
2 General concepts of nutrient flux and stability

2.1 INTRODUCTION

Water can carry a wide array of dissolved substances, including every bioelement [human urine, for example, contains up to 80 dissolved compounds (Botkin, 1990)]. Thus the fluxes of many important nutrients are closely connected with the hydrological cycle, nutrients with gaseous forms such as N_2 and CO_2 being partial exceptions. The concentration of any given dissolved substance in the waters on the earth's surface is variable, both in space and time. The dissolved substances in a particular unit volume of water depend on the recent history of that water. Passage of water through rocks and soil dissolves chemical compounds, whole processes such as diffusion, the mixing of water from different sources, and evaporation causes changes in concentrations. These processes go on even in the absence of biota, and it will be useful to begin the mathematical description of these nutrient dynamics in physical systems without the complication of biota.

The mathematical approach used through much of this book is that of compartmental modelling. This approach has been described in detail by Sheppard (1962), Jacquez (1972) and Anderson (1983), among others. It assumes that a system can be divided into a finite number of compartments or pools, each of which is internally homogeneous and connected to other compartments. Associated with each compartment is a variable that represents an amount of matter, energy or nutrients in that compartment at a given time. A differential equation describes the dynamic changes in the amount of matter, energy or nutrient in each compartment through time, as these are affected by fluxes into and out of the compartments. As an example of a compartment, think of a well-mixed lake containing uniformly distributed dissolved phosphorus and no biota. Streams flowing into the lake bring input fluxes of phosphorus and outflows carry out phosphorus. The changes in the amount of phosphorus in the lake depend on the instantaneous difference between inflows and outflows. This is an idealization, since no body of water containing perfectly homogeneously distributed dissolved substance exists in reality. However, it is a useful idealization that may often

be accurate enough to serve as a good first approximation. It is necessary, in any case, to understand the dynamics of such imaginary systems before one can go on to more realistic situations.

Although the most common application of compartmental models (often called 'box and arrow diagrams') has been to quantitative areas of physiology, such as pharmacokinetics, compartmental modelling became an important tool in ecology over two decades ago. Perhaps the earliest pioneer in compartmental modelling in ecology was A. J. Lotka, whose book, *Elements of Physical Biology*, published in 1924, contained conceptual models of the nitrogen, phosphorus and other material cycles in the form of a number of connected compartments (plants, animals, carcasses, manure, soil and so forth).

In more recent times compartmental modelling became popular under the name of 'systems ecology', developed by a number of ecologists, including E. P. and H. T. Odum (1955), who modelled the energy flow in a coral reef community, J. S. Olson (1965), who modelled flows of caesium in a forest, and G. Van Dyne (1966), who developed early models of energy flow in grasslands. Since that time, it has been customary to use compartment models to describe and predict the movement of substances through ecosystems. Here we will start with the simplest compartmental model, one with a single compartment.

2.2 SINGLE COMPARTMENT OR POOL

In modelling the flow of matter, one starts with basic conservation principles. The principle of conservation of mass states 'the rate of change of mass in a specified region of space equals the rate at which mass enters that region minus the rate at which the mass leaves' (Denn, 1986).

Let us apply this to a situation in which there is a constant volume V (for example, 1 cc) of water, containing solute of initial concentration C_0 , in a pool (Figure 2.1). Let water, at a constant rate, q (l s^{-1} , where 1 litre, l, is

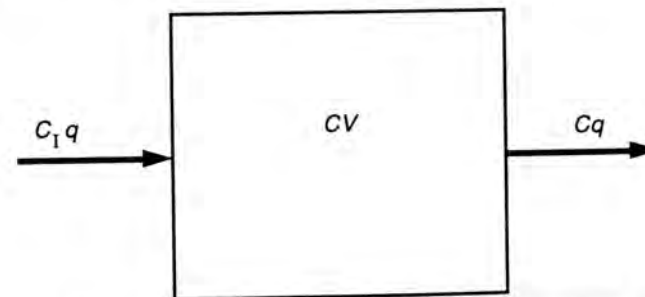


Figure 2.1 Single-compartment model of a solute of concentration C in a water body with an inflow C_1V and an outflow CV of solute. If the initial concentration is C_0 , the time course of concentration is given by Equation (2.3).

approximately 1 kg in weight), enter the pool and let there also be the same constant outflow q . Assume that at time $t = 0$ a dissolved solute with concentration C_1 (g solute l^{-1}) is present in the input water and assume further that the pool is rapidly mixed. The solute is assumed to be low enough in concentration to make up a negligible fraction of the volume in the pool, input water and outflow water. The problem now is to determine the concentration of the solute in the tank, which we will define as $C(t)$, for all times $t > 0$.

A straightforward way to approach this problem is to consider the water in the pool to be a compartment and to apply the mass conservation law to the total mass of solute in the compartment. This total mass is the concentration $C(t)$ times the volume of water in the pool V , or CV (I will usually abbreviate $C(t)$ to C from now on). The inflow of mass of solute, or the *input loading* is C_1q and the outflow is Cq . The law of conservation of mass then states

(Rate of change of mass of solute contained in compartment)
= (rate at which mass enters) – (rate at which mass leaves)

In symbolic terms,

$$d(CV)/dt = C_1q - Cq \quad (2.1)$$

where $d(CV)/dt$ represents the rate of change of CV . The quantities V , q and C_1 are all constants; thus, $dV/dt = 0$, so $d(CV)/dt = VdC/dt + CdV/dt = VdC/dt$, and Equation (2.1) becomes

$$VdC/dt = q(C_1 - C) \quad (2.2)$$

Equation (2.2) is a linear equation because in the terms where C occurs it is always as the first power of C . The equation can be solved to obtain the solution

$$C = C_1(1 - e^{-(q/V)t}) + C_0e^{-(q/V)t} \quad (2.3)$$

which can be checked by substitution of C from Equation (2.3) into Equation (2.2). In Equation (2.3) C_0 , formally a constant of integration, represents the initial condition on concentration at time $t = 0$. The solution (2.3) is a general solution of the differential equation in the sense that C_0 can be chosen to fit all possible initial conditions of C . The constant C_1 is the steady-state equilibrium concentration, to be discussed below. The ratio q/V , the exponential coefficient of time, t , sets the time scale of the dynamics of the variable C through time. This coefficient of time in the exponent is of special importance in linear differential equations and is referred to as an *eigenvalue*. A first-order linear differential equation such as Equation (2.1) has one eigenvalue. Eigenvalues will be encountered frequently throughout this text. They become especially important in describing the dynamics of multicompartments, which have as many eigenvalues as compartments. Concentration C given by Equation (2.3) is plotted in Figure 2.2 for

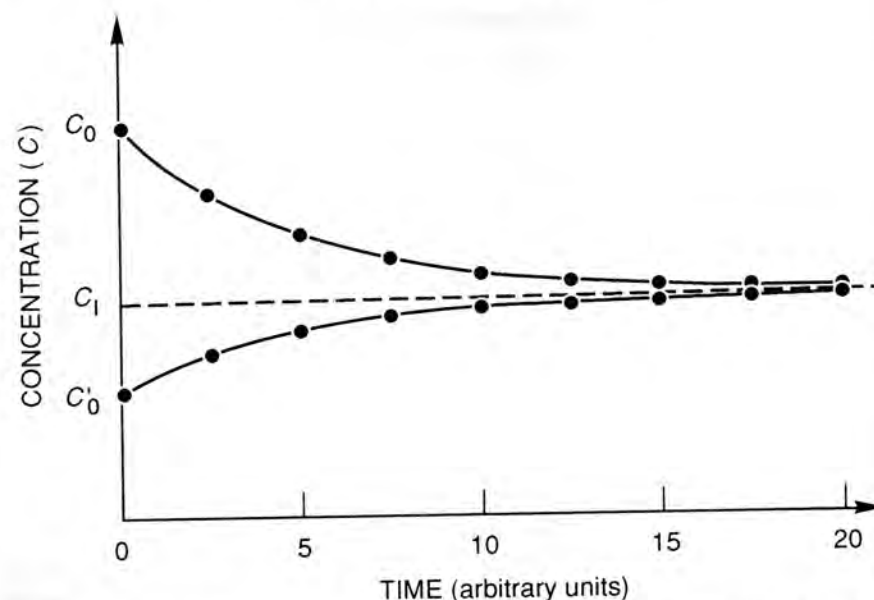


Figure 2.2 Plot of concentration C as a function of time for two different starting concentrations, C_0 and C'_0 [from Equation (2.3)]. The ratio q/V is set to 0.20. $T_R = 5.0$ is the return time to a fraction e^{-1} of the initial deviations $(C_0 - C_1)$ and $(C'_0 - C_1)$

both the case in which $C_0 > C_1$, meaning that the concentration is started out above the steady-state level, and that in which $C'_0 < C_1$. In both cases the solution approaches C_1 through time.

2.3 PROPERTIES OF THE SOLUTION

The solution, Equation (2.3), though very simple, contains many of the basic properties that we will be interested in trying to look for in more complex models. These are as follows.

Steady-state equilibrium

As $t \rightarrow \infty$, the concentration approaches a constant value

$$C^* = C_1 \quad (2.4)$$

where the $*$ signifies that the variable is at steady-state equilibrium.

Transient behaviour

The part of the solution (2.3) that depends on t is called the transient

component of the solution:

$$(C_0 - C_1)e^{-(q/V)t}$$

This transient component damps away or 'decays' as time t increases, becoming quite small as t reaches large values (several multiples of V/q), leaving only the steady-state component of the solution, C_1 .

Stability

For any starting value of C , C_0 (C_0 can plausibly only be zero or a positive value), the solution returns to $C^* = C_1$ (Figure 2.2). Thus, the system is both locally and globally stable. **Local asymptotic stability** (also called Lyapunov stability) means that there is at least a small region around C^* such that, following a perturbation of C to any point in this region, the solution returns towards C^* ('asymptotically' meaning that the solution literally never reaches C^* , because $e^{-(q/V)t}$ is always positive, no matter how large t is). **Global asymptotic stability** means that the solution returns asymptotically towards C^* for all possible starting values of C . In linear systems such as Equation (2.1), local stability always implies global stability. Many systems in nature, however, are non-linear and some of these may be locally stable but not globally stable. Such systems may not return to the same equilibrium following a large perturbation. Cases of this will occur in some of the complex biotic systems studied later.

Resilience

Resilience is a type of stability, sometimes called 'relative stability'. Assume that a system is at least locally stable and so will return to steady-state equilibrium following a perturbation. Resilience is a measure of the rate at which the system approaches steady state following the perturbation. To formalize this somewhat, suppose as before that the concentration in Equation (2.1) is perturbed to C_0 . How quickly does the perturbation decay to some fraction of its original value? (It is conventional to take as this fraction e^{-1} , where $e = 2.718 \dots$ is the natural logarithm.) From the solution, Equation (2.3), it is clear that when $e^{-(q/V)t}$ becomes equal to e^{-1} , the initial deviation $(C_0 - C^*)$ will have returned to a fraction e^{-1} of C^* . This occurs at a time $t = T_R$, where

$$T_R = 1/(q/V) = V/q \quad (2.5)$$

The value T_R is called the **return time to equilibrium** and its inverse is a measure of resilience:

$$\text{Resilience} \sim 1/T_R \quad (2.6)$$

An equivalent way to calculate the return time to equilibrium, T_R , which will be useful in much more general applications, is to integrate the area

under the curve in Figure 2.2, normalized by the initial size of the perturbation away from C^* , $C_0 - C^*$. The appropriate integral for the one-compartment system under consideration is

$$\begin{aligned} T_R &= \int_0^\infty dt (C - C^*) / (C_0 - C^*) \\ &= [(C_0 - C^*) / (C_0 - C^*)] \int_0^\infty dt e^{-(q/V)t} \\ &= -(V/q) e^{-(q/V)t} \Big|_0^\infty = V/q \end{aligned}$$

which is exactly the same as Equation (2.5). This expression is generalizable to a system of n compartments, with concentrations $C_i(t)$, where i is the compartment number, by performing summations within the integral

$$T_R = \frac{1}{\sum_{i=1}^n (C_{i,0} - C_i^*)^2} \int_0^\infty dt \sum_{i=1}^n (C_i(t) - C_{i,0})^2 \quad (2.7)$$

Expression (2.7) can also be used for non-linear systems, in which the $C_i(t)$ values cannot be solved for analytically, but can be determined numerically by means of computer simulations.

Residence time

Assume that a molecule of solute has just entered the compartment pictured in Figure 2.1. What is the expected time it will reside in the system given that the compartment is in steady state? Since C^*V is the amount of solute mass in the compartment, and hence is a measure of the number of solute molecules, and C^*q is a measure of the number of solute molecules both entering and leaving the compartment per unit time, the average time any one molecule stays in the compartment is

$$T_{res} = (C^*V) / (C^*q) = V/q \quad (2.8)$$

where T_{res} is called the **residence time**. The mean residence time, also called the turnover time of the system, is equal in this case to the return time, T_R .

The mean residence time can be thought of as a measure of the rate of flushing or dilution of the solute. If there is an initial concentration, C_0 , in the compartment and the input water starting at time $t = 0$ is pure (without solute), then the concentration at any later time is described by the equation

$$dC/dt = -(q/V)C \quad (2.9)$$

the solution of which is

$$C = C_0 e^{-(q/V)t} \quad (2.10)$$

At time $t = T_R$, $C(t) = C_0 e^{-1} \cong 0.34C_0$, at time $t = 2T_R$, $C(t) \cong 0.12C_0$, and so forth.

2.4 EXAMPLE OF RESIDENCE TIME CALCULATIONS

Canfield *et al.* (1984) computed the mean residence times for several bioelements in Acton Lake in Ohio (Figure 2.3). This calculation is not as simple as it would appear because the stream inputs are variable both in flow rates and concentrations. Thus one cannot use an instantaneous value of input, such as q in Equation (2.8).

The volume of the lake was estimated to be $95.5 \times 10^5 \text{ m}^3$ and this volume was assumed to be well mixed, except for some vertical stratification. The water residence time was calculated by summing daily mean stream discharges into the lake until a volume of water equal to two whole lake volumes had been discharged into the lake (water loss due to evaporation was assumed negligible). The average water residence time was assumed to be half of this measured time.

Stream solute inputs were obtained by calculating flow-weighted concentration averages for the streams. An average input concentration (mean concentration in mg l^{-1}), C_i , was obtained for each bioelement, and the stream water discharge rate, $q(\text{l d}^{-1})$ where d stands for days), was calculated. The total mass (mg), N_T , of a particular bioelement in the lake was found by sampling three vertical layers of the lake. The average concentration of each layer j , C_j , was multiplied by the layer volume, V_j , and then the masses of the layers were summed, or

$$N_T = \sum_{j=1}^3 C_j V_j \text{ (mg)} \quad (2.11)$$

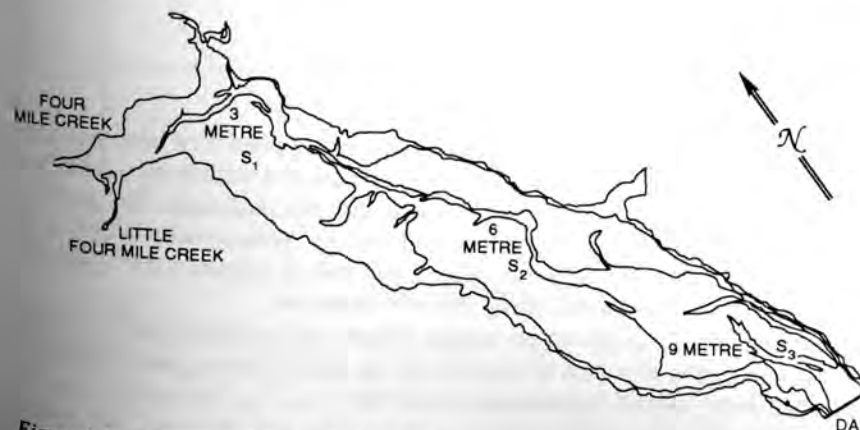


Figure 2.3 Diagram of Acton Lake, Ohio.

Table 2.1 Residence times (days) for selected elements in Acton Lake (from Canfield *et al.*, 1984)

Ca	Mg	Cl	Na	K	Fe	Mn
77	104	105	105	144	930	1800

The residence time, in units of d is, in analogy with Equation (2.8),

$$T_{\text{res}} = N_T / (C_1 q) (d) \quad (2.12)$$

The results of the residence times for one of four of the dates for which these were computed by Canfield *et al.* (1984) are shown in Table 2.1.

Note that calcium (Ca) has the shortest residence time, while iron (Fe), manganese (Mn) and potassium (K) are the longest, and magnesium (Mg), chlorine (Cl) and sodium (Na) have intermediate values. These values indicate the degree to which the bioelements react within the lake. Na and Cl are known to be fairly non-reactive in the lake and hence demonstrate 'conservative' behaviour, that is, behaviour expected in terms of the conservation equation (2.1). Mg also seems to exhibit conservative dynamics. Some of the elements displaying long residence times, such as Fe and Mn, may have already been stored in large amounts in bottom sediments and have been undergoing resuspension from these sediments during the period of measurement, thus indicating a relatively high concentration in the water column of the lake at an earlier time. Ca, which showed a relatively short residence time, may have been precipitating during the time of measurement as calcite, so that the water column concentration was correspondingly low.

The study by Canfield *et al.* (1984), and others like it, show that it is insufficient simply to model only the compartment and its hydrological inflows and outflows even in the idealized abiotic case. The interactions of the solute with the sediment must also be considered. An extension of the model to do this is considered in the next section.

2.5 LOSS RATE TO SEDIMENTS

Nutrient retention is the percentage of nutrient supplied to a lake that does not leave via outflow. It can be studied by means of a slightly more complex equation that considers nutrient exchange with the sediments. One particular nutrient budget model is that introduced by Vollenweider (1969), with explicit reference to phosphorus. Here I will follow Chapra's (1975) presentation based on this model, using my own notation.

Suppose that, in addition to stream inflows and outflows, there is a loss to the sediments. This can be represented by another term, subtracted from the right hand side of Equation (2.1), so that

$$V dC/dt = I_n - qC - vAC$$

or

$$dC/dt = (I_n/V) - [(q + vA)C]/V \quad (2.13)$$

where

A = surface area of the lake (m^2), assumed to be the surface area of the sediments as well, v = the apparent settling rate of total phosphorus (m d^{-1}), and I_n = shorthand for the input of nutrient mass per unit time, or qC_1 ($\text{mg m}^{-2} \text{d}^{-1}$).

The solution of Equation (2.13) is

$$C = [I_n / (q + vA)] \{1 - e^{-(q + vA)C/V} t\} + C_0 e^{-(q + vA)C/V} t \quad (2.14)$$

This solution, which is plotted in Figure 2.4 for zero and non-zero values of loss rate to the sediments, vA , is different in two important ways from Equation (2.3), in which the loss rate to the sediments was ignored (see Figure 2.4). The steady-state value ($t \rightarrow \infty$) is now

$$C^* = I_n / (q + vA) \quad (2.15)$$

reflecting the fact that the loss rate to the sediments, vAC , causes the

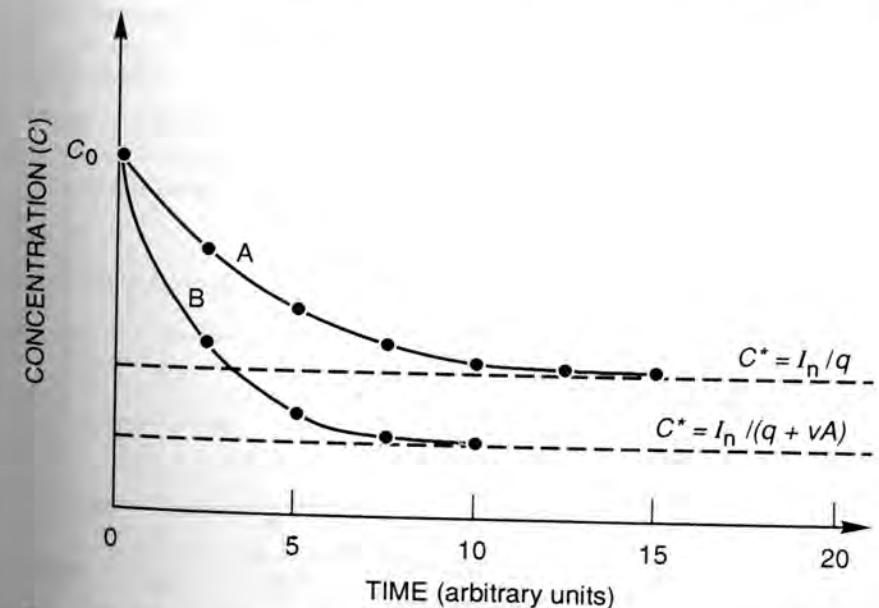


Figure 2.4 Effects of loss rate to the sediments, vA , on the nutrient concentration as a function of time. In curve A, the loss rate to the sediments is zero. In curve B this loss rate was chosen to be of the same magnitude as the loss rate q from the system. Note that the loss rate to the sediments affects both the steady-state concentration and the rate of return to steady state.

steady-state value of nutrient in water to be lowered. The second difference is that the return time to steady state, T_R , is now

$$T_R = V/(q + vA) \quad (2.16)$$

that is, the return time is lowered by a factor $q/(q + vA)$, indicating that resilience has increased. This results from the retentive power of the sediments. When there is no loss rate to sediments, $v = 0$, so that C^* and T_R reduce to the earlier results of Equations (2.4) and (2.5).

Example: From Equation (2.16), it is possible to derive the phosphorus retention coefficient, R_p , of the lake, defined as the rate of mass lost to the sediments, vAC^* , divided by the rate of mass input to the lake:

$$R_p = vAC^*/I_n = v/(q_s + v) \quad (2.17)$$

where

$q_s (= q/A)$ = the rate of water inflow per unit lake area, or areal water load.

Chapra (1975) fitted Equation (2.17) to data on R_p and q_s for 15 southern Ontario lakes (from Kirchner and Dillon, 1975) using least squares. The fit is shown in Figure 2.5, where the resulting settling velocity, v , is 16 m/year.

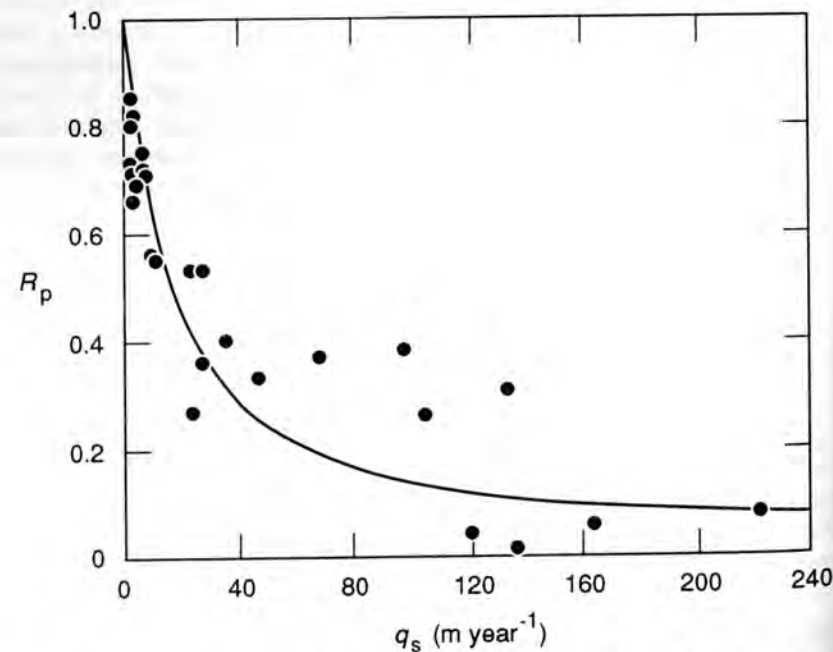


Figure 2.5 Fit of Equation (2.17) to data on the retention coefficient, R_p , as a function of the rate of water inflow per unit of lake area, q_s , from data from 15 southern Ontario lakes. [Adapted from Chapra (1975) based on data from Kirchner and Dillon (1975).]

2.6 FEEDBACK FROM SEDIMENTS

It appears from a number of studies (e.g. Hayes *et al.*, 1952; Rigler, 1978) that there is a net retention of some nutrients, such as phosphorus, in the sediments of lakes, as described in the preceding model. However, not all of the nutrients taken up by the sediments remain there. Some fraction may be regenerated into the water column at a later time. The explicit consideration of sediment release has been included in models by Lorenzen *et al.* (1976) and others. This problem is worth considering in detail here for two primary reasons. First, the coupled lake-sediment system has some dynamic properties that are far different from the lake system alone. Second, the study of the system requires some mathematics that will be convenient to refer to in later sections of the book in discussions of more complex systems. Nonetheless, this section can be skipped by readers without loss of continuity.

Let us refer back to Equation (2.13), which describes solute dynamics in a single compartment, such as a lake, where there is loss to the sediments. Assume now that the sediments are able to release some of the nutrient back into the water. To take this into account, let C_s be the concentration of the nutrient in the sediments (g m^{-3}), $V_s (\text{m}^3)$ be the volume of sediments in close-enough contact with the water that the nutrient is exchangeable with the water column, and k_s be the rate constant for release of the bioelement into the water (Figure 2.6). Separate equations are needed to describe C and C_s . As before, determining these equations is simply a matter of applying conservation laws. The equations are, first in words and then in symbols,

(Rate of change of nutrient mass in water) = (input rate due to water inflow) - (loss rate due to water outflow) - (deposition rate to sediments) + (regeneration from sediments)

or

$$V dC/dt = I_n - qC - vAC + Ak_sC_s \quad (2.18a)$$

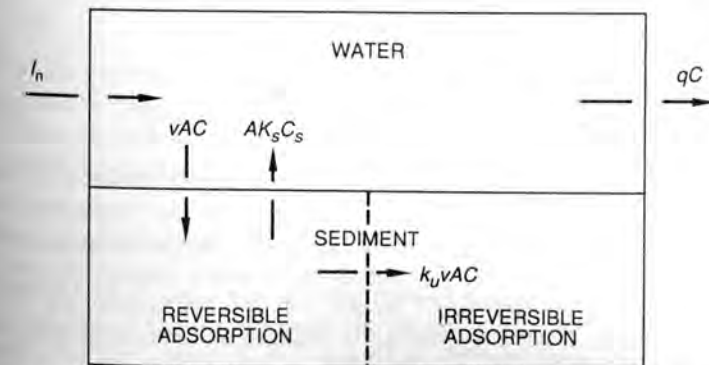


Figure 2.6 Schematic diagram of solute dynamics in a water body that includes exchange of nutrients with sediments.

and

(Rate of change of nutrient in available form in sediment) = (input due to deposition from water column minus rate at which nutrient becomes permanently unavailable) - (losses due to regeneration into water column)

or

$$V_s \frac{dC_s}{dt} = vAC(1 - k_u) - Ak_s C_s \quad (2.18b)$$

where k_u ($0 \leq k_u \leq 1$) is the fraction of input from the water column to the sediments that becomes permanently inaccessible to any further circulation in the system, due to irreversible adsorption in the sediments or an equivalent process. Note that this loss is assumed to occur at a rate proportional to the concentration of solute, C , in the water.

This pair of coupled equations is linear and thus can be solved analytically. However, the derivation of the solution is complex and is, therefore, omitted. The solution, which, because of its length is shown in full form only in Appendix A (Equations A.1a and A.1b), is identical with that of Lorenzen *et al.* (1976) with some changes in notation.

The solutions shown in Equations (A.1a and A.1b) for the dynamic behaviour of the system of water column and sediment are too complicated to lead to any quick insights into system dynamics. However, the steady-state solutions are simple enough to comment on directly. Let us first consider these and then discuss some aspects of the transient behaviour.

Steady-state solutions

When the coupled water-sediment system is subjected to the load I_n for a long enough period of time ($t \rightarrow \infty$), the transient dynamics decay, leaving only the constant terms in Equations (A.1a and A.1b):

$$C^* = C_1 C_5 / (C_2 C_5 - C_3 C_4) = I_n / (q + vk_u A) \quad (2.19a)$$

$$C_s^* = C_4 C_1 / (C_2 C_5 - C_3 C_4) = I_n v (1 - k_u) / [k_s (q + vk_u A)] \quad (2.19b)$$

Note that C^* in Equation (2.19a) has a form that is very similar to Equation (2.15). The term $vk_u A$ in Equation (2.19a) represents the permanent loss to the sediments, as does vA in Equation (2.15). Reversible exchange with the sediments does not affect C^* . The steady-state solute temporarily stored in sediments, C_s^* , is a multiple of C^* by $v(1 - k_u)/k_s$, the ratio of the fluxes of solute to and from temporary storage in sediments. These equations can be examined in various limits.

Case 1: There is no permanent loss of nutrients from the system (i.e. $k_u = 0$).

Then

$$C^* = I_n / q = C_1$$

$$C_s^* = I_n v / (q k_s) = C_1 v / k_s$$

so that the amount of nutrient in the water is the same as if no sediment were present. The effect of increasing k_u from zero is to decrease both C^* and C_s^* .

Case 2: The regeneration rate k_s increases indefinitely.

$$\text{As } k_s \rightarrow \infty$$

$$C^* = I_n / (q + vk_u A)$$

$$C_s^* \rightarrow 0$$

Although one might intuitively expect an increase in regeneration to cause an increase in C^* , the only effect is a decrease in C_s^* . The reason for this is simply that C^* does not depend on the regeneration rate, only on the loss rate to the sediments.

Case 3: The loss rate to sediment, v , increases indefinitely.

$$\text{As } v \rightarrow \infty$$

$$C^* \rightarrow 0$$

$$C_s^* \rightarrow I_n (1 - k_u) / (k_s k_u A)$$

Hence an unlimited increase in v causes water column solute to go to zero and available sediment concentration to approach a constant. C_s^* does not increase indefinitely because there is a loss to permanent storage in the sediments. However, if $k_u \rightarrow 0$, so that the rate of permanent loss increases,

$$C^* = I_n / q$$

$$C_s^* \rightarrow \infty$$

that is, the storage of nutrient in the sediment increases indefinitely. The return flux to the water column balances the loss from the water column to the sediment, keeping the concentration in the water column the same as if there were no sediment.

Transient solutions

The behaviour of the transient solutions of Equations (2.18a,b), describing the dynamics of the system from the initial conditions to the steady state, depends on the values of two quantities derived from the equations, the eigenvalues. The single eigenvalue of a one-compartment system was discussed earlier. This two-compartment system has two eigenvalues, λ_1 and

λ_2 . Because these are rather complex, they are shown in Appendix A. The fact that there are now two eigenvalues rather than one eigenvalue, as there was in the analyses of the single-compartment models [Equations (2.1) and (2.13)], means that there are two time scales of system behaviour, the inverses of the two eigenvalues. One example will illustrate the importance of these two time scales.

Example: Assume that the rate of bioelement regeneration from sediments, k_s , is small. If k_s/V_s is small enough [compared with $(q + vA)/V$], the two eigenvalues can be shown from Equation (A.2) to be approximately

$$\lambda_1 \cong -(q + vA)/V \quad (2.20a)$$

$$\lambda_2 \cong -(Ak_s/V_s)(q + vk_sA)/(q + vA) \quad (2.20b)$$

where $|\lambda_2| \ll |\lambda_1|$. The effects of these two time scales can be seen by considering the case in which the initial bioelement concentrations (phosphorus in this case) in the water column and sediments, C and C_s , are both at steady-state values; $C^* = 4.03 \times 10^{-6}$ and $C_s^* = 4.8 \times 10^{-2}$ at time $t = 0$, at which point the loading I_n is stopped. Parameter values from Lorenzen *et al.* (1976) are used: $A = 10^8 \text{ m}^2$, $V = 3.8 \times 10^9 \text{ m}^3$, $q = 9 \times 10^8 \text{ m}^3 \text{ year}^{-1}$, $I_n = 45000 \text{ kg of P year}^{-1}$, $V_s = 10^7 \text{ m}^3$, $v = 36 \text{ m year}^{-1}$, $k_s = 0.0012 \text{ m year}^{-1}$ and $k_u = 0.6$.

Concentrations C and C_s are plotted on a logarithmic scale in Figure 2.7. Note that there is an initial rapid decrease in C , which largely reflects the rapid washout of phosphorus initially in the water column of the lake. This rate of increase is governed primarily by the eigenvalue with larger absolute value λ_1 . This is followed, however, by a much slower decline, as shown by the less steeply sloped second part of the curve in Figure 2.7. The concentration in the lake only slowly reaches its steady-state value, over a longer time scale determined by λ_2 . This smaller (or in larger systems the smallest) eigenvalue is often referred to as the critical or dominant eigenvalue, as it governs the long-term dynamics of the system. This is because the phosphorus held in the sediments is slowly released and partially compensates for the loss of external input I_n . It is important to note that the sediments perform a buffering action in the lake (see also the model by Jorgensen *et al.*, 1975). The buffering of the lake is important in two respects. First, when there is a sudden jump in input of solute to the lake, this will be partially compensated for by increased sediment uptake. The second aspect, or reverse side of the coin, however, is that if the solute input is decreased (say, by a reduction in sewage input) this will be offset to some extent by increased net flux from the sediments to the water column for some period of time before the input reduction has an effect.

The models discussed up to now are a vast simplification of actual systems. A real body of water is rarely a single well-mixed compartment, as lakes tend to stratify into layers that increase in density with depth and

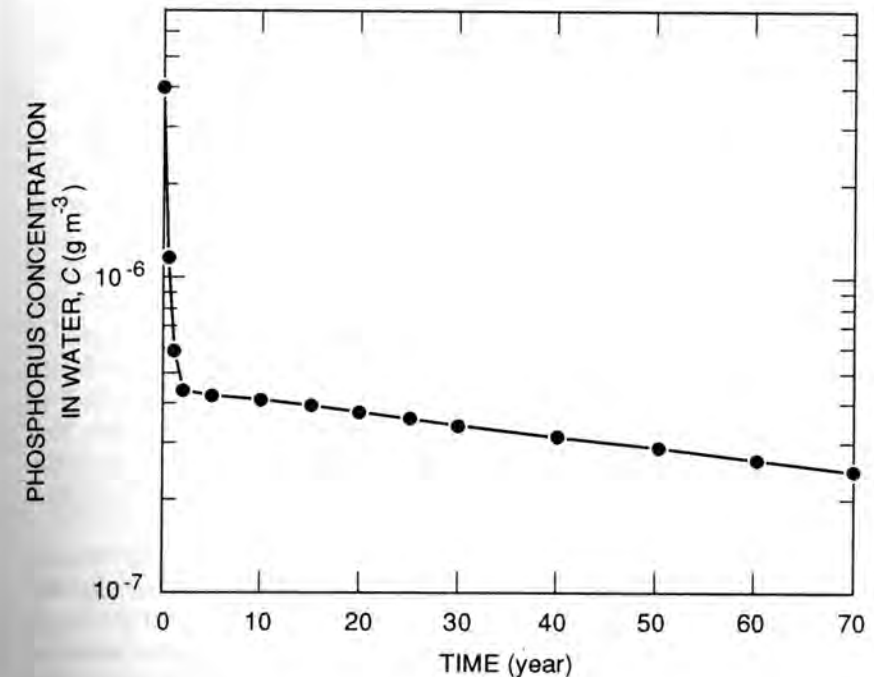


Figure 2.7 The response of the phosphorus concentration in a lake modelled by Equations (2.18a,b) to a cessation of phosphorus input, I_n . There are two distinct parts of the transient behaviour; a sharp drop described by the eigenvalue $\lambda_2 = -3.3$ and a slower decline described by the eigenvalue $\lambda_1 = -0.011$ (see text for discussion).

which do not mix (for very shallow lakes, however, the one-compartment assumption is often a good approximation). It may often be reasonable, however, to partition the lake into just two layers, an epilimnion and a hypolimnion, each of which is relatively well mixed. A number of models of this form exist, including that of Imboden (1974).

I will not consider this complication of the abiotic system. However, it should be remarked that separation of the water column into an epilimnion and hypolimnion (where the epilimnion is the upper layer of warm water in lakes that may form during summer above cooler denser water of the hypolimnion) may be important in models when the hypolimnion is likely to become anaerobic (low in available oxygen). Lakes with anaerobic hypolimnia have smaller values of phosphorus retention than do lakes with aerobic hypolimnia. Phosphorus retention in the hypolimnion often involves complex reaction of the orthophosphate, or dissolved inorganic form of phosphorus, with oxides of iron, manganese and other metals. These form insoluble precipitates under aerobic conditions, but at low levels of dissolved

oxygen (or low redox potentials) these precipitates are dissolved (Day *et al.*, 1989). The existence of anaerobic conditions can thus increase the normal release rate of phosphorus (see, for example, Nürnberg, 1984).

2.7 SERIES OF LAKES

Lakes and reservoirs are frequently connected in chains, and an effect on one, whether it is an increase or a decrease in bioelement loading, may propagate to others downstream. Thus, a series of lakes must be considered to be one connected system. It is useful here to consider a model for the propagation of effects in a sequence of lakes, because it is an analogue, in some sense, for the propagation of bioelement effects through a food web (though a very simple one in which there are no feedbacks). A number of models of this type have been constructed. For example, O'Connor and Mueller (1970) modelled chloride concentration in the Great Lakes, represented as a series of boxes connected by flows. Each box receives precipitation and runoff and is subjected to evaporation.

Another system that has been modelled is a system of four shallow eutrophic lakes in Sweden, which Ahlgren (1980) represented schematically (Figure 2.8). A given lake i has a runoff input, $q_i C_{i,i}$, and an input of sewage, J_i (no volume of water is associated with this sewage), a sediment retention factor, R_i , and a concentration, C_i . Therefore, the equations for this system are [generalizing from Equation (2.13) and assuming no evaporative losses, so that water flow accumulates additively],

$$V_1 dC_1/dt = (q_1 C_{1,1} + J_1)(1 - R_1) - q_1 C_1 \quad (2.21a)$$

$$V_2 dC_2/dt = (q_1 C_1 + q_2 C_{1,2} + J_2)(1 - R_2) - (q_1 + q_2)C_2 \quad (2.21b)$$

$$V_3 dC_3/dt = [(q_1 + q_2)C_2 + q_3 C_{1,3} + J_3](1 - R_3) - (q_1 + q_2 + q_3)C_3 \quad (2.21c)$$

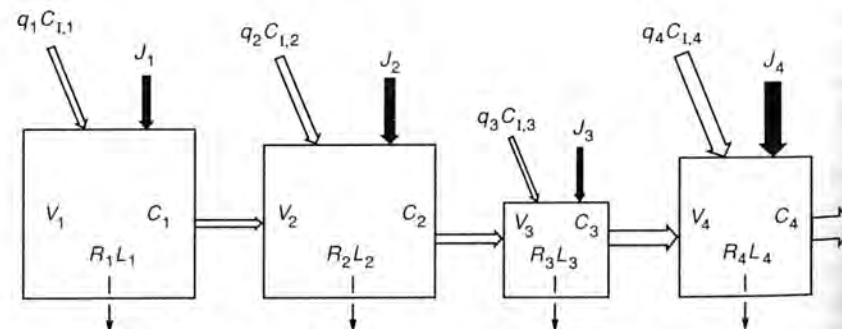


Figure 2.8 Scheme of a series of lakes with solute concentrations C_i , modelled by Ahlgren (1980). The terms $R_i L_i$ represent retention rates in sediments, where the L_i 's are inputs to the lakes; e.g. $L_1 = q_1 C_{1,1} + J_1$.

$$V_4 dC_4/dt = [(q_1 + q_2 + q_3)C_3 + q_4 C_{1,4} + J_4](1 - R_4) - (q_1 + q_2 + q_3 + q_4)C_4 \quad (2.21d)$$

where the nutrients retained in the sediments are here removed directly from the inflow, and so are not proportional to the concentration in the lake. Thus, the retention factors, R_i , are not expressed by vA_i , as they would otherwise be [in analogy with Equation (2.13)].

A rather remarkable thing about the complex set of equations (2.21) is that they are analytically soluble, and without much difficulty, since they form a 'cascade' sequence with no feedbacks. One can solve for the behaviour of the concentration C_1 in the highest lake in the drainage first, and use the result as part of the input to the next lake below it in the sequence, and so forth. To illustrate the method, while avoiding complexity, we compute only the first two lake concentrations, C_1 and C_2 . The solutions are shown in Appendix B for a special case where the initial concentrations of all the lakes are equal to zero. It is clear that the solutions of successive lake concentrations become more and more complicated. However, formulae for variables at any stage in the sequence of this type of cascade are available (e.g. Bailey, 1964).

Ahlgren (1980) used the data in Table 2.2 to specify the Equations (2.21a,b,c,d) for phosphorus. The different values of $C_{1,i}$ reflect different land usages around the lakes, with Lake no. 4 surrounded by a relatively greater amount of farmland. The water discharge values, q_i , were found by multiplying specific runoff values per unit area of land by the sizes of the drainage areas, A_i .

Until 1970, all four lakes received domestic and industrial sewage. In 1970 the complete diversion of all sewage was begun. Measurements of phosphorus and nitrogen in the lakes were begun at that point. To compare the data with theory, computer simulations were performed by Ahlgren (1980) on Equations (2.21). In Figure 2.9 comparisons are made between simulation results and data for phosphorus concentrations after 1970, both including and ignoring retention. Although a retention of $R=0.44$ was expected, based on relevant studies of similar lakes, the assumption of zero

Table 2.2 Data used for the parameter values of Equations (2.21) (Based on data in Ahlgren, 1980)

Lake no....	1	2	3	4
Drainage area, A (km ²)	50.7	94.0	128	264
Lake area, A_i (km ²)	6.1	2.67	1.0	1.6
Lake volume, V (10 ⁶ m ³)	15.4	14.3	3.0	5.3
Runoff, q (l s ⁻¹ km ⁻²)*	5.2	5.2	5.2	5.2
Runoff P concentration, D (g m ⁻³)	0.1	0.05	0.05	0.05
Sewage P loading (g m ⁻² year ⁻¹)	0.16	0.5	2.2	2.1

*1978 value.

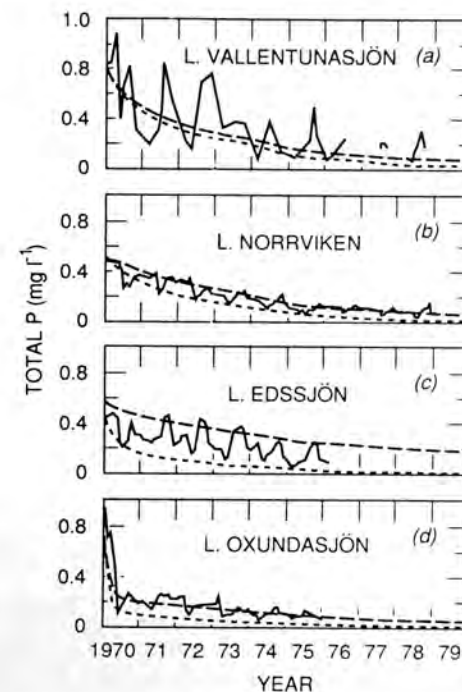


Figure 2.9 Comparisons of data on total phosphorus concentration in four Swedish lakes (Figure 2.8) after diversion of sewage effluents (solid lines) with model simulations (dotted and dashed lines). In the dashed model curves, the retention $R_p = 0$, while in the dotted curves $R_p = 0.44$. (From Ahlgren, 1980.)

retention worked better in the model. Ahlgren attributed this to excessive phosphorus release from the sediments. Ahlgren also applied the model to nitrogen, but the results were less satisfactory, probably due to denitrification losses or less accurate input data.

The derivation of this cascade solution for solute in a series of lakes is an appropriate place to introduce an additional stability concept, that of resistance.

Resistance

Resistance can be defined in a manner similar to Harrison and Fekete (1980) as the relative magnitude of the change in a specified component of system following a unit change in one of the fluxes, either an input, an output, or a flow between compartments in the system.

The concept of resistance is related to the sensitivity analysis that modellers frequently undertake to see how variables in their model respond

to changes in inputs, fluxes, rate coefficients or other quantities in the model. There is no one overall resistance of a system, but a variety of different resistances associated with changes in various fluxes and the resultant deviations in compartments of interest. Taking Ahlgren's lakes as an example, suppose there is a sudden increase in phosphorus input in sewage, J_1 , so that the total input of sewage to the first lake, J_1 , increases by a certain amount. What is the effect on the concentrations, C_1, C_2, C_3 and C_4 of the four lakes? From Ahlgren's parameter values, these values were computed through time following an increase in J_1 (Figure 2.10). One can compute the percentages of the final changes of C_1, C_2, C_3 and C_4 relative to the fractional change of J_1 (which is 0.1), or

$$\text{Fractional change in } C_i = [(C_i^{**} - C_i^*)/C_i^*] \quad (2.22)$$

where C_i^* is the steady-state value of C_i before the perturbation and C_i^{**} is the steady-state value after the perturbation. The resistance will be defined here as the inverse of this fractional change in C_i , so that resistance increases as this relative fractional change decreases. The computed resistances for the four lakes, if expressed as the inverses of the fractional changes in C_i for the unit change in J_1 , were approximately Resistance₁ = 1.0834, Resistance₂ = 2.522, Resistance₃ = 5.866 and Resistance₄ = 8.510, where greater values denote greater resistance to change. It is clear that in this case the

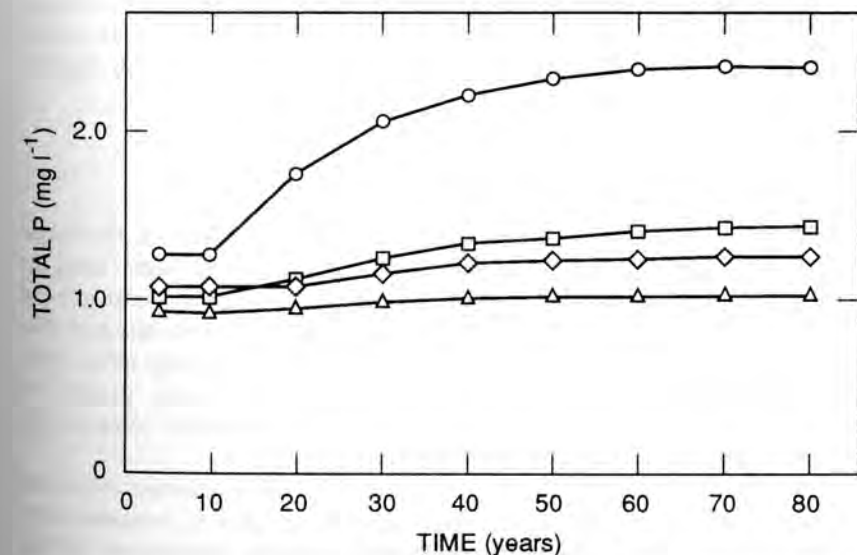


Figure 2.10 Response of concentrations of phosphorus in four connected lakes to a 100% increase in sewage input to Lake 1 in year 10: Lake 1 (circles), Lake 2 (squares), Lake 3 (diamonds) and Lake 4 (triangles). [Based on Ahlgren's (1980) model, Equation (2.22).]

compartments further removed from the perturbation have the greatest resistance.

Resistance can also be thought of as having a temporal component; that is, not only is the magnitude of change important, but also how long it takes that change to occur. In the present case, $\text{Resistance}_2 = 74.56$ at 3 years and 57.27 after 10 years. Clearly, on a short time scale, the resistance to change is high.

The cascading compartment model is a special case of a more general model in which compartments are linked sequentially, but where flows can occur in either direction. Solution of the equations of such a model is much more difficult than solution of the cascade model equations, but the more general model has wider applicability. It has been used for such purposes as the modelling of the nutrient dynamics of connected ocean basins. Wulff (1989) for example, computed the temporal nutrient budgets in the Baltic Sea, and Sarmiento *et al.* (1988) examined the causes of anoxia (severe reduction in oxygen) in the Mediterranean Sea with such models.

The models discussed above are idealizations of real systems. Input flows of water and concentrations of bioelements usually undergo significant temporal fluctuations, as do outflows and the amount of water in the lake. Evaporation and direct precipitation also may have significant effects. While the simple models analysed above fail to take into account these complicating factors, it is possible to derive more general models, based on conservation laws, to represent systems of almost any degree of complexity. Computations of nutrient loading, for example, have been carried out for highly complex spatially heterogeneous and temporally varying cases (e.g. Huff *et al.*, 1973; Bolla and Kutas, 1984).

2.8 SUMMARY AND CONCLUSIONS

The purpose of this chapter has been to introduce some of the basic concepts of flow of solutes through a system and, at the same time, to introduce the types of stability that are most frequently applied in studies of food webs. The systems analysed here are all simple linear systems, and also 'passive' ones in the sense that the compartments do not actively affect their inflows or outflows. Such systems are appropriate starting places for development of concepts and models, as they do not exhibit some of the really surprising features of systems with biotic elements.

The single-compartment model of a nutrient in water solution subjected to an external loading and losses that are proportional to concentration illustrated the principles of steady state and transient components of the solution. The linear system analysed was both locally and globally stable; that is, it recovered to steady state from all plausible perturbations. The rate of recovery is termed resilience and identified with the eigenvalue of the system or the inverse of the return time to equilibrium. In linear systems this

return time is equal to the turnover time or residence time of nutrient in the compartment.

Nutrient dynamics in real systems, even in the absence of biota, are much more complex than can be represented by a single-compartment model. There are interactions of the nutrient solute with sediments or solid components of clay and soil. Coupled equations are required to describe the nutrient dynamics between the aqueous and solid phases. Losses to sediments, both temporary and permanent, can affect the dynamics of the nutrient in the water body. A series of connected compartments, allowing either one-way or two-way flow, may be necessary to describe the nutrient dynamics of many systems that are not internally homogeneous. Another aspect of stability, resistance, is used to measure the inverse of the amount of change of a given compartment to changes in one or more of the flux rates in the system. The speed of change is also important. A system that appears to be highly resistant over a short time period may undergo great changes in response to flux rate changes over a long time period.

One of the useful results shown so far is the equality of mean residence time, T_{res} , a key concept of nutrient flow, and return time of a system to steady state, T_R , an important stability concept. This equality will be shown to be at least a good approximation in the more complex systems studied in later chapters.