

2 One-dimensional models in discrete time

So far, we have assumed that demographic events happen continuously over time and can thus be written as rates. For many biological species with overlapping generations and continuous reproduction this is a valid approximation. However, many other populations, like annual plants, have discrete generations and many species have clearly defined breeding seasons. These are better modeled in a discrete time framework. More fundamentally, we have already discussed that the effect of biological events (like birth) on the population dynamics is often not immediate as it is assumed in an ODE system, but only becomes apparent after some time delay. While in continuous time this leads to complex difference-differential equations, effects of time delay (by one time unit or generation) are automatically included in discrete time models. In this section, we will consider a population with dynamics given by the following first-order, autonomous (= constant coefficient) difference equation,

$$N_{t+1} = R(N_t), \quad t \in \mathbf{N}. \quad (1)$$

An initial value N_0 is specified and the reproduction function R can take any shape. The simplest example is the linear difference equation

$$N_{t+1} = RN_t \quad (2)$$

of geometric growth (for $R > 1$) or decline (for $0 < R < 1$). Geometric growth has the explicit solution

$$N_t = R^t N_0. \quad (3)$$

Very few other discrete time systems have explicit solutions. Next, we need to include density-dependent population regulation. Rather than “dropping down” a model, we want to construct a model from biological principles.

2.1 Non-linear discrete population growth

Consider a fish population of adult stock size N_t . From one breeding season to the next (t to $t+1$), the survival probability for any adult is given by s . (For $s = 0$, we have the special case of no generation overlap). During breeding season, the adults produce a number of $L_t = bN_t$ larvae. We assume that larvae grow up to reproductive age during one season. Surviving larvae are recruited to the adult population. We thus need a model for larval survival.

1. Assume that the larvae L develop according to (continuous time) logistic decline, i.e.,

$$\frac{\partial L_t(\tau)}{\partial \tau} = -m_1 L_t(\tau) - m_2 L_t^2(\tau), \quad (4)$$

where m_1 measures mortality due to extrinsic (e.g. abiotic) factors and m_2 the density dependent component (e.g., due to competition for resources). With $L_t(0) = bN_t$ and

a time Δ between seasons we get

$$L_t(\Delta) = \frac{bN_t m_1}{(bN_t m_2 + m_1) \exp[m_1 \Delta] - bN_t m_2}. \quad (5)$$

We thus get

$$N_{t+1} = sN_t + L_t(\Delta) = sN_t + \frac{c_1 N_t}{1 + c_2 N_t} \quad (6)$$

with positive constants

$$c_1 = b \exp[-m_1 \Delta] \quad , \quad c_2 = b \frac{m_2}{m_1} (1 - \exp[-m_1 \Delta])$$

This is the *Beverton-Holt model* for stock recruitment. For $s = 0$, the model is also called the *Verhulst model*.

2. An alternative approach assumes that larvae (or juveniles) do not compete primarily among themselves, but with their adult conspecifics. This will be true, in particular, if adult fish eat eggs and larvae of their own species (which is indeed true for many species, where predation is purely size-dependent). We then get

$$\frac{\partial L_t(\tau)}{\partial \tau} = -m_1 L_t(\tau) - m_2 N_t L_t(\tau), \quad (7)$$

which simply results in

$$L_t(\Delta) = bN_t \exp[-(m_1 + m_2 N_t) \Delta]. \quad (8)$$

We then get a so-called *Ricker model* for stock recruitment

$$N_{t+1} = sN_t + N_t \exp[r(1 - N_t/K)] \quad (9)$$

with constants

$$r = \log[b] - m_1 \Delta \quad , \quad K = \frac{\log[b] - m_1 \Delta}{m_2 \Delta}.$$

3. Finally, we can assume that density-dependent competition is entirely among adults (e.g. for breeding places). Then we get a discretized version of logistic growth

$$N_{t+1} = rN_t \left(1 - \frac{N_t}{K}\right), \quad (10)$$

where $r = s + b$ accounts for the surviving adult and juvenile individuals from the previous generation.

Recruitment in the Beverton-Holt model is called *normal compensation*. It increases monotonically with stock size and reaches an asymptote for $N_t \rightarrow \infty$ at $L_{\max}(\Delta) = c_1/c_2$. In contrast, recruitment for the Ricker model is *over-compensating*. Here, $L_{\max}(\Delta)$ runs through an intermediate maximum and approaches zero for $N_t \rightarrow \infty$. As a consequence, the reproduction function of the Ricker model is usually non-monotonic. The same holds true for the discrete logistic growth model. All three models can be derived in many different ways and for various underlying mechanisms. They are archetypical models of theoretical ecology.

2.2 Discrete versions of continuous models

One special application of discrete models consists simply of an observation in discrete time intervals of a population with continuous birth and death. Thus, we simply set $N_t = N(t \cdot \Delta)$. An explicit reproduction function can be derived if and only if the ODE can be solved. For logistic growth, in particular, we obtain

$$N_{t+1} = \frac{K}{1 - (1 - K/N_t) \exp[-r]} = \frac{\lambda N_t}{1 + (\lambda - 1)N_t/K} \quad (11)$$

with $\lambda = \exp[r]$. We recognize this as a special case of the Beverton-Holt model with $s = 0$, $c_1 = \lambda$, and $c_2 = (\lambda - 1)/K$. Note that we do not get the discrete logistic growth as the corresponding model. This correspondence also implies that the Beverton-Holt model (with $s = 0$) is explicitly solvable. In more general, we can define a corresponding discrete model for every autonomous ODE model. The converse is not true, however. In this sense, there are “more” discrete models than continuous models. As we will see, they also show a larger variety of phenomena.

2.3 Equilibria and Stability of Discrete Dynamics

Consider a general discrete dynamical system (1-dim., etc) with continuously differentiable reproduction function,

$$N_{t+1} = F(N_t) \quad ; \quad F'(N) := \frac{\partial F(N)}{\partial N} \text{ continuous} \quad (12)$$

We can then characterize equilibria as follows

1. Equilibria (or fixed points) of the dynamics are all intersections of the reproduction function with the line of slope 1,

$$F(N^*) = N^* \quad (13)$$

2. Let

$$\Lambda := \left. \frac{\partial F(N)}{\partial N} \right|_{N^*}.$$

Then N^* is locally (asymptotically) stable for $|\Lambda| < 1$ and locally unstable for $|\Lambda| > 1$.

Proof: Consider some starting value N_0 close to an equilibrium point N^* . Due to the mean value theorem, there is a $c \in (N_0, N^*)$ such that

$$\left. \frac{\partial F(N)}{\partial N} \right|_{N=c} = \frac{F(N_0) - F(N^*)}{N_0 - N^*} = \frac{F(N_0) - N^*}{N_0 - N^*}.$$

Since the derivative of $F(N)$ is continuous, we have

$$\left| \left. \frac{\partial F(N)}{\partial N} \right|_c \right| < 1$$

if $|\Lambda| < 1$, and thus $|F(N_0) - N^*| < |N_0 - N^*|$. We thus get a sequence N_i that converges to the equilibrium point N^* . Similarly, we are (locally) driven away from the optimum for $|\Lambda| > 1$.

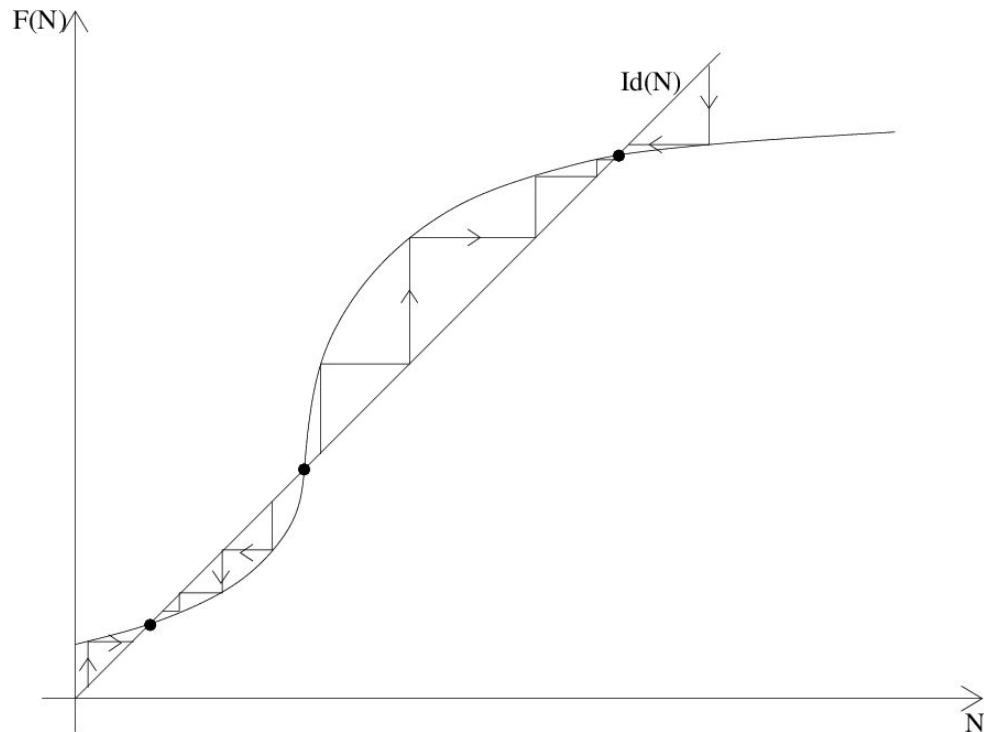


Figure 1: Cobwebbing method to determine the stability of equilibria.

Cobwebbing We can represent the discrete dynamics easily using the cobwebbing method:

- Start at N_0 , go (vertically) to $F(N_0)$.
- Project (horizontally) to the identity line to get $N_1 = F(N_0)$.
- Go vertically to $F(N_1)$ and iterate.

Depending on the slope Λ near an equilibrium point, we get four types of characteristic behavior.

1. $0 < \Lambda < 1$: monotone convergence.
2. $-1 < \Lambda < 0$: oscillating convergence (damped oscillations)
3. $\Lambda > 1$: monotone divergence
4. $\Lambda < -1$: oscillating divergence (driven oscillations)

2.4 Analysis of the Beverton-Holt and the Ricker model

Beverton Holt model Consider the dynamics of the Beverton-Holt model defined by

$$N_{t+1} = F(N_t) = sN_t + \frac{c_1 N_t}{1 + c_2 N_t}. \quad (14)$$

- We have

$$N(1 - s)(1 + c_2 N) = c_1 N$$

and thus $N_1^* = 0$ and

$$N_2^* = \frac{c_1 - 1 + s}{c_2(1 - s)}$$

- With

$$F'(N) = \frac{\partial F(N)}{\partial N} = s + \frac{c_1}{(1 + c_2 N)^2} \leq s + c_1 = F'(0)$$

and $F'(N_2^*) = s + \frac{c_1}{(1 + (c_1 - 1 + s)/(1 - s))^2} = 1 + \frac{(1 - s)(1 - s - c_1)}{c_1} < 1$ for $s + c_1 > 1$ and thus $N_2^* > 0$. We get monotonic approach of N_2^* for $s + c_1 > 1$ and monotonic approach of $N_1^* = 0$ otherwise.

Lemma In general, if $F(N)$ is continuous and monotonic on a closed interval $I \subseteq \mathbf{R}_+$ (e.g., $I = [0, \infty)$) with $F(I) \subseteq I$, then every sequence $N_i = F^i(N_0)$ with $N_0 \in I$ converges monotonically to a fixed point of F or to ∞ .

Proof For $F(N_0) > N_0$, we have $F(F(N_0)) \geq F(N_0)$ because of monotony, and thus $N_0 < F(N_0) \leq F(F(N_0)) \leq \dots$. The sequence will either converge to some N^* or diverge to infinity. In the former case, we have $F(N^*) = N^*$ since F is continuous. The case $F(N_0) < N_0$ works analogously, $F(N_0) = N_0$ is trivial.

Ricker model Consider now the Ricker model (we use $s = 0$, without restriction under rescaling),

$$N_{t+1} = F(N_t) = N_t \exp[r(1 - N_t/K)]. \quad (15)$$

- We obtain equilibria at $N_1^* = 0$ and $N_2^* = K$.

- We have

$$F'(N) = \left(1 - \frac{Nr}{K}\right) \exp[r(1 - N/K)].$$

and thus

$$\Lambda_1 = F'(0) = \exp[r] > 1, \quad (16)$$

$$\Lambda_2 = F'(K) = 1 - r. \quad (17)$$

- We have a unique maximum of $F(N)$ at $N_{\max} = K/r$ (and, of course a minimum $N_{\min} = 0$).

We thus can distinguish three dynamical regimes (see, for example, *Populus*, density-dependent population growth, “discrete logistic” = Ricker)

1. For $r < 1$, the interval $I = [0, N_{\max}]$ contains both equilibrium points. Since we have $F(N)$ monotonically increasing in I , with $F(I) \subseteq I$, we obtain monotonic convergence to the stable equilibrium $N_2^* = K$ for every start value $N_0 \in I$. For start values $N_0 \notin I$, we have $F(N_0) \in I$ and the same applies after the first step.
2. For $1 < r < 2$, we have no longer monotonic convergence, but still $|\Lambda_2| < 1$. Hence, $N_2^* = K$ is still asymptotically stable and approached by damped oscillations.
3. For $r > 2$, we have $|\Lambda_2| > 1$ and therefore do no longer have a stable equilibrium. In particular, we get oscillating divergence for the equilibrium at $N_2^* = K$. Since the Ricker model has a finite maximum population size, we can ask what happens.

2.5 Limit cycles

The basic idea to gain further insights of the long-term dynamics of the Ricker model and similar systems is to consider the iterated map

$$F^{(2)}(N) = F(F(N)) \quad \text{resp.} \quad F^{(k)}(N) = F(\dots F(F(N))) \quad k\text{-fold} \quad (18)$$

across k seasons. Obviously, this is again a discrete dynamical system and can be studied in the same way as the original one. Concerning its long-term behavior, we observe the following elementary facts:

1. Equilibria of F are also equilibria of $F^{(2)}$ and of every higher iteration $F^{(k)}$.
2. For the derivative of $F^{(2)}$ at the fixed points, we have, using the chain rule,

$$\frac{\partial F^{(2)}(N)}{\partial N} = \frac{\partial F(Z)}{\partial Z} \Big|_{Z=F(N)} \cdot \frac{\partial F(N)}{\partial N}. \quad (19)$$

and accordingly iterated for $F^{(k)}$. For equilibria N^* of $F(N)$, in particular, this means

$$\frac{\partial F^{(k)}(N)}{\partial N} \Big|_{N=N^*} = \left(\frac{\partial F(N)}{\partial N} \Big|_{N=N^*} \right)^k. \quad (20)$$

Thus, stable equilibria of F remain stable for all higher iterations, and unstable equilibria remain unstable.

3. Additional (stable or unstable) equilibria of iterated maps $F^{(k)}$ can occur if the original dynamics F leads to cycling.

Definition and basic properties: Limit Cycles

1. A point N_0 is called a *point of period k* or a *k -cycle point* if it is a fixed point (equilibrium) of the k -fold iterated map $F^{(k)}(N)$, but not a fixed point of any map $F^{(k')}$ with $1 \leq k' < k$. Its orbit

$$\{N_0, F(N_0), \dots, F^{(k-1)}(N_0)\} =: \{N_0, N_1, \dots, N_{k-1}\}$$

is called the corresponding k -cycle. Note that all points N_i in the cycle are fixed points of $F^{(k)}$.

2. A limit cycle is asymptotically stable, if and only if the corresponding cycle points are asymptotically stable equilibria of the k -fold mapping. In particular, we obtain via the chain rule

$$\Lambda^{(k)} = \frac{\partial F^{(k)}}{\partial N} = \prod_{i=0}^{k-1} \left. \frac{\partial F(N)}{\partial N} \right|_{N=N_i} \quad (21)$$

for the derivative of $F^{(k)}$ at all points of the cycle. The cycle and the corresponding fixed points of $F^{(k)}$ are asymptotically stable if $|\Lambda^{(k)}| < 1$ and unstable if $|\Lambda^{(k)}| > 1$.

3. We define the characteristic exponent (or Floquet exponent)

$$\lambda = \frac{1}{k} \log |\Lambda^{(k)}| = \frac{1}{k} \sum_{i=0}^{k-1} \log \left| \left. \frac{\partial F(N)}{\partial N} \right|_{N=N_i} \right|. \quad (22)$$

Obviously, the cycle is stable for $\lambda < 0$ and unstable for $\lambda > 0$.

2.6 Example: Discrete logistic growth

As an example, we consider logistic growth

$$N_{t+1} = F(N_t) = rN_t \left(1 - \frac{N_t}{K} \right), \quad (23)$$

which behaves similar as the Ricker equation, but is easier to analyze. We have a maximum of $F(N)$ at $N = K/2$, where $F(K/2) = rK/4$. There are two equilibria at $N_1^* = 0$ and at $N_2^* = K(r-1)/r$. With $F'(N) = r(1 - 2N/K)$, we obtain $F'(0) = r$ and $F'(N_2^*) = 2 - r$.

1. For $0 < r < 1$, we have a single stable equilibrium at $N_1^* = 0$ and the population dies out.
2. For $1 < r < 3$, a second equilibrium N_2^* appears and is stable, while N_1^* is unstable. Approach to the stable equilibrium is monotonic for $r < 2$ and oscillating for $r > 2$.
3. For $r > 3$, both equilibria N_1^* and N_2^* are unstable and we can expect limit cycles or other types of limit behavior.

Finally, for a reasonable biological model, r should not be larger than 4 since otherwise $F(N)$ can get larger than K and then negative in the next iteration. To study the dynamics via iterated maps, assume $K = 1$ for simplicity. We then obtain:

$$F(N) = rN(1 - N) \quad (24)$$

$$F^{(2)}(N) = r(rN(1 - N))(1 - rN(1 - N)) = r^2N(1 - N)(1 - rN + rN^2) \quad (25)$$

$$\frac{\partial F^{(2)}(N)}{\partial N} = r(1 - 2rN(1 - N))r(1 - 2N) \quad (26)$$

(Note that, in general, we have the symmetry $F^{(k)}(1 - N) = F^{(k)}(N)$.) We find equilibria $F^{(2)}(N) = N$ for

$$N_1^* = 0 \quad , \quad N_2^* = \frac{r - 1}{r} \quad , \quad N_{3,4}^* = \frac{1 + r \pm \sqrt{(r - 1)^2 - 4}}{2r} \quad (27)$$

Obviously, $N_{3,4}^*$ exist for $r \geq 3$. We also find that $F(N_3^*) = N_4^*$ and vice-versa $F(N_4^*) = N_3^*$. The corresponding derivatives are

$$\Lambda_1^{(2)} = r^2 \quad \Lambda_2^{(2)} = (2 - r)^2 \quad , \quad \Lambda_{3,4}^{(2)} = 4 + 2r - r^2 \quad (28)$$

- At $r = 3$, we have $N_2^* = N_3^* = N_4^*$. We see that, by increasing r beyond this threshold, the previously stable equilibrium N_2^* turns unstable. At the same time two new equilibria of $F^{(2)}(N)$, N_3^* and N_4^* , appear and are stable: $|\Lambda_{3,4}^{(2)}| < 1$ for $3 < r < 1 + \sqrt{6} \approx 3.45$. This is the typical signature of a pitchfork bifurcation. For the original map $F(N)$, the number of equilibria does not change. The new equilibria for $F^{(2)}$ correspond to a stable limit cycle with period 2.
- For $r > 1 + \sqrt{6}$, we have $\Lambda_{3,4}^{(2)} < -1$ and the equilibria N_3^* and N_4^* of $F^{(2)}$ turn unstable. For the iterated map $F^{(4)}$ this means that the slope at both equilibria increases to $(\Lambda_{3,4}^{(2)})^2 > 1$, thereby generating, once again, two new equilibria in a pitchfork bifurcation. We thus obtain a 2-cycle for $F^{(2)}$, corresponding to a 4-cycle for $F(N)$, in each case. In general, every time when a stable equilibrium of $F^{(k)}$ becomes unstable, we get two new stable equilibria of $F^{(2k)}$, and thus a limit cycle with the period $2k$. This is the so-called *period doubling cascade* of the logistic map and many similar discrete maps (such as the Ricker model).

2.7 Chaos

For the logistic map, we get a series of critical values r_{2^k} (with $r_2 = 3$ and $r_4 = 1 + \sqrt{6} \approx 3.45$), above which stable cycles of period 2^k exist. As it turns out, this sequence quickly converges to a finite value $r_c = r_\infty \approx 3.57$. We can ask what happens beyond this point. As an example, we can consider the logistic map with $r = 4$ and dissect the interval $[0, 1]$ as follows

1. Two intervals $I_0 = [0, 1/2]$ and $I_1 = [1/2, 1]$. Both intervals are mapped by $F(N)$ to the full domain $[0, 1]$.
2. Dissect I_0 such that $I_{00} = [0, q]$ is mapped by F to I_0 and $I_{01} = [q, 1/2]$ is mapped to I_1 . Similarly, dissect I_1 into I_{10} and I_{11} .
3. Iterate this: $I_{000} \subset I_{00}$ is mapped by F to I_{00} and by $F^{(2)}$ to I_0 ; $I_{001} \subset I_{00}$ is mapped to I_{01} and then to I_1 , etc. In general, $I_{i_0 i_1 i_2 \dots i_k} \subset I_{i_0}$ with $i_j \in \{0, 1\}$ is mapped by F to $I_{i_1 i_2 \dots i_k} \subset I_{i_1}$ and by $F^{(k)}$ to I_{i_k} .
4. In general, if (e.g.) $N \in I_{0100}$, then $N \in I_0$, $F(N) \in I_1$, $F^{(2)}(N) \in I_0$, $F^{(3)}(N) \in I_0$. We can identify each point with an infinite interval nesting (dyadic transformation).
5. Points with periodic nesting correspond to periodic orbits. There are points with every period, starting with $I_{0000\dots}$ and $I_{1111\dots}$, which encode the (unstable) fixed points.
6. All points on interval boundaries are attracted by 0 (dense set: population on the verge of extinction; this is special for $r = 4$).
7. Almost all points (with no period in the nesting) must have orbits of infinite length. We also see that orbits of very close points can differ widely after even a few generations. This is the signature of *chaos*.
8. For the special case $r = 4$, there is an explicit solution for the dynamics

$$N_k = \sin^2[2^{k-1}\pi\theta] \quad \text{where} \quad \theta = \frac{1}{\pi} \sin^{-1}[N_0^{1/2}]. \quad (29)$$

We see that we get aperiodic orbits for all irrational θ .

These observed phenomena are not specific to $r = 4$, but occur for most values $r > r_c$. We can summarize them as follows:

- There are infinitely many periodic points, with all kinds of periods, even and odd.
- For most r values, we obtain chaos, indicated by orbits of infinite length that never come back to a starting point. Another characteristic of chaotic solutions is that very small initial differences are magnified due to the mapping. This means that the long-term predictability of the system gets lost (butterfly effect).
- As analog to the Floquet exponent for finite cycles, one defines the *Lyapunov exponent*

$$\lambda = \lim_{k \rightarrow \infty} \frac{1}{k} \sum_{i=0}^{k-1} \log \left| \frac{\partial F(N)}{\partial N} \Big|_{N=N_i} \right| \quad (30)$$

for any point N_0 with infinite orbit. A positive Lyapunov exponent indicates that small initial differences are magnified and the resulting orbit is chaotic.

- The chaotic regimes are interlaced by intervals with stable limit cycles with low period (e.g. 3-cycles).

Periodicity and Chaos in Biology Our examples show that even very simple models (in one dimension!) can give rise to very complex phenomena. Periodic dynamics are a frequent observation in biology, also in population dynamics. There can be multiple causes for such cycles. With discrete dynamics, cycling is created by an overshooting of the equilibrium, which is typical of many systems where regulation is not immediately effective, but acts with a certain delay. Essentially the same behavior is seen in continuous delay ODE's. Chaotic behavior in biology has been speculated a lot. From a theoretical point of view, we should expect chaos in particular for systems with higher dimension (multiple interacting species). Even with continuous dynamics, chaos exists in dimension ≥ 3 . However, convincing empirical evidence is hard to obtain. In particular, it is often difficult (or impossible) to distinguish long cycles and/or stochastic noise from "real" deterministic chaos. Finally, true chaos is never strictly possible in populations with a discrete number of individuals. Nevertheless, chaos is a field where biology has inspired mathematics and has helped to found chaos theory as a research field (Robert May 1974, 1976).