Conclusion

This chapter has introduced you to some representative models of temporal and spatial variation of temperature, and the effect of temperature on biological activity. Although they are interesting in themselves, you will find temperature models like these used in simulations of complex systems. For example, a model of lake temperature could be used in conjunction with a temperature-activity model and a model of photosynthesis as input for a model of algal productivity. Temperature-activity models are essential for simulations in which physiological rates of plants or poikilothermic animals are important components.

CHAPTER 13

COMPARTMENTAL MODELS OF BIOGEOCHEMICAL CYCLING

In several previous chapters we considered various ecological models of growing and interacting populations. In this chapter we will study some ecological models for simulating flow of energy and material through organisms and their environment. These biogeochemical models focus on transfer through components of ecosystems, without considering individual organisms. Our approach will be to examine comparatively simple models that illustrate the principles of biogeochemical models. The techniques of compartmental modeling learned here will be useful in the next several chapters.

13.1 The Concepts of Material and Energy Flow

The concept of flow of materials between different components of the biosphere was worked out early in the twentieth century. For example, Lotka's (1925) box-and-arrow diagram for a global cycle of carbon would be at home (with slightly modified data) in current ecology textbooks. This analytical approach was evidently on Elton's mind as he worked out the first food web for an ecosystem in 1923 (Hutchinson 1978). The same approach influenced Lindeman (1942) in the first attempt to measure energy flow through an ecosystem.

One of the early attempts to obtain a complete, detailed description of energy content and flows in a single ecosystem was Odum's (1957) work on Silver Springs, Florida. The results of this research may be summarized in an energy-flow diagram (Figure 13.1). Similar diagrams are the basis of most ecosystem models.

The diagrams show the amount and direction of flow among components of an ecological community, and between the community and its environment. To develop a complete diagram, one must know for each component the standing crop, and the energy or material inputs and outputs. The organisms in the system may be grouped in a variety of ways; a common division is by trophic level. Depending on the interests and

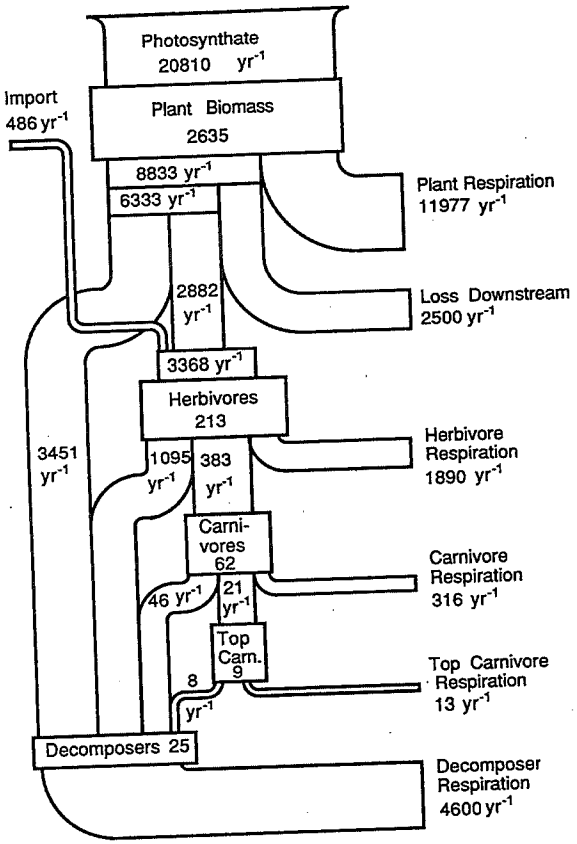

Figure 13.1. An energy diagram of the biological community in Silver Springs, Florida. Based on diagrams by Odum (1957) and by Patten (1971).

objectives of the modeler, a given trophic level may be subdivided in a variety of ways.

13.2 Block Diagrams and Compartment Models

Block diagrams are useful conceptual tools for developing simulations of flow, with each component of the system represented by a rectangular block. The blocks are connected by arrows showing flow of energy or material between components, or between components and the environment. The system may include all biological components of a community, or only a portion, depending upon the modeler's definition of the system. Once the system has been defined, everything else is "environment". Inputs to the system are termed driving or forcing functions. Figure 13.2 is an example of a block diagram.

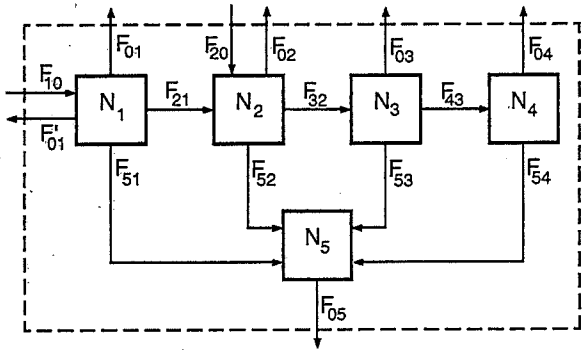

Figure 13.2. A simple block diagram of the Silver Springs energy flow compartmental model, modified from Patten (1971).

The blocks within a diagram may be defined with words. However, letters with subscripts to designate compartments, N_1 and N_2 for example, are more convenient because they may be used directly in writing computer programs. Between compartments, the flows F_{12}, F_{32}, etc., will have subscripts indicating receiving and donating blocks. Conventionally, a subscript of 0 indicates the environment. In this book, the first number in the subscript of a flow will represent the receiving compartment, and the second the source compartment. You should be aware that this subscript order may be reversed by different modelers working in different biological fields. No standardization exists.

In the Silver Springs model (Figure 13.2), N_1 = producers, N_2 = herbivores, N_3 = carnivores, N_4 = top carnivores, and N_5 = decomposers. F_{10} and F_{20} are the two driving flows from the environment. F_{01}, F_{02}, F_{03},

F_{04} and F_{05} represent respiratory losses to the environment from the system. F'_{01} represents the physical loss of plant biomass carried downstream and out of the system by water currents.

Under steady-state conditions, the sum of system inputs, F_{10} and F_{20}, must equal the sum of the system outputs, F_{01}, F_{02}, F_{03}, F_{04}, F_{05} and F'_{01}. Also at steady state, the sum of the inputs to any block must equal the sum of outputs from that block.

The units for the blocks will depend on the system. Usually they express mass or energy on the basis of volume or area. Typical units might be grams of dry weight per square meter, grams of organic carbon per cubic meter, or kilocalories per square meter. The flows will use the same units together with units of time, such as grams per square meter per day, or grams of organic carbon per square meter per year.

A compartmental model is a more formal statement of the block diagram, and includes the equations describing the flows between compartments. Sheppard (1948) apparently was the first to use "compartment" in this sense (Godfrey 1983). The flows or fluxes are used in the equations to provide an energy or material balance for each compartment. The rate of change for each compartment is found by adding the flows into the compartment and the flows out of the compartment. For the Silver Springs model these are

$$\frac{dN_1}{dt} = F_{10} - F_{21} - F_{01} - F_{51} - F'_{01} \tag{13.1}$$

$$\frac{dN_2}{dt} = F_{21} + F_{20} - F_{02} - F_{32} - F_{52} \tag{13.2}$$

$$\frac{dN_3}{dt} = F_{32} - F_{43} - F_{03} - F_{53} \tag{13.3}$$

$$\frac{dN_4}{dt} = F_{43} - F_{04} - F_{54} \tag{13.4}$$

$$\frac{dN_5}{dt} = F_{51} + F_{52} + F_{53} + F_{54} - F_{05} \tag{13.5}$$

Each flow is defined by an equation which usually involves a rate coefficient. We will designate the rate coefficients as f_{ij}. A large number of equations could be used to model flow between compartments, but only a few useful equations are encountered frequently. Some of these are described in Table 13.1. A variety of other examples may be found in Godfrey (1983).

$F_{ij} = k$	Flow from compartment j to i is constant, and is independent of time and system state.
$F_{ij} = f_{ij}N_j$	Flow to i is proportional to the content of j. This is a linear equation with control by the donor compartment only, with rate constant f_{ij}.
$F_{ij} = f_{ij}N_i$	Flow to i is proportional to the content of i. This is a linear equation describing control of flow by the receptor compartment.
$F_{ij} = f_{ij}N_iN_j$	Flow to i is controlled by both donor and receptor compartments in a cross-product manner. This is the mass-action approach. The equation is nonlinear.
$F_{ij} = f_{ij} \cdot f(\text{time})$	Flow from j to i is a function of time. An example is a sine function (Equation 11.2).
$F_{ij} = f_{ij}N_i(1 - g_{ij}N_i)$	Flow from j to i is controlled by a positive linear term and a negative non-linear term, much like the logistic equation.
$F_{ij} = \frac{f_{ij}N_i}{K + N_i}$	Flow from j to i is limited with a hyperbolic term as in Michaelis-Menten kinetics.

Table 13.1. Some useful equations for describing flow between compartments. F_{ij} is the instantaneous flow to compartment i from compartment j, and f_{ij} is the rate coefficient. N_i indicates the content of compartment i.

Compartment models of the type described here are often implemented on computers by solving the system of equations with matrix algebra. This method will be discussed in Chapter 16. For the present, we will solve the equations with a direct approach. Because most of the equations of flow are functions of the size of the compartments, it is necessary

to use the two-stage numerical approach with Euler integration. For clarity of programming, the first stage should be separated into two parts as described in Section 6.2. That is, the various flows F will all be calculated, and then the net changes of content for each compartment will be determined to complete the first stage. Then, following the usual second stage procedures, values of the compartments will be updated.

13.3 The Silver Springs Model

We will continue working with the Silver Springs model as an example. It is not better than similar and more recent models. However, it is familiar and relatively uncomplicated, and it still appears in general ecology textbooks. The set of equations given in this section define the flows in the block diagram of Figure 13.2, and have been modified from Odum (1957) and Patten (1971):

(A. Forcing:)
$$F_{10} = M + R\sin\left(2\pi\frac{(T-11)}{52}\right)$$

$$F_{20} = k$$

F_{10} is the energy input from photosynthesis, assumed to be proportional to light intensity. M is the annual mean photosynthesis, and R is the range of the annual fluctuation around the mean. F_{20} is the energy in 70 loaves of bread fed daily to catfish by the tourist concession at the springs.

(B. Feeding:)
$$F_{21} = \tau_{21}N_1$$

$$F_{32} = \tau_{32}N_2$$

$$F_{43} = \tau_{43}N_3$$

Feeding is donor-dependent in this system, with τ_{ij} the linear coefficient having units of inverse weeks (wk^{-1}).

(C. Mortality:)
$$F_{51} = \mu_{51}N_1$$

$$F_{52} = \mu_{52}N_2$$

$$F_{53} = \mu_{53}N_3$$

$$F_{54} = \mu_{54}N_4$$

Here μ_{ij} is a coefficient of donor-dependent mortality, with units of wk^{-1}.

(D. Respiration:)
$$F_{01} = \rho_{01}N_1$$

$$F_{02} = \rho_{02}N_2$$

$$F_{03} = \rho_{03}N_3$$

$$F_{04} = \rho_{04}N_4$$

$$F_{05} = \rho_{05}N_5$$

Here ρ_{ij} is a coefficient of donor-dependent respiration, with units of wk^{-1}.

(E. Export:)
$$F'_{01} = \lambda_{01}N_1$$

λ_{01} is a coefficient of the loss downstream of small plants and pieces of plants that break loose from the plants that grow in the Silver Spring system. The coefficient has units of wk^{-1}.

After the F_{ij} values are calculated with the equations given above, the first stage in the two-stage Euler procedure is completed with the calculation of the ΔN_i values:

$$\Delta N_1 = (F_{10} - F_{21} - F_{51} - F_{01} - F'_{01})\,\Delta t$$

$$\Delta N_2 = (F_{20} + F_{21} - F_{32} - F_{52} - F_{02})\,\Delta t$$

$$\Delta N_3 = (F_{32} - F_{43} - F_{53} - F_{03})\,\Delta t$$

$$\Delta N_4 = (F_{43} - F_{54} - F_{04})\,\Delta t$$

$$\Delta N_5 = (F_{51} + F_{52} + F_{53} + F_{54} - F_{05})\,\Delta t$$

The second stage of the Euler integration is completed as usual, with

$$N_i \longleftarrow N_i + \Delta N_i$$

Exercise 13-1: Write and implement a program to simulate energy flow through Silver Springs using the model equations above. For

the various compartment sizes and flows, use values given below derived from Odum (1957). The values of mean annual standing crop given in Figure 13.1 (units of kcal m^{-2}) are suitable for initial compartment sizes:

$$N_1 = 2635 \qquad N_2 = 213 \qquad N_3 = 62 \qquad N_4 = 9 \qquad N_5 = 25$$

The values of rate coefficients (units of yr^{-1}) can be calculated by inserting yearly values for the flows and for standing crops into the flow equations for mortality, feeding, respiration and export. This process yields coefficients as follows:

$$\mu_{51} = 1.310 \qquad \mu_{52} = 5.141 \qquad \mu_{53} = 0.742 \qquad \mu_{54} = 0.889$$
$$\tau_{21} = 1.094 \qquad \tau_{32} = 1.798 \qquad \tau_{43} = 0.339$$
$$\rho_{01} = 4.545 \qquad \rho_{02} = 8.873 \qquad \rho_{03} = 5.097 \qquad \rho_{04} = 1.444$$
$$\rho_{05} = 184.0 \qquad \lambda_{01} = 0.94$$

For the driving functions, use the following values:

$$k = 486 \text{ kcal m}^{-2} \text{ yr}^{-1} \qquad R = 175 \text{ kcal m}^{-2} \text{ wk}^{-1}$$
$$M = 400 \text{ kcal m}^{-2} \text{ wk}^{-1}$$

Most of the rate coefficients above are based on annual flows through the system; weekly values may be found with division by 52. Use weeks as the time unit for your simulation, with $\Delta t = 0.1$ week as the unit for Euler integration. Larger Δt values will produce unstable results.

Write your program to plot the contents of each compartment for each week, including initial values. Your output will be a graph with five separate lines, each showing the content of a model compartment.

After you have entered the program into your computer, make an initial trial run, setting $R = 0$. This procedure will keep F_{10} constant. The system should tend rapidly to a steady-state condition. If it does not, then check your program for errors.

After this initial check, carry out a 3-year simulation, beginning with the first week in January. Set $R = 175$ kcal m^{-2} wk^{-1}.

Exercise 13-2: A crude simulation of ecological succession may be obtained with the model above by setting the solar input to a constant value ($R = 0$) and reducing the starting size of all compartments to some minimum value (such as 5 kcal m^{-2}). Allow the simulation of the system to proceed for about 150 weeks to stabilize. Again use $\Delta t = 0.1$ week.

Exercise 13-3: Modify the Silver Springs model above by employing nonlinear feeding equations as follows:

$$F_{21} = \tau'_{21} N_1 N_2$$

$$F_{32} = \tau'_{32} N_2 N_3$$

$$F_{43} = \tau'_{43} N_3 N_4$$

Numerical values for the coefficients may be found by inserting the values for flows and standing crop sizes (Figure 13.1) and solving. This produces the following values for the coefficients:

$$\tau'_{21} = 0.00513 \qquad \tau'_{32} = 0.0290 \qquad \tau'_{43} = 0.0376$$

As in Exercise 13-1, run the simulation for a 3-year period, plotting the energy content of the five compartments. The larger excursions of the compartment contents produced by the nonlinear flows should be apparent.

13.4 Global Carbon-Cycle Model

The increased concentration of carbon dioxide that has been measured in the earth's atmosphere has caused concerns about global warming. There exist real controversies on the relative roles of burning fossil fuels and clearing tropical forests in producing the increase. The relative ability of terrestrial plants and the oceans to serve as reservoirs for the increase in carbon is also controversial. Complex compartmental models are important tools in working with analysis and prediction of the carbon cycle. Bolin (1981) has outlined a simple model of the carbon cycle that shows many of the expected characteristics of the cycle. We will use a modified version of this model as an introduction to the important subject of carbon cycle modeling, and as a further illustration of ecological compartment models.

In this model, carbon is distributed among seven compartments (Figure 13.3). The principal pool of the atmosphere can exchange carbon with both oceanic and terrestrial components. The oceans are represented by only two compartments, one for the mixed layers near the surface that come into contact with the atmosphere, and another for the deeper, more

isolated waters. The terrestrial component is made up of four compartments: short-lived vegetation with a rapid carbon turnover, including annual plants and vegetative parts such as leaves; long-lived vegetation, particularly the woody trunks, stems and roots of trees; detritus, defined as dead and decomposing organic matter, sometimes called litter, duff, or humus; and organic material in the soil.

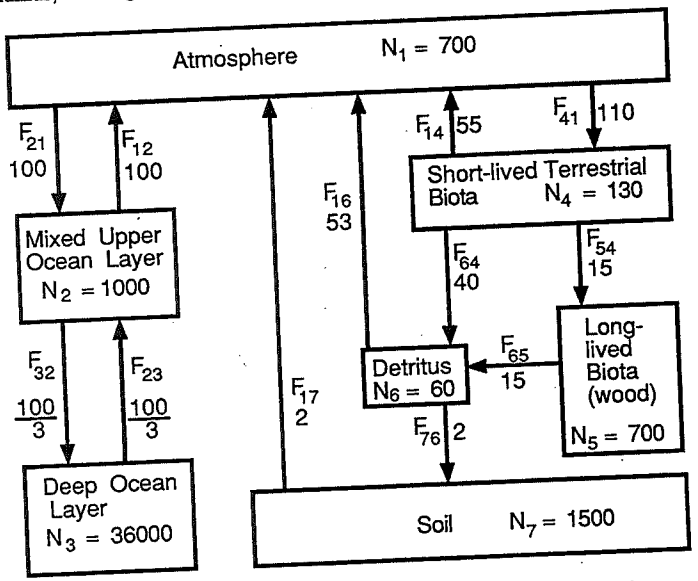

Figure 13.3. Block diagram of the equilibrium carbon cycle, modified from Bolin (1981). Pool sizes are in units of 10^{15} grams (=gigatons; GT). Transfers between compartments are in units of GT year^{-1}.

With two exceptions, the flows between compartments are linear, first-order, donor-controlled flows. That is, flow to compartment i from compartment j is described with

$$F_{ij} = k_{ij} N_j \tag{13.6}$$

The two exceptions are the flows representing uptake of atmospheric carbon by terrestrial plants, and the transfer of carbon dioxide from the ocean

to the atmosphere. In the first case, flow between plants and the atmosphere is controlled by both donor and receptor compartments. Within broad limits, a larger biomass of plants should be able to take up more atmospheric carbon than a smaller quantity of plants. Also, an increase in atmospheric CO_2 may stimulate plant growth, so that the transfer to plants may occur at a greater rate. However, the transfer is not directly proportional to the concentration of atmospheric CO_2; that is, a doubling of the CO_2 concentration would almost certainly not double the flow of carbon. Bolin (1981) suggested a linearized version of a nonlinear equation. Yearsley and Lettenmaier (1987) used the following nonlinear equation for this transfer:

$$F_{41} = k_{41} N_4 \left(1 + \beta \ln \frac{N_1}{(N_1)_0}\right) \tag{13.7}$$

Here, $(N_1)_0$ is the equilibrium value for the atmospheric carbon, N_1 is the current concentration, and β is a photosynthetic coefficient. The equation is semi-empirical, and indicates that uptake of atmospheric carbon is proportional to the amount of plant material when the atmosphere is at the equilibrium level of 700 GT. As atmospheric carbon rises above the equilibrium level, plants will be able to take up only a part of the increased atmospheric CO_2 .

The second instance of nonlinear flow is the transfer from the ocean to the atmosphere. This transfer is made complex by the chemical buffering system of the ocean. Bolin (1981) suggested that the flow could be described with

$$F_{12} = k_{21} \left((N_1)_0 + \xi \frac{(N_1)_0}{(N_2)_0} [N_2 - (N_2)_0]\right) \tag{13.8}$$

The equilibrium values for the atmosphere and mixed-layer are given with $(N_1)_0$ and $(N_2)_0$. The current value of the mixed layer is N_2, and ξ is a buffering constant. k_{21} (not a misprint) is the constant for the flow to compartment 2 from 1. This equation may be written in a much simpler form when appropriate constants are inserted. The result is:

$$F_{12} = N_2 - 900 \tag{13.9}$$

This form of the equation will hold for all reasonable values of an increase in the CO_2 content of the mixed layer. Elaborations of Bolin's basic model and more complex models may be found in papers by Yearsley and Lettenmaier (1987), Mulholland et al. (1987), and Detwiler and Hall (1988).

Exercise 13-4: On your computer, implement the global carbon model from the above information. As an early step in your program, solve for the transfer coefficients for the various flows (except F_{12} and F_{41}) using Equation 13.6. That is, find $k_{ij} = F_{ij}/N_j$. Use the whole-number equilibrium values in Figure 13.3. Because the model is sensitive to errors in the fourth or fifth significant digit for these constants, it is easiest to have the computer solve for these k_{ij} values and retain them.

Write your program using two-stage Euler integration, following the procedure described in Sections 13.2 and 13.3. That is, first calculate all the flows F_{ij} using Equation 13.6, but for F_{12} use Equation 13.9, and for F_{41} use Equation 13.7 with $\beta = 0.10$ and $k_{41} = 110/130$. Then find all the compartmental changes ΔN_i, and finally perform the updates for the new values of N_i. For this simulation set $\Delta t = 0.1$ year.

Begin your simulation with the equilibrium pool values from Figure 13.3. Plot the values of the various pools N_i through time for 20 years to be sure they remain at equilibrium.

After you are sure your program is working with the equilibrium values, alter your program so that a slug of 10 GT of carbon is added to the atmosphere at the beginning of year 10. This simulates the burning of a large amount of fossil fuel in that year. Follow the result of the perturbation for 90 years. For this simulation, the graphical output should show the departure of each pool from its equilibrium value, rather than pool size. That is, your x-axis should run from 0 to 100 years, and your y-axis from -10 to +10 GT.

Exercise 13-5: Modify the program of Exercise 13-4 to simulate a single incident of massive destruction of forest and release of carbon by burning of the wood. This is easily done by removing 10 GT from the compartment of long-lived biota at the same time that 10 GT is added to the atmosphere.

Exercise 13-6: For more than a century atmospheric carbon has been increasing principally because of combustion of fossil fuels including coal and oil. The amount of carbon added to the atmosphere each year has also increased. The amount of carbon from fossil sources added to the atmosphere each year by human activity may be described quite accurately with

$$\text{GT added each year} = 0.5\, e^{0.03t}$$

where t is the number of years since 1900 (Rotty 1981).

Modify your program from Exercise 13-4 to simulate the addition of carbon from fossil fuel combustion for an 80 year period, 1900-1980. At least initially most of the added carbon accumulates in the atmospheric pool N_1. As output from your program, plot the cumulative carbon input to the atmosphere from fossil fuel combustion, and the change in the atmosphere from equilibrium. Then alter your program so that it will plot the distribution of the added carbon among the seven pools over the 80-year period. Initially, almost 100% of the added carbon will be in the atmosphere; this should decline to about 30% after 80 years, with 70% distributed among the other compartments.

13.5 Simulated Food Chain

Elliot et al. (1983) based a model of a planktonic grazing food chain on a general model of predation developed by Wiegert (1975, 1979). The model is instructive because it attempts to include a number of realistic factors in the transfer of material through the food chain. Some of these factors you have encountered previously in Chapters 7 and 8 for homogeneous populations, including self-limitation of population size, saturation of predators, and minimal prey density. The basic four-compartment model of the planktonic food chain is shown in Figure 13.4.

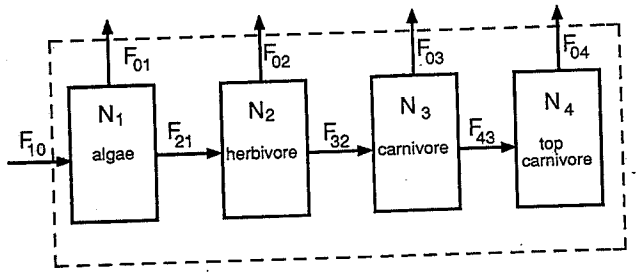

Figure 13.4. A block diagram for a simple 4-compartment model of a planktonic grazing food chain.

The model is simplified so that non-grazing losses from each compartment are combined in a single term. That is, rates of respiration, non-grazing mortality, etc., are all lumped together in a single factor to model loss to the environment. This flow to the environment from each of the four compartments is given by

$$F_{0i} = \lambda_{0i} N_i \qquad (13.10)$$

where N_i is compartmental density (measured in units of mass) and λ_{0i} is the rate constant for loss, with units of time^{-1}.

The system is driven by a flow into compartment 1 from the environment, F_{10}. This flow will be a constant in the simulation described here. However, it may be made a function of time, for example a sine function as in the Silver Springs simulation above.

The predatory or grazing transfers of mass between all the compartments are modeled with equations having the same form. The equations include terms for both donor and receptor control:

$$F_{21} = \tau_{21} N_2 [D_{21} R_{21}]_+ \tag{13.11}$$

$$F_{32} = \tau_{32} N_3 [D_{32} R_{32}]_+ \tag{13.12}$$

$$F_{43} = \tau_{43} N_4 [D_{43} R_{43}]_+ \tag{13.13}$$

In these equations τ_{ij} is the feeding rate constant for grazing transfer to compartment i from j. It may also be thought of as the rate constant for exponential growth of N_i, whenever D_{ij} and R_{ij} are held constant.

The + subscript for the bracketed term is used to indicate that this term must be positive or zero. That is,

$$[x]_+ = x \quad \text{if} \quad x \geq 0$$

$$[x]_+ = 0 \quad \text{if} \quad x < 0$$

(Note that this is not equivalent to absolute value.) In these equations, this convention prevents the flow from being negative, and having the prey feeding on the predator. (The terminology is easily programmed in BASIC with the statement IF X < 0 THEN X = 0.)

The explanations of the D and R components of these equations will be given for the specific example of F_{21}, the flow to compartment 2 from compartment 1. Only the subscripts need to be altered to find the equivalent terms for F_{32} and F_{43}.

D_{21} is a term for the donor control of flow to compartment 2 from 1. The term may take several forms, including $D_{21} = 1$ to indicate simple receptor control of flow. Wiegert (1979) suggests the following as a realistic expression:

$$D_{21} = \left[1 - \left(\frac{\alpha_{21} - N_1}{\alpha_{21} - \gamma_{21}}\right)_+\right]_+ \tag{13.14}$$

The function of the + subscripts is important and is described above. α_{21} is a constant that represents a saturating density of prey N_1. When prey density N_1 is greater than α_{21}, then D_{21} is equal to 1. Thus, F_{21} in Equation 13.11 will not be decreased because of a lack of prey. γ_{21} is a constant that represents some minimal density of prey. If prey density N_1 drops below γ_{21}, then D_{21} drops to zero. In this case, F_{21} in Equation 13.11 will become zero also, and there will be no feeding on the prey. (γ_{21} may represent for example the number of hiding places for prey, where they can be safe from predation.)

R_{21} is the term in Equation 13.11 for receptor control of the flow F_{21}. In this model it describes self-limitation of the predator population, with a modified logistic function. Weigert's (1979) expression was:

$$R_{21} = \left[1 - \left(1 - \frac{\lambda_{02}}{\tau_{21}}\right)\left(\frac{N_2 - \alpha_{22}}{\gamma_{22} - \alpha_{22}}\right)_+\right]_+ \tag{13.15}$$

Again, the + subscripts are important. λ_{02} is the rate constant for loss from compartment 2. α_{22} is a constant indicating the density at which predators begin to interact and to compete with each other. When N_2 exceeds α_{22}, R_{21} drops below 1 because of the predators' self-interference. γ_{22} represents the limiting maximum density of predators, so that R_{21} will decline as N_2 approaches γ_{22}.

This model system is extremely flexible, and can be used to simulate many features of the grazing food chain of aquatic ecosystems. The equations and constants may be modified to provide a variety of possible simulations, involving changes in refuge size, maximal densities, predation rates, and loss rates. These variations will produce widely varying results. The density of compartments may reach equilibrium, or oscillate in stable and unstable ways.

Exercise 13-71: Write a program for simulating planktonic grazing with the 4-compartment model of food chains described above. As described in Section 13.2, use a two-stage Euler integration, with the first stage subdivided into two parts. That is, for stage one first calculate the flow rates between components of the system with Equations 13.10 through 13.15, and then find the ΔN_i values by summing rates. For stage two, update the compartment values. It should be adequate to set $\Delta t = 0.1$ for the simulation of planktonic grazing.

The following coefficients were suggested by Elliot et al. (1983) as reasonable estimates for the grazing planktonic food chain in some freshwater systems:

$\lambda_{01} = 0.10$ $\lambda_{02} = 0.46$ $\lambda_{03} = 0.37$ $\lambda_{04} = 0.20$
$\tau_{21} = 1.15$ $\tau_{32} = 0.74$ $\tau_{43} = 0.27$
$\alpha_{21} = 20.0$ $\alpha_{32} = 15.0$ $\alpha_{43} = 5.0$
$\gamma_{21} = 5.0$ $\gamma_{32} = 2.0$ $\gamma_{43} = 0.50$
$\alpha_{22} = 10.0$ $\alpha_{33} = 5.0$ $\alpha_{44} = 1.0$
$\gamma_{22} = 30.0$ $\gamma_{33} = 20.0$ $\gamma_{44} = 20.0$

Use a constant input for this system of $F_{10} = 20.0$. For initial values of the compartments, use the following:

$N_1 = 10.0$ $N_2 = 2.0$ $N_3 = 5.0$ $N_4 = 1.0$

In this simulation, units of time and units of mass are arbitrary. As output for this simulation, plot values of the compartmental densities N_i against time for 0 to 240 units of time.

Exercise 13-8: Modify the simulation of Exercise 13-7 to show the effect of limiting the maximum density of the top carnivore. This modification might be needed for a simulation with a species that is more territorial, for example. Thus, in your program reduce the constant for maximum top carnivore density, γ_{44}, from 20 to 10 units and then rerun the simulation.

Conclusion

This chapter has introduced you to some of the concepts and techniques of working with models of material and energy flow through large-scale systems. In succeeding chapters you will work with compartmental models of smaller systems, and many of the methods you have learned here will be useful. The direct two-stage Euler approach has been described for implementing these models on the computer. The more elegant matrix approach will be taken up in Chapter 16. The three examples described in this chapter were relatively simple and designed to promote understanding of methodology. However, the same techniques may be applied to more complex, diverse systems. The simulation programs become longer, and the results less intuitively obvious, but the fundamental methods still apply.

CHAPTER 14
DIFFUSION MODELS

In the compartmental ecological systems of the previous chapter, the mechanisms of transport of material and energy between compartments were relatively straightforward. In physiological models, the mechanisms of transport are frequently the subject of interest. These mechanisms usually fall into three general categories: diffusion, active transport, and fluid flow. Each of these presents different problems requiring different modeling approaches. We will consider the first two mechanisms in this chapter. Fluid flow and other transfers among physiological compartments will be discussed in the next chapter.

A solution is made by dissolving some matter (solute) in a fluid (solvent). A solution may be described by its mass concentration, which is the mass of the solute per unit volume of solution. Molecules of solute are dispersed through the solvent by diffusion, a result of the thermal movements of the solvent molecules colliding with the molecules of solute.

14.1 Transport by Simple Diffusion

A simple model of transport of material by diffusion between a single compartment and an unchanging environment was discussed in Section 1.5. Frequently we are interested in diffusion between compartments, for example between two adjacent cells (Figure 14.1). Across a membrane separating the two compartments, net material transfer will proceed from the compartment of higher concentration to the compartment of lower concentration. The rate of transfer will be proportional to the difference in concentrations. For the simple model here, we will assume constant compartmental volumes and uniformity of concentration inside compartments.

The following equation describes forward diffusion from compartment i to j:

$$\left(\frac{dQ_i}{dt}\right)_f = \frac{-kQ_i}{V_i} \tag{14.1}$$