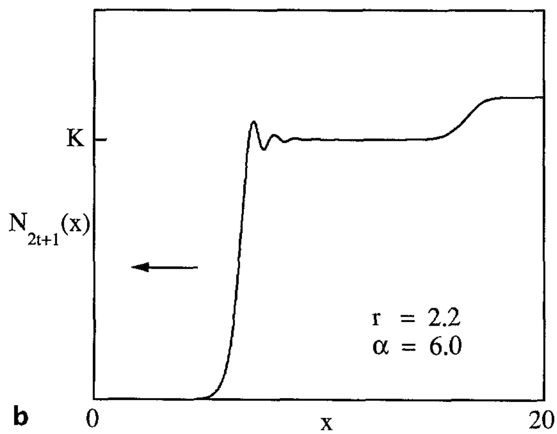


Fig. 9a,b. A travelling two-cycle. The integrodifference equation employed in Figs. 7 and 8 exhibits a travelling two-cycle for still larger *r*. The wave alternates between two profiles, all the while moving to the left

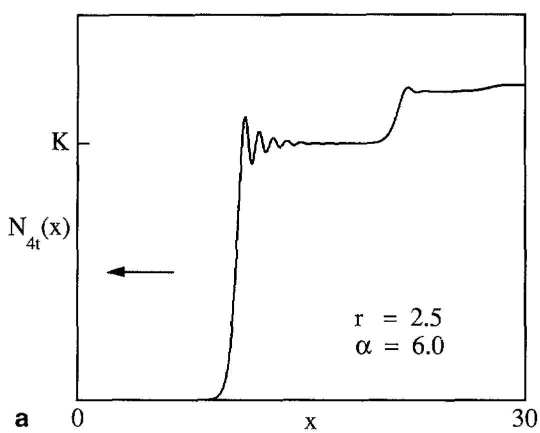


Fig. 10a

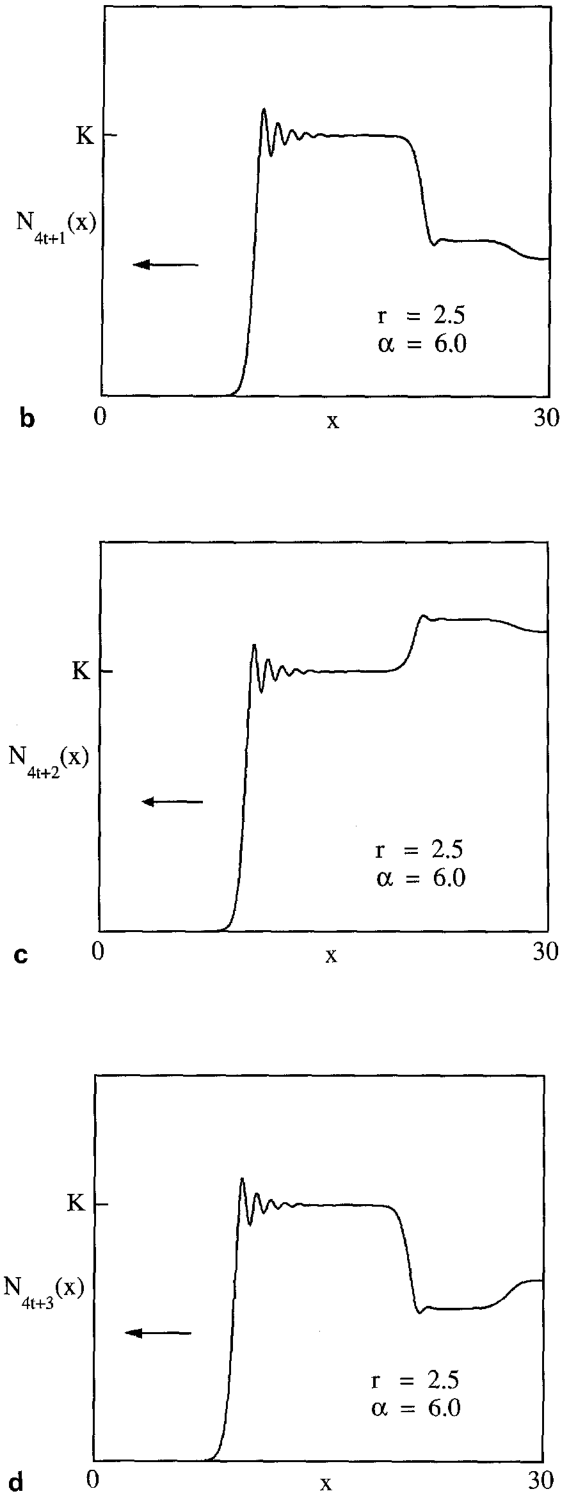


Fig. 10a–d. A travelling four-cycle. The integrodifference equation of Figs. 7, 8, and 9 exhibits a travelling four-cycle wave after loss of stability of the travelling two-cycle. The wave alternates between four profiles, all the while moving to the left

6 Waves of pursuit and evasion

One can also study the travelling waves that arise in systems of integrodifference equations. The simplest ecological scenario is perhaps that of a predator and a prey that grow and disperse in synchrony but with different diffusivities.

Consider, for example, the (rescaled) system of difference equations for a predator and prey (Kot 1989)

$$N_{t+1} = N_t \exp[r(1 - N_t - P_t)] \tag{94a}$$

$$P_{t+1} = bN_t P_t \tag{94b}$$

where N_t is the number of prey and P_t is number of predators at time t. In the absence of the predator, a high r prey ($r > 2$) exhibits oscillatory or chaotic behavior (May 1975; May and Oster 1976). In the presence of the predator, but with no dispersal, the nontrivial equilibrium

$$(N^*, P^*) = \left(\frac{1}{b}, 1 - \frac{1}{b}\right) \tag{95}$$

is asymptotically stable (see Fig. 11) for

$$1 < b < 2 \tag{96a}$$

$$0 < r < \frac{4b}{3 - b}. \tag{96b}$$

A high r prey may, in other words, be kept in check by a predator. For $b < 1$, the predator dies out and the prey exhibits its natural propensities. For $b > 2$, oscillations reappear by way of a Hopf bifurcation. Finally, for $r > 4b/(3 - b)$, stability is lost via a subcritical flip bifurcation (Neubert and Kot 1991).

In the presence of the predator and dispersal, it is natural to consider

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k_1(x - y)N_t(y) \exp\{r[1 - N_t(y) - P_t(y)]\}\, dy \tag{97a}$$

$$P_{t+1}(x) = \int_{-\infty}^{+\infty} k_2(x - y)bN_t(y)P_t(y)\, dy \tag{97b}$$

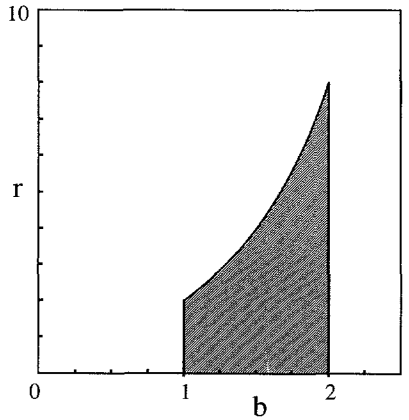


Fig. 11. Stability region for a simple discrete-time predator-prey model (Eqs. (94)). The nontrivial equilibrium corresponding to coexistence of the predator and prey is asymptotically stable for parameters within the shaded region

with

$$k_1(x-y) = \tfrac{1}{2}\alpha_1 \exp(-\alpha_1|x-y|) \tag{98a}$$

$$k_2(x-y) = \tfrac{1}{2}\alpha_2 \exp(-\alpha_2|x-y|) \tag{98b}$$

as our governing equations. This system has been studied with an eye to diffusive instability by Kot (1989); it was shown that overdispersal of the predator (relative to the prey) can lead to a cascade of diffusion-driven period-doubling bifurcations. There has not been a detailed analysis of system (97) concerning travelling waves. However, it is clear, from numerical simulations, that system (97) may exhibit many of the same waves that one associates with systems of reaction-diffusion equations.

Dunbar (1983, 1984) observed two varieties of travelling waves of passive pursuit and evasion in a reaction-diffusion system based upon a Lotka–Volterra predator-prey model. One variety exhibited monotonicity in the final approach of the waveform to the steady state (*à la* Chow and Tam 1976); the other variety exhibited damped oscillations. System (97) possesses both varieties of waves. Figures 12 and 13 illustrate simulations of system (97) that exhibit these two waveforms.

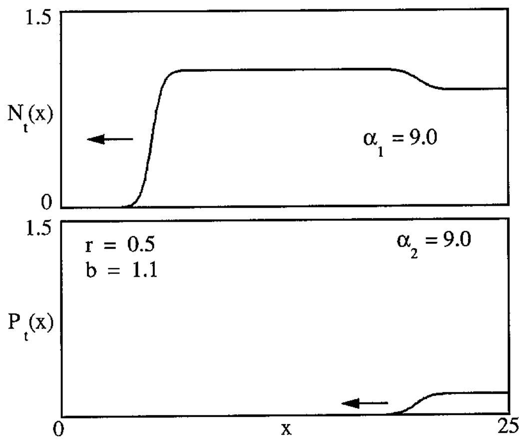


Fig. 12. Simple travelling waves of pursuit and evasion for a predator-prey system with bilateral-exponential contact distributions for both predator and prey. The predators do not actively pursue; the dispersal is passive. However, the prey population wave propagates ahead of the predator wave in such a way as to give the impression of pursuit and evasion. Solutions were obtained by numerically integrating system (97) using the extended trapezoidal rule

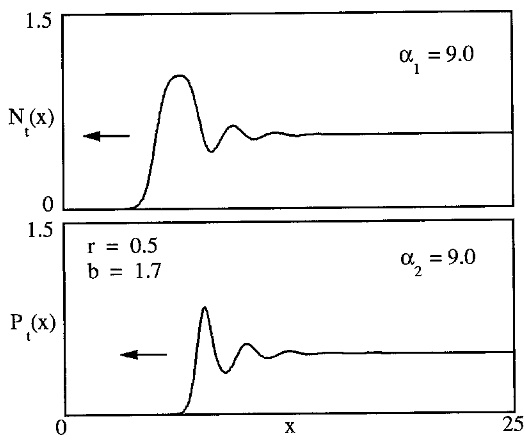


Fig. 13. Travelling waves of pursuit and evasion with exponentially damped oscillations. These waves were obtained by numerically integrating system (97) using the extended trapezoidal rule

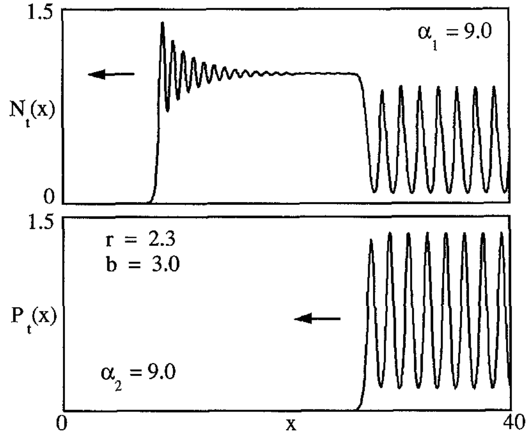


Fig. 14. Travelling wave trains in a system with oscillatory kinetics. The underlying system of difference equations (Eqs. (94)) has undergone a Hopf bifurcation and exhibits oscillatory kinetics. The corresponding system of integrodifference equations (Eqs. (94)) possesses travelling wave trains

There is also an extensive literature, built around the seminal papers of Kopell and Howard (1973) and Howard and Kopell (1977), on travelling wave train solutions for reaction-diffusion systems with limit cycle kinetics. The limit cycle acts, in effect, as a pacemaker: each oscillation gives rise to a wave which propagates as the result of diffusion. System (97) also exhibits such phenomena. Figure 14 highlights the travelling wave train that appears in a simulation of system (97). I am currently endeavoring to extend some of the more rigorous arguments for reaction-diffusion systems to systems of integrodifference equations.

7 Discussion

Many modellers appear to have a marked antipathy toward the use of integrals in their models. This has lead to some interesting paradoxes in the history of modelling. Models with distributed delays, Volterra integrodifferential equations, are, for example, more general and, in many instances, easier to deal with than delay-differential equations (Cushing 1977; Burton 1983). Yet delay-differential equations are prevalent in the literature, perhaps because of their simpler appearance. Similarly, it might be argued (Mollison 1977) that continuous-time spatial contact models are preferable to reaction-diffusion models because of the flexibility that contact distributions provide. Nevertheless, continuous-time spatial contact models are far from common. For continuous-time models, there are alternative formulations that employ continuous dependent and independent variables; integral formulations are often viewed as something of a luxury.

The situation is rather different when we turn to discrete-time models that allow for dynamics and dispersal. There are, in fact, a variety of formulations that have been offered in lieu of integrodifference equations. The more prominent of these alternatives are coupled (or cellular) maps, coupled lattice maps, and cellular automata (Jackson 1990). These are not, however, in any sense equivalent to integrodifference equations. Cellular maps (Yamada and Fujisaka 1983; Kaneko 1984; Waller and Kaprall 1984) typically take space and time to be discrete, even if the dependent variable is continuous. Coupled lattice maps (Oono and Kohmoto 1985; Oono and Yeung 1987) and cellular automata (Wolfram 1983, 1984) take the extreme approach of letting space, time, and the dependent variable all be discrete. Continuity, of course, is a severe constraint on the behavior of a model, as may be seen in moving from the logistic difference equation to the logistic differential equation. Integrodifference equations, because they maintain continuity of space and the dependent variable, are easier to analyze than these alternative formulations. The occurrence of discrete, nonoverlapping generations in a biological population may force us to turn to discrete-time models; it should not, by itself, force us to give up continuity in space and number.

I have studied a variety of integrodifference equations. In the simplest instances, integrodifference equations behave like reaction-diffusion equations, despite the dissimilar appearance of the actual models. Scalar integrodifference equations with compensatory growth exhibit simple travelling waves like those of scalar reaction-diffusion equations. The critical speed of these waves is, in many instances, determined from a straightforward linearization. For carefully chosen redistribution kernels, one may approximate the shape of the waveform with a method developed for reaction-diffusion equations. With the occurrence of overcompensation, scalar integrodifference equations suddenly exhibit travelling waves far more complicated than those of scalar reaction-diffusion equations. However, the complexity is that which we might predict from our knowledge of difference equations: overcompensatory integrodifference equations may exhibit a cascade of period-doubling flip bifurcations that result in travelling cycles. Systems of integrodifference equations, in turn, are reminiscent of systems of reaction-diffusion equations, again modulo discreteness in time. In sum, integrodifference equations readily incorporate the varied dispersal patterns found in nature; they allow us to model populations with discrete, nonoverlapping populations; and they allow us to build upon our knowledge of continuous-time reaction-diffusion models. At the same time, they are substantially easier to analyze than a variety of alternative discrete-time models.

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