

5 The Improved Euler Method

As you discovered in Exercise 5-3, reducing the time increment Δt decreases the error, but also causes a proportional increase in computer time required to perform a given integration. Complex biological simulations require highly accurate integration to work properly and will cause increases in computer times that become inconvenient, expensive, and so on. Hence, there has been a lot of mathematical research on methods which reduce the error other than by decreasing Δt .

Most of the error in the simple Euler method applied to the growth model occurs because it proceeds as if the slope in the interval Δt has constant value which is a function of N_t . In fact, the slope changes continuously between N_t and $N_{t+\Delta t}$.

The Improved Euler is based on finding a better estimate of slope within interval Δt . (The description here is based on the general notation of Equations 5.1-5.3 above.) First one finds an estimate of slope at y_t and an estimate of slope at $y_{t+\Delta t}$. The improved slope is the average of these two estimates. The equations which accomplish this estimation are as follows:

$$\Delta y'_t = f(y_t) \Delta t \quad (5.8)$$

$$y'_{t+\Delta t} = y_t + \Delta y'_t \quad (5.9)$$

$$\Delta y''_t = f(y'_{t+\Delta t}) \Delta t \quad (5.10)$$

$$\Delta y_t = \frac{\Delta y'_t + \Delta y''_t}{2} \quad (5.11)$$

$$y_{t+\Delta t} = y_t + \Delta y_t \quad (5.12)$$

This set of equations, $\Delta y'_t$ is the first estimate of the slope and is used to find the second estimate, $\Delta y''_t$. These two estimates are averaged in Equation 5.11, and the average is used to update y_t in Equation 5.12. The technique is illustrated graphically in Figure 5.2. The analogous equations for exponential growth (Equation 1.3) would be:

CHAPTER 12

TEMPERATURE AND BIOLOGICAL ACTIVITY

Models of temperature are important in most fields of biological inquiry because of the effect temperature has on rates of biological activity. This is produced primarily by effects of temperature on chemical reaction rates. At low temperatures reaction rates become vanishingly small, and biological activity all but ceases. At high temperatures competing reactions, such as the denaturation of vital proteins are favored, and organisms begin to lose their integrity. Biological activity is primarily confined to temperatures between 0 and 100° Celsius. This chapter will describe some methods for modeling seasonal and daily variation of temperature and heat balance, and for describing the effect of temperature on rates of biological processes.

12.1 Seasonal and Daily Variation in Temperature

Temperature of the environment is largely a function of solar radiation. For this reason environmental temperatures tend to follow sinusoidal patterns like those of light intensity in the previous chapter. Temperature also partly depends on the quantity of heat stored in the environment as a result of solar inputs. If solar radiation were stored and reradiated uniformly, the temperature curve would be the integral of the solar sine curve. Analytically, the integral of a sine function is a negative cosine function:

$$\int \sin x \, dx = -\cos x + c \quad (12.1)$$

A negative cosine curve is identical to the sine curve, except that it lags the sine curve by 90° (i.e., it is out of phase by one-fourth wavelength). This relationship is diagrammed in Figure 12.1. The cosine approximation of temperature is inadequate, because the earth's surface is not homogeneous; air, land, and water can absorb, circulate and exchange heat energy at different rates. At most locations on the earth's surface, air temperature lags solar intensity by 3 to 4 weeks, rather than 13 weeks as

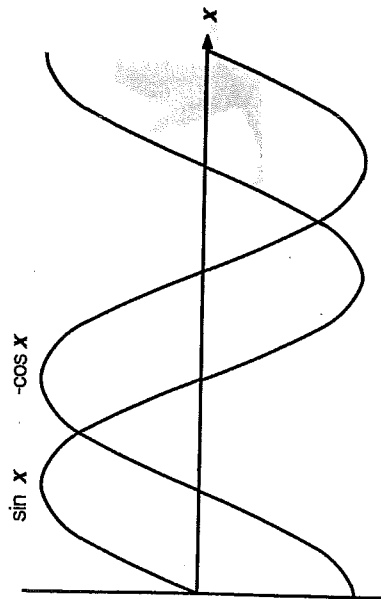


Figure 12.1.1. Comparison of sine curve with its integral, the negative cosine curve.

predicted by the negative cosine curve. If we use the 4-week figure and assume that average annual air temperature is 10°C with a range of 12°C for average daily temperatures on either side of the annual mean, we can find the average daily temperature for any week with

$$T = 10 + 12 \cdot \sin\left(2\pi \frac{W - 15}{52}\right) \quad (12.2)$$

This can be compared with a model for light intensity from Chapter 11:

$$I_d = 400 + 200 \cdot \sin\left(2\pi \frac{W - 11}{52}\right) \quad (12.3)$$

In many simulations, extremes of temperatures are more important than means. Webb et al. (1975) developed a model for air temperature of an Oregon forest which was composed of three elements: mean, daily temperature, daily temperature range, and daily temperature excursion. Air temperature at any hour of any day is found with the relationship

$$\text{Air Temperature} = \text{Mean} + (\text{Range})(\text{Excursion}) \quad (12.4)$$

The following equations were used to find each of these components:

$$\text{Mean} = 10 + 8 \sin\left(2\pi \frac{D - 107}{365}\right) \quad (12.5)$$

$$\text{Range} = 7 + 2 \sin\left(2\pi \frac{D - 107}{365}\right) \quad (12.6)$$

$$\text{Excursion} = \sin\left(2\pi \frac{H - 17}{24}\right) \quad (12.7)$$

Equation 12.5 indicates that mean daily temperature has an annual average of 10°C , and a range of 8°C . This is multiplied by the sine function which starts its 365-day cycle on day 107 (17 April); the peak mean temperature of 18°C will come on day 198 (17 July). Equation 12.6 indicates that the average daily fluctuation of $\pm 7^{\circ}\text{C}$ in temperature will take place on days 107 and 290; the maximum fluctuation of $\pm 9^{\circ}\text{C}$ will occur on day 198. Equation 12.7 provides the timing of the daily temperature variation, with the minimum at 0400 (4 am) and a maximum at 1600 (4 pm). In these three equations, time is expressed as D , Julian calendar days, and as H , hours, from 0 to 24 with solar noon at 12.

Exercise 12-1: Write a program to simulate air temperature in an Oregon forest, using Equations 12.4-12.7. Perform time increments in nested FOR-NEXT loops, using the outer loop to increment days, and the inner loop for hours. Set up your program to produce graphical output showing air temperature for each hour during the weeks of 1-7 January and 4-10 July. Then modify your program to produce a graph of air temperature over the 24-hour period of your birthday. (This will be useful for planning your birthday picnic in an Oregon forest.)

12.2 Heat Balance in Biological Systems

Heat balance determines the temperature of natural objects and organisms. If an object is absorbing or generating heat faster than it is giving off heat, obviously its temperature must rise. In this section we will consider the heat balance of an entire lake, and also of a desert-dwelling mammal.

The major source of heat energy input for a lake is solar radiation striking its surface. It is not surprising that the heat content and water temperature of a lake will follow an approximate sine function on an annual basis. The energy budget equation which describes the heat content

of a lake is

$$Q_{t+\Delta t} = Q_t + (I_t + S_t - E_t - O_t) \quad (12.8)$$

where Q_t is the heat content of a lake at time t , and $Q_{t+\Delta t}$ is the heat content one week later. Heat content is measured on the basis of the exposed surface of the lake, as calories cm^{-2} . The other components of the equation are I_t , the effective radiation coming in through the lake's surface; S_t , the sensible heat transfer by conduction or convection to or from the atmosphere; E_t , the heat lost or gained by evaporation or condensation; and O_t , the heat lost as radiation to the atmosphere. These four components are rates, and are each expressed below as calories $\text{cm}^{-2} \text{ week}^{-1}$.

Radiation input by weeks may be described by the following equation:

$$I_t = 2800 + 1400 \sin \left(2\pi \frac{w-11}{52} \right) \quad (12.9)$$

The form of this equation and the constants have been described above (e.g. Equation 12.2). Sensible heat transfer is based on Newton's law of cooling (see Chapter 1) and is given by

$$S_t = k(T_a - T_w) \quad (12.10)$$

where T_w is the surface temperature of the water and T_a is the temperature of the air overlying the water. Air temperature may fluctuate as in Equation 12.2. The transfer coefficient will vary with wind velocity; you may assume that it has a value of 100 calories $\text{cm}^{-2} \text{ week}^{-1} \text{ } ^\circ\text{C}^{-1}$.

Evaporation removes heat from the lake and may be described by the equation

$$E_t = RH(P_w - P_a) \quad (12.11)$$

The various terms in this equation are defined as follows. R is a rate constant that depends on wind velocity. Assuming an average wind velocity of 10 m sec^{-1} , R will have an approximate value of 1.0 gram $\text{mmHg}^{-1} \text{ cm}^{-2} \text{ week}^{-1}$. H is the latent heat of evaporation and is a function of water temperature. Over the range of 0 to 50°C, H may be approximated by this equation:

$$H = 595.8 - 0.54T_w \quad (12.12)$$

P_w is the saturation water vapor pressure, which is also a function of surface water temperature. P_w is approximated by a cubic equation (Chapter 3):

$$P_w = 4.57 + 0.357T_w + 0.0065T_w^2 + 0.00047T_w^3 \quad (12.13)$$

P_a is the partial pressure of water vapor in the air and is quite variable. For purposes of this simulation we may assume a constant 80 percent

relative humidity, so that P_a will be a function of air temperature as follows:

$$P_a = 3.66 + 0.286T_a + 0.0052T_a^2 + 0.00037T_a^3 \quad (12.14)$$

According to the Stefan-Boltzmann law, thermal radiation of the lake to the atmosphere is a function of the absolute temperature of the lake surface, raised to the fourth power. The atmosphere will also radiate to the lake as a function of atmospheric temperature. The relationship between atmospheric temperature and radiation is not simple (Hutchinson 1957). We will employ a simple equation that relates the net thermal radiation between a lake and the atmosphere to the difference between air temperature and water temperature:

$$O_t = 77(T_w - T_a) \quad (12.15)$$

where O_t is the net thermal radiation with units of calories $\text{cm}^{-2} \text{ week}^{-1}$.

Exercise 12-2: Prepare a flowchart for a program to simulate water temperature of a lake based on the heat-balance model described with Equations 12.8-12.15. Then implement your program using the given transfer coefficients and rate constants. The output of your program should consist of a graph showing lake temperature for 104 weeks (2 years). Assume the lake has an initial temperature of 6°C on January 1, and that the lake circulates continuously throughout the year. Also assume the lake to have an average depth of 10 meters, so that

$$(T_w)_t = \frac{Q_t}{1000} \quad (12.16)$$

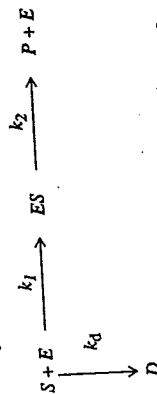
based on the specific heat of water of 1 calorie $\text{gram}^{-1} \text{ } ^\circ\text{C}^{-1}$. Although this simulation appears complex because of the number of equations involved, it is in fact greatly simplified and ignores many important features of the lake environment, including stratification. Section 12.7 below describes a model that includes stratification. For more information on models of heat balance for lakes, see Hutchinson (1957) and Wetzel (1983).

Exercise 12-3: Like most mammals placed in a hot environment, camels regulate their body temperatures partially by evaporative cooling (sweating) if they have enough drinking water. However, a partly dehydrated and thirsty camel exposed to heat will conserve water, and rather than sweating will allow its body temperature to increase. This takes advantage of the decreased rate of transfer of

where k_2 and k_1 are rates at temperatures C_2 and C_1 . The equation is useful over relatively narrow ranges of temperature. Prosser and Brown (1961) discuss this problem further.

12.4 Effect of Temperature on Enzyme Activity

The amount of product produced by a reaction catalyzed by an enzyme depends on two reactions that have different rates. One reaction is the actual formation of product; the other is the denaturation of the enzyme. These reactions may be written together as follows:



where E is the active form of the enzyme, D is the denatured form, P is the product, S is the substrate, and ES is the enzyme-substrate compound. The rate of product formation is

$$\frac{dP}{dt} = k_2[ES] \quad (12.24)$$

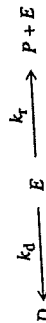
If substrate is in excess and k_2 is the rate constant for the limiting reaction, we may assume that ES is in equilibrium with E and S , so that k_1 is given by

$$k_1 = \frac{[ES]}{[E][S]} \quad (12.25)$$

If this equation is rearranged and substituted into Equation 12.24, then

$$\frac{dP}{dt} = (k_2 k_1 [S]) [E] = k_r [E] \quad (12.26)$$

where k_r is an overall constant involving k_1 , k_2 , and substrate concentration $[S]$, which will be essentially constant if in great excess. The reaction now simplifies to



The effect of temperature on k_r may be modeled using a modification of Equation 12.20:

$$(k_r)_T = (k_r)_0 \exp \left(\frac{A_r T}{T + 273} \right) \quad (12.27)$$

where T indicates temperature in $^{\circ}\text{C}$.

The denaturation rate constant, k_d , also depends on temperature, and may be described by an equation similar to 12.27. Because of the very high activation energy involved, the reaction has a very high value of A_d , which is equivalent to a very high Q_{10} value. Here we will assume that denaturation is controlled totally by kinetic effects. The equation would be much the same if instead we were to assume a temperature effect on the equilibrium constant involved in the denaturation reaction.

Exercise 12-4: Using the equations above, write a program to simulate the effect of temperature on an enzyme-catalyzed reaction. Base your measurement of rate of product formation (i.e. activity of enzyme) on amount of product that is obtained after the reaction has proceeded for some arbitrarily specified period of time. Because denaturation of the enzyme depends on time, the optimum temperature shown by your simulation will partly be a function of length of this time period, as shown in Figure 12.3. A flowchart for the program is shown in Figure 12.2. Implement your simulation using the following values:

$$\begin{aligned}
 (k_r)_0 &= 1 & (k_d)_0 &= 0.0001 & A_r &= 18 \\
 A_d &= 55 & E_0 &= 2 & t_{\max} &= 20
 \end{aligned}$$

Set $\Delta t = 0.01$. The output of your simulation should be a graph of the amount of product vs. temperature, for temperatures from 0 to 80°C . Your graph should resemble a typical optimum temperature curve like those of Figure 12.3.

12.5 Models of Temperature Effects on Biological Activity

Many models have been published to describe effect of temperature on rates of biological processes. The available literature is so large that Watt (1976) described it as "truly awesome". Many of these models attempt to use simple enzyme effects for complex biological processes involving many enzymes. In general, such models assume that a single enzyme will limit rates in complex systems like a developing embryo or feeding animal. The response of the whole organism is assumed to be similar to that of the limiting enzyme. This assumption is usually incorrect, because different enzymes can be limiting at different temperatures.

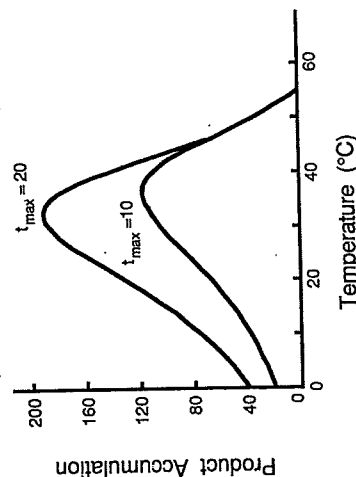


Figure 12.3. Curves showing simulation results of response of enzymes to different temperatures.

Overall response of a biological process to temperature is a composite of the response curves of all enzymes that might limit the rate within the temperature range for the organism. An overall response curve may be very different from that produced by a single enzyme. For example, Sharpe and DeMichele's (1977) model of development rate at different temperatures was based on Eyring's transition-state theory (Johnson et al. 1954, Eyring and Urry 1965). Assuming a single limiting enzyme, the model uses six constants that must be estimated from data. They note that the composite curve from multiple limiting enzymes could be described with their equation. The constants then would be simply regression coefficients for an empirical equation.

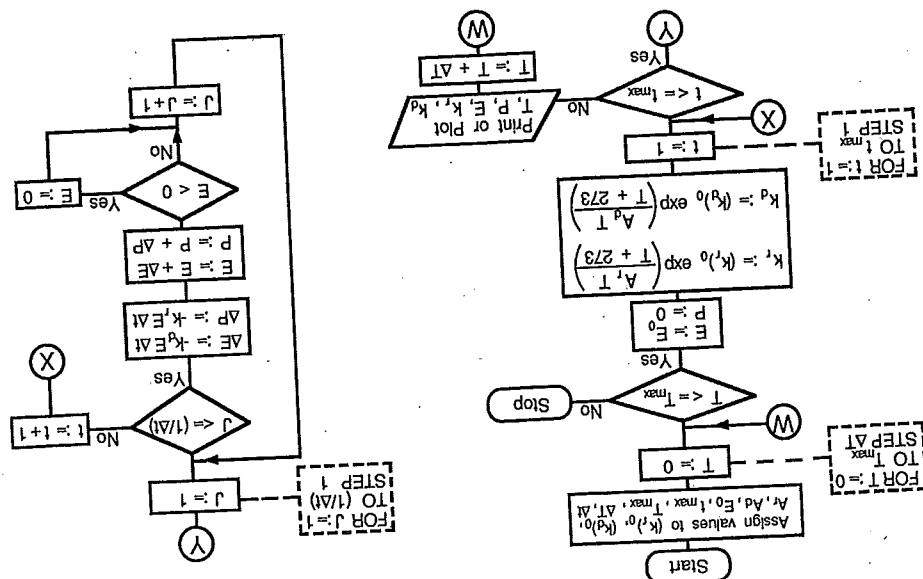
We present here two empirical equations which have been used to describe effects of temperature on biological rates. Below optimum temperature the rate rises approximately exponentially; above optimum it descends sharply.

O'Neill et al. (1972) developed an equation which results in a curve with the necessary form, and at the same time is based on constants which may be readily derived from most experimental data. The equation has the following form:

$$k_T = k_{\max} U^x \exp(xV) \quad (12.28)$$

where

$$U = \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \quad (12.29)$$



with increasing temperature. The second, exponential term describes the rate of denaturation of a limiting enzyme, which causes the rate to decline. As temperature increases, the two terms compete, and k_T reaches a maximum value at the optimum temperature. Above this temperature, the second term predominates because its rate of change per degree is much greater than the first term.

The constants k_1 and k_2 may be determined with nonlinear curve-fitting techniques. In actual practice, the values of the constants and the values of the temperature optimum, maximum and minimum may all be evaluated with techniques that permit the least-squares estimation of several coefficients.

Exercise 12-5: Write a program which determines k_T with Equation 12.28 for temperatures between 0 and 48°C. Use the following values for constants in the equation:

$$T_{\text{opt}} = 37 \quad T_{\text{max}} = 42 \quad Q_{10} = 2.5 \quad k_{\text{max}} = 100$$

Output for your program should be a curve showing k_T plotted against temperature in °C.

Exercise 12-6: Moner (1972) obtained the following values for growth rate (inverse of division time) for the ciliated protozoan *Tetrahymena pyriformis* at different temperatures:

°C	Rate	°C	Rate	°C	Rate
14	0.0023	21	0.0073	28	0.0129
15	0.0029	22	0.0087	29	0.0131
16	0.0036	23	0.0093	30	0.0132
17	0.0041	24	0.0100	31	0.0131
18	0.0048	25	0.0110	32	0.0111
19	0.0060	26	0.0117	33	0.0059
20	0.0066	27	0.0121	34	0.0000

Produce a graph of these data with a simple connect-the-dots routine, plotting rate vs. °C. From the plot, estimate the constants needed for the O'Neill model (Equation 12.28).

Write a program as in Exercise 12-5 to draw a curve of k_T vs. temperature from 10°C to 40°C, using your estimates of the constants. On the same graph, plot the actual data points to examine the accuracy of the model equation. You will discover that the

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$$V = \frac{T - T_{\text{opt}}}{T_{\text{max}} - T_{\text{opt}}} \quad (12.30)$$

$$x = \frac{W^2 \left(1 + \sqrt{1 + 40/W}\right)^2}{400} \quad (12.31)$$

Here, k_T is the rate of the process at temperature T , k_{max} is the rate at the optimum temperature T_{opt} , and T_{max} is upper lethal temperature. Temperatures are all measured in °C. W is defined as follows:

$$W = (Q_{10} - 1) (T_{\text{max}} - T_{\text{opt}}) \quad (12.32)$$

The Q_{10} value should be estimated from the nearly linear increasing portion of the rate curve. The principal advantage of Equation 12.28 over other exponential equations is that its constants are readily found from plots of most real data. Its disadvantage is the obscure theory behind Equations 12.31 and 12.32. For temperatures above T_{max} it is necessary to set $k_T = 0$, because the equation is not designed to predict values beyond that point.

Logan (1988) reviewed a number of empirical equations that can produce temperature-rate curves resembling those of Figures 12.3 and 12.4. One of the more useful empirical models is partly based on an exponential function like the O'Neill equation above:

$$k_T = k_1 \left(\frac{\tau_1^2}{\tau_1^2 + k_2} - \exp(-\tau_2) \right) \quad (12.33)$$

In this equation, k_T is the rate at temperature T , k_1 and k_2 are empirical constants, and τ_1 and τ_2 are determined from experimental temperature data as

$$\tau_1 = T - T_{\text{min}} \quad (12.34)$$

$$\tau_2 = \frac{T_{\text{max}} - T_1}{T_{\text{max}} - T_{\text{opt}}} \quad (12.35)$$

The maximum and optimum temperatures for the reaction rate are defined as in the O'Neill model above. T_{min} is determined from the data, and is the low temperature at which the reaction rate drops effectively to zero. The bracketed part of Equation 12.33 contains two terms which compete to determine the rate. The first term (left-hand) resembles the Michaelis-Menten relationship, and will produce a sigmoid rise in the rate

Suppose that an egg is laid in an environment with temperatures alternating between 10°C and 20°C on a 12-hour cycle. If the egg begins to develop at the start of a 12-hour period of 10°C, development will proceed as follows:

Time period	Rate	Development	Sum	Total hrs
12 hrs at 10°C	0.01	0.12	0.12	12
12 hrs at 20°C	0.03	0.36	0.48	24
12 hrs at 10°C	0.01	0.12	0.60	36
12 hrs at 20°C	0.03	0.36	0.96	48
4 hrs at 10°C	0.01	0.04	1.00	52

Exercise 12-8: Write and implement a program based on the rate-summation method to find duration of development when temperature varies. Include in your program a sequence of DATA statements giving length of the period, temperature, and the rate at that temperature. Your program should read a DATA statement, and then calculate the proportion of development that occurs during the period, sum up the development to that time, and check to find if it exceeds 1.00. If not, data for the next period should be read. The portion of the final period required to complete development should be calculated. Output from your program should be in a tabular form, as given above. Test your program using a cycle of alternating 6-hour periods of rates of 0.022 and 0.034 at 12°C and 18°C respectively. Assume egg development begins at the start of a period with the higher rate.

12.7 Model of a Stratifying Lake

The heat-balance model of a lake in Section 12.2 was not very realistic because heat was assumed to be uniform throughout the water column. In fact, most heat is absorbed near the surface and carried down through the water column. One method for modeling lake temperature is to divide the lake vertically into separate compartments. For this method, heat transport is assumed to occur only in the vertical dimension between compartments. Each compartment represents one meter of depth below 1 cm² of surface, so the volume of each compartment is 100 cm³. Heat content of each compartment is measured in calories; in this model, water at 0°C has a caloric content of 0. Thus, temperature of any compartment is its heat content divided by 100 cal °C⁻¹.

Solar radiation provides the principal heat input. Absorbed energy contributes to the heat content of a compartment at depth z as described

model is quite sensitive to small differences in the estimate of Q_{10} . You should try using various Q_{10} values to improve the fit of the plotted line to the data.

Exercise 12-7: As in Exercise 12-6, produce a rate vs. temperature graph of Moner's (1972) data. From the plot, estimate the values of T_{opt} , T_{max} and T_{min} needed for Logan's Equation 12.33. Then use the CURNLFIT program (Chapter 3) to estimate the constants k_1 and k_2 . (To do this, you will need to read in the temperature as x -values and the rates as y -values. Put Equation 12.33 into CURNLFIT using k_T as Y , T as X , and your estimates of T_{min} , T_{max} , and T_{opt} as constants; use k_1 as coefficient A and k_2 as coefficient B .) For initial approximate values needed by CURNLFIT, use 3 times the measured maximum rate for k_1 (coefficient A), and 2 times ($T_{max} - T_{min}$) for k_2 (coefficient B).

12.6 Modeling Development in Variable Temperatures

Most plants, animals and microbes grow and develop in environments with fluctuating temperatures. Several methods are available for applying rate equations to development in varying temperatures. These models can have important practical application; for example, models for simulating the development of insect eggs or larval stages can permit agricultural controls to be applied most efficiently for maximum effectiveness. We will examine here a simple rate-summation model for predicting development in changing temperatures (Messenger and Flitters 1959, Grainger 1959, Tanigoshi and Browne 1978).

The rate-summation technique estimates duration of development based on the amount of time spent at a given temperature. This time is multiplied by the development rate, determined from constant temperature experiments. The time-rate product indicates how much development occurs during the period. Time-rate products are summed consecutively until the sum reaches unity, at which point the simulated development is complete. Consider a hypothetical example for eggs of a species of insect which experimentally have shown the following development rates at two temperatures:

Constant Temperature	Duration	Rate (1/duration)
10°C	100 hrs	0.01 hr ⁻¹
20°C	33.3 hrs	0.03 hr ⁻¹

by a modification of Equation 11.8:

$$(I_a)_z = I_z - I_{z+1} = I_0 \left(e^{-\eta(z-1)} - e^{-\eta z} \right) \quad (12.36)$$

where I_a is energy absorbed per unit time, I_z is amount of solar energy reaching the top of compartment z , I_{z+1} is the amount at the bottom, η is the absorption coefficient and I_0 is the surface intensity.

Other types of heat transfer between the lake and the atmosphere are assumed to occur only at the surface. The remaining terms in the heat balance model (Equation 12.8) are

$$Q_0 = S - O - E \quad (12.37)$$

where Q_0 is the heat transport across the surface per unit of time, S is a sensible heat exchange (convective or conductive), O is heat radiated to the atmosphere, and E is heat transfer by evaporation or condensation.

In addition to the solar energy absorbed, each compartment will have its energy content altered by the transport of heat to the compartment from the adjacent warmer layer, and by the transport of heat from the compartment to the adjacent cooler layer. We will assume that the warmer layer is at a shallower depth, and the cooler layer is deeper. Amount of heat Q_z transported from compartment z to compartment $z+1$ is assumed to be a function of the temperature difference and the eddy diffusivity coefficient, A_z , as follows:

$$Q_z = F A_z (T_z - T_{z+1}) \quad (12.38)$$

where F is a proportionality constant. In finding heat transfer for the bottom compartment, assume the sediments have the same temperature as the bottom layer of water. The eddy diffusivity coefficient is a function of both the force that produces mixing, i.e. wind, and the force that resists the mixing, i.e. the density gradient; water of greater density lies beneath water of lesser density. The eddy diffusivity coefficient may be approximated with

$$A_z = A_{\min} + 0.9 A_{z-1} \exp [-G (\rho_{z+1} - \rho_z)] \quad (12.39)$$

A_0 will be the wind-induced surface value for eddy diffusivity. (To find A_z for the bottom compartment of water, assume the sediments to have a density value of 1.5). The constant 0.9 describes the exponential decrease in the surface value of eddy diffusivity with increasing depth. G is a constant of proportionality. A_{\min} is the minimum eddy diffusivity, with a value of approximately 0.01 cal cm^{-2} . ρ_z and ρ_{z+1} are the densities of water in compartments z and $z+1$. Water density is a function of

temperature, and may be obtained from the following empirical quadratic equation which applies very well over the range of normal lake temperatures:

$$\rho_z = 0.999884 + (5.75 \times 10^{-5}) T_z - (7.27 \times 10^{-6}) T_z^2 \quad (12.40)$$

Exercise 12-9: Write a program to simulate the warming of a lake in the spring, assuming an initial temperature of 4°C for all depths. Let the lake have a depth of 20 meters (i.e. 20 compartments), with compartment 1 representing the depth interval 0-1 m. The compartmental temperature values should be stored in a subscripted array. Losses and additions of heat in each compartment may be calculated with the equations above. The calculation of temperatures should be a two-part process. In the first part, the densities for all the compartments are calculated, and then the change in heat content and temperature is calculated for each of the compartments in turn, top to bottom:

$$\Delta T_z = [(I_a)_z + Q_{z-1} - Q_z] / 100 \quad (12.41)$$

with the values for I_a and Q coming from Equations 12.36 and 12.38. For compartment 1, the heat transfer across the surface can be considered to be Q_0 (Equation 12.37).

In the second stage the changes are applied to each compartment to update its temperatures:

$$T_z \leftarrow T_z + \Delta T_z$$

Remember to set the temperature of the sediments (compartment 21) to equal the temperature of compartment 20. Use the following values in setting up your simulation; some represent daily versions of weekly values in Exercise 12.2:

$$\begin{aligned} I_0 &= 350 & A_0 &= 0.5 & O &= -20 & E &= 70 \\ S &= 30 & \eta &= 0.40 & F &= 100 & G &= 2000 \end{aligned}$$

Run your simulation for 30 days; the surface temperature should approach 26°C . Plot depth-temperature curves at least for times 0 and 30. Your output should consist of a graph showing temperature on the x -axis, and depth on the y -axis. Your graph may be clearer if you plot temperatures of each compartment as connected line segments, rather than as connected points. Graphs for comparison with actual lakes may be found in any textbook of limnology, for example Hutchinson (1957) or Wetzel (1983).

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