

2

Simple Population Models

2.1 Introduction

2.1.1 Biological Population Dynamics

A biological population is a collection of individuals that has identifiable emergent properties not possessed by individual organisms. These properties include the population's size, its growth rate, its immigration and emigration rates, its age and size structure, and its spatial distribution. The dynamic behaviour of a population relates to changes in these properties through time. One objective of population modelling is to describe and possibly explain how a population's properties change through time.

Mathematical equations used to model biological populations provide an abstract representation of their dynamics. This requires emphasis because the equations in many population models can exhibit dynamic behaviours that biological populations either do not or could not exhibit; models are, after all, only models. For example, a mathematical model might predict that under some circumstances the modelled population was made up of a negative number of organisms or produced a negative number of recruits. Such obvious discrepancies between the behaviour of the mathematical equations and possible biological behaviours are of little consequence because usually they are easily discovered and avoided. Unfortunately, purely mathematical behaviours can also arise that are less obvious in their effects. It is thus sensible to understand the dynamic behaviour of any equations used in a modelling exercise to avoid ascribing nonsensical behaviours to innocent populations.

2.1.2 The Dynamics of Mathematical Models

The purpose of this chapter is to give a brief introduction to the properties of models and how their dynamic behaviours are dependent upon both their particular mathematical form and the particular values given to their parameters. To do this we will consider some of the mathematical models that are commonly used in both ecology and fisheries to describe population dynamics. We will also be distinguishing between models that do not include age structure and those that do. This is a natural progression,

First, we will consider exponential population growth and its relationship to both the logistic model of population growth, commonly used in basic fisheries models, and age-structured models, such as those used in the analysis of yield-per-recruit. This will lead us to a more detailed study of the logistic population growth model. As we shall see, the discrete logistic model can exhibit a wide range of dynamic behaviours, ranging from monotonically damped equilibria (a smooth rise to a stable equilibrium population size) to chaotic behaviour (unpredictable sequential behaviour). The simple age-structured models we will consider will demonstrate that if the right information is available, we can investigate how the productivity of any population is distributed between new recruits to the population and the growth of individuals already in the population.

2.2.1 All Assumptions Should Be explicit

A model can be viewed as a purely abstract mathematical system, or we can make the step of relating its variables and parameters to the real world. An explicit listing of a model's assumptions about its relation to reality, along with their implications, should be standard practice but is not as common as it ought to be. The most important assumptions of simple exponential population growth are (Slobodkin, 1961; Pianka, 1974):

1. **All animals in the population have identical ecological properties.** This means that morphology, genetics, and behaviour have no effect on population dynamics. Age-structured models are one way to alter this assumption. In addition, we are dealing with a single population or stock; that is, either there is no immigration ($I = 0$) or emigration ($E = 0$), or alternatively, ($E = I$) immigration equals emigration; we are ignoring biogeography.
2. **There are no significant time delays in population processes.** The whole population responds immediately to any changes in population size irrespective of season, geographical scale, or distance. Age-structured models also affect this assumption, at least by introducing time lags between reproduction and growth.
3. **The parameters of the model are constants.** This ignores random variations as well as seasonal and environmentally induced natural variations in such things as maximum population size and maximum

population growth rate. It also ignores long-term changes in parameter values—it assumes stationarity.

These assumptions, about the relation between the model and reality, are either unlikely or unrealistic, but for the moment, they are necessary if we are to keep the model simple (Slobodkin, 1961). Wherever we have used the term *population* in the aforementioned three assumptions, we could have used the term *stock*. The idea is that the model is concerned with a self-sustaining population that does not depend upon immigration to maintain its size. By making our assumptions explicit, we are helping to determine how to interpret the terms of our mathematical model. The assumptions also determine the domain of applicability (meaning the range of situations to which the model is expected to relate; Lakatos, 1970). It is excellent practice to inspect statements about the assumptions of models in the literature to see if one can add to the list given.

2.3 Density-Independent Growth

2.3.1 exponential growth

Population growth at its abstract simplest can be imagined as a population growing in an unlimited environment. An example, which might approximate this theoretical possibility of unrestricted growth, could arise where resources may not yet be limiting for a colonizing species when it first arrives in a new and empty location. Large parts of the world's human population are still growing as if this were the case, but sadly they will soon discover that resources are, in fact, limited. Further examples might be the populations of organisms that first colonized the new volcanic island of Surtsey, which started to form in November 1963 off Iceland, or on the remains of the volcanic island of Krakatoa, which blew up in August 1883 (Krebs, 1985). The initial, accelerating growth exhibited by such populations is described as exponential growth.

If birth and death rates are constant at all population sizes, it implies a constant proportional increase in population size each time period. The rate at which a population's size changes can be described by

$$\frac{dN}{dt} = (b - d)N \equiv rN \quad (2.1)$$

In this differential equation (Lotka, 1925, p. 101), dN/dt translates as the rate of change of the population size N relative to time t , b is the birth rate, d is the death rate, and the symbol \equiv denotes “is equivalent to.” In ecology textbooks, where $r = (b - d)$, r is often termed the intrinsic rate of increase,

the “instantaneous rate of population growth,” or even the “per-capita rate of population growth” (Krebs, 1985, p. 212). The point to note is that the per capita growth rate ($b - d$), or r , is a constant and is assumed independent of population size N . Not surprisingly, this type of growth is termed density independent. Good summaries of population growth can be found in many ecological texts (e.g., Begon and Mortimer, 1986; Caughley, 1977; Caughley and Sinclair, 1994; Christiansen and Fenchel, 1977; Krebs, 1985; Pianka, 1974).

There is a possible source of confusion over the term *rate*. A constant birth rate at all population sizes does not mean that the same absolute number of offspring will be produced at all population sizes, but rather that the population increases by the same proportion at all sizes. Thus, a growth rate of 0.1 implies a population of 100 will increase by 10, while a population of 1,000 will increase by 100. As population size increases, the absolute number by which the population grows in each time interval will also increase, but the proportional increase will stay constant.

Equation 2.1 is a differential equation relating the rate of change of population size to time. This can be integrated to produce an equation describing the expected numbers in the population at any time after some given starting population size and time. The integral of Equation 2.1 is

$$N_t = N_0 e^{(b-d)t} \equiv N_0 e^{rt} \equiv N_{t-1} e^r \quad (2.2)$$

where N_t is the expected population size at time t and N_0 is the population size at time zero (the starting population size). Because the irrational constant e is used (Jeffrey, 1969), this model is termed exponential growth, and that phrase often brings to mind a continuously increasing population. However, depending upon the balance between births and deaths, exponential growth can describe a population going to extinction, staying stable, or growing rapidly (Figure 2.1; Berryman, 1981; Krebs, 1985). In simple whole-population models, Equation 2.2 is of limited use. Knowledge of its properties is worthwhile, however, as it is used in age-structured models that follow individual cohorts whose numbers only decline after birth.

Note that exponential increase produces an accelerating curve in which the proportional increase in population size is constant each time period (Equation 2.2, Figure 2.1, Example Box 2.1), but where the absolute numbers of individuals entering the population each time period increases more quickly with time. In the case of exponential decrease this is a decelerating curve where the proportional decrease is constant throughout but the actual number dying each time period reduces so the population approaches zero ever more slowly with time. This distinction between constant proportional rates of change and increasing or decreasing absolute numbers of individuals is an important one to grasp when considering the exponential model of population changes. The intuitions concerning this phenomenon may come more easily if one recognizes that this process is analogous to compound interest

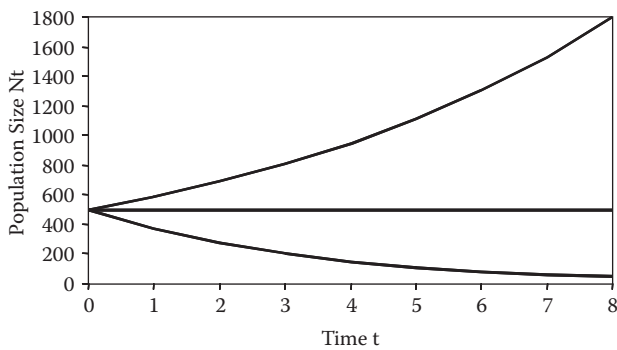


Figure 2.1
Population growth curves from Equation 2.2 under different net balances of birth and death rates (Berryman, 1981). When the net reproductive rate is positive, the exponential increase produces an accelerating curve, leading to ever-increasing population sizes. When there are more deaths than births, an exponential decrease produces a decelerating curve that approaches zero ever more slowly (Example Box 2.1). Obviously, when births balance deaths, an equilibrium ensues.

in financial terms. Positive interest rates lead to exponential growth, and this is a common property for anything that is increased or decreased by a constant proportion through a series of time periods.

2.3.2 Standard Transformations

The mathematical form of exponential population growth has a number of properties that can simplify our representation of population growth processes. The most important property for the practice of population dynamics is that a natural logarithm transformation linearizes the pattern of growth (natural logs, denoted *Ln*, are logs to base *e*). Thus,

$$Ln(N_0e^{rt}) = Ln(N_0) + Ln(e^{rt}) = Ln(N_0) + rt$$

(2.3)

In a population growing exponentially, a plot of the natural log of numbers against time should produce a straight line, and the gradient would be an estimate of the growth rate *r* and the intercept an estimate of *Ln(N₀)* (Equation 2.3).

2.3.3 Why Consider equilibrium Conditions?

Exploited populations rarely appear to be in equilibrium. Nevertheless, to understand a mathematical model's properties it is usual to consider under what conditions equilibrium could be attained. At equilibrium, by definition, the rate of change of population size with respect to time will be zero (*dN/dt* = 0), and with Equation 2.2 that could occur under two conditions.

EXAMPLE BOX 2.1

Three exponential curves in Excel. Each population starts with five hundred individuals, and how it grows depends on whether the birth rate (row 1) is greater than the death rate (row 2). The equation in column B must be copied into columns C and D, and down to whatever time is required. By calculating down to a time of eight (row 21) and plotting the numbers for the three populations (columns B to D) against time (column A), one should be able to generate curves similar to Figure 2.1. The growth model is Equation 2.2. Investigate the properties of this growth model by varying any of the parameters in B1:D3. Try setting the vertical axis of the plot of exponential growth to a logarithmic scale or plot the natural log of numbers against time (put =Ln(B5) into column E, etc.). See Appendix A for guidance with the use of Excel in fisheries.

	A	B	C	D
1	b: births	0.1	0.1	0.1
2	d: deaths	0.04	0.1	0.125
3	N₀	500	500	500
4	Time	Pop 1	Pop 2	Pop 3
5	0.0	=B\$3*EXP((B\$1-B\$2)*\$A5)	500	500
6	0.5	=B\$3*EXP((B\$1-B\$2)*\$A6)	500	493.8
7	1.0	=B\$3*EXP((B\$1-B\$2)*\$A7)	500	487.7
8	1.5	'	500	481.6
9	2.0	'	500	475.6
10	Cont. down	Copy down	Copy down	Copy down

The trivial case is when $N = 0$, i.e., the population is extinct (because with no immigration, at all subsequent times N will equal 0). The more interesting case biologically is when the birth rate exactly equals the death rate and both are positive. With Equation 2.2 this is what is termed an *astable equilibrium*, in which any perturbation to the birth or death rates will disrupt the equilibrium and lead to either an exponential increase or a decrease toward extinction.

If the birth and death rates stay constant but there is a perturbation to the population size (possibly immigration or emigration), a new equilibrium population size will result. The key point being that the population does not return to its previous equilibrium. At equilibrium, $N_{t+1} = N_t$, so there can be no change in numbers from time t to time $t + 1$. Hopefully, it is clear that there can be an *astable equilibrium* at any population size as long as births equal deaths. When not in equilibrium the populations will either increase to infinity or contract to extinction at a rate dependent upon how dissimilar births are from deaths.

2.4 Density-Dependent Models

2.4.1 An upper Limit and Persistence

Few general characteristics can be ascribed to all biological populations. However, as Linnaeus implied (Stauffer, 1960), Malthus pointed out (Malthus, 1830), and the world's human population will soon discover, no population can grow indefinitely because all populations live in limited environments. Thus, positive exponential growth can only be a relatively short-term phenomenon. Another general property of populations is that most are believed to persist despite random environmental perturbations (although long-term persistence is not guaranteed as the continuing spate of extinctions around the world testifies). Unfortunately, our first model, Equation 2.2, allows for very little other than indefinite growth or extinction. While it is true that some “weedy” species exhibit a boom and bust lifestyle (Andrewartha and Birch, 1954), if there is to be population self-regulation, then an obvious option is to alter the simple exponential model to account for the general properties of a maximum population size and persistence.

2.4.2 The Logistic Model of growth

One of the simplest models to be derivable from exponential growth is the logistic model. It is worth noting that in the past a number of fisheries were managed using equilibrium analyses of continuous models based upon the logistic (details will be given when we consider surplus production models in Chapter 11). It has also been suggested that at least part of the sad history of failures in fishery advice and management stems from this combination (Larkin, 1977); this suggestion is often followed by implied abuse at the logistic and its implications, as well as the people who use it. However, invective against the logistic is misplaced. The logistic is simply a convenient model of linear density-dependent effects (similar fisheries advice would have come from any equilibrium analysis using a linear model of population regulation). Beverton and Holt (1957) pointed out the weaknesses inherent in using the logistic population growth curve, but they recognized that in the absence of detailed information this approach might still have value if used carefully. They stated:

It is when such detailed information does not exist that the sigmoid curve theory, by making the simplest reasonable assumption about the dynamics of a population, is valuable as a means of obtaining a rough appreciation from the minimum of data. (Beverton and Holt, 1957, p. 330)

The exponential population growth model was density independent in its dynamics; that is, the birth and death rates were unaffected by the population

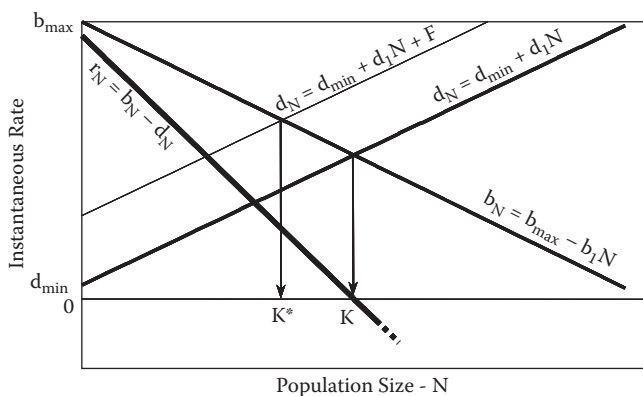


Figure 2.2

Comparison of the influence of population size on the instantaneous rate of increase in a density-dependent model (after Pianka, 1974, p. 86; this is fundamental population biology and Pianka's discussion of these relationships is highly recommended). The death (d_N) and birth (b_N) rates are both described by linear equations (see Equation 2.4), hence the term *linear density dependence*. The junction of the two is where births balance deaths, leading to the equilibrium population size K , and with an imposed fishing mortality F , a new, lower equilibrium, K^* , is produced.

size. If population growth was regulated such that the difference between births and deaths was not a constant but became smaller as population size increased and greater as the population decreased, then the likelihood of runaway population growth or rapid extinction could be greatly reduced. Such a modification of the dynamic response with respect to density is what makes such models density dependent. In a density-dependent model, the population rate of increase (as a balance between births and deaths) alters in response to population size changes (Figure 2.2).

A decline in the rate of increase in a density-dependent model can be brought about by a decline in the birth rate with population size, or an increase in the death rate, or a combination of the two. We will consider the general case where both rates are affected by population size, but the same outcomes would derive from just one being affected.

The simplest model to include density dependence would be where the birth and death rates are linearly related to population size (Figure 2.2; Pianka, 1974). For this to be the case instead of the rates being a simple constant, we would have to include population size and some modifying parameter in a linear equation (Equation 2.4).

If fishing were able to take a constant proportion from the stock, this would be equivalent to an added density-independent increment to the death rate (the fine line in Figure 2.2, $d_N = d_{\min} + d_1 N + F$), leading to a new equilibrium at K^* (these terms are explained later; see Example Boxes 2.2 and 2.3 and Figure 2.5). The modification this would make to the reproductive rate r_N is not shown (the new r_N line would pass through K^*). Linearly relating birth

and death rates to population size would be represented by a change in the gradient terms:

$$\begin{aligned}b_N &= b_{\max} - b_1 N \\d_N &= d_{\min} + d_1 N\end{aligned}\quad (2.4)$$

where b_{\max} and d_{\min} are the birth and death rates when population size, N , is very small, and b_1 and d_1 are parameters that scale the rates at which the birth and death rates change with population size. Equation 2.4 implies that births decrease linearly as N increases and the death rate increases linearly as population increases (Figure 2.2). These changes introduce the possibility of population regulation. If the terms in Equation 2.4 are substituted for b and d in Equation 2.1, our original model becomes

$$\frac{dN}{dt} = [(b_{\max} - b_1 N) - (d_{\min} + d_1 N)]N \quad (2.5)$$

which can be rearranged:

$$\frac{dN}{dt} = [(b_{\max} - d_{\min}) - (b_1 + d_1)N]N = (b_{\max} - d_{\min})N - (b_1 + d_1)N^2 \quad (2.6)$$

This has the effect of putting the intercepts ($b_{\max} - d_{\min}$), which is the rate of population increase when population density is very low, together in one term. The properties of the model can be explored by determining the conditions required for equilibria to exist (where $dN/dt = 0$); thus,

$$(b_{\max} - d_{\min})N = (b_1 + d_1)N^2 = (b_{\max} - d_{\min}) = (b_1 + d_1)N^* \quad (2.7)$$

and therefore (Pianka, 1974),

$$N^* = K = \frac{(b_{\max} - d_{\min})}{(b_1 + d_1)} = \frac{r}{(b_1 + d_1)} \quad (2.8)$$

where N^* or K is the equilibrium population size, often called the carrying capacity in the logistic equation, referring to the hypothetical maximum number or biomass that the environment can maintain if no changes occur. Pearl and Reed (1922) were the first to use the term K to represent the population upper limit. By including these density-dependent effects, this population model is using a form of negative feedback. Thus, as population size increases, the birth rate decreases (possible mechanisms could include increased competition or reduced growth, which would affect fecundity or reduce energy allocated to reproduction) or the death rate increases (possibly due to starvation, cannibalism, or predator aggregation).

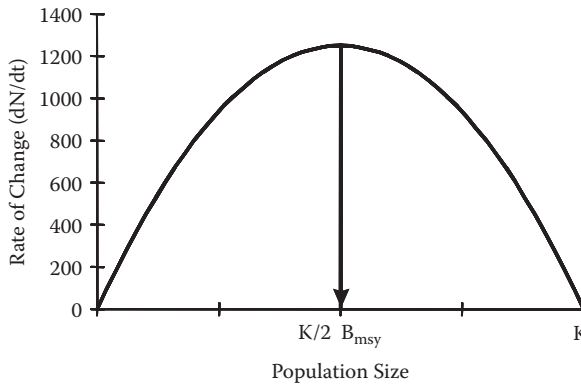


Figure 2.3

Plot of the equilibrium rate of change of population size vs. population size (production vs. stock size curve; Schaefer, 1954). Maximum productivity occurs at half K (in terms of biomass, this is B_{msy}); equilibria occur at zero and K . The symmetry of the production curve about $K/2$ is unrealistic. Permitting asymmetry of the production curve will be considered in Chapter 11.

If we simplify the model (reparameterize by amalgamating constants) by letting $r = (b_{\max} - d_{\min})$, then from Equation 2.6 the rate of population change becomes

$$\frac{dN}{dt} = rN - (b_1 + d_1)N^2 = rN \left(1 - \frac{(b_1 + d_1)N}{r} \right) \quad (2.9)$$

and making the further substitution of $K = r/(b_1 + d_1)$, i.e., $1/K = (b_1 + d_1)/r$, leads to

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (2.10)$$

which is the more common form of the well-known logistic equation (Krebs, 1985). The derivation of K reveals why the two parameters, r and K , are always strongly correlated. Equation 2.10 tells us about the rate of change of population size (related to stock production). By searching for where this is maximum we find that the maximum rate of population change occurs when $N = K/2$ (Figure 2.3).

Thus, a population growing according to the logistic equation will grow at its fastest rate when it is at half the theoretical equilibrium population size. In addition, the population growth rate (dN/dt) will be zero when the population is extinct and when it is at its maximum equilibrium size, the carrying capacity. Integrating Equation 2.10 produces the continuous solution to the logistic equation (Equation 2.11), giving the expected population size N_t at time t after some starting time and initial population size N_0 . By setting

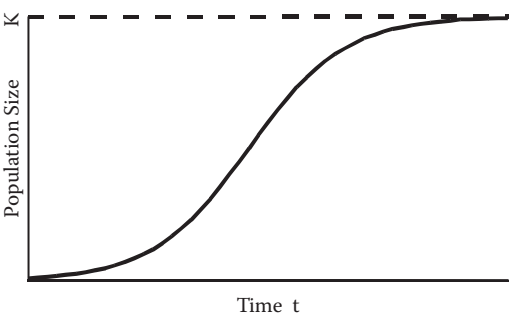


Figure 2.4
Population trajectory when growing according to the logistic curve (Equation 2.11). The top dashed line represents the asymptotic carrying capacity K . Maximum growth rate is at $K/2$, where the inflection exists in the curve. Note the classic *sigmoid* shape described by Beverton and Holt (1957).

$(K - N_0)/N_0 = \gamma$, where K refers to the equilibrium population size, t is time, and r is the maximum rate of population change, then

$$N_t = \frac{K}{1 + \frac{(K - N_0)}{N_0} \frac{1}{e^{rt}}} = \frac{K}{1 + \gamma \cdot e^{-rt}} \tag{2.11}$$

Following the population trajectory through time for this logistic model generates the familiar S-shaped curve (Figure 2.4; Pearl and Reed, 1922). First, there is accelerating growth with a rapid increase in population size before the compensation of density-dependent regulation has much effect (when $(1 - N/K) \sim 1.0$). The acceleration slows until a maximum rate of increase is reached at half the maximum population size. After that, there is a deceleration of growth rates in a way symmetric to the manner in which it accelerated (due to the symmetry of the production curve; Figure 2.3), and the asymptotic population size is eventually reached when $(1 - N/K) \sim 0.0$.

One aspect of the continuous logistic curve that should be noted is the smoothness of the population growth trajectory. There are no oscillations or population overshoots beyond the asymptotic value. This is due to the differential equations dealing with infinitesimals and the instantaneous response to any change in population size that this implies.

2.4.3 Discrete Logistic Model

Differential equations implicitly introduce the assumption of no significant time delays. The assumption that the population can respond immediately to changed population size appears unrealistic. It might be approximated in a large homogeneous population where births and deaths occurred continuously through time and generations overlapped completely. It is also

possible to add explicit time delays to differential equations (Nicholson, 1958). However, for populations in seasonal environments, especially with nonoverlapping generations or discrete cohorts, a discrete time model may be more appropriate. Such models can be referred to as difference equations because they are literally formed to illustrate the difference between time intervals. A logistic model setup as a difference equation could be

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right)$$

(2.12)

which is Equation 2.10 converted to discrete time intervals instead of infinitesimals. If there were an extra source of mortality, such as fishing mortality, this could be included by adding an extra term (C_t is the catch at time t):

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right) - C_t$$

(2.13)

2.4.4 Stability Properties

The exponential model of population growth was astable (any perturbation led either to extinction or runaway growth). The discrete logistic model, however, has more interesting properties. Density-dependent growth means it is more capable of compensating for increases in mortality brought on by such things as fishing. Again, an equilibrium exists where $N_{t+1} = N_t$, which can be represented by a diagonal line on a phase diagram (Figure 2.5, Examples Boxes 2.2 and 2.3) in which time is implicit. The logistic model has

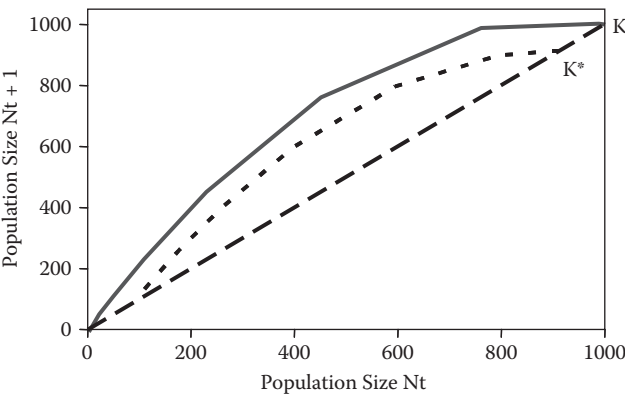


Figure 2.5 Phase diagram of the discrete logistic growth. The diagonal line of equilibrium is $N_{t+1} = N_t$. The upper curved line is the productivity beyond replacement (i.e., beyond the equilibrium line) at each possible population size. The equilibrium carrying capacity is at K . With an extra constant source of mortality (e.g., $C_t > 0$; see Figure 2.2), a lower equilibrium carrying capacity K^* is obtained at the end of the dotted lower curved line. Strictly, this applies only to nonoscillatory situations (see Example Boxes 2.2 and 2.3).

EXAMPLE BOX 2.2

The discrete logistic population growth model (Equation 2.13). By plotting population size (column B) against time (column A), and varying the r , K , and N_0 parameters, one should be able to generate the equivalent to Figure 2.4. Time is implicit in column B because each cell after B5 refers to the cell immediately above. That is, the cell for N_{t+1} refers to the cell for N_t , immediately above, and hence the time steps are implicit. Investigate the influence of a constant catch level, C_t , by varying the value in D1; be sure to increase the starting population size in B3 to be greater than the constant catch level or else the population would instantly go negative. Negative numbers are avoided by using $=\text{Max}(\text{Eq 2.13},0)$. For convenience, the final population size is copied to D3 to aid with the interpretation of the graph. Column C, which duplicates N_{t+1} , should only be copied to one row less than N_t .

	A	B	C	D
1	r: growth	0.5	Ct	0
2	K: popmax	1000		
3	N ₀	50	N ₂₀	=B25
4	Time	Nt	Nt+1	
5	0	=B3	=B6	
6	1	=max(B5+\$B\$1*B5*(1-B5/\$B\$2)-\$D\$1,0)	=B7	
7	2	=max(B6+\$B\$1*B6*(1-B6/\$B\$2)-\$D\$1,0)	=B8	
8	3	=max(B7+\$B\$1*B7*(1-B7/\$B\$2)-\$D\$1,0)	=B9	
9	4	Copy Down to at least Row 25	Copy down	
10	Continue down to row 25		to row 24	

a nonlinear relationship between successive generations (the curved line on the phase diagram, Figure 2.5). The population must take a value somewhere on the curved trajectory, the actual shape of which will be determined by the particular parameter values adopted in the model.

The productivity, above that required to replace the breeding population at any time, is that which, if the predictions of this simplistic model held in practice, could be cropped without damaging the population. That is, the difference between the curve of the production line and the dashed equilibrium line is the hypothetical quantity that could be harvested from the population in a sustainable fashion. The maximum difference, which occurs at $K/2$, is known as the maximum sustainable yield (MSY), and this is the origin of the idea (Schaefer, 1954, 1957).

The stock biomass needed to generate this level of productivity is the B_{msy} (pronounced B.M.S.Y.). This simplistic/historical view underlies the intuitions that many people have about population productivity in fisheries.

EXAMPLE BOX 2.3

The phase diagram for the discrete logistic equation. From the spreadsheet in Example Box 2.2, plot N_{t+1} (column C) against N_t (column B) as a solid line with no dots and vary the parameters r , K , and N_0 until the graph approximates Figure 2.5. To include the equilibrium line, type in, select, and copy H23:I24, as below, then “paste special” these data onto the graph ticking the “New Series” and “Categories (X values) in First Column” boxes, formatting the series to represent a dashed line. At any population size, the distance between the curved line and the equilibrium line is an estimate of the surplus production. You should adjust the value of the constant catch, C_t , in D1, and observe how this affects the final equilibrium, i.e., where the curved line crosses the straight line of equilibrium. To retain multiple curved lines one can copy columns B and C, as values, into columns further to the right and, as before, copy and paste special them into the graph. In this way, one can duplicate Figure 2.5.

	G	H	I	J
23		0	0	
24		1000	1000	

When we discuss stock production models in Chapter 11, we will see why this notion is too simplistic and too risky a view of what is possible.

2.4.5 Dynamic Behaviour

Equation 2.12 (Equation 2.13 with C_t set to zero) has a wide variety of different behaviours depending upon the value given to its r parameter. The fact that very complex dynamic behaviour can be obtained from a simple deterministic difference equation was highlighted by May (1973). This was surprising at the time because the model is a completely deterministic equation and the belief had been that the behaviour of deterministic equations should be capable of being completely understood in an analytical fashion. There are four characteristic forms of dynamic behaviour expressed by the model (Table 2.1, Figure 2.6, Example Box 2.4).

Clearly there are a number of complex behaviours that Equation 2.13 can exhibit, and most of these relate to imbalances in the density-dependent compensation for changes in population size. This is a remarkable field of research, and the visual patterns that can be produced once one starts investigating chaos are undoubtedly fascinating. The detailed dynamics of a model in chaos are unpredictable. Given the state of the model at a given time, it is impossible to predict with certainty what will happen at a later

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TABLE 2.1
Dynamic Behaviour of Equation 2.12 Given a K Parameter Set at 1,000 and the Following Different r Parameter Values

r Values	Description of Behaviour
$0 < r \leq 1$	Monotonically damped equilibrium. No oscillations, leading smoothly to a stable equilibrium.
$1 < r < 2.03$	Damped oscillatory equilibrium. Oscillates but, given enough time, will return to a single equilibrium point following a perturbation.
$2.03 < r < 2.43$	Stable limit cycles, 2. The model system oscillates in a cyclic fashion with two alternative population levels.
$2.43 < r < 2.54$	Stable limit cycles, 4. The model system oscillates in a cyclic fashion with four alternative population levels.
$2.54 < r < 2.57$	Stable limit cycles, ≥ 4. These cycles continue but reach higher orders, first 8, then 16, but then it becomes difficult to distinguish events from chaotic behaviour.
$\sim 2.575 < r$	Chaos. Unpredictable behaviour that changes depending on starting conditions.

Note: See Figure 2.6 for representations of the types of behaviour described. The values of r listed are only approximate, but the behaviour itself may be investigated in Example Box 2.4.

point in time. However, the phase plot for the discrete logistic model illustrates the notion of a strange attractor, and indicates that beneath the chaotic behaviour there are constraints operating on the behaviour of the model. In this case the chaotic behaviour of the various population sizes possible is constrained to lie on a parabola (Figure 2.7; cf. Figure 2.3).

Monotonically damped equilibria occur when changes in the population size are sufficiently slow that the density-dependent mechanisms are able to compensate perfectly, leading to smooth and orderly population growth. This can only occur if the growth rate does not rise through the limits indicated in Table 2.1. If the rate of population increase is too high, then the linear density-dependent compensation built into the model is inadequate to counteract the rapid changes in population size that can occur. At this stage, we would say that nonlinear density-dependent effects are being expressed.

With damped oscillatory equilibria the under- and overcompensation are limited in their lack of balance so that a relatively stable equilibrium eventually arises. With stable limit cycles, the under- and overcompensation for population size changes interact in such a way as to oscillate in a stable manner between multiple quasi-stable states (Figure 2.6). Finally, when the growth rate passes the chaos threshold, the degree of under- and overcompensation is so great that unpredictable behaviour arises (though constrained within the bounds of the strange attractor).

Fascinating though an examination of chaos theory can be (Gleick, 1988; Lauwerier, 1991), a question remains about exactly how useful knowing about such matters is going to be in the modelling of natural populations.

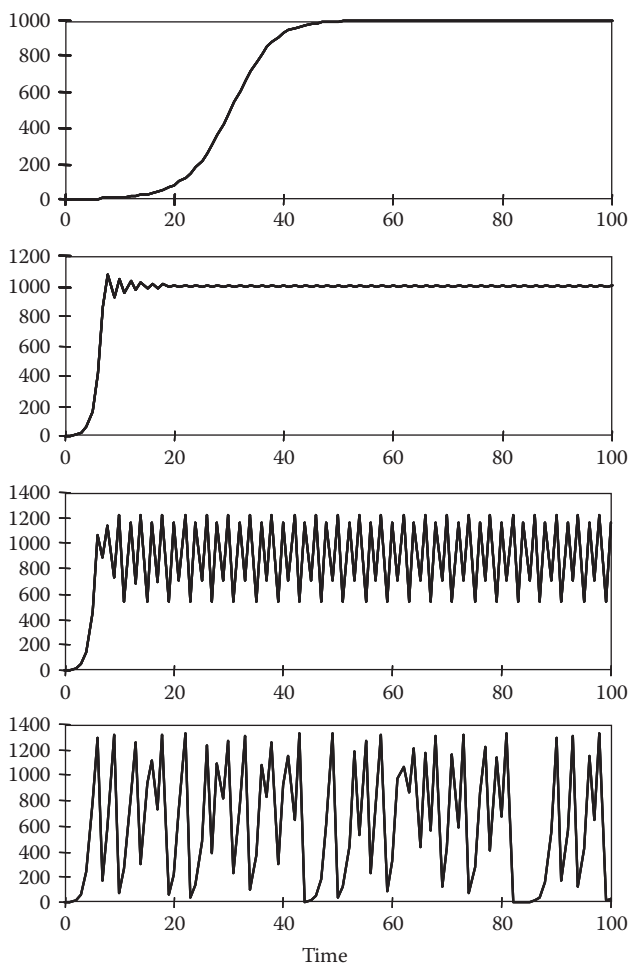


Figure 2.6
Examples of the dynamic behaviour exhibited by the discrete logistic when K was set at 1,000, N_0 set to 1, $C_i = 0$, and each panel is the product of a different r value. Four different r values are illustrated: an r of 0.25 (top; monotonically damped equilibrium), r of 1.85 (second; damped oscillatory equilibrium), r of 2.5 (third; four-way stable limit cycle), and an r of 3 (bottom; chaos). In chaos, if the starting population size N_0 is altered, even only slightly, a completely different and unpredictable outcome is produced (Example Box 2.4).

There are few publications concerning the population dynamics of marine species that use chaos theory in their explanations. Some publications are even explicit in denying that observations of apparently random behaviour are brought about by the nonlinearity introduced by overcompensation in a density-dependent model. Instead, it is claimed that the randomness in observations is brought about by population responses to stochastic environmental effects (Higgins et al., 1997).

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EXAMPLE BOX 2.4

Investigation of a model's dynamic behaviour. Alter the model described in Example Boxes 2.2 and 2.3 by extending time down to 100, N_t (column B) by copying down to row 105 and N_{t+1} (column C) down to row 104. Plot, as points, columns B and C in a new graph in two series (B5:C55 and B56:C104). Colour the first series blue and the second series red. In this way, if the population eventually reaches equilibrium, its form should be more discernible in the phase diagram as a red point. By comparing the phase diagram with a plot of N_t against time (column B against A; cf. Figure 2.6), the manner in which the dynamics alters with changes to r , K , and N_0 can be followed. Using Table 2.1 as a guide, investigate the boundaries of the different dynamic behaviours.

Investigate the impact of a constant fishing mortality rate by setting C_t to >0 . Is the impact the same on all the dynamical behaviours? See Section 2.5 for a discussion.

For an alternative model equation in column B, replace $B5+r*B5*(1-B5/K)$ with $r*B5*\exp(-K*B5)$ and copy down. With the alternative equation the meaning of the parameters has changed, so start with r set to 2.0, K set to 0.0005, and N_0 set to 50. Find the boundaries between the different dynamical behaviours in this model. Is it more or less robust than the logistic?

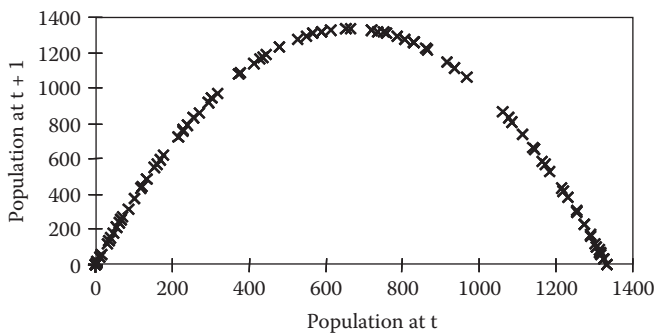


Figure 2.7
The time phase diagram for the discrete logistic equation exhibiting chaos (see Figure 2.6). The points plotted are the first one hundred population sizes when the population started at a size of 1, has a K of 1,000, and an r of 3. The order of appearance on the parabola appears to be random, but the population sizes are obviously constrained to lie on a definite line. The pattern arising from this constraint is known as a strange attractor. Note the upper limit to stock size is no longer K .

An inspection of the time phase diagram (Figure 2.7; in which the dynamic behaviour of a model system is illustrated) provides one with an indication of the bounds within which biological behaviour can occur as compared to mathematical behaviour. Such inspections permit one to determine which combinations of parameter values will lead to what would be pathological or impossible biological behaviour. In this way, such behaviours could be excluded by constraining the parameter values possible. It should be noted that complex dynamic behaviour in a model should therefore be considered with suspicion unless there are good biological reasons to think that such behaviour could be expected.

2.5 Responses to Fishing Pressure

Density-dependent effects compensate for population changes by altering the population growth rate. However, they may under- or overcompensate and so lead to oscillations (see the logistic model in Example Box 2.4). Overcompensation occurs when a population's growth rate is reduced too much, and undercompensation is where the growth rate is not reduced enough. Undercompensation can lead to a population rising to levels beyond its theoretical asymptotic equilibrium. The imposition of extra density-independent mortality onto a model population can often stabilize a relatively unstable situation.

If a constant catch mortality is imposed, this can reduce the variation in a model population's behaviour through effectively offsetting any undercompensation. Of course, if there is no undercompensation, then additional mortality through fishing will simply increase the mortality rate at a given population size (overcompensation). In addition, if the increased mortality is too great, it can lead to a population collapse (see Example Box 2.4).

Maximum productivity occurs at half the maximum population size with lower productivity at either side (Figures 2.3 and 2.4). Thus, we would expect to be able to harvest a population safely more intensively when the biomass was only at half its equilibrium level than we could at other levels (Figure 2.8). This theory is overly simple, but nevertheless one can determine theoretical sustainable harvest rates for population levels below, at, and above the theoretical optimum population size (Figure 2.8), which means these amounts can be harvested each time period without altering the population size.

In each case the harvest rate would equal the surplus production at the given population size. Populations that are harvested when they are near their maximum population size have more resilience to perturbations (such as fishing pressure) than populations harvested when at lower population sizes. The sensitivity to perturbations becomes extreme toward the lower population sizes (Figure 2.9). In practice, with the model, this means more

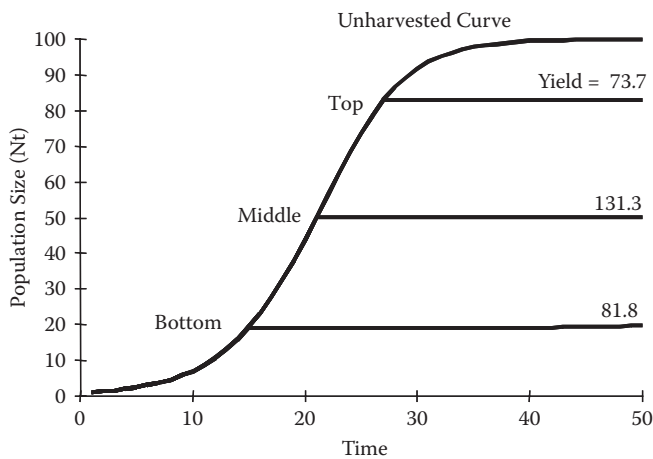


Figure 2.8
A population growing according to a discrete logistic population model with a regular harvest being taken at three different levels of standing crop ($K = 100$, $r = 0.25$, and $N_0 = 1$). The upper and lower levels' total sustainable yield is slightly less than half that from the middle level (Pitcher and Hart, 1982). In this model, 3.51 units are harvested each time period from the top population, while 6.25 and 3.8957 units can be taken from the middle and bottom populations, respectively. The fourth decimal place is necessary with the bottom curve because it is very sensitive to changes in harvest rate (see Figure 2.9 and Example Box 2.4).

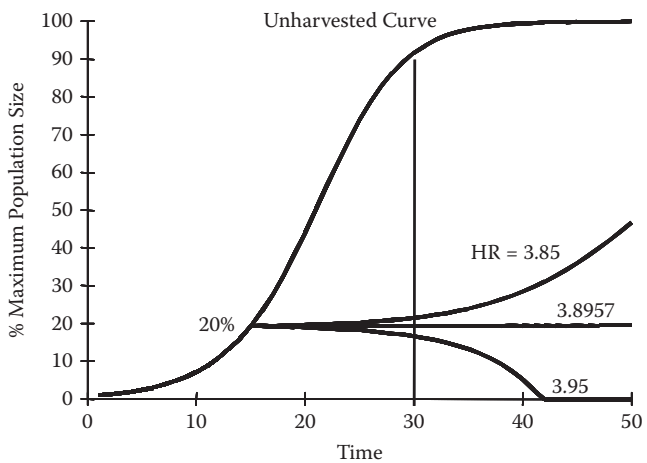


Figure 2.9
Sensitivity to changes in harvest rate of a population growing according to a discrete logistic population model with a regular and constant harvest being taken at a population size approximately 20% of the maximum. Taking 3.8957 population units per time period leads to a constant population size. A slight deviation in this harvest rate (HR) leads to either rapid population growth or a rapid decline to extinction. See Example Box 2.4.

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The models we have dealt with so far may not be thought to have much relevance to fisheries. However, if we extend the logistic model to include catch we obtain

where B_t is stock biomass at time t , r is the intrinsic rate of growth, K is the unfished or virgin biomass equivalent to the carrying capacity, and C_t is the catch taken over time t . It is common practice to assume that catch is proportional to fishing effort and stock size (though this is only the case if the catchability coefficient, q , does not vary through time or with stock size). If we implement these further changes, then Equation 2.14 becomes a dynamic version of the surplus production model proposed by Schaefer (1954, 1957):

where E is the fishing effort and q is a parameter describing fishing gear efficiency (the catchability coefficient is the proportion of the stock biomass B taken by one unit of effort, i.e., $C_t = qE_tB_t$). This was the general form of model used in our simple fishery simulation (Figure 2.9), and we will see more of this and other slightly more complex models when we discuss surplus production models.

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(MSY) toward investigating alternative harvesting strategies. Also, models are no longer constrained to express only linear or symmetrical responses to changes in population density. There is no point in criticizing the logistic equation when the actual problem was that it was inappropriate to use a linear relation between density-dependent effects and population size. The changes in methods mentioned earlier should lead to the production of better fisheries management advice. Unfortunately, it is also more capable of leading to the conclusion that one's data are inadequate for the production of useful advice. Using the old equilibrium methods and inappropriate models, definite management advice could usually be produced. However, the equilibrium methods often produced completely inappropriate conclusions. It is far better to know that one's data are uninformative than to provide bad advice.

2.7 Age-Structured Models

2.7.1 Age-Structured and exponential growth Models

An age-structured model attempts to capture the composite behaviour of the cohorts making up a population, which entails following the development and changes in each cohort separately. This is an improvement over a simple whole-population model for the obvious reason that different aged animals tend to have different growth rates and be different sizes (weights). A larger individual will clearly contribute more biomass to a catch than a smaller one, and generally will contribute a higher egg production. If the necessary information is available, then an age-structured model has the potential to reflect natural population processes and the impacts of harvesting better than simpler models.

If the model concerns a good biological population or stock, then immigration and emigration will be, or is assumed to be, minimal. If this is the case, then once a cohort has recruited, the numbers in that cohort or age class can only decline. How this decline is modelled determines the design of the model. In the introduction to this chapter, it was pointed out that at least some age-structured models have a relationship with the exponential model of population growth. The explanation is quite simple when we remember that the exponential model of population growth can be used to model a declining population. An equation denoting the changing numbers within a cohort can be represented as

$$N_{t+1} = N_t e^{-Z} \quad (2.16)$$

where N_t is the number in the cohort at time t , Z is the total rate of instantaneous mortality (fishing + natural mortality), and e^{-Z} is the

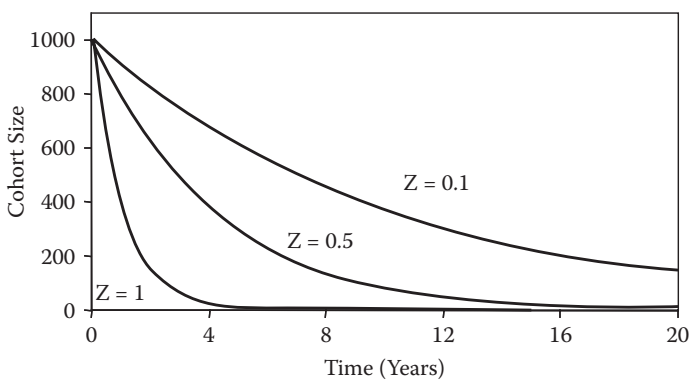


Figure 2.10
Cohort declines with different levels of total mortality (see Equation 2.16). Because e^{-Z} has a negative exponent, it can never be greater than 1 and equates to the proportion of each cohort that survives over each time interval.

proportional survivorship. The relationship with the exponential growth model (Equation 2.2) is clear, but note that the Z value is given as negative, indicating that there can only be an exponential decline in cohort size through time (Figure 2.10).

2.7.2 Annual versus instantaneous Mortality rates

The use of the exponential term in Equation 2.16 is fundamental to population modelling. At the start of this chapter (after Equation 2.1) it was pointed out there was a possibility of confusion over rates of change referring to either proportional changes or absolute changes in population size. One place where this is often a problem and which leads us into an important foundation of fisheries science is the confusion over annual and instantaneous rates of change.

An important aspect of the relationship between fish stocks and fishing is captured by the notion of the mortality imposed by fishing. As in Section 2.5, in a model, fishing constitutes an extra source of mortality that can greatly influence the dynamics of both the natural population and the model. Before we can determine if a level of fishing is sustainable, we would, ideally, obtain an estimate of the level of mortality introduced by the fishing activities. An important distinction is the one between annual mortality (easily understood) and instantaneous mortality rate (less easy to grasp intuitively).

Fishing mortality is invariably referred to by the capital letter F , which refers to the instantaneous rate of fishing mortality. If this is mistaken for the proportion of the fish stock caught annually (the annual mortality, often H for the harvest rate or A for annual), then confusion can arise, especially if F is greater than or equal to 1 (Figure 2.10).

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Outcome of Applying a Constant Mortality Rate Apportioned among Shorter and Shorter Time Periods That Add to One Year

Time Period	Fraction of a Year (Number of Times the Rate Applied)	Mortality Rate Applied Each Time Period	Number Remaining after One Year
6 months	0.5 (2)	0.34657	426.97
3 months	0.25 (4)	0.17329	467.11
1 month	0.08333 (12)	0.05776	489.70
1 week	0.019231 (52)	0.01333	497.68
1 day	0.00274 (365)	0.00189	499.67
½ day	0.00137 (730)	0.00095	499.84
3 hours	0.000342 (2920)	0.00024	499.96
Infinitesimal	~0.0 (∞)	~0.0	500.00

$(1 - e^{-0.693147}) = (1 - 0.5) = 0.5$, the annual mortality rate derived from the instantaneous rate. To apply this rate twice in a year, we divide 0.693147 by 2; to apply it each week we divide by 52. Note how as the time interval becomes shorter, the number remaining approaches the expected five hundred.

It is also common knowledge that if interest is compounded at intervals shorter than a year, then the overall effect is greater over a year than if it were merely compounded once. Hence, we would expect that, given a particular proportional decrease, the effect, if compounded daily, would be greater than if compounded weekly, which would be greater than if compounded monthly (Table 2.2). Equally obviously, it is also a more gradual process. If this procedure of shortening the time over which the interest is compounded is taken to extremes and very tiny periods of time are used, this would approximate the infinitesimals for which the exponential format of the equations operate (Table 2.2).

The exponential function acts to produce proportional changes out of events (such as a mortality) acting over very small time intervals on the same population. This is the same as compounding a negative interest rate many times. The repeated application of a constant proportional decline (divided into however many time intervals are being considered) is what leads to the changes being able to be represented by the exponential equation. The

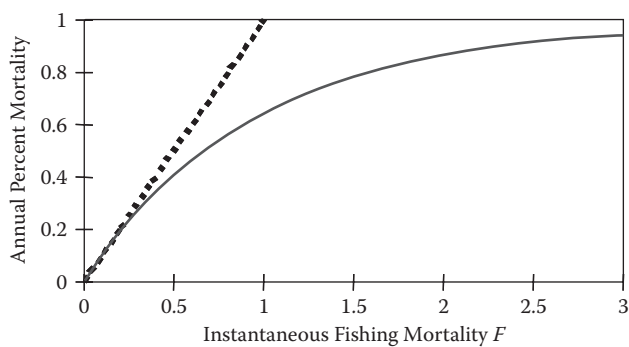


Figure 2.11
The relationship between instantaneous and annual fishing mortality. Note that at low levels of F the two are approximately equal (the curve approximates the straight dotted line, which is a 1:1 reference line), but with F values greater than about 0.2 the equivalence disappears and much larger values of F are required to increase the annual proportion killed by fishing. The relationship is asymptotic with extremely high levels of instantaneous fishing mortality required to catch 100% of the population in a single year.

instantaneous rate of fishing mortality is denoted F , and this is related or translated to the annual mortality due to fishing (the harvest rate, H) using

$$\begin{aligned} \text{Proportional Annual Mortality} = H &= 1 - e^{-F} \\ F &= -\ln(1 - H) \end{aligned} \tag{2.17}$$

A general symbol for annual mortality would be useful, but we cannot use lowercase f , as this is one of the generally accepted symbols for fishing effort (and sometimes fecundity). We cannot use M , as this is generally used to designate instantaneous natural mortality. Some people use E to represent the exploitation rate, but that can also be confused with effort and also commonly refers only to recruited or legal-sized fish. In this book, we will use the letter H to indicate annual fishing mortality, the harvest rate.

The important distinction to understand is the one between the F that everyone tends to talk about, the instantaneous rate, and H , the proportion of the stock taken as catch each year (Figure 2.11).

2.7.3 Selection of a Target Fishing Mortality

An important question to answer is what level of fishing mortality to impose on a stock and the manner in which the catch should be harvested. In fisheries management several standard reference or target levels of fishing mortality exist, and a number of these derive from the analysis of yield-per-recruit. A yield-per-recruit analysis is the simplest form of age-structured population model. A discussion of these methods will thus provide a gentle introduction to age-structured modelling and suggest some fishing targets.

2.8 Simple Yield-per-Recruit

2.8.1 Is There an Optimum Fishing Mortality Rate?

Most exploited aquatic populations are made up of a number of discrete cohorts of different ages. In polar, temperate, and subtropical regions, most commercial species produce one cohort each year. Even in the tropics, despite breeding seasons sometimes being extended throughout much of the year, similar cohort-based population structure can be discerned (even if it is just size based, a form of ecological-cohort). Russell's (1931) equation of stock dynamics can be applied to each cohort separately in an age-structured population. The effects of age structure on stock dynamics become especially important when individual growth and the time delays of ageing are taken into account.

A common intuition is that total yield from a fishery will always increase with increases in total effort. However, this idea was shown to be incorrect before the 1930s. When trying to formalize this idea, the first problem was to find a clear demonstration of what was, at the time, a counterintuitive notion. Also, there is the implication that if maximizing effort does not necessarily maximize catch, is there such a thing as an optimal fishing rate that would lead to a maximum yield? Russell (1942) provided a nice empirical demonstration that the optimal harvest was not necessarily taken by fishing as hard as possible (i.e., that an intermediate fishing mortality could give a bigger yield in an age-structured population).

Russell's (1942) example fished a hypothetical fish species at two different levels (Table 2.3). The major implication of having a high harvest rate of 80% mortality per annum (an $F = 1.609$) relative to a lower rate of 50% per annum (an $F = 0.693$) is that in this particular example, despite basically the same number of fish being taken, the total catch weight was over 60% greater with the lower F . This result stems simply from the lower catch rate leaving more fish in the sea for longer so that they grow to a heavier weight before being caught. At the lower harvest rate there is a greater biomass caught and the number of fish remaining in the sea after fishing is also greater. Hence, the lower fishing mortality yields a larger catch and yet is more risk averse (Table 2.3, Example Box 2.5). Even if the population were not in equilibrium the same principle holds. The benefit in yield remains clear, but obviously the potential stable population size cannot be determined or compared.

By carrying out these analyses for a wider range of different fishing mortality rates one can search for the fishing mortality rate that would be expected to produce the maximum yield from the fishery. This is commonly termed F_{\max} (pronounced F max) and was a common fisheries target mortality rate in the past (Figure 2.12).

The yield drops off at very low levels of F (Figure 2.12) because very few fish are caught. This type of analysis suggests that an obvious refinement to fishing would be to use selective fishing gear that only catches the larger individuals

TABLE 2.3
Comparison of the Effects of Two Fishing Mortality Rates on a Hypothetical Fishery in Which Natural Mortality Is Ignored

Age	Mean Wt kg	Annual Mortality of 80% <i>F</i> = 1.61 <i>H</i> = 0.8			Annual Mortality of 50% <i>F</i> = 0.69 <i>H</i> = 0.5		
		Stock Size #	Catch #	Catch Wt kg	Stock Size #	Catch #	Catch Wt kg
1	—	1,000.0	—	—	1,000.0	—	—
2	0.082	200.0	800.0	65.6	500.0	500.0	41.0
3	0.175	40.0	160.0	28.0	250.0	250.0	43.8
4	0.283	8.0	32.0	9.1	125.0	125.0	35.4
5	0.400	1.6	6.4	2.6	62.5	62.5	25.0
6	0.523	0.3	1.3	0.7	31.3	31.3	16.3
7	0.700	0.1	0.3	0.2	15.6	15.6	10.9
8	0.850	0	0.1	0	7.8	7.8	6.6
9	0.925	0	0	0	3.9	3.9	3.6
10	0.990	0	0	0	2.0	2.0	1.9
11	1.000	0	0	0	1.0	1.0	1.0
Yield	—	1,250.0	1,000.0	106.1	1,999.0	999.0	185.6

Note: The total number of fish caught in each case is effectively the same, but the total yield is much greater with the lower fishing mortality, more stock numbers remain, and presumably that stock has a greater resilience. # refers to numbers of fish. (Data from Russell, 1942.)

Each cohort assumes one thousand recruits each year, with mortality held constant so the system is in equilibrium. The population with the lower fishing mortality ends with a higher standing stock and the greatest yield. As an exercise, construct an Excel worksheet to duplicate this table (see Example Box 2.5).

in which the gains through individual growth would be maximal. The tabular approach is too simple (Table 2.3), however, because it ignores natural mortality and differing vulnerability to fishing gear of different sized/aged animals. If these factors are included, the problem would then be one of estimating the optimal size (or equivalent age class) at first capture for a given *F*.

One aspect of standard yield-per-recruit analysis that must be emphasized is that this analysis only takes into account growth and mortality; generally recruitment variation is not included. Because recruitment is not modelled explicitly but is assumed to be constant (hence yield-per-recruit), the standard yield-per-recruit analysis does not attend to the issue of whether the fishing rate predicted to produce the maximum yield is likely to be sustainable.

2.8.2 What is the Optimum Age or Size at First Capture?

If fishing gear can be made to be age (meaning average size) selective, this opens the possibility of attempting to catch some cohorts while avoiding others

EXAMPLE BOX 2.5

Simplified yield-per-recruit. This Excel sheet calculates the yield from two different schedules of natural (annual M) and fishing (annual H) mortality: (C1:C2) and (F1:F2). The annual harvest rate (in C3 and F3 for the two populations) is used to calculate the animals captured (in columns D and G). The total mortality in C3 and F3 determines the survivorship $=C6-(C6*C\$3)$ in C7 and copied down; with $=F6-(F6*F\$3)$ in F7 and copied down). By summing the respective columns (using $=sum(C6:C16)$ in C17, etc.), the standing stock (N total) and yield (catch Kg total) from each fishery can be determined. By saving as values (edit/paste special/values) in columns to the right, along with their respective mortality rates, build up the information required to duplicate Figure 2.12. By setting the natural mortality to zero, the contents of Table 2.3 can be duplicated. The age at first capture (tc) is used later in Example Box 2.6.

	A	B	C	D	E	F	G	H
1	Annual H		0.8			0.5		
2	Annual M		0.1			0.1		
3	Total A		=C1+C2			=F1+F2		
4	tc		1			1		
5	Weight Kg	Age	N	Catch N	Catch Kg	N	Catch N	Catch Kg
6	0.042	0	1000.0			1000.0		
7	0.082	1	100.0	=C6*C\$1	=A7*D7	400.0	=F6*F\$1	=A7*G7
8	0.175	2	10.0	=C7*C\$1	=A8*D8	160.0	200.0	35.0
9	0.283	3	1.0	8.0	2.3	64.0	80.0	22.6
10	0.400	4	0.1	0.8	0.3	25.6	32.0	12.8
11	0.523	5	0.01	0.08	0	10.2	12.8	6.7
12	0.700	6	0	0.01	0	4.1	5.1	3.6
13	0.850	7	0	0	0	1.6	2.0	1.7
14	0.925	8	0	0	0	0.7	0.8	0.8
15	0.990	9	0	0	0	0.3	0.3	0.3
16	1.000	10	0	0	0	0.1	0.1	0.1
17	Totals		1111.1	888.9	82.2	1666.6	833.2	124.7

(i.e., treating the cohorts differently). If individual growth is an important component of productivity, then we would wish to catch cohorts selectively and would also want to include the effects of natural mortality in the analysis.

In Australia, a fine example of the value of fishing for the right-sized animals is seen in the banana prawns (*Penaeus merguensis*) of the northern prawn fishery (Pownall, 1994). This species is found in large breeding aggregations (fishers refer to these as boils); they are relatively short-lived and start

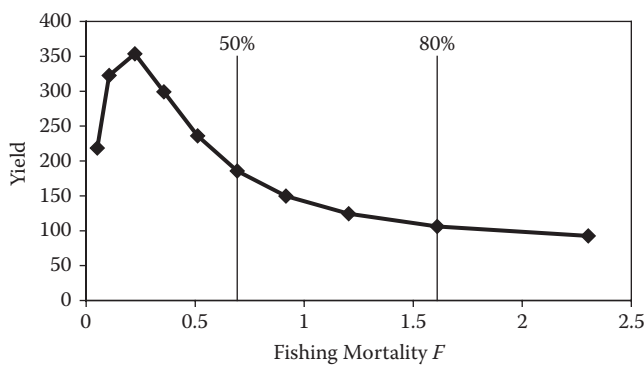


Figure 2.12
The equilibrium yield-per-recruit obtained from Russell’s (1942) example with different annual harvest rates (5, 10, 20, and 30%, up to 90%). Given zero natural mortality and assuming fish are all equally vulnerable to fishing from age class 1, then the optimal fishing mortality, the F_{max} , in terms of maximum yield, is $F = 0.223$, or 20% annual harvest rate (Table 2.3 and Example Box 2.5).

life as very small animals. The best prices for prawns are obtained for the larger individuals, so it would be bad economics to begin the harvest of the banana prawns too early.

The fishing season is very short, with catch rates becoming unprofitable after only a few weeks (nowadays often just three to four weeks). Year-to-year variations in catch are considered to be the result of variation in recruitment and not in fishing effort, so the assumption has been made that despite the high fishing mortality there will always be sufficient prawns to provide adequate recruitment in subsequent years. The opening date for the banana prawn season was set by an economic analysis and model of the fishery that was developed early on.

The northern prawn fishery is open from April until the end of November with a midseason closure in June and July. By opening the fishery in April new season banana prawns have had a chance to grow to a larger, more valuable size. Catchability of banana prawns is also higher in April as they congregate for spawning. Owing to these factors, effort is focused mainly on banana prawns following the opening of the fishery. (Dann and Pascoe, 1994, p.11)

The Australian management of banana prawns is based on a yield-per-recruit argument (optimum size of individual animal), and an effort has been made to ensure that the animals at least approach this size before they are fished. Where the management is risky is in the assumption that unrestrained fishing effort will not affect subsequent recruitment. Short-lived fast-growing species like tropical prawns can certainly be recruitment overfished (see next section; Garcia et al., 1989). However, in species with highly variable recruitment it is hard to detect recruitment failure until after it has happened.

Given the objective of maximizing yield (total catch), analytical methods were developed in the 1950s for calculating the optimum age or size at which to first begin capture for a particular fishing mortality. However, standard yield-per-recruit analyses do not attend to whether such catches would be sustainable (i.e., they ignore absolute recruitment). If a species grew to a large size before it was mature and suffered a significant natural mortality, the equilibrium yield-per-recruit analysis could lead to recommending that heavy fishing be imposed upon immature individuals. The development of the alternative technique of egg-per-recruit analyses, which takes yield-per-recruit one step further, is an attempt to avoid the risk of recruitment overfishing.

2.8.4 The Model Structure and Assumptions

The assumption of equilibrium is quite unrealistic because in many fisheries recruitment variation leads to the age structure of the population changing markedly with time. However, this assumption simplifies the model considerably and is useful for introducing the ideas involved. It is a major weakness of the method, however, and implies that any results should be assumed to be uncertain and potentially risky. This is one reason F_{\max} is no longer considered a safe management target. In our cohort model we assume that R individuals of age t_r are recruited (become vulnerable to possible capture) to the fishery each year. Hence, by definition, t_r is the minimum age at which fish could be targeted by the fishery. Note that there is a distinction between being vulnerable and being targeted. To add a little

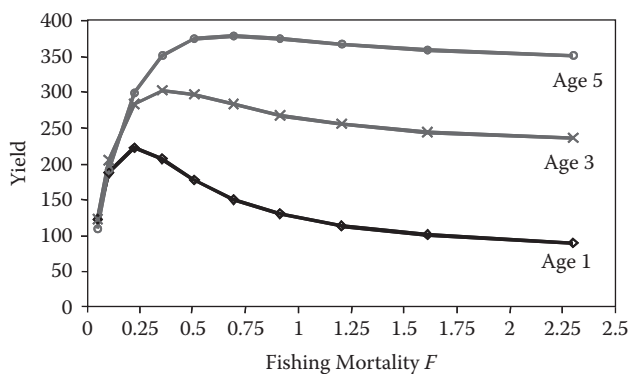


Figure 2.13
Yield-per-recruit from Russell’s (1942) example with $M = 0.1054$ (annual = 10%) included. Calculations are repeated assuming fish are vulnerable to fishing from three different age classes onwards. The yield curves suggest that the optimal yield would be obtained with a fishing mortality of $F = 0.693$ or $H = 50\%$, with fish capture starting at age 5 (see Example Box 2.6). The global optimum is different again with $t_c = 8$ and $F = \infty$.

EXAMPLE BOX 2.6

To take account of the age of first capture, replace the contents of C7 in Example Box 2.5 with =if(B7>=C\$4,C6-(C6*C\$3),C6-(C6*C\$2)). Copy this down to C16. This is now equivalent to Equation 2.19. In D7 put =if(B7>=C\$4,C6*C\$1,0) and copy down. Do the equivalent changes in columns F and G. Now, by changing the ages of first capture in C4 and F4 it should be possible to develop the information needed to duplicate Figure 2.13.

There are many ways to implement the same model. The mortality rates could be put in columns as *if* statements, turning on if the age were greater or equal to the age at first capture. One could use the formal Equations 2.20 to 2.23. As an exercise, put together an alternative worksheet that implements these formal equations.

more realism, we will also impose natural mortality to underlay the fishing mortality. To keep things simple to start with, we will assume that once fish are recruited (at age t_r), they are subject to a constant rate of instantaneous natural mortality, M . Fishing mortality effects are then added to the model, and this can be done in a number of ways. In our simplest of models we will arrange things so that we can set the age at first capture (t_c) to be greater than the age at recruitment. With this arrangement, because of targeting, fish are not vulnerable to harvesting before the age t_c , but thereafter they are subject to a constant rate of fishing mortality, F (again, measured as an instantaneous rate). To allow for those fisheries where older, larger fish are no longer

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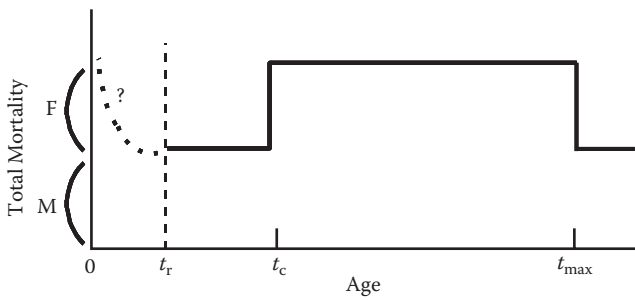


Figure 2.14
A diagram of the assumptions made in simple yield-per-recruit analysis. Here t_r is the age at recruitment, t_c is the age at first possible capture, and t_{\max} is the age at which fish cease to be vulnerable to fishing. The model does not consider the dynamics of individuals younger than t_r years of age but simply assumes that there are R recruits of this age entering the stock each breeding period. M and F are the constant instantaneous rates of natural and fishing mortality, respectively. Knife-edge selection is shown by the vertical rise in mortality at t_c .

selected, the model structure is completed by assuming that fish older than t_{\max} years of age are no longer vulnerable to fishing so that only natural mortality remains. Note that the model assumes both knife-edge recruitment at age t_r and knife-edge selection at t_c ; i.e., either none or all fish in an age class are either recruited or not or are vulnerable to harvesting or not, and once vulnerable, all age classes are equally vulnerable (Figure 2.14).

2.8.5 The Model equations

To generate yield-per-recruit information in a comparative manner for various ages at first capture (Figure 2.13) we need to translate Russell's (1942) example into our first version of an age-structured model. In the empirical depiction of the imposition of fishing mortality and growth (Table 2.3), all ages or cohorts experienced the same level of fishing mortality.

Obviously, as a year concludes, the members of one age class progress to become the members of the next age class. We require an equation with which we can follow the progression of a particular cohort of individuals as they proceed through the possible age classes. The cohort begins at age t_r with a particular level of recruitment R and then, through time, the numbers will decline as natural and fishing mortality have their respective impacts. A representation of the numbers N at t_r , N_0 is $N_{t_r} = N_0 = R$.

We need to find a way to model natural mortality acting throughout the life of the animals in a cohort, while fishing mortality only acts between ages t_c and t_{\max} . As per the equation for exponential decline (Equation 2.14), the numbers at any age $t + 1$ will be

$$N_{t+1} = N_t e^{-(M+F_t)}$$

(2.18)

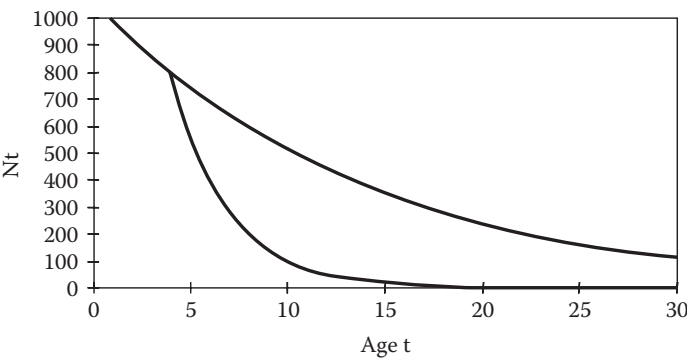


Fig ure 2.15
The age structure of a cohort starting with an R of 1,000 at age 1 ($t_r = 1$), an age of first capture ($t_c = 5$), no t_{max} , an M of 0.075, and an F of 0.25. The upper line is what would happen if fishing mortality was zero for all ages. This exhibits a standard exponential decline of numbers through time. The lower curve is identical to the upper until age 5, when fishing mortality is added, whereupon the numbers drop far more precipitously. Without F there is still 0.1% of the initial cohort left by the age of 60, while with an F of 0.25 the same population level is reached by the age of 17. Fishing can obviously affect the age structure of a stock.

This is simply an exponential decline where the growth rate is negative and equal to M plus F (the exponential term represents survivorship and is equivalent to $1 - H$). Note there are two sets of subscripts, those for time or age (t) and those for ages vulnerable to selective fishing (i). The value of F is only greater than zero for ages where $i \geq t_c$, the age of first capture t_c , and $\leq t_{max}$. The exponential decline brought about by natural mortality is made more severe by the onset of fishing mortality (Figure 2.15).

If this model is run, and the population is assumed to be in age-structured equilibrium, the curves in Figure 2.15 also represent the age structure of the population. Clearly, fishing mortality can have a major impact on the age structure, effectively removing all older animals. This occurs even without size selectivity because it is an expression of the repeated application of a constant mortality rate. The older a fish is, the greater the number of years the cohort will have been exposed to mortality.

This analysis only describes how the population changes in terms of numbers, whereas we need to know how much yield would be obtained under different regimes of age at first capture and different levels of F . The number dying at any time N_Z is simply the difference between the numbers at time $t + 1$ and time t :

$$N_Z = N_t - N_{t+1}$$

(2.19)

Remember that N_{t+1} will always be less than N_t . By substituting Equation 2.18 into Equation 2.19, replacing the N_{t+1} , we obtain

$$N_Z = N_t - N_t e^{-(M+F_i)} = N_t (1 - e^{-(M+F_i)}) \quad (2.20)$$

where the term in large brackets is the proportion that dies from all causes (cf. Equation 2.17). This is simply the complement of the survivorship ($e^{-(M+F)}$). Equation 2.20 determines the number of individuals of age t that die as the cohort proceeds to time $t + 1$. The numbers that die due to fishing mortality (i.e., the number caught, N_{ct}) is simply the fraction (F/Z) of the numbers that die, where Z is the total instantaneous mortality rate:

$$N_{ct} = \left(\frac{F_i}{F_i + M} \right) N_t (1 - e^{-(M+F_i)}) \quad (2.21)$$

This is now known as the Baranov catch equation, though the equation's properties were also examined by others (Beverton and Holt, 1957). Remember that F_i is the instantaneous fishing mortality at age i , which is zero before age t_c and constant afterwards. The total numbers caught under any particular regime of age at first capture and constant fishing mortality are simply the sum of all the N_{ct} . To convert this to a yield, Y , the numbers caught at each age are multiplied by the average weight w_t for each age:

$$Y = \sum_{t=t_c}^{t_{\max}} w_t N_{ct} \quad (2.22)$$

Finally, the yield in Equation 2.22 is that expected for a recruitment of R or N_0 . To generate the strict yield-per-recruit calculations, we need to divide the estimated yield, Y , by the initial recruitment to scale the calculations to units of yield-per-recruit (Equation 2.23). A common alternative would be to carry out the calculations with an initial recruitment of one:

$$\frac{Y}{R} = \sum_{t=t_c}^{t_{\max}} w_t N_{ct} \quad (2.23)$$

Using Equation 2.23, the data required to generate Figure 2.13 can be produced. This can then be used to compare different harvesting strategies for different species, which perhaps have different levels of natural mortality operating (Figure 2.16).

As natural mortality becomes very large, an analysis of yield-per-recruit on a timescale of years becomes less useful because it simply predicts that fishing mortality should become extremely large for the youngest age class in the fishery (Figure 2.16). In such circumstances (e.g., with prawns), data would be required from shorter time intervals such as months, whereupon useful answers could again be determined.

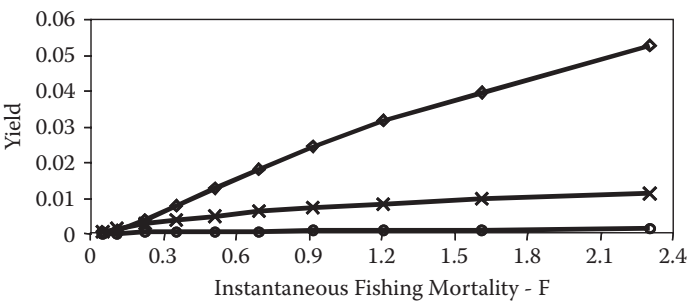


Figure 2.16
Annual natural mortality of 0.75 ($M = 1.386$) with a range of F fishing mortality rates measured over a year and three different ages at first capture. The order of the three age at first capture lines is reversed relative to Figure 2.13. Here the upper curve is the yield for a harvesting from year 1, the middle line is for year 3, and the lower line (almost coincident with the x axis) is for harvesting at year 5. The reversal of the lines arises because with high levels of M , most fish die before growing to a large size, so it is optimal for yield to catch them earlier. It may not be optimal in terms of allowing animals to reach maturity and breed, but that is a different objective for the fishery. Note the greatly reduced yield that has occurred because the weight at age data was not changed.

2.8.6 Yield-per-recruit Management Targets

The expected outcomes from a yield-per-recruit analysis are a target fishing mortality (the mortality rate to aim for) and a target age at first capture. Age at first capture would be used to set regulations regarding gear type (e.g., mesh sizes, hook sizes, escapement holes, minimum sizes) or season start date, while the target fishing mortality (related to the amount of fishing effort) could be used to set a constant fishing rate harvesting strategy (one of the options possible when managing a fish stock). This all assumes the overall objective is to maximize yield from the fishery.

Remember that yield-per-recruit (YPR) analyses by themselves do not attend to the sustainability of the predicted optimal F values. The actual target mortality chosen should reflect this fact. An obvious target fishing mortality to choose might be taken to be the fishing mortality, F_{max} , which gives rise to the maximum yield (in Figure 2.13, this would be approximately $F_{max} = 0.69$, starting on age class 5; in Figure 2.16, $F_{max} = 2.4$ or greater, starting on age class 1). Empirical evidence indicates that, in part, because of uncertainties inherent in equilibrium YPR analyses, F_{max} tends to be too high and leads to stock declines. Instead of F_{max} , many fisheries around the world are now being managed using an $F_{0.1}$ (pronounced F zero point one) strategy (Hilborn and Walters, 1992). The value of $F_{0.1}$ is determined numerically by finding the fishing mortality rate at which the slope of the YPR curve is 10% of the slope at the origin (Figure 2.17).

Hilborn and Walters (1992) considered the introduction of the $F_{0.1}$ strategy to be remarkable:



$F_{0.1}$ policies may be one of the most significant changes in fisheries harvesting practice since the earlier widespread acceptance of MSY. They are significant not because of any theoretical breakthrough, or any intrinsic elegance, but simply because they provide a replacement for F_{\max} and MSY and appear to often be robust. (Hilborn and Walters, 1992, p. 461)

2.8.7 Management Targets and Limits

As stock assessments have improved, the objectives of fishery management have also become more sophisticated (Haddon, 2007). The classical MSY target is now seen to be a risk-prone strategy. Instead, it is becoming more common to adopt both target reference points (TRPs), which define a desirable state for a fishery and fish stock, and limit reference points (LRPs), which define a state

below which the stock should not go (Smith, 1997). Meaningful management action is required if ever a LRP is approached by the stock. Both TRPs and LRPs refer to fishery or stock performance measures that can relate to a range of things, including (ideally) spawning stock biomass, or fishing mortality rates, or any measure that characterizes the state of the stocks. These reference points should be linked with preagreed decision rules that govern management action. Thus, if a LRP is passed, then some remedial action should be defined that will drive the stock back toward the TRP.

By definition, overfishing is said to occur when a stock is being fished at a higher rate than the prescribed limit fishing mortality for the given fishery. Similarly, a stock is said to be overfished if its biomass is below the prescribed limit reference point. If a stock is large but is being fished too hard, it is possible for overfishing to occur while a stock is not yet overfished. Similarly, a depleted stock may be rebuilding and only being fished lightly, and so be overfished without overfishing occurring.

2.8.8 Uncertainties in Yield-per-recruit Analyses

Unfortunately, there are a number of limitations to the yield-per-recruit analyses that go toward adding appreciable uncertainty to the estimates of optimum age/size at first capture and optimum fishing mortality (estimates of all parameters can only be made with limited statistical precision). Using $F_{0.1}$ instead of F_{\max} is an attempt to mitigate for these uncertainties.

Yield-per-recruit (YPR) analyses assume that the fishery concerned has reached an equilibrium with the given fishing mortality. This is a very severe limitation for some, especially intrinsically unstable, fisheries (especially those with high recruitment variability). It also assumes that natural mortality and the growth characteristics of the population are constant with stock size. There is also the problem that management measures that can be taken to implement the recommended age limits can only be implemented using size-selective gear. Age classes are rarely uniform in size, so the outcome will never be as optimistic as that predicted. With annual species, YPR recommendations can be enforced through using closed seasons.

Finally, setting or estimating F is a very difficult process requiring an accurate estimate of the population size and good records of total commercial catch. One always ends with an estimate of F ; there is no real way of eliminating the inherent uncertainty in any fisheries assessment parameter. One method of trying to avoid recruitment overfishing is to conduct egg-per-recruit analyses as well as the more traditional yield-per-recruit.

2.8.9 Types of Overfishing

While implementation of the predictions of the yield-per-recruit approach may be difficult, if the primary objective of management is to maximize yield of biomass from a fishery, then this sort of analysis is fundamental. If one is

dealing with a fishery in which most fish are being caught before they reach their optimum for yield, then growth overfishing is said to occur. If a stock is being fished so hard there are appreciable impacts upon subsequent recruitment, then there is said to be recruitment overfishing.

There are sometimes good (or at least economic) reasons for catching a species at less than its optimum size/age for yield—perhaps, if the optimal price is obtained for individuals smaller than that optimum for yield. In such cases it might be better to perform a dollar-per-recruit analysis, although with the volatility of fish prices this would probably not be practical. On the other hand, fishing a stock so hard that recruitment overfishing is the result can lead to a vicious cycle of stock reduction until it collapses (i.e., recruitment overfishing is risk prone and not risk averse).

