7 Single-species stock assessment

7.1 Introduction

It is not easy to keep track of the rates of birth, death and reproduction of a large number of individuals. It is even more difficult to predict how a change in any one of these parameters, such as increased mortality, will affect the population in the future, because this will depend on numerous interactions within and among species, often against a backdrop of year-to-year variability in the environment. Indeed, fishery scientists have the additional problem of studying animals that are usually visible only when they have been brought over the side of a ship! Yet understanding the population biology of fished species is essential to meet one of the main objectives of fishery science, that of maximizing yields to fisheries while safeguarding the long-term viability of populations and ecosystems (Chapter 1).

The aim of this chapter is to provide a brief overview of single-species stock assessment. 'Brief' is certainly an understatement, given that many books are devoted primarily to this subject, including specialist volumes relevant to particular taxa or regions. For derivations of the methods introduced in this chapter we particularly recommend Hilborn and Walters (1992) and Quinn and Deriso (1999). Fisheries science is a quantitative subject, so students should be prepared to embrace the minimal mathematics included here. We have put much of this in separate boxes and point out key references for those who want more detail.

7.2 Balancing birth and death

Traditionally, the Holy Grail in fisheries science was to find the **maximum sustainable yield** (MSY), the largest catches that can be taken over the long-term without causing the population to collapse. From a strictly biological point of view, this makes sense. However, this is by no means the only objective of fishery management, and it may ignore the goals of the fishers themselves, who are often more concerned with employment and maximizing profit from the catch (Chapters 1, 6 and 11). Even if the objective is to maximize yield, precaution suggests managers should aim for yields below the theoretical MSY (section 7.3). In the meantime, MSY is a good starting point for understanding the biology of exploitation.

For a given level of fishing mortality to be sustainable, there must be a balance between the mortality, which reduces population biomass, and reproduction and growth, which increase it (Russell, 1931; Fig. 7.1). Mortality and reproduction are not entirely independent, but fluctuate within limits set by abiotic factors such as weather, and biotic factors such as competition and predation (Begon *et al.*, 1996a; Chapter 4). The balance that is struck through biotic factors is due to density dependence, the relationship between population density and per capita birth, growth or death (Fig. 7.2). Density dependence gives populations the resilience required to sustain elevated mortality from fisheries.

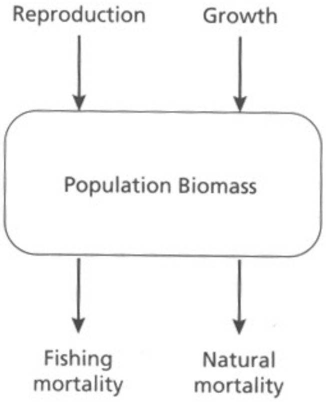

Fig. 7.1 Population biomass depends on growth, reproduction, natural mortality and fishing mortality.

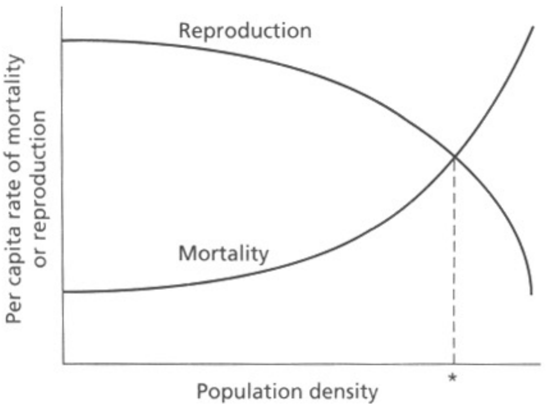

Fig. 7.2 Density dependence in per capita rates of birth and death. At the equilibrium (*) these processes balance one another.

7.3 Surplus production models

Surplus production models are used to search for the largest fishing mortality rates that can be offset by increased population growth, normally measured as changes in population biomass per unit time. They are a good starting point because they capture the basic logic of density dependence, and the simplest ones can be thought of as 'null models' that underlie the theory of sustainable exploitation for terrestrial as well as aquatic organisms (Milner-Gulland & Mace, 1998; Reynolds *et al.*, 2001). Surplus production models use data that have been aggregated to some extent across age classes. These models appear in the literature under several aliases, including **production models, stock production models, surplus yield models** or **biomass dynamic models**.

Suppose that a population grows in a classical logistic (sigmoid) fashion, beginning slowly at first and then reaching a maximum rate of increase, before slowing down again as it reaches maximum total biomass, B_{max} (Fig. 7.3a). The maximum biomass of the population is traditionally said to occur at the carrying capacity of the environment, although many fish populations fluctuate so wildly that it is easier to deal with this concept in theory than in practice (Chapter 4). The slowdown in population growth at high densities would be due to density-dependent processes such as competition for resources, cannibalism or the spread of disease (section 4.2.4). The impact of density dependence can be seen most clearly by plotting the rate of change of the total population biomass against total population biomass (Fig. 7.3b). The rate of population growth also shows the 'surplus' yield available to a fishery (Fig. 7.3c), and so the maximum sustainable yield (MSY) is found at the highest point on this curve.

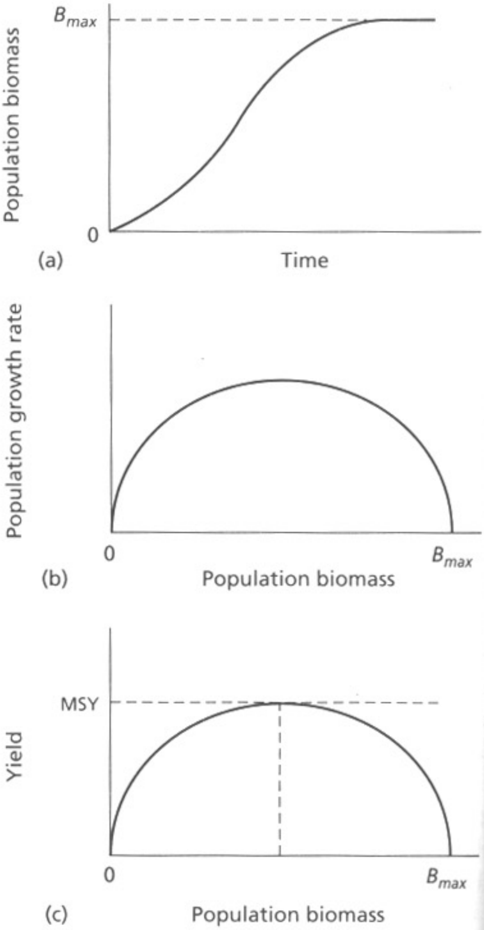

Fig. 7.3 (a) Logistic population growth. (b) Populations grow most quickly at intermediate sizes up to a maximum total biomass, B_{max}. (c) The maximum sustainable yield (MSY) in biomass occurs at a level of fishing mortality that places the population at an intermediate size.

7.3.1 Stability

We have now found MSY on a surplus yield curve, but in the real world MSY is a very small target indeed! Furthermore, it is a moving target, due to temporal changes in the productivity of the ocean and the fisheries that can be supported (Chapter 2). Before we discuss

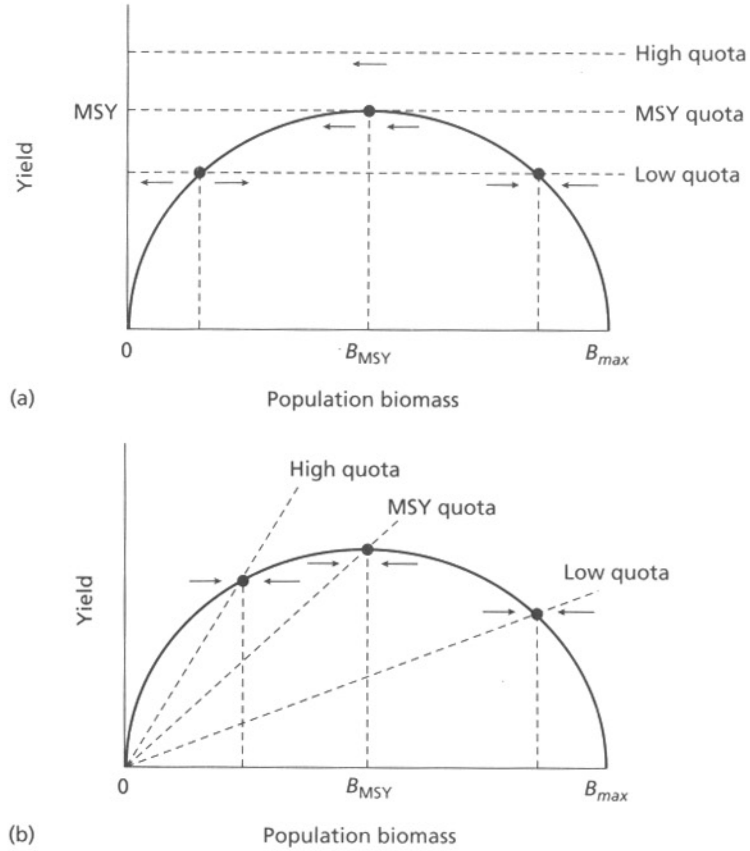

Fig. 7.4 Stability of surplus production models under various fishing quotas. Arrows indicate population trajectories. (a) Constant biomass caught. (b) Constant proportions of biomass caught.

ways of finding MSY using real data, we must consider what happens when we miss the target, because this is inevitable; our population estimates will never be perfect, nor will enforcement of quotas (catch controls, section 17.2.2) or other restrictions be sufficiently exact to score a direct hit on MSY. The yield curves in Fig. 7.4 correspond to those shown in Fig. 7.3 with arrows added to indicate stability of various catch rates.

First, consider the case where a constant biomass is caught (Fig. 7.4a). Suppose that this fixed quota had been set too high (above MSY—'high quota' in Fig. 7.4a). For all population sizes, yield would exceed the surplus production so the population would be driven to extinction. Now consider the case where MSY is estimated perfectly, and the quota is equal to MSY. The fate of the population depends on whether it is initially above or below B_{MSY}. If the population is larger than B_{MSY}, it will stabilize at B_{MSY}. This is due to density dependence (i.e. initial productivity will be less than mortality), and as it is fished the population will decrease until production and mortality balance. However, if the population is initially smaller than B_{MSY}, the surplus production will always be less than the quota and the population will go extinct. What if the quota is too low ('low quota' in Fig. 7.4a)? If the population is larger than B_{MSY} a stable equilibrium will be reached, though the yield to the fishery will be less than at MSY because density dependence reduces productivity. If the population is smaller than B_{MSY}, the equilibrium is unstable and the population will either increase to the equilibrium point at the higher population size or crash. This consideration of stability conditions shows that one should *never* try to exploit populations at the MSY using constant catch rates: any reduction of the population below the theoretical point for maximum yield will crash the population. If a constant number of individuals is removed from the population, the MSY equilibrium is not stable.

The situation is better if we exploit at levels that are in proportion to the size of the population (Fig. 7.4b). For example, a fixed percentage of the population might be caught ($Y = pB$), where Y is the yield (biomass caught) and p is the proportion of population biomass, B. Here, perturbations of the population in either direction from the MSY point will be followed by a return to the equilibrium as long as the quota crosses the yield curve. For example, if the population is larger than B_{MSY}, the quota will exceed MSY and the population will be driven downwards to a stable equilibrium. Similarly, if the population biomass is less than B_{MSY}, the quota will be less than the surplus production that results from a release from density dependence in small populations. The population biomass will therefore increase to a stable equilibrium with the quota. But we are not out of the water yet!

7.3.2 Models of population growth

We derived the dome-shaped production model (Fig. 7.3) from a function that describes the growth rate of the population according to population size. The general form for continuous time is:

$$\frac{dB}{dt} = g(B) - Y \tag{7.1}$$

where B is the exploitable population biomass at time t, $g(B)$ is the surplus production as a function of biomass, and Y is the yield to the fishery (in biomass). In words, the rate of change with time in the population biomass is equal to the surplus production minus the yield to the fishery. The equation we used in Fig. 7.3 for $g(B)$ will be familiar to population biologists as the classical logistic equation of population growth. It is usually called a **Schaefer curve** by fisheries biologists, after Schaefer (1954) who used it to develop a mathematical basis for fitting surplus production models. This equation expresses the change in the biomass of the population with time:

$$g(B) = rB\left[1 - \frac{B}{B_{\max}}\right] \tag{7.2}$$

where r is the intrinsic rate of population increase, i.e. the difference in biomass between per capita birth and death rates in the absence of density dependence, and $B_{\max}$ is the maximum biomass of individuals that the population can contain, i.e. the so-called carrying capacity. In a fished population the yield, Y, is subtracted from the right-hand term (as in equation 7.1). At equilibrium, where density-dependence compensates for the additional mortality from exploitation, $dB/dt = 0$, and $g(B) = Y$.

The **Fox curve** is an alternative to the Schaefer (i.e. logistic) model of population growth (Fox, 1970). It is often used, because it may be more appropriate for biomass measurements than the logistic equation which is traditionally used in other contexts for numbers of individuals:

$$\frac{dB}{dt} = rB\left[1 - \frac{\log_e B}{\log_e B_{\max}}\right] \tag{7.3}$$

Here the inflection point corresponding to that in Fig. 7.3(a) occurs at less than half of the maximum theoretical population size, and so the maximum population growth rate and MSY are also to the left of the logistic cases shown in Figs 7.3(b) and 7.3(c).

A third alternative is the **Pella–Tomlinson model** (Pella & Tomlinson, 1969). This function has a parameter, m, added to the Schaefer logistic model, such that

$$\frac{dB}{dt} = rB - \frac{r}{B_{\max}}B^{m} \tag{7.4}$$

If $m = 2$ this equation is identical to Schaefer's original equation. When $m < 2$ the production model produces a maximum toward the left, and when $m > 2$ the maximum is toward the right. This Pella–Tomlinson approach allows for flexibility in the shape of production curves.

7.3.3 Fitting models to data

The choice of production curves is actually the least of our worries. More serious is the second phase of the procedure, namely how to fit these models to real data, to estimate MSY and the level of fishing effort at which it occurs. As we shall see, failure to do this properly has been implicated in the most dramatic stock collapse in the history of fishing.

The methods of fitting these models rely on the assumption that an index of abundance (such as commercial catch rates) can be related to true abundance, e.g.

$$I_t = qB_t \tag{7.5}$$

where I_t is the index of relative abundance at time t (usually measured in years), B_t is the population biomass at time t, and q is the **catchability coefficient** (section 10.2.4). The latter term relates the **catch per unit effort** (CPUE) to population biomass:

$$\mathrm{CPUE} = qB \tag{7.6}$$

It is important to remember that catchability will change with improvements in technology and in response to changes in the distribution and behaviour of the population (sections 4.3 and 10.2.4).

Techniques for model fitting fall under two main categories, **equilibrium methods** and **non-equilibrium methods**. The latter can be further subdivided into process-error or observation-error methods.

Equilibrium methods

Equilibrium methods are often used to fit the Schaefer model, but they can be applied to the other models too. Schaefer (1954) developed a method for estimating MSY and the level of fishing effort at which MSY is achieved f_{MSY}, based on catch and effort data. The basic idea is to make the *very dangerous assumption* that each year's catch and effort data represent an equilibrium (or steady-state) situation, where the catch is equal to the surplus production at that level of fishing effort. Effort might be measured as the number of boats at sea per year, or number of traps baited per year or number of person-days spent spear fishing. CPUE is then regressed against effort over a series of years, producing a negative relationship (high fishing effort yields low CPUE). In part, this negative relationship may be driven by the fact that both the independent and the dependent variables contain fishing effort, providing some correlation even where none exists! This problem notwithstanding, with a little mathematical juggling, the parameters from this regression can be used to fit the familiar dome-shaped production curve.

The equilibrium method depends critically on the assumption that historical catch rates are in equilibrium with the population (Hilborn & Walters, 1992). This assumption is dangerous because temporal changes in CPUE will rarely be a sole reflection of density-dependent responses of the population to fishing mortality. Rather, CPUE reflects ongoing reductions in standing stock, because fishing effort often increases year by year as a fishery develops. Consider the case of the orange roughy, *Hosplostethus atlanticus* (Trachichthyidae) fishery off north-western New Zealand (Fig. 7.5). This fishery built up rapidly until declining catch rates precipitated a considerable reduction in the total allowable catch in 1989–90 (Field & Clark, 1996). In this case, it would have been wrong to assume that the yield in any one year resulted from density-dependent responses bringing the population into equilibrium with high rates of fishing mortality, especially for a species like the roughy which does not reach maturity until it is over 20 years old. Instead, this fishery was mining the population, and the time series of CPUE data could not be used with any confidence. For this reason, the researchers stayed well clear of the equilibrium assumption and employed more sophisticated methods. Many fisheries take 'one-way trips' toward increased effort over time, and the result is that stocks are given credit for greater resiliency than they deserve.

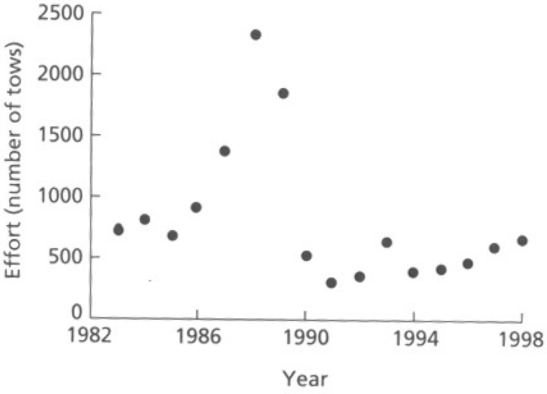

Fig. 7.5 Changes in fishing effort over time for an orange roughy fishery at the Challenger Plateau, New Zealand. The fishery first developed in 1981. After Field & Clark (1996, unpublished data).

Non-equilibrium methods

Process-error methods first transform the production curves into linear forms, and then use multiple regression to fit the models to data (Walters & Hilborn, 1976; Schnute, 1977). Catch and effort data are still used, but without the assumption that the population is in equilibrium. As with all statistical fitting techniques, the parameters in the fitted equation depend on the assumption made about the ways in which errors are distributed in the data. Process-error methods assume that catch and effort data have been measured without error, and all error is attributed to the functional relationship between population growth rate and population size (Hilborn & Walters, 1992; Polacheck *et al.*, 1993; Quinn & Deriso, 1999). That is, we assume error in equation 7.1 rather than 7.5. With this assumption, multiple linear regression is used to estimate the parameters of the production curve. In the case of a Schaefer curve, this means estimating r, $B_{\max}$ (equation 7.2) and the catchability coefficient, q, to relate catch per unit effort to population biomass. This method depends on having good variation (contrast) in the time series of catch and effort data. Otherwise, the estimates can go seriously astray.

Observation-error methods assume that the underlying production relationship is correct, and that all the error occurs in the relationship between true stock size and the index used to measure it (Pella & Tomlinson, 1969). Formally, this is the opposite of the process-error method above, because now the error is assumed to be in equation 7.5 rather than in equation 7.1. The time series for stock sizes is estimated by making an initial estimate of stock biomass. Then the model is used to predict stock sizes for the rest of the time period. One then compares observed and expected population sizes or catches, and uses statistical methods to adjust the parameter values to minimize the difference between the observed and expected values. For the Schaefer curve one thus estimates the same three parameters as with the regression methods, as well as the initial stock biomass. The latter might be the same as $B_{\max}$ if the time series extends back to the start of the fishery. This technique is reviewed by Hilborn and Walters (1992), Polacheck *et al.* (1993), and Quinn and Deriso (1999). Again, the quality of the estimates depends greatly on the quality of the data. We return to a direct comparison of the performance of the three methods for fitting models to data after we see one of them in action.

7.3.4 Surplus production models in action

Of the three methods discussed, the classical equilibrium method has the longest and most sordid history, principally because it presided over the infamous collapse of the Peruvian anchovy *Engraulis ringens*. This fish accounted for > 25% of global marine landings in 1970 (Fig. 1.4; section 4.2.2). It is instructive and sobering to see the disastrous consequences of the equilibrium assumption before we move on to a direct comparison of its performance with the other two methods.

The Peruvian anchovy population is found in the Peru Coastal Current, which runs close the shore of Peru and northern Chile. Anchovy are pelagic fishes, filtering chains of phytoplankton as well as zooplankton, fish eggs and fish larvae from the water. Spawning peaks in September and October, with a smaller secondary peak in February and March (Laws, 1997). The young grow rapidly and recruit to the fishery when they are about 5 months old and 8–10 cm in length. They spawn at age 1 year and may live for 4 years. Most anchovy are caught by Peruvian purse-seiners, and converted to fishmeal to be sold to foreign countries for use in animal feeds. In the 1970s, the fishery accounted for about a quarter of Peru's foreign revenues.

Figure 7.6(a) shows the relationship between CPUE and effort in the anchovy fishery. The parameters from this relationship were used to fit the production curve in Fig. 7.6(b), using Schaefer's equilibrium method. The data include estimates of the biomass taken by seabirds, some 18% of the human catch. You may not be impressed with the extrapolation on the right side of the curve! Such is the nature of the parameter fitting technique, which allows extrapolation well into the unknown, for those brave enough to make the journey. The curve indicates a potential MSY of about 11 million tonnes. After subtracting an average of 1.5 million tonnes for seabirds, this leaves about 9.5 million tonnes for the fishery. It was reassuring to see that since the mid-1960s, the fishery's effort was about right for taking this yield. This was no accident since, in 1965, the Peruvian government brought in regulations that limited annual catches to 7.5 million tonnes. However, it proved difficult to enforce the regulations because the fishing fleets and fishmeal processing plants were greatly overcapitalized and, by 1970, the annual target of 7.5 million tonnes could have been processed in less than 40 days (Laws, 1997). Thus, there were considerable economic pressures for catches to exceed limits.

In January–February 1972 a research vessel survey recorded unusually low numbers of juvenile anchovy. At the same time, oceanographers recorded an intrusion of warm tropical water off the Peruvian coast. This soon developed into a full-blown El Niño event (section 2.3.2). The adult fish relocated to pockets of cool water and tended to move south. Adults were easy to catch in large numbers during March and April, but catches soon declined markedly. By July the earlier hints of low recruitment developed into loud alarms. Faced with this double blow of declining catches and failed recruitment, a management panel recommended a halt to the commercial fishery until they were sure that recruitment from the current cohort of adults proved successful. In

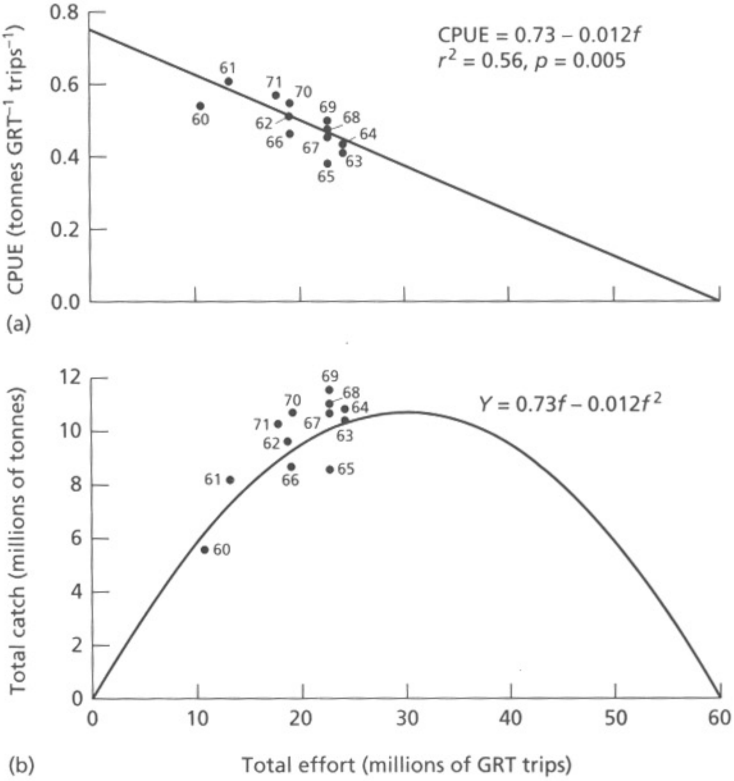

Fig. 7.6 Surplus production model for the Peruvian anchovy (*Engraulis ringens*). (a) Catch per unit effort (CPUE) vs. fishing effort, including both the commercial fishery and the catch taken by seabirds. (b) Schaefer production curve fitted from parameters derived from (a). GRT is gross registered tonnage, a measure of fishing vessel size. After Boerema and Gulland (1973).

fact, some fishing was allowed in the southern part of the fishery in November, because the adult stock seemed reasonably healthy there. But this was false hope. The stock collapsed and the fishery failed. The collapse put fishers out of work, left processing plants idle, and led to serious economic and social problems in Peru. Moreover, many of the seabirds that once fed on the anchovy starved and died. The anchovy stock did not recover quickly after this collapse, contrary to the hope for a stock with a high intrinsic rate of natural increase. Instead, it fluctuated at low abundance, suffering from the continuing effects of an overcapitalized industry and further moderate El Niños in 1976, 1982–83 and 1987. In the 1990s, however, the stock finally grew in size, and anchovy yields now exceed those of any other fished species (Fig. 1.4, Table 3.3).

A tournament of production models

Would the other two techniques for fitting production curves ('process-error' and 'observation-error' methods) have done any better? Polacheck *et al.* (1993) made a direct comparison between all three methods by using them with three data sets from very different fisheries. Each method was used to fit the Schaefer form of the surplus production function (equation 7.2) to these data. Figure 7.7 shows that in two cases the equilibrium method was the most optimistic, with a process-error method being marginally more optimistic for one species, the New Zealand rock lobster *Jasus edwardsii*. A hint that the classical equilibrium method is too optimistic is illustrated by the data for the South Atlantic albacore *Thunnus alalunga* (Scombridae). This method predicted an MSY of just over 28 000 tonnes, which would be caught at fishing effort of just over 100 million hours (Fig. 7.7a). The fishery has been under this in most years, yet CPUE declined steadily over the period to only 30% of its initial value. The overfished state of this fishery is better predicted by the observation-error method, which proved to be the most conservative in all three cases. The highly over-optimistic predictions of the equilibrium method for Namibian hake (Fig. 7.7c) illustrate the problems

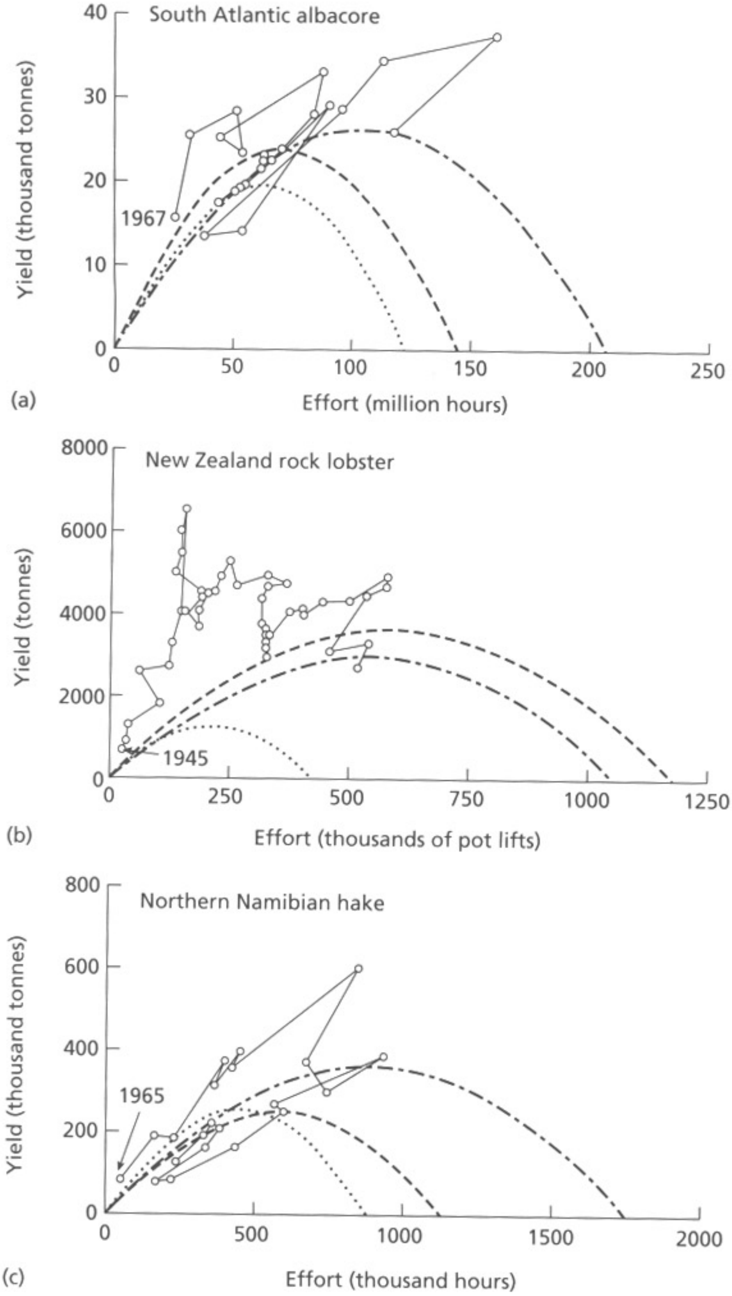

Fig. 7.7 Three kinds of production models fitted to catch and effort data for: (a) South Atlantic albacore; (b) New Zealand rock lobster; and (c) northern Namibian hake. Actual data ——; equilibrium method - - - -; observation error . . . .; process error – – –. After Polacheck *et al.* (1993).

mentioned in section 7.3.3 for the orange roughy (Fig. 7.5): in the early years of the hake fishery some of the 'surplus' production estimated by the equilibrium method included removal of some of the initial standing stock (Butterworth & Andrew, 1984).

Monte Carlo simulations were used by Polacheck *et al.* (1993) to compare the performance of the process-error and observation-error techniques. These added noise to the catch rates as predicted by the model to see how each technique handled it in terms of bias and precision. The observation-error method performed best, with the process-error method proving very imprecise.

The authors concluded that 'under no circumstances should agency staff, conference organizers, reviewers, managers or journal editors accept assessments or publications that are based on (equilibrium) or process-error estimators only'.

General lessons about production curves and MSY

Several lessons have been learned the hard way about the use of production curves and MSY, particularly from traditional methods that rely on the equilibrium assumption. First, fisheries are rarely in equilibrium. The build-up of the Peruvian anchovy fishery in the early 1960s is typical (Fig. 1.4). Such build-ups render catch and effort data much less informative about density-dependent changes in population growth than they appear. Second, everything we know about marine ecology suggests that stability is the exception rather than the rule (Chapters 2 and 4). In the case of the anchovy fishery, the El Niño had a catastrophic effect on the productivity of the anchovy stock. Third, catch and effort data are difficult to work with because CPUE is affected by advances in fishing technology and changes in the behaviour of the quarry, both of which are difficult to account for. Thus, the tendency of the anchovy to concentrate in pockets of cool water allowed fishers to maintain high catch rates despite sharp reductions in total stock size. Fourth, production curves suggest that the surest way to find the optimal fishing effort is to overfish the population, so that a predicted drop in yield at high effort is clearly discernible! In practice, overfishing often happens because fishers are attempting to earn a livelihood by competing for a common resource (Chapters 6 and 11), but this leads to a pervasive ratchet mechanism of resource exploitation, whereby it is much easier to allow effort to increase than to bring in regulations that decrease it. So, by the time we find out where yields drop with high fishing mortality, it will probably be too late to restrict the fishery. Finally, we must remember that surplus production models pool the various processes that determine population productivity. For some fisheries this may not be good enough. For example, in most marine fishes larger/older individuals will contribute disproportionately to reproduction, and they are often more valuable per kilogram. Yet their greater percentage contribution to the catch is ignored by surplus production models.

While early experiences such as the Peruvian anchovy collapse gave production models a bad name, it would be wrong to paint them all with the same brush. The more sophisticated production models described are considerable improvements over equilibrium methods, and can outperform some of the more complex approaches presented later in this chapter (Punt, 1992). Furthermore, most methods of parameter fitting do not rely on complicated computer models and expensive fisheries data. Thus, they can provide useful guidance in fisheries where there are insufficient resources for time-consuming and costly research vessel surveys and analyses of age structure and growth rate. As we will see, the more auxiliary data that are available, the more sophisticated the model that can be used.

7.4 Delay–difference models

Delay–difference models, also known as **Deriso/Schnute** models, are surplus production models in the sense that data are aggregated over most age classes. But this technique goes further, by using not only population biomass data from previous years, but also incorporating information concerning instantaneous rates of natural mortality, body growth and recruitment (Deriso, 1980; Schnute, 1985; Fournier & Doonan, 1987). Thus, the approach is intermediate between the simple methods based on relative abundance, catch and effort data described above, and fully age-structured models such as the statistical catch-at-age and yield-per-recruit methods described in sections 7.6 and 7.7. Delay–difference models are so named because they allow for a time delay between spawning and recruitment, and they use difference equations, in which time changes in discrete steps (as opposed to differential equations, where time is continuous). The basic approach is to build a population model out of submodels that can describe survival, body growth and recruitment next year. Thus, the surviving biomass next year is predicted from the surviving biomass from last year, adjusted for body growth, plus next year's recruitment. Delay–difference models assume 'knife-edge' maturity and vulnerability to fishing (i.e. all individuals reach maturity at the same age and become equally vulnerable to fishing at the same age, sections 9.3.1 and 9.3.4), and that natural mortality is constant with age.

The simplest delay–difference model, which dates back to Allen (1963) and Clark (1976), is derived in Box 7.1.

The Allen–Clark model has only two components, survival and recruitment. Modern models add a third

Box 7.1
The Allen–Clark delay-difference model.

The following treatment, which follows Quinn and Deriso (1999), excludes stability conditions and generalizations to other models. First, we derive the equilibrium population size, and then add fishing. The adult population abundance next year, N_{t+1}, is the sum of the number of survivors this year, plus recruitment next year. Thus,

$$N_{t+1} = l_t N_t + D(N_{t+1-b}) \tag{1}$$

where l_t is the annual survival against natural sources of mortality and D represents a stock-recruitment function, applied to adults backdated to the time of hatching b years ago. Note that this assumes that l_t is the same for all recruits. We can use whatever function seems appropriate to express recruitment according to population size, such as a 'Beverton–Holt' curve or a 'Ricker' curve (section 4.2.1).

The equilibrium population size, N_*, is given by

$$N_* = \frac{D(N_*)}{1 - l_*} \tag{2}$$

Equation 2 meets the condition that there should be a balance between natural mortality $(1 - l)$, and recruitment: if mortality is high, recruitment must be high too, thereby offsetting these losses. This concept is developed further in section 7.8.

Now we can add fishing. Let:

$$S_t = N_t - C_t \tag{3}$$

where S_t is the number of adults that escape from the fishery and C_t is the number of adults caught. Equation 1 becomes

$$N_{t+1} = l_t S_t + D(S_{t+1-b}) \tag{4}$$

This means that the number of individuals next year will be the sum of adults that have escaped both fishing and natural mortality, plus recruitment. Note the assumption that fishing occurs in a single pulse at the start of the year and that there is only natural mortality for the remainder. We can use this equation to find the maximum sustainable yield with respect to optimal escapement from the fishery. Since $C_t = N_t - S_t$ (equation 3),

MSY = maximum (with respect to S) of $N_* - S$

= maximum (with respect to S) of $lS + D(S) - S$

At this point the population is not changing in size. Therefore, the first derivative of $[lS + D(S) - S]$ with respect to S will be equal to zero. This is solved to give

$$\frac{dD(S_m)}{dS} = 1 - l \tag{5}$$

In other words, the MSY occurs at the value of optimal escapement, S_m, where the rate of change in recruitment is equal to the rate of natural mortality. Clark (1976) gives conditions for determining whether this equilibrium point is stable.

As an example, Clark (1976) used this model for Antarctic fin whales *Balaenoptera physalus*. This required a stock-recruitment function for equation 4. Clark used the following equation, with r representing the intrinsic rate of population increase and N_{max} as the maximum number of individuals that the population can contain:

$$D(S) = rS\left[1 - \frac{S}{N_{max}}\right] \tag{6}$$

The parameters were $r = 0.12$, $N_{max} = 600\ 000$, and $l = 0.96$. When these are used in equation 2, the result is solved to calculate the equilibrium population size in the absence of fishing:

$$N_* = N_{max}\left[1 - \frac{1-l}{r}\right] \tag{7}$$

$$= 400\ 000.$$

MSY is found by solving equation 5 to find the optimal escapement:

$$r\left[1 - \frac{2S_m}{N_{max}}\right] = 1 - l \tag{8}$$

$S_m = 200\ 000$ whales

While this is an elegant example of a simple delay–difference model, the predicted optimal escapement seems quite low, and depends critically on the parameters used for life histories and maximum population sizes, as well as the form of the stock-recruitment relationship.

component, body growth, which is applied to both those animals that had already been born, as well as new recruits. Thus, we now model next year's biomass, B_{t+1}, rather than just the number of individuals. A full derivation of this technique has been carried out by Schnute (1985), and the approach has been reviewed by Hilborn and Walters (1992) and Quinn and Deriso (1999). The method assumes that both fishing and natural mortality are constant for all individuals after recruitment. As before (Box 7.1), recruitment is modelled by whatever stock-recruitment relationship best fits the data (section 4.2.1).

The incorporation of fundamental life-history and recruitment information makes it possible to obtain good fits of the model to relative abundance data (e.g. CPUE or survey information). However, good fits may be achieved by several different combinations of growth, mortality and recruitment parameters. It is therefore important to pin down as many parameters as possible beforehand, using auxiliary information on life histories, other similar stocks, and so on. A good technique for doing this formally involves Bayesian inference (section 7.9.1).

7.4.1 Delay–difference models in action

A delay–difference model was used by Collie and Walters (1991) to calculate potential equilibrium yields for stocks of the yellowtail founder *Limanda ferruginea* (Pleuronectidae), a commercially important flatfish that is exploited in coastal waters from southern New England to the Grand Banks of Newfoundland. This species generally recruits to the fishery at 1–2 years of age in the southern part of their range, and 4–5 years in the north. Catches from several stocks of this species have followed a roller coaster pattern, rising rapidly during the late 1960s, dropping equally rapidly in the 1970s, and rising again in the early 1980s. These changes have roughly followed population abundance.

Collie and Walters (1991) assumed a natural survival value of 0.82. The authors set proportions of fish recruiting at each age according to findings from previous studies, and used commercial CPUE as their main index of population abundance, supported by research vessel surveys. They converted CPUE to population biomass using equation 7.6 and used weight at age data to determine growth parameters. Recruitment parameters were calculated by fitting a Ricker curve to spawner and recruit abundance data.

The resulting delay–difference model provided a good fit to the CPUE data, as shown for the Grand Banks stock (Fig. 7.8). However, the authors noted that the parameters had large confidence limits, and many different combinations of parameters could achieve this fit. Thus, equally good fits could be obtained if the population were small but productive or large but unproductive. The importance of this became clear when they looked at the predicted equilibrium yields for the Grand Banks fishery for different values of parameter *a*, the density-independent parameter from the Ricker spawner–recruit relationship (equation 4.2, section 4.2.1). Recall that higher values of *a* indicate that

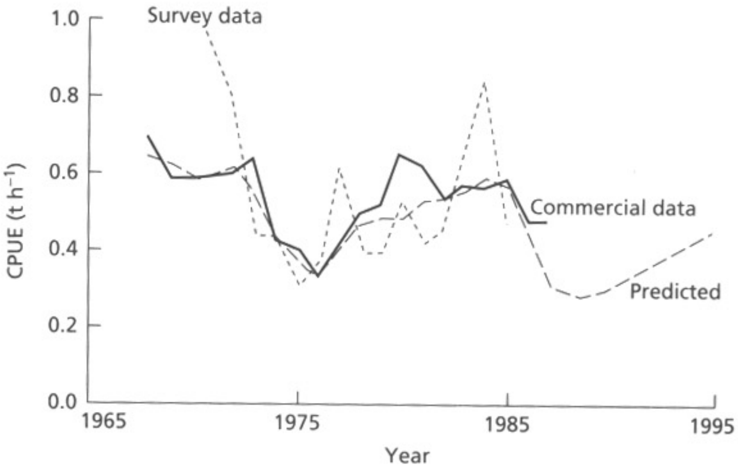

Fig. 7.8 Delay–difference model fit to catch per unit effort data of Grand Banks yellowtail flounder. After Collie & Walters (1991).

Table 7.1 Annual equilibrium yields (thousands of tonnes) from a delay–difference model for Grand Banks yellowtail flounder. The data show different combinations of potential exploitation rates and values of *a* from Ricker spawner–recruitment functions. The **bold** type shows the highest yields for each value of *a*. From Collie and Walters (1991).

Exploitation rate (%)	Ricker *a* value				
	0.0	0.3	0.6	0.9	1.2
20	14.7	13.5	12.7	13.4	16.8
30	**16.6**	16.8	16.8	18.5	23.7
40	13.6	**17.0**	**18.9**	22.1	29.6
50	2.4	12.0	17.6	**23.5**	33.8
60	0.0	0.0	9.9	20.1	**34.2**
70	0.0	0.0	0.0	5.4	24.8

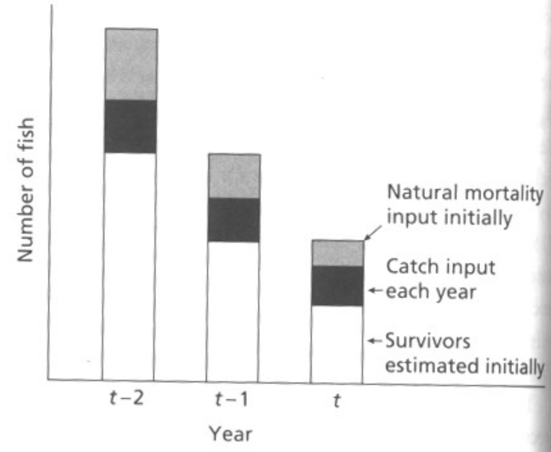

Fig. 7.9 Virtual population analysis for a fish with three age cohorts. Beginning with the current year, *t*, we can rebuild the historical stock sizes by adding the numbers that were caught by the fishery or that died from natural causes to the numbers of survivors.

the gradient of the spawner–recruit curve is steeper at the origin (more recruits per spawner) and that the curve will be more domed. As Table 7.1 shows, the more domed the spawner–recruit relationship, the higher the equilibrium yields will be.

This example thus illustrates that the benefits of the excellent fit that can be achieved by delay–difference models may come with a cost of considerable uncertainty about management recommendations if the parameters are uncertain. In particular, as with the other surplus production models presented above, time-series data must be handled cautiously when used to make inferences about population dynamics. Results such as those in Table 7.1 can show the model's sensitivity to parameter uncertainty, and point toward auxiliary information that should be collected to solve the problem. Many scientists now prefer to take advantage of advances in computing power to use fully age-structured models rather than the two age groups represented by delay–difference models.

7.5 Virtual population analysis

Virtual population analysis (VPA) uses commercial catch data to calculate stock sizes and mortality rates of age-based or length-based cohorts. VPA does not by itself indicate how many individuals can be caught to meet a given objective, nor does it predict the future. In fact, it explains the past. For, if we know the historical age structure of a population, we can then see the consequences of changes in mortality rates, based on methods such as yield-per-recruit calculations (section 7.7). Our use of the term VPA is equivalent to **sequential population assessment** as reviewed along with other age-structured models by Megrey (1989).

If we know how many fish from a given cohort were caught one year, we have a minimum estimate of how many must have been alive the previous year. If we add natural mortality, we have the total mortality for that year and the total number that must have been alive the year before. One can then work backwards, year by year, deriving annual estimates of numbers of survivors and mortality rates. With a good picture of past and present population dynamics, one can then make the forecasts needed to assess management options. For fisheries targeting particularly short-lived species, these calculations can be done on a shorter time scale such as months rather than years, provided that the catch and age or length-cohort data are collected on that time scale.

The basis of VPA is illustrated in Fig. 7.9. For a given cohort (year class) this year, we calculate the number that must have been alive the previous year by adding the number caught by the fishery this year to the number estimated to have died of natural causes over the same period. First, we adopt a standard formulation in population biology to account for both natural and fishing mortality, which we call the **exponential decay equation** (Box 7.2):

Box 7.2
Equations of death.

Suppose we wish to follow the survival of a cohort (year class) though time. The number of individuals alive at any time t in the future will be a function of the number alive now, minus mortality. If we call the initial population size N_t, then the number alive one time unit later, N_{t+1}, will be given by the exponential decay equation:

$$N_{t+1} = N_t e^{-(F+M)} \tag{1}$$

By convention, the symbol F is used to denote the instantaneous rate of fishing mortality. (Note the capital letter, to distinguish it from f for fishing effort.) M is the instantaneous rate of natural mortality and e is the base of the natural logarithm ($e = 2.71828$). Thus, the total mortality is given by $F + M$, which, again by convention in fisheries, is denoted Z.

An example of how the number of individuals alive in the future depends on instantaneous rates of mortality is shown in Fig. B7.2.1.

We can use equation 1 to calculate the rate of change in numbers alive with time. This is simply the first derivative of the equation:

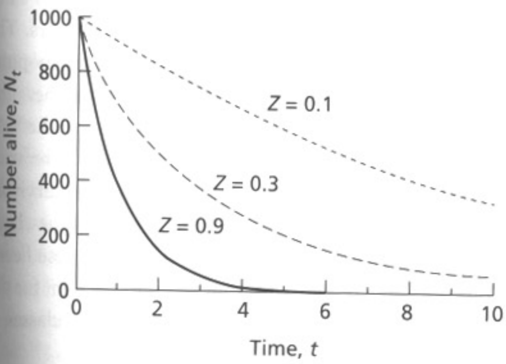

Fig. B7.2.1 Death of a cohort: number alive over time, for three levels of instantaneous total mortality (Z).

$$\frac{dN}{dt} = -FN - MN \tag{2}$$

We can also use equation 1 to calculate the number of individuals caught by the fishery. First we calculate the number of fish that die. This is the difference between N_t and N_{t+1}, i.e.

$$\text{deaths} = N_t - N_t e^{-Z} = N_t(1 - e^{-Z}) \tag{3}$$

The number of individuals caught over that time is the proportion of deaths due to fishing mortality:

$$C_t = \frac{F}{Z} N_t (1 - e^{-Z}). \tag{4}$$

This is referred to as the **catch equation**, with $Z = F + M$.

For example, suppose we start with 1000 fish, and they die from fishing at the instantaneous rate of mortality $F = 0.5$, and from natural causes $M = 0.1$ per year. How many will be alive after 4 years? The exponential decay equation 1 can be generalized to

$$N_t = N_0 e^{-Zt} \tag{5}$$

where N_0 is the number alive initially. Therefore

$$N_t = 1000 e^{-(0.6 \times 4)} = 91 \text{ fish}.$$

How many fish were caught by the fishery in the first year? From the catch equation 4 we calculate the proportion of mortality due to fishing:

$$C = \left[\frac{0.5}{0.6}\right] 1000 (1 - e^{-0.6})$$

$$C = 376 \text{ fish}$$

Similarly, 75 fish died of natural causes, producing a total first year's mortality of 451. This total could, of course, also have been calculated by putting $Z = 0.6$ into the exponential decay equation 1 and subtracting the result from 1000.

$$N_{t+1} = N_t e^{-(F+M)} \tag{7.7}$$

Here N_{t+1} is the number of individuals alive at time $t+1$, N_t is the number alive at time t, M is the instantaneous rate of natural mortality, and F is the instantaneous rate of fishing mortality. We will be seeing a lot of this equation in this chapter, and we describe ways of estimating natural mortality in section 9.3.6.

We also calculate the numbers caught at time t, C_t, from fishing mortality and natural mortality at time t using the **catch equation**, which is also derived in Box 7.2.

$$C_t = \frac{F_t}{F_t + M_t} N_t (1 - e^{-(F_t+M_t)}) \tag{7.8}$$

When catch is multiplied by the mean weight of individuals, and summed over age classes, we have the total yield in biomass to the fishery.

To do a VPA, we use the exponential decay and catch equations 7.7 and 7.8. Here we illustrate the concept by following one cohort backwards through time, and hence use only one subscript, t, although it is customary to add a second subscript to denote age, in order to keep track of multiple cohorts.

Step 1. Calculate the 'terminal abundance' (i.e. for the most recent year, t) of the oldest cohort from the catch equation 7.8, rearranged to give N_t. Use an estimate of terminal F_t, as well as M, which is assumed constant for all ages in all years.

$$N_t = \frac{C_t}{(F_t/Z_t)(1 - e^{-Z_t})} \tag{7.9}$$

Step 2. Calculate the previous year's fishing mortality for the cohort by substituting equation 7.7 into the catch equation 7.8. The previous year is now t:

$$C_t = \frac{F_t}{Z_t} N_{t+1}\, e^{Z_t} (1 - e^{-Z_t}), \text{ hence}$$

$$C_t = \frac{F_t}{Z_t} N_{t+1} (e^{Z_t} - 1) \tag{7.10}$$

We can substitute for $Z_t = F_t + M$ to get

$$C_t = \frac{F_t}{F_t + M} N_{t+1} (e^{F_t+M} - 1) \tag{7.11}$$

Since we know the catch, C_t, the stock size from step 1, N_{t+1}, and M, F_t is the only unknown in equation 7.11. Unfortunately, equation 7.11 cannot be solved for F_t directly, but it can be solved numerically with a computer.

Step 3. For the younger ages, calculate N_t again, by inserting F_t (as calculated in Step 2) into an appropriate modification of equation 7.7. That is,

$$N_t = N_{t+1} e^{(F_t+M)} \tag{7.12}$$

After using equation 7.9 to calculate the number of oldest individuals, we work back year by year, using equation 7.11 for fishing mortality and equation 7.12 for abundance, as shown schematically in Fig. 7.9. A worked example of a VPA is given in Box 7.3.

Although VPA estimates of annual fishing mortality and population size depend on the initial estimates for the most recent year, their proportional dependence on these becomes smaller as one works backwards through time. This gives greater confidence in estimates from earlier years, which can be fine-tuned as new population estimates are generated each year. As a rule of thumb, the method works best when F/Z is between 0.5 and 1.0.

For the most recent years, where estimates of F and population size cannot benefit from much hindsight, the use of 'tuning fleets' is important to infer population numbers at age (Pope & Shepherd, 1985). Thus, although VPA in theory does not require fishing effort data, in practice it is hard to get away without it. **Tuning fleets** may be research vessels making regular surveys, or commercial fleets where fishing activity has been well quantified over a number of years. For example, we might know the total number of days fishing per year for a fleet of beam trawlers using a certain mesh size in a certain region over a 10-year period. If we know how mesh size or engine power have changed, we can also correct the data to account for this. Then, we can plot historical population numbers, based on VPA, against effort by our tuning fleets in those years. The relationship can be used to predict very recent population numbers from recent tuning fleet catches and effort. If the tuning fleet predictions are far off the VPA predictions, a closer look at the data would be warranted. Some VPA software, such as **extended survivors analysis (XSA)** used routinely in European fisheries, have options for 'tuning' the VPA according to these fleets. Thus XSA can weight different fleets to account for the efficiency with which they target different age classes.

7.5.1 Age-based cohort analysis

A clever approximation of virtual population analyses was developed by Pope (1972). Within limits, this gives very similar results to VPA, without the need for iterative calculations of fishing mortality, F. Thus, numerical solutions are unnecessary. As with VPA, we use catch data and initial guesstimates of F and M to work backwards through time to reconstruct previous values of F and stock structure. However, Pope's ingenuity was to simplify the calculations by assuming that all

Box 7.3

Example of virtual population analysis.

Table B7.3.1

Age (t)	Catch numbers	Stock size	Fishing mortality (F)
1	70	487	0.172
2	90	335	0.349
3	80	194	0.600

Table B7.3.1 shows catches through time for a cohort of fish. We assume that $M = 0.2$ and is constant for all ages. Of course in reality M will vary, but the smaller it is relative to F, the less important this is. We begin with the oldest fish, aged 3, and set the terminal value of $F_3 = 0.6$.

Step 1. From equation 7.9, the stock size of age 3 fish that would have yielded a catch of 80 will be:

$$N_3 = \frac{C_3}{(F_3/Z_3)(1 - e^{-Z_3})}$$

$$= \frac{80}{(0.6/0.8)(1 - e^{-0.8})}$$

$$= 194 \text{ fish}$$

Step 2. From equation 7.11 we can calculate the value of F that must have occurred the previous year to yield the catch of 90 age 2 fish while leaving 194 survivors.

$$C_2 = \frac{F_2}{F_2 + M} N_3 (e^{F_2+M} - 1)$$

$$90 = 194 \frac{F_2}{F_2 + 0.2} (e^{F_2+0.2} - 1)$$

$$F_2 = 0.349$$

(solved by iteration: a simple approach is to insert the right-hand side of the equation into a spreadsheet and have F in the equation refer to a column in which values of F vary up and down).

Step 3. We use this value of F with equation 7.12 to calculate the stock size for age 2 fish.

$$N_2 = N_3\, e^{(F_2+M)}$$

$$= 194\, e^{0.349+0.2}$$

$$= 335 \text{ fish (depending on rounding)}$$

We repeat Steps 2 and 3 to work backwards through time.

fish are taken instantaneously halfway through the year, rather than continuously (Fig. 7.10). Thus, the number of fish alive at the moment just before fishing mortality ($N_{t+0.5}$) will be solely a function of natural mortality acting on the cohort since the start of the year. Then fishing reduces the stock all at once, producing the entire year's catch (C_t), followed again by natural mortality.

The number of fish alive just before fishing takes place ($N_{t+0.5}$) will be the number alive at the start of the year (N_t), reduced by half of the year's natural mortality, $M/2$:

$$N_{t+0.5} = N_t e^{-M/2} \tag{7.13}$$

After the entire year's catch (C_t) is taken instantaneously, we are left with

$$N_t e^{-M/2} - C_t \tag{7.14}$$

Now these fish suffer natural mortality for the rest of the year, leaving the number alive at the end of the year (N_{t+1}):

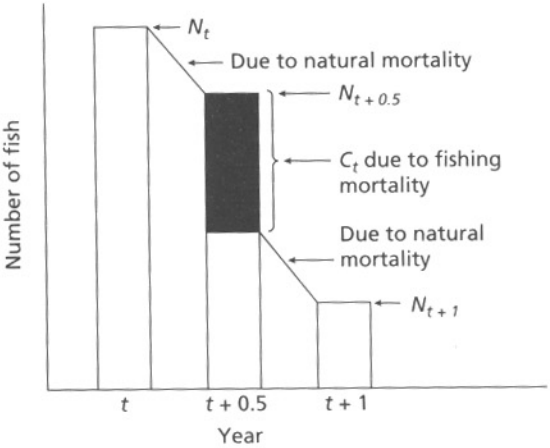

Fig. 7.10 Age-based cohort analysis. The logic is the same as for virtual population analysis (Fig. 7.9), but the year is broken into two parts, with the catch assumed to have occurred instantly in the middle of the year.

Box 7.4
Example of age-based cohort analysis.

Table B7.4.1 shows the same catches at age as for our VPA example (Box 7.3), with a comparison between the VPA results and cohort analyses, calculated below. As before, we take $M = 0.2$, and our initial estimate of F for the terminal age class (3-year-olds) as 0.6.

Step 1. The first step is identical to the VPA calculation, i.e. we calculate the number of age 3 fish, N_3, from the rearranged catch equation 7.9, to give:

$N_3 = 194$ fish

Step 2. The difference from VPA is that this is substituted into equation 7.16 as N_{t+1} to calculate the number of fish from that cohort that would have been alive the previous year:

$$\begin{aligned} N_2 &= (N_3 e^{M/2} + C_2) e^{M/2} \\ &= (194 e^{0.2/2} + 90) e^{0.2/2} \\ &= 336 \text{ fish} \end{aligned}$$

This is only one fish away from our calculation of 335 using VPA (Box 7.3).

Step 3. Now we calculate F on age 2 fish, using the exponential decay equation (equation 1 in Box 7.2):

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

This is rearranged to give:

$$F_t = \ln\left[\frac{N_t}{N_{t+1}}\right] - M$$

Thus, F for age 2 fish is given by:

$$\begin{aligned} F_2 &= \ln\left[\frac{N_2}{N_3}\right] - M \\ &= \ln\left[\frac{336}{194}\right] - 0.2 \\ &= 0.349 \end{aligned}$$

This is identical to the VPA result, or within about 0.002 of it, depending on rounding. Note that, unlike VPA, we have circumvented the iterative calculation of F. We continue working our way back through time repeating Steps 2 and 3 to build up the historical pattern of age-based stock sizes and fishing mortalities each year. When we perform Steps 2 and 3 again to calculate stock sizes and fishing mortality on age 1 fish, the results are also virtually identical to the VPA analyses shown in the table.

Table B7.4.1

		Stock size		Fishing mortality (F)	
Age (t)	Catch numbers	VPA	Cohort	VPA	Cohort
1	70	487	488	0.172	0.173
2	90	335	336	0.349	0.349
3	80	194	194	0.600	0.600

$$N_{t+1} = (N_t e^{-M/2} - C_t) e^{-M/2} \qquad (7.15)$$

Since we are trying to find the number of fish alive at the start of the year, we rearrange this equation to give the fundamental equation:

$$N_t = (N_{t+1} e^{M/2} + C_t) e^{M/2} \qquad (7.16)$$

This gives the number of fish alive at the start of the year based on the catch through the year and the number alive at the start of the following year. The catch is estimated in the usual way, from the fishery, and we can use whatever means are available to estimate M (section 9.3.6) and take an initial assumption about F, which generally proves fairly unimportant to the final result, as for the case of VPA. A worked example of age-based cohort analysis is presented in Box 7.4.

Pope (1972) showed that this method approximates VPA quite well for values of M as high as 0.3 and F as high as 1.3. If M and F are larger, then the method still works if the catch times are divided into smaller units than 1 year. One can also substitute $M/(1 - e^{-M})$ for $e^{-M/2}$, which gives an even better approximation to VPA, especially for larger values of M (MacCall, 1986b).

7.5.2 Length-based cohort analysis

Length-based cohort analysis was developed for species that cannot be aged. The principle is the same as for age-based cohort analysis, but animals are separated into length classes (Jones, 1981). The technique can be implemented by statistical packages such as FiSAT, developed by the Fisheries and Agriculture Organization (FAO) Fisheries Department and the International Center for Living Aquatic Resources Management (ICLARM).

First, length groups are converted to age groups based on the von Bertalanffy growth equation (sections 3.4.2 and 9.3.3). Thus,

$$t(L_1) = t_0 - \frac{1}{K}\log_e\left(1 - \frac{L_1}{L_\infty}\right) \qquad (7.17)$$

where $t(L_1)$ is the age of individuals in length interval L_1. t_0, K and L_∞ are parameters of the von Bertalanffy growth equation (section 9.3.3). Thus, the time interval, Δt, between two successive age classes, $t(L_2) - t(L_1)$, becomes:

$$\Delta t = \frac{1}{K}\log_e\left[\frac{L_\infty - L_1}{L_\infty - L_2}\right] \qquad (7.18)$$

The fundamental equation from age-based cohort analysis (equation 7.16) is modified to replace the time interval (assumed to be 1 year) with the converted age intervals. That is, the term $e^{M/2}$ is replaced with a term representing the fraction of a given length class that survive natural mortality from the time they are in L_1, until half of the time period has elapsed before they reach L_2:

$$N_{L_1} = [N_{L_2} T_{L_1,L_2}{}^{M/2K} + C_{L_1,L_2}]T_{L_1,L_2}{}^{M/2K} \qquad (7.19)$$

where N_{L_1} is the number of individuals that survive to reach length L_1, corresponding to an age $t(L_1)$, C_{L_1,L_2} is the number of individuals between lengths L_1 and L_2 that are caught, and T_{L_1,L_2} represents the fraction from equation 7.18:

$$\frac{L_\infty - L_1}{L_\infty - L_2}.$$

The procedure for carrying out a length-based cohort analysis is similar to the age-based approach. First, we modify the age-based form of the catch equation (Box 7.2) for use with length classes, and apply it to the oldest length class:

$$C_{L_1,L_2} = \frac{F}{Z}N_{L_1}(1 - e^{-Z\Delta t}). \qquad (7.20)$$

For the oldest age class we take $e^{-Z\Delta t} = 0$, because theoretically, the age corresponding to Δt being larger than the largest length class is infinite. We thus substitute zero for $e^{-Z\Delta t}$, plug the catch numbers for the largest length class into the left-hand side of equation 7.20, and make an initial guess of the terminal value of F/Z to calculate the N_{L_1} the number of individuals in the oldest length class. An example is shown in Box 7.5.

Once we have calculated the stock sizes corresponding to each length interval, we can calculate fishing mortality rates. The basic formula is:

$$F = M\frac{F/Z}{1 - F/Z} \qquad (7.21)$$

where F and Z refer to length class L_1,L_2. F/Z is derived from catches and stock numbers, i.e.

$$\frac{F}{Z} = \frac{C_{L_1,L_2}}{N_{L_1} - N_{L_2}} \qquad (7.22)$$

The final step is to convert numbers in each length class to actual numbers in the stock. However, we cannot do this until we know how long each individual spends in each time interval and sum across the intervals. The mean number of individuals in each age class per year is calculated as:

$$\overline{N}_{L_1,L_2} = \frac{N_{L_1} - N_{L_2}}{Z\Delta t} \qquad (7.23)$$

Thus, the total is the sum across each length class, i, weighted by its time interval:

$$\sum_i(\overline{N}_{L_i,L_{i+1}})\Delta t. \qquad (7.24)$$

As with age-based cohort analysis, this method requires an initial estimate of mortality (F/Z), but the

Box 7.5

Length-based cohort analysis for a hypothetical species.

Suppose the following data apply to a fished species: L_∞ = 120 cm, $K = 0.3$, $M = 0.2$, and F/Z is initially guessed to be 0.8. Therefore $M/2K = 0.2/(2 \times 0.3) = 0.33$. The sizes of individuals in the last two length classes, the numbers caught, and their corresponding values of T are shown in Table B7.5.1.

Applying the length-based catch equation (equation 7.20) to the oldest age class:

$$C_{100,\infty} = 25 = 0.8(N_{100})(1 - 0)$$

$$N_{100} = 31.2$$

Working backwards to the next largest length class using the fundamental length-based cohort equation 7.19:

$$N_{90} = (31.2 \times 1.5^{0.33} + 30)1.5^{0.33} = 75.1$$

To calculate F from these data, we apply equations 7.22 and 7.21. Thus, for the length category 90–100 cm,

$$F/Z = 30/(75.1 - 31.2) = 0.683$$

$$F = (0.2 \times 0.683)/(1 - 0.683) = 0.43$$

Length group (cm)	Number caught	T
L_1–L_2	C_{L_1,L_2}	$(L_\infty - L_1)/(L_\infty - L_2)$
90–100	30	(120–90)/(120–100) = 1.50
100–∞	25	–

Table B7.5.1

calculations for older year classes do not rely heavily on the initial input. However, it is still important to estimate M and the growth parameters as well as possible.

7.6 Statistical catch-at-age methods

Statistical catch-at-age methods, also known as **stock synthesis**, or **integrated analysis**, are an alternative to VPA for estimating stock sizes. As their name suggests, these techniques are age based, which places them with age-based VPA and cohort analyses into the family of **age-structured stock assessment methods**. They are used routinely in many stock assessments. The basic idea is to develop a population dynamics model from first principles and then relate the model's predictions (e.g. of the annual catches) to the observed data. Statistical methods are used to find the best set of model parameters that will fit the observations. This is an extremely flexible approach. It also provides a way of overcoming a problem with VPA (section 7.5), namely that abundance estimates for the most recent year classes tend to be imprecise and require 'tuning'. Furthermore, most modern catch-at-age methods do not require estimates of M that are needed for VPA. One disadvantage of catch-at-age methods is that the computational procedures are considerably more complex than those required for VPA. Thus, the estimation of parameters requires non-linear regression, which effectively precludes the use of computer spreadsheets. In the following, we collapse a great deal of detail into a snapshot of the method. The historical roots of the approach, which includes catch curve analyses and developments by Doubleday (1976), Paloheimo (1980), Fournier and Archibald (1982), and Deriso *et al.* (1985), are reviewed by Deriso *et al.* (1985), Megrey (1989), and Quinn and Deriso (1999). These references should be consulted by anyone wanting more than the brief overview we provide below.

A well-known early example of a statistical catch-at-age model is called **CAGEAN** (Catch-AGE Analysis; Deriso *et al.*, 1985). The model uses the same catch equation and exponential decay equation that we encountered in Box 7.2 and used for VPA. Rather than beginning with fishing mortality on the terminal (oldest) age class, CAGEAN estimates the annual recruitments and the numbers-at-age in the first year of the analysis. To simplify the estimation, it is assumed that there is **separable fishing mortality**. That is, fishing mortality can be described by the product of an age-dependent vulnerability to the fishery, and a year-specific factor.

The values for these parameters are obtained by fitting the model to the observed data. CAGEAN can use catch-at-age and fishing effort data, and place constraints on the extent to which recruitment deviates from a pre-specified spawner–recruit relationship. We define a function based on the weighted sum of squared deviations between the model's predictions and the observed data. Non-linear least-squares regression is used to minimize these deviations to find the best fit parameters. In contrast to VPA, CAGEAN does not assume that catches are known exactly. For catch-at-age data, the sum of squares term is given by:

$$SSQ(\text{catch}) = \sum_a \sum_t [\text{predicted } C_{a,t} - \text{observed } C_{a,t}]^2 \tag{7.25}$$

where $C_{a,t}$ is the catch of animals age a during year t. The predicted catches are based on the catch equation and the exponential decay equation (Box 7.2).

The basic approach can be extended in many ways. For example, Smith and Punt (1998) assess a stock of gemfish *Rexea soladri* (Gempylidae, close relatives of the Trichiuridae) off eastern Australia for which catch-at-age data are missing from some years, although length-frequency data are available for most years. The underlying model is sex- as well as age-structured and most of the parameters are therefore sex specific, to capture the impact of sexual dimorphism.

The statistical approach used by statistical catch-at-age models to estimate parameters is an improvement over the *ad hoc* approach used by VPA. Furthermore, one need not guess at terminal fishing mortalities. Various authors (e.g. Deriso *et al.*, 1985) have developed methods for quantifying the uncertainty surrounding key model outputs such as the time series of spawner and recruit abundance. Incorporation of auxiliary information such as fishing effort or independent estimates of natural mortality are very helpful for estimating the parameters needed to fit models to catch data. Indeed, the flexibility of this technique for accommodating such additional information is a major asset. Proponents of VPA-related techniques such as cohort analysis counter that these methods are computationally simpler and more transparent, with a solid track record in many well-studied fisheries.

7.7 Yield-per-recruit models

At the beginning of this chapter we identified four factors influencing population biomass that must be in balance if we are to exploit sustainably: reproduction, body growth, fishing mortality and natural mortality (see Fig. 7.1). We also saw that surplus production models lump these together and ignore age structure. Models that keep the components separate fall under the '**dynamic pool**' approach. With the information provided by analyses such as VPA and statistical catch-at-age analyses, we can use **yield-per-recruit models** to seek fishing mortality rates that achieve the best trade-off between the sizes of individuals caught, and the number of individuals available for capture. If fishing mortality rates are set too high, too many individuals will be taken before they have had a chance to grow. This is loosely termed '**growth overfishing**'. If fishing mortality is too low, although the individuals will be large when captured, the total yield will be low. This logic can be seen if we follow the fate of a single cohort through time (Fig. 7.11). The optimal age at which to capture these fish is A.

The fundamental yield-per-recruit model assumes a steady state, i.e. that recruitment is constant, and hence the age structure of the population is the same as we would see if we followed a single cohort through time. Hence, yield is measured 'per recruit' (Beverton & Holt, 1957). We will therefore need to incorporate recruitment in a later section of this chapter. The model also assumes that fishing and natural mortality are constant from the moment that the fish become vulnerable to fishing gear. We can actually relax these assumptions when yield-per-recruit models are put into practice to see the effects of different ages at first capture and exploitation patterns, thereby informing decisions for management. Obviously, fishers will want to catch the largest total biomass rather than the largest yield per recruit. We keep track of total biomass later, by multiplying yield per recruit by the projected numbers of recruits, given various potential rates of fishing mortality.

The fundamental yield-per-recruit model gives the yield, Y (in biomass) to the fishery as:

$$Y = \sum_{t_c}^{t_{\max}} F_t N_t W_t \tag{7.26}$$

where t_c and $t_{\max}$ are the ages of first capture and maximum ages of cohorts, respectively, F is the instantaneous rate of fishing mortality, N is the number of individuals alive, and W is their mean weight. Strictly, the summation sign should be an integral, since age is a continuous variable. However, age is usually recorded

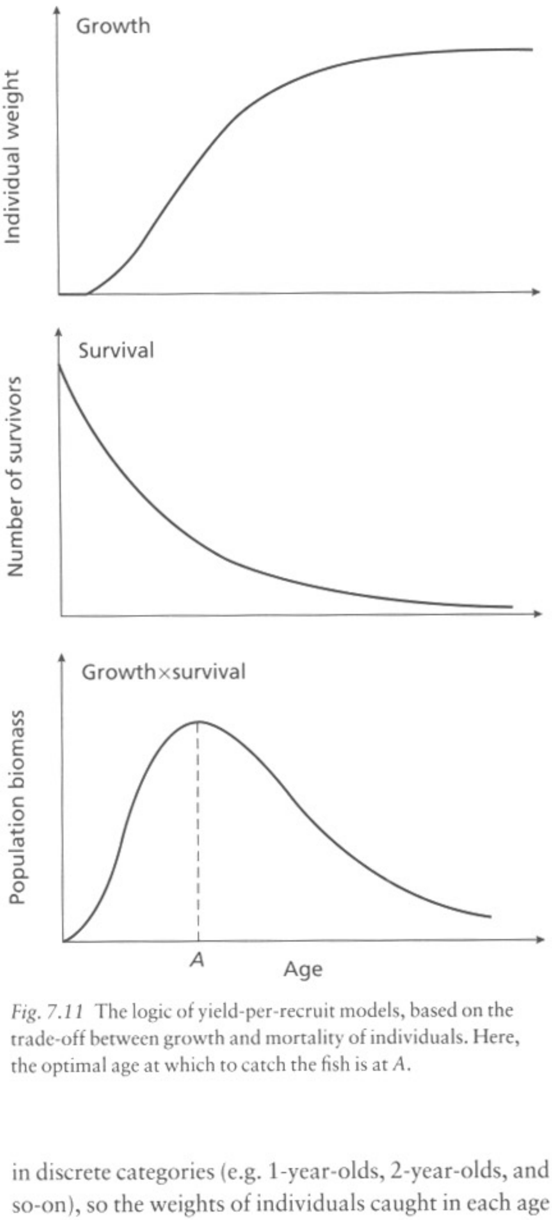

Fig. 7.11 The logic of yield-per-recruit models, based on the trade-off between growth and mortality of individuals. Here, the optimal age at which to catch the fish is at *A*.

in discrete categories (e.g. 1-year-olds, 2-year-olds, and so-on), so the weights of individuals caught in each age class can be simply added together.

Box 7.6 provides a worksheet for calculating yield per recruit for a single cohort of fish. This shows that if $F = 0.6$, about 1 kg of fish would be caught for every fish that initially recruited to the fishery. The total biomass of fish left behind in the sea would be about 2.4 kg. We usually want to find the value of F that meets some objective such as providing a high yield to the fishery, while maintaining the stock at a reasonable size. Thus, we repeat the calculations for a range of fishing mortalities, and plot yield per recruit and population biomass per recruit vs. F (Fig. 7.12). The maximum yield per recruit occurs at $F_{\max} = 0.23$. If current F were 0.9, then a reduction in fishing mortality to $F_{\max}$ would nearly double the yields and increase the stock size fivefold. The latter would give us a better safety margin against recruitment failure, as shown by the population biomass per recruit. For species with high M, yield-per-recruit curves are often much more flat-topped than in our example, which is typical for relatively slow-growing species such as cod. If curves are very flat-topped, practitioners are forced to rely on targets other than maximum values of these curves (section 7.10).

It would be unrealistic to expect M and F to be constant with age, since younger fish tend to suffer high natural mortality, but low fishing mortality until they are large enough to become vulnerable to fishing gears. Yield-per-recruit analyses can accommodate age-specific mortalities. Indeed, researchers often investigate the effects of changing mesh size by setting $F = 0$ for the youngest age classes of fish ('knife-edged selection'). This allows exploration of the joint effects of changing age at capture and mean F.

Long-term forecasts from yield-per-recruit models typically assume a stable age structure through time. This may often be unrealistic, given the erratic temporal changes in recruitment typical of most fish stocks (Chapter 4). Indeed, yield-per-recruit models by themselves ignore impacts of fishing mortality on recruitment: this requires an explicit link to a stock-recruitment curve (section 7.8). Moreover, errors in M may have important effects on the predictions when M is high relative to F. Temporal variation in M and F are also ignored, as is density dependence in growth and maturity, which may change with different levels of fishing mortality.

7.7.1 Yield-per-recruit models in action

Atlantic croaker *Micropogonias undulatus* are members of the family Sciaenidae, known as drums. Croakers are named after the noises they make during the spawning season. They are one of the most abundant inshore bottom fishes along the east coast of the United States, including the Gulf of Mexico. They are also one of the most important species for commercial and recreational fisheries. Croakers spend the autumn

Box 7.6
Example of yield-per-recruit calculations for a single cohort of fish.

Table B7.6.1 follows the fate of a single cohort of fish. The weights are of individuals at each age. The number alive is at the start of the year per 100 fish recruiting, based on an assumed natural mortality (*M*) of 0.2, and a hypothetical fishing mortality (*F*) of 0.6. The numbers alive and catch numbers at the end of the year are based on the exponential decay equation and the catch equation, respectively (Box 7.2). The population biomass is calculated as (weight × number surviving) and catch weights (yields) are (weight × catch numbers).

These calculations are repeated for a range of potential fishing mortalities, yielding the data in Table B7.6.2, which are plotted in Fig. 7.12.

Table B7.6.1

Age (years)	Weight (kg)	Number alive	Population biomass (kg)	Catch numbers	Catch weight (kg)
1	0.6	100	60	41	25
2	0.9	45	40	19	17
3	2.1	20	42	8	17
4	4.1	9	37	4	15
5	6.3	4	26	2	11
6	8.4	2	15	1	6
7	10.0	1	8	0.3	3
8	11.2	0.4	4	0.2	2
9	12.6	0.2	2	0.1	1
10	13.5	0.1	1	0.0	0
Sum (kg)			237		98
Sum/Recruit (kg)			2.37		0.98

Table B7.6.2

Fishing mortality (*F*)	Yield per recruit (kg) (*Y*/*R*)	Biomass per recruit (kg) (*B*/*R*)
0.0	0	21.46
0.1	1.12	12.94
0.2	1.36	8.27
0.3	1.32	5.60
0.4	1.2	4.00
0.5	1.08	3.01
0.6	0.98	2.37
0.7	0.89	1.93
0.8	0.83	1.63
0.9	0.77	1.42
1.0	0.73	1.26

and winter in oceanic waters. They spawn from July until November along the US east coast, probably on the continental shelf edge. In spring, adults as well as larvae and juveniles move into estuaries, where they remain until early autumn. Most individuals reach maturity at 1 year of age.

Atlantic croaker are caught by haul-seines, pound nets and gill nets (Chittenden, 1991). Once they move

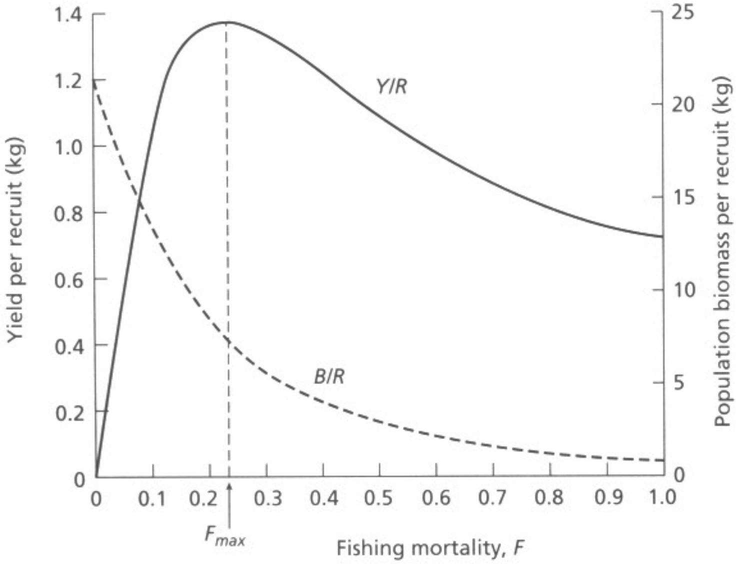

Fig. 7.12 Yield per recruit (*Y/R*) and population biomass per recruit (*B/R*) for a single cohort of fish, for various potential fishing mortalities, *F*. The results are for fish of ages 1–10, and natural mortality, $M = 0.2$ (see Box 7.6).

offshore they are caught by otter trawl and gill-net fisheries. Commercial landings have fluctuated drastically over the past 60 years, ranging from 20 000 tonnes from 1937 to 1940, to 29 000 tonnes in 1945, and plunging to less than 1000 tonnes from 1967 to 1971 before recovering to 13 000 tonnes in 1977 and 1978 (Barbieri *et al.*, 1997). There has been a decline since 1987, and recreational catches peaked in 1991 when approximately 21 million fish were caught.

Barbieri *et al.* (1997) used a yield-per-recruit model to investigate whether mortality was too high in two Atlantic croaker fisheries, and to make recommendations about the effects of reduced mortality on young fish through bycatch reduction devices and minimum size limits. Figure 7.13 shows the predicted effects of various values of *F* and mean age at first capture, t_c, on yield per recruit. Two fisheries are shown, each simulated twice—once with $M = 0.20$, and once with $M = 0.35$, to cover the probable range of the true value of *M*, which is uncertain. In lower Chesapeake Bay (Fig. 7.13a, b), analyses of landings showed that the current value of t_c is 2 years of age. Surprisingly, it appears that a reduced age at first capture might actually increase yields, but this might be a risky strategy for a small benefit. The relationship with *F* is flat-topped for all ages of first capture. Total mortality $Z (= F + M)$, is thought to be about 0.6. However, the breakdown between *F* and *M* is unclear. If $M = 0.20$ (Fig. 7.13a), *F* would be 0.4, which is below but near the maximum. If $M = 0.35$ (Fig. 7.13b), *F* would be 0.25, and there is more room for higher yields with increasing *F*.

The situation is quite different for the North Carolina fishery (Fig. 7.13c, d). Here, *Z* is much higher, at 1.3. If *M* is low, reducing the age at first capture would be a bad idea. Indeed, the mean age at first capture, which is 1 year in this fishery, should be increased considerably. This is not so important if *M* is high (Fig. 7.13d). Note how much more peaked the yield-per-recruit surface is if *M* is low than if *M* is high. *F* is estimated to be either 1.1 if *M* is low, or 0.75 if *M* is high. In either case, this stock appears to be overexploited.

Since there was no indication of growth overfishing in Chesapeake Bay, Barbieri *et al.* (1997) suggested that that fishery should be regulated at the *status quo* until estimates of current mortality rates are improved. In contrast, the North Carolina fishery needed a higher mean age at first capture and lower fishing mortality. The authors noted that the differences may actually reflect the fact that the North Carolina data came from 1979 to 1981, whereas the Chesapeake Bay data came from 1988 to 1991. The early period coincided with the occurrence of unusually large fish. Whether the differences between the Chesapeake Bay and North Carolina fisheries reflect temporal or spatial patterns, this study shows that it is important to be careful about generalizing from one fishery to another.

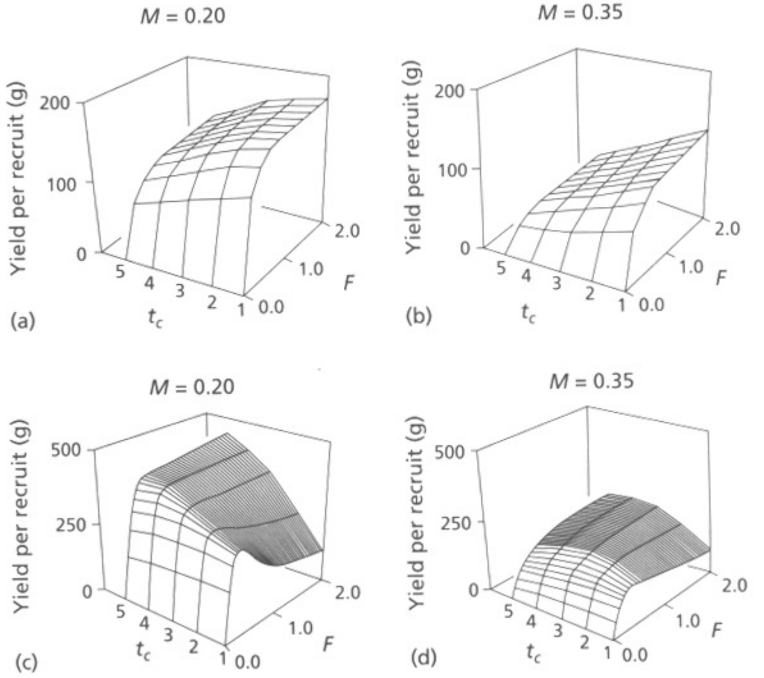

Fig. 7.13 Yield-per-recruit curves for Atlantic croaker *Micropogonias undulatus*. These are based on various combinations of mean age at first capture, t_c, and fishing mortality, F. (a) Lower Chesapeake Bay, assuming $M = 0.2$; (b) Lower Chesapeake Bay, assuming $M = 0.35$; (c) North Carolina, assuming $M = 0.2$; (d) North Carolina, assuming $M = 0.35$. After Barbieri *et al.* (1997).

7.8 Incorporating recruitment

We discussed recruitment briefly in section 7.4.1, but largely ignored it in our discussion of yield-per-recruit models. This is risky when recruitment is related to spawning stock size (Chapter 4). Thus, while yield-per-recruit models handle 'growth overfishing' very elegantly, they need to be integrated with recruitment if we are to avoid **'recruitment overfishing'**, which is defined as a reduction in spawning stock biomass to the point where recruitment is impaired.

The simplest way to incorporate recruitment is to consider semelparous species with a life span of 1 year. These species, such as squid, spawn once and then die (section 3.4.3). Each year's fishery consists entirely of last year's recruitment, and the stocks are not buffered by multiple year classes, nor by small individuals that are temporarily safe from the fishery (e.g. Rosenberg *et al.*, 1990; Basson *et al.*, 1996). Here, spawner–recruit relationships must be used to find a target for **escapement**: the number of fish allowed to survive (Pauly, 1985; Beddington *et al.*, 1990). If recruitment is plotted against spawning stock size over a number of years, we can ask what level of recruitment would be needed to maintain the population in the face of fishing mortality. The higher the mortality, the higher the recruitment has to be for the population to be in equilibrium.

7.8.1 Replacement lines

Replacement lines help us to understand how changes in F affect the recruitment rates of exploited stocks.

The theory of replacement lines was first developed by fishery scientists (Beverton & Holt, 1957), but has since been applied to other studies of population dynamics. As an example, we have chosen a Ricker spawner–recruit curve (Fig. 7.14). First, consider Fig. 7.14(a), with a diagonal line that has a slope of 1.0, showing the replacement level where recruitment balances spawning stock size. We can predict the trajectory of a population from any starting stock size by following from a point on the x-axis to the recruitment curve, and then taking this as the next generation to be plotted again on the x-axis, following up to the recruitment curve, and so-on. This is equivalent to reflecting the recruitment back to the spawning stock size in the following generation through the one-to-one replacement line. In Fig. 7.14(a), the population will approach a stable

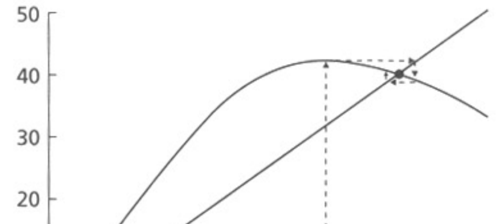

Fig. 7.14 Population trajectories for a Ricker spawner–recruitment relationship. (a) The replacement line intersects the spawner–recruit curve, leading to a stable equilibrium. (b) The replacement line corresponding to higher fishing pressure exceeds the spawner–recruit curve, leading to a population collapse.

equilibrium, oscillating above and below it as it does so. In Fig. 7.14(b), a steeper replacement line has been drawn, to accommodate higher fishing mortality. Here, recruitment is not high enough to sustain the population, and it will crash.

Replacement lines can be used to predict the sustainability of fisheries if the slope of the replacement line is adjusted according to the level of fishing mortality (Shepherd, 1982). A doubling of mortality, for example, will result in a doubling of the slope of recruitment needed to replace the stock (if patterns of growth and maturation are constant). Yields can also be predicted, thereby building a useful bridge to methods such as yield-per-recruit models, which otherwise ignore impacts of fishing mortality, F, on future recruitment (section 7.7). Recall from section 4.2.1 (equation 4.3) the flexible Shepherd spawner–recruit relationship that relates the abundance of spawners (S) to that of recruits (R). This can also be written as:

$$R = \frac{aS}{1 + (S/b)^c} \tag{7.27}$$

where a is the slope of the curve at the origin (maximum R/S at low stock sizes), b is the biomass at which recruitment is reduced to half the level it would have been under density independence only, and c controls the degree to which the spawner–recruit curve is asymptotic or dome shaped. If stock size S is measured as stock biomass B, we can substitute B for S and rearrange the equation to estimate B (Shepherd, 1982):

$$B = b(aB/R - 1)^{1/c} \tag{7.28}$$

equation 7.28 contains biomass per recruit (B/R), which we can calculate using yield-per-recruit models (section 7.4). We can also translate B/R into recruitment as $R = B/(B/R)$. Finally, if we know recruitment, we can calculate yield based on yield per recruit as $Y = R(Y/R)$. This concept is shown graphically in Fig. 7.15. Fig. 7.15(a) and (d) are the standard outputs from a yield-per-recruit model, showing the effect of different values of fishing mortality on population biomass per recruit and yield per recruit, respectively. Fig. 7.15(c) shows the relationship between recruitment and stock sizes (e.g. based on observations over a number of years). The replacement line has been added to Fig. 7.15(c) for a trial value of fishing mortality (F_{trial}) by giving it a slope that is the inverse of B/R for F_{trial}, using the translation step shown in Fig. 7.15(b). Equilibrium stock size is found where this line crosses the function relating recruits to population biomass. This is multiplied by yield per recruit to give the total yield (Fig. 7.15e).

7.8.2 Replacement lines in action

The concepts discussed above are illustrated for the North Sea cod *Gadus morhua* stock in Fig. 7.16. In this study, Cook *et al.* (1997) fitted a Shepherd spawner–recruit curve to data for 1963–94. The worrying result is that the spawner–recruit curve is below the replacement line. This is especially clear during the early years when stock sizes were high. Indeed, as predicted by the theory, this stock has been declining toward the origin. Recruitment exceeded the replacement line in only 8

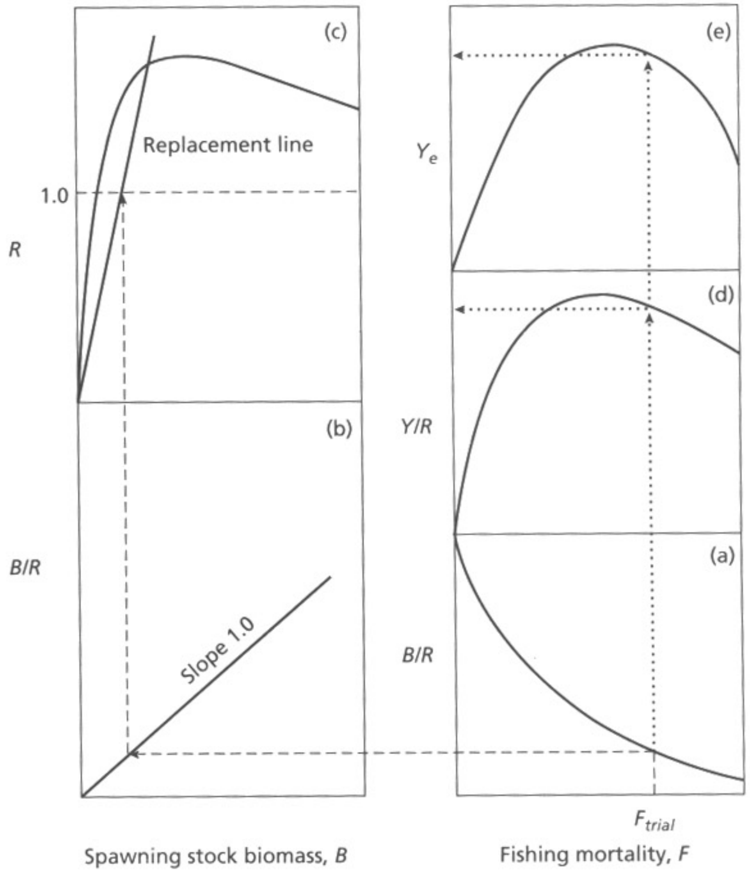

Fig. 7.15 Graphical links between yield-per-recruit calculations and a spawner–recruit relationship. A trial value of fishing mortality (F_{trial}) in (a) predicts spawning stock biomass per recruit (B/R), based on a yield-per-recruit calculation. This is converted to spawning stock biomass, B, in (b). A replacement line in (c) has slope = $1/(B/R)$. This is used to convert B/R into equilibrium spawning stock biomass, at the intersection of the replacement line and the stock-recruitment relationship. Equilibrium spawning stock biomass is then multiplied by yield per recruit in (d) to give total equilibrium yield, Y_e, in (e). After Sissenwine and Shepherd (1987).

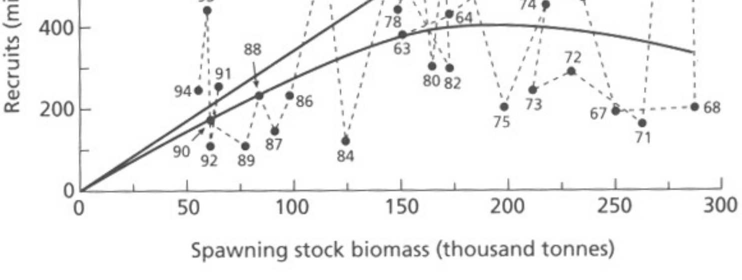

Fig. 7.16 Stock-recruitment curve and replacement line for North Sea cod. The numbers represent data for various years. After Cook *et al.* (1997).

of 31 years. Cook *et al.* (1997) also fitted Ricker and Beverton–Holt spawner–recruit curves to the same data. The values of F at which the population was predicted to crash were 0.91 (Shepherd), 1.05 (Ricker) and 1.13 (Beverton–Holt). These were perilously close to the contemporary estimate of $F = 0.91$ for that stock. We appear to be playing Russian roulette with the whims of recruitment. As we go to press, a major re-building programme is being proposed for this stock.

7.9 Confronting risk and uncertainty

There is uncertainty in most fisheries data. The values used for population size, commercial catches, natural mortality and fishing mortality are all estimates rather than true values. Even if we could estimate these perfectly, our projections into the future would still be uncertain. Although these facts are obvious to everyone, the structure of most decision-making processes still encourages the production of single 'best estimates' by fisheries biologists (Hilborn *et al.*, 1993a; Francis & Shotton, 1997). This is risky because it involves throwing away information.

Formal decision analyses allow us to face uncertainty directly. The process can be broken down into five parts (Hilborn, 1996; Punt & Hilborn, 1997).

1 Identify alternative hypotheses about the state of the fishery. For example, the population biomass may be 750 000 tonnes or 950 000 tonnes.

2 Determine the relative weight of evidence in support of each alternative. For example, the probability of 750 000 tonnes is 0.1 and the probability of 950 000 tonnes is 0.5.

3 Identify alternative management actions. For example, consider setting the quota to 100 000 tonnes or 150 000 tonnes.

4 Evaluate the distribution and expected value of each performance measure, given the management action and probability of each alternative hypothesis about the state of the stock. For example, if the biomass is 750 000 tonnes and you set the quota to 100 000 tonnes, you can expect the stock size after 5 years to be 50% of the virgin biomass.

5 Present these results to the decision-makers.

An example of this approach is a decision table for the New Zealand hoki *Macruronus novaezelandiae* (order Gadiformes) fishery in New Zealand (Table 7.2). This table focuses on alternative hypotheses for virgin stock size, but it could be adapted to whatever uncertain aspect of the fishery was of interest. The first row gives alternative potential virgin stock sizes, and beneath each of these (in parentheses) is the probability that it is true. We describe how the probabilities are calculated in the next section (7.9.1). Three potential management actions (in this case quotas) are considered in the left column. Each cell of the table shows the predicted outcome of each management action, in terms of the ratio of stock biomass after 5 years of exploitation to the hypothesized virgin biomass. These values are usually calculated using Monte Carlo simulations (reviewed by Punt & Hilborn, 1997). The expected values in the right-most column are the means for these cells, e.g. $0.66 = (0.51 \times 0.099) + (0.63 \times 0.465) + \ldots (0.81 \times 0.003)$. If only the most probable virgin stock size (950 000 tonnes) had been considered, comparison with the mean expectations shows that this would have led to underestimates of the stock sizes after 5 years of

Table 7.2 A decision table to evaluate the consequences of a variety of alternative catch quotas, given various potential virgin biomasses, for the New Zealand hoki *Macruronus novaezelandiae*. Values in parentheses are the probabilities of each virgin biomass, cell entries are the ratio of the stock biomass after 5 years to the virgin biomass, and expectations are means of each of these ratios when multiplied by their probability. After Hilborn *et al.* (1994).

	Alternative hypotheses (virgin biomass 10^3 t)						Expectation
Quota (10^3 t)	750 (0.099)	950 (0.465)	1150 (0.317)	1350 (0.096)	1550 (0.020)	1750 (0.003)	1047
100	0.51	0.63	0.70	0.75	0.78	0.81	0.66
150	0.26	0.45	0.56	0.63	0.69	0.72	0.49
200	0.22	0.26	0.42	0.52	0.59	0.64	0.34

exploitation. This is particularly true under the higher quotas, because, for example, the 31.7% chance that the virgin stock size was actually 1 150 000 tonnes would have been ignored.

7.9.1 Bayesian analysis

Two main approaches have been used to calculate probabilities of alternative hypotheses being correct: Bayesian analyses and resampling methods.

Bayesian analysis provides a way of making probabilistic inference by combining prior information with current information. It is based on Bayes' theorem, developed by the Reverend Thomas Bayes in 1763 (Box 7.7). The good reverend has reached sainthood in the eyes of many contemporary theorists.

Bayesian inference was used to establish the probabilities of the alternative hypotheses for virgin stock biomass of the New Zealand hoki (Table 7.2). We will not go into the mathematics here, but refer readers to McAllister *et al.* (1994), Walters and Ludwig (1994), Punt and Hilborn (1997), and Francis and Shotton (1997). Bayesian analysis contains two key elements: specification of prior distributions of each alternative hypothesis, and calculation of the goodness of fit of available data to each of these alternatives.

The **prior distribution** summarizes all information about a parameter, except for the data used in the likelihood calculations, in the form of a probability distribution. This information can include previous experience with other stocks, knowledge about the behaviour or life history of the animal, and so on. Specifying these 'priors' is not easy, and is sometimes criticized on the grounds that the final probabilities of each parameter may be warped by errors in the prior distribution. But this criticism can be levelled at any modelling technique to some extent. For example, non-Bayesian analyses of fish stocks often make a default assumption that the instantaneous rate of natural mortality, M, is 0.2. Effectively, this is also a specified 'prior', although it is not called that in traditional analyses. In practise, one should check how important such assumptions are in all analyses, including ones using Bayes' Theorem, by running sensitivity analyses on a range of parameter values. An advantage of Bayesian analyses is that specification of priors is a formal procedure that cannot be swept under the carpet, and it can incorporate many kinds of information simultaneously. The data that can be used in a Bayesian analysis are exactly the same as those used in non-Bayesian analysis (e.g. indices of population size, age-composition data, etc.).

Box 7.7
Bayes' Theorem.

Suppose we wish to calculate the probability that either of two hypotheses, H_1 and H_2, is correct, based on prior information and a current observation (R). In its simplest form for discrete parameters, Bayes' Theorem says that the probability of H_1 given the prior information and the current observation R is proportional to the product of the prior probability of H_1 and the probability of R, given H_1 (Edwards, 1992). In formal notation, the latter is written $P(R|H_1)$. Thus:

$$P(H_1|R) = k \times P(H_1) \times P(R|H_1) \qquad (1)$$

where k is a constant of proportionality, which is the same in the similar equation for H_2. It is given by

$$1/k = [P(H_1) \times P(R|H_1)] + [P(H_2) \times P(R|H_2)] \qquad (2)$$

For example, suppose you know from experience that 1/3 of lobsters in a population are males and 2/3 are females. Furthermore, 3/4 of males have large claws and 1/2 of females have large claws. You trap a lobster that has large claws. What is the probability that it is a male?

Let H_1 be that the lobster is a male, so that $P(H_1) = P(\text{male}) = 1/3$.

Let H_2 be that the lobster is a female, so that $P(H_2) = P(\text{female}) = 2/3$.

Let R be the fact that the lobster you have caught has large claws.

Based on the above prior information, $P(R|H_1) = 3/4$ and $P(R|H_2) = 1/2$. Therefore, $1/k = (1/3 \times 3/4) + (2/3 \times 1/2) = 7/12$. Hence, $k = 12/7$. Therefore, $P(H_1|R) = 12/7 \times 1/3 \times 3/4 = 3/7$. The probability that the large-clawed lobster is a male is 3/7.

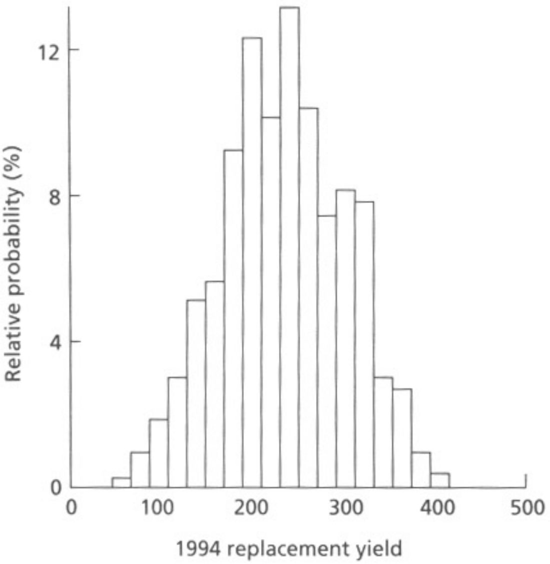

Fig. 7.17 Probabilities of various potential replacement yields for the Bering–Chukchi–Beaufort Seas stock of bowhead whales *Balaena mysticetus*. After Punt and Hilborn (1997).

The results of a Bayesian analysis are usually summarized by the **posterior distributions** for quantities of interest to management. The posterior probability of some variable is the probability that it is the true value after accounting for its prior probability and the information content of the available data.

An example of the use of Bayesian methods is provided by recent assessments of the Western Arctic population of bowhead whales *Balaena mysticetus*, conducted by the Scientific Committee of the International Whaling Commission (IWC). A key output from the assessment is the current replacement yield (i.e. the catch that will keep the population of animals aged 1 and older at its current size). This distribution is used by the IWC to set catch limits for this population. The assessments were based on an age- and sex-structured population dynamics model (Punt, 1999) and used data collected during visual and acoustic surveys off Point Barrow, Alaska. Various prior distributions were specified, including the pre-exploitation size of the population, the population size at which MSY is achieved, the age at maturity, and survival rates for adults and juveniles (IWC, 1995). The data are not particularly informative about current replacement (Fig. 7.17). The IWC based its catch limits on the lower fifth percentile of this distribution to allow a high probability of some further recovery.

7.9.2 Resampling methods

An alternative approach to setting probabilities is to use resampling methods such as bootstrapping. These methods use existing data from the fishery to generate probabilities for alternative hypotheses. They are straightforward and often faster computationally than Bayesian analyses, although this advantage is becoming less important as computers get faster and Bayesian algorithms improve. It may also be comforting to avoid the formal setting of priors, although it is still important to admit the full extent of uncertainty in each parameter.

As an example of the resampling approach, we will consider a study of the orange roughy *Hoplostethus atlanticus* fishery on the Chatham Rise, east of New Zealand (Francis, 1992). The response that this study generated, including debate about whether Bayesian methods would be superior, shows that computational approaches to risk assessment are still experiencing growing pains (Hilborn *et al.*, 1993b; Francis, 1993). Orange roughy are deep-water fish, which aggregate on seamounts such as the Chatham Rise during spawning. Trawlers target spawning aggregations, and catch most fish below 750 m from mid-June to mid-August. As with the roughy fishery on the Challenger Plateau (Fig. 7.5), this fishery grew rapidly in the early 1980s, and well beyond the sustainable level for a fish that matures in its mid-20s.

Francis (1992) used a population model that combines yield-per-recruit analysis with life-history parameters and a Beverton–Holt spawner–recruit relationship to estimate maximum sustainable yield. The management objective of the New Zealand Ministry of Agriculture and Fisheries was to aim for 'maximum constant yield', defined in this case as two-thirds MSY. This required a reduction in the total allowable catch (TAC) toward 7500 tonnes. This was only a quarter of the existing TAC for 1989–90 of 28 637 tonnes. How quickly should these painful cuts be brought in? Socio-economic concerns needed to be weighed against the probability of a collapse. This is where risk analysis came in, and embraced the uncertainty in stock assessment.

Figure 7.18 shows the probability of fishery collapse within 5 years for alternative rates of TAC reduction. A collapse was defined as the stock being reduced to the

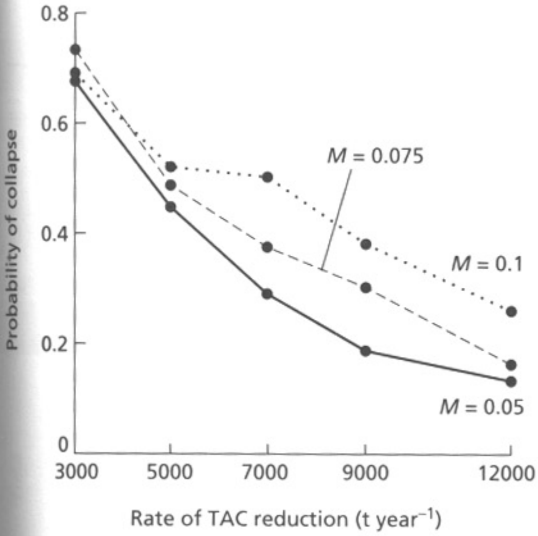

Fig. 7.18 Risk analysis for orange roughy *Hoplostethus atlanticus* on the Chatham Rise, New Zealand. This shows the probability of collapse within 5 years according to various rates of reduction of the total allowable catch toward a target of 7500 t y^{-1}. Each line represents a different assumption for the instantaneous rate of natural mortality, *M*. After Francis (1992).

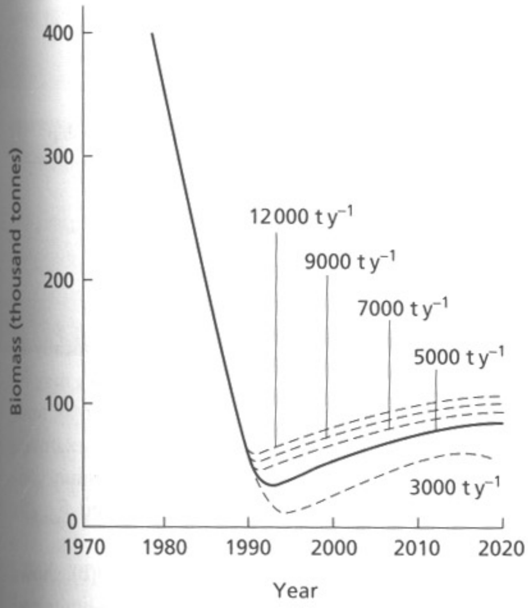

Fig. 7.19 Traditional presentation of management advice for orange roughy *Hoplostethus atlanticus* on the Chatham Rise, New Zealand. Each projection of stock biomass from 1990 assumes an instantaneous rate of natural mortality, *M* of 0.05, for various rates of reduction of the TAC. After Francis (1992).

point where the TAC was not catchable with a fishing mortality rate of less than 1.0 per year. The solid line in Fig. 7.18 was generated with an estimate of natural mortality, $M = 0.05$, which is the best guess. If higher rates of *M* are assumed, there is greater urgency to reduce the catch because these suggest that total mortality must be higher.

Figure 7.19 shows the more traditional way of presenting management advice from a stock assessment. These forecasts of stock biomass for different rates of TAC reduction show different management options, but they do not incorporate uncertainty in natural mortality, survey indices or recruitment. This therefore does not show the dangerous situation of the fishery depicted in Fig. 7.18, i.e. a 30–50% chance of collapse even if the TAC is reduced at the rate of 7000 t y^{-1}, depending on the natural rate of mortality.

In summary, there is little excuse for ignoring the uncertainty that is inherent in stock assessments. We have the mathematical underpinnings (e.g. Bayes' Theorem), and the computational power. Perhaps the biggest remaining obstacle is a pervasive feeling that decision-makers can only handle recommendations based on single point values. This can be an expensive mindset: during the collapse of the northern cod *Gadus morhua* in the north-western Atlantic in the 1980s there was conflicting information about the state of the stock, depending on inferences from offshore catches, inshore catches or government surveys. Yet uncertainty was filtered during the decision process under the ethos that 'one message goes to the minister' (Harris, 1998). Unfortunately, the wrong message got through, contributing to the destruction of the fishery and the loss of 40 000 jobs. An alternative approach, advocated by Hilborn *et al.* (1993a), would be to allow decision-makers to have decision tables such as Table 7.2 and graphs like Figs 7.17 and 7.18. These could be presented to them by fishery scientists who could run on-the-spot scenarios in response to 'what if' questions asked by the decision-makers. These could include economic as well as biological alternatives. We return to methods of incorporating uncertainty in bioeconomic models in Chapter 11.

7.10 Biological reference points

Biological reference points are derived from models of populations, to serve as benchmarks in making man-

Table 7.3 Some examples of biological reference points. F = instantaneous fishing mortality; B = spawning stock biomass; R = recruitment.

Symbol	Definition
F_{MSY}	F giving maximum sustainable yield (also called F_m)
F_{MCY}	F giving maximum consistent yield, i.e. largest long-term yield without reducing population below a predetermined level, such as 0.2 virgin biomass, with a prespecified probability. May also be given relative to F_{MSY}, e.g. $(2/3)F_{\mathrm{MSY}}$
F_{crash}	F that would drive the population to extinction
F_{max}	F where total yield or yield per recruit is highest
$F_{0.1}$	F where slope of yield per recruit vs. F is one-tenth of its value near the origin (Fig. 7.20)
F_{pa}	F set according to a specific precautionary approach
F_{lim}	F set as the highest that is acceptable by some specified criterion
F_{low}	F in an equilibrium population where recruitment per spawning stock biomass in 90% of years has been above the replacement level
F_{med}	F in an equilibrium population where recruitment per spawning stock biomass in half of the years has been above the replacement level
F_{high}	F in an equilibrium population where recruitment per spawning stock biomass in 10% of years has been above the replacement level
F_{LOSS}	F that would drive the stock to the lowest observed spawning stock size (LOSS)
$F_{x\%}$	F in an equilibrium population where recruitment per spawning stock biomass is x% of the corresponding unfished population
B_{MSY}	B corresponding the maximum sustainable yield
B_{LOSS}	The lowest B ever observed
B_{lim}	The B limit set as the lowest that is acceptable by some specified criterion
B_{pa}	The B set within a precautionary approach
$B_{x\%\,R}$	The B at which the average recruitment is x% of the maximum of the underlying spawner–recruitment relationship

agement recommendations. Fishing rates that would give the theoretical MSY were once considered a good target, but there has been a stampede away from this objective due to the difficulty of estimating MSY accurately (section 7.3.1; Punt & Smith, 2001). Indeed, the FAO's Code of Conduct and the UN Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks posit MSY as a limit, not a target. Fishing mortality should not exceed the theoretical point at which MSY would be achieved (F_{MSY}) and stock biomass should not drop below the MSY level (B_{MSY}).

A variety of biological reference points are listed in Table 7.3. Many of these are reviewed by Smith *et al.* (1993) and Caddy (1998). Some apply specifically to particular kinds of models, and different ones may be adopted as either target reference points or as limit reference points (not to be exceeded). For example, production models show that F_{MCY} (maximum consistent yield) is a safer target than F_{MSY}, and F_{crash} is definitely a good thing to avoid (Fig. 7.20a).

The yield-per-recruit curve in Fig. 7.20(b) shows F_{max} and $F_{0.1}$, which are usually reported as limits and targets, respectively, when this modelling technique is used. $F_{0.1}$ is the value of F on the yield-per-recruit curve where the slope of yield is one-tenth of its initial slope at the origin (Gulland, 1983; Deriso, 1987). For each

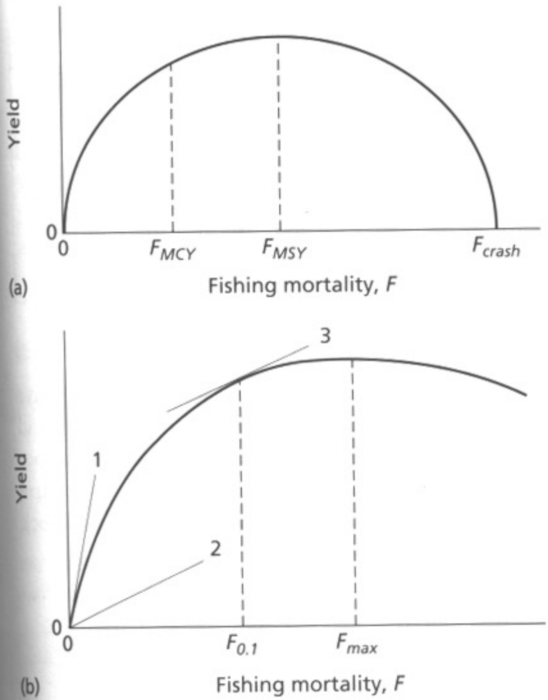

Fig. 7.20 Biological reference points. (a) Surplus production model; (b) yield-per-recruit model. $F_{0.1}$ is found by following the numbered steps indicated: (1) find slope at origin; (2) plot line with 10% of this slope; (3) find tangent to curve at this slope.

unit increase in F, the yield per recruit will increase by one-tenth of the amount at which it was first increasing when F was very low. $F_{0.1}$ will always be less than $F_{\max}$, thereby maintaining the stock at a safer level. Indeed, $F_{0.1}$ also has the very useful practical advantage of allowing a more precise target than $F_{\max}$ when the yield-per-recruit curve has a wide flat top, as in the Atlantic croaker analyses for lower Chesapeake Bay (Fig. 7.13). For that case, $F_{0.1}$ was 0.27 and 0.64 assuming low and high values of M, respectively (Barbieri *et al.*, 1997). Remember that there is no theoretical underpinning for selecting the value of 0.1 as the percentage of initial F.

The study of the pros and cons of various biological reference points, including their integration with socioeconomic objectives, is a hot topic in fisheries. Reference points are intimately linked to considerations of risk, because they are the targets or limits considered as acceptable benchmarks to aim for or to avoid at all costs. We have come a long way from targeting MSY using equilibrium production models. But can we really get away with considering exploitation of one species at a time, and ignoring interactions among species? This is the subject of the next chapter.

Summary

- The aims of stock assessment are to describe the population biology of fished species and to find ways of maximizing yields to fisheries while safeguarding the long-term viability of populations.
- For a given level of fishing mortality to be sustainable, there must be a balance between the forces that reduce population biomass (natural and fishing mortality) and those that increase it (reproduction and growth).
- Many quantitative methods have been developed for single-species stock assessment. Fishery scientists who work on stock assessment have made key contributions to the wider understanding of the dynamics of exploited animal populations.
- Surplus production models aggregate production across age classes. Equilibrium surplus production methods have received a bad name because they were based on faulty assumptions, but modern 'observation-error' methods are a considerable improvement and can perform well.
- Delay–difference models are a stepping stone between production models and fully age-structured models, requiring a minimum of data on body growth and recruitment.
- Virtual population analyses is used to describe age-specific stock structure. VPA does not by itself indicate how many individuals can be caught to meet a given objective, nor does it predict the future.
- Statistical catch-at-age analysis is an extremely flexible method for estimating stock size. Unlike VPA, estimates of natural mortality are not required, but one must be cautious about juggling numerous parameters at once.

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Summary (*Continued*)

- Yield-per-recruit models are run using the information provided by analyses such as VPA or statistical catch-at-age analyses, to seek fishing mortality rates that achieve the best trade-off between the sizes of individuals caught, and the number of individuals available for capture.
- Yield-per-recruit models need to be integrated with recruitment if recruitment overfishing is to be avoided. Recruitment overfishing is a reduction in spawning stock biomass to the point where recruitment is impaired.
- Advances in methods of stock assessment are being matched by new ways of converting this information into management advice. These include explicit incorporations of risk and uncertainty and the use of precautionary biological reference points.

Further reading

Many books are devoted to single-species stock assessment, and many fisheries laboratories do their assessments using software that they have developed or customized. The excellent books by Hilborn and Walters (1992) and Quinn and Deriso (1999) give detailed accounts of stock-assessment methods and contain many worked examples. They have to be consulted if you intend to do your own assessment! Sparre and Venema (1998) provide a clear description of stock assessment methods in tropical fisheries.