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2. The nutrient replenishment is sufficiently rapid so that the culture continues to grow normally.

We are able to choose the appropriate stock nutrient concentration, the flow rate, and the size of the growth chamber.

In this example the purpose of the model will be twofold. First, the progression of steps culminating in precise mathematical statements will enhance our understanding of the chemostat. Second, the model itself will guide us in making appropriate choices for such parameters as flow rates, nutrient stock concentration, and so on.

4.3 FORMULATING A MODEL

A First Attempt

Since a number of factors must be considered in keeping track of the bacterial population and its food supply, we must take great care in assembling the equations. Our first step is to identify quantities that govern the chemostat operation. Such a list appears in Table 4.1, along with assigned symbols and dimensions.

<table>
<thead>
<tr>
<th>Table 4.1</th>
<th>Chemostat Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Quantity</strong></td>
<td><strong>Symbol</strong></td>
</tr>
<tr>
<td>Nutrient concentration in growth chamber</td>
<td>C</td>
</tr>
<tr>
<td>Nutrient concentration in reservoir</td>
<td>C₀</td>
</tr>
<tr>
<td>Bacterial population density</td>
<td>N</td>
</tr>
<tr>
<td>Yield constant</td>
<td>$Y = 1/\alpha$</td>
</tr>
<tr>
<td>Volume of growth chamber</td>
<td>V</td>
</tr>
<tr>
<td>Intake/output flow rate</td>
<td>F</td>
</tr>
</tbody>
</table>

We also keep track of assumptions made in the model; here are a few to begin with:

1. The culture chamber is kept well stirred, and there are no spatial variations in concentrations of nutrient or bacteria. (We can describe the events using ordinary differential equations with time as the only independent variable.)

At this point we write a preliminary equation for the bacterial population density $N$. From Fig. 4.2 it can be seen that the way $N$ changes inside the culture chamber depends on the balance between the number of bacteria formed as the culture reproduces and the number that flow out of the tank. A first attempt at writing this in an equation might be,
An Introduction to Continuous Models

\[
\frac{dN}{dt} = KN - FN \tag{11}
\]

where \( K \) is the reproduction rate of the bacteria, as before.

To go further, more assumptions must be made; typically we could simplify the problem by supposing that

2. Although the nutrient medium may contain a number of components, we can focus attention on a single growth-limiting nutrient whose concentration will determine the rate of growth of the culture.

3. The growth rate of the population depends on nutrient availability, so that \( K = K(C) \). This assumption will be made more specific later, when we choose a more realistic version of this concentration dependence than that of simple proportionality.

Next we write an equation for changes in \( C \), the nutrient level in the growth chamber. Here again there are several influences tending to increase or decrease concentration: inflow of stock supply and depletion by bacteria, as well as outflow of nutrients in the effluent. Let us assume that

4. Nutrient depletion occurs continuously as a result of reproduction, so that the rule we specified for culture growth and that for nutrient depletion are essentially going to be the same as before. Here \( \alpha \) has the same meaning as in equation (6b).

Our attempt to write the equation for rate of change of nutrient might result in the following:

\[
\frac{dC}{dt} = -\alpha K(C)N - FC + FC_0 \tag{12}
\]

\(\text{(wrong):}\)

- minus for depletion during growth
- minus for depletion due to outflow
- plus due to replenishment from stock solution

Corrected Version

Equations (11) and (12) are not quite correct, so we now have to uncover mistakes made in writing them. A convenient way of achieving this is by comparing the \textit{dimensions} of terms appearing in an equation. These have to match, clearly, since it would be meaningless to equate quantities not measured in similar units. (For example 10 msec\(^{-1}\) can never equal 10 lb.)
By writing the exact dimensions of each term in the equations, we get

\[ \frac{dN}{dt} = K(C)N - FN \]

Dimensions: \( \frac{\text{number}}{\text{volume} \times \text{time}} = \frac{1}{\text{time} \cdot \text{volume}} \cdot \frac{\text{number}}{\text{time} \cdot \text{volume}} \)

From this we see that

1. \( K(C) \), the growth rate, must have dimensions of 1/time.
2. The second term on the RHS is incorrect because it has an extra volume dimension that cannot be reconciled with the rest of the equation.

By considering dimensions, we have uncovered an inconsistency in the term \( FN \) of equation (11). A way of correcting this problem would be to divide \( FN \) by a quantity bearing dimensions of volume. Since the only such parameter available is \( V \), we are led to consider \( FN/V \) as the appropriate correction. Notice that \( FN \) is the number of bacteria that leave per minute, and \( FN/V \) is thus the effective density of bacteria that leave per minute.

A similar analysis applied to equation (12) reveals that the terms \( FC \) and \( FC_0 \) should be divided by \( V \) (see problem 6). After correcting by the same procedure, we arrive at the following two corrected versions of equations (11) and (12):

\[ \frac{dN}{dt} = K(C)N - \frac{FN}{V}, \quad (13a) \]

\[ \frac{dC}{dt} = -\alpha K(C)N - \frac{FC}{V} + \frac{FC_0}{V}, \quad (13b) \]

As we have now seen, the analysis of dimensions is often helpful in detecting errors in this stage of modeling. However, the fact that an equation is dimensionally consistent does not always imply that it is correct from physical principles. In problems such as the chemostat, where substances are being transported from one compartment to another, a good starting point for writing an equation is the physical principle that mass is conserved. An equivalent conservation statement is that the number of particles is conserved. Thus, noting that

\[ NV = \text{number of bacteria in the chamber}, \]

\[ CV = \text{mass nutrient in the chamber}, \]

we obtain a mass balance of the two species by writing

\[ \frac{d(NV)}{dt} = K(C)NV - FN, \quad (14a) \]

\[ \frac{d(CV)}{dt} = -\alpha K(C)NV - FC + FC_0, \quad (14b) \]
(problem 9). Division by the constant $V$ then leads to the correct set of equations (13a, b).

For further practice at formulating differential-equation models from word problems an excellent source is Henderson West (1983) and other references in the same volume.

4.4 A SATURATING NUTRIENT CONSUMPTION RATE

To add a degree of realism to the model we could at this point incorporate the fact that bacterial growth rates may depend on nutrient availability. For low nutrient abundance, growth rate typically increases with increasing nutrient concentrations. Eventually, when an excess of nutrient is available, its uptake rate and the resultant reproductive rate of the organisms does not continue to increase indefinitely. An appropriate assumption would thus be one that incorporates the effect of a saturating dependence. That is, we will assume that

5. The rate of growth increases with nutrient availability only up to some limiting value. (The individual bacterium can only consume nutrient and reproduce at some limited rate.)

One type of mechanism that incorporates this effect is Michaelis-Menten kinetics,

$$K(C) = \frac{K_{\text{max}}C}{K_n + C},$$

shown in Figure 4.3. Chapter 7 will give a detailed discussion of the molecular events underlying saturating kinetics. For now, it will suffice to note that $K_{\text{max}}$ represents an upper bound for $K(C)$ and that for $C = K_n$, $K(C) = \frac{1}{2}K_{\text{max}}$.

Figure 4.3 Michaelis-Menten kinetics: Bacterial growth rate and nutrient consumption $K(C)$ is assumed to be a saturating function of nutrient concentration. See equation (15).
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Our model equations can now be summarized as follows:

\[
\frac{dN}{dt} = \left( \frac{K_{\text{max}}C}{K_n + C} \right) N - \frac{FN}{V} \quad (16a)
\]

\[
\frac{dC}{dt} = -\alpha \left( \frac{K_{\text{max}}C}{K_n + C} \right) N - \frac{FC}{V} + \frac{FC_0}{V} \quad (16b)
\]

In understanding these statements we draw a distinction between quantities that are variables, such as \( N \) and \( C \) and those that are parameters. There is little we can do to control the former directly, as they undergo changes in response to their inherent dynamics. However, we may be able to select values of certain parameters (such as \( F \), \( C_0 \), and \( V \)) that will influence the process. (Other parameters such as \( K_{\text{max}} \) and \( K_n \) depend on the types of bacteria and nutrient medium selected in the experiment.)

It is of interest to determine what happens as certain combinations of parameters are varied over a range of values. Conceivably, an increase in some quantities could just compensate for a decrease in others so that, qualitatively, the system as a whole remains the same. Thus, while a total of six parameters appear in equations (16a,b) the chemostat may indeed have fewer than six degrees of freedom. This idea can be made more precise through further dimensional analysis of the equations in order to rewrite the model in terms of dimensionless quantities.

4.5 DIMENSIONAL ANALYSIS OF THE EQUATIONS

As shown in Table 4.1, quantities measured in an experiment such as that of the chemostat are specified in terms of certain conventional units. These are, to a great extent, arbitrary. For example a bacterial density of \( 10^5 \) cells per liter can be written in any one of the following equivalent ways:

\[
N = 10^5 \text{ cells/liter},
\]

\[
= 1 \text{ (unit of } 10^5 \text{ cells)/liter},
\]

\[
= 100 \text{ cells/milliliter},
\]

\[
= N^* \tilde{N}.
\]

Here we have distinctly separated the measured quantity into two parts: a number \( N^* \), which has no dimensions, and a quantity \( \tilde{N} \), which represents the units of measurement and carries the physical dimensions. The values \( 10^5, 1, 100 \), and \( N^* \) all refer to the same observation but in terms of different scales. As time evolves, \( N \) and \( N^* \) might change, but \( \tilde{N} \) is a constant, reflecting the fact that the scale of measurement does not change.

All of the original variables can be expressed similarly, as follows:

\[
\text{measured quantity} = \text{scalar multiple} \times \text{unit carrying dimensions},
\]

\[
N = N^* \times \tilde{N},
\]

\[
C = C^* \times \tilde{C},
\]

\[
t = t^* \times \tau.
\]
We shall see presently that advantage is gained by expressing the equations in terms of such dimensionless quantities as $N^*, c^*$, and $t^*$. To do so, we first substitute the expressions $N^* \hat{N}$, $c^* \hat{C}$, $t^* \tau$ for $N$, $C$, and $t$ respectively in equations (16a,b) and then exploit the fact that $\hat{N}$, $\hat{C}$, and $\tau$ are time-independent constants. We obtain

$$\frac{d(N^* \hat{N})}{d(t^* \tau)} = \left( \frac{K_{max} c^* \hat{C}}{K_n + c^* \hat{C}} \right) N^* \hat{N} - \frac{F}{V} (N^* \hat{N}). \quad (17a)$$

$$\frac{d(c^* \hat{C})}{d(t^* \tau)} = -\alpha \left( \frac{K_{max} c^* \hat{C}}{K_n + c^* \hat{C}} \right) N^* \hat{N} - \frac{FC^* \hat{C}}{V} + \frac{FC_0}{V}. \quad (17b)$$

Now multiply both sides by $\tau$, divide by $\hat{N}$ or $\hat{C}$, and group constant terms together. The result is

$$\frac{dN^*}{dt^*} = \frac{\tau K_{max}}{K_n / \hat{C} + c^*} \frac{C^*}{\hat{C}} \left( N^* - \frac{\tau F}{V} N^* \right), \quad (18a)$$

$$\frac{dC^*}{dt^*} = -\alpha \frac{\tau K_{max} \hat{N}}{\hat{C}} \frac{C^*}{\hat{C}} \left( N^* - \frac{\tau F}{V} C^* + \frac{\tau FC_0}{VC} \right). \quad (18b)$$

By making judicious choices for the measuring scales $\hat{N}$, $\tau$, and $\hat{C}$, which are as yet unspecified, we will be able to make the equations look much simpler and contain fewer parameters. Equations (18a,b) suggest a number of scales that are inherent to the chemostat problem. Notice what happens when we choose

$$\tau = V/F, \quad \hat{C} = K_n, \quad \hat{N} = \frac{K_n}{\alpha \tau K_{max}}.$$

The equations now can be written in the following form, in which we have dropped the stars for notational convenience.

$$\frac{dN}{dt} = \alpha_1 \left( \frac{C}{1 + C} \right) N - N, \quad (19a)$$

$$\frac{dC}{dt} = -\left( \frac{C}{1 + C} \right) N - C + \alpha_2. \quad (19b)$$

The equations contain two dimensionless parameters, $\alpha_1$ and $\alpha_2$, in place of the original six ($K_n$, $K_{max}$, $F$, $V$, $C_0$, and $\alpha$). These are related by the following equations:

$$\alpha_1 = \frac{\tau K_{max}}{F},$$

$$\alpha_2 = \frac{\tau FC_0}{VC} = \frac{C_0}{K_n}.$$

In problem 8 we discuss the physical meaning of the scales $\tau$, $\hat{C}$, and $\hat{N}$ and of the new dimensionless quantities that appear here.

We have arrived at a dimensionless form of the chemostat model, given by equations (19a,b). Not only are these equations simpler; they are more revealing. By the above we see that only two parameters affect the chemostat. No, other choice of $\tau$, $\hat{C}$, and $\hat{N}$ yields less than two parameters (see problem 10). Thus the chemostat has two degrees of freedom.
somewhere (at an initial point) and has an orientation consistent with increasing values of time. We shall presently see that these ideas have a natural and important generalization to systems of differential equations.

5.2 SYSTEMS OF TWO FIRST-ORDER ODEs

In modeling biological systems, which are generally composed of several interacting variables, we are frequently confronted with systems of nonlinear ODEs. The ideas of Section 5.1 can be extended to encompass such systems; in the present section we deal in great detail with systems of two equations that describe the interaction of two species. The reason for dealing almost exclusively with these will emerge after some preliminary familiarity is established.

Let us therefore turn attention to a system of two autonomous first-order equations, a prototype of which follows:

\[
\frac{dx}{dt} = f_1(x, y), \tag{5a}
\]

\[
\frac{dy}{dt} = f_2(x, y). \tag{5b}
\]

Technically, we assume that \( f_1 \) and \( f_2 \) are continuous functions having partial derivatives with respect to \( x \) and \( y \); this ensures existence of a unique solution given an initial value for \( x \) and \( y \). A solution to system (5) would be two functions, \( x(t) \), and \( y(t) \), that satisfy the equations together with the initial conditions, if any.

As a preliminary to understanding the equations, let us consider an approximate form of these equations, whereby derivatives are replaced by finite differences, as follows:

\[
\frac{\Delta x}{\Delta t} = f_1(x, y), \tag{6a}
\]

\[
\frac{\Delta y}{\Delta t} = f_2(x, y). \tag{6b}
\]

The changes \( \Delta x \) and \( \Delta y \) in the two independent variables are thus specified whenever \( x \) and \( y \) are known, since
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\[ \Delta x = f_1(x, y) \Delta t, \quad (7a) \]
\[ \Delta y = f_2(x, y) \Delta t. \quad (7b) \]

These equations can be interpreted as follows: Given a value of \( x \) and \( y \), after some small increment of time \( \Delta t \), \( x \) will change by an amount \( \Delta x \) and \( y \) by an amount \( \Delta y \). This is represented pictorially in Figure 5.5, where a point \((x, y)\) is assigned a vector with components \((\Delta x, \Delta y)\) that describe changes in the two variables simultaneously. We see that equations (6) and (7) are mathematical statements that assign a vector (representing a change) to every pair of values \((x, y)\).

![Diagram of Figure 5.5](image)

**Figure 5.5** (a) Given a point \((x, y)\), (b) a change in its location can be represented by a vector \(v\).

In calculus such concepts are made more precise. Indeed, we know that derivatives are just limits of expressions such as \(\Delta x/\Delta t\) when ever-smaller time increments are considered. Using calculus, we can understand equations (5a,b) directly without resorting to their approximated version. (A review of these ideas is presented in Section 5.3, which may be skipped if desired.)

### 5.3 CURVES IN THE PLANE

In calculus we learn that the concepts *point* and *vector* are essentially interchangeable. The pair of numbers \((x, y)\) can be thought of as a point in the cartesian plane with coordinates \(x\) and \(y\) [as in Figure 5.6(a)] or as an arrow strung out between the origin \((0, 0)\) and \((x, y)\) that points to the location of this point [Figure 5.6(b)]. When the coordinates \(x\) and \(y\) vary with time or with some other parameter, the point \((x, y)\) moves over the plane tracing a curve as it moves. Equivalently, the arrow twirls and stretches as its head tracks the position of the point \((x(t), y(t))\). For this reason, it is often called a *position vector*, symbolized by \(x(t)\).
As previously remarked, since the solution of a system of equations such as (5a,b) is a pair \((x(t), y(t))\), the idea that a solution corresponds geometrically to a curve carries through from the one-dimensional case. To be precise, the *graph* of a solution would be a curve \((t, x(t), y(t))\) in the three-dimensional space, depicting the time evolution of the values of \(x\) and \(y\). We shall use the fact that equations (5a,b) are autonomous to suppress time dependence as before, that is, to depict solutions by trajectories in the plane. Such trajectories, each representing a solution, together make up a phase-plane portrait of the system of equations under consideration.

We observed in Section 5.2 that \((\Delta x, \Delta y)\) given by equations (7a,b) is a vector that depicts both the magnitude and the direction of changes in the two variables. A limiting value of this vector,

\[
\left( \frac{dx}{dt}, \frac{dy}{dt} \right), \tag{8a}
\]

is obtained when the time increment \(\Delta t\) gets vanishingly small in \((\Delta x/\Delta t, \Delta y/\Delta t)\). The latter, often symbolized

\[
\frac{dx}{dt} \tag{8b}
\]

represents the *instantaneous change* in \(x\) and \(y\), and can also be depicted as an arrow attached to the point \((x(t), y(t))\) and tangent to the curve. This vector is often called the *velocity vector*, since its magnitude indicates how quickly changes are occurring.

A summary of all these facts is collected here:

---

**A Summary of Facts about Vector Functions (from Calculus)**

1. The pair \((x(t), y(t))\) represents a curve in the \(xy\) plane with \(t\) as a parameter.
2. \(x(t) = (x(t), y(t))\) also represents a position vector: a vector attached to \((0, 0)\) that points to the position along the curve, that is, the location corresponding to the value \(t\).
3. The vector \(dx/dt\), which is just the pair \((dx/dt, dy/dt)\) has a well-defined geometric meaning. It is a vector that is tangent to the curve at \(x(t)\). Its magnitude, written \(|dx/dt|\) represents the speed of motion of the point \((x(t), y(t))\) along the curve.
4. The set of equations (5a,b) can be written in vector form,

\[
\frac{dx}{dt} = F(x) .
\]

Here the vector function \(F = (f_1, f_2)\) assigns a vector to every location \(x\) in the plane; \(x\) is the position vector \((x, y)\), and \(dx/dt\) is the velocity vector \((dx/dt, dy/dt)\).
Figure 5.6 (a) Point and (b) vector representations of a pair \((x, y)\). (c) A curve \((x(t), y(t))\) can also be represented by moving vector \(x(t)\), as in (d).
5.4 THE DIRECTION FIELD

From concepts that arise in calculus we surmise that solutions to ODEs, whether in one dimension or higher, correspond to curves, and differential equations are "recipes" for tangent vectors to these curves. This insight will now be applied to reconstructing a qualitative picture of solutions to a system of two equations such as (5). For such autonomous systems each point \((x, y)\) in the plane is assigned a unique vector \((f_1(x, y), f_2(x, y))\) that does not change with time. A solution curve passing through \((x, y)\) must have these vectors as its tangents. Thus a collection of such vectors defines a direction field, which can be used as a visual guide in sketching a family of solution curves, collectively a *phase-plane portrait*. Example 4 clarifies how this is done in practice.

**Example 4**

Let

\[
\begin{align*}
\frac{dx}{dt} &= xy - y, \\
\frac{dy}{dt} &= xy - x,
\end{align*}
\]

and let \(f_1(x, y) = xy - y, f_2(x, y) = xy - x\). In the following table the values of \(f_1\) and \(f_2\) are listed for several values of \((x, y)\).

<table>
<thead>
<tr>
<th>(x)</th>
<th>(y)</th>
<th>(f_1(x, y))</th>
<th>(f_2(x, y))</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>-1</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>-1</td>
</tr>
<tr>
<td>-1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>0</td>
<td>-1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>-1</td>
<td>2</td>
<td>-2</td>
</tr>
<tr>
<td>-2</td>
<td>-1</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

After tabulating arbitrarily many values of \((x, y)\) and the corresponding values of \(f_1(x, y)\) and \(f_2(x, y)\), we are ready to construct the direction field. To each point \((x, y)\) we attach a small line segment in the direction of the vector \((f_1(x, y), f_2(x, y))\).
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See Figure 5.7. The slope $\Delta y/\Delta x$ of the line segment is to have the ratio $f_1(x, y)/f_2(x, y)$. Notice that a vector $(f_1(x, y), f_2(x, y))$ has the magnitude $\sqrt{f_1(x, y)^2 + f_2(x, y)^2}$, which we shall not attempt to portray accurately. This magnitude represents a rate of motion, the speed with which a trajectory is traced. A cluttered picture emerges should we attempt to draw the vectors $(f_1, f_2)$ in their true sizes. Since we are interested in establishing only the direction field, making all tangent vectors some uniform small size proves most convenient.

![Diagram of direction field with points and vectors]

Figure 5.7 Several points $(x, y)$ and the direction vectors $(f_1, f_2)$ associated with them have been sketched above for equations (9a,b).

Two notable locations in example 4 are the points $(0, 0)$ and $(1, 1)$, at both of which $f_1 = 0$ and $f_2 = 0$. Neither $x$ nor $y$ changes given these initial values; the terms steady state, equilibrium point, or singular point are synonymously used to denote such locations. Presently we will see that such points play a central role in determining global phase-plane behavior.

The chore of tabulating and sketching direction fields is in principle straightforward but tedious. Rather than belabor the process we might consign the job to a computer, as we have done in Figures 5.8 (a,b). A simple BASIC program run on an IBM personal computer produced these results.
Figure 5.8 (a) Computer-generated vector field for example 4. The vectors point away from the points to which they are attached. For example, along the positive x axis, they point down. (b) Hand-sketched solution curves for example 4. The directions are ascertained by noting whether vectors point into or out of the region at the boundary of the square. (Computer plot by Yehoshua Keshet.)
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From the direction field thus generated one gets a good general idea of solution curves consistent with the flow. Through every point in the plane there is a curve (by existence of a solution) and only one curve (by uniqueness). Thus curves may not intersect or touch each other, except at the steady states designated by heavy dots in Figures 5.7 and 5.8. Rules governing the possible pattern of curves will be outlined in a subsequent section.

As a word of caution, note that a phase-plane diagram is not a quantitatively accurate graph. In practice, because only a finite number of tangent vectors can be drawn in the plane, there will always be some small error in the curve that we inscribe. Such initially small mistakes could propagate if they result in an improper choice of tangent vectors along the way. For this reason, solution curves drawn in this way are approximate. There may be cases where ambiguity arises close to a steady state and where it is difficult to distinguish between several alternatives. Such situations call for a more rigorous technique. Before turning to these matters, we investigate a more systematic way of establishing the direction field in a computationally efficient way.

5.5 NULLCLINES: A MORE SYSTEMATIC APPROACH

Rather than arbitrarily plotting tabulated values, we prepare the way by noticing what happens along the locus of points for which one of the two functions, either \( f_1(x, y) \) or \( f_2(x, y) \) is zero. We observe that

1. If \( f_1(x, y) = 0 \), then \( dx/dt = 0 \), so \( x \) does not change. This means that the direction vector must be parallel to the \( y \) axis, since its \( \Delta x \) component is zero.
2. Similarly, if \( f_2(x, y) = 0 \), then \( dy/dt = 0 \), so \( y \) does not change. Thus the direction vector is parallel to the \( x \) axis, since its \( \Delta y \) component is zero.

The locus of points satisfying one of these two conditions is called a nullcline. The \( x \) nullcline is the set of points satisfying condition 1; similarly, the \( y \) nullcline is the set of points satisfying condition 2. Because the arrows are parallel to the \( y \) and \( x \) axis respectively on these loci, it proves helpful to sketch these as a first step. Example 5 illustrates the procedure.

**Example 5**

For equations (9a,b) the nullclines are loci for which

1. \( \dot{x} = 0 \) (the \( x \) nullcline); that is, \( xy - y = 0 \). This is satisfied when \( x = 1 \) or \( y = 0 \). See dotted lines in Figure 5.9(a). On these lines, direction vectors are vertical.
2. \( \dot{y} = 0 \) (the \( y \) nullcline); that is, \( xy - x = 0 \). This is satisfied when \( x = 0 \) or \( y = 1 \). See the dotted-dashed line in Figure 5.9(a). On these lines direction vectors are horizontal.
Figure 5.9 Nullclines and flow directions for example 5. (a) Nullclines, which happen to be straight lines here, are sketched in the xy-plane and assigned vertical or horizontal line segments in (b). (c) Directions are determined by tabulating several values and inscribing arrowheads. (d) Neighboring arrows are deduced by preserving a continuous flow.

Points of intersection of nullclines satisfy both $\dot{x} = 0$ and $\dot{y} = 0$ and thus represent steady states. To identify these and determine the directions of flow, several guidelines are useful.
Rules for determining steady states and direction vectors on nullclines

1. Steady states are located at intersections of an $x$ nullcline with a $y$ nullcline.
2. At steady states there is no change in either $x$ or $y$ values; that is, the vectors have zero length.
3. Direction vectors must vary continuously from one point to the next on the nullclines. Thus a change in the orientation (for example, from pointing up to pointing down) can take place only at steady states.

We note that $(0, 0)$ and $(1, 1)$ are the only two steady states in example 5. It is important to avoid confusing these with other intersections, for example $(1, 0)$ and $(0, 1)$, for which only one of the two nullcline conditions is satisfied. Generally it is a good idea to distinguish between the $x$ and $y$ nullclines by using different symbols or colors for each type.

It should be remarked that in affixing orientations to the arrows along nullclines we can economize on algebra by being aware of certain geometric properties. For instance, in example 5 we observe the following patterns of signs:

<table>
<thead>
<tr>
<th>$x$</th>
<th>$y$</th>
<th>$f_1(x, y)$</th>
<th>$f_2(x, y)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-$</td>
<td>1</td>
<td>$-$</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>$-$</td>
<td>$+$</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>$-$</td>
<td>0</td>
<td>$-$</td>
</tr>
<tr>
<td>0</td>
<td>$+$</td>
<td>0</td>
<td>$-$</td>
</tr>
<tr>
<td>$+$, $&gt;1$</td>
<td>1</td>
<td>$+$</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>$+$, $&gt;1$</td>
<td>0</td>
<td>$+$</td>
</tr>
<tr>
<td>0</td>
<td>$+$</td>
<td>$-$</td>
<td>0</td>
</tr>
<tr>
<td>$-$</td>
<td>0</td>
<td>$-$</td>
<td>$+$</td>
</tr>
</tbody>
</table>

It is evident that on opposite sides of a steady-state point (along a given nullcline) the orientation of arrows is reversed. This is a property shared by most systems of equations with the exception of certain singular cases. (We shall be able to distinguish these exceptions by calculating the Jacobian $J$ and evaluating it at the steady state in question. If $\det J \neq 0$, the property of arrow reversal holds.) In most cases where we encounter $\det J \neq 0$, it suffices to determine the direction vectors at one or two select places and deduce the rest by preserving continuity and switching orientation as a steady state is crossed. Thus the arrow-nullcline method can reveal a fairly complete picture with relatively little calculation (see example 6).

**Example 6**
Consider the equations

$$\frac{dx}{dt} = x + y^2,$$

(10a)
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\[ \frac{dy}{dt} = x + y. \] \hspace{1cm} (10b)

The \( x \) nullcline is the curve \( 0 = x + y^2 \); the \( y \) nullcline is the line \( 0 = x + y \). Steady states are thus \((0, 0)\) and \((-1, 1)\). The Jacobian of system (10) is

\[ J(x_0, y_0) = \begin{pmatrix} 1 & 2y \\ 1 & 1 \end{pmatrix}. \]

Thus \( \det J(0, 0) = 1 \neq 0 \), \( \det J(-1, 1) = -1 \neq 0 \), so the property of arrow reversal holds. It suffices to tabulate two values, for example, as follows:

<table>
<thead>
<tr>
<th>( x )</th>
<th>( y )</th>
<th>( \dot{x} = x + y^2 )</th>
<th>( \dot{y} = x + y )</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td>(-y)</td>
<td>(+)</td>
<td>0</td>
</tr>
<tr>
<td>+</td>
<td>(-x)</td>
<td>(+)</td>
<td>0</td>
</tr>
</tbody>
</table>

After drawing these two arrows, all others follow by the above method. (See Figure 5.10.)

Figure 5.10 Nullclines and arrows for example 6, equations (10a,b).

5.6 CLOSE TO THE STEADY STATES

The examples we have seen give evidence to the notion that dramatic local change in the flow pattern can only take place in the vicinity of steady-state points. We now invoke a metaphorical magnifying glass to scrutinize the behavior close to these locations. In the discussions of Chapter 4, we established that close to a steady stat
Continuous Processes and Ordinary Differential Equations

(\( \bar{x}_0, \bar{y}_0 \)) [defined by \( f_1(\bar{x}_0, \bar{y}_0) = f_2(\bar{x}_0, \bar{y}_0) = 0 \)] the nonlinear system (5) behaves very nearly like a linear one,

\[
\frac{dx}{dt} = a_{11}x + a_{12}y, \\
\frac{dy}{dt} = a_{21}x + a_{22}y,
\]

where \( a_{ij} \), related to partial derivatives of \( f_1 \) and \( f_2 \), make up the coefficient of the Jacobian matrix \( J(\bar{x}_0, \bar{y}_0) \) as follows:

\[
J(\bar{x}_0, \bar{y}_0) = \begin{pmatrix}
a_{11} & a_{12} \\
a_{21} & a_{22}
\end{pmatrix} = 
\begin{pmatrix}
\frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\
\frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y}
\end{pmatrix}_{(\bar{x}_0, \bar{y}_0)}.
\]

This result is important, as it reduces the problem to one we understand well. It remains to interpret the phase-plane equivalents of solutions to systems of linear ODEs (described in Chapter 4). This will give us the local picture of the flow pattern about the steady states.

**Example 7**

Equations (9a,b) can be linearized about the steady states \((0, 0)\) and \((1, 1)\). The Jacobian is

\[
J(\bar{x}_0, \bar{y}_0) = \begin{pmatrix}
y & x - 1 \\
y - 1 & x
\end{pmatrix}_{(\bar{x}_0, \bar{y}_0)}.
\]

One obtains

\[
J(0, 0) = \begin{pmatrix}
0 & -1 \\
-1 & 0
\end{pmatrix}, \quad J(1, 1) = \begin{pmatrix}
1 & 0 \\
0 & 1
\end{pmatrix}.
\]

Thus close to \((0, 0)\) the system behaves much like the linearized version,

\[
\frac{dx}{dt} = -y, \quad \frac{dy}{dt} = -x.
\]

Similarly, close to \((1, 1)\) the linearized equations are

\[
\frac{dx}{dt} = x, \quad \frac{dy}{dt} = y.
\]

A summary of properties of linear systems (of two ordinary differential equations) is given in Table 5.1, in which we consider only the real, distinct eigenvalues case.
Table 5.1  Linear Systems of two ODEs

<table>
<thead>
<tr>
<th>Full algebraic notation</th>
<th>Equivalent Vector–Matrix Notation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Equations</td>
<td>[ \frac{dx}{dt} = a_{11}x + a_{12}y ]</td>
</tr>
<tr>
<td></td>
<td>[ \frac{dy}{dt} = a_{21}x + a_{22}y ]</td>
</tr>
<tr>
<td>dx/dt = Ax, A = \begin{pmatrix} a_{11} &amp; a_{12} \ a_{21} &amp; a_{22} \end{pmatrix}</td>
<td></td>
</tr>
<tr>
<td>Significant quantities</td>
<td>[ \beta = a_{11} + a_{22}, ]</td>
</tr>
<tr>
<td></td>
<td>[ \gamma = a_{11}a_{22} - a_{12}a_{21}, ]</td>
</tr>
<tr>
<td></td>
<td>[ \delta = \beta^2 - 4\gamma ]</td>
</tr>
<tr>
<td>Characteristic equation</td>
<td>[ \lambda^2 - \beta\lambda + \gamma = 0 ]</td>
</tr>
<tr>
<td></td>
<td>[ \lambda_{1,2} = \frac{-\beta \pm \sqrt{\delta}}{2} ]</td>
</tr>
<tr>
<td>Eigenvectors</td>
<td>[ \lambda_1 + \lambda_2 = \beta, \quad \lambda_1\lambda_2 = \delta ]</td>
</tr>
<tr>
<td></td>
<td>[ \lambda_1, \lambda_2 = \text{Tr } A, \quad \lambda_1\lambda_2 = \det A ]</td>
</tr>
<tr>
<td>Identities</td>
<td>[ \lambda_1 + \lambda_2 = \text{Tr } A, \quad \lambda_1\lambda_2 = \det A ]</td>
</tr>
<tr>
<td></td>
<td>[ \lambda_1, \lambda_2 = \frac{\text{Tr } A \pm \sqrt{\text{disc } A}}{2} ]</td>
</tr>
<tr>
<td>Eigenvectors</td>
<td>[ \begin{pmatrix} a_{12} \ \lambda_1 - a_{11} \end{pmatrix}, \begin{pmatrix} a_{12} \ \lambda_2 - a_{11} \end{pmatrix} ]</td>
</tr>
<tr>
<td></td>
<td>[ v_1, v_2 \text{ such that } (A - \lambda I)v_i = 0 ]</td>
</tr>
<tr>
<td>Solutions</td>
<td>[ x = c_1a_{12}e^{\lambda_1 t} + c_2a_{12}e^{\lambda_2 t}, ]</td>
</tr>
<tr>
<td></td>
<td>[ y = d_1e^{\lambda_1 t} + d_2e^{\lambda_2 t}, ]</td>
</tr>
<tr>
<td></td>
<td>where ( d_1 = c_1(\lambda_1 - a_{11}), \quad d_2 = c_2(\lambda_2 - a_{11}). )</td>
</tr>
</tbody>
</table>
5.7 PHASE-PLANE DIAGRAMS OF LINEAR SYSTEMS

We observe that a linear system can have at most one steady state, at (0, 0) provided \(\gamma = \det A \neq 0\). In the particular case of real eigenvalues there is a rather distinct geometric meaning for eigenvectors and eigenvalues:

1. For real \(\lambda_i\), the eigenvectors \(v_i\) are directions on which solutions travel along straight lines towards or away from \((0, 0)\).
2. If \(\lambda_i\) is positive, the direction of flow along \(v_i\) is away from \((0, 0)\), whereas if \(\lambda_i\) is negative, the flow along \(v_i\) is towards \((0, 0)\).

Proof of these two statements is given below.

**An Interpretation of Eigenvectors**

Solutions to a linear system are of the form

\[
x(t) = c_1 v_1 e^{\lambda t} + c_2 v_2 e^{\lambda t}.
\]

Recall that \(c_1\) and \(c_2\) are arbitrary constants. If initial conditions are such that \(c_1 = 0\) and \(c_2 = 1\), the corresponding solution is

\[
x(t) = v_2 e^{\lambda t}.
\]

For any value of \(t\), \(x(t)\) is a scalar multiple of \(v_2\). (This means that \(x(t)\) is always parallel to the direction specified by the vector \(v_2\).) If \(\lambda\) is negative, then for very large values of \(t\), \(x(t)\) is small. In the limit as \(t\) approaches \(+\infty\), \(x(t)\) approaches the steady state \((0, 0)\). Thus \(x(t)\) describes a straight-line trajectory moving parallel to the direction \(v_2\) and towards the origin.

A similar result is obtained when \(c_1 = 1\) and \(c_2 = 0\). Then we arrive at

\[
x(t) = v_1 e^{\lambda t}.
\]

The solution is a straight-line trajectory parallel to \(v_1\).

It follows that any solution curve that starts on a straight line through \((0, 0)\) in either direction \(\pm v_1\) or \(\pm v_2\) will stay on that line for all \(t\), \(-\infty < t < \infty\) either approaching or receding from the origin. Note also from the above that a steady state can only be attained as a limit, when \(t\) gets infinitely large, because time dependence of solutions is exponential. This tells us that the rate of motion gets progressively slower as one approaches a steady state.

Solution curves that begin along directions different from those of eigenvectors tend to be curved (because when both \(c_1\) and \(c_2\) are nonzero, the solution is a linear superposition of the two fundamental parts, \(v_1 e^{\lambda t}\) and \(v_2 e^{\lambda t}\), whose relative contributions change with time). There is a tendency for the "fast" eigenvectors (those associated with largest eigenvalues) to have the strongest influence on the solutions. Thus trajectories curve towards these directions, as shown in Figure 5.11.
Real Eigenvalues

Assuming that eigenvalues are real and distinct (with $\gamma \neq 0$, $\beta^2 - 4\gamma > 0$ where $\beta$, $\gamma$ are as defined in Table 5.1 and equation (16), the behavior of solutions can be classified into one of the three possible categories:

1. Both eigenvalues are positive: $\lambda_1 > 0, \lambda_2 > 0$.
2. Eigenvalues are of opposite signs: e.g., $\lambda_1 > 0, \lambda_2 < 0$.
3. Both eigenvalues are negative: $\lambda_1 < 0, \lambda_2 < 0$.

In these three cases the eigenvectors also are real. Both vectors point away from the origin in case 1 and towards it in case 3. In case 2 they are of opposite orientations, with the one pointing outwards associated with the positive eigenvalue. Figure 5.11(a–c) illustrates this point.
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All solutions grow with time in case 1 and decay with time in case 3; hence in each case the point \((0, 0)\) is an unstable or a stable node, respectively. Case 2 is somewhat different in that solutions approach \((0, 0)\) along one direction and recede from it along another. This unstable behavior is descriptively termed a saddle point (see Figure 5.11(e)).

Complex Eigenvalues

For \(\lambda = a \pm bi\), we distinguish between the following cases:

4. Eigenvalues have a positive real part \((a > 0)\).
5. Eigenvalues are pure imaginary \((a = 0)\).
6. Eigenvalues have a negative real part \((a < 0)\).

Note that when the linear equations have real coefficients, complex eigenvalues can occur only in conjugate pairs since they are roots of the quadratic characteristic equation.

The eigenvectors are then also complex and have no direct geometric significance. In building up real-valued solutions, recall that the expressions we obtained in Section 4.8 were products of exponential and sinusoidal terms. We remarked on the property that these solutions are oscillatory, with amplitudes that depend on the real part \(a\) of the eigenvalues \(\lambda = a \pm bi\). In the \(xy\) plane, oscillations are depicted by trajectories that wind around the origin. When \(a\) is positive, the amplitude of oscillation grows, so the pair \((x, y)\) spirals away from \((0, 0)\); whereas if \(a\) is negative, it spirals towards it. The case where \(a = 0\) is somewhat special. Here \(e^{at} = 1\), and the amplitude of such solutions does not change. These trajectories are disjoint closed curves encircling the origin, which is then termed a neutral center. In this case a somewhat precarious balance exists between the forces that lead to increasing and decreasing oscillations. It is recognized that small changes in a system that oscillates in this way may disrupt the balance, and hence a neutral center is said to be structurally unstable. Cases 4, 5, and 6 are illustrated in Figure 5.12.

5.8 CLASSIFYING STABILITY CHARACTERISTICS

From certain combinations of the coefficients appearing in the linear equations, we can deduce criteria for each of the six classifications described in the previous section. We shall catalog the nature of the eigenvalues and thus the stability properties of a steady state using three quantities,

\[
\beta = a_{11} + a_{22} = \text{Tr } A, \tag{16a}
\]

\[
\gamma = a_{11}a_{22} - a_{12}a_{21} = \det A, \tag{16b}
\]

\[
\delta = \beta^2 - 4\gamma = \text{disc } A, \tag{16c}
\]

where \(A\) is the \(2 \times 2\) matrix of coefficients \((a_{ij})\) and \(A = J(x_0, y_0)\). [See equation (12)] and \(\text{Tr } (A) = \text{trace, } \det (A) = \text{determinant, and } \text{disc } (A) = \text{discriminant of } A\).
Figure 5.12 Solution curves for linear equations (11a,b) when eigenvalues are complex with (a) positive, (b) zero, and (c) negative real parts.
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Criteria stem from the fact that eigenvalues are related to these by

\[ \lambda_{1,2} = \frac{\beta \pm \sqrt{\delta}}{2}. \quad (17) \]

Consult Figure 5.13 for a graphical interpretation of the arguments that follow.

For real eigenvalues, \( \delta \) must be a positive number. Now if \( \gamma \) is positive, \( \delta = \beta^2 - 4\gamma \) will be smaller than \( \beta^2 \) so that \( \sqrt{\delta} < \beta \). In that case, \( \beta + \sqrt{\delta} \) and \( \beta - \sqrt{\delta} \) will have the same sign [see Figures 5.13(a) and 5.13(c)]. In other words, the eigenvalues will then be positive if \( \beta > 0 \) [case 1, Figure 5.13(a)] and negative if \( \beta < 0 \) [case 3, Figure 5.13(c)]. On the other hand, if \( \gamma \) is negative, we arrive at the conclusion that \( \sqrt{\delta} \) is bigger than \( \beta \). Thus \( \beta + \sqrt{\delta} \) and \( \beta - \sqrt{\delta} \) will have opposite signs whether \( \beta \) is positive or negative [case 2, Figure 5.13(b)].

**Example 8**

In Section 5.6 we saw that the Jacobian of equations (9a,b) for the two steady states (0, 0) and (1, 1) are

\[ J(0, 0) = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}, \quad J(1, 1) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \]

Thus for (0, 0), \( \beta = 0 \) and \( \gamma = -1 \); so (0, 0) is a saddle point. For (1, 1), \( \beta = 2 \) and \( \gamma = 1 \); so (1, 1) is an unstable node.

**Example 9**

Consider the system of equations

\[ \frac{dx}{dt} = 2x - y, \quad \frac{dy}{dt} = 3x + 2y. \]

Then

\[ \beta = (2 + 2) = 4, \quad \gamma = (2)(2) + (1)(3) = 7, \]

\[ \delta = \beta^2 - 4\gamma = 16 - 28 = -12. \]

Since \( \beta^2 < 4\gamma \), the eigenvalues will be complex. Since \( \beta = 4 > 0 \), the behavior is that of an unstable spiral.

**Example 10**

Consider the system

\[ \frac{dx}{dt} = -4x + y, \quad \frac{dy}{dt} = x - 2y. \]

Then

\[ \beta = (-4 - 2) = -6, \quad \gamma = (-4)(-2) - (1)(1) = 7, \]

\[ \delta = \beta^2 - 4\gamma = 36 - 28 = 12. \]

Since \( \beta < 0 \) and \( \gamma > 0 \), the system is a stable node.
Figure 5.13 Eigenvalues are those values $\lambda$ at which the parabola $y = \lambda^2 - \beta \lambda + \gamma$ crosses the $\lambda$ axis. Signs of these values depend on $\beta$ and on the ratio of $\sqrt{\delta}$ to $\beta$ where $\delta = \beta^2 - 4\gamma$. When $\gamma > 0$, both eigenvalues have the same sign as $\beta$. If $\delta < 0$, the parabola does not intersect the $\lambda$ axis, so both eigenvalues are complex.
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For eigenvalues to be complex (and not real) it is necessary and sufficient that \( \delta = \beta^2 - 4\gamma \) be negative. Then

\[
\lambda = \frac{\beta \pm i\sqrt{-\delta}}{2}.
\]

Cases 4, 5, and 6 then follow for positive, zero, or negative \( \beta \) respectively.

To summarize, the steady state can be classified into six cases as follows:

1. Unstable node: \( \beta > 0 \) and \( \gamma > 0 \).
2. Saddle point: \( \gamma < 0 \).
3. Stable node: \( \beta < 0 \) and \( \gamma > 0 \).
4. Unstable spiral: \( \beta^2 < 4\gamma \) and \( \beta > 0 \).
5. Neutral center: \( \beta^2 < 4\gamma \) and \( \beta = 0 \).
6. Stable spiral: \( \beta^2 < 4\gamma \) and \( \beta < 0 \).

The \( \beta\gamma \) parameter plane, shown in Figure 5.14, consists of six regions in which one of the above qualitative behaviors obtains. This figure captures in a com-

![Parameter Plane Diagram](image)

**Figure 5.14** To get a general idea of what happens in a linear system such as

\[
\dot{x} = a_{11}x + a_{12}y, \quad \dot{y} = a_{21}x + a_{22}y,
\]

we need only compute the quantities

\[
\beta = a_{11} + a_{22}, \quad \gamma = a_{11}a_{22} - a_{12}a_{21}.
\]

The above parameter plane can then be consulted to determine whether the steady state \((0, 0)\) is a node, a spiral point, a center, or a saddle point.
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prehensive way the fundamental characteristics of a linear system. Notice that the region associated with a neutral center occupies a small part of parameter space, namely the positive $\gamma$ axis.

The stability and behavior of a linear system, or the properties of a steady state of a nonlinear system can in practice be ascertained by determining $\beta$ and $\gamma$ and noting the region of the parameter plane in which these values occur. See examples 8, 9, and 10.

.9 GLOBAL BEHAVIOR FROM LOCAL INFORMATION

Systems of nonlinear ODEs may have multiple steady states (see examples 5 and 6). Close to the steady states, behavior is approximated by the linearized equations, a fact that does not depend on the degree of the system; that is, it holds true in general for $n \times n$ systems.

An attribute of $2 \times 2$ systems that is not shared by those of higher dimensions is that local behavior at steady states can be used to reconstruct global behavior. By this we mean that stability properties of steady states and various gross features of the direction field determine a flow in the plane in an unambiguous way. The reason bigger systems of equations cannot be treated in the same way is that curves in higher dimensions are far less constrained by imposing a continuity requirement. A result that holds in the plane but not in higher dimensions is that a simple closed curve (for example, an ellipse or a circle) separates the plane into two disjoint regions, the “inside” and the “outside.” It can be shown in a mathematically rigorous way that this limits the ways in which curves can form a smooth flow pattern in a planar region. Problem 16 gives some intuitive feeling for why this fact plays such a central role in establishing the qualitative behavior of $2 \times 2$ systems.

The terminology commonly used in the theory of ODEs reflects an underlying analogy between abstract mathematical equations and physical flows. We tend to associate the behavior of solutions to a $2 \times 2$ system with the motion of a two-dimensional fluid that emanates or vanishes at steady-state points. This at least imparts the idea of what a smooth phase-plane picture should look like. (We note a slight exception since saddle points have no readily apparent fluid analogy.) By smooth, or continuous flow we understand that a small displacement from a position $(x_1, y_1)$ to one close to it $(x_2, y_2)$ should not cause a drastic change in the direction of the flow.

There are a limited number of ways that trajectories can be combined to create a flow pattern that accommodates the local (steady-state) properties with the global property of continuity. A partial list follows:

1. Solution curves can only intersect at steady-state points.
2. If a solution curve is a closed loop, it must encircle at least one steady state that cannot be a saddle point (see Chapter 8).

Trajectories can have any one of several asymptotic behaviors (limiting behavior for $t \rightarrow +\infty$ or $t \rightarrow -\infty$). It is customary to refer to the $\alpha$-limit set and $\omega$-limit set, which are simply the sets of points that are approached along a trajectory for
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$t \to -\infty$ and $t \to +\infty$ respectively. Limit sets may include any of the following (see Figure 5.15):

1. A steady-state point.
2. Infinity. (Trajectories emanating from or approaching infinitely large values in phase space are said to be unbounded.)
3. A closed-loop trajectory. (A trajectory may itself be a closed curve or else may approach or recede from one. Such solution curves represent oscillating systems; see Chapters 6 and 8.)
4. A cycle graph (a set containing a finite number of steady states connected by an equal number of trajectories).

Figure 5.15 Limit sets described in text: (a) steady-state point, (b) infinity, (c) closed-loop trajectory, (d) cycle graph, (e) heteroclinic trajectory, (f) homoclinic trajectory, and (g) limit cycle.
Certain types of trajectories are further distinguished by name since they represent interesting or important properties. Three of these are listed here:

5. A **heteroclinic trajectory** connects two (different) steady states. (The term connects is often used loosely to convey that an orbit tends to each of the steady states for \( t \to \pm \infty \).)

6. A **homoclinic trajectory** returns to the same steady state from whence it originates.

7. A **limit cycle** is a closed orbit that is the \( \alpha \) or \( \omega \) limit set of neighboring orbits (see Figure 5.15 and Chapter 8).

It has been shown that by linearizing a set of (nonlinear) equations about a given steady state, we can understand local behavior rather thoroughly. Indeed, this behavior falls into a small number of possible cases, six of which were described in Figure 5.14. (We did not go into details of several other singular cases, for example, if \( \text{det } A = 0 \) or \( \text{disc } A = 0 \). These are discussed in several sources in the references.)

Suppose we arrive at a prediction that some steady state is a spiral, a node, or a saddle point according to linear theory. The nonlinearity of the equations might distort that local behavior somewhat, but its basic features would not change. An exception to this occurs when linearization predicts a neutral center. In that case, somewhat more advanced analysis is necessary to establish whether this prediction holds true. A hint for why this prediction is not trustworthy has been given previously and involves the concept of structural stability. Briefly, even though the effect of nonlinearities is small near a steady state, it may suffice to disrupt the delicate balance of a neutral center. What happens when the delicate rings of a neutral center are broken? We postpone discussion of this to a later chapter.

### 5.10 Constructing a Phase-Plane Diagram for the Chemostat

To demonstrate how to apply the theory given in Chapters 4 and 5 to a given situation, we return to the example of the chemostat. In Section 4.5 we discovered the following set of dimensionless equations depicting bacterial density \( N \) and nutrient concentration \( C \):

\[
\frac{dN}{dt} = \alpha_1 \left( \frac{C}{1 + C} \right) N - N, \tag{18a}
\]

\[
\frac{dC}{dt} = -\left( \frac{C}{1 + C} \right) N - C + \alpha_2. \tag{18b}
\]

As we saw, these nonlinear equations have two steady states, one of which represents a stable level of nutrient and cells. We now apply the method of phase-plane analysis to this example. Because only positive values of \( N \) and \( C \) are biologically meaningful, we shall restrict attention to the positive quadrant of the \( NC \) plane.