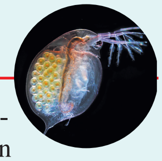
CASE STUDY 2b Hosts, Parasites, and Time-Travel



In Case Study 2c you will derive a model for the dynamics of the genotypes of *Daphnia* and its parasite. Recall that we are modeling a situation involving two possible host genotypes (A and a) and two possible parasite genotypes (B and b). Parasites of type B can infect only hosts of type A, while parasites of type b can infect only hosts of type a. You will then derive an explicit solution of a simplified version of the model in Case Study 2d. This will give the frequency of host genotype A and parasite genotype B as functions of time. These functions are

(1)

$$q(t) = \tfrac{1}{2} + M_q \cos(ct - \phi_q)$$

$$p(t) = \tfrac{1}{2} + M_p \cos(ct - \phi_p)$$

where $q(t)$ is the predicted frequency of host genotype A at time t and $p(t)$ is the predicted frequency of the parasite genotype B at time t. In these equations ϕ_q, ϕ_p, and c are positive constants, and M_q and M_p are positive constants that are strictly less than $\frac{1}{2}$ (the biological significance of these constants is explored in Case Study 2a).

In this part of the case study you will use Equations 1 to make predictions from the model that can be compared with data from the experiments.

Recall that, in the experiment, a host from a fixed layer of the sediment core was challenged with infection by a parasite from either the same layer, a layer above the fixed layer (that is, from its future), or a layer below it (that is, from its past). We can view different depths in the sediment core as representing different points of time in the history of the *Daphnia*-parasite interaction (see Figure 1). In this way Equations 1 can equally be viewed as specifying the frequency of the host and parasite genotypes as functions of location in the sediment core. Increasing values of t correspond to shallower points in the core as shown in Figure 2.

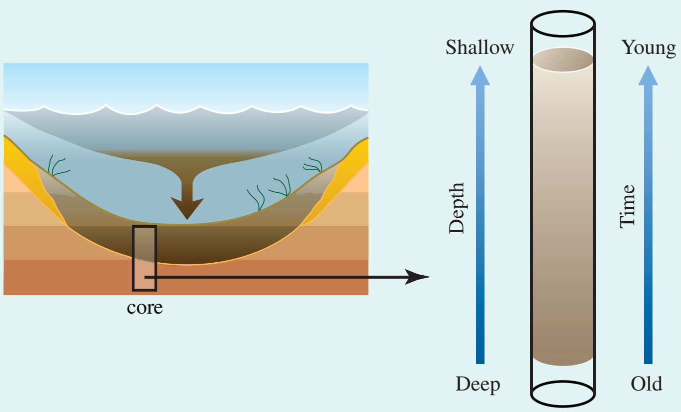


FIGURE 1

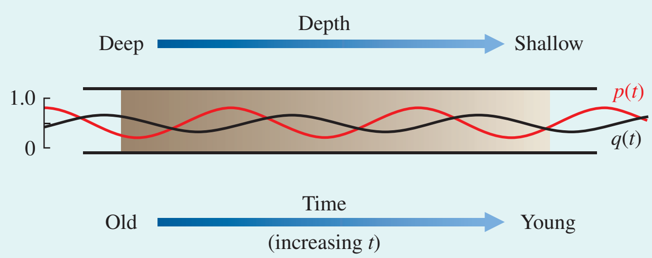


FIGURE 2

In the experiment introduced in Case Study 2 on page xlvii, researchers chose a fixed depth τ and extracted a layer of sediment of width W centered around this depth. This layer is shown in Figure 3.

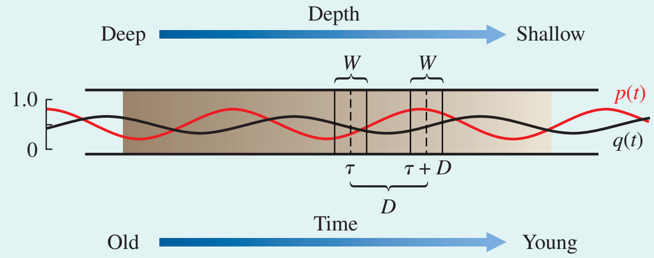


FIGURE 3

After the contents of this layer were completely mixed, hosts and parasites were extracted at random from the mixture. Researchers also took deeper and shallower layers (that represent the past and the future for hosts located in the layer at τ) and completely mixed each. The center of these layers was a distance D from the center of the focal layer (see Figure 3). They then challenged hosts from the layer at τ with parasites from their past (that is, from the layer with $D < 0$), present (the layer at τ), and future (the layer with $D > 0$). For each challenge experiment the fraction of hosts becoming infected was measured.

We can use our model to predict the fraction of hosts infected. To do so, we first need to know the predicted frequency of hosts of type A in the layer at τ as well as the frequency of the parasites of type B in the layer at $\tau + D$.

1. Consider a focal layer at location τ with width W as shown in Figure 4.

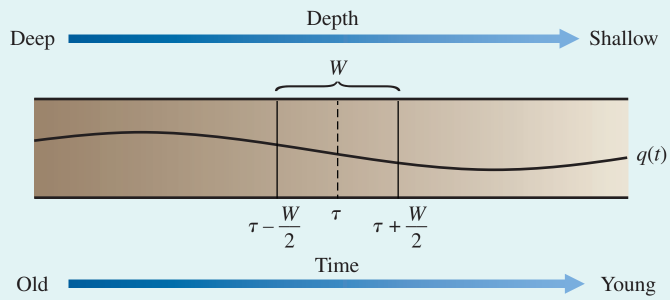


FIGURE 4

The frequency of host type A will vary across the depth of this layer as specified by the function $q(t)$. Show that, when this layer is completely mixed, the frequency of A in the mixture is given by

$$q_{\text{ave}}(\tau) = \frac{1}{2} + M_q \cos(c\tau - \phi_q)\,\frac{2\sin\left(\frac{1}{2}cW\right)}{cW}$$

Hint: You might want to use the trigonometric identity

$$\sin(x + y) - \sin(x - y) = 2\cos x \sin y$$

2. Consider another layer at a location a distance D from τ, again with thickness W, as shown in Figure 5. The frequency of parasite type B will vary across depth in this layer, as specified by the function $p(t)$. Show that, when this layer is completely mixed, the frequency of B in the mixture is given by

$$p_{\text{ave}}(\tau + D) = \frac{1}{2} + M_p \cos(c(\tau + D) - \phi_p)\,\frac{2\sin\left(\frac{1}{2}cW\right)}{cW}$$

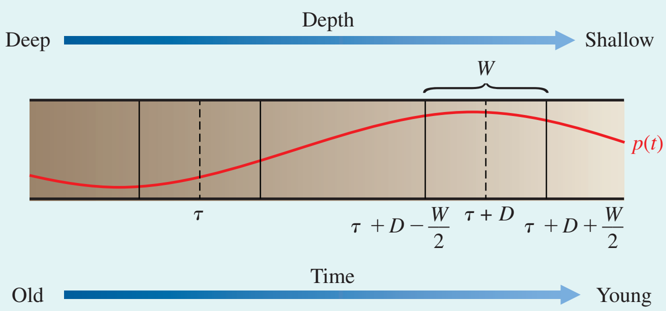


FIGURE 5

3. Suppose that hosts from the layer at τ are challenged with parasites from the layer at $\tau + D$. Use the facts that only B parasites can infect A hosts and only b parasites can infect a hosts to explain why the fraction of hosts infected in this challenge experiment is predicted to be

$$I(\tau) = p_{\text{ave}}(\tau + D)q_{\text{ave}}(\tau) + [1 - p_{\text{ave}}(\tau + D)][1 - q_{\text{ave}}(\tau)]$$

The final step is to recognize that the experiment was actually conducted with several different, randomly chosen depths τ. Therefore we need to average $I(\tau)$ in Problem 3 over the possible depths. Because $I(\tau)$ is periodic, we need only average over one period of its cycle. Its average is therefore

$$F = \frac{1}{T}\int_0^T I(\tau)\,d\tau$$

where $T = 2\pi/c$ is the period of $I(\tau)$.

4. Show that

$$\textbf{(2)} \qquad F(D) = \tfrac{1}{2} + M_p M_q \cos(cD - \phi^*)\,\frac{4\sin^2\left(\frac{1}{2}cW\right)}{c^2W^2}$$

where $\phi^* = \phi_p - \phi_q$.

Hint: You might want to use the trigonometric identity

$$\cos x \cos y = \tfrac{1}{2}(\cos(x + y) + \cos(x - y))$$

Equation 2 was used in Case Study 2a to predict the experimental outcome expected under different conditions.