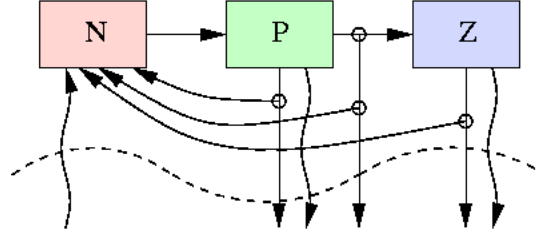


NPZ Models Edit

For a simplified example of a biological model, let us consider an NPZ system: nutrients ($N \equiv b_1$) are taken up by phytoplankton ($P \equiv b_2$), which are grazed upon by zooplankton ($Z \equiv b_3$). The rate at which the net biomass of phytoplankton is reduced depends upon the product of the concentrations of the phytoplankton and the zooplankton – essentially assuming that the grazing increases proportional to the number of encounters between predator and prey during a short time interval. A fraction a of the grazed material is assimilated, while the rest, along with any dead zooplankton, is recycled immediately back into dissolved nutrients.



NPZ model structure

We must define precisely what we mean by a variable such as P .

- the net biomass per unit volume of water in all the primary producers – the photosynthesizing organisms
- the density of some particular species, sets of species, or range of sizes
- chlorophyll fluorescence
- usual approach based on a “currency” – a property, such as the number of moles of nitrogen, which is conserved during interactions. When, for example, a zooplankter feeds on a phytoplankton cell, some of the prey’s nitrogen is incorporated into the zooplankter’s biomass and some may become detritus or be excreted. In theory, though, we can account for all of it. To relate such variables to measurements, we need either to measure the amount of nitrogen directly or use formulae which express the ratio of properties such as wet weight or carbon content to the number of moles of nitrogen. Such conversions can be difficult when the variable represents a changing assemblage of different species; however, as noted by Redfield (19xx), some ratios are relatively constant across a wide range of organisms.

Based on nitrogen as a currency, then, we can make the biological dynamics more specific, using a combination of linear and quadratic rules: the phytoplankton grow by taking up nutrient and are grazed by the zooplankton

$$\frac{\partial}{\partial t}P = \mu PN - gPZ - d_P P \quad (1)$$

The zooplankton assimilate a fraction of the grazed material and lose nitrogen by respiration and grazing by predators

$$\frac{\partial}{\partial t}Z = agPZ - d_Z Z \quad (2)$$

The nutrient is lost to phytoplankton and regenerated from the unassimilated grazed material and the decay of zooplankton

$$\frac{\partial}{\partial t}N = -\mu PN + (1 - a)gPZ + d_P P + d_Z Z \quad (3)$$

Some of the all-too-numerous problems with this model include:

- The term “phytoplankton” stands for a wide variety of different species. If the different varieties always appeared in the same ratio, one might begin to believe that a single growth rate μ for the assemblage as well as a simple grazing rule could indeed be used. But different phytoplankton species are dominant at different times and/or in different places; how much of this diversity must be included before we can understand the system better?
- Nutrients, too, come in many flavors. Dissolved nitrogen appears as both nitrate, nitrite, and ammonia, with different organisms having different abilities to use these variants. And phytoplankton do not live by nitrogen alone; over the past xx years, the work of Martin(19xx) and others has demonstrated that growth is often limited by the scarcity of iron rather than of nitrogen.
- Zooplankton not only come in many different species, they may also have a complicated life cycle, with changes in form, behavior, foraging ability, and size. Passing through these stages may take a year; some copepods, for example, have a dormant stage for over-wintering. Can we learn much by using a single variable Z and glossing over all the complexity, or do we need to include at least some of this kind of detail.
- Can we close the system with the zooplankton, representing their losses by predation and death as $d_Z Z$, or do we need to include higher trophic levels? For that matter, what about bacteria, protozoa, ...?

Many of these issues depend upon the question being asked; the choices made will depend on the degree to which one is trying to make a model for a small-scale ecosystem perhaps with interests in only a limited component (e.g., copepods in Massachusetts Bay) or a global scale model to look at overall distributions.

In addition, there are mathematical issues to consider:

- What are appropriate functional forms \mathcal{B}_i ? How do the characteristics of the dynamics change as we alter them?
- What are appropriate values for the coefficients such as g ? Can these be estimated from laboratory experiments or by fitting the model to data?
- As the model becomes more complex, we inevitably introduce more and more poorly known constants and functional forms. At what point are we putting in so much that the model becomes statistically meaningless?
- How do we verify a model? While we may be able to show that a model utterly fails, most comparisons with data (and the data, of course, is still extremely sparse) tend to be of the “this looks like that” variety. Even more rigorous statistical comparisons cannot validate a model, since more than one dynamical system may produce similar enough behavior (see xx).

The Quadratic NPZ Model

With these questions deferred, let us examine the behavior of the Quadratic NPZ model. The system has five parameters (μ , g , d_P , a , d_Z) as well as one which is less obvious, stemming from the closed nitrogen cycle. If we sum the three equations, we find

$$\frac{\partial}{\partial t}(N + P + Z) = 0$$

so that the initial value of $N_T = N(0) + P(0) + Z(0)$ is unchanged during the evolution. We can incorporate that information directly and reduce the number of equations to two:

$$\begin{aligned}\frac{\partial}{\partial t}P &= P[\mu(N_T - P - Z) - gZ - d_p] \\ \frac{\partial}{\partial t}Z &= Z[agP - d_Z]\end{aligned}\tag{Q - NPZ}$$

If μ decays exponentially with depth we find a **range of solutions** with the characteristics depending on depth. **Diffusion** smooths out the slowly decaying oscillations.

STEADY STATES: We begin the analysis of such a system by looking for the equilibrium or steady-state solutions. Setting the right-hand sides of (Q-NPZ) to zero gives three such states

- 1) $P = Z = 0$, $N = N_T$
- 2) $Z = 0$, $N = d_P/\mu$, $P = N_T - d_P/\mu$ for $N_T > d_P/\mu$
- 3) $P = d_Z/ag$, $Z = (\mu N_T - \mu d_Z/ag - d_P)/(\mu + g)$, $N = N_T - P_Z$ for $N_T > d_Z/ag + d_P/\mu$

The **figure** summarizes the behavior of this system of equations as one parameter ($depth \propto \ln(\mu)$) is varied: we have steady states with only N for small uptake rates, then states with both N and P , and finally states with non-trivial values for all three variables when the uptake rate becomes high enough. Time evolution pictures also show that the approach to steady state occurs via a decaying oscillation for small μ values.

STABILITY: Once we know the steady states, we must also consider their **stability**: what happens if we perturb the fields slightly away from the equilibrium values? Movement and mixing in the ocean provide such perturbations: if we consider transporting some water and organisms vertically in the situation shown in the figure, the values will no longer be consistent with the local equilibrium conditions. By studying the stability, we can gain insight into the ways the system will adjust under physical forcing. (We do, however, have to recognize that the physically-induced perturbations may not always be small; later, we shall look at the conditions under which this kind of approximation may or may not be valid).

The steady states are defined by

$$\mathcal{B}_i(\bar{b}_1(\mathbf{x}), \bar{b}_2(\mathbf{x}), \dots, \bar{b}_N(\mathbf{x})|\mathbf{x}) = 0$$

(under the assumption that the reaction terms have no explicit time-dependence (c.f. section xx). If we perturb each field

$$b_i = \bar{b}_i(\mathbf{x}) + b'_i(\mathbf{x}, t)$$

we have

$$\frac{\partial}{\partial t} b'_i = \mathcal{B}_i(\bar{b}_1 + b'_1, \bar{b}_2 + b'_2, \dots, \bar{b}_N + b'_N) - \mathcal{B}_i(\bar{b}_1, \bar{b}_2, \dots, \bar{b}_N)$$

(letting the \mathbf{x} dependence be implicit). If the perturbations are small, we can Taylor-expand the right hand side to find

$$\frac{\partial}{\partial t} b'_i \simeq b'_1 \frac{\partial}{\partial \bar{b}_1} \mathcal{B}_i(\bar{b}_1, \bar{b}_2, \dots, \bar{b}_N) + b'_2 \frac{\partial}{\partial \bar{b}_2} \mathcal{B}_i(\bar{b}_1, \bar{b}_2, \dots, \bar{b}_N) \dots + b'_N \frac{\partial}{\partial \bar{b}_N} \mathcal{B}_i(\bar{b}_1, \bar{b}_2, \dots, \bar{b}_N)$$

so that the perturbations satisfy the matrix equation

$$\frac{\partial}{\partial t} b'_i = \mathcal{B}_{ij} b'_j \quad , \quad \mathcal{B}_{ij} \equiv \left. \frac{\partial \mathcal{B}_i}{\partial b_j} \right|_{\mathbf{b}=\bar{\mathbf{b}}} \quad (4)$$

We can write

$$b'_i(t) = \exp[t\mathcal{B}_{ij}] b'_j(0)$$

where the matrix exponential can be defined in terms of the eigenvalues and eigenvectors of \mathcal{B}_{ij} :

$$\exp(t\mathcal{B}_{ij}) = v_{ik}^{-1} e^{\sigma_k t} v_{kj}$$

Here the k^{th} column of v_{ik} is the eigenvector corresponding to eigenvalue σ_k

$$\mathcal{B}_{ij} v_{jk} = v_{ik} \sigma_k$$

When the real part of every eigenvalue is negative, all perturbations will eventually decay and we call the equilibrium stable; if the real part of one or more is positive, that mode will grow to large amplitude (when the Taylor approximation breaks down) and we call the equilibrium unstable. Purely imaginary eigenvalues correspond to neutral modes which simply oscillate; the linearized equations are not entirely adequate. As we shall discuss later, the transient behavior even of a stable system can show considerable temporary growth, so that an asymptotic stability result may be misleading, but it is at least a start.

For the Q-NPZ model, the matrix \mathcal{B}_{ij} is

$$\mathcal{B}_{ij} = \begin{pmatrix} \mu(N_T - \bar{P} - \bar{Z}) - g\bar{Z} - d_P - \mu\bar{P} & -(\mu + g)\bar{P} \\ ag\bar{Z} & ag\bar{P} - d_Z \end{pmatrix}$$

which simplifies for the three equilibria to

$$\bar{P} = \bar{Z} = 0 \quad , \quad \mathcal{B}_{ij} = \begin{pmatrix} \mu N_T - d_P & 0 \\ 0 & -d_Z \end{pmatrix}$$

$$\bar{Z} = 0, \quad \bar{P} = N_T - d_P/\mu \quad , \quad \mathcal{B}_{ij} = \begin{pmatrix} -\mu\bar{P} & -(\mu + g)\bar{P} \\ 0 & ag\bar{P} - d_Z \end{pmatrix}$$

$$\bar{P} = d_Z/ag, \quad \bar{Z} = (\mu N_T - \mu d_Z/ag - d_P)/(\mu + g) \quad , \quad \mathcal{B}_{ij} = \begin{pmatrix} -\mu\bar{P} & -(\mu + g)\bar{P} \\ ag\bar{Z} & 0 \end{pmatrix}$$

For a 2×2 real matrix, at least one of the eigenvalues will have a positive real part if the trace (Tr , the sum of the diagonal elements) is positive or the determinant (Det , the product of the diagonal elements minus the product of the off-diagonal elements) is negative. Thus the $\bar{P} = \bar{Z} = 0$ state becomes unstable when $\mu N_T > d_P$ – phytoplankton have enough nutrient to grow. The $\bar{P} \neq 0$, $\bar{Z} = 0$ state will become unstable when $ag\bar{P} > d_Z$; at this point, the phytoplankton have sufficient biomass to support zooplankton growth. In both cases, the determinant switches from positive to negative before the trace becomes positive. Finally, the state with both \bar{P} and \bar{Z} non-zero will always have negative Tr and positive Det , so that all perturbations will decay.

MONOD FORM: When uptake and grazing have limitations of the form $R/(R + R_{1/2})$, the system can become **unstable** and devolve into limit cycles. Without diffusion, the oscillations have different frequencies with depth and the signal becomes very noisy; with diffusion **the fields** become smooth.