$\dot{Q}$ decreases linearly as it approaches the fixed point; therefore $Q(t)$ is increasing and concave down, as shown in Figure 2.2.5. ■

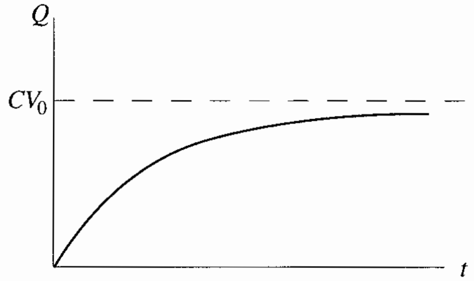

Figure 2.2.5

EXAMPLE 2.2.3:

Sketch the phase portrait corresponding to $\dot{x} = x - \cos x$, and determine the stability of all the fixed points.

Solution: One approach would be to plot the function $f(x) = x - \cos x$ and then sketch the associated vector field. This method is valid, but it requires you to figure out what the graph of $x - \cos x$ looks like.

There's an easier solution, which exploits the fact that we know how to graph $y = x$ and $y = \cos x$ *separately*. We plot both graphs on the same axes and then observe that they intersect in exactly one point (Figure 2.2.6).

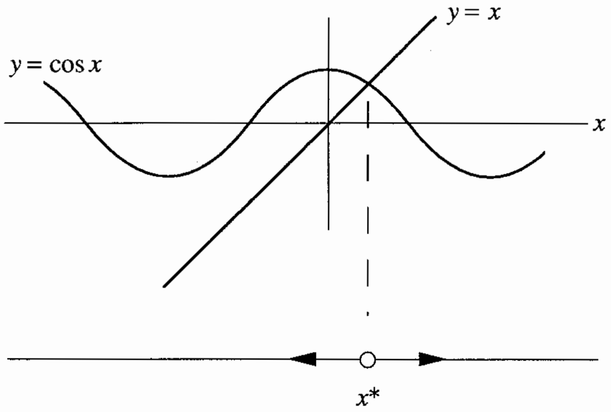

Figure 2.2.6

This intersection corresponds to a fixed point, since $x^* = \cos x^*$ and therefore $f(x^*) = 0$. Moreover, when the line lies above the cosine curve, we have $x > \cos x$ and so $\dot{x} > 0$: the flow is to the right. Similarly, the flow is to the left where the line is below the cosine curve. Hence x^* is the only fixed point, and it is unstable. Note that we can classify the stability of x^*, even though we don't have a formula for x^* itself! ■

2.3 Population Growth

The simplest model for the growth of a population of organisms is $\dot{N} = rN$, where $N(t)$ is the population at time t, and $r > 0$ is the growth rate. This model predicts exponential growth: $N(t) = N_0 e^{rt}$, where N_0 is the population at $t = 0$.

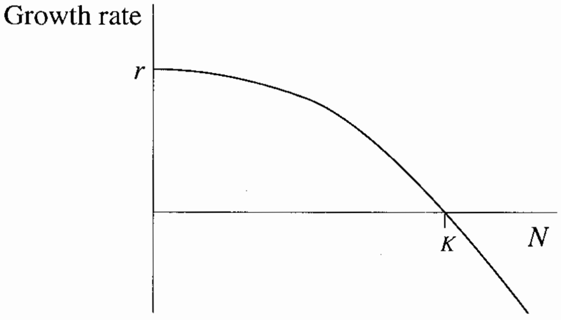

Figure 2.3.1

Of course such exponential growth cannot go on forever. To model the effects of overcrowding and limited resources, population biologists and demographers often assume that the per capita growth rate $\dot{N}/N$ decreases when N becomes sufficiently large, as shown in Figure 2.3.1. For small N, the growth rate equals r, just as before. However, for populations larger than a certain ***carrying capacity*** K, the growth rate actually becomes negative; the death rate is higher than the birth rate.

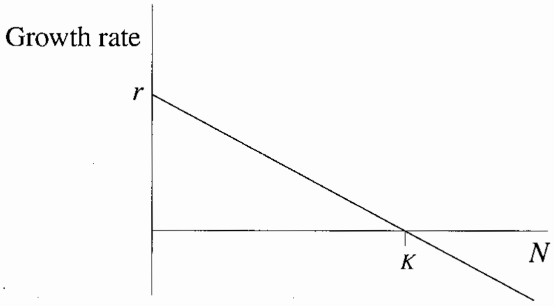

Figure 2.3.2

A mathematically convenient way to incorporate these ideas is to assume that the per capita growth rate $\dot{N}/N$ decreases *linearly* with N (Figure 2.3.2).

This leads to the ***logistic equation***

$$\dot{N} = rN\left(1 - \frac{N}{K}\right)$$

first suggested to describe the growth of human populations by Verhulst in 1838. This equation can be solved analytically (Exercise 2.3.1) but once again we prefer a graphical approach. We plot $\dot{N}$ versus N to see what the vector field looks like. Note that we plot only $N \geq 0$, since it makes no sense to think about a negative population (Figure 2.3.3). Fixed points occur at $N^* = 0$ and $N^* = K$, as found by setting $\dot{N} = 0$ and solving for N. By looking at the flow in Figure 2.3.3, we see that $N^* = 0$ is an unstable fixed point and $N^* = K$ is a stable fixed point. In biological terms, $N = 0$ is an unstable equilibrium: a small population will grow exponentially fast and run away from $N = 0$. On the other hand, if N is disturbed slightly from K, the disturbance will decay monotonically and $N(t) \to K$ as $t \to \infty$.

In fact, Figure 2.3.3 shows that if we start a phase point at *any* $N_0 > 0$, it will always flow toward $N = K$. Hence *the population always approaches the carrying capacity.*

The only exception is if $N_0 = 0$; then there's nobody around to start reproducing, and so $N = 0$ for all time. (The model does not allow for spontaneous generation!)

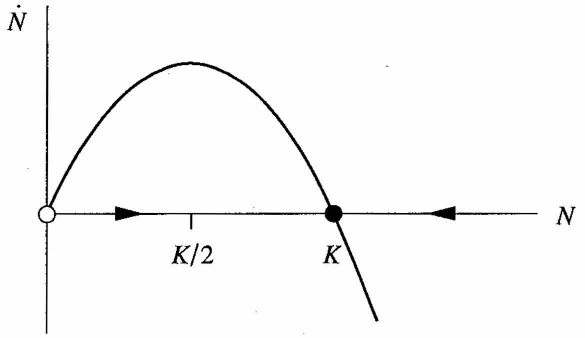

Figure 2.3.3

Figure 2.3.3 also allows us to deduce the qualitative shape of the solutions. For example, if $N_0 < K/2$, the phase point moves faster and faster until it crosses $N = K/2$, where the parabola in Figure 2.3.3 reaches its maximum. Then the phase point slows down and eventually creeps toward $N = K$. In biological terms, this means that the population initially grows in an accelerating fashion, and the graph of $N(t)$ is concave up. But after $N = K/2$, the derivative $\dot{N}$ begins to decrease, and so $N(t)$ is concave down as it asymptotes to the horizontal line $N = K$ (Figure 2.3.4). Thus the graph of $N(t)$ is S-shaped or *sigmoid* for $N_0 < K/2$.

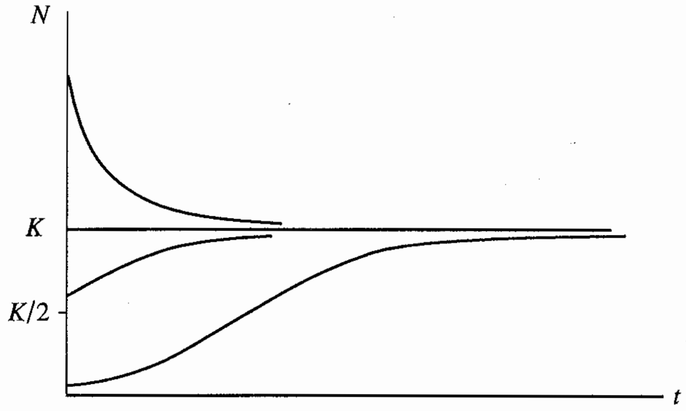

Figure 2.3.4

Something qualitatively different occurs if the initial condition N_0 lies between $K/2$ and K; now the solutions are decelerating from the start. Hence these solutions are concave down for all t. If the population initially exceeds the carrying capacity ($N_0 > K$), then $N(t)$ decreases toward $N = K$ and is concave up. Finally, if $N_0 = 0$ or $N_0 = K$, then the population stays constant.

Critique of the Logistic Model

Before leaving this example, we should make a few comments about the biological validity of the logistic equation. The algebraic form of the model is not to be taken literally. The model should really be regarded as a metaphor for populations that have a tendency to grow from zero population up to some carrying capacity K.

Originally a much stricter interpretation was proposed, and the model was argued to be a universal law of growth (Pearl 1927). The logistic equation was tested in laboratory experiments in which colonies of bacteria, yeast, or other simple organisms were grown in conditions of constant climate, food supply, and absence of predators. For a good review of this literature, see Krebs (1972, pp. 190–200). These experiments often yielded sigmoid growth curves, in some cases with an impressive match to the logistic predictions.

On the other hand, the agreement was much worse for fruit flies, flour beetles, and other organisms that have complex life cycles, involving eggs, larvae, pupae, and adults. In these organisms, the predicted asymptotic approach to a steady carrying capacity was never observed—instead the populations exhibited large, persistent fluctuations after an initial period of logistic growth. See Krebs (1972) for a discussion of the possible causes of these fluctuations, including age structure and time-delayed effects of overcrowding in the population.

For further reading on population biology, see Pielou (1969) or May (1981). Edelstein–Keshet (1988) and Murray (1989) are excellent textbooks on mathematical biology in general.

2.4 Linear Stability Analysis

So far we have relied on graphical methods to determine the stability of fixed points. Frequently one would like to have a more quantitative measure of stability, such as the rate of decay to a stable fixed point. This sort of information may be obtained by *linearizing* about a fixed point, as we now explain.

Let x^* be a fixed point, and let $\eta(t) = x(t) - x^*$ be a small perturbation away from x^*. To see whether the perturbation grows or decays, we derive a differential equation for η. Differentiation yields

$$\dot{\eta} = \tfrac{d}{dt}(x - x^*) = \dot{x},$$

since x^* is constant. Thus $\dot{\eta} = \dot{x} = f(x) = f(x^* + \eta)$. Now using Taylor's expansion we obtain

$$f(x^* + \eta) = f(x^*) + \eta f'(x^*) + O(\eta^2),$$

where $O(\eta^2)$ denotes quadratically small terms in η. Finally, note that $f(x^*) = 0$ since x^* is a fixed point. Hence

$$\dot{\eta} = \eta f'(x^*) + O(\eta^2).$$

Now if $f'(x^*) \neq 0$, the $O(\eta^2)$ terms are negligible and we may write the approximation