

Thus we can state that if we observe a continuously growing population in discrete time intervals and the observed (discrete) intrinsic growth rate is  $R_0$ , then the real (continuous) growth rate is given by  $r = \ln(1 + R_0)$ . However, the qualitative features are preserved as in the Euler discretization.

#### 6.1.4 Logistic growth in discrete and continuous time

Consider the logistic differential equation

$$y' = ay(1 - y), \quad y(0) = y_0. \quad (6.3)$$

Euler discretization (with  $\Delta t = 1$ ) gives

$$y(n+1) = y(n) + ay(n)(1 - y(n)) = (1+a)y(n) \left(1 - \frac{y(n)}{\frac{1+a}{a}}\right), \quad (6.4)$$

which is a discrete logistic equation. We have already solved (6.3) and we know that its solutions monotonically converge to the equilibrium  $y = 1$ . However, if we plot solutions to (6.4) with, say,  $a = 4$ , we obtain the picture presented in Fig. 6.1. Hence, in general it seems unlikely that we can use the Euler discretization as an approximation to the continuous model.

Let us, however, write down the complete Euler scheme:

$$y(n+1) = y(n) + a\Delta t y(n)(1 - y(n)), \quad (6.5)$$

where  $y(n) = y(n\Delta t)$  and  $y(0) = y_0$ . Then

$$y(n+1) = (1 + a\Delta t)y(n) \left(1 - \frac{a\Delta t}{1 + a\Delta t}y(n)\right).$$

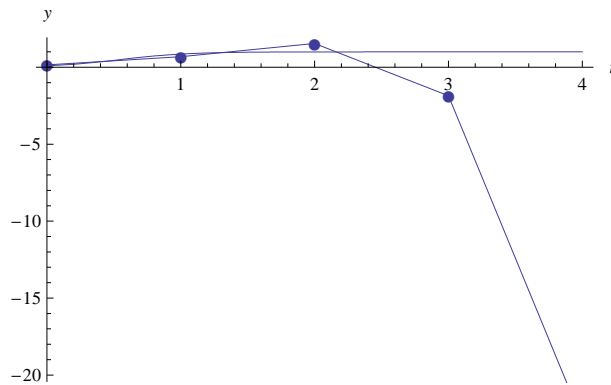


Fig. 6.1. Comparison of solutions to (6.3) and (6.4) with  $a = 4$ .

Substitution

$$x(n) = \frac{a\Delta t}{1 + a\Delta t} y(n) \quad (6.6)$$

reduces (6.5) to

$$x(n+1) = \mu x(n)(1 - x(n)). \quad (6.7)$$

Thus, the parameter  $\mu$  which controls the long time behaviour of solutions to the discrete equation (6.7) depends on  $\Delta t$  and, by choosing a suitably small  $\Delta t$  we can get solutions of (6.7) to mimic the behaviour of solutions to (6.3). Indeed, by taking  $1 + a\Delta t < 3$  we obtain convergence of solutions  $x(n)$  to the equilibrium

$$x = \frac{a\Delta t}{1 + a\Delta t}$$

which, reverting (6.6), gives the discrete approximation  $y(n)$  which converges to 1, as the solution to (6.3). However,

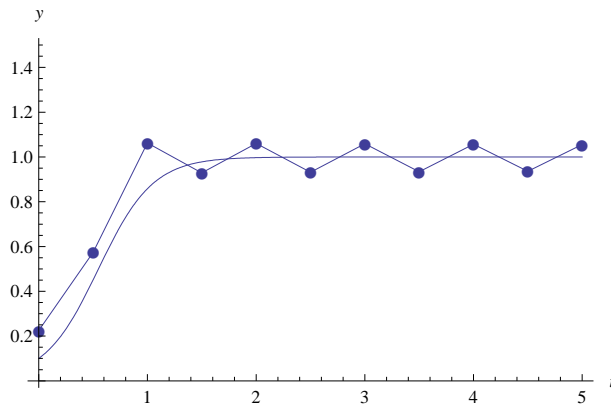


Fig. 6.2. Comparison of solutions to (6.3) with  $a = 4$  and (6.7) with  $\mu = 3$  ( $\Delta t = 0.5$ ).

as seen on Fig 6.2, this convergence is not monotonic which shows that the approximation is rather poor. This can be remedied by taking  $1+a\Delta t < 2$  in which case the qualitative features of  $y(t)$  and  $y(n)$  are the same, see Fig. 6.3).

We note that above problems can be also solved by introducing the so-called non-standard difference schemes which consists in replacing the derivatives and/or nonlinear terms by more sophisticated expressions which, though equivalent when the time step goes to 0 produce, nevertheless, qualitatively different discrete picture. In the case of the logistic equation such a non-standard scheme can be constructed replacing  $y^2$  not by  $y^2(n)$  but by  $y(n)y(n + 1)$ .

$$y(n + 1) = y(n) = a\Delta t(y(n) - y(n)y(n + 1)).$$

In general, such a substitution yields an implicit scheme but in our case the resulting recurrence can be solved for

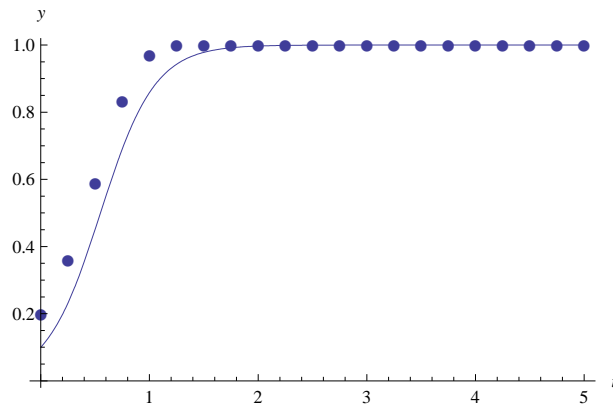


Fig. 6.3. Comparison of solutions to (6.3) with  $a = 4$  and (6.7) with  $\mu = 2$  ( $\Delta t = 0.25$ ).

$y(n+1)$  producing

$$y(n+1) = \frac{(1+a\Delta t)y(n)}{1+a\Delta ty(n)}$$

and we recognize the Beverton-Holt-Hassel equation with  $R_0 = 1 + a\Delta t$  (and  $K = 1$ ).

Consider now the logistic equation

$$N' = rN \left(1 - \frac{N}{K}\right).$$

The first type of discretization immediately produces the discrete logistic equation (1.24)

$$N_{k+1} = N_k + rN_k \left(1 - \frac{N_k}{K}\right),$$

solutions of which, as we shall see later, behave in a dramatically different way than those of the continuous equation.

This is in contrast to the exponential growth equation discussed earlier.

To use the time-one map discretization, we re-write (4.14) as

$$N(t) = \frac{N_0 e^{rt}}{1 + \frac{e^{rt}-1}{K} N_0}.$$

which, upon denoting  $e^r = R_0$  gives the time-one map

$$N(1, N_0) = \frac{N_0 R_0}{1 + \frac{R_0-1}{K} N_0},$$

which, according to the discussion above, yields the Beverton-Holt model

$$N_{k+1} = \frac{N_k R_0}{1 + \frac{R_0-1}{K} N_k},$$

with the discrete intrinsic growth rate related to the continuous one in the same way as in the exponential growth equation.

### 6.1.5 Discrete models of seasonally changing population

So far we have considered models in which laws of nature are independent of time. In many real processes we have to take into account phenomena which depend on time such as seasons of the year. The starting point of modelling is as before the balance equation. If we denote by  $B(t)$ ,  $D(t)$ ,  $E(t)$  and  $I(t)$  rates of birth, death, emigration and immigration, so that e.g. the number of births in time interval  $[t_1, t_2]$  equals  $\int_{t_1}^{t_2} B(s) ds$ . Then, the change in the size of the popu-