10 Exploited Resources

THE EXAMPLE OF GRAZING SHEEP

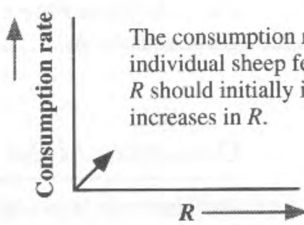
We introduce this chapter with a simple example drawn from practical ecology. Sheep eat grass and ultimately convert some of that grass to wool. Let's say that we can manage the number of sheep on a pasture and that we would like to graze sheep in a way that maximizes the long-term yield of wool. To manage the pasture sensibly, we need to consider sheep numbers, grass abundance, and grass productivity. We begin by exploring what happens to grass abundance as we change the number of sheep on the pasture. We need to know two things:

1. The amount of grass that an individual sheep eats per unit time and how that amount changes as the abundance of the grass increases. This is the **functional response** of the sheep (Solomon 1949).
2. The rate at which the grass grows under different levels of foraging. We will assume a discrete logistic curve for grass growth—thus grass will eventually reach a carrying capacity, K, set by its own resource levels (e.g., water, fertilizer, and sunlight) in the absence of any sheep. We subtract from this logistic growth rate the amount of grass mortality (per unit time) due to grazing. This mortality is the product of the number of sheep times the functional response of each sheep.

The Consumer's Functional Response

First, we need some labels. Let's call grass density R (for resource) and call the sheep's grass consumption rate simply "consumption rate" (with units of mass of grass eaten per sheep per unit time).

At relatively low grass densities, sheep must spend much time searching for patches of grass. As grass levels increase, search times for sheep decrease with the result that overall consumption rates increase.



The consumption rate of an individual sheep feeding on grass R should initially increase with increases in R.

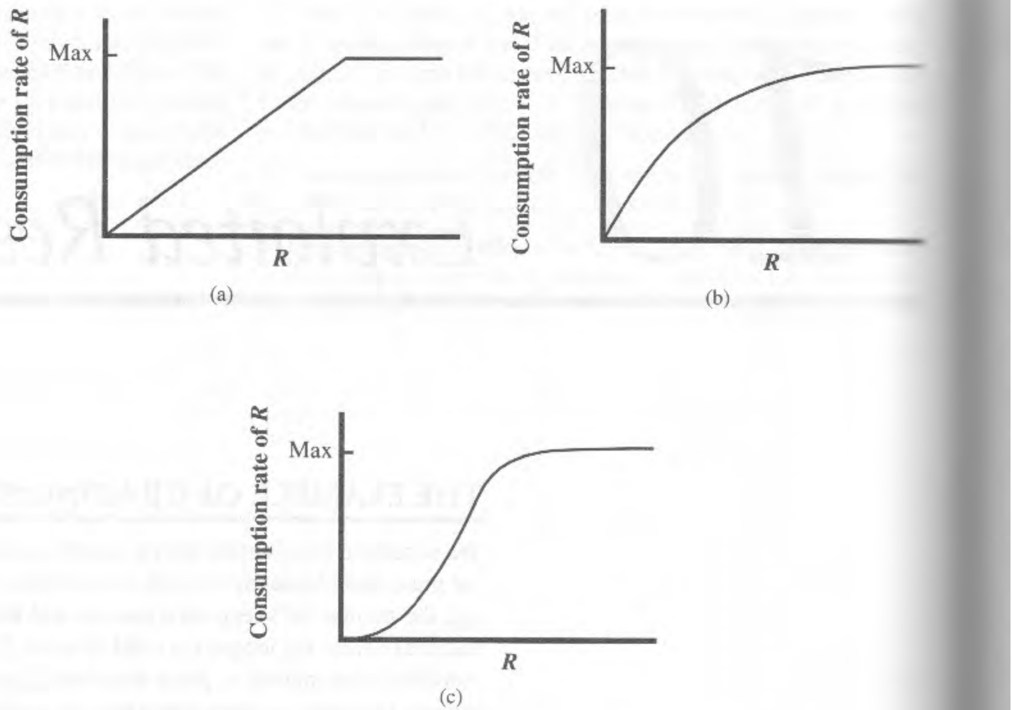


Figure 10.1
Different possible shapes for the functional response: (a) A linear approach to this maximum, (b) a gradual approach to the maximum, and (c) a logistic, S-shaped approach to the maximum.

When grass is very abundant, locating it is no longer the bottleneck for sheep consumption. Instead sheep will reach a maximum consumption rate set by how quickly they can chew, swallow, and digest grass. We can imagine three different approaches to this maximum, as depicted in Figure 10.1.

In Chapter 11 we derive these different functional responses based on features of the consumer's behavior. For now, we simply note that these different shapes are possible for different kinds of animals. For example, a small mammal or a warbler feeding on cocoons and larvae of moths shows an S-shaped, or type 3, functional response, but a wasp that lays its eggs in sawfly cocoons shows a type 2 functional response, as do wolves responding to caribou density. These varying responses are shown in Figure 10.2.

Innate Growth of the Resource Population

Recall from Chapter 5, where we introduced single-species density dependent growth, that the continuous logistic growth rate for the total population as a function of its own density is a hump-shaped curve. Thus we would get something like the curve shown in Figure 10.3, which plots the grass growth rate, dR/dt, as a function of grass density, R.

Dynamics of the Resource Population under Exploitation

The next step is to combine the plot of resource growth from Figure 10.3 with the plot of resource consumption by sheep—the functional response in Figure 10.1. Since the plots have the same axes, we can superimpose them to examine the changes in grass numbers from both sources. Let's assume a type 3 functional response for sheep as a starting point. The total consumption of grass depends also on how many sheep are grazing. This introduces an additional consideration: Assume that sheep have **additive effects** on grass consumption such that 10 sheep consume grass 10 times faster than a

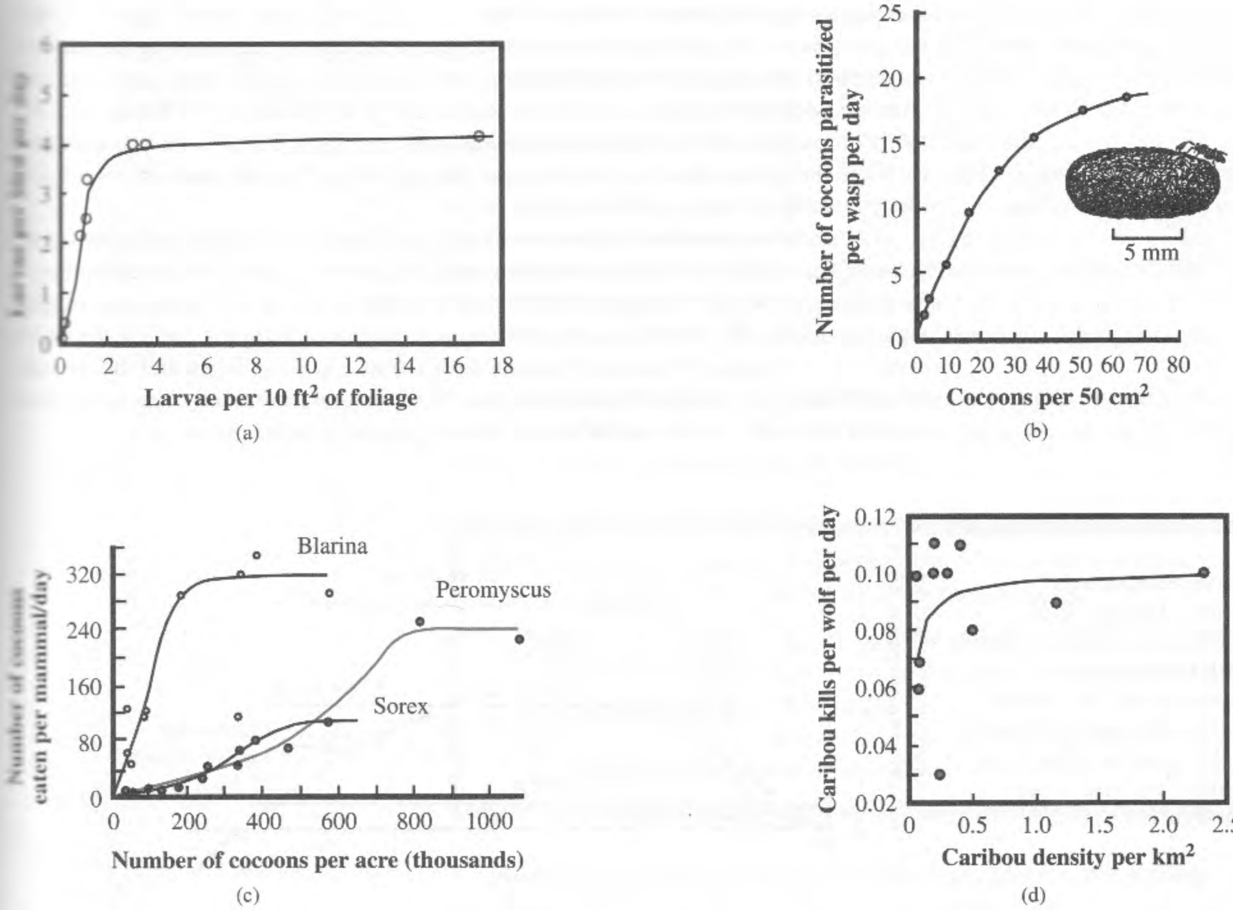


Figure 10.2
Various functional responses. (a) Functional response of baybreasted warblers to changes in the density of spruce budworm (a moth) larvae in New Brunswick (Mook 1963). (b) The chalcid wasp *Dahlbominus fuscipennis* parasitizing cocoons of the sawfly *Neodiprion setifer* in laboratory cages (Burnett 1956). (c) Small mammals feeding on sawfly cocoons; *Peromyscus* is a mouse, and the other two species are shrews (Holling 1959). (d) Wolves feeding on caribou (Dale et al. 1994).

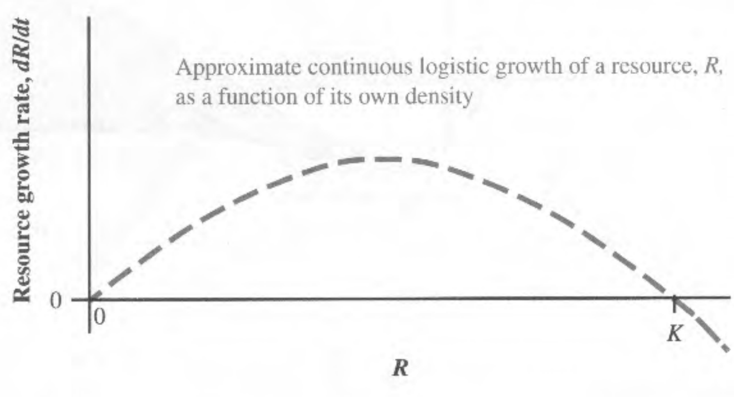


Figure 10.3
This dashed curve shows how grass would grow in the absence of any grazing if its population growth rate were roughly a continuous logistic.

single sheep for each grass level, and 100 sheep consume 100 times more grass per unit time than a single sheep, and so on. While this seems like a reasonable assumption, it would be violated if sheep interact with each other in ways that influence their ability to forage. For example, if the average sheep spends more time fighting with other sheep at high sheep numbers, then this would certainly cut into the time it has available for feeding on grass. In this case, 100 sheep might eat far less than 100 times the amount that a single sheep would eat if it were alone on the same pasture. Conversely, a single sheep scanning for predators might forage less efficiently than a small tight flock with many vigilant eyes. Thus there are several sound biological reasons why the additive assumption might not be realistic. For now we put these complications aside and deal with the additive case. (We return to possible sheep interference in Chapter 12.) The total consumption of multiple sheep is illustrated in Figure 10.4 for three quantitative levels of sheep: one sheep, a few sheep, and more sheep. The latter two curves are simply increasing multiples of the first.

Let's take a closer look at the one-sheep case. First, we extract a curve for the net growth rate of grass—the difference between the growth of grass and its consumption by sheep—as shown in Figure 10.5. Then we plot the net growth of grass—the stippled region in Figure 10.5—which is the difference between recruitment and consumption, as shown in Figure 10.6. In other words, with a single grazing sheep and the dynamical rates for gain and loss plotted in Figure 10.6, the grass eventually reaches a stable equilibrium at R^*, not far below K, the carrying capacity of the grass.

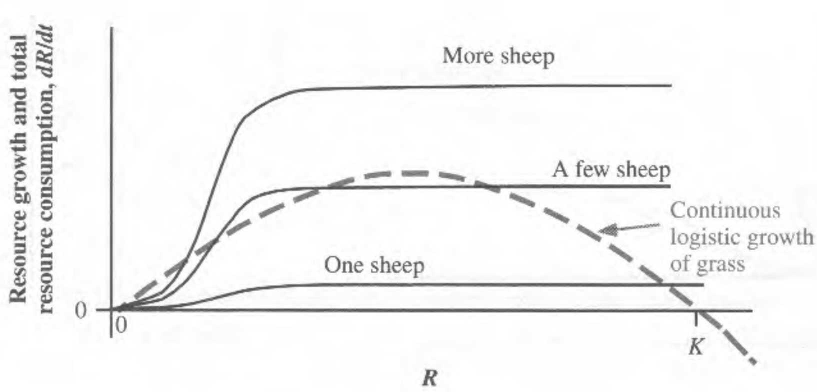


Figure 10.4
Total resource consumption by different numbers of sheep. Total resource consumption is the functional response (which has units of per consumer) multiplied by the number of consumers. Thus it represents the rate of loss of the resource (grass) and can be compared to the rate of gain given by the dashed continuous logistic curve.

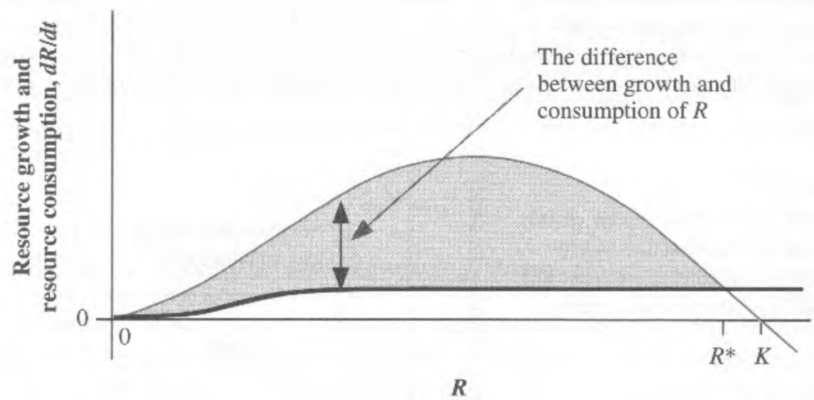


Figure 10.5
The stippled region shows the *net* growth of grass—the difference between the grass recruitment curve (logistic) and the consumption of grass by a single sheep.

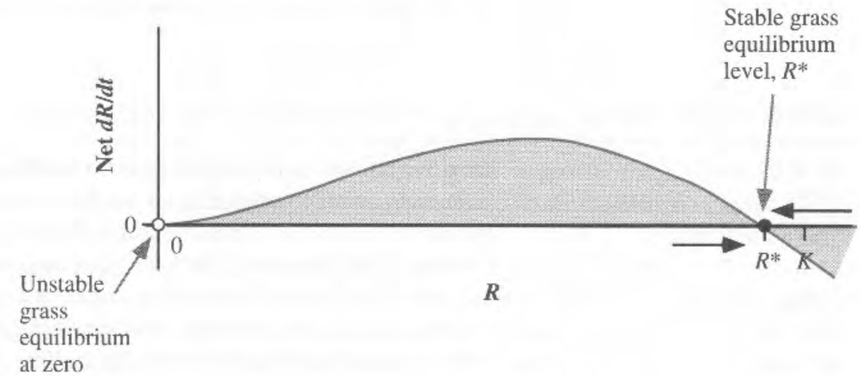


Figure 10.6
The net resource growth rate (gain minus loss) from Figure 10.5. By definition, an equilibrium occurs when the net growth rate is 0. Two resource levels yield an equilibrium here: zero grass, which is unstable, and R^*, which is a stable equilibrium point.

In Figure 10.7 we next explore the situation for a few sheep. To plot *net* grass growth we modify Figure 10.7 to plot only the difference between grass recruitment and its consumption by sheep, as shown in Figure 10.8. In Figure 10.8 there are three non-trivial equilibrium points labeled, 1, 2, and 3, and the trivial equilibrium point at $R = 0$. The equilibrium points labeled 1 and 3 are stable (dark circles) but number 2 is unstable (open circle) since resource levels will tend to grow away from it, either to increase to the level of stable grass equilibrium 3 or to decrease to stable grass equilibrium 1. The arrows show the direction of resource growth in the vicinity of the different equilibria. An arrow pointing to the right means that resources increase for that level of R since recruitment exceeds consumption (plotted on the y axis). Conversely, an arrow pointing to the left means that resources decrease at that level of R since consumption exceeds resource recruitment.

A similar curve can be constructed for the more sheep case. It shows only a single feasible equilibrium point, which is stable. In summary, we get the following three cases for the three qualitative levels of sheep.

Problem: Be sure that you understand how Figure 10.9 was constructed for the case of more sheep. Then answer the following questions.

1. Why are the stable equilibrium grass levels less than the value of K for grass?
2. How is it possible to determine the stability of each equilibrium point simply by looking at the plots of net dR/dt?
3. Why does the plot for a few sheep have two humps for the net recruitment rate but the plots for more sheep and one sheep have only one hump?

Now let's consider the effect of a continuous change in the number of sheep rather than simply three discrete values. We return to Figure 10.4 and imagine not just three consumption curves but many, each representing a different number of sheep; that is, we mentally fill in the intermediate levels of sheep between the three curves. In this way

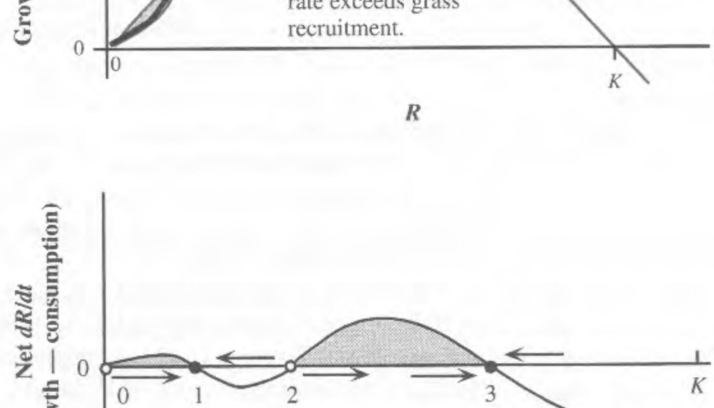


Figure 10.7
As in Figure 10.5 but for the case of a few sheep.

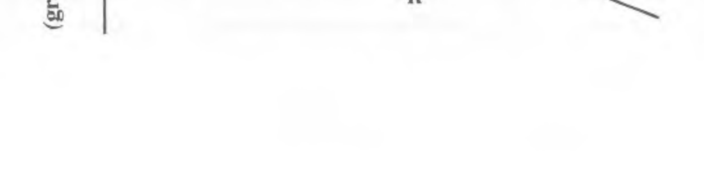


Figure 10.8
As in Figure 10.6 but for a few sheep. Four levels of grass now yield an equilibrium. Equilibrium points 1 and 3 are stable, but point 2 is unstable. The horizontal arrows indicate either increasing or decreasing R, based on whether dR/dt is positive or negative.

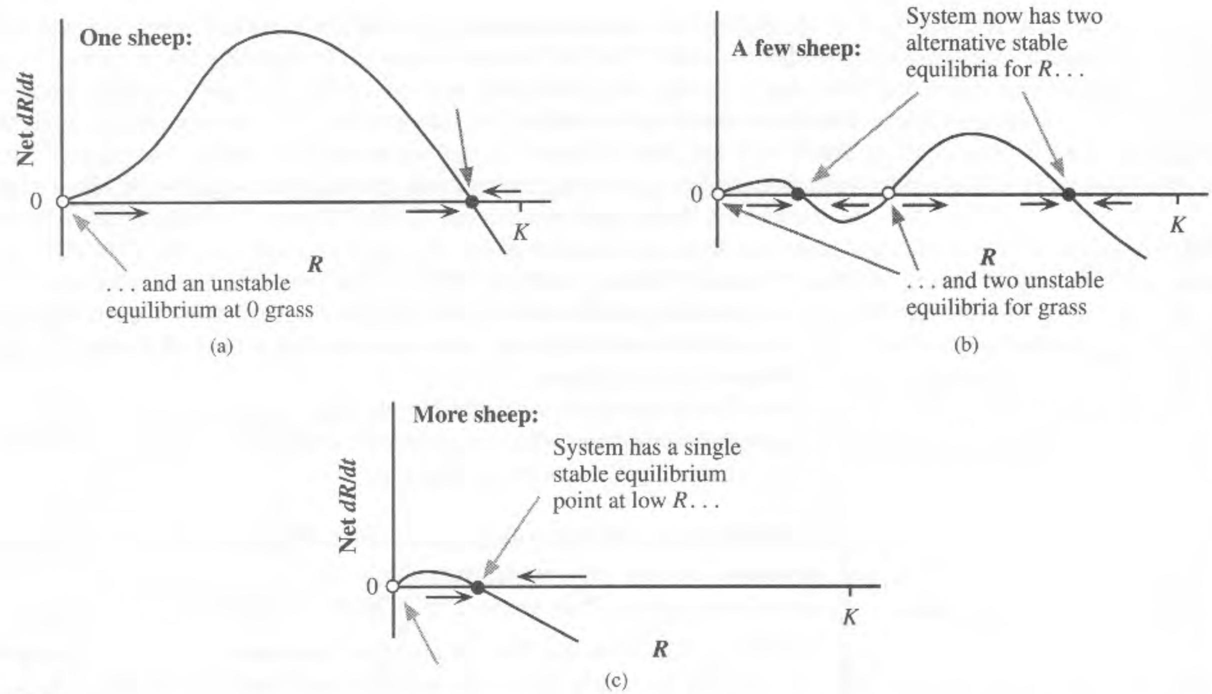
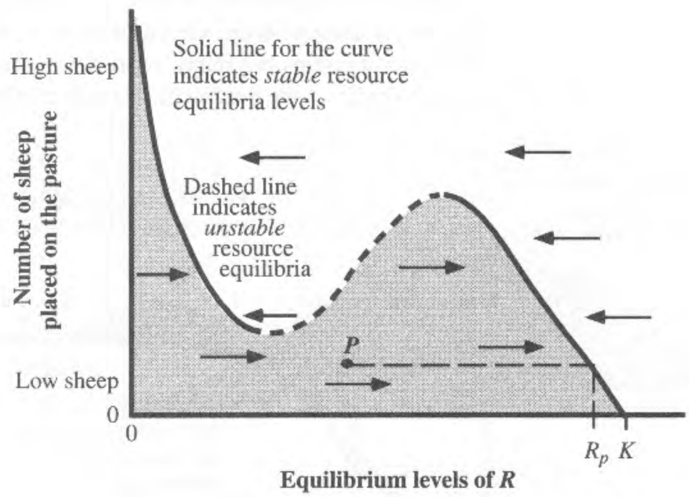


Figure 10.9
A summary of the changing dynamics for resources with different numbers of sheep on the pasture: (a) one sheep, (b) a few sheep, and (c) more sheep. Stable equilibrium points for R are indicated by filled dots and unstable points by open dots.

Figure 10.10
Similar to the case of Figure 10.9, but now the equilibrium levels of the resource (grass) are plotted for continuous changes in the number of sheep. Any point in the stippled region represents a particular combination of sheep and grass that leads to positive net growth for the grass. The curve itself yields zero net growth, by definition. Above the curve (in the unshaded region), grass growth is negative. For example, if grass and sheep were at point P and the number of sheep were fixed, grass levels would increase until they reached point R_P.



we can explore the continuous decrease in *equilibrium* grass abundance as sheep numbers increase. Starting with zero sheep, the grass is at K, and, as sheep are added, the combined consumption curve intersects the recruitment curve to the left of K. The equilibrium grass levels drop as more sheep are added. This relationship is plotted as a smooth curve in Figure 10.10.

While it might seem more natural to plot the number of sheep on the x axis in Figure 10.10, since it is the independent variable in this thought experiment, the later development (in Chapter 12) will be simplified by switching axes. Then the x axis represents the equilibrium resource level that is reached for each number of sheep on the y axis. Between the T_1 and T_2 levels of sheep, the multiple equilibrium points correspond to the multiple equilibrium points illustrated in Figure 10.9 for the case of a few

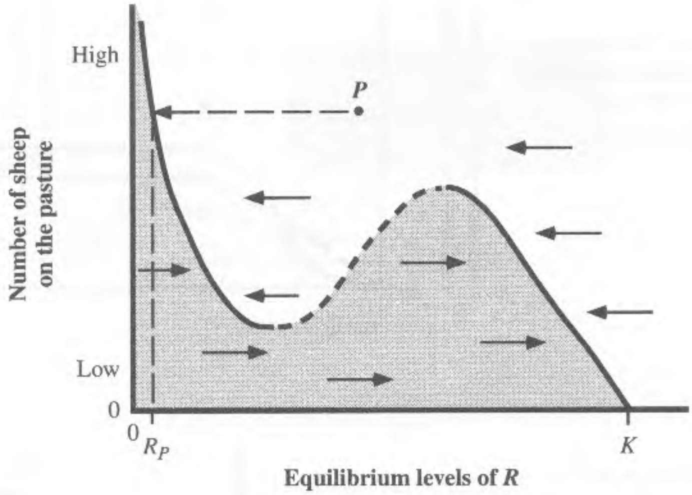


Figure 10.11
As in Figure 10.10, but now the initial grass and sheep numbers, *P*, are outside the positive growth region for grass. Grass declines until it comes to rest at R_P^*.

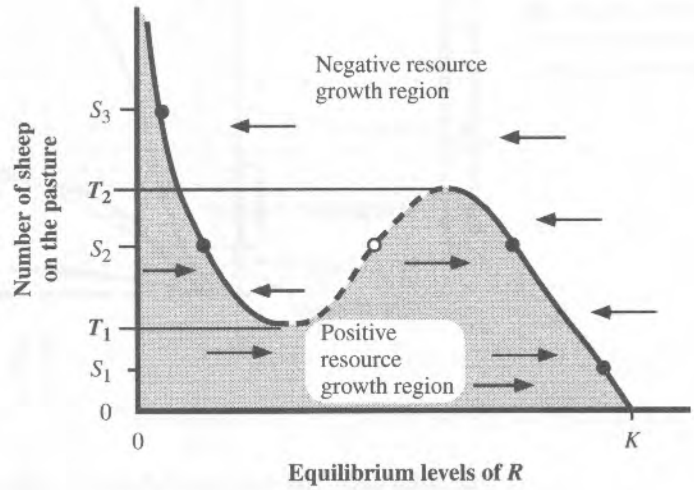


Figure 10.12
This is simply Figure 10.10 plotted again to highlight the two transition levels of sheep. The number of sheep at T_1 marks the threshold sheep level that begins the transition between a single nontrivial equilibrium point for grass to the three equilibrium points illustrated in Figure 10.9. As the number of sheep increase still more, a new threshold number of sheep is reached at T_2. Above T_2 sheep, the grass population returns to a single stable equilibrium at a low grass level. The sheep levels S_1, S_2, and S_3 loosely correspond to those of one sheep, a few sheep, and more sheep, respectively, in Figures 10.4 and 10.9.

sheep. For all points below the curve (i.e., in the stippled region), the number of sheep is low relative to resource recruitment rates, so resources can increase. For example, when there are no sheep, grass will increase until it reaches a stable equilibrium at *K*. Imagine that the system starts at point *P* in Figure 10.10. At this point, the number of sheep is relatively low and grass, *R*, is at about *K*/2. Since *P* falls in the stippled region, resources will increase, as shown by the arrows pointing to the right, until they hit the equilibrium curve for this low number of sheep. But, if the number of sheep is high and the initial resource level is again at *K*/2, then the starting point *P* would be outside the stippled region. Grass levels would then decrease, as shown by the horizontal arrows pointing to the left, until resources reach the equilibrium curve for that particular number of sheep, as shown in Figure 10.11.

Threshold Consumer Levels for a Type 3 Functional Response

Figure 10.12 is a plot of Figure 10.10 again but special emphasis is added to show the levels of sheep marking a transition in the stability properties of the equilibria; these sheep levels are labeled T_1 and T_2. The number of sheep labeled T_1 marks the threshold for the transition from a situation wherein a single stable equilibrium resource level exists (low sheep numbers, e.g., sheep level S_1) to those intermediate sheep numbers that yield three nontrivial equilibrium resource levels (e.g., sheep level S_2) indicated by

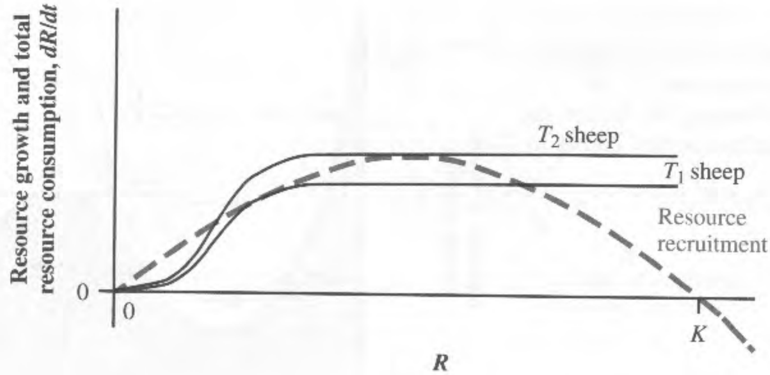


Figure 10.13
The total sheep consumption curves for the two threshold sheep numbers, T_1 and T_2, overlaid on the grass recruitment curve, as in Figure 10.4.

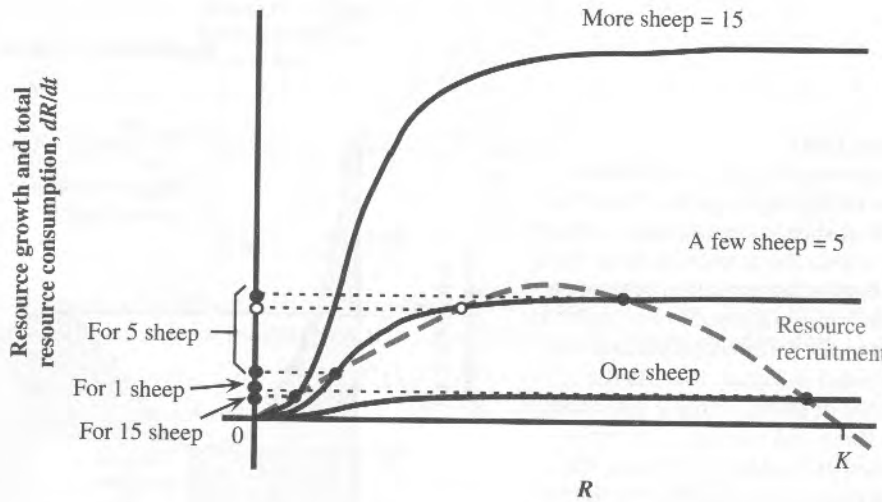


Figure 10.14
The solid dots correspond to stable equilibria, and the open dot corresponds to the unstable equilibrium when there are five sheep. These equilibria are projected to the y axis to show the values of dR/dt for these R values.

the solid dots. The number of sheep T_1 marks the threshold sheep level that begins the transition between these two behaviors. The total consumption associated with T_1 sheep is depicted in Figure 10.13. Finally, as sheep levels increase still more (i.e., climbing up the y axis), a new threshold number of sheep is reached at T_2, which marks the next and final transition. Above T_2 sheep, there is a return to a single stable, but low level, of resource. The total consumption associated with T_2 sheep is also depicted.

Maximizing Yield of a Managed Resource

Let's now suppose that we want to optimize the number of sheep on the pasture for maximized wool production. If too few sheep are grazed, then there won't be many sheep to produce wool. If too many sheep are grazed, then the grass will be overexploited; the sheep will have little to eat and therefore each sheep's ability to convert grass into wool will be diminished. Presumably, some intermediate number of sheep will be best, but how can we solve for this number? We specify wool production per sheep as proportional to food consumption per sheep times the number of sheep, which equals the total food consumption of the population of sheep grazing on the pasture. That is,

$$\boxed{\text{Wool production rate} \propto \text{total grass consumption, } \frac{dR}{dt}.}$$

The right-hand side of this expression is the y axis on the plots in Figures 10.4 and 10.9, but now we wish to plot dR/dt versus number of sheep and look for a maximum. Let's look at Figure 10.4 again, but let's now supply some actual numbers for the different levels of sheep to make things quantitative, as shown in Figure 10.14.

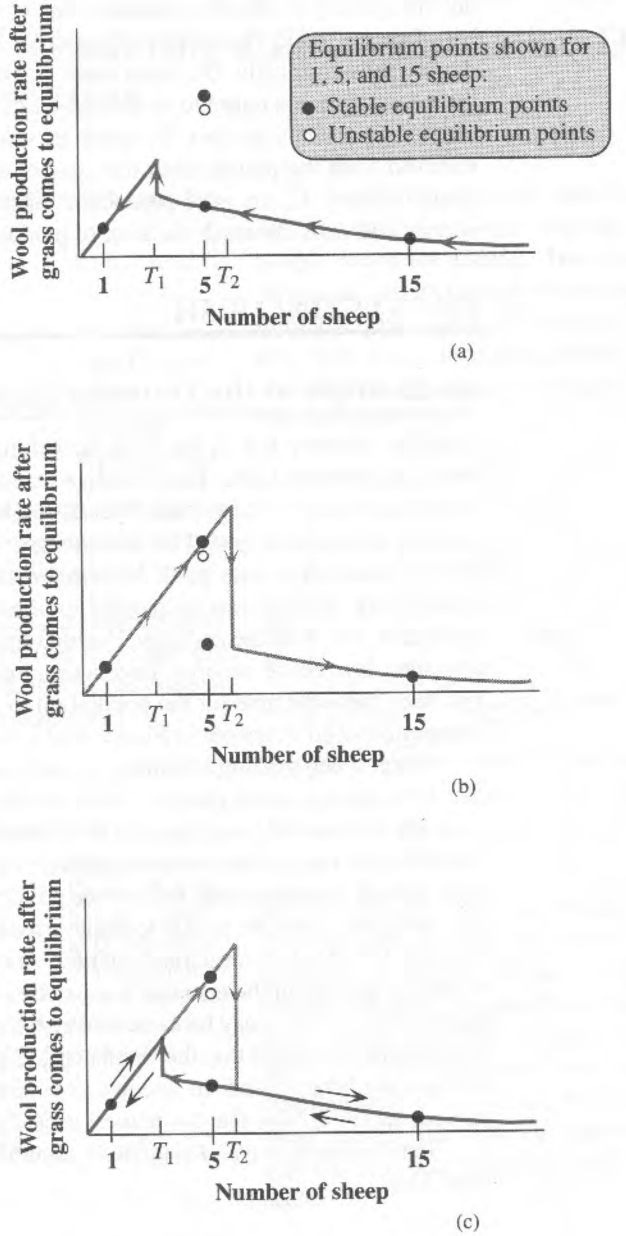


Figure 10.15 Equilibrium wool production as a function of the number of sheep grazing on the pasture. Two different curves are possible: (a) the pasture begins in a highly overgrazed state, and sheep are successively removed, or (b) the pasture begins in an ungrazed state, and sheep are successively added. (c) The two curves superimposed.

In Figure 10.15 we go one step further by plotting these equilibria dR/dt levels on the y axis of Figure 10.14 as a continuous function of the number of sheep on the x axis. We get two different curves, depending on whether we begin with no sheep and successively add sheep to the pasture or begin with an overstocked pasture and successively remove sheep. These alternative curves are a direct result of the emergence of the unstable equilibria points at intermediate numbers of sheep, indicated by the dashed portion of the curve in Figure 10.10. To the left of T_1, the two curves superimpose, and to the right of T_2, the two curves superimpose. Since an unstable equilibrium cannot be reached, there is no corresponding wool production rate for the five-sheep example (the open dot in Figure 10.14).

The optimum number of sheep to maximize wool production is exactly T_2. However, the important message here is that the dynamical behavior of resource populations under exploitation can be complex. Thresholds or *breakpoints* which, if exceeded, can abruptly and discontinuously move resources to new and undesirable levels. Also, *hysteresis* may occur with the curves for sheep addition and sheep subtraction not being identical. Each contains a breakpoint, but these break points can be at different levels. Consequently, it is not always easy to find the optimum level of sheep on the pasture. If the optimum number of sheep, T_2, in Figure 10.15(b) is exceeded by even a single sheep, then wool production falls drastically, to a much lower stable level. If that single sheep is then removed, the system does not return to its previous level, but instead rides the thin red curve in Figure 10.15(c). Only modest increases in wool yield are produced as more sheep are removed from the pasture until the number of sheep drops to T_1. When the number of sheep is below T_1, the wool production takes a giant leap upward. However, wool production still does not reach the level of production that was achieved at exactly T_2 sheep.

HARVESTING FISH

An Example of the Peruvian Anchovy

Peruvian anchovy live in the cool, upwelling, nutrient-rich waters along the coast of Peru and northern Chile. Reproductive maturity is reached at about 1 year of age and the typical anchovy lives about 3 years. Anchovy occur in large schools and are caught near the surface with nets. This was the largest fishery in the world until it collapsed in 1972 in association with an El Niño that disrupted these cold currents and diminished productivity. Fishing was suspended to allow the stocks to recover, but there was no immediate return of the anchovy. Populations of seabirds that feed on the anchovy also remained low. Since anchovy have a rapid generation time, we can assume that there has been adequate time for the population to return to its former level since the fishing suspension. But, as shown in Figure 10.16, it hasn't. Why hasn't it?

In the sheep-grazing example, we had complete control over the number of sheep that were grazed on the pasture. When we harvest trees from a forest or fish or whales from the sea, natural forces beyond the control of the forester or the fisher or the whaler influence the size of the resource available for harvesting. However, the theory that we have already developed will help us see possible outcomes of different resource harvesting strategies. Often the goal is to achieve **the maximum sustainable yield (MSY).** The word *sustainable* is an important qualifier since the maximum yield in any single year is to simply harvest all the resource that exists at that time. However, this is not sustainable since next year there may be no resource. A bit later, we show how to estimate the MSY, but for now we accept that the estimated MSY for Peruvian anchovy was about 9 to 10 million tons/year, based on average conditions for several years before the El Niño episode in 1972. Note that the harvest exceeded MSY in 1970 and in 1966–67.

Two common ways of regulating natural resources like fisheries are explained in Box 10.1.

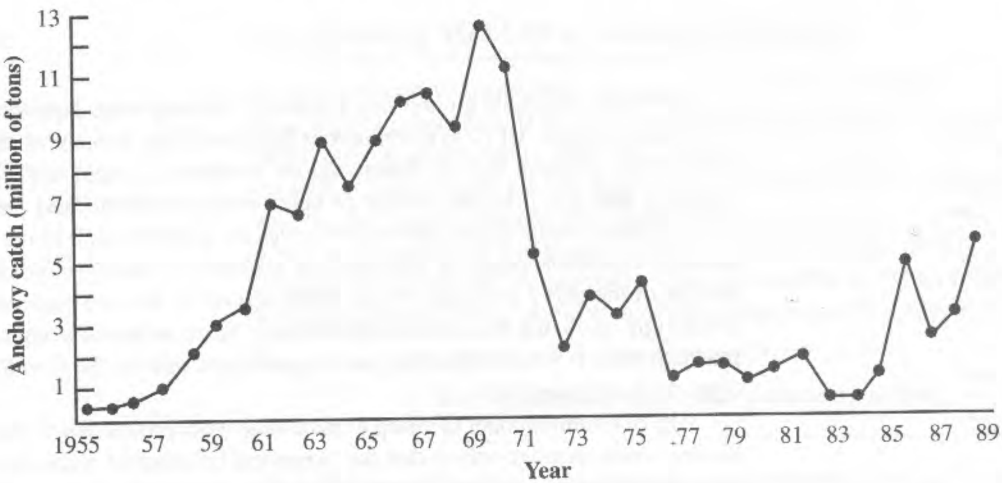


Figure 10.16
Total catch for the Peruvian anchovy fishery. After the collapse in 1972, fishing was greatly reduced but the population had only slightly recovered by 1989. After Krebs 1994.

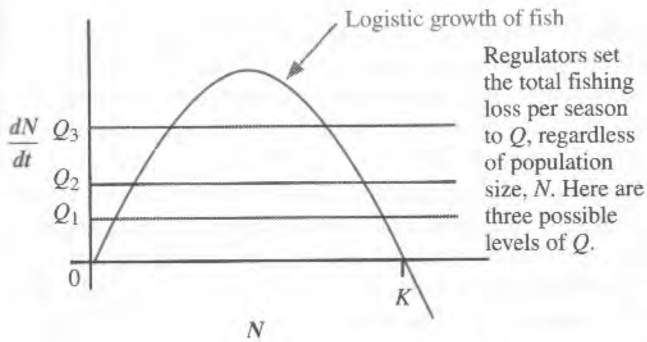
Box 10.1 *Methods of Regulating a Fishery or Other Dynamic Natural Resources*

As with the sheep, we begin by setting up a growth and loss expression for fish:

$$\underset{\text{a fishing season}}{\text{Net growth of a fish population in}} = \underset{\substack{\text{logistic}\\ \text{recruitment}\\ \text{curve of the fish}\\ \text{(per season)}}}{rN\left(\frac{K-N}{K}\right)} \quad \underset{\text{minus}}{-} \quad \underset{\substack{\text{total losses}\\ \text{from}\\ \text{fishing}\\ \text{(per season).}}}{L} \qquad \text{(a)}$$

Now we focus on the loss part of this equation, which is the part that governments can regulate. We may distinguish two methods for regulating the losses due to fishing.

1. **Fixed quota.** Total losses to fishing, L, are regulated by setting a limit, Q, on the number of fish harvested per season, regardless of the number of fish in the population, as illustrated in the following diagram.

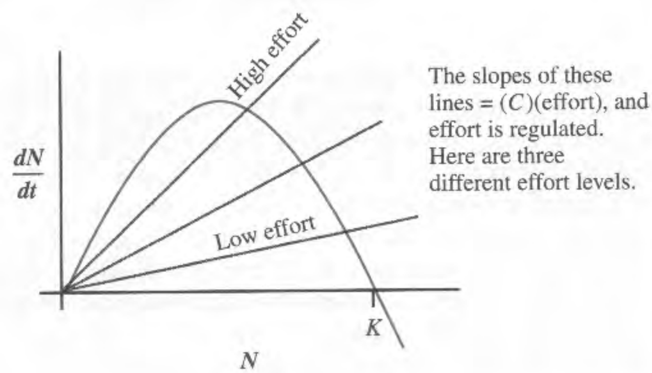


2. **Fixed effort quotas.** We can expand the loss part of Eq. (a) as follows:

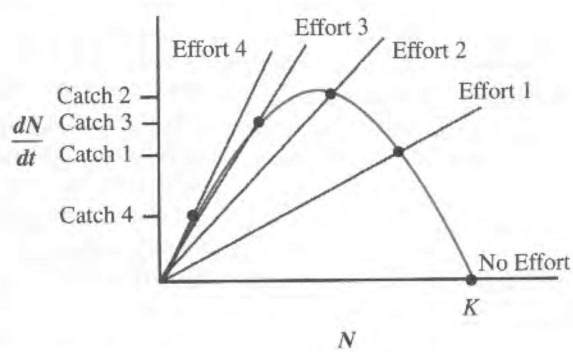
$$L = (\text{fishing effort})(C)(N). \qquad \text{(b)}$$

Here the losses, L, are a product of three factors: the amount of fishing effort (which increases with the amount of time spent fishing, the number of fishing boats, the area the boats cover per day, etc.), a parameter of "fish catchability," C, and the size of the fish population, N. Fish catchability measures the efficiency of each unit of fishing effort. Fish catchability therefore has units of fish caught per effort expended per fish. We assume that C is a constant. Then, Eq. (b) says that all else being equal, the more fish in the population, the more effort expended trying to catch those fish, and the easier the fish are to catch, then the more fish will be caught in a given time period.

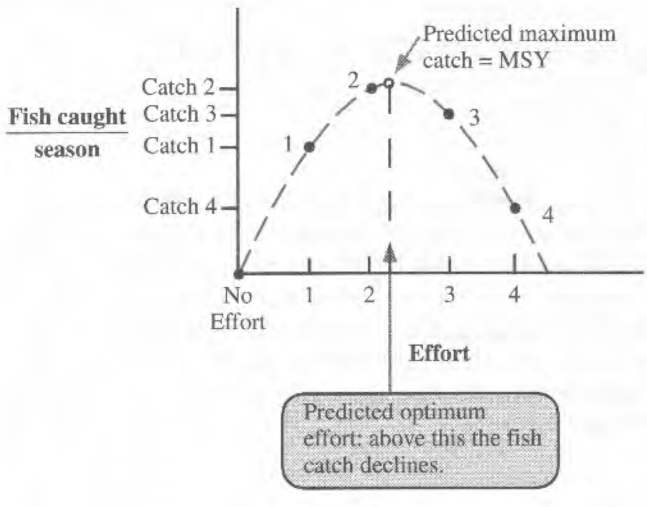
Equation (b) also says that the harvested losses represent a type 1 functional response by the consumers—the people doing the fishing. The numbers of fishers and the "foraging" effort of each fisher are combined into a single term: the "fishing effort." Thus the analog of Figure 10.14 in this case, where the number of fish caught increases linearly with the fish population size (as by Eq. b), looks something like the following.

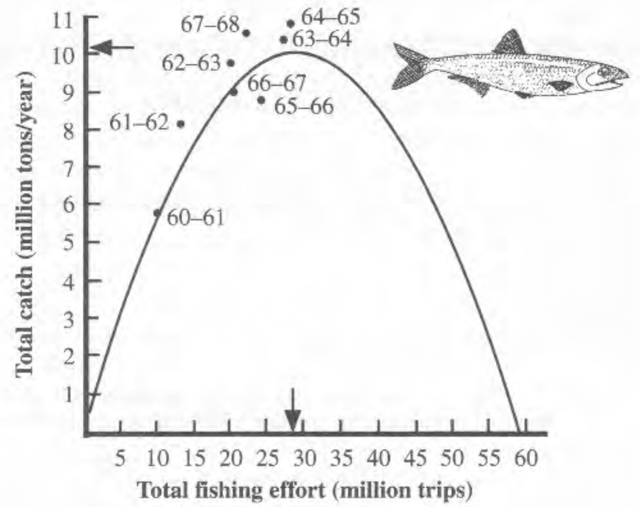


Regulation is effected by limiting the "effort" term in Eq. (b). This may be done by restricting the number of fishing permits, the length of the fishing season, or restricting regions where fishing is allowed. Variations in fishing effort from year to year will lead to different catches, which will trace out the recruitment curve (assuming that it remains constant from year to year). For example, the following diagram shows five different efforts in five different years applied to a fish population and the resulting catches for each.



The following diagram shows those same fish catches plotted against the effort values instead of against fish population size, N.





This plot also yields a hump-shaped curve, like the logistic curve. This is a key result since this figure shows that, even without knowing the absolute fish population size, N, the optimum effort and the MSY can still be estimated simply by the relative position of the yield–effort curve. The optimum effort and the MSY are shown with arrows in the preceding figure. If, additionally, the catchability constant, C, is known, then fish population size, N, and the corresponding r and K may also be estimated from the yield–effort curve (we work through some examples later in this chapter).

Figure 10.17
The relationship between total fishing effort and total catch for the Peruvian anchovy fishery. The effects of humans and sea birds are combined in these data. The parabola is based on a continuous logistic equation fitted to these data. Arrows indicate the estimate for MSY and appropriate fishing effort. After Krebs (1994) from Boerema and Gulland (1973).

The catch versus Peruvian anchovy data and a fitted curve are shown in Figure 10.17. Note that during this period the anchovy did not appear to be severely overexploited.

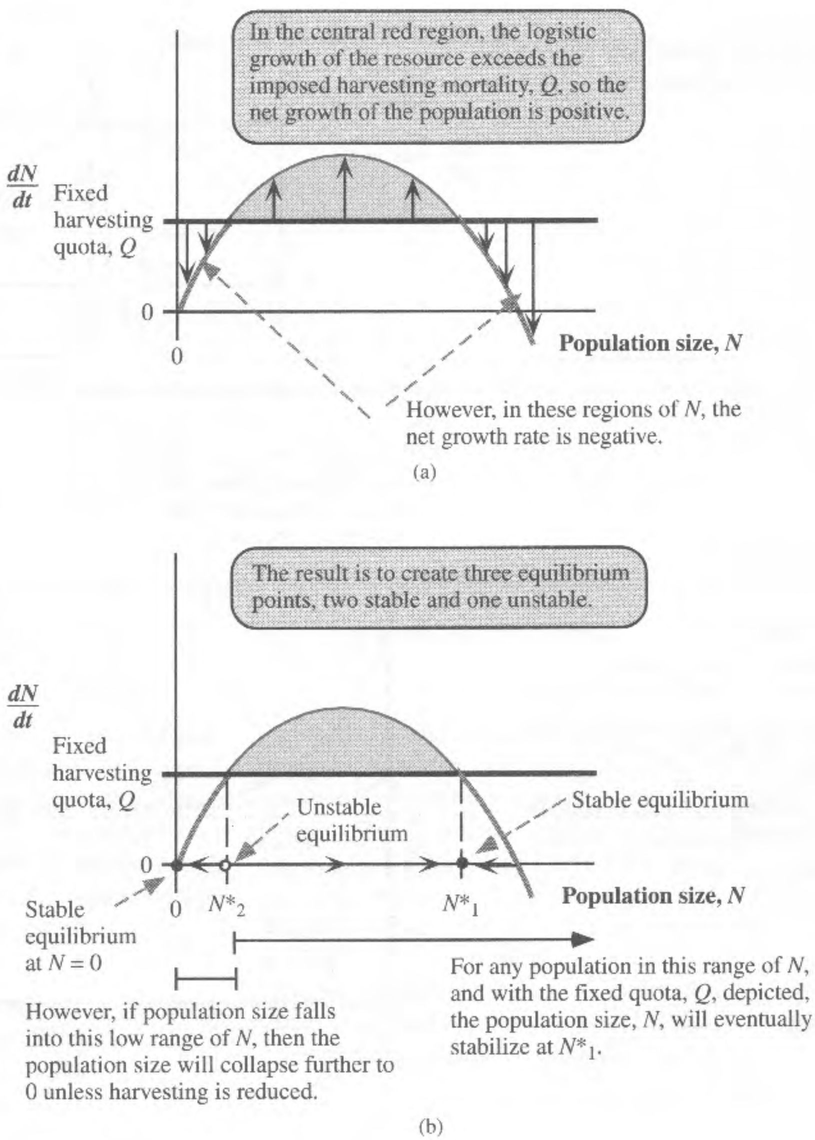
Obviously several complications may affect all this. Fishing effort is normally modified from year to year—but with climatic changes, the recruitment curve, and the r and K for the fish population are also changing yearly. Additionally, the fish population may not grow according to a logistic equation. A full model might require knowledge of the age structure of the fish population. Density-dependence might be different for different ages, and the functional form of the density-dependence could contain several higher-order terms. Recall the more complicated single-species models that we explored in Chapter 5. Finally, the catchability, C, may not be a constant but instead a function of effort and/or fish population size, N. In this case, we would not have type 1 functional response curves but perhaps type 2 or type 3 curves. As we have already shown, the latter can yield break points and alternative stable states. Finally, the fish population is also being exploited by several natural predators, and we usually have little knowledge of their abundance and functional responses.

The task for government resource regulators is to prevent a **tragedy of the commons** by keeping the fishing industry from "killing the goose that laid the golden egg." It is in the best interest of each individual to prevent the overexploitation of the common fishery that they collectively depend on, yet at any particular time it is in the short-term economic best interest of each fisher to maximize his or her catch. Thus we have the classic problem of what is best in the short term for the individual, if followed by all individuals, leads to the collapse of the fishery and thus a bad situation for all who depend on it for their livelihood.

As we have indicated, one possible way to prevent the collapse of the fishery is for governments to impose a fixed-quota harvest (Box 10.1). This imposes a limit on short-term profits so as to maximize longer term profits and the continued viability of the natural resource. For example, regulatory agencies could put a limit on the number of fish that can be caught per season. The fishing season would close after the limit is reached.

Figure 10.18 illustrates the impact of fixed quota harvesting on a resource population with intrinsic logistic growth. We seek to maximize the fish yield in terms of dR/dt. There are two equilibria in Figure 10.18. The one to the right of the hump's peak is sta-

Figure 10.18
Growth of a logistically growing resource under a fixed-harvesting quota.



ble, and therefore the yield at N_1^* is sustainable. However, the one to the left is unstable, and therefore the yield associated with N_2^* would be unsustainable at the same quota level. If the quota were increased, the horizontal line would march up the y axis, giving higher allowed yields. The MSY occurs when the quota is raised to the point that it just equals the peak of the logistic hump, as depicted in Figure 10.19.

For logistic recruitment, the population size will be at $K/2$ when the MSY is reached. Therefore the MSY will equal

$$\begin{aligned}\text{MSY} &= \frac{dN}{dt} \quad \text{at} \quad \frac{K}{2} = \frac{rK/2}{K}\left(K - \frac{K}{2}\right) \\ &= \frac{rK}{4}.\end{aligned} \tag{10.1}$$

It shouldn't take long to see a major problem with regulation for a fixed-quota level $Q_{\max}$. If $Q_{\max}$ is exceeded in a single year, perhaps because it was misidentified by government regulators or because environmental conditions change so that the recruitment parabola becomes lower, then resource levels will be depressed the following year to a level below $K/2$. Now, assuming the same quota level, the fish population will

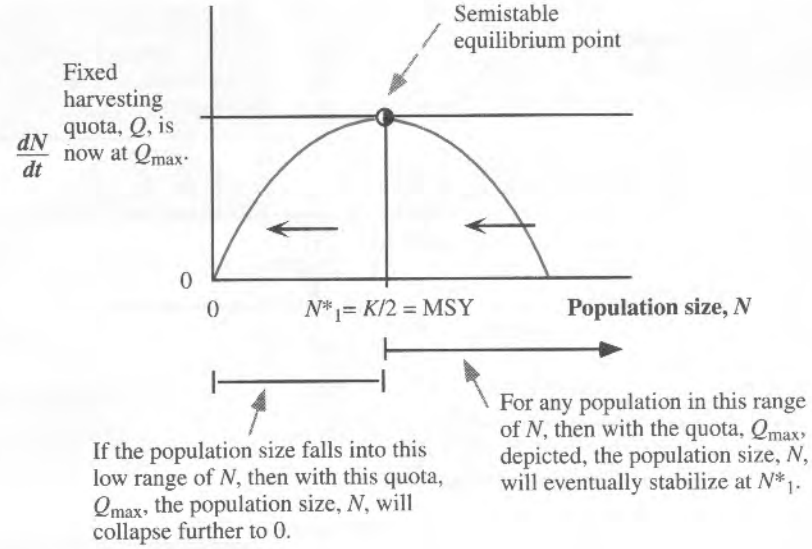


Figure 10.19
A much higher fixed-quota harvest. This harvest will produce the MSY.

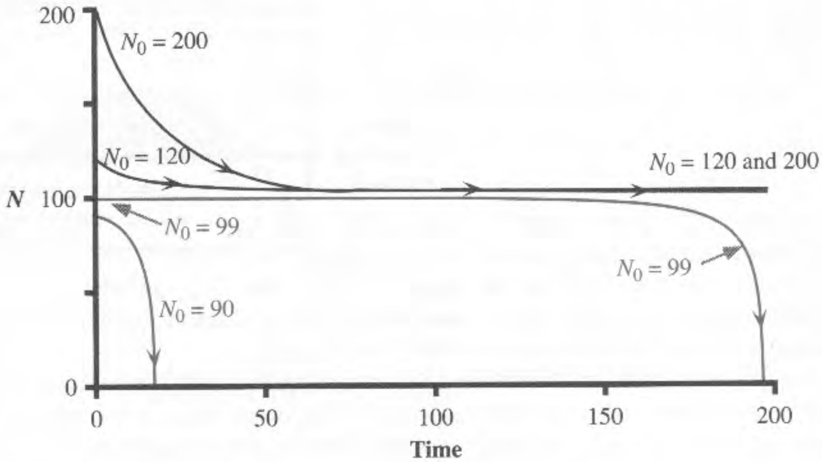


Figure 10.20
Harvesting at the maximum sustainable level for four different initial population sizes: 90, 99, 120, and 200. For this example, $r = 1$, $K = 200$, and Q_{max} is 50. Since $K/2 = 100$, any population slipping below $N = 100$ eventually crashes unless Q is reduced.

approach the stable equilibrium of zero, sliding the fish population into extinction. Therefore harvesting will need to be suspended or greatly reduced until the resource level can return to a level greater than R^* so that the quota Q_{max} will again produce a stable equilibrium. An example of a logistic population being harvested at the MSY is shown in Figure 10.20 for $K = 200$. The initial fish population size is shown at four alternative levels, and for each the population is followed over time.

In this example, the two populations that dipped below $N = 100$ ($= K/2$) fell to extinction. The MSY can be approached only from population sizes above $K/2$. If regulators take quick action and reduce the harvest rate as soon as they notice that the fish population is being overexploited, it will rebound, as Figure 10.21 illustrates.

Why didn't the Peruvian anchovy population rebound like this after fishing was suspended? The anchovy had not gone extinct but were at very low levels. One of our assumptions may be wrong, or there may be more going on than is accounted for by this simple logistic model of fish growth. We will see how this question might be answered a little later in the chapter.

In real systems we typically have little knowledge of the actual level of the resource population, let alone the exact shape of the recruitment curve, and yearly variations in climate influence the shape of this curve anyway. Thus it is easy to overestimate Q_{max}, setting off a population decline and thus producing less than optimal long-term yields (May et al. 1979). A fixed-effort harvesting scheme avoids some of the stability pitfalls of the fixed-quota method, as demonstrated in Boxes 10.2 and 10.3). A fixed-effort

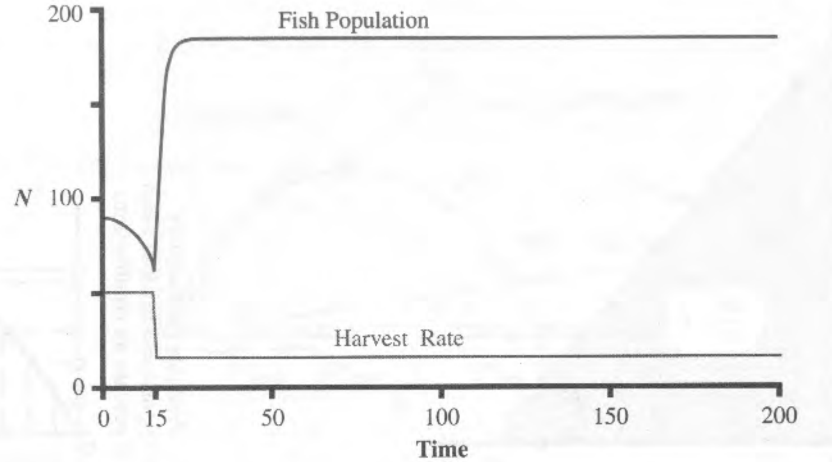


Figure 10.21
This is the same example as in Figure 10.20 for an initial population size of 90. The fish population is on its way to a crash. Now, however, at time 15, the harvest rate is reduced from 50 to 15. With this adjustment the fish population recovers.

Box 10.2

In Figure 10.22, we develop a curve similar to that in Figure 10.15 for a type 1 functional response instead of a type 3 response. This situation corresponds to the fixed-effort regulation of a fishery discussed in Box 10.1. We label the resource population size R and the consumer population as predators P. For example, governments could regulate the number of fishermen, P, as a means of controlling fishing effort.

Solution:

Now we plot the relationship between the levels of R at equilibria (on the x axis) and the number of predators, P, in Figure 10.23. The dots on the x axis in Figure 10.22 are carried over here for each level of prey, and projected (by dashed lines) to the appropriate number of predators. Then a line has been drawn to connect these dots. Figure 10.23 is the analog of Figure 10.12 for a type 1 functional response.

The final step is to produce the analog of Figure 10.15. The open squares on the y axis in Figure 10.22 show the equilibrium level of dR/dt associated with the indicated predator numbers on each total consumption curve. These values are plotted on the y axis in Figure 10.24 against the corresponding predator numbers on the x axis.

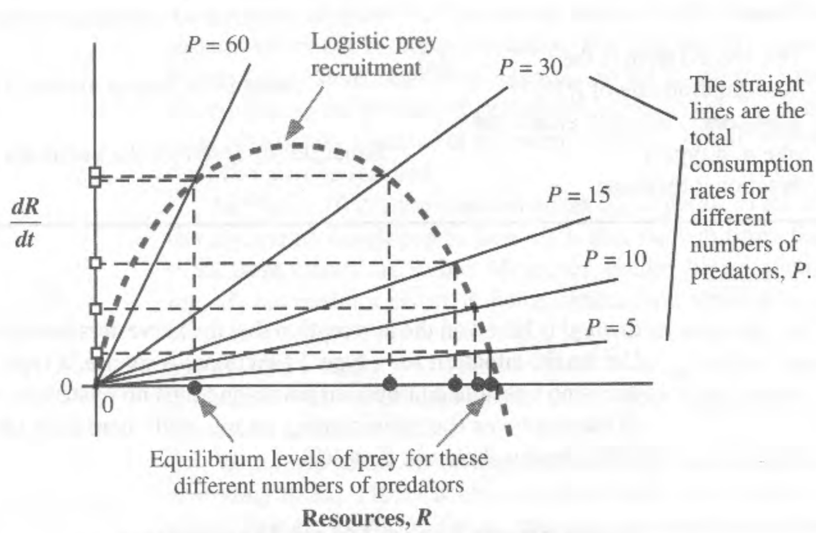


Figure 10.22

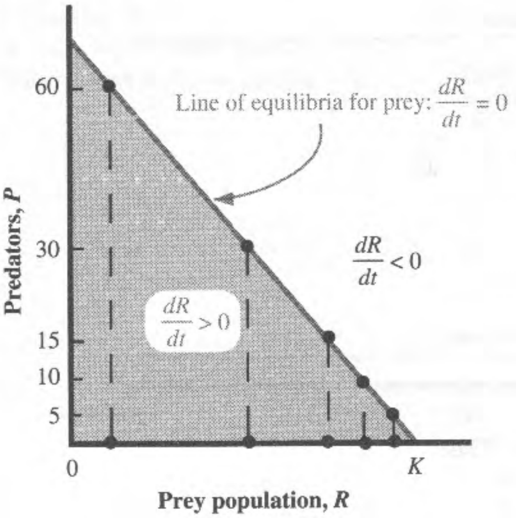


Figure 10.23

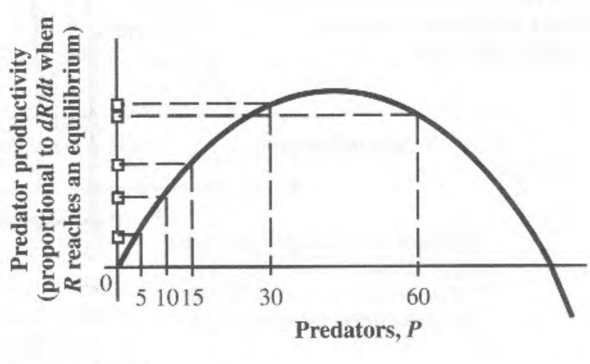


Figure 10.24

Box 10.3

Derive an algebraic expression for the graphical relationship between dR/dt and predator numbers that was developed in Box 10.2.

Solution:

Given a type 1 functional response of predators, with a population size P and a resource population R that grows logistically in the absence of harvesting, we may write

$$\frac{dR}{dt} = \underbrace{rR\left(1-\frac{R}{K}\right)}_{\text{The first term is the logistic equation for } R.} - \underbrace{aPR}_{\text{The second term is the consumption rate of } R \text{ by } P \text{ predators, each with encounter rate } a\text{: a type 1 functional response.}} \qquad \text{(c)}$$

We let R^* be the equilibrium level of R and solve for R^* by setting Eq. (c) to 0.

$$rR^*\left(1-\frac{R^*}{K}\right) = aPR^*.$$

Rearranging, we get

$$R^* = K\left(1-\frac{aP}{r}\right).$$

At R^*, consumer productivity = aPR^* (from Eq. (c)), and thus the turnover of resources at this equilibrium is

$$\text{Consumption rate of all } R \text{ at } R^* = aPK\left(1-\frac{aP}{r}\right). \qquad \text{(d)}$$

Equation (d) describes the **parabola** plotted in Figure 10.24.

method is based on the assumption that the harvesters have a type 1 functional response. Unlike the situation for a type 3 functional response, a type 1 functional response produces no unstable equilibrium points and thus no hysteresis. However, overexploitation of the resources (i.e., diminishing returns with increasing effort) is still possible, as we have already shown in Box 10.1.

More about Fixed-Effort Harvesting

Because of the desirable stability features of the type 1 functional response (Box 10.3), the regulation of total resource harvesting can be accomplished most successfully by a

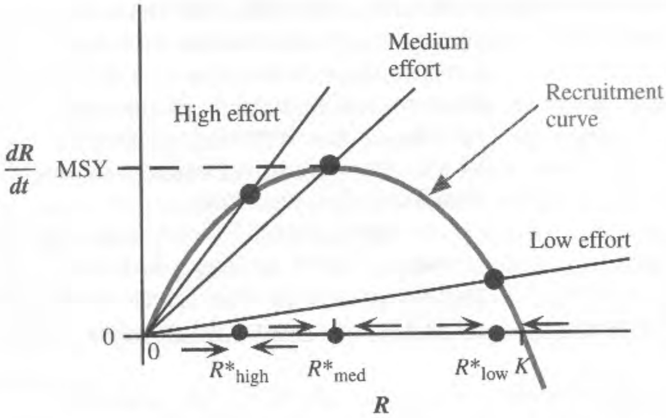


Figure 10.25
Fixed-effort harvesting of a resource, R. The medium harvesting effort produces the MSY and an equilibrium resource level of $K/2$.

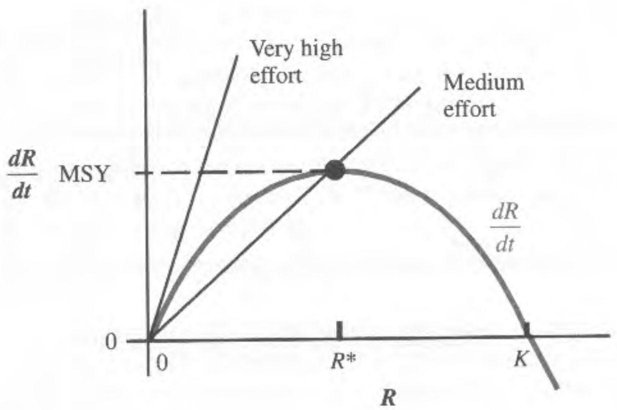


Figure 10.26
The only equilibrium R for the very high effort is zero resource.

fixed-effort regulation of harvesting. Recall from Box 10.1 that the total yield (or catch) of resource to all harvesters is the product of three different terms:

$$\text{Total yield} = \begin{bmatrix} \text{capture effort expended} \\ \text{by all harvesters} \end{bmatrix} [\text{catchability}][\text{resource level}]. \tag{10.2}$$

Regulating the first term sets the total yield, and the resource level adjusts accordingly. An example of the overall harvest in terms of dR/dt based on three different levels of capture effort per resource (assuming that catchability remains constant) is shown in Figure 10.25. Here, regulatory agencies do not fix the total quota per season, but instead try to regulate the amount of capture effort expended. To do this successfully, they must be able to obtain a census of the number of fish, R, and adjust effort accordingly so that the MSY can be reached.

In Figure 10.25, the medium effort corresponds to the MSY. Note, however, from the arguments developed in Box 10.1, that the equilibria fish numbers corresponding to all three efforts are stable. Moreover, unlike the situation with fixed-quota harvesting, if the medium effort is being maintained through regulation, but the resource level temporarily falls below R^*_{med}, the recruitment rate still exceeds the harvest rate and resource levels will increase back to R^*_{med} when conditions return to normal. Resources will not become extinct unless very high capture efforts are maintained, as illustrated in Figure 10.26.

With fixed-effort harvesting, the total yield varies with the resource population size according to Eq. (10.2) If the population size were to drop below R^*, then the yield would drop below MSY. The appropriate response by regulators would be to reduce the allowable effort to let resource levels increase back to R^* or beyond. However, competition among the harvesters would act in the opposite direction. In the face of diminishing catch, harvesters will apply political pressure to increase allowable effort so that yields can go up again, restoring their profit margins. At the same time, with a diminshed supply of resources, the marketplace will often respond with increased prices. This provides an additional incentive to overexploit declining resources. If allowed, such pressures could ultimately ratchet up the effort, forcing the resource to still lower levels. Thus economic pressures interacting with biological harvesting can produce a positive feedback situation that can result in the extinction of the common resource, even with fixed-effort regulation.

As before, the MSY yield occurs at $K/2$ and therefore from Eq. (10.1), MSY $= rK/4$. Of course, r and K are largely invisible to us without a lot of careful field studies. However, the catch at the MSY is measurable and from it we can at least calculate the product rK for this exploited fish population:

$$rK = 4(\text{MSY}). \tag{10.3}$$

Then if we know the catchability of fish, we can extract more information about the fish population. Using Eq. (10.2), we get

$$\frac{\text{Total catch}}{\text{season}} = (C)(\text{effort})(\text{R}).$$

At the MSY, the effort is effort* and the resulting catch is $rK/4$; therefore

$$\frac{rK}{4} = (C)(\text{effort}^*)\left(\frac{K}{2}\right),$$

and

$$r = 2(C)(\text{effort}^*). \tag{10.4}$$

From Eq. (10.3), this result implies that

$$K = \frac{4(\text{MSY})}{2(C)(\text{effort}^*)}. \tag{10.5}$$

Exercise: An effort of 10 boats per fishing season results in a total season's catch of 20,000 fish. The catchability constant $C = 0.001$/boat. What is the fish population size, N?

Answer:

$$N = \frac{\text{Catch}}{(C)(\text{effort})} = \frac{20{,}000}{(0.001)(10)} = 2 \text{ million fish.}$$

Exercise: The MSY of a population has been determined by trial and error to be 30,000 fish produced by an optimum effort of 25 boats fishing per season. What are r and K for this fish population?

Answer:

$$r = 2(0.001)(25 \text{ boats}) = 0.05/\text{season}$$

and

$$K = \frac{4(30{,}000)}{0.05} = 2.4 \text{ million fish.}$$

Exercise: A woman lives in the only home by a small lake. The bass population in the lake has a logistic recruitment curve with $r = 0.1$/day and a carrying capacity of 100. She decides to continue fishing every day until she catches 4 bass. What will happen to the bass population if she continues this policy? Suppose that she changes her fishing so that she fishes every day for just 2 hours, regardless of how many fish she catches. Assume that her catch is linearly related to the bass population size (i.e., her "handling time" is negligible), and, when the bass are at carrying capacity, her 2-hour fishing effort translates into an average catch of 8 fish. What will happen to the bass population if she continues this policy?

Fixed-effort harvesting may result in instabilities if the resource recruitment curve is lopsided because the strength of density-dependence for fish population growth is nonlinear, perhaps because of an Allee effect, as shown in Figure 10.27. The equilibrium to the left of the recruitment curve hump is unstable. If the fish population is reduced below the level corresponding to the peak of the hump, it will crash, even if harvesting is suspended or reduced to a very low level as the crash occurs.

Exercise: For the situation depicted in Figure 10.27, if effort is maintained such that the MSY is reached, will the resulting equilibrium be stable to temporal changes in the level of R^*?

In Figure 10.28, the fish population begins at the equilibrium level associated with a harvest rate of 0.45/fish/time. The fish recruitment curve is asymmetric like the curve in Figure 10.27. At time 25, an El Niño occurs and the fish population crashes, either by 10% or 40%. In response to this crash, regulators drop the harvest rate at time 35 by 80%, in an effort to protect the fishery.

As Figure 10.28 shows, for the milder population crash of 10%, this reduction in harvest was sufficient to resurrect the fish population, which rebounded to reach a new plateau higher than the first one because of the now reduced harvest rate. Under identical conditions, the greater population crash of 40%, even though followed by an equivalent reduction in harvest rate, was not enough to prevent the fish population from continually crashing to zero.

If the harvest rate were reduced to zero, instead of just 80% of its former level, then in both cases (and in fact in every case for this model), the fish population would rebound and reach its carrying capacity. However, with the Peruvian anchovy, the population behaved differently: it seemed to reach a new stable equilibrium at a very low population level following the crash. Note that there is only one nontrivial stable equilibrium point in Figure 10.27; hence this model does not account for the existence of an alternative stable state at low fish numbers. What could account for this discrepancy?

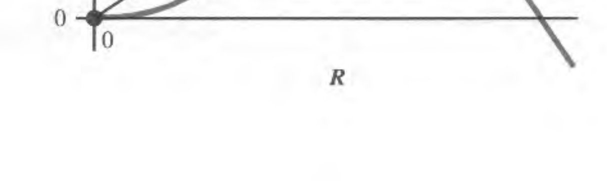
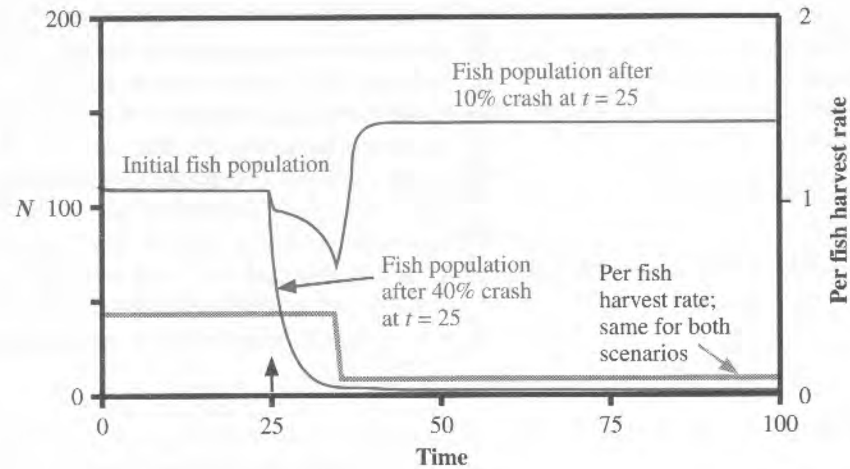


Figure 10.27
Instabilities in fixed-effort harvesting resulting from a lopsided resource recruitment curve.

Figure 10.28
Time courses for a fish population, N, for two different scenarios of fixed-effort harvesting following a crash in the fish population. The harvest rate is the same for both scenarios—the harvest is reduced at time 35 by 80%.



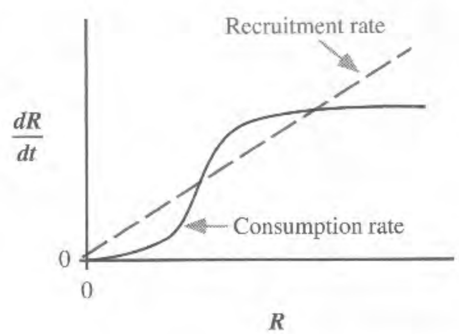
One possibility is that fishing boats have type 3 functional responses. Then a situation like that of intermediate sheep levels depicted in Figures 10.4 and 10.5 would result: two alternative stable equilibria would exist, one at high fish levels and one at low fish levels. However, most fishing boats spend much more time searching for fish than hauling in fish, and there is no evidence that they are usually at or close to some saturation point in harvesting rates that would yield a type 3 functional response.

A more likely alternative recognizes that fish and people are not the only players in this ecological interaction. The exploited fish have many nonhuman predators, including larger fish, sea birds, and marine mammals. If these predators have a type 3 functional response to their fish prey, then it is entirely possible that human overexploitation of fish might force the fish population to the lower of one or several alternative stable equilibria maintained by their natural enemies. To fully understand the dynamics of interacting prey and predators, we need to understand the numerical response of natural predator populations, as well as the within-predator functional response. In Chapter 12 we explore this theme in some detail.

PROBLEMS

1. You have a herd of milk cows and an overgrazed 10-acre pasture. Assume that the functional response of cows to grass on the pasture is a type 2. What is the relationship between cow numbers (y axis) and equilibrium grass levels (x axis)? Also describe graphically the total milk production as you graze more and more of your herd and state why it has the shape that you draw.

2. In the following diagram, the recruitment rate in the absence of predators and the death rate due to predator consumption is plotted for a particular prey species, R. The consumption curve is the functional response (showing total consumption of R) by a fixed number, x, of predators.



Draw the *net* growth curve of R for the prey species in the presence of this fixed number of consumers. Label all equilibrium points for the prey and state whether they are stable or unstable. Now answer the following questions:

a. What type of functional response do the predators have?

b. Do the resources (prey) show intraspecific density dependence?

c. Sketch the curve of equilibrium prey levels as a function of predator numbers.

3. An effort of 20 boats per fishing season results in a total season's catch of 10,000 fish. The catchability constant $C = 0.001$/boat. What is the fish population size, R? The MSY of this population has been determined by trial and error to be 20,000 fish produced by an optimum effort of 30 boats fishing per season. What are r and K for this fish population?

4. Suppose sheep interfere with each other at higher sheep densities, such that the combined functional responses of multiple sheep increases less than linearly with the number of sheep on the pasture. How would you qualitatively modify Figure 10.14 to incorporate this behavior and how would this change the general shape of the wool production curve shown in Figure 10.15?