

Dynamic Population Models

T. Legović

Ruder Bošković Institute, Zagreb, Croatia

E-mail: legovic@irb.hr

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3.1 A DEFINITION OF A POPULATION MODEL

By a population we mean the number of alive organisms in a given area. We are interested in predicting how this number will change in future. For this purpose we create models which include processes that are responsible for a population change. For example, if

organisms reproduce in the area of study, the process of reproduction should be included in the population model because it results in population change.

A model which expresses population processes mathematically is called a *mathematical model*. Usually, mathematical models we are interested in result in *population conservation equations*. A common characteristic of these equations is to express mathematically the following:

Population at the time instant $t + \Delta t$ = population at time instant t
 + sum of processes which cause population to increase in the unit time Δt
 – sum of processes which cause population to decrease in the unit time Δt .

If we can express all the encompassed processes as a function of the existing population or of a past value of the population which we presently know, we have a *predictive model*.

For example:

$$N(t + \Delta t) = N(t) + [\Sigma f_i(N(t), t) - \Sigma g_j(N(t), t)] * \Delta t \quad (3.1)$$

where $N(t)$ stands for the population in a time instant, t (known); $N(t + \Delta t)$ is the population in the time instant $t + \Delta t$ (unknown), f_i is the i -th contribution to population growth and g_j is the j -th contribution to population decline (known) in the time interval Δt (known).

Once, $N(t + \Delta t)$ is computed we substitute this value to the right side instead of $N(t)$ and compute $N(t + 2\Delta t)$. Continuing this process as long as we wish, we are predicting population value into the future.

The above example is of a mathematical model in discrete form, as opposed to a continuous form which will be seen in examples that follow.

3.2 THE FIRST LAW (MODEL) OF POPULATION DYNAMICS: MALTHUS LAW

Let us start with a very simple model and turn it into a mathematical model.

Assume that at the time, t , which we set to be zero, we have $N(t = 0) = N_0$ organisms. The number is known because we can count or estimate the number of organisms.

We ask the following question:

What will be the number of organisms at time $t = 1$ which we denote by $N(t = 1) = N_1$?

Here, the time unit is arbitrary; it may be 1 h, one day, one month, or whatever we find useful.

We write:

$N_1 = N_0$ (i.e., the no. of organisms with which we started) + the number of organisms which were born (between $t = 0$ and $t = 1$) – the number of organisms which died (between $t = 0$ and $t = 1$) + the number of immigrated organisms (between $t = 0$ and $t = 1$) – the number of emigrated organisms (between $t = 0$ and $t = 1$).

For simplicity, let us close our area of study so that immigration and emigration are not possible.

Then, we are left with:

$N_1 = N_0$ (i.e., the no. of organisms with which we started) + the number of organisms which were born (between $t = 0$ and $t = 1$) – the number of organisms which died (between $t = 0$ and $t = 1$).

Now we need ecologists to tell us how many organisms are born and how many die per capita in a unit of time. Let us denote by a the number of organisms that are normally born for each existing individual of our population in a unit of time. Similarly, let us denote by b the number of organisms that normally die per existing individual. Hence the number of born individuals in a unit of time will be $a * N_0$. Similarly, the number of died individuals in a unit of time will be $b * N_0$. Now we can put these numbers into the above equation:

$$N_1 = N_0 + a * N_0 - b * N_0. \quad (3.2)$$

To further simplify this equation, we denote by r the difference between a and b . Hence:

$$N_1 = N_0 + r * N_0 = (1 + r)N_0. \quad (3.3)$$

Here r is called the *biotic potential*. If the biotic potential is zero (i.e., the number of born is equal to the number of died organisms in a unit of time), then obviously:

$$N_1 = N_0$$

That is, the number in the next time instant will be the same as the number we started with.

Let us now make one key assumption which will enable us to predict the population number far into the future: assume that the biotic potential r is constant for all time instants in the future. Then, after the second time instant we have:

$$N_2 = N_1 + r * N_1 = (1 + r)N_1 \quad (3.4)$$

Now insert N_1 from Eq. (3.3) into Eq. (3.4) and get:

$$N_2 = (1 + r)(1 + r)N_0 = (1 + r)^2 N_0.$$

We can generalize the population after any time instant t into the future:

$$N_t = (1 + r)^t N_0 \quad \text{where } t = 1, 2, 3, \dots \quad (3.5)$$

Furthermore, by using our key assumption, note from Eqs. (3.3) and (3.4) we can generalize:

$$N_{t+1} = (1 + r)N_t. \quad (3.6)$$

Eq. (3.6) is our first mathematical model.

This model is called the *first law of population growth* or the *Malthus law*.

The expression Eq. (3.5) is called the solution to Eq. (3.6) given the initial value N_0 .

Namely, to arrive at Eq. (3.5) from Eq. (3.6) we needed to know what was the value of a population at the time $t = 0$.

In mathematics Eq. (3.6) is called a difference equation.

Note also that Eq. (3.6) assumes a jump from t to $t + 1$ and that we do not know anything about the population between t and $t + 1$. For this reason Eq. (3.6) is called discrete as opposed to continuous equation.

To see the difference between discrete and continuous equation let us turn Eq. (3.6) into a continuous equation.

First rewrite Eq. (3.6):

$$N_{t+1} - N_t = rN_t \quad (3.7)$$

Now assume that we are not going to jump from t to $t + 1$ but from t to $t + \Delta t$ where Δt is much smaller than 1. Eq. (3.7) becomes:

$$N_{t+\Delta t} - N_t = r_{\Delta t}N_t\Delta t \quad (3.8)$$

Now two things must be explained.

1. Why we wrote $r_{\Delta t}^*$ instead of r . This is because r was a number which denoted the difference between born and dead per individual in one unit of time while $r_{\Delta t}^*$ denotes the difference which occurred in Δt which is smaller than 1, and hence $r_{\Delta t}^*$ is smaller than r .
2. Why did we put Δt on the right side? In Eq. (3.7) it did not need to be there because Δt was equal to 1. Eq. (3.8) reads as follows: on the left side is the number of organisms and so it must be on the right side. But the right side reads:

$$[(\text{no. of born} - \text{no. of dead}) / (\text{one organism} * \Delta t)] * \text{no. of organisms} * \Delta t$$

Hence, no. of organisms * Δt cancels out and what remains is the number of born – number of dead for the whole population. So, the left side has the same units as the right side.

Now dividing with Δt we have:

$$(N_{t+\Delta t} - N_t) / \Delta t = r_{\Delta t}N_t$$

We can further shrink Δt into the infinitesimal increment dt and we have:

$$(N_{t+dt} - N_t) / dt = r_{dt}N_t$$

The left side is the derivative dN/dt which denotes the rate of change of the population at the time instant t . Let us denote r_{dt} by r_c , and we have:

$$dN/dt = r_cN \quad (3.9)$$

where r_c is the instantaneous difference between per capita birth and death. Also, the subscript c stands for the continuous case.

Eq. (3.9) is called the continuous form (as opposed to the discrete form given by Eq. (3.6)) of the Malthus law of population growth. Of course, the word “growth” refers to our expectation that r and r_c are positive because if they are zero the law should be called the first law of population stagnation and if they are negative the law should be called the first law of population decline.

In mathematics, Eq. (3.9) is called a differential equation.

Given $N(t = 0) = N_0$ the solution to Eq. (3.9) is:

$$N(t) = N_0e^{r_c t} \quad (3.10)$$

Hence, the solution to Eq. (3.6) is a geometric growth (Eq. (3.6)) and the solution to Eq. (3.9) is an exponential growth (Eq. (3.10)).

By equating Eq. (3.5) to Eq. (3.10) we see that in the case that $r_c = \ln(1 + r)$ the two dynamics coincide in the points of geometric growth.

When do we expect that Eqs. (3.5) and (3.10) will adequately represent population dynamics in nature?

There are two hypotheses that need to be satisfied. First is that population reproduction and death must not be influenced by a finite environment. However, if r and r_c are positive, the population will grow and sooner or later the population will start to deviate from the first law.

Hence, we expect that the first law will apply as long as the population is much smaller than limitations in food supply or space.

The second assumption is that the population must be large enough so that individual differences in organism reproduction and death do not matter. When the population falls below a certain number, individual-based models are more appropriate (Gourney and Nisbet, 1998).

3.3 THE SECOND LAW OF POPULATION DYNAMICS: VERHULST LAW

The first law of population dynamics does not account for the finite environment in which food supply and space are limited. Verhulst (1838) modified Eq. (3.9) by assuming that population growth, besides the Malthus term needs to be multiplied by a linearly decreasing term of N , resulting in the equation:

$$dN/dt = r_c(1 - N/K)N \quad (3.11)$$

where K is the largest population that food sources in the environment can support.

K is called the *carrying capacity* of the environment.

It is clear that Eq. (3.11) is close to Eq. (3.9) when $N \ll K$ (because N/K does not differ much from zero). As N approaches K , the right side of Eq. (3.11) approaches zero and the population becomes constant. If $N > K$ the right side of Eq. (3.11) is negative, which means that the population decreases to K .

Given the initial population $N(t = 0) = N_0$, the solution to Eq. (3.11) is:

$$N(t) = \frac{K}{1 - \left(1 - \frac{K}{N_0}\right)e^{-r_c t}} \quad (3.12)$$

A population whose dynamics is described by Eq. (3.11) and function (3.12) is said to follow the *second law of population dynamics* or *Verhulst law*. The population is called *logistic*.

A graph of the function (3.12) for three initial values is given in Fig. 3.1.

Carrying capacity of the environment is $K = 200$. For all three populations: $r_c = 0.1$.

The logistic population is often taken when constructing models of populations that interact with each other and thus forming multipopulation models.

Let us consider harvesting the logistic population which is proportional to N so that the dynamics is given by (Schaefer, 1954):

$$dN/dt = rN(1 - N/K) - eN \quad (3.13)$$

where e is a harvesting effort (proportional to the number of fishing days and number of fishing tools). The effort which leads to the maximum sustainable yield (MSY) is given by

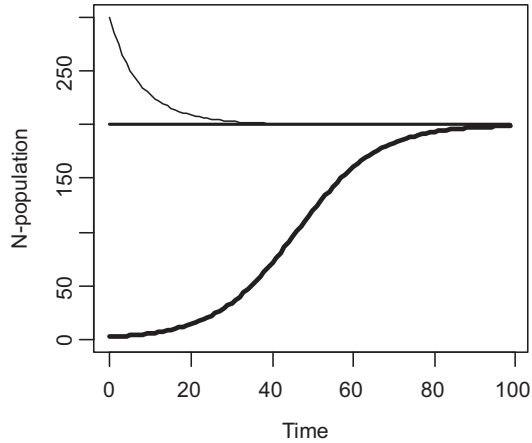


FIGURE 3.1 Dynamics of three logistic populations. $N_1 = 300$, $N_2 = 200$, $N_3 = 2$.

$e_{opt} = r/2$ and the corresponding stationary value of N is $N^* = K/2$. The maximum sustainable yield is given by:

$$MSY = rK/4. \quad (3.14)$$

The resulting value $N^* = K/2$ is stable and the strategy is termed a stable harvesting strategy. This means that as long as e is set approximately equal to e_{opt} no monitoring is needed.

On the other side, if one uses a harvesting quota, i.e., a constant value in Eq. (3.13) instead of eN , the MSY is also given by Eq. (3.14) but now $N^* = K/2$ is unstable in the sense that if the population drops below $K/2$ and due to existing uncertainties in the environment this will certainly happen, the population tends to extinction. Hence, to use this strategy and save the population from extinction, first the adequate monitoring must be put into place.

In case we do have an appropriate monitoring in place, the dynamic control (bang–bang theory) states that the optimum harvesting procedure is:

- If $N > K/2$ harvest the population to $K/2$;
- If $N = K/2$ harvest $rK/4$;
- If $N < K/2$ do not harvest.

The above result is understandable because being at the $N = K/2$ gives the maximum yield. Hence, when N is above that point, it is most advantageous to harvest until $K/2$ is reached. On the other side, when $N < K/2$ the population should recover at the maximum rate, i.e., it should not be harvested at all.

3.4 A LOGISTIC POPULATION IN PERIODIC ENVIRONMENT

In the second law of population dynamics r_c and K are taken to be constant. On the other side, it is clear that food supply changes daily, seasonally, or from one year to the other.

Let us take the carrying capacity to be a periodic function of time. In the simplest case we may assume that:

$$K(t) = K_0 + K_1 \sin \omega t \quad (3.15)$$

where K_0 is the average value of the carrying capacity, K_1 is the amplitude of periodic variation, and ω is the circular frequency: $\omega = 2\pi/T$ where T is the period.

Upon inserting Eq. (3.15) into Eq. (3.11) and integrating, one gets a complicated expression which describes the dynamics of logistic population in the periodic environment. The dynamics has roughly two parts: a transient starting with N_0 that continues toward a periodic behavior.

Two limiting cases have been identified (May, 1976):

1. $r_c T \gg 1$. This case means that the population reacts quickly because r_c is large while the carrying capacity changes slowly because the period is large. The population has plenty of time to adapt to changing environment and hence it follows it closely. The asymptotic dynamics is given approximately with:

$$N(t) \approx K_0 + K_1 \sin \omega t \quad (3.16)$$

2. $r_c T \ll 1$. In this case the environment changes rapidly and the population is averaging changes in carrying capacity. The asymptotic dynamics is approximately constant:

$$N(t) = \sqrt{K_0^2 - K_1^2} \quad (3.17)$$

It is interesting that in case (1) the average value of the population is K_0 while in case (2) it is smaller. In case (2) as K_1 increases to K_0 , the population $N(t)$ decreases to 0.

Fig. 3.2 shows dynamics of a population in cases (1) and (2).

If one were to harvest a logistic population in the periodic environment given by expression (3.16) according to proportional harvesting strategy (Legović and Perić, 1984) so that the dynamics of the population is given by

$$dN/dt = rN[1 - N/K(t)] - eN$$

then the optimum harvesting effort which produces the maximum sustainable average yield (MSAY) is again $e_{opt} = r/2$. In case the population follows the periodic change in $K(t)$ then the MSAY is the same as in the peaceful environment, i.e., $MSAY = rK_0/4$. But if the population is unable to track changes in $K(t)$, then MSAY is smaller and is given by:

$$N(t) \approx r \left(\sqrt{K_0^2 - K_1^2} \right) / 4 \quad (3.18)$$

Since populations in nature are all in between the two considered extremes, we conclude that in the periodic environment, MSAY will be smaller than MSY in the peaceful environment.

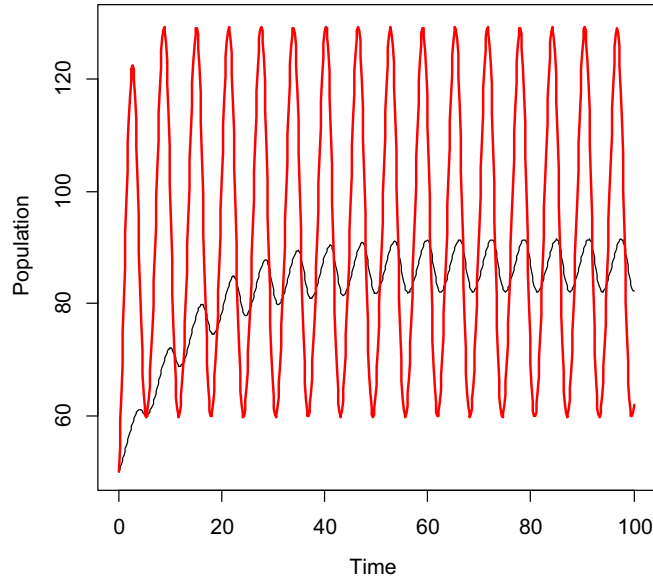


FIGURE 3.2 Dynamics of two logistic populations with periodic carrying capacity $K(t) = 100 + 50 \sin(t)$. $r_c = 1$, $r_c = 0.1$ (black line).

3.5 A LOGISTIC POPULATION IN A RANDOM ENVIRONMENT

Environment may be constant for a while, it may have a periodic component but it may also have a random component. This means that some environmental parameters may vary by chance, hence their extent and timing cannot be predicted. We are interested to find out the population dynamics in such an environment.

If we consider a logistic population immersed in a random environment, it is clear that both r and K may vary in an unpredictable fashion.

Consider a simpler case (Beddington and May, 1977):

$$dN/dt = r(t)N - \langle r \rangle N^2/K \quad (3.19)$$

where $r(t) = \langle r \rangle + g(t)$. $\langle r \rangle$ is the mean and $g(t)$ is the uncorrelated white noise with the mean equal to 0 and variance s^2 . Such a white noise is denoted by:

$$g(t) = [0, s^2]. \quad (3.20)$$

With the above white noise, the effect of random environment on the biotic potential of the population of organisms is defined (Fig. 3.3). The case is not general because a random variation is included only in the linear term of Eq. (3.19) and not in the nonlinear term. The solution to Eq. (3.19) will be a distribution which will have a transient part and later it will have a stationary phase. We are interested to find out the mean value that N will attain after a long time.

The mean value is:

$$\langle N \rangle = K(r - s^2/2)/r \quad (3.21)$$

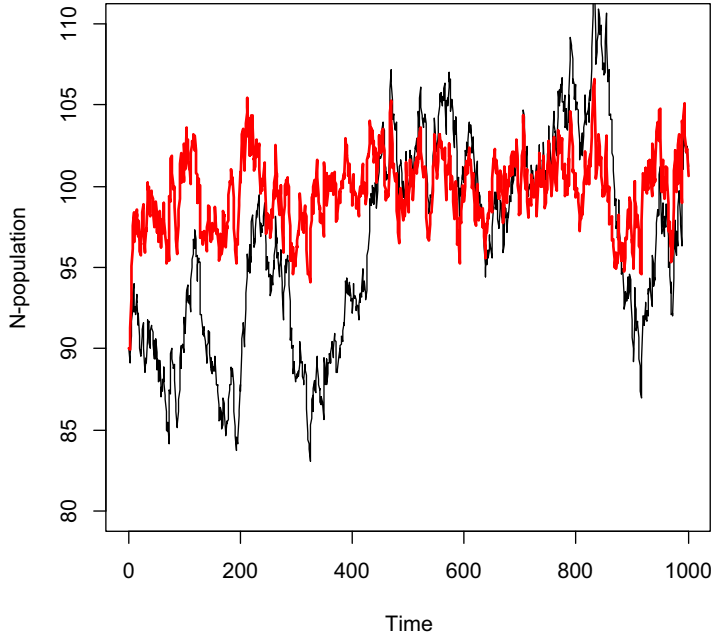


FIGURE 3.3 Dynamics of two simulations are shown: $\langle r \rangle = 0.01$ (black), 0.1 (red (gray in print versions)) with $g(t) = [0,0.01]$, $K = 100$.

We see that the mean value of N is not K but smaller by a factor of $Ks^2/2r$ so that in case the variance $s^2 = 2r$, the mean value is zero. Of course, the population will reach extinction for values of s^2 which are smaller than $2r$.

In case we were to harvest the population with a proportional harvesting rate eN , after a long time (asymptotically) the population mean value will reach:

$$\langle N \rangle = K(r - e - s^2/2)/r \quad (3.22)$$

The optimum harvesting effort which will produce the maximum sustainable average yield (MSAY) is:

$$e_{opt} = r/2 - s^2/4 \quad (3.23)$$

while the corresponding MSAY is:

$$\text{MSAY} = (K/4r)(r - s^2/2)^2. \quad (3.24)$$

The mean value of N during the optimum harvesting will reach:

$$\langle N_{opt} \rangle = (r - s^2/2)K/2r \quad (3.25)$$

We see that e_{opt} , MSAY, and N_{opt} will be smaller in the random environment than in peaceful environment.

We see that in all simulations regardless of whether the population reacts faster (with larger r) or slower (with smaller r), the average value $\langle N \rangle$ is smaller than K .

The message is that the expected average value of N will be smaller in a random environment than in the peaceful environment and that a decrease will grow with the variance of environmental fluctuation.

3.6 PREY–PREDATOR MODELS

The interaction most often found in ecosystems is the one in which predator feeds on prey. The first model of this type was formulated by Lotka (1925). Volterra (1926) independently published the same model in connection to the question by D’Ancona of why the number of predatory fishes rose during the First World War. The model is:

$$dN/dt = rN - bNP \quad (3.26)$$

$$dP/dt = cNP - mP \quad (3.27)$$

In the absence of predator, prey population is assumed to follow Malthus law. Predator population is assumed to feed on prey proportionally to prey population N and predator population P . This interaction is called bilinear collision in an analogy to a collision among two kind of particles.

Given the initial values $N(t = 0) = N_0$ and $P(t = 0) = P_0$ the solution is a pair of periodic functions (Fig. 3.4). A characteristic of these periodic functions is that the peak of prey

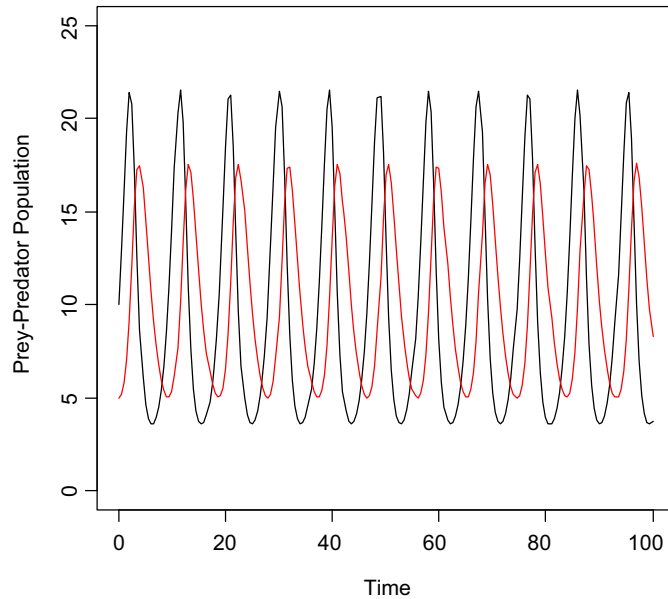


FIGURE 3.4 Prey (black)–predator (red (gray in print versions)) dynamics in the Lotka–Volterra model. $r = 1$, $b = 0.1$, $c = 0.05$, $m = 0.5$.

precedes the peak of predator in such a way that when the prey population peaks, the predator population grows with the maximum rate, and when the predator population is at the maximum, the prey population decreases maximally.

If one uses a proportional fishing eN of prey and eP of predator, where e is a common harvesting effort, one easily shows that the nonextinction equilibrium value (i.e., $N^* \neq 0$, $P^* \neq 0$ when $dN/dt = 0$ and $dP/dt = 0$) is:

$$N^* = (m + e)/c; \quad P^* = (r - e)/b$$

It turns out that N^* is the same as the average value $\langle N \rangle$ of the corresponding periodic function and so is $P^* = \langle P \rangle$.

From the above expressions we see that: if e decreases, N^* decreases and P^* increases.

The above statement constitutes the Volterra principle and represents the answer to the D’Ancona question: Predatory fishes increased and prey fishes decreased because the fishing effort in the Adriatic Sea decreased during the First World War, i.e., most of the fisherman were drafted and sent to battlefields.

Although the above prey–predator model was successful in explaining the D’Ancona question, it is used today mostly as a didactical tool because in the absence of predators we would expect that the prey population is governed by the second law of population growth. When the first term in the right side of Eq. (3.26) is replaced with the right side of Eq. (3.11) we get:

$$dN/dt = rN(1 - N/K) - bNP \quad (3.28)$$

$$dP/dt = cNP - mP \quad (3.29)$$

The dynamics of the model is shown in Fig. 3.5. The dynamics of both prey and predator tends to an equilibrium point in a form of damped oscillations.

It is easy to show that for this model too the Volterra principle is valid.

The above model can be made more realistic by allowing the predator to show saturation in the presence of plenty of prey. One way of taking saturation into account leads to the Rosenzweig and MacArthur (1963) model:

$$dN/dt = rN(1 - N/K) - V_{max}NP/(h + N) \quad (3.30)$$

$$dP/dt = cV_{max}NP/(h + N) - mP \quad (3.31)$$

In this model $V_{max}N/(h + N)$ is the Michaelis and Menten (1913) term, familiar in enzyme kinetics (Wiki, 2016). The term is nearly proportional to N when $h \ll N$ and then the prey–predator interaction does not differ significantly from bNP . But when $N \gg h$ then the term is nearly constant and then the prey–predator interaction is proportional to P .

The model has three equilibrium states:

(0,0)—when both prey and predator disappear. This equilibrium is always unstable.

(K,0)—when predator becomes extinct. This equilibrium will be stable if the predator is too inefficient to catch prey or if its mortality is too high, i.e., if $cV_{max}K/(h + K) < m$.

($N^* = mh/(cV_{max} - m)$, $P^* = (r/V_{max})(h + N^*)(1 - N^*/K)$)—when both prey and predator coexist. For this equilibrium to be stable the following condition must hold:

$m/(cV_{max} - m) \leq K/h \leq (cV_{max} + m)/(cV_{max} - m)$ (Gurney and Nisbet, 1998).

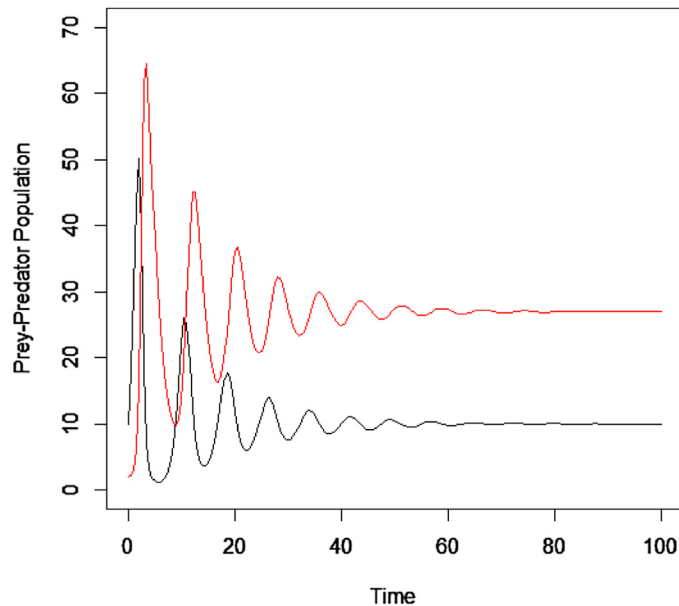


FIGURE 3.5 Prey (black)–predator (red (gray in print versions)) dynamics with $r = 1.5$, $K = 100$, $b = c = 0.05$, $m = 0.5$, and $N_0 = 10$, $P_0 = 2$.

If K is too small, the predator cannot maintain itself and it goes to extinction, while if K is too high, the predator cannot control the prey sufficiently quickly and the solution tends to a periodic behavior of both prey and predator. In between these two extremes, the equilibrium is stable.

The fact that when K increases the equilibrium is destabilized is termed the paradox of enrichment. When we are dealing with aquatic systems, this phenomenon can also be termed the paradox of eutrophication.

Fig. 3.6 shows a dynamics when the nonextinction equilibrium is stable. The behavior is qualitatively the same as the damped oscillations in Fig. 3.5, except that Fig. 3.6 shows the plot in (N, P) space.

Fig. 3.7 shows a dynamics when the equilibrium is unstable. The prey and predator populations tend to a periodic behavior when the paradox of enrichment occurs.

Proportional harvesting of predator only or prey and predator with a common harvesting effort may stabilize an otherwise unstable equilibrium point.

This means that with harvesting one may control the paradox of enrichment and it is possible to prevent it from occurring. However, too intensive harvesting of prey and predator will result in the extinction of predator.

We conclude with the following laws regarding a prey–predator community:

1. If predator is inefficient in catching the prey, it will tend to extinction and the prey will tend to its carrying capacity.
2. If the prey does not have too high carrying capacity and the predator is efficient in catching the prey, a stable equilibrium will occur in which both prey and predator will coexist.

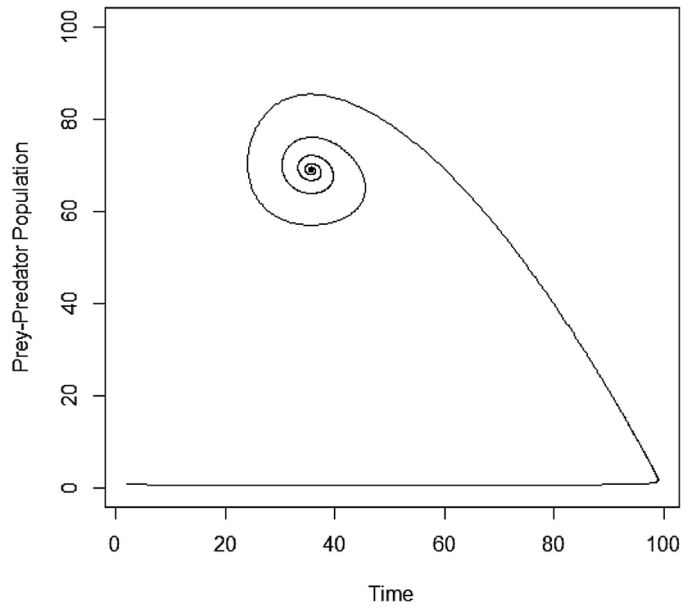


FIGURE 3.6 Dynamics of Rozenzweig-McArthur model for $r = 1.5$, $K = 100$, $V_{max} = 1.2$, $h = 50$, $c = 1$, $m = 0.5$.

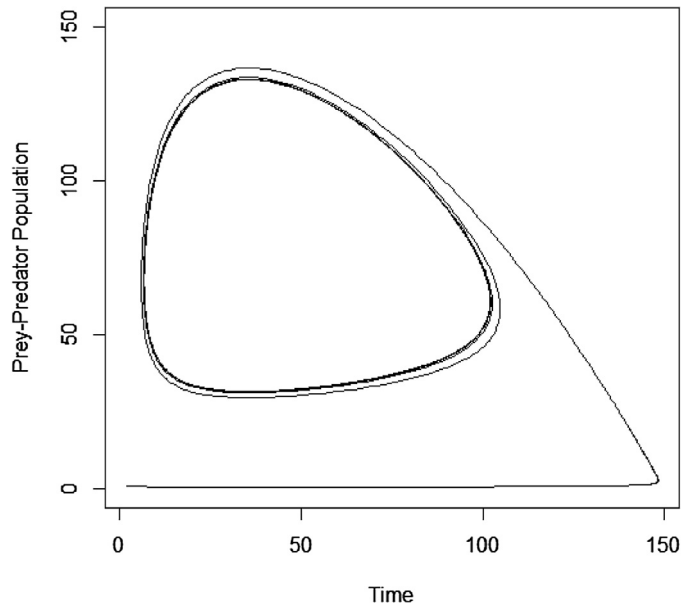


FIGURE 3.7 Dynamics of Rozenzweig-McArthur model for $r = 1.5$, $K = 150$, $V_{max} = 1.2$, $h = 50$, $c = 1$, $m = 0.5$.

3. If prey has a high carrying capacity and the predator is sufficiently efficient to persist, a periodic behavior of both prey and predator will occur and we have the paradox of enrichment.
4. If one applies harvesting of predators only, its population will decrease or it may go to extinction depending on the intensity of harvesting, while the prey population will increase to a stable equilibrium point. The paradox of enrichment will not occur.
5. If both prey and predators are harvested with the same harvesting effort, an otherwise unstable prey–predator system may be stabilized and the paradox of enrichment will not occur. If harvesting is too high, the predator will tend to extinction.

3.7 MODELS OF COMPETITION

In nature, one often observes a competition between populations for nesting space or the source of food (Begon et al., 2006). This competition is called interspecific as opposed to intraspecific which gave the quadratic term in the right hand side of the logistic equation (i.e., rN^2/K).

To consider a simple competition model, assume first the existence of two logistic populations in a finite environment. Each population has its own carrying capacity and biotic potential. Assume further that each population affects the dynamics of the other by drawing on its resources, i.e., both populations are amensals to each other. This can be modeled in such a way that in the nonlinear term of the logistic equation for the first population instead of N_1/K one writes $(N_1 + aN_2)/K$ where a stands for the intensity of amensalism that population N_2 exerts on N_1 . In the similar way one can modify the equation for the second population.

The resulting model is the Lotka–Volterra competition model:

$$dN_1/dt = r_1N_1(1 - (N_1 + aN_2)/K_1) \quad (3.32)$$

$$dN_2/dt = r_2N_2(1 - (N_2 + bN_1)/K_2) \quad (3.33)$$

Constants a and b determine the intensity of the corresponding amensalisms.

If *ecological niches* have zero intersection, i.e., if the two populations do not feed on the same source or do not occupy the same space, they do not compete, and then $a = b = 0$. In this case, the above model remains a model of two independent logistic populations N_1 and N_2 . If ecological niches intersect at least partially then $a > 0$ and $b > 0$. In case that population N_1 releases toxic material that kills members, or disables development, of the second population, the coefficient b may be large.

There exist four equilibrium solutions. First is the $(N_1^*, N_2^*) = (0,0)$ —the total extinction when both populations disappear. Then we have two equilibrium solutions when one of the two populations goes to extinction: $(N_1^*, N_2^*) = (K_1, 0)$ and $(N_1^*, N_2^*) = (0, K_2)$. Finally, one equilibrium solution exists in which both populations are present. Assume $N_1 > 0$ and $N_2 > 0$. From $dN_1/dt = 0$ and $dN_2/dt = 0$ Eqs. (3.32) and (3.33) give:

$$K_1 - N_1^* - aN_2^* = 0 \quad (3.34)$$

$$K_2 - N_2^* - bN_1^* = 0 \quad (3.35)$$

By solving these equations for N_1^* and N_2^* we get:

$$N_1^* = (K_1 - aK_2)/(1 - ab) \quad (3.36)$$

$$N_2^* = (K_2 - bK_1)/(1 - ab). \quad (3.37)$$

where $ab < 1$, $K_1 > aK_2$ and $K_2 > bK_1$.

It turns out that the nonextinction equilibrium is a stable node as long as $N_1^* > 0$ and $N_2^* > 0$. Since $a > 0$ and $b > 0$, $N_1^* < K_1$ and $N_2^* < K_2$.

When a and b are very small we can safely neglect ab because it is of a second-order smallness and we have approximately

$$N_1^* \approx K_1 - aK_2 \quad (3.38)$$

$$N_2^* \approx K_2 - bK_1 \quad (3.39)$$

Suppose $a = b = 1$ and K_1 is different from K_2 .

Eqs. (3.34) and (3.35) become:

$$K_1 - N_1^* - N_2^* = 0 \quad (3.40)$$

$$K_2 - N_2^* - N_1^* = 0 \quad (3.41)$$

This system cannot be satisfied for any values $N_1^* > 0$ and $N_2^* > 0$. Therefore the nonextinction equilibrium does not exist and we have competitive exclusion of one population.

Let us summarize the fate of the two competing populations:

$(1/b) < K_1/K_2 > a$	The equilibrium is unstable and the first population wins, so we have competitive exclusion of the second population;
$(1/b) < K_1/K_2 < a$	The equilibrium is unstable, whether the first or second population wins will be determined by initial population values but here too we have competitive exclusion of one population;
$(1/b) > K_1/K_2 < a$	The equilibrium is unstable and the second population wins so here we have competitive exclusion of the second population;
$(1/b) > K_1/K_2 > a$	The equilibrium is stable and we have coexistence of populations.

We see that in three out of four cases, the competition will cause exclusion of one population.

Let us look at another simple model of species (N_1 and N_2) competition for food (F).

$$dF/dt = I - aFN_1 - bFN_2 \quad (3.42)$$

$$dN_1/dt = aFN_1 - m_1N_1 \quad (3.43)$$

$$dN_2/dt = bFN_2 - m_2N_2 \quad (3.44)$$

where I is the inflow of food into the environment occupied by N_1 and N_2 populations; $a(b)$ is the specific efficiency of $N_1(N_2)$ to take the existing food F and $m_1(m_2)$ is the specific mortality rate of $N_1(N_2)$.

Possibly three equilibrium solutions exist. The first is $(I/m_1, m_1/a, 0)$ and represents the extinction of N_2 . The second is $(I/m_2, 0, m_2/b)$ and represents the extinction of N_1 .

Let us assume that both $N_1^* \neq 0$ and $N_2^* \neq 0$, then from the second equation we have:

$$F^* = m_1/a \quad (3.45)$$

and from the third:

$$F^* = m_2/b \quad (3.46)$$

This is possible only if the two populations are identical in the efficiency of taking food and in mortality. Since in general $m_1 \neq m_2$ and $a \neq b$, the equilibrium will not exist.

In case $m_1/a > m_2/b$, N_1 will reach equilibrium but F will continue to decrease toward m_2/b and hence dN_1/dt will become negative and N_1 will tend to extinction.

The dynamics of the N_1 and N_2 is given in Fig. 3.8.

This model shows that the exclusion of one population due to competition for food will happen always, hence the competitive exclusion principle.

In conclusion, we have the following law: competition among participating populations in a community raises a chance of population extinction. Whether the extinction of less efficient populations will happen faster or slower or even not at all, will depend on spatial characteristics of the environment especially shelter and on fluctuating (seasonal) sources of food, both of which we have not considered here. However, for conservation purposes, where one analyses the chance of survival of a specific population, taking into account natural characteristics of the environment is crucial.

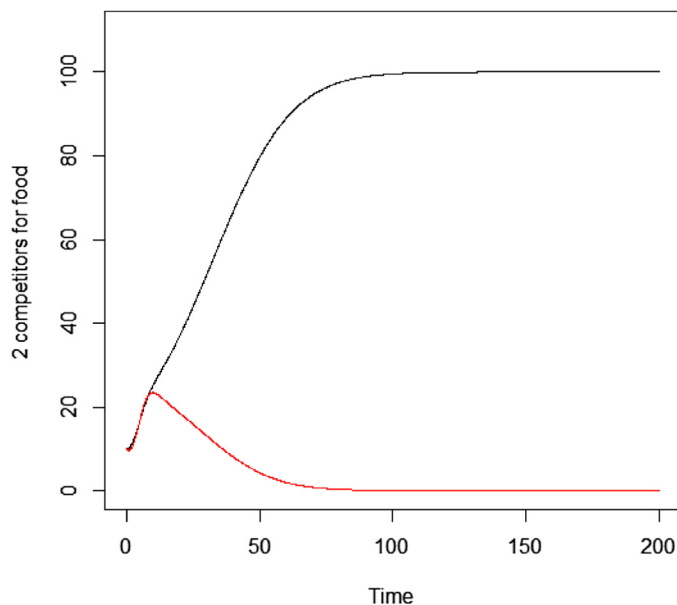


FIGURE 3.8 Two populations competing for food. $I = 10, a = 0.01, b = 0.02, m_1 = 0.1, m_2 = 0.3$. Since $m_1/a < m_2/b$ the first population wins.

3.8 MODELS OF COOPERATION

Recently, cooperation among populations has been found to be much more frequent than thought historically (Bronstein, 2016).

In the simplest case the presence of a commensal population increases the carrying capacity of the other population. The same may be assumed of the other population. Hence the mutualism is a consequence of two commensal interactions: first population helping the second and the second helping the first.

A model of two logistic populations with a mutualism may be written as:

$$dN_1/dt = r_1N_1(1 - N_1/(K_1 + aN_2)) \quad (3.47)$$

$$dN_2/dt = r_2N_2(1 - N_2/(K_2 + bN_1)) \quad (3.48)$$

There exist four equilibrium solutions: $(0,0)$, $(K_1,0)$, $(0, K_2)$, and the nonextinction point $(N_1^* \neq 0, N_2^* \neq 0)$:

$$N_1^* = (K_1 + aK_2)/(1 - ab) \quad (3.49)$$

$$N_2^* = (K_2 + bK_1)/(1 - ab) \quad (3.50)$$

$$\text{where } ab < 1. \quad (3.51)$$

We see that $N_1^* > K_1$ and $N_2^* > K_2$.

Given that Eq. (3.51) is satisfied, the nonextinction equilibrium is a stable node, i.e., the populations tend to the equilibrium without oscillations.

If $r_1 = r_2 = r$, the characteristic return time (T_c) to the nonextinction equilibrium is:

$$T_c = 1/r[1 - \sqrt{ab}] \quad (3.52)$$

As ab increases, the return time to the equilibrium will be longer.

We may now formulate the following law:

If two species interact forming a mutualistic community, sooner or later their populations will exceed carrying capacity of the environment.

In case $ab \geq 1$, the above law will also hold simply because some other variable in the finite environment not included in the model will eventually stop the growth of both populations.

Dynamics of two mutualistic populations is shown in Fig. 3.9.

The above model can easily be generalized to a mutualistic community with N_i , $i > 2$ populations. Then the above law will hold for all the participating populations.

In case we harvest all the populations with the same harvesting effort, resulting in the proportional harvesting, we will discover that maximizing the yield (Y):

$$Y = e(\sum_i N_i) \quad (3.53)$$

will lead to a maximum sustainable yield (MSY) and none of the participating populations will disappear (Legović and Geček, 2012). This is a consequence of obligatory cooperation. In case some or all populations exist without interaction with the rest of the community some of them may tend to extinction as a consequence of attempting to reach MSY (Legović and Geček, 2010).

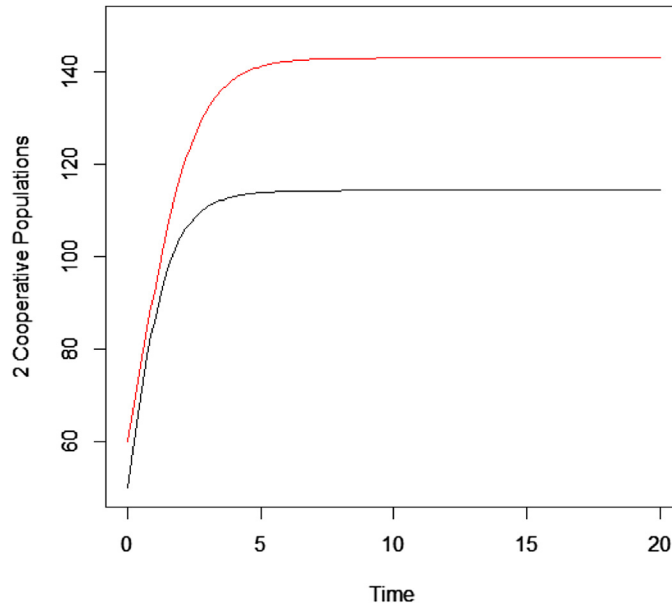


FIGURE 3.9 Dynamics of two populations with mutualism. $R_1 = 1.5$, $K_1 = 100$, $r_2 = 1$, $K_2 = 100$, $a = 0.1$, $b = 0.2$.

In conclusion, we may state the law: mutualism enhances the persistence of participating populations although the return to the equilibrium may take longer.

3.9 FOOD CHAINS

Food webs that we find in ecosystems are composed of many populations and even a greater number of interactions. Since they are essentially nonlinear, it is difficult and time-consuming to construct adequate models and even more difficult to analyze and consequently to understand their dynamics. However, food chains are a class of ecosystems which are relatively easy to construct and analyze.

A food chain can be represented by the following graph of flow of matter: (Fig. 3.10)

Where S is a food source for the first population, N_1 , also called the first trophic level. The first trophic level, N_1 , is a food source for the second trophic level, N_2 , and so on until the last trophic level N_n . N_n is also called the top trophic level or the top predator. Such a food chain is



FIGURE 3.10 Food chain with n trophic levels.

said to be composed of n trophic levels. Since the graph in Fig. 3.10 represents a flow of biomass, starting from N_1 , one has also to include the export of biomass due to mortality, so that each of the trophic levels has a direct outflow from the system.

To avoid the spatial effects which would further complicate the issue, we shall place the food chain into a well mixed biological reactor that will represent a lake, a river, or a coastal sea.

Let us consider the food chain corresponding to the graph in Fig. 3.10. Assume that all that is consumed by one trophic level is turned into biomass of the next trophic level and that we measure biomass of all trophic levels in the units of S . For example if S represents phosphorus in water, than we would measure the amount of phosphorus in each trophic level in a unit of volume. In Eqs. (3.28) and (3.29) this would mean that $b = c$.

Equations of the food chain of length n are:

$$dS/dt = DI - b_1SN_1 - DS \quad (3.54)$$

$$dN_1/dt = b_1SN_1 - b_2N_1N_2 - DN_1 \quad (3.55)$$

$$dN_2/dt = b_2N_1N_2 - b_3N_2N_3 - DN_2 \quad (3.56)$$

...

$$dN_{n-1}/dt = b_{n-1}N_{n-1}N_n - b_nN_{n-1}N_n - DN_{n-1} \quad (3.57)$$

$$dN_n/dt = b_nN_{n-1}N_n - DN_n \quad (3.58)$$

There are n extinction equilibrium points:

$$1. (S^*, N_1^*, \dots, N_n^*) = (I, 0, \dots, 0) \quad (3.59)$$

$$2. (S^*, N_1^*, \dots, N_n^*) = (D/b_1, I - D/b_1, 0, \dots, 0) \quad (3.60)$$

$$3. (S^*, N_1^*, \dots, N_n^*) = (b_2I/(b_1 + b_2), D/b_2, b_1I/(b_1 + b_2) - D/b_2, 0, \dots, 0) \quad (3.61)$$

...

To find the last, $(n + 1)$ -th, equilibrium point (the non-extinction equilibrium) we note that from the last, $(n + 1)$ -th, equation describing the dynamics of the n -th trophic level, one gets:

$$N_{n-1}^* = D/b_n = a_{n-1}D \quad (3.62)$$

Inserting into the $(n - 1)$ -th equation:

$$N_{n-3}^* = D(b_n + b_{n-1})/(b_nb_{n-2}) = a_{n-3}D, \text{ etc.} \quad (3.63)$$

where $a_{n-1}, a_{n-3}, a_{n-5}, \dots$ are functions of b_i constants only.

The equilibrium values $N_{n-1}^*, N_{n-3}^*, N_{n-5}^*, \dots$ are linear functions of the dilution rate, D but not of the inflow concentration I . Starting with N_{n-1}^* , whether the series will end with N_1^* or with N_2^* will depend on whether the number of trophic levels is even or odd.

Assume the food chain has an even number of trophic levels.

Then $n = 2k$ where k is a natural number.

The above series will terminate with $N_1^* = a_1D$.

Now substitute N_1^* into the first equation and get:

$$S^* = I/(1 + a_1b_1) = \beta_1I \quad (3.64)$$

Now substitute S^* into the second equilibrium equation and get:

$$N_2^* = b_2 I / (b_2 + a_{n-2} b_1 b_2) - D / b_2 = \beta_2 I - \gamma_2 D \quad (3.65)$$

Continue in the same manner through all the odd numbers successively until the n -th equation. The obtained equilibrium values of the even trophic levels are:

$$N_{2i}^* = \beta_{2i} I - \gamma_{2i} D \quad \text{where } i = 1, \dots, k. \quad (3.66)$$

Now assume the food chain has an odd number of trophic levels.

Then $n = 2k + 1$. The above series will terminate with $N_2^* = a_2 D$.

Substituting this value into the second equation, one obtains:

$$S^* = (1/b_1 + b_2 a_2 / b_1) D. \quad (3.67)$$

Now substitute S^* into the first equation and get N_1^* :

$$N_1^* = I / (1 + b_2 a_2) - D / b_1 = \beta_1 I - \gamma_1 D. \quad (3.68)$$

Substituting into the third, fifth, ... until the last equation successively will lead to the equilibrium value of odd trophic levels. These equilibrium values will be linear functions of I and D only:

$$N_{2i+1}^* = b_{2i+1} I - \gamma_{2i+1} D, \quad i = 1, \dots, k. \quad (3.69)$$

From the above, we have following conclusions:

1. In a food chain with a binary collision among prey and their predator population and an even number of trophic levels, the equilibrium concentration of the first trophic level and all other odd trophic levels is independent of an increase in the concentration of the nutrient in the inflow. They are proportional to the inflow of water.
2. In a food chain with an odd number of trophic levels, the equilibrium concentration of the first trophic level and all other odd trophic levels increases with increasing inflow concentration of the limiting nutrient and decreases with the inflow rate of water.
3. From (1) and (2) it follows that the equilibrium concentration of the top trophic level does not depend on whether the chain is even or odd. The concentration will always increase with increasing nutrient concentration in the inflow and decrease with increasing water flow.
4. Increase of nutrient concentration in the inflow will result in more nutrient being trapped in the food chain which is easily seen from the summation:

$$I = S^* + N_1^* + \dots + N_n^* \quad (3.70)$$

The reader is welcome to attempt the analysis of food chains in which instead of bilinear collision among prey and predator populations, Michaelis–Menten interaction is used.

3.10 CYCLING OF MATTER

Apart from food chains, in food webs of ecosystems one finds that nutrients cycle among various trophic levels.

3.10.1 A Model of Nutrient, Phytoplankton, and Dead Matter

Perhaps one of the simplest ecosystems with a nutrient cycle is the one which contains the source of nutrients, I , nutrient concentration in a lake, S , phytoplankton, N , death of phytoplankton mN , dead matter, M , and decomposition of dead matter, rM . By decomposition, nutrients will be released and will again be available for uptake by phytoplankton. The dilution rate is D .

A graph denoting transport of nutrient in such an ecosystem is shown in Fig. 3.11.

Equations of the ecosystem immersed in a continuous culture reactor are:

$$dS/dt = D(I - S) - aSN + rM \quad (3.71)$$

$$dN/dt = aSN - mN - DN \quad (3.72)$$

$$dM/dt = mN - rM - DM \quad (3.73)$$

where a , D , m , and r are positive.

In the above formulation, it is assumed that phytoplankton, N , takes up the nutrient, S , according to the bilinear collision. As we mentioned earlier, this interaction allows us to state conclusions about a change in parameters if they are not far from original values which lead the system to steady state.

Furthermore, the death of phytoplankton and the remineralization process follow a first-order kinetics.

The system (3.71–3.73) has only two equilibrium points.

The extinction of N and M : $(S^*, N^*, M^*) = (I, 0, 0)$ and the nonextinction steady state.

The nonextinction steady state: $(S^* > 0, N^* > 0, M^* > 0)$ is obtained from Eqs 3.71–3.73 as follows. From (3) in steady state:

$$M^* = mN^*/(r + D) \quad (3.74)$$

From Eq. (3.72) in steady state:

$$S^* = (m + D)/a \quad (3.75)$$

From Eq. (3.71) in steady state, upon substitution of Eq. (3.74) and Eq. (3.75) and by rearranging:

$$N^* = D[I - (m + D)/a]/[m + D - rm/(r + D)] \quad (3.76)$$

In order that S^* , N^* , and M^* be positive, the following condition must be met:

$$I > (m + D)/a \quad (3.77)$$

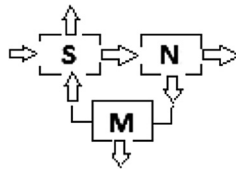


FIGURE 3.11 A graph of nutrient cycling among three components: concentration in water, concentration in the first trophic level, and dead matter.

If incoming nutrient concentration is too small, death rate of phytoplankton, m , or dilution rate, D , are too high, phytoplankton population would be washed out of the reactor. Since organic matter would have no source, it would be washed out too and eventually the extinction state will be reached.

We can now predict what will happen asymptotically to an ecosystem for which the models (3.71) and (3.72) is representative in case characteristics of the environment are changed. For example:

1. An increase in nutrient concentration in the inflow, I , will cause a linear increase in N^* and M^* , but S^* will not be changed.
2. An increase in dilution rate, D , means that the ecosystem is progressing from a relatively stagnant lake to a river. Such a change will increase S^* while N^* and M^* will decrease.
3. An increase in remineralization only, r , will not change S^* while N^* and M^* will decrease.
4. An increase of specific death rate of phytoplankton only, m , will cause S^* and M^* to increase and N^* to decrease.
5. An increase in the efficiency of phytoplankton uptake only, a , will cause S^* to decrease while N^* and M^* will increase.

In case we change the bilinear collision interaction with the more realistic Michaelis–Menten form, the model changes into:

$$dS/dt = D(I - S) - aSN/(h + S) + rM \quad (3.78)$$

$$dN/dt = aSN/(h + S) - mN - DN \quad (3.79)$$

$$dM/dt = mN - rM - DM \quad (3.80)$$

In steady state:

$$S^* = (m + D)h/[a - (m + D)] \quad (3.81)$$

$$N^* = (r + D)M^*/m \quad (3.82)$$

where $a > m + D$ and $I > (m + D)h/[a - (m + D)]$.

In steady state, substitution into Eq. 3.72, gives M^* :

$$M^* = mD[I - S^*]/[(m + D)(r + D) - rm] \quad (3.83)$$

where $(m + D)(r + D) > rm$.

The qualitative conclusion with regard to an increase in I is the same as in the previous model: S^* will not change while M^* and N^* will increase linearly.

A comparison to the case with no cycling, i.e., when m and r are zero, shows that cycling of nutrient increases S^* and decreases N^* .

3.10.2 Food Chain With Two Trophic Levels and Cycling of Nutrients

Consider a cycling of nutrient with an ecosystem composed of nutrient, prey, and predator.(Fig. 3.12)

$$dS/dt = D(I - S) - aSN + rM \quad (3.84)$$

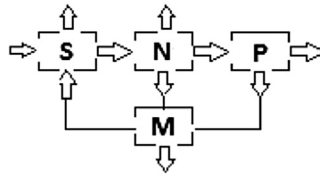


FIGURE 3.12 A graph of nutrient cycling among four components: nutrient in water, first trophic level, second trophic level, and dead matter.

$$dN/dt = aSN - bNP - m_1N - DN \quad (3.85)$$

$$dP/dt = bNP - m_2P - DP \quad (3.86)$$

$$dM/dt = m_1N + m_2P - rM - DM \quad (3.87)$$

In steady state:

$$I = S^* + N^* + P^* + M^* \quad (3.88)$$

$$N^* = (m_2 + D)/b \quad (3.89)$$

$$S^* = (DI + rM^*)/[D + a(m_2 + D)/b] \quad (3.90)$$

$$aS^* - bP^* = m + D \quad (3.91)$$

$$mN^* + m_2P^* = (r + D)M^* \quad (3.92)$$

Concerning an increase in I we have the following conclusions: S^* and M^* will increase, N^* will not change, and P^* will increase because it is the top trophic level. In addition, the total quantity of nutrient captured in the ecosystem will increase.

Using the above model, one can analyze how food chains, with even and odd number of trophic levels and with cycling of nutrients, differ from the respective food chains where cycling is negligible.

3.11 CONCLUSIONS

In this chapter we have gradually progressed from the first law of isolated population dynamics in an infinite environment to the second law, which we expect to hold in a finite peaceful environment. We then examined the dynamics of an isolated population in periodic and random environment including its harvesting. From interactions of two populations we analyzed prey–predator, competition, and mutualism. As examples of simple food webs we briefly considered food chain and food chain with cycling of a nutrient. The treatment serves to see how more complicated systems of populations in nature, being nonlinear, will inevitably lead to unexpected results that could have not been guessed by intuition only. Furthermore, more complicated models inevitably lead to greater variety of effects that are not seen in simpler models. One could have also noticed that for all the populations to persist in progressively more complicated ecosystems, a greater number of conditions must be satisfied. This is particularly easy to see when analyzing food chains. Consequently, more

complicated ecosystems are likely to be more vulnerable to at least one population loss due to either natural or man-made perturbations.

3.12 A BRIEF HISTORY OF POPULATION MODELING

We do not have reliable historical data on when the process of mathematical modeling of population dynamics started. The first recorded model of population dynamics that we know of was proposed and solved by Leonardo di Pisa (better known as Fibonacci (1175–1250)) in 1202 in his famous book *Liber abaci*. The problem he was concerned about is:

“If one puts a pair of rabbits in a place surrounded on all sides by a wall. How many pairs of rabbits can be produced from that pair in a year if it is assumed that starting with the second month, each pair becomes productive and every subsequent month, each productive pair brings to life one new pair?” The model produced a series of numbers for the pairs of rabbits: 0 (before rabbits were put into the cage), 1 (an instant after the first pair was introduced), 1 (a month later), 2 (two months later), 3, 5, 8, 13, 21, ..., 233 (after twelfth month). The series extended much further in t is known today as the Fibonacci series. Johannes Kepler (1571–1630) showed that the successive numbers in the series satisfy the following recursive (difference or iterative) equation:

$$N_{t+2} = N_t + N_{t+1} \quad \text{for } t = 0, 1, \dots$$

The model is a second-order difference equation and it requires two starting values $N_0 = 0$ and $N_1 = 1$ to be solved uniquely. This was done by Daniel Bernoulli who obtained (Bacaër, 2011):

$$N_t = (1/\sqrt{5})((1 + \sqrt{5})/2)^t - (1/\sqrt{5})((1 - \sqrt{5})/2)^t$$

The first law of population dynamics Eq. (3.6) was stated by Leonhard Euler in 1748 (Bacaër, 2011). The law has been unjustly named after Thomas R. Malthus who in 1798 wrote that the human population in England grows according to the geometrical law. In addition, he assumed that quantity of food grows linearly (i.e., along the straight line). Since geometric growth exceeds any linear growth given enough time, he predicted a great starvation and a catastrophe for human population in future. Subsequent data on human population and food production showed that Malthus was wrong about both assumptions: neither has human population grown geometrically until now nor the food production grown linearly. Hence his fear of a catastrophe for human population was unfounded. To get a feeling about the magnitude of his numerical error it suffices to consider present data versus Malthus prediction. According to his prediction, today’s human population would be about 256 billion while there would be enough food to feed 9 billion. In fact, human population is about 7.3 billion (as of July 2015) and the present food production is sufficient to feed 57 billion people.

Verhulst (1838) suggested a logistic population model. Given the data on human population during 1961 when human population has grown by 2% per year and assuming $r = 0.039$ one predicts that the carrying capacity for earth is 10 billion. By carefully examining UN data until 2010, Gonzalo et al. (2013) predicted that the human population on Earth will reach 10 billion by 2050 and will start to decrease.

First prey–predator model was suggested by Lotka (1925). Volterra (1926) independently published the same model and used it to determine the cause of predatory fish populations increase in the Adriatic Sea during the First World War. Volterra subsequently analyzed a number of properties of food web models. In fact, germination of many ideas on dynamics of populations of organisms using mathematical models took place between 1923 and 1940 (Scudo and Ziegler, 1978). That development gave rise to expanded interest after the Second World War and an explosion of activity following the advent of computers which enabled simulation and numerical analysis of complicated ecosystem models. The development has been fueled further by a growing need to understand dynamics of populations in ecosystems to protect them better and find ways to reduce human impact.

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